

CHAPTER 3

ASPECTS OF SEABIRD BIOLOGY THAT BEAR ON VULNERABILITY TO AND RECOVERY FROM DISASTERS

Part A: Seabird Populations and Genetics

POPULATION DEFINED

The word "population" is commonly used to refer to any group of organisms, whether the group is part of a species inhabiting a local area, all members of a particular species, or all members of all species within a region. The biological definition of a population, however, involves a group of organisms that actually interbreed and share a common gene pool. A population differs from a species, which (according to biological definitions) is a group of organisms with the potential to interbreed. If dispersal of individuals from their place of birth to a breeding site is restricted, a population will include only the residents of a local area, but if dispersal is more widespread, the population may include all members of the species. Each population in turn may consist of two or more subpopulations or demes—groups of individuals that reside in a local area and that interbreed with members of other such groups. For seabirds, colonies and regions may or may not constitute separate populations, depending on levels of gene flow among sites. For example, colonies of thick-billed murres within the North Atlantic appear to constitute a single population and apparently are genetically isolated from colonies in the north Pacific (Birt-Friesen *et al.* 1992).

Some species appear to comprise "metapopulations"—networks of subpopulations that become extinct and are recolonized by immigrants from other sites over time periods ranging from a few generations to tens of thousands of years. Generally, subpopulations of a metapopulation are geographically isolated but exchange migrants on either a regular or intermittent basis (Levins 1969). The rate at which subpopulations disappear depends on conditions within the site as well as stochastic (random) processes, whereas the rate of colonization of new sites and recolonization of previous sites depends on dispersal rates. For example, subpopulations of muskoxen thrive, grow, and disappear over periods of a few generations, only to form again due to immigration of animals from neighboring sites (P. deGroot, Queen's University, pers. com.). Many species of gulls also appear to represent metapopulations.

In such species, at one point in time, individual subpopulations may constitute "sources" of immigrants or "sinks" for immigrants. The degree to which productivity exceeds mortality in certain subpopulations, which will then act as exporters or "sources" of breeders to other sites, will depend on the current state of the environment for these subpopulations. Some subpopulations will, at one point in time, not produce sufficient recruits to offset annual

mortality and will act as demographic "sinks," requiring immigration to prevent extinction. Whether a subpopulation represents a source or a sink at one point in time will depend on its demographic characteristics and on the current and local state of its environment. The status of a subpopulation is independent of population size or density: in theory, as little as 10% of a metapopulation can act as a source and still maintain up to 90% of the population in temporary sinks (see Pulliam 1994). For Pulliam (1994) many species could function as a network of source and sink populations. We emphasize that a given subpopulation can alternatively act as a source and a sink depending on fluctuations in the quality of the local environment.

In such a context, the goal of ecological restoration is to find ways to shift local subpopulations with demographic "deficits" to a state of demographic stability. For example, the control of the introduced raccoon on the colony of ancient murrelets on Limestone Island, British Columbia, has shifted the status of that particular colony from a sink, maintained by the neighboring predator-free Reef Island colony, to a colony that is again self-sustained (J-L. Martin, pers. com.).

IMPORTANCE OF DELIMITING POPULATIONS

For many reasons, understanding the dynamics and geographic limits of populations is essential for management and conservation:

- Species that consist of numerous localized populations may not naturally recolonize areas from which they are extirpated, either because levels of dispersal are too low (Cairns and Elliot 1987) or because migrants lack key adaptations to local conditions and thus do not survive or reproduce. In such species, populations that are decimated or extirpated through natural or anthropogenic disturbances may require human assistance for recovery (see Chapter 4). For example, common murrelets have failed to repopulate colonies in southern Quebec from which they were extirpated by eggging and shooting in the late 1800s and early 1900s (e.g., Tuck 1961). In species that are essentially panmictic (populations characterized by random breeding) or that constitute metapopulations, subpopulations may recover from disturbance relatively quickly and without assistance. For example, double-crested cormorants have recolonized many sites from which they were exterminated by pesticides and human predation in the 1950s and 1960s (see Nettleship and Duffy 1995).
- Protection of healthy populations (i.e., current sources of immigrants) is critical to the longevity of species. Protection of populations that currently act as demographic sinks will be efficient only if we are able to identify and act upon the causes of the reproductive deficit. The removal of the human-caused perturbation(s) to the population (e.g., introduced predators, habitat destruction) is an efficient means of restoration and protection of such sink populations. However, if a population is currently acting as a sink, but with no apparent factor explaining its demographic deficit, the decision to restore that population will require additional, sometimes subjective, information. For example, the decision may depend on our ability to estimate the value of such a population as a potential demographic source in the future, or as a stepping stone in maintaining the functional integrity of the metapopulation.

