The California Current Marine Bird Conservation Plan
Chapter 4
Demography and Population Dynamic Models as a Cornerstone of Seabird Conservation and Management in the California Current
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Demography and Population Dynamic Models as a Cornerstone of Seabird Conservation and Management in the California Current

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CHAPTER 4. DEMOGRAPHY AND POPULATION DYNAMIC MODELS AS A CORNERSTONE OF SEABIRD CONSERVATION AND MANAGEMENT IN THE CALIFORNIA CURRENT

Seabirds of the CCS face many conservation challenges. The primary challenge is to maintain or restore populations in the face of habitat destruction, introduction of nonnative predators, prey depletion and bycatch mortality from fisheries and oil spills, among others.

Population dynamics for all species reflect, ultimately, four processes: reproduction, survival, recruitment and movement (combination of immigration and emigration). Seabird life histories are characterized by long adult life spans, low reproductive rates and deferred maturity. Once breeding begins it can be intermittent (in some species not all breeding-age adults attempt to reproduce every year) (1, 2). These life history characteristics make seabirds of the CCS vulnerable, particularly to events that kill breeding age birds (3).

The past few decades have been characterized by a multitude of disturbances to seabirds, including several major oil spills, of which the Exxon Valdez Oil Spill is surely the most prominent (4, 5).

Events such as these oil spills have focused the attention of the public, government agencies, and the scientific community on two linked questions: What are the long-term impacts to seabird populations of anthropogenic disturbance? And, can seabirds recover from these impacts? An increased understanding of major oceanographic perturbations, such as El Niño (ENSO) and the Pacific Decadal Oscillation (PDO), and the various impacts of commercial fisheries has led to a growing recognition of the complexities involved in trying to address these two important questions.

Yet despite these serious challenges, there are two recent developments providing additional hope and tools for the conservation biologist and wildlife manager. The first is that in the past few decades there have been great advances in our understanding of seabird population biology; in part, this has been fueled by the recent development of sophisticated methods to estimate demographic parameters (6). The second is that there has been extensive elaboration of theoretical models and frameworks with the potential to be applied to seabird populations. These include metapopulation models (7), source/sink models (8), and stochastic population models, including population viability analyses (9, 10).
4.1 THE DEMOGRAPHIC COMPONENTS OF POPULATION CHANGE

We view population dynamics (and as discussed later, metapopulation dynamics) as fundamentally important in formulating and evaluating all conservation and management programs (11), because we must be able to detect and subsequently effect change in population dynamics for conservation to succeed. These changes must be detectable at the level of both an entire population and a sub-population.

Therefore it is helpful to consider what we call the Fundamental Law of Population Dynamics. Versions of this law have been introduced by various authors; here we present a relatively simple version (see McDonald and Caswell (12) for a more comprehensive treatment).

For ease of explanation we consider a simple life history, one that corresponds to no known seabird. Suppose, for a hypothetical seabird species, that individuals attain sexual maturity at age 1 year, that they breed (or at least can breed) at that age, and that every year thereafter they may or may not breed (if still alive). Given that, the seabird version of the Fundamental Law states that the number of adults at time, \( t+1 \), symbolized \( N_{\text{adults}}(t+1) \), is a function of just four demographic processes: (1) adult survival from time \( t \) to \( t+1 \); (2) reproductive success per adult, at time \( t \); (3) survival of those offspring from time \( t \) to \( t+1 \); and (4) net immigration (net immigration = immigration - emigration) of individuals during the interval \((t, t+1)\).

As an equation we can write:

\[
N_{\text{adults}}(t+1) = N_{\text{adults}}(t) \times \{\text{adult survival from } t \text{ to } t+1 \}
+ \text{reproductive success at time } t \times \text{offspring survival from } t \text{ to } t+1
+ \text{net immigration (= immigration - emigration) from } t \text{ to } t+1.
\]

Note that the middle line of the equation corresponds to new 1-year-olds (i.e., new adults or “recruits”) who were born the previous year.

For species with more complex life histories, the notation gets a bit more complicated, but the idea is the same: population dynamics can be explained in terms of just these four processes, which in theory, can be directly observed—some more easily than others.

One complication is that, in almost all seabirds, adulthood is not reached at age 1 year. For simplicity, we might treat age of first breeding as being fixed at some age, but it would be more realistic to treat it as a demographic parameter (usually symbolized as \( \alpha \)), meaning that, even within a single seabird population, individuals show variation in the age at which they first breed. For this reason we prefer to reformulate the parameter “age of first breeding” and instead consider “probability of breeding among those who have never bred before,” which we will symbolize \( \beta \). Thus, \( \beta \) can be thought of as a measure of recruitment probability. Furthermore, \( \beta \) will demonstrate age specificity, just as survival and reproductive success are also age specific. At a young enough age, \( \beta \) will be zero; minimum age of first breeding corresponds to the youngest age at which \( \beta \) is greater than zero.

As formulated above, all adults are being followed through time, whether or not they are breeders. Hence “reproductive success” is averaged over all adults. For studying population dynamics (analytically and from a monitoring point of view), it is helpful to separate this process into two separate components: probability that an adult breeds (or attempts to breed), and reproductive success among those individuals that breed (or attempt to breed).

What we refer to as “breeding probability” has also been termed “breeding propensity” (13). Furthermore, “breeding probability” is divided into two parameters: first, the probability that an individual that has never bred before is breeding in that year, what we have called \( \beta \), and second, the probability an experienced adult attempts to breed that year, which we shall refer to as \( \gamma \). Thus, we have added two parameters to the original four, i.e., \( \beta \) and \( \gamma \).

Finally, it may be helpful to separate survival probability among juveniles (young of the year, also termed Hatching Year birds) from survival probability among subadults, thereby creating one more parameter.

Thus, we can parameterize seabird demographic processes determining population growth in terms of seven parameters: (1) adult survival, (2) subadult survival, (3) juvenile survival, (4) reproductive success per breeder, (5) probability that an adult that has never bred before breeds in a given year, (6) probability an experienced adult breeds in a given year, and (7) net immigration. This formulation, developed for seabirds, would be entirely appropriate for other long-lived birds, such as eagles (14).

Many different parameterizations of population dynamics are possible. We justify this particular parameterization for two reasons. First, this parameterization has a strong empirical, biological basis. For example, there is good evidence that juvenile and subadult survival differ substantially, but—more to the point—juveniles and subadults often spend their lives in disparate regions and therefore are likely influenced by different mortality factors.
Another example is the value of distinguishing reproductive success among breeders from the probability an adult attempts to breed. Different factors are likely to affect these two parameters. For example, if nest sites are indeed limiting, provision of additional nest sites will markedly improve breeding probability but will have little influence on reproductive success.

Second, the parameters identified are accessible to monitoring. For example, many long-monitoring programs (including many ongoing studies on the Isle of May, Britain (15, 16); on the Farallon Islands, USA (17); and research conducted by the British and French Antarctic research programs in the Southern Ocean (18, 19)) estimate reproductive success per breeder (or per breeding pair) on an annual basis. (i.e., parameter 4 above). Uniquely banded individuals are not required to estimate reproductive success. As a result, good comparative data are available (comparing years, populations, and species).

It is more difficult, however, to estimate adult breeding probability. Good estimates require monitoring banded individuals (20, 21). Separating these two parameters is useful because it allows us to address uncertainty regarding one parameter (breeding probability) but not the other (reproductive success).

Finally, we note that reproductive success has been variously defined; here we consider reproductive success to be the number of chicks (offspring) reared to fledging (or independence) per breeding individual or per breeding pair. Thus, reproductive success subsumes components such as clutch size, hatching success, fledging success, “breeding success” (number of chicks fledged per egg laid), number of broods, etc.

Below we consider each demographic parameter, focusing on the significance of each parameter for determining seabird population dynamics and summarizing the state of knowledge regarding this parameter.

A parameter may be significant with respect to conservation efforts because it constrains population growth, but the parameter must be labile if it is to serve as a management tool. For example, theoretical investigations demonstrate that reduction in age of first breeding can have a sizeable impact on the population growth rate, \( \gamma \). However, some evidence suggests that minimum age of first breeding is genetically constrained (23, 24), and therefore aiming to reduce minimum age of first breeding is unlikely to be an effective means of conserving seabirds.

### 4.2 REVIEW OF DEMOGRAPHIC PARAMETERS

#### (1) Adult survival.

Earlier views of adult survival considered this a species-specific, time-constant parameter. There is now evidence that adult survival in seabirds varies temporally, spatially, and age-specifically, and that changes in adult survival are associated with corresponding population fluctuations (25-30).

A recent example of temporal variability in adult survival was Jones et al.’s (30) study of Least Auklets (Aethia pusilla) breeding in the western Aleutian Islands, Alaska from 1990 to 2000. Annual adult survival probability varied from 74.7% to 95.3% and averaged 87.3% during the study period. Annual variation in adult survival was most parsimoniously explained by annual variation in the North Pacific Index (NPI), a measurement of atmospheric pressure in the north Pacific that indicates relative sea surface temperature and primary productivity in the region. This was the first direct evidence that variation in adult survival of a Pacific alcid species was related to large-scale climatic/oceanographic variation. Because of the Auklet’s low trophic position as a planktivore, adult survival for this species was positively correlated with ocean climate through the influence of climatic variation on primary productivity. The strength of this interaction was compounded by increased gull predation during low productivity years, when the gulls’ usual fish prey was scarce.

In the case of Brandt’s Cormorants (Phalacrocorax penicillatus) breeding on the Farallon Islands, adult survival was positively correlated with sea surface temperature, a well-established index of local food availability (31). These results implicate variability in food resources due to ocean climate as a major source of variation in adult survival, as well as in breeding probability and reproductive success (see below). This variation has significant effects on population trajectories.

Another example of annual variation in adult survival was provided by Harris et al.’s (32) study of Atlantic Puffins (Fratercula arctica). Between 1973 and 1980 survival averaged an astounding 97.5%; between 1981 and 1994 survival was only 92.4%. In other words, in the latter period adult mortality tripled compared with the 1970s. In addition, in 1990/1991 survival was only 80.6% (S.E.=2.6%), a more than doubling of mortality compared with the rest of the 1981-1994 period. The authors concluded that the “catastrophically low” survival in 1990/91 and the decadal shift in baseline survival were due to environmental perturbation, but there was no direct evidence for this.
A species showing marked decadal changes in adult survival due to fisheries-induced mortality (bycatch) is the Wandering Albatross (Diomedea exulans). This species has been especially well-studied demographically; two detailed long-term studies have been conducted at sites in different oceanographic regions, one in the Crozet Islands in the Indian Ocean (18, 33, 34), and the other at South Georgia Island in the South Atlantic Ocean (19). Weimerskirch (33) found that adult survival from 1966 to 1976 was just under 90% compared with 96% in more recent years (1986-1994), and concluded that low adult survival in the earlier time period (due to entanglement in fishing gear and shooting by fishermen) was the most significant factor contributing to substantial population declines. Conversely, the increase in adult survival in recent years was associated with population stability.

Both food supply and predation pressure had significant effects on adult survival of Black-legged Kittiwakes (Rissa tridactyla) in Britain and Ireland. Oro and Furness (35) found that annual variation in adult survival was best modeled as a function of both sandeel and Great Skua (Catharacta skua) abundance, the main prey and predator of the Kittiwake.

Not only does adult survival for a given species vary temporally, but there is ample evidence that adult survival also varies spatially. A striking example is provided by Spendelow et al. (36) who demonstrated substantial differences in survival of adult Roseate Terns (Sterna dougallii) among four colonies in New York State and New England (USA). To complicate the picture even further, the pattern of annual variation in adult survival differed among the four sites.

Another species for which extensive data on adult survival have been gathered at separate sites is the European Shag (Phalacrocorax aristotelis). Earlier work on the Isle of May (16, 37, 38) considered that adult survival was fairly constant from year to year. This was in contrast to the situation for European Shags on the Farne Islands, Britain (less than 100 km distant), which experienced several episodes of high adult mortality, owing to “red tide” (paralytic shellfish poisoning; (16)). More recently, however, high adult mortality for European Shags on the Isle of May was reported by Harris and Wanless (39) in winter 1994, apparently due to poor feeding conditions. Common Guillemots (Uria aalge) at three Scottish colonies also demonstrated spatial variation in adult survival (38, 40, 41).

Adult survival typically does not remain constant with increasing age. A common theoretical pattern of age-dependent survival is an increase in survival with age to a midlife optimum, followed by decline as the oldest birds senesce (42-47). Previous studies on age-dependent survival in seabirds have described the curve as a constant (31, 48, 49), negative-linear function (43, 50, 51), or a constant that exhibits senescent decline in older ages (19, 32, 37, 52-56). One study, Ainley et al. (57), found increased survival for birds age > 10. Rattiste and Lilleleht (58), and Ratcliffe et al. (59) fit the fully quadratic age-dependent survival function that Botkin and Miller (43) predicted for long-lived birds. Data from the Farallones for Western Gulls, Brandt’s Cormorants, Common Murres, and Cassin’s Auklets all showed some level of age-dependent relationship with survival and some showed age-dependent breeding propensity as well (PRBO unpublished data).

Population modeling results bear out the potential significance of even small changes in adult survival, a point we return to later. For example in the Common Murre (Uria aalge) population model developed by Nur et al. (60), a decrease in survival from 0.933 to 0.905, resulted in a change in population growth rate from +1.1% per year to -1.9%; in other words, a decrease of 3.0% in adult survival (in relative terms; absolute difference = 0.028) produces a change of 3.0% in the population trajectory. Similar results have been obtained for other species (18, 19, 61).

(2) Subadult survival.

Knowledge of this parameter is fragmentary at best for nearly all seabird species. And although it may be desirable to distinguish juvenile survival from subadult survival, many studies have been unable to make this distinction.

An additional problem is that studies of subadult survival based on capture/recapture (as opposed to band recovery) are unavoidably biased because of dispersal (11, 23). This is less of a problem for studies of adult survival because of high breeding philopatry. If the strength of natal philopatry varies from year to year, this will bias estimates of temporal variation in subadult survival. Studies of subadult survival based on band recoveries, on the other hand, have not usually had enough resolution to identify temporal or spatial variation in survival rates. An exception to this generalization is provided by the work of Baillie and Mead (62): they used band recoveries to determine that subadult Common Murres (as well as juvenile, first-year birds) suffered high mortality as a result of severe oil pollution during winter 1980/81.
Despite incomplete data, the picture that emerges is that subadult survival is apparently quite variable between years or between decades. For example, there was marked variation in immature survival for Wandering Albatrosses in the Crozet Islands; overall survival in the first four years of life after fledging varied from as little as 21% (for cohorts born in 1970-1976) to 50% (for those born in 1986-1994; (18)).

Furthermore, variation in immature survival (but not adult survival) was strongly correlated with fishing effort (18). The study by Croxall et al. (19) similarly concluded that mortality of Wandering Albatross subadults due to long-line fishing was responsible for a large proportion of the overall population decline. Murphy et al. (63) suggested that the population decline of Common Murres at Bluff, Alaska, was due principally to an increase in over-winter mortality of subadults, which may have resulted from competition with a fishery. Annual variation in the mortality of immature Black-legged Kittiwakes (Rissa tridactyla) was not in concert with that of adults, indicating that the decline in numbers of adults at a colony in England during the late 1960s was due to mortality factors acting during the subadult period (64). Among European Shags, survival of immatures (juveniles and subadults) was much more variable between years than was survival of adults (37).

Temporal variation in survival during the immature period (including both juvenile, post-fledging survival, and subadult survival) was also suggested for Roseate Terns (65), Atlantic Puffins (66), and Brandt’s Cormorants (67). For the last-mentioned species, Nur and Sydeman (31) demonstrated that immature survival was correlated with environmental conditions (as indexed by sea surface temperature) during both the first year of life and the third year of life (when individuals first return to the natal colony).

For additional studies of subadult survival see Spear et al. (51); Ainley et al. (57); Gaston et al. (68); and a review by Hudson (69). Beissinger and Nur (70) provide re-analyses of data originally presented by Birkhead and Hudson (71); these analyses demonstrated that subadult survival (but not juvenile survival) was similar among different Common Murre populations and similar among Common and Thick-billed Murres (Uria lomvia). We might expect subadult and adult survival to be more similar (year by year and site by site) than are juvenile and adult survival; nevertheless, because subadults and breeding adults are usually found in disjunct areas, different mortality influences may be at work.

(3) Juvenile survival.

Even less is known about juvenile survival than about subadult survival. For this parameter there appears to be great variation among populations. For example, four different population estimates for first-year survival in Common Murres varied from 0.47 to 0.67 (70); yet for other populations, first-year survival may be 0.40 or less (60). Estimates from five studies of Herring Gulls (Larus argentatus) (72), ranged from 50-82% (median = 78%).

Some of the studies cited in the previous section may bear more directly on variation in juvenile survival than subadult survival, but it is not possible to disentangle the two. Not surprisingly, such large variation in first-year survival can have large impacts on population growth trajectories (see “Sensitivity to Population Parameters,” below). An example of the great magnitude of variation possible was already presented for Wandering Albatrosses; survival from the time of fledging (at an age of c. 12 months) to age 5 was more than twice as high for the 1980s than the 1970s (50% vs. 21%). These results indicate a great potential for improvement in survival of juveniles and subadults as a means to restore or to stabilize declining or depleted populations.

Hatchwell and Birkhead (27) examined which demographic parameters were responsible for growth of the Skomer (Britain) Common Murre population in the 1980s, compared with the 1970s. They concluded (from indirect evidence) that a change in juvenile or subadult survival, or both, was the major factor explaining why the population grew in the 1980s, but not in the 1970s.

Population modeling for the Common Murre on the Farallon Islands (60) demonstrated that 40% juvenile survival results in average population growth of only 1.1%, whereas 60% juvenile survival results in a rapidly growing population, at the rate of 8% per year; both survival estimates are within the range observed for this species (70). Note also that juvenile mortality is less than three times that of adult mortality in the Herring Gull (on average, 0.28 vs. 0.12, respectively; (72)), while it is five to eight times that of adult mortality in the Common Murre. While there will be, inevitably, a gap between adult and juvenile mortality, conservation efforts may be successful in closing that gap somewhat.
By using a Leslie matrix and assuming that a population is
censused immediately before the breeding pulse (e.g.,
immediately before offspring production), it is easy to
show that the effect of a specified change in juvenile (i.e.,
first-year) survival is identical to the same magnitude
change in reproductive success (12, 73). This is because
the elements of the top row of the projection matrix are
the number of female offspring produced which survive to
age 1 per female. Thus the population consequences are
identical whether 80% of breeders raise a chick and 50%
of the chicks survive to age 1 or 50% of breeders raise a
chick and 80% of the chicks survive.

(4) Reproductive success.

More data are available on this parameter than any other.
It is well-established that reproductive success varies from
year to year, from decade to decade, and that much of this
variation is related to food availability for breeders (16,
74-80).

For example, a decline in North Sea herring stocks was
associated with decline in Black-legged Kittiwake reproduc-
tive success (chicks fledged per pair) and a decline in
population growth rate (81). Whereas a major decline in
reproductive success is likely to presage a population
decline, it does not follow that all fluctuations in reproduc-
tive success are similarly influential. Furthermore, at
least for some species, as stated by Harrison (82), “an
occasional bumper crop of young may be a more impor-
tant attribute of an enduring species than the vicissitudes
of success and failure in individual years.”