- Knowledge about the geographic limits of populations is also important for determining the impact of natural and anthropogenic mortality. For example, a small, localized oil spill may have little impact on a large, geographically widespread population, such as the North Atlantic population of thick-billed murres, but may have a catastrophic effect on a small, demographically isolated population, such as red-legged kittiwakes on Buldir Island.
- Population data are required to determine the effective size of a population. The effective size is the number of individuals that actually contribute to the gene pool of the population, and may be one or two orders of magnitude lower than the census size due to unequal breeding success and population bottlenecks. For example, the North Atlantic population of thick-billed murres consists of approximately 2.5 million breeding pairs (Nettleship and Evans 1985), but appears to have an effective size of only ~10,000 females (Friesen *et al.* 1997).

Thus, although seabird colonies are attractive units for conservation and restoration due to their generally well-defined geographic limits, the population is the more appropriate unit toward which effort should be applied.

METHODS OF DELIMITING POPULATIONS

The geographic limits of a population can be delineated using one or more of four basic approaches.

Demographic Data

The direction and extent of gene flow among local populations can be approximated from demographic data such as dispersal information (e.g., Rockwell and Barrowclough 1987). Such information provides estimates of the geographic limits of a population, the extent to which it represents a metapopulation, and the identity of source and sink populations. Although dispersal data provide direct measures of contemporary movements, accurate estimates of gene flow also require information about lifetime fitness (the contribution of recruits to the next generation) of both resident individuals and migrants. Unfortunately, generation of the required data involves long-term mark-and-recapture studies (such as banding data) and is extremely labor-intensive, especially for seabirds that have secretive nesting habits, such as marbled murrelets. Furthermore, demographic data do not account for historical gene flow, which may be one of the most important forces defining populations, especially in species occurring at high latitudes because of the effects of Pleistocene glaciers. This is especially true of metapopulations: subpopulations may exchange few or no migrants over human lifespans, but may be connected by infrequent, mass movements of individuals. For example, band returns suggest that little or no dispersal has occurred among colonies of thick-billed murres in the North Atlantic during the past 100 years, but intensive hunting and eggging at the colony at Ydre Kitsigsut (Greenland) appeared to result in movement of thousands of individuals to a neighboring site at Arsuk Fjord (Nettleship and Evans 1985). Furthermore, genetic data suggest that Atlantic colonies of thick-

billed murres were founded by large numbers of birds from one ancestral population following recession of the Pleistocene glaciers (Friesen *et al.* 1997).

Morphometrics

Morphological differences among animals from different subpopulations can provide a suggestion of the extent to which they represent genetically isolated populations. For example, Warheit (1996) was able to identify breeding populations of common murres from the north Pacific based on morphometric variation of skeletal elements. This approach has the advantage of being relatively quick and inexpensive, but rigorous analysis requires that birds be killed. Furthermore, it provides only an indirect measure of the amount of gene flow, may be confounded by environmental forces, and does not provide an indication of the extent to which a population represents a metapopulation or consists of sources and sinks.