For species with single-egg clutches (procellariiforms,
many alcids), reproductive success is usually high (67-
80%). There is little evidence that for such species, boost-
ing reproductive success beyond levels that are already
relatively high will be effective in raising seabird numbers;
a point that is quantitatively demonstrated below (see
“Sensitivity of Population Growth to Population
Parameters”). Few studies have reported average reproduc-
tive success as high as 80%; this may present an upper
bound to what a seabird can achieve. However, where
reproductive success is unusually low, management efforts
would be particularly well rewarded.

Seabirds can be divided into two categories: those with
single-egg clutches and those with multiple-egg clutches.
The recovery potential for species with multiple-egg
clutches (and especially those with a clutch of 3 or more)
is much greater than for those with single-egg clutches.
For example, a review of population studies of seabirds
(83) indicated that Common Murre populations (clutch
of one egg) rarely grew at more than 10% per year
(excluding cases with known immigration), yet often
cormorant or gull populations (typically with clutches of
3-4 eggs, and 2-3 eggs, respectively) grew at much faster
rates. The small clutch size for some seabirds, therefore,
constrains their ability to recover or to take advantage of
good conditions.

As a result, the effects of good and bad years are not
symmetric: in a bad year, reproductive success can be
depressed much more (relative to the long-term average)
than it can be elevated in a good year. This asymmetry is
applicable to all seabirds, but appears to be stronger for
the single-egg clutch species (75). For example, for
Common Murres on the Farallon Islands, in an excep-
tionally good year reproductive success increases by 20%
relative to the long-term average, while for two cormorant
species, reproductive success in an exceptionally good year
is 100% above the long-term average.

Finally, we note that reproductive success is affected by
age of mate and years of experience with the same mate
(84-87). The dependency of reproductive success on these
factors should be taken into account when considering
the impact of oil spills and other perturbations. That is,
individuals that lose their mate or simply change mates,
generally have lower reproductive success in their first and
subsequent seasons (up to the fourth year in Short-tailed
shearwaters (Puffinus tenuirostris) (87), when breeding
with the new mate).
(5) Probability of first breeding, \( \beta \).

Recall that we divided breeding probability into two components: (1) the probability an individual of breeding age breeds for the first time, \( \beta \), and (2) breeding probability among experienced breeders, \( \beta \). Good information on \( \beta \) is difficult to obtain for the reasons given below; a good example, however, is provided by McDonald and Caswell (12) for the Florida Scrub-jay (Aphelocoma coerulescens).

It is helpful to think of \( \beta \) for a given age (call it \( \beta_x \)) as the ratio of two quantities:

\[
\beta_x = \frac{V(x)}{N(x)}
\]

where \( V(x) \) is the number of first-time breeders of age \( x \), and \( N(x) \) is the number of individuals of age \( x \) who have not bred at a younger age.

Rather than reporting \( \beta_x \), many studies report the age-specific distribution of first-time breeders, i.e., they report \( V(x) \). This is surely useful information, but only provides limited insight into \( \beta_x \). There are two difficulties with inferring \( \beta_x \) (even qualitatively) on the basis of \( V(x) \) alone.

The first difficulty is that individuals first observed breeding at a given age may have bred before, but were not observed by the investigator. Pradel et al. (23) describe how this probability can be estimated using capture-recapture (or sighting-resighting) data. Thus, differences between populations (between species, between years, etc.) may confound attempts to detect differences in \( \beta_x \).

The second difficulty is that, though \( V(x) \) may be directly observable (not withstanding differences in detection probability), \( N(x) \) is generally not directly observable for seabirds. \( N(x) \) reflects the total number of individuals who have yet to breed, some of which may attempt to breed at age \( x \) (and thus be observed) and some of which may remain non-breeders at age \( x \). Non-breeders may not attend the breeding colony or are otherwise not observed, which presents difficulty in estimating the denominator. Note that \( N(x) \), which represents the pool of individuals available to first breed at age \( x \), is simply the difference between total number of individuals of age \( x \) (thus reflecting survival to age \( x \)) and the number of individuals of age \( x \) who have previously bred (thus reflecting \( \beta \) at age \( x-1 \), \( x-2 \), etc.). Thus, differences in survival (of immatures and adults) can also confound attempts to detect differences in \( \beta_x \).

As noted, few studies have attempted to estimate \( \beta_x \); instead observed ages of first breeding have been reported. These latter studies have indicated much interspecific variation in age of first breeding, for example with respect to body size (24, 88). In addition, there appears to be variation within species as well. For example, Common Murres on the Isle of Canna (Britain) were observed first breeding at ages 3 and 4 (89). Skomer Common Murres bred at ages 4 to 6 years (71).

Age of first breeding is likely to reflect, in part, breeding opportunities; the colony on the Isle of Canna was a fast-growing one with (presumably) many available breeding sites. Brooke (20) observed that age of first breeding for Manx Shearwaters (Puffinus puffinus) increased from 6 yrs in the 1970s to 7 yrs in the 1980s on the island of Skokholm (Britain). Age of first breeding may be flexible, but there are likely physiological limitations on the ability of any restoration program to reduce age of first breeding beyond a certain age.

It is unrealistic to assume that all individuals will begin breeding at the same age; instead, there is usually a range of ages in which \( \beta \) increases as age increases, eventually (but not always) reaching a plateau (23, 90). As a result, age of first breeding can vary substantially even within a year and within the same population.

For example, some Western Gull (Larus occidentalis) females start breeding at age 4, but a considerable number do not start breeding until ages 7, 8, 9, or 10 (91). Spear et al. (51, 91) attribute this variation, in part, to intense competition for mates, due to a skewed sex-ratio in the population. As a result of this competition, age of first breeding is delayed. A similar wide range of age of first breeding was reported for Common Murres by Harris et al. (92), and for Cassin’s Auklets by Pyle (84).

In summary, parameter \( \beta \) appears to be very flexible. For many species, a large pool of non-breeders provides a potential source of first-time breeders, if competition is lessened (93), if excess sites are provided, or as a result of high mortality of established breeders. An example is provided by catastrophic red tide mortality of European Shags on Farne Island, which allowed many new individuals to recruit (49). We view this pool of non-breeders as a source to be tapped by restoration efforts.
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(6) Breeding propensity (breeding probability among experienced breeders), \( \gamma \).

This parameter also shows much variation between and within species. Fisher (94) found that many Laysan Albatrosses (*D. immutabilis*) on Midway Island skipped breeding in 1964/65 and 1968/69; the 1964/65 observations were associated with an El Niño event in 1965. On the other hand, among Western Gulls (*Larus occidentalis*) on the Farallon Islands who are experienced breeders, breeding probability is close to 100%, year in and year out (95).

Skipping (i.e., non-breeding among experienced breeders) reflects individuals present at the colony not attempting to breed and individuals absent from the colony; the extent of skipping is undoubtedly underestimated, because skipping birds are often absent or inconspicuous.

In the Short-tailed Shearwater (21), 12% of adults did not attend the colony in a given year and 19% maintained burrows but did not lay an egg. In the Newell’s Shearwater (*P. auricularis newelli*), breeding probability was estimated to be less than 55% (185) in contrast with the closely related Manx Shearwater where it was estimated to be 80% (20). In the Sooty Shearwater, Hamilton and Moller (96), based on data provided by Richdale (97), estimated that 55% of breeding-age individuals did not breed in a given year. Use of that parameter value in a population-dynamic model produced a sharply declining population (96). Ainley et al. (185) also attributed declining population trends of Newell’s Shearwaters to the low proportion of breeding-age adults that actually bred.

Albatrosses generally skip breeding in the year following successful breeding; Croxall et al. (19) also found that some successful breeders skipped two years in a row, and that some individuals also skipped breeding in the year following unsuccessful breeding. At least among Procellariiformes, the failure to attempt breeding (among experienced breeders) is commonplace.

Skipping of breeding appears commonplace among cormorants and shags as well, and the incidence of such appears quite variable. Aebischer (38) attributed a population crash among European Shags on the Isle of May to extensive non-breeding of experienced adults. Aebischer and Wanless (16) report that a second population crash could also be attributed to failure to breed among adults. Other cormorant species demonstrating a pattern of intermittent breeding include the Guanay Cormorant (*Phalacrocorax bougainvillea*) (98) and Galapagos Flightless Cormorant (*Nannopterum harrisi*) (99). Nur and Sydeman (100) found that breeding probability of Brandt’s Cormorants (who had previously bred) varied markedly between years, ranging from 8% to 85% (mean = 59%), and that the variation was related to food availability. Intermittent breeding has also been reported for gulls and terns (101-103) and for Common Murres (104).

The effect of this non-breeding is similar to that of reproductive failure among those attempting to breed. That is, production of young is the same whether 100% of adults attempt to breed with 40% success or 50% attempt to breed with 80% success. However, attempting and failing to raise young is likely more stressful to parents than not breeding at all (105).

(7) Immigration and emigration.

Population growth of seabird colonies is undoubtedly influenced by immigration and emigration, yet we have little good information on these parameters. Models of single populations have de-emphasized the role of immigration/emigration because it is difficult to incorporate into the usual age-structured or unstructured models. As long as immigration equals emigration, then the population dynamics of a single population would not be sensitive to the actual immigration rates (though genetic variability would be affected).

In contrast, immigration/emigration is an explicit part of metapopulation models (see below), and so this parameter cannot be ignored in such models. Emigration is difficult to study because individuals are leaving the focal colony (by definition) and death is hard to distinguish from emigration. The number of immigrants can, in some cases, be quantified, but the pool from which they come is much harder to identify.