Traditional Genetic Methods

Protein electrophoresis may also be used to estimate the geographic limits of populations, the extent to which a population represents a metapopulation, and the identity of source and sink sites. This approach has the advantage of being relatively quick and inexpensive, but it often necessitates that birds be killed and requires highly trained personnel and specialized laboratory facilities. Also, protein electrophoresis often is not suitable for measuring genetic subdivision in populations that breed at high latitudes due to low levels of variability (Evans 1987); because most of these populations were established following recession of the Pleistocene glaciers, insufficient time has elapsed for evolution of population-specific protein markers. Furthermore, due to the low mutation rates at most protein loci, classical electrophoresis measures rates and directions of evolutionary gene flow, which may be very different from contemporary values. Thus, populations may have been genetically isolated for tens of thousands to hundreds of thousands of years, but may have very similar electrophoretic profiles due to historical association. For example, protein data suggest that the North Atlantic population of thick-billed murres is essentially panmictic (Friesen 1992), even though band returns indicate that very little gene flow occurs among colonies today.

Recent Molecular Methods

Recent innovations in molecular and theoretical genetics, especially the polymerase chain reaction (PCR, or DNA amplification), provide potentially accurate and sensitive methods of measuring the direction and magnitude of gene flow among populations. PCR uses a modification of the fundamental cellular process that replicates DNA to generate millions of copies of specific target genes. The gene that is amplified is determined by the choice of primers—short pieces of DNA that match regions flanking the gene of interest and that provide initiation sites for DNA replication. Thus, PCR enables researchers to focus on genes with high levels of variability and has several advantages over previous methods of genetic analysis. Most importantly for the present purposes, PCR enables variation in DNA to be compared directly

among individuals from different sites (e.g., Kocher *et al.* 1989, Birt-Friesen *et al.* 1992, Quinn 1992, Wenink *et al.* 1994). Furthermore, it allows researchers to focus their attention on genes that have slower or faster mutation rates and that, therefore, provide measures of historical and recent levels of gene flow, respectively. Unfortunately, many existing PCR-based protocols are slow and laborious (e.g., analysis of DNA sequences or microsatellite loci), produce results that are not reproducible and are difficult to interpret (e.g., analysis of randomly amplified polymorphic DNA [RAPDs]), or provide data for one gene only (often mitochondrial DNA, which is not typical of the rest of the genome; Wilson *et al.* 1985). However, recent technical developments, such as denaturing gradient gel electrophoresis (DGGE) and the analysis of single-stranded conformational polymorphisms (SSCPs; Lessa and Applebaum 1993), provide rapid, inexpensive, and sensitive methods of comparing genetic variation among individuals. For example, use of single-stranded conformational polymorphisms or denaturing gradient gel electrophoresis in conjunction with targeted amplification of nuclear genes is a powerful new technique that combines the strengths of classical protein electrophoresis with those of cutting-edge DNA-based techniques (Palumbi and Baker 1994). However, even this method does not provide a measure of gene flow within the last few generations.

The most powerful approaches to delineating populations involve use of contemporary molecular techniques in combination with dispersal and demographic information, enabling accurate estimation of both gene flow and population structure. However, few such studies exist, and none on seabirds have been published.

OTHER USES OF POPULATION MARKERS

Morphometric and genetic markers have several applications for wildlife management and conservation, in addition to their uses for defining populations.

Preservation of Genetic Diversity

As a population declines, its genetic resources become depleted (Allendorf and Leary 1986, Gilpin and Soulé 1986). Initially this depletion involves loss of rare variants (alleles) from the population, but ultimately it includes loss of individual variation (heterozygosity). Both these effects decrease the species' ability to cope with environmental perturbations, such as climatic changes and disease epidemics (e.g., O'Brien and Evermann 1988, Vrijenhoek 1994). Eventually, a declining population may reach a threshold size below which inbreeding, deleterious alleles, and stochastic events may result in extinction. Loss of a population will result in reduction of overall genetic diversity, which may compromise the species' longevity. Thus, genetically differentiated populations must be managed as independent units; in contrast, if a species is essentially panmictic, protection of individual subpopulations may be less critical.

Environmental Impact Assessment

Morphometric and genetic variation can provide markers for monitoring the impact of human activities on sensitive or remote ecosystems, such as marine systems and the high Arctic. They also can enable the identification of breeding populations of animals killed during migration or winter. For example, many seabirds killed by oil spills are migrating or wintering; the "affected" zone, or the population of seabirds that was affected by an oil spill and that requires a restoration effort, may be very different and geographically distant from the actual spill zone (see Chapters 1 and 4).

Environmental Monitoring

Knowledge of the geographic limits of a population is required to identify appropriate reference or "control" sites from which to obtain baseline data for monitoring, restoration, and modeling (e.g., to determine if a seabird colony has recovered "normal" functioning following an oil spill; see Chapter 7). Demographic parameters may be very different for genetically isolated populations, even if they occur in ecologically similar areas.

Captive Management and Translocation

Delineation of populations is also essential for captive breeding and translocation, to prevent both inbreeding and crosses between genetically incompatible individuals (e.g., Hansen and Loeschcke 1994; see Chapter 9). For example, after a captive breeding program was designed to restore the dusky seaside sparrow by hybridizing the last remaining males with females of the morphologically similar Scott's seaside sparrow, genetic analyses indicated that Scott's seaside sparrow was not the most closely related subspecies to the dusky seaside sparrow. Therefore, Scott's seaside sparrow was not the most appropriate choice for captive breeding (Awise and Nelson 1989).

Determination of Population Uniqueness and Identification of Cryptic Species

Population markers can be used to determine if a colony is unique (e.g., endemic or genetically distinct), information that may then be used to rank conservation and restoration efforts (see Chapter 4). Most importantly, genetic data can lead to the identification of cryptic species—populations that are similar in appearance but that represent separate, noninterbreeding species. For example, genetic comparisons revealed that North American and Asiatic subspecies of the marbled murrelet actually represent reproductively distinct species that have been genetically isolated for five to six million years (Friesen *et al.* 1996). Therefore, these two taxa must be managed independently.

Improved Basic Knowledge for Management

Finally, demographic, morphometric, and genetic data can lead to improved general understanding of the dynamics of small, potentially endangered populations. For example, a correlation between genetic variation and disease resistance in small populations has been postulated but not directly demonstrated (O'Brien and Evermann 1988).

Part B: Seabird Ecology

INTRODUCTION

Seabirds are important and visible components of marine ecosystems worldwide. They are highly mobile animals capable of long-distance movements and are often found thousands of kilometers from land (Harrison 1983). They tend to breed on inaccessible coastal habitats, often in large, dense aggregations, and are often highly conspicuous victims of oil spills and other environmental disasters. These factors generate considerable public interest, thereby placing seabirds at the forefront of marine conservation issues.

In this section, we (1) evaluate aspects of the ecology and natural history of seabirds that make individuals and populations vulnerable to human impacts and (2) describe the utility of seabird life history studies in designing, implementing, and evaluating seabird restoration programs. It is beyond the scope of this chapter to review the relative importance of numerous conservation problems facing seabirds. For a recent synopsis of management issues for seabirds, see Duffy and Nettleship (1992) and references therein.

SEABIRD BIOLOGY AND VULNERABILITY

As marine organisms, seabirds appear to be more vulnerable to a variety of human anthropogenic factors than do other forms of marine life that have been studied. We use the term "vulnerability" to indicate both the number of individuals impacted and the capacity for populations to recover from perturbation. A number of biological characteristics relate to the susceptibility of seabirds to human impacts.

Sociality

Many seabirds are highly gregarious, often breeding in large colonies, some numbering in the hundreds of thousands (e.g., Wittenburger and Hunt 1985, Hunt *et al.* 1986). Sociality influences both the number of affected individuals and the capacity for seabird populations to recover. For example, coloniality and behavioral mechanisms promoting grouping behavior place large numbers

of individuals at risk in the event of an oil spill or other anthropogenic impact. From the standpoint of recovery, some seabird species require other individuals or a minimum group size to stimulate reproductive activities (the "Allee effect," Allee *et al.* 1949). Reed and Dobson (1993) review another phenomenon, known as "conspecific attraction," that relates to the recruitment of birds to colony sites occupied by individuals of the same species. Conspecific attraction in relation to foraging also places large numbers of birds at risk in small areas. Lastly, some seabird colonies may serve as "information centers" (Ward and Zahavi 1973, Wittenburger and Hunt 1985, Clode 1993). If colonies of certain species function as information centers, this phenomenon may limit the capacity of small groups to successfully find and exploit available resources.