Species vary in their tendency to immigrate/emigrate in regard to both dispersal of young and dispersal of adults. Terns and cormorants, for example, show a great deal of dispersal, even among breeding adults (1). Or, to put it another way, site tenacity is low; this makes it difficult to designate critical breeding areas to be acquired and managed. Spendelow et al. (36) found that dispersal of breeding adult Roseate Terns was considerable, and it varied among colonies, ranging from 1% to 12% per year.
In general, seabird species show a considerable amount of dispersal at the post-fledging juvenile stage. Dispersal during the juvenile stage may or may not lead to effective emigration among breeding individuals. Harris (26) found that pre-breeding Atlantic Puffins from the Isle of May visited colonies at other islands, and appeared to return to the natal colony only if there were few breeding vacancies at the visited colony. The fact that many puffins returned to their natal colony to breed should not be taken to imply that puffins are constrained to do so. Another example is offered by Ainley et al. (57) who found that skuas visited a number of colonies as young pre-breeders, but most eventually returned to within meters of their natal sites and those that emigrated were attracted by unusual opportunities of ample food availability.

This tendency to sample a number of colonies before settling improves the likelihood of successful restoration and emphasizes that dispersal (immigration/emigration) needs to be explicitly included in restoration models.

A review of population recovery of marine birds indicated that immigration played a role in many growing populations (83). Immigration can play a role in restoration in several ways. In establishing a new colony (or reestablishing an extirpated colony) all individuals are, at first, immigrants. Among growing colonies, immigration will often reinforce population growth. On the other hand the establishment of a new colony may siphon off individuals (increased number of emigrants from the established colony) leading to no net change in the larger metapopulation.

Many seabirds are specifically attracted to extant colonies. Coulson (106) found that, among growing colonies, small colonies were the most attractive to Black-legged Kittiwakes seeking to breed. In contrast, Birkhead (107) found that Common Murres were most attracted to high-density subcolonies, but were most likely to settle in medium-density subcolonies (because high-density subcolonies had few vacancies). Heubeck et al. (108) observed that small kittiwake colonies declined at faster rates than did large colonies, suggesting that kittiwakes were more likely to emigrate from small colonies. As a consequence, the recovery prospects for a small colony that has been severely depleted may be poor. The prospects for a completely extirpated colony are even worse.

Whereas a number of studies have provided insight into patterns of immigration and emigration, it has been much more difficult to estimate actual immigration and emigration rates. A common assumption has been that immigration and emigration are negligible. In some cases, this view may be justified (38). However, at least some studies seem to contradict that view.

For example, Harris (26) concluded that 23% or more of Atlantic Puffin chicks fledged on the Isle of May and surviving to breed, breed at a different colony, i.e., not on the Isle of May. Austin et al. (109) concluded that Short-tailed Shearwaters showed “substantial, and probably opportunistic immigration.” Wandering Albatross female dispersal was estimated to be 24% (i.e., that fraction of individuals bred in a colony other than their natal colony); even among females that bred in one colony, 11% switched colonies and bred in a second colony (18).

The same statistics for males were half that of females. Immigration of Common Murres was considered by Parish (110) to be an important factor in explaining rapid population growth of Tatoosh Island (Washington state) in the 1980s.

Multi-strata mark-recapture models are important tools that can be used to quantify movement of animals between physical sites as well as transition probabilities between states such as breeding/non-breeding (111, 112). These methods can provide unbiased estimates of site fidelity (113), movement rates between subpopulations (36), and can even estimate probabilities associated with unobservable states (114).

(8) Sex ratio and mating system.

In addition to the seven primary demographic parameters enumerated above (which are the focus of this section), there are two factors that will also influence population dynamics: the sex ratio and the mating system.

Often, population dynamic models of seabirds assume an equal sex ratio. There is evidence that the sex ratio is not uniform, either among offspring (115-117), or among adults (51). Mating systems will also influence population dynamics if individuals of one sex mate with several individuals of the other sex. Although monogamy is the norm in seabirds (86), there are exceptions (118). As a result of deviations from either an equal sex ratio or monogamy, one sex will be the limiting sex.

Population models need to take into account which sex is limiting or if both are (though perhaps at different times of the life cycle). We do not discuss this further but note that software is now available to model such complexities (RAMAS/GIS 4.0).
(9) Stochasticity.
In the last decade, population models that incorporate stochasticity (i.e., variation in demographic parameters due to random effects) have become increasingly prevalent. The result is a model that is probabilistic, rather than deterministic. The reasons for developing stochastic, probabilistic models are manifold.

The first is that nature is in fact stochastic. Not only is the environment unpredictable, but so, too, 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. For example, a stochastic population model for the Farallon Common Murre developed by Nur et al. (60), predicted that on average the population would grow by 1.1% per year. Most interestingly, in the face of a very variable, unpredictable environment (as observed on the Farallones), there was a 10% chance the population would shrink by 21% or more after 10 years and a 10% chance that the population would grow by 53% or more after 10 years.

A third reason for incorporating stochasticity is that deterministic models do not accurately predict average response. Instead, greater environmental and demographic variability tends to depress population growth rates (119). The final reason for incorporating stochasticity is that the deleterious effects of stochasticity are strongest for the smallest populations (e.g., incipient or decimated colonies; see Allee effect below).

The effects of stochasticity on populations are often categorized in a four-part manner (120, 121):

1. Genetic variability. Even in identical environments the genotypic makeup of two populations will differ due to genetic drift and founder effects. This source of variation will in turn affect vital rates.

2. Demographic stochasticity. This can be thought of as “The Law of Small Numbers.” The number of adults surviving in a finite population from one year to the next reflects the true underlying survival probability (which may vary among years, see “Environmental stochasticity,” below) and sampling effects.

To see this, suppose we have a population of 10 individuals, each with a survival probability of 0.5. There is a 0.1% chance that in any one year, all 10 individuals will die (= (.5)10, assuming each individual lives or dies independently of the others) and an equal chance that all 10 will live. Similar arguments apply to production and survival of young. Demographic stochasticity also applies to each sex. Suppose there are 5 males and 5 females in the population with survival probability of 0.5 each. There is a 3% chance that all males will die (= (.5)5) and a 3% chance that all females will die. Thus there is only a 94% chance (= .97 x .97) that at least 1 male and 1 female will survive among the initial 10 in a single time period (e.g., 1 year). Conversely, there is a 6% chance that either no males survive or no females survive.

3. Environmental stochasticity. This refers to variations in demographic parameters due to environmental fluctuation. For example, if feeding conditions are good in a given year, survival and fecundity tend to be high.

4. Environmental catastrophe. This is a variation on #3 but is rare and drastic in its effects.

Stochastic forces #3 and #4 apply to both small and large populations, but forces #1 and #2 are negligible for very large populations.

Because Farallon Common Murre population size is very large (60,000 or more individuals), the stochastic population model of Nur et al. (60) only included environmental stochasticity (catastrophic or mundane). However, anyone wishing to investigate small populations should include the effects of genetic and demographic stochasticity.

Not only are small populations more subject to stochasticity, but their vulnerability to stochastic variation decreases the probability of long-term persistence. An anomalous year in which few or no individuals survive has greater impact on long-term population growth than an anomalous year in which everyone survives.

Because no environment is truly constant with time, environmental stochasticity should always be considered in the development of realistic population models.

However, in using empirical data as a basis for estimating the magnitude of environmental stochasticity to be included in a model, one needs to be careful to exclude sampling variance from that estimate. Even if, in the extreme case, a parameter is truly constant with time, any empirical study will detect year to year variation in the estimate of that parameter for each year studied, simply because the estimates are drawn from a finite sample size. Failure to exclude sampling variance could lead to overestimating the magnitude of environmental stochasticity in a parameter.

Finally, a literature search was conducted on all the breeding species of the CCS to determine what is known of the demographic parameters and to identify the gaps in knowledge. This exercise revealed a number of gaps (Table 4.1) for most of the species.
## Table 4.1 - Demographic parameters of CCS breeders and knowledge gaps (indicated by blank cells).

<table>
<thead>
<tr>
<th>COMMON NAME</th>
<th>Distribution</th>
<th>Population Status</th>
<th>Age at First Breeding Propensity</th>
<th>Juvenile Survival</th>
<th>Breeding Propensity</th>
<th>Reproductive Success</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laysan Albatross</td>
<td>Diomedea immutabilis</td>
<td>increasing</td>
<td>8 (8-9)</td>
<td>0.95</td>
<td>0.64 (0.4-0.78)</td>
<td>90% b.f.</td>
</tr>
<tr>
<td>Black-vented Shearwater</td>
<td>Puffinus opisthomelas</td>
<td>increasing</td>
<td>5.7 (3-7)</td>
<td>0.79-0.95</td>
<td>1st=0.67, 2nd=0.76, 3rd=0.79-0.82, 6-37th=0.861</td>
<td></td>
</tr>
<tr>
<td>Leach’s Storm-petrel</td>
<td>Oceanodroma leucorhoa chapmani</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Leach’s Storm-petrel</td>
<td>O. l. socorroensis</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Leach’s Storm-petrel</td>
<td>O. l. cheimomnestes</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Black Storm-petrel</td>
<td>Oceanodroma melania</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Ashy Storm-petrel</td>
<td>Oceanodroma homochora</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Fork-tailed Storm-petrel</td>
<td>Oceanodroma furcata</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Least Storm-petrel</td>
<td>Oceanodroma microsoma</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Magnificent Frigatebird</td>
<td>Fregata magnificens</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Brown Pelican</td>
<td>Pelecanus occidentalis</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Double-crested Cormorant</td>
<td>Phalacrocorax auritus</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Least Cormorant</td>
<td>Phalacrocorax penicillatus</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Pelagic Cormorant</td>
<td>Phalacrocorax pelagicus</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Heermann’s Gull</td>
<td>Larus heermanni</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Ring-billed Gull</td>
<td>Larus delawarensis</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>Mew Gull</td>
<td>Larus canus</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
<tr>
<td>California Gull</td>
<td>Larus californicus</td>
<td>increasing</td>
<td>3 (2-4)</td>
<td>2.7 (1-4)</td>
<td>0.74</td>
<td>0.74 (0.4-0.90)</td>
</tr>
</tbody>
</table>
Table 4.1 – Demographic parameters of CCS breeders and knowledge gaps (indicated by blank cells).

<table>
<thead>
<tr>
<th>COMMON NAME</th>
<th>Distribution</th>
<th>Population Status</th>
<th>Age at First Breeding</th>
<th>Adult Survival</th>
<th>Breeding Propensity</th>
<th>Reproductive Success</th>
<th>Juvenile Survival</th>
<th>breeding (b.f.) natal (n.f.) fidelity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western Gull</td>
<td>CA, OR, WA, CN</td>
<td>CA</td>
<td>5 (4-6)</td>
<td>0.9 (ENSO = 0.7)</td>
<td>0.945 (.78-.99)</td>
<td>fl-1st:&lt;0.5, 1st-2nd:0.65</td>
<td>75% b. f., 42% n. f.</td>
<td></td>
</tr>
<tr>
<td>Glacous-winged Gull</td>
<td>OR, WA, CN</td>
<td>increasing</td>
<td>5.4 (4-7)</td>
<td>0.83-0.87</td>
<td>1.67 (1.4-1.8)</td>
<td>1st=4, 2nd=6, 3rd=62</td>
<td>85-94% b. f.</td>
<td></td>
</tr>
<tr>
<td>Gull-billed Tern</td>
<td>CA</td>
<td>decreasing</td>
<td>5</td>
<td></td>
<td>0.68</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caspian Tern</td>
<td>CA, OR, WA, CN</td>
<td>3 (2-4)</td>
<td>0.87-0.91</td>
<td></td>
<td>1.1 (0.6-1.6)</td>
<td>0-1:0.55 ; 1-4:0.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Royal Tern</td>
<td>CA, MX</td>
<td>(2-6)</td>
<td>(0.69-0.77)</td>
<td></td>
<td>0.68</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elegant Tern</td>
<td>CA, MX</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.97</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arctic Tern</td>
<td>WA</td>
<td>decreasing</td>
<td>3-4</td>
<td>0.82-0.87</td>
<td></td>
<td>Gulf of AK;1.16; Cooper l:(0.21-0.86)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forster's Tern</td>
<td>CA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0-1.6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Least Tern</td>
<td>CA, MX1</td>
<td>increasing</td>
<td>3 (2)</td>
<td>0.88 (0.84-0.94)</td>
<td>0.47</td>
<td>0.80-0.82</td>
<td>36-86% b.f., 16% n.f.</td>
<td></td>
</tr>
<tr>
<td>Black Skimmer</td>
<td>CA</td>
<td>3 (2-4)</td>
<td></td>
<td></td>
<td></td>
<td>NY(0.25-0.91) TX(0-2)</td>
<td>76% b. f.</td>
<td></td>
</tr>
<tr>
<td>Common Murre</td>
<td>CA, OR, WA, CN</td>
<td>4(2-9)</td>
<td>0.87-0.95</td>
<td></td>
<td></td>
<td>CA:8(1-9); WA:35(09-71)</td>
<td>57-78% n.f.</td>
<td></td>
</tr>
<tr>
<td>Pigeon Guillemot</td>
<td>CA, OR, WA, CN</td>
<td>decreasing?</td>
<td>3</td>
<td>0.8 (.76-.89)</td>
<td>(0-0.8)</td>
<td>CA:1.0; WA:0.82, 0.89</td>
<td>0-1st breed=0.4</td>
<td></td>
</tr>
<tr>
<td>Marbled Murrelet</td>
<td>CA, OR, WA, CN</td>
<td>decreasing?</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.833 (0-1.53)</td>
<td></td>
</tr>
<tr>
<td>Xantus's Murrelet</td>
<td>CA, MX2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.28, 0.3</td>
<td></td>
</tr>
<tr>
<td>Craveri's Murrelet</td>
<td>MX</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.72 (0.3-1.36)</td>
<td></td>
</tr>
<tr>
<td>Ancient Murrelet</td>
<td>WA, CN</td>
<td>decreasing</td>
<td>3 (2-4)</td>
<td>0.83-0.87</td>
<td>1.44-1.69</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cassin's Auklet</td>
<td>CA, OR, WA, CN, MX</td>
<td>decreasing</td>
<td>3 (1-4)</td>
<td>0.75</td>
<td>CN:0.65</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhinoceros Auklet</td>
<td>CA, OR, WA, CN</td>
<td></td>
<td>3</td>
<td>0.62</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tufted Puffin</td>
<td>CA, OR, WA, CN</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.563 (0.13-0.92)</td>
<td></td>
</tr>
</tbody>
</table>

SEFI: Species Endangered for the Future.
4.3 ENVIRONMENTAL VARIATION IN EACH PARAMETER

Studies conducted in the CCS and other temperate as well as polar areas indicate a large degree of annual variability in demographic parameters (100). Reproductive success is the best documented of the seven parameters, but adult survival and juvenile/subadult survival also show marked variation.

With the ENSO events of 1982/1983, 1991/1992, and 1997/1998 there has accumulated a large body of evidence that demographic parameters can be strongly influenced by such global-climate events. The concept that decadal-scale variation can also be strongly evident in demographic parameters has emerged recently. In many cases, changes at this longer timescale (c. decadal) are associated with changes in oceanographic regimes.

A major oceanographic regime shift was observed in about 1976 (122) and more recently in about 1999 as well. For Cassin's Auklets on Southeast Farallon Island, there was a marked change in nearly all demographic parameters before and after the shift in 1999: reproductive success increased by 50% comparing 1991 to 1997 with 1999 to 2002; adult survival increased by 9% during the same time period; and breeding probability increased by 10% (Nur et al. in review).

Other examples of decadal-scale changes in adult survival are summarized in Nur and Sydeman (100). In the Antarctic, Jenouvrier et al. (123) observed decadal changes in southern fulmar adult survival, while Barbraud and Weimerskirch (124) observed long-term changes in Emperor Penguin survival.

With respect to reproductive success, two different temporal patterns for birds of the CCS can be identified. The Common Murre on SEFI displays a skewed pattern of moderately high success in most years, with a few exceptional years of very low (or no) success (e.g., in strong ENSO years (25)). Brandt's Cormorants on SEFI provide an example of a second pattern: reproductive success varies strongly between years, but deviations are both positive (“boom” years) and negative (“bust” years). Thus, Brandt's Cormorants show a normal distribution of reproductive success by year, but Common Murres do not.

Spatial Variation

Relatively few studies have examined spatial variation in demographic parameters for the same species or subspecies, but there are some examples relevant to the California Current. Examples include variation in juvenile and subadult survival in Common Murres (125), variation in adult survival in Cassin's Auklets (126-128), and variation in reproductive success and adult survival for Rhinoceros Auklets (129).

In particular, a recent study examined variation in reproductive success parameters across the California Current and Alaska Current (Sydeman et al. unpublished) at 12 colonies, for three seabird species, comparing reproductive success before and after the El Nino event of 1997/1998. Whereas these researchers found strong effects on marine birds throughout the CCS and southern Gulf of Alaska, they also found that different populations demonstrated differences in the timing of the diminishment of breeding success: some populations showed a decline in 1997 while others declined in 1998.

The magnitude of spatial variation (and correlation across populations) in demographic parameters will depend on which factors are most important in determining the realized values. To the extent that basin-wide factors (oceanographic regime and ENSO events) are most important, we would expect that spatial variability would be muted. To the extent that local factors are most important we would expect substantially higher spatial variation. Oil spills and predation are examples of local factors, especially predation at the colony. Prey can vary on a local scale and there is increasing evidence that local factors (at least as indicated by oceanographic conditions) are associated with variation in reproductive success at Triangle Island (130) and on the Farallon Islands (131).
Evidence of the strong influence of food availability on demography, often driven by climate variability, is presented in Chapter 5. Adult survival, breeding probability (including both beta and gamma), and reproductive success have all been shown to vary with indices of food availability (31, 35, 59, 100, 131, 181).

For example, for Western Gulls and Pelagic Cormorants breeding on Southeast Farallon Island, there was a strong relationship between indices of rockfish abundance (direct or indirect) and reproductive success (132). In some cases, a correlation with an environmental index has been demonstrated and it has usually been inferred that such a correlation implies a link with food availability (123, 132).

Juvenile survival and subadult survival have been much more difficult to study. Nevertheless, studies of Brandt’s Cormorants on the Farallon Islands have demonstrated that the probability a locally fledged bird survived until age 3 (when large numbers of individuals begin breeding) was correlated with SST recorded both for the year of fledging and SST in the third year of life when individuals first return to the colony to breed (31). For Cassin’s Auklets on the Farallon Islands, Nur et al. (in review) demonstrated a correlation between the proportion of a cohort recruiting and the Northern Oscillation Index (NOI) in the winter before the fourth year of life, the modal year of recruitment for this population.

Predation is also a strong influence on seabird populations (see Chapter 6), especially predation at seabird colonies (both of breeding adults and of eggs or chicks). In some cases, predators are native predators while in others they are non-native. Studies by Sydeman et al. (133) and Nur et al. (134) identified predation as the most important factor influencing population status and population vulnerability for Ashy Storm-Petrels and Xantus’s Murrelets. For the former, predation on adults and subadults by Western Gulls (a native species, which has increased its spread on Southeast Farallon Island, overlapping with the Ashy Storm-Petrel population) has been the concern; for Xantus’s Murrelet, both mouse and Barn Owl (Tyto alba) predation of both chicks and adults was the issue.