Foraging Ecology

Most seabirds represent mid- to upper-trophic-level predators in marine food webs. Although seabird diet varies substantially by species, location, and time (by day, season, year, and decade), seabirds largely feed on moderate-sized marine zooplankton (e.g., free-floating copepods and euphausiids), schooling pelagic fish, and ages 0 and 1 demersal fish. These prey are often patchily distributed in oceanic environments (Hunt and Schneider 1987). In response, seabirds concentrate on prey patches where they may be more (or less) susceptible to mortality factors. Seabirds are also visual-pursuit predators. Many species swim (or fly) through the water column in search of prey. This type of foraging behavior, demonstrated by alcid, penguins, and cormorants, places birds at risk of contact with both surface oil and fishing nets at depth.

Demographic Parameters

Knowledge of demographic traits of seabirds is essential for evaluating the vulnerability of seabird populations, rather than individuals, to anthropogenic impacts (cf. Wiens *et al.* 1984) and for planning and implementing restoration programs. Most seabird species are characterized by high adult survival probabilities (often greater than 80% per year), low levels of productivity (often less than 0.5 young/year per adult), delayed maturity and age at first breeding (often greater than five years), low recruitment probabilities (often less than 35%), variable annual breeding probabilities (often less than 100%), and low levels of dispersal. Combined, these life history traits predict a low rate of intrinsic increase and population recovery. Additionally, these characteristics indicate that if an impact increases the mortality rate of breeding adults or subadults, effects at the population level will be long-lasting and the time needed for recovery will be substantial. Conversely, if an impact affects reproductive success, effects on the population may be minimal, requiring little or no recovery (unless the impact is chronic). Moreover, although the number of individuals suffering mortality may be estimated (e.g., Piatt *et al.* 1990, Page *et al.* 1990), it is impossible to measure the effects of mortality on the population without prior information on the size, structure, productivity, and dispersal characteristics of the population in question.

SEABIRD BIOLOGY AND RESTORATION

Many of the factors that make seabirds vulnerable to anthropogenic impacts should also be considered when planning and implementing restoration programs. Below we consider some of the same aspects of seabird biology that have been mentioned above, but from the standpoint of population recovery.

Demographic Parameters

In addition to assessing vulnerability, demographic data provide a strong biological basis for planning seabird restoration projects. While we are not suggesting that demographic and life history data are a prerequisite for each and every restoration project, knowledge of life history and demographic parameters can vastly improve the design and evaluation of restoration programs. In addition, long-term (i.e., greater than ten years) life history studies, if available, provide information on (1) the range of parameter values that may be witnessed during restoration, (2) interdependencies of life history traits that may influence the outcome of restoration efforts, and (3) the traits that are most likely to promote population growth and persistence—i.e., the traits that, if manipulated, would have the greatest value as a restoration tool. To adequately investigate the factors that are most likely to influence population growth and recovery, data from demographic studies must be synthesized via stochastic population dynamics modeling and sensitivity analyses (e.g., Burgman *et al.* 1993; see Chapter 11 for discussion of modeling).

Below we review the seabird demographic parameters that are likely to be influential in seabird population dynamics, hence restoration. Our hope is to provide a "shopping list" of desired inputs for planning restoration via demographic analyses. As an introductory comment, we remind readers that seabird populations are age-structured (Furness and Monaghan 1987). By this we mean that when estimating and evaluating demographic parameters, one must consider how parameter values change with age. Gaston *et al.* (1994) provide a recent example for thick-billed murre. A review of age-specific life history traits is beyond the scope of this chapter, but recent reviews of this topic are available (Wooller *et al.* 1992, Forslund and Part 1995). Demographic parameters that should be considered when designing a restoration program include the following.

Adult survival (from breeding age to death)

Early views considered this a time-constant parameter. There is now considerable evidence that adult survival in seabirds varies from year to year and decade to decade, and, furthermore, that changes in adult survival are associated with corresponding population dynamics (Coulson and Thomas 1985, Harris 1991, Croxall and Rothery 1991, Hatchwell and Birkhead 1991, Sydeman 1993). Given the generally high survival of most seabirds, enhancing adult survival may be difficult to accomplish, but if possible might provide an effective means of promoting population growth and recovery. However, aside from managing food resources (by limiting fisheries), controlling predators, and reducing net fisheries bycatch of adult birds, techniques to enhance this parameter have yet to be developed.

Juvenile and subadult survival (from fledging to age 1, age 1 to breeding age)

Knowledge of these life history parameters is fragmentary, at best, for nearly all seabird species and, where known, often involves species (i.e., large larids) that are not in need of restoration efforts. Little is known about whether juvenile or subadult survival varies from year to year, if temporal fluctuations are as great (or greater) than variation in adult survival, and if there is a strong relationship between fluctuations in adult and subadult survival. Moreover, estimates of juvenile and subadult survival based on capture/recapture (or capture/resighting) methods are subject to biases due to dispersal (this may be less of a problem for studies of adult survival because of high breeding philopatry). Nonetheless, indications are that both juvenile and subadult survival have important, if not critical, roles in the population dynamics of many seabirds (Buckley and Downer 1992, Nur *et al.* 1994). As an example, Hatchwell and Birkhead (1991) concluded, albeit indirectly, that a change in juvenile or subadult survival must have been the major demographic factor explaining why the Skomer Island common murre population grew in the 1980s but not in the 1970s. As suggested above, enhancing survival could provide an effective means of restoring seabird populations, although techniques for such an undertaking for adults, let alone juveniles and subadults (which spend less time at a colony site), have yet to be developed. However, given that subadult and juvenile survival is often considerably lower than adult survival, there is greater room for improvement, which may then promote population recovery.

Reproductive success

Substantial data are available on this parameter, although it may be one of the less important parameters in relation to understanding population dynamics and planning restoration for seabirds. It is well established that reproductive success varies from year to year and from decade to decade, and that much of this variation is related to marine climate and food availability in some systems (e.g., Furness and Monaghan 1987, Ainley *et al.* 1995b). For example, a decline in North Sea herring stocks was associated with declines in black-legged kittiwake reproductive success and population growth rates (Coulson and Thomas 1985). Whereas a major change in reproductive success may presage population growth or decay, it does not follow that all fluctuations in reproductive success are similarly influential. For example, consider species with single-egg clutches (e.g., procellariiforms and many alcids): reproductive success is high relative to the species' capacity for productivity—i.e., generally 65-80% of all eggs result in free-flying fledglings in these species. Consequently, boosting reproductive success beyond levels that are already relatively high may be difficult and will not be an effective means of restoring populations. Conversely, when reproductive success is low relative to the potential success rate, restoration efforts focused on enhancing productivity will be more effective. Another consideration in relation to enhancing reproductive success might be that for seabird populations, one or two strong cohorts may sustain recruitment for many years (e.g., Ainley *et al.* 1990). In this case, improving reproductive success might again accomplish little with respect to population growth.

Breeding probability

This parameter is important to restoration because it may be more easily manipulated. Overall breeding probabilities may be considered as two separate components: (1) the probability of breeding among experienced breeders and (2) the probability of breeding among individuals entering the reproductive population for the first time. Good information on these parameters usually requires monitoring banded individuals through time; thus, it is generally scarce.