Predation rates may appear relatively small yet still have population-level impacts. For example, the predation rate may be on the order of 3% of the population for Ashy Storm-Petrels mentioned above (133), but even additional mortality of this magnitude can mean the difference between a declining and an increasing population.

A study on Black-legged Kittiwakes in the Shetlands, demonstrated that both food, mediated through the abundance of juvenile sand lance, and predation by Great Skuas, were significant influences on demographic parameters (35). In particular, sand lance abundance influenced both adult survival and reproductive success. Great Skuas in the Shetlands (at Foula Island) surprisingly also demonstrated adult survival rates that were dependent on sand lance abundance (59). That is, both the seabird prey and the seabird predator demonstrated a correlation of adult survival with sand lance (principal prey of the kittiwake).
4.6 MORTALITY DUE TO ANTHROPOGENIC PERTURBATION

Mortality due to fisheries is discussed in Chapter 6 and that due to oil pollution in Chapter 7. Both have serious impacts on seabird populations and are of grave concern. With regard to bycatch, as noted above, even a relatively low mortality rate (of 1 to 3% per year of the total population) can cause population decline where otherwise there would be stability. For Common Murres, mortality due to gillnetting has been considered to be instrumental in diminishing population size in Central California (135).

Oil pollution exerts an impact both episodically, due to major oil spills, and chronically, due to chronic oiling. Major oil spills receive the most attention (136, 137) and rightfully so, since mortality can be very high. This mortality usually consists of both adults and immatures. Loss of breeding-age adults is the greatest concern with loss of immatures less so, since only a fraction of these age classes would otherwise recruit into the breeding population. Other impacts on demography can be more subtle. For example, reproductive success can be disrupted if an individual loses its mate; a “widowed” bird may not pair at all in the subsequent season or may have reduced success if it does.

However, chronic oiling is also a serious concern. Nur et al. (138) evaluated oiling rates obtained from beached bird surveys for several CCS seabird species. For Common Murres in central California, they estimated that chronic oiling accounted for an additional adult mortality of 2% per year and for juveniles an additional mortality of 7%. Data from other species (grebes, loons, and scoter species) did not suggest mortality rates as high as for Common Murres, consistent with the finding of Page et al. (136), who investigated mortality of seabirds as a result of the Apex Houston spill.

4.7 DENSITY DEPENDENCE: NEGATIVE AND POSITIVE

Density dependence has been discussed extensively with respect to seabirds (2, 139). Density dependence can be negative (survival and reproduction decrease with increasing population density) or positive (increase in these parameters with increasing population size). In addition, dispersal can be a function of population size.

Density dependence is of great conservation significance since it can lead to population regulation (i.e., stabilization of population size) if the dependence is negative, or can lead to population destabilization (thus increasing the probability of population crashes and extinction) if it is positive. The decrease in survival and/or reproduction as population size or density gets to be especially small is referred to as the Allee effect and was first described for animal species 70 years ago.

Recent analyses by Nur and Sydeman (132) examined density dependence in four species on the Farallones that have been studied over a 23 to 30 yr period (Western Gulls, Brandt’s Cormorants, Pelagic Cormorants, Common Murres). These authors found no correlation between breeding population size in a given year and reproductive success in the same year, in fact the correlations tended to be positive (though not significant). Other parameters were not examined in this study, though Nur and Sydeman (31) found no relationship between adult survival and population size for Brandt’s Cormorants.

In contrast, Frederiksen and Bregnballe (140) found evidence for density dependence in adult survival of European Cormorants (Phalacrocorax carbo sinensis), which appeared to be a result of differences in over-winter survival. This subspecies is found in freshwater and sheltered marine habitats, and so the relevance of this example is low for the CCS.

For seabirds breeding in the CCS or in the Gulf of Alaska, there is no evidence that we know of indicating either negative or positive density dependence for any demographic parameter. However, both remain of potentially great concern. As population size increases to especially high levels (e.g., colonies with more than 100,000 breeding pairs), density dependence may be a factor, especially for breeders that must forage for food for the chick. At the same time, were colonies or populations to decrease to very low levels, this may be of concern, too.
4.8 ALLEE EFFECT

In contrast to the lack of direct evidence for negative density dependence, positive density dependence appears to be an important factor in a wide range of seabird species—but only at low population densities. For many species, if population size or density falls below a certain threshold value, this results in reduced population growth rate, termed the “Allee effect” (named after the ethologist W.C. Allee).

The Allee effect is discussed by Lande (141) and Simberloff (142) and has been incorporated into population models of the Spotted Owl (Strix occidentalis). In the Common Murre, there is good evidence that reproductive success increases with density at the colony (71), apparently due to better protection from predators at high density compared with low. Other examples of deleterious effects on seabirds of breeding at low density are given by Wittenberger and Hunt (143). Hudson (69) considered implications of positive density dependence for murre population dynamics. He modeled a scenario where an oil spill (or similar catastrophic mortality) could lead to long-term population decline, which accelerates as density decreases, eventually resulting in population extinction.

Because positive density dependence (a generalization of the Allee effect) appears to be of widespread significance for colonially-breeding seabirds, it would be important to minimize the Allee effect for target populations. For some species, this may mean taking steps to ensure that colony size or population density does not dip below the threshold level at which the Allee effect exerts itself.

Small colonies suffer a double penalty; in addition to the Allee effect, they are subject to the deleterious effects of demographic and genetic stochasticity. For seabirds, which generally display low fecundity, the most expeditious way to increase colony size is through immigration. This may include recruitment of additional individuals to a colony using attraction techniques (144).

4.9 RELATIONSHIPS BETWEEN DEMOGRAPHIC PARAMETERS

An empirical question rarely addressed in the seabird literature is, “How correlated are the demographic parameters with each other?”

Population fluctuations will be much stronger if demographic parameters positively covary; conversely, fluctuations will be dampened, and population stability will be enhanced, if parameters covary negatively. Where patterns of covariation over time have been examined, positive covariation has generally been present. Examples include Cassin’s Auklet (Nur et al. in review) and Southern Fulmar (123). For Black-legged kittiwakes, reproductive success and adult survival were both related to prey availability (35). More studies are needed, but so far the indication is that parameters covary positively.

How much does each parameter contribute to changes in population growth?

From a management perspective, this question is of great interest. However, answering it has not been easy. One approach has been to vary each demographic parameter a fixed percentage and examine effects on population growth. A second approach has been to examine elasticity or sensitivity of the Leslie population matrix (145). In this second approach, one examines the absolute or proportional change in the population growth rate as a result of infinitesimally small changes in individual demographic parameters. Both approaches usually yield similar results; often, adult survival is identified as the parameter most sensitive with respect to determining population growth, while population growth rate is not very sensitive to changes in reproductive success.

There are some complications to consider. First, conclusions may be affected by the choice of which rate to vary, mortality or survival. Thus, one investigator may vary mortality by a relative 5% (e.g., change adult mortality from 0.20 to 0.19, implying that survival changed from 0.80 to 0.79), while the other may vary survival by a relative 5% (e.g., change adult survival from 0.90 to 0.95, implying that mortality changed from 0.10 to 0.05). If we do not realize this, we may be led to conclude that population growth rate is sensitive to differences in survival but not to differences in mortality, which is logically inconsistent.
Calculation of elasticity and sensitivity avoids this problem, though one needs to develop a population matrix model in order to derive these measures. In addition, a second complication is that the number of age classes in the model will determine the magnitude of sensitivity and elasticity for each age class. Thus, if one models a seabird with 9 age classes (e.g., 0, 1, 2, 3, 4, 5, 6, 7, and 8+ year olds), one may include that the parameter with the greatest sensitivity is survival of 8+ year olds. However, if one models the same population, this time with 50 age classes, one might conclude that sensitivity is greatest for survival of 0 year olds (i.e., juvenile survival). The only difference is that one model lumped individuals of 8 to 50+ years of age (thereby creating one large “older adult” age class) and the other did not.

However, there is a third and most serious complication: the approach of calculating elasticity and sensitivity does not take into account the magnitude of variability in a demographic parameter and how sensitive it is to changes in the environment. That is, if we are interested in comparing “good” (e.g., cold water) years with “poor” years (e.g., warm water), one should take into account that adult survival may only change by 5% between a good and bad year, but reproductive success may change by 50%. This was the magnitude of the difference in parameters observed for Cassin’s Auklets by Nur et al. (in review). These authors concluded that the observed change in reproductive success (a change of 50%, comparing the warm-water regime of the 1990s prior to 1998 to the cold-water regime starting with 1999) was as influential in determining a change in the population growth rate as a change in adult survival of 5%. As a result, they concluded that reproductive success and adult survival were equally important in explaining changes in population trajectory for this population.

4.10 STABILITY VERSUS VOLATILITY OF SEABIRD POPULATIONS

In the CCS little negative density dependence is apparent, thus stability is rare. What apparent stability of seabird populations is observed is not mainly a result of regulation. In addition, demographic parameters fluctuate strongly over time (from year to year and from decade to decade), this leads to further population fluctuations. Climate-driven changes in ocean regimes appear to be cyclical (cold-water and warm-water phases alternating, for example (122)).

Thus, conditions for population growth alternate between favorable and unfavorable, leading to corresponding population growth and decline, respectively. This alternating pattern can both abate unchecked growth and lead to reversals of population declines of CCS seabird species. However, to the extent that populations decline to extremely low levels and are subject to the Allee effect (an effect yet to be confirmed by CCS seabird populations), there is concern for the inherent instability that may result.
4.11 METAPOPULATION MODELS

The first metapopulation model was that of Levins (146). The general idea is that a metapopulation consists of several distinct populations that are linked by dispersal (immigration and emigration).