The breeding probability of experienced breeders appears to vary substantially among species and even within species. "Skipping" (i.e., nonbreeding among experienced breeders) reflects both individuals present at the colony but not attempting to breed and individuals absent from the colony. Because skipping birds are absent or inconspicuous, the extent of skipping is probably underestimated. In the short-tailed shearwater, 12% of adults did not attend the colony in a given year and 19% maintained burrows but did not lay an egg (Wooller *et al.* 1989). Similarly, in the Manx shearwater, breeding probability was estimated to be 80% (Brooke 1990). Aebischer (1986) attributed a population crash in the European shag on the Isle of May, Scotland, to extensive lack of breeding by experienced adults.

The probability that a sexually mature bird will enter the reproductive population for the first time also varies greatly among and within species. When competition for space or mates is intense, breeding probability among potential new recruits may be low. For example, few western gull females on Farallon Island, California, start breeding at age 4, when they are physiologically capable of producing eggs. Most start at ages 5, 6, or 7, when they are more competitive for territory-holding males (Spear *et al.* 1995a). Moreover, 4- and 5-year-old male western gulls are more likely to recruit in years when food is abundant (Spear *et al.* 1995a). A similarly wide range of age at first breeding has been reported for common murres by Halley and Harris (1993) and other species (Bradley and Wooller 1991). Because variability in the age at first breeding is high, we consider activities that alter the factors that affect the age at first breeding to be a potentially powerful restoration tool. For many seabird species, a pool of nonbreeders provides a potential source of recruits to be tapped. As an example, a catastrophic red tide mortality of breeding shags on the Farne Islands, England, allowed many new individuals to be recruited in subsequent years (Potts *et al.* 1980). Similarly, if territories, nest sites, or mates are made available through restoration activities, population growth and recovery may be facilitated (see Chapter 9).

Age of first breeding

The distribution of age at first breeding is not normal; most individuals initiate breeding earlier in life, and few breed for the first time in the various older age classes. For this reason we are more interested in minimum or modal age of first breeding rather than average age of first breeding: the latter reflects the tail end of the distribution (individuals who recruit only late in life), and factors influencing this tail have been discussed above. Certainly there is interspecific variation in age of first breeding, for example, with respect to body size (Croxall and Gaston 1988, Gaillard *et al.* 1989, Nur 1993) and longevity (Bradley and Wooller 1991). In addition, there appears to be variation within species as well. For example, common murres on the Isle of Canna, Scotland, were observed breeding for the first time at ages 3 and 4 (Swann and Ramsay 1983). Only a single

individual murre from the Farallon Islands, California, has been observed breeding at age 3, with most recruiting at ages 5 to 7 (W. Sydeman, unpubl. data). At Skomer Island, Wales, common murrelets bred at four to six years (Birkhead and Hudson 1977). As with breeding probabilities, age of first breeding is likely to reflect reproductive opportunities. For example, the colony on the Isle of Canna was a fast-growing colony, presumably with many available breeding sites.

Immigration and emigration

We have very little good information on this parameter for seabirds. Emigration is inherently difficult to study because, by definition, individuals are leaving the study colony, 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. Nonetheless, a review of population recovery of marine birds indicated that immigration has played a key role in many growing or recovering populations (Nur and Ainley 1992). Immigration can play a role in restoration in several ways: when establishing a new colony (or re-establishing an extirpated colony), all individuals are, at first, immigrants; and among growing colonies, immigration will often reinforce population growth. On the other hand, the establishment of a new colony may siphon off individuals from an established colony, thereby leading to no net change in the larger metapopulation (see discussion below and in Chapter 3a).