In Levins’ model there are an infinite number of available patches and each empty patch is colonized, with a certain probability; if the patch is occupied with a population then that population may go extinct with a certain probability. In Levins’ model there are no internal population dynamics: local populations are either extinct or full.

In more recent years, more realistic models have been developed (7, 147-151), and application of metapopulation models to problems of conservation and management has proliferated (152). Examples of recent bird metapopulation models include Stith et al., (153); Smith et al., (154); Akcakaya et al., (155); LaHaye et al., (156); Buckley and Downer, (1); Wootten and Bell, (157); Stacey and Taper, (158); we discuss most of these below. Source/sink models (see below) can be considered a particular kind of metapopulation model.

Stith et al. (153), drawing on previous work of Harrison (149), present a good overview of types of population structure that are either examples of types of metapopulations or are examples of population structures that would not qualify as true metapopulations.

The central idea is that a metapopulation consists of populations that are semi-isolated. If populations are so isolated that they virtually never exchange immigrants, then this would not qualify as a metapopulation.

In contrast, according to Harrison (149), a patchily-distributed species is not a metapopulation if dispersal between patches is very common and/or individuals inhabit several patches in one lifetime. Other investigators disagree, however (e.g., Spendelow et al., (36); Buckley and Downer, (1)), and consider any set of populations linked by dispersal to constitute a metapopulation.

A second important point is that a common configuration for a metapopulation may consist of a single large “core” or “mainland” population surrounded by a number of smaller “satellite” or “island” populations. The latter would be prone to extinction, but the core population is considered to have high probability of persistence.

The single population models discussed above (e.g., that of the Farallon Common Murre (60), can be thought of as a special case of a metapopulation model.
However, even a small amount of dispersal can affect persistence of local populations, especially if the local populations are small (and thus prone to extinction, see above). This last point was demonstrated by Stacey and Taper (158) in modeling the fate of small, local Acorn Woodpecker (Melanerpes formicivorus) populations. In the absence of immigration, these populations would rapidly go extinct, but a moderate immigration rate would suffice to maintain the metapopulation for hundreds of years. Metapopulation models can be used to assess the persistence (or other aspects of the population dynamics) at the level of an individual, localized population, or to assess the dynamics of the entire metapopulation.

Two factors influencing metapopulation dynamics are dispersal rates between local populations (as mentioned above) and environmental correlation among the patches. The more correlation among populations, the more likely several populations will suffer the same environmental catastrophe at once. This point relates to the concept of “spreading of risk” (159, 160). If, however, all local populations are subject to the same red tide or same oil spill, then no risk has been spread at all.

Akcakaya and Ginzburg (161) used a metapopulation model to consider the long-term persistence of Mountain Gorilla (Gorilla gorilla beringei) metapopulations. In an uncorrelated environment the long-term persistence of several small populations was indeed greater than a single large population, thus demonstrating “spreading of risk.” However this advantage was overcome if correlation among the several small populations was moderately strong. For strong environmental correlation in demographic parameters (156), a single large population will persist longer than several small populations, even if they are connected by dispersal.

Definition of sinks and sources

Pulliam and colleagues have recently focused attention on the importance of sink and source populations with respect to population dynamics on a local and regional scale (162, 163).

A “sink” population is one in which local production of new recruits is less than mortality of established individuals, and therefore the population is not self-sustaining; it can only be sustained by immigration from other, more productive populations.

A “source” population, on the other hand, is productive enough so that an excess of potential recruits is produced. This can lead to growth of the source population or to emigration of potential recruits to other, mostly sink, populations, or to both. A network of source and sink populations can be formed, joined by immigrants/emigrants; this may be referred to as a “landscape” of populations.

An important implication of the source/sink paradigm is that population dynamics cannot be understood at the level of a single population, which may either be a source or sink, but rather at the level of the entire network or landscape. Furthermore, Pulliam (163) demonstrated that a single source population can effectively maintain a large number of sink populations; in fact, most of the individuals in a metapopulation may be breeding in sink populations and yet the overall network of source/sink populations may be self-sustaining.

In short, conservation efforts need to be directed, above all, at source populations not sinks; it is only source populations that allow sink populations to persist.

One difficulty with the sink/source paradigm is that it is empirically difficult to identify which populations are actually sources and which sinks. At minimum one would require information on survival, recruitment, and reproductive success specific to each population; information that is rarely available. But even this information may not be sufficient: Watkinson and Sutherland (164) demonstrate that with high immigration and negative density dependence, what appears to be a sink population may actually be a source population. That is, in the absence of immigration/emigration a population may be self-sustaining (thus meeting the definition of a source population) but when there are many immigrants, fecundity or survival, or both, may be depressed at the higher population density.
A second difficulty with the sink/source paradigm is that a population may be a source at one point in time and a sink at another point in time.

Wootton and Bell (157) developed a metapopulation model for the Peregrine Falcon (*Falco peregrinus*) in California. They considered there to be two subpopulations linked by dispersal: the Northern California population, which they argued is a source population, and the Southern California population, which they argued is a sink population. Current management efforts are geared towards the Southern California population, and involve release of captive-bred individuals. Management efforts, they argue, would be more productive if they were directed at stabilizing and increasing the Northern source population rather than the Southern sink population.

**Implications of sink/source population dynamics**

The future of a metapopulation does not lie with sink populations, it lies with source populations. For colonial seabirds, small populations are especially likely to be sinks. This is due to the manifestation of the Allee effect, which appears to apply to all vertebrate species, at least to some degree (150).

For species, such as Common Murres, the Allee effect appears to be prevalent over a considerable range of population sizes and population densities (see above). Examples of likely sink populations would be small colonies that are being re-established or being “incremented”—i.e., exactly the targets of some restoration programs (165).

A conservation program that invests in sink populations rather than in source populations is unlikely to succeed in the long-term. Sink populations, by definition, are incapable of sustaining their own growth. However, as stated above, population status can change over time, with the possibility of sink populations becoming source populations with changing conditions.

In contrast, it is precisely source populations that are incapable of sustaining the growth rate of the entire metapopulation. Pulliam and colleagues (162, 166) have shown that a stable metapopulation may be sustained by only a few source populations, in the midst of many sink populations. Since it is only the source populations that are sustaining the population, and only the source populations that are capable of leading to future growth, then clearly the lion’s share of attention in a conservation program should be paid to source, or potential source, populations.

The long-term value of a sink population is minimal. It is simply wishful thinking to think that a sink population will be able to repopulate the geographic range of a metapopulation should the mother colony undergo a population crash. Alternatively, one can investigate ways in which sink populations can be improved, thus transforming sink populations into self-sustaining populations.
In other words, a valuable objective of a conservation program would be to improve reproductive success in relation to mortality, on a site-by-site basis, thus turning sink populations into source populations. Since a newly (re)established colony will almost always be small, it is more likely to be a sink than a source—at least in its initial phase. Once an erstwhile sink population reaches a threshold population size it may now be self-sustaining, but the initial increase in population size (from small, sink colony to large, self-sustaining colony) will not be due to internal recruitment but rather due to recruitment from elsewhere. This is not to say that all small colonies are sinks, but just that it is more likely for a small colony to be a sink than for a large colony.
4.12 UTILITY OF POPULATION MODELS

Caswell (145) explained the utility of population models to conservation biology by way of an analogy to medical practice. A patient (the population) is examined to assess its condition, the causes of any problems are diagnosed, treatments are prescribed to address the problems, and a prognosis predicts eventual outcomes of treatment.

Population assessment is primarily a matter of determining the population growth rate ($\lambda$). This may be accomplished either by examining changes in population numbers (directly or via index), or by well-designed mark-recapture studies that provide data for estimation of vital rates that can be used to construct a model, then derive the model’s dominant eigenvalue ($\lambda$). Although assessment can be made without knowledge of vital rates, they are necessary for diagnosis and treatment, and are ultimately the best means of assessment as well.

Diagnosis attempts to determine why the population is in trouble. The best tool for this is retrospective perturbation analysis. Diagnosis requires examination of differences in vital rates and population growth rates from the population of concern versus either a) itself during a time period when the population was not in trouble, or b) a separate population that is not currently in trouble. Life table response experiments (LTRE) provide the framework for the diagnosis (145, 182). Given actual comparative data from the population during periods with different population trajectories, LTRE will quantify the contributions of vital rates to the change in $\lambda$.

Prescriptions are perturbations enacted by management on specific vital rates in order to alter $\lambda$. Because this approach is forward looking, the proper tool for evaluating management prescriptions is prospective perturbation analysis. This technique investigates the relative effects of changing different vital rates on overall population growth rate. Such analyses are generally made by sensitivity (183) or elasticity calculations (184). Sensitivity is the incremental change in $\lambda$ due to an incremental change in a vital rate; however, such calculations are misleading due to the different scales of different vital rates (e.g., fecundity vs. survival) (167). One solution to the scaling issue is elasticity, defined as the proportional change in $\lambda$ related to a proportional change in vital rate. More recently, Link and Doherty (168) introduced methods for a variance stabilizing transformation to deal with scaling issues.

Hamilton and Moller (96) examined sensitivity of population growth rate of Sooty Shearwaters to small changes in adult mortality, and found that the population trajectory was not particularly sensitive to this parameter, but was more sensitive to changes in juvenile mortality. This finding runs counter to the conventional understanding that population trajectories of long-lived species such as seabirds are most sensitive to changes in adult mortality rates. Indeed, Russell presents evidence from several studies supporting the latter argument, including a model of the sensitivity of $\lambda$ to variations in adult survival and reproductive success in Wandering Albatrosses.

Buckley and Downer (1) conducted perturbation analyses on several idealized seabird species by taking into account the expected range of variation in each parameter, and came to the conclusion that subadult survival—but not adult survival or first-year survival—was one of the most important parameters determining long-term population growth and persistence. Seather and Bakke (169) examined 49 bird species (including 0 seabird species) and found that covariance of vital rates influenced the contribution of a vital rate to $\lambda$, a consideration that is often overlooked.

An important question to consider is whether or not a prescription that perturbation analysis indicates would have a large effect on $\lambda$ and actually provides a practical and realistic response. The answer to this depends on technical, economic, and political feasibility that must be considered both separately and jointly. Nichols and Hines (170) suggested a metric whereby elasticities of vital rates could be considered relative to costs of management actions, and provided an equation for calculating proportional change in $\lambda$ per dollar spent.

Prognosis aims to predict a population's fate via population viability analyses (PVA). PVA uses stochastic models with fluctuating population size and varying vital rates to predict population size, and probability of population persistence for a defined time horizon under certain specific conditions (171). PVAs are inherently risky as they attempt to forecast the future fate of the population, but can be valuable so long as they are understood to be projections that are conditional on the population model(s) at hand.
If managers and policymakers could be educated to understand the probability projections from models representing different management regimes, PVAs could become a more useful conservation tool. Whereas PVAs have become more and more commonly applied to birds and mammals recently (9, 155, 172-175), there apparently have been few developed for seabirds. We know of only three examples: that of Hamilton and Moller (96) for Sooty Shearwaters and that of Sydeman et al. (133) for Ashy Storm-petrels (Oceanodroma homochroa) and Xantus's Murrelets (Synthliboramphus hypoleucus).

Population dynamic and metapopulation models serve an important role in planning and evaluating conservation programs. Evaluation of management actions should include quantifying the possible benefits of active and passive conservation efforts, as well as measuring the costs of not implementing conservation efforts. Population modeling permits different conservation scenarios to be evaluated using a common yardstick.

Population models provide a good framework for exposing areas where we have insufficient information as well as allow us to evaluate the significance of these sources of uncertainty.

In one case, for example, a small gap in knowledge may have a big influence on the prognosis for a population and influence the evaluation of alternative restoration programs; in another case, ignorance of parameter values may be greater, but the impact on the future course of the population may be small.

An example of the second case is provided by results of a metapopulation model of Southern California Spotted Owl population dynamics (156). Dispersal among fifteen populations, thought to form a single metapopulation, was not known, but the available evidence indicated very low rates of dispersal. Specifically, observations of two color-band ed populations 10 km apart indicated no exchange of individuals over a five year period. Therefore LaHaye et al. (156) carried out metapopulation simulations in which dispersal was moderate (4% between neighboring populations), low (2%), very low (1%), or none (0%). It turned out that predictions of their model were insensitive to the presumed level of dispersal. Thus dispersal was clearly a parameter with insufficient information (and one that might be picked upon should the metapopulation model become implicated in a litigation effort), yet not one that had an important consequence for model predictions.

Population models (and models in general) require one to be explicit about assumptions. These assumptions, and the sensitivity of population model predictions to them, can and should be evaluated directly. For example, a model may assume the presence or absence of density dependence, either negative or positive, and this would need to be considered when assessing the appropriateness of the model. A different type of assumption may relate to the efficacy of conservation action. Following an oil spill, for example, little is known about the subsequent fate of “rehabilitated” birds despite good estimates regarding the number of oiled birds treated and released (176). One can create a model to compare predictions regarding impact and subsequent recovery from a spill assuming that (1) some or all rehabilitated birds die within a specified time 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 (1), (2), and (3).
Select examples of population models

To illustrate the general points made above, we conclude by considering a few recent seabird models that have, in our view, produced valuable insights and serve as examples of potential avenues of investigation.

First, Hamilton and Moller (96) conducted a PVA of Sooty Shearwaters. They determined that predator control was the key ingredient to assure long-term persistence of Sooty Shearwater populations, and that control of adult predation was much more effective than control of chick predation. However, one of their other conclusions also bears repeating: "Less reliance should be placed on the predictions of population trends or extinction probabilities than on the model's guidance to the relative efficacy of management actions." This is a view with which we concur.

Shannon and Crawford (177) used modeling to investigate population dynamics of African Penguins (Spheniscus demersus) at Dassen Island, South Africa in relation to egg harvesting and oil pollution. The authors were able to estimate the extent of commercial egg harvesting on the population during the early 20th century, back-calculate pre-egg-harvesting population size, and determined that there was no sustainable egg harvest plan; even harvesting 1% of annual egg production negatively affected population growth rate. Simulations projected the 50-year population under 7 different chronic and catastrophic oiling scenarios, both with and without rehabilitation.

Cuthbert et al. (178) developed stochastic population models of Hutton’s Shearwaters (Puffinus huttoni), an endemic, endangered seabird from New Zealand that may be negatively impacted by introduced mammalian predators. Data were available from the species of interest to estimate adult survival and fecundity, but juvenile survival and age of first breeding were taken from similar species. Sensitivity analyses indicated that breeding parameters, the previous focus of research, had little influence on l, and that further research was needed to 1) obtain more precise estimates of adult survival, and 2) obtain data on juvenile and adult mortality sources. This exercise enabled managers to prioritize research needs and focus management efforts where they would be most productive.

Another example of the utility of a population model in developing and evaluating conservation plans and programs is provided by a population model developed by Ainley et al. (in press) for the Newell’s Shearwater on Kauai.

The Kauai population appears to be declining, which is of concern since the vast majority of Newell’s Shearwaters breed on this island (Ainley et al., in press). A principal objective of the study was to evaluate the impact of different mortality sources of anthropogenic origin. These included “fallout” of newly fledged juveniles, attracted to lights on the island; collisions with power lines, resulting in mortality of adults and subadults; and mortality of adults and subadults during the breeding season, due to introduced predators. In addition, in the past decade a mitigation program had been instituted: juveniles which had “fallen out” were routinely picked up and subsequently released. While this program (Save Our Shearwaters, SOS) did not eliminate “fallout” mortality, it undoubtedly reduced mortality.

The authors evaluated the contribution of each anthropogenic source of mortality to the overall rate of population decline. Model results demonstrated the greatest impact was mortality due to introduced predators; of least impact was residual mortality due to fallout, i.e., fledging mortality occurring despite the presence of the SOS program. Power line collisions were of intermediate importance. However, fallout mortality would be of much greater importance were the SOS program to cease.

With these results in hand, one can discuss costs and benefits of different restoration programs. The most desirable program combines high benefit with low cost. Thus, burying of power lines (at least in key flyway areas) may be more feasible (and less costly) than attempting to eradicate introduced predators on Kauai, even though the latter has greater overall effect on population trends.
4.13 MODELING EFFORTS FOR CALIFORNIA CURRENT SYSTEM SPECIES

Nur et al. (60) created age-structured models with environmental and demographic stochasticity for three species of California Current System seabirds: Common Murre, Brandt’s Cormorant, and Western Gull. The models were integrated with a toxic spill module that predicted mortality given season, size, and drift direction of an oil spill. Density dependence was included in the Western Gull model, but not in the models for the other two species. Food availability could be manipulated directly, or as a function of sea surface temperature and consequences observed. Four simulations were run under different scenarios: status quo, oil spill, reduced prey availability, and El Niño.

Sydeman et al. (133) presented results of PVA for two California Current system endemic species: the Ashy Storm-Petrel and the Xantus’s Murrelet. They demonstrated that predation was likely a key component determining population persistence or likely extinction. In the case of the Ashy Storm-Petrel, predation by Western Gulls (which in recent years had become especially numerous in proximity to Ashy Storm-Petrel breeding sites) appeared to be sufficient to account for the entire observed population decline in the past two decades. Given current demographic parameters, the population faced a high (45%) probability of being reduced to less than 500 breeders within 50 years.

For the Xantus’s Murrelet, the most important demographic process accounting for the observed population decline of 3-5% per year was apparently low reproductive success, mainly due to mouse predation. Reduction of mouse predation on eggs by 50% had the potential to reverse the population decline.

In addition, adult Xantus’s Murrelets suffered from predation by Barn Owls (Tyto alba), but even complete elimination of Barn Owl predation was insufficient to arrest the population decline. Furthermore, Sydeman et al. (179) recommended that the Xantus’s Murrelet population be considered “threatened” since there was at least a 30% (and up to 80%) probability that the largest known colony would be reduced to less than 500 breeders within 20 years.

Parrish et al. (180) studied the demography of Common Murres at Tatoosh Island, Washington from 1991-1999, a period of ~3% annual decline. Age-specific vital rates drawn from the literature were used to develop a number of plausible population models that were compared to the observed population decline. Models included effects of climate, direct predation by Bald Eagles on adults, and indirect reductions in fecundity due to eagle-facilitated gull and crow predation on unguarded murre eggs. Direct and indirect eagle pressure on the Tatoosh Island murre population were implicated in the population decline, but emigration was not quantified.
4.14 RESEARCH AND MONITORING RECOMMENDATIONS

1. Include assessments of adult survival as an essential component of all seabird monitoring programs in the CCS.

2. Study sources of adult, nestling and egg mortality for all seabird species.

3. Conduct research to determine which demographic parameters are most sensitive to temporal environmental variability. This will facilitate the development of predictive population models.

4. As possible, add measurements of demographic parameters to long-term seabird monitoring programs.

5. Conduct research into how demographic parameters co-vary through time to aid in the development of predictive models.

6. Investigate spatial variation of species demographic parameters for metapopulation modeling efforts.

4.15 CONSERVATION AND MANAGEMENT RECOMMENDATIONS

1. Identify and quantify sources of mortality for seabird species of concern.

2. Increase the use of modeling in decision making and as a practical conservation tool in general.

3. Train new experts (i.e. graduate students) in quantitative population biology and the use of population dynamics modeling for seabird conservation.
CHAPTER 4 LITERATURE CITED


Chapter 4. Demography and Population Dynamic Models as a Cornerstone of Seabird Conservation and Management in the California Current


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