The majority of seabirds were once thought to be intensely philopatric (Bradley and Wooller 1991), but more recent studies have indicated that this may not be a general pattern. For example, Porter and Coulson (1987) published an accounting of factors affecting philopatry and recruitment in kittiwakes. They found that about 11% of each cohort return to breed at their natal colony and noted that this proportion was time-constant (1952-84). Coulson and de Mévergnies (1992), in a regional survey of kittiwake colonies in Britain, indicated that roughly 35% were philopatric, while 45% emigrated. In Atlantic puffins, Harris and Wanless (1991) suggested that approximately 50% of young emigrated, revising earlier conclusions (Harris 1984) that the majority of young were philopatric. Halley and Harris (1993) showed that during the prospecting period, immature common murrelets visited colonies close to their natal colony more frequently than colonies farther away. Finally, Bradley and Wooller (1991) concluded that recruitment and philopatry in long-lived birds were influenced by many factors including sex, age, food and nest site availability, population size and density, and expected longevity. In conclusion, if intercolony movement and recruitment occurs rarely, this behavior will not have major demographic implications. Nevertheless, immigration and emigration rates should be accurately estimated because this parameter may have substantial implications for restoration of small, incipient seabird colonies.

Coloniality and Density-Dependence

As discussed above, many seabirds are gregarious, reproducing in large colonies. The relationship between coloniality, density, social behavior, and life history parameters is fundamental to seabird restoration. Colonial breeding in seabirds may or may not act to constrain or promote population growth and recovery if density-dependent population-regulating mechanisms are operating. By

this, we mean that fecundity, survival, or recruitment is a function of population size (or an equivalent such as population density), either negatively (i.e., increasing population density reduces survival, fecundity, or recruitment) or positively. The concept of negative density-dependence is ubiquitous in both the scientific and lay literature, and yet the evidence for negative density-dependence in seabirds is not robust. This is not to say there is no evidence (reviews are provided by Birkhead and Furness 1985, Croxall and Rothery 1991), but rather that direct evidence is often lacking. An example of one prevalent view is provided by Baker *et al.* (1990), who argued that catastrophic mortality of marine birds (with specific reference to the *Exxon Valdez* oil spill) was actually "good" for these species, as it served to reduce intraspecific competition.

One example of possible negative density-dependent reproductive success is provided by Hunt *et al.* (1986) on five seabird species nesting on the Pribilof Islands, Alaska. They compared two colonies, one very large (2.5 million seabirds) and one large (250,000 seabirds). In four species, chick growth at the very large colony was reduced compared to the large colony. However, there was no significant difference in reproductive success between the colonies for any of the species. These results may suggest the operation of negative density-dependence at very high population levels, but they do not demonstrate the action of similar density-dependence at intermediate or low levels of density.

On the other hand, a positive correlation between reproductive success and breeding density may be important in some species or populations, especially at low densities. For these species or populations a technique that increases breeding density would be a worthwhile restoration tool. Allee *et al.* (1949) first recognized that the population dynamics of social species may be positively density-dependent when population size is low. They postulated that mating success, reproductive success, and recruitment may be limited by a critical density that must be exceeded before a resource (habitat or prey) can be properly exploited. With respect to seabird restoration, this implies that a threshold group size is needed to establish productive colonies. An example of the Allee effect is provided by wedge-capped capuchin monkeys: as group size increased from 5 to 30 individuals, so too did per capita production of young (Robinson 1988). In the common murre, there is good evidence that reproductive success increases with density at the colony (Birkhead 1977), apparently due to better protection from predators. Hudson (1985) also considered the implications of positive density-dependence for murre population dynamics: he modeled a scenario in which an oil spill (or similar catastrophic mortality) could lead to long-term population decline, eventually resulting in population extinction. Whether Allee effects occur in other seabird populations is not well known, but it seems likely. Thus, in planning seabird restoration, one would not want to disturb colonies in which density was close to or below an Allee threshold. Furthermore, as minimum colony size and density (numbers per unit area—i.e., the Allee threshold) have not been established for most seabird species, a review of available data would be enlightening with respect to designing recovery programs.

Other density-dependent aspects of coloniality in seabirds (e.g., breeding phenology and synchrony, productivity) are also important and bear upon issues of colony establishment and population growth. First, we distinguish between spatial and temporal aspects of coloniality. Coloniality itself represents differences in spatial dispersion. In contrast, chronology and synchrony are reflective of temporal clustering of pairs within colonies. Information on dispersion within seabird colonies is

an important element of seabird breeding ecology. For example, data on the spatial configuration of murre colonies may be useful in deploying decoys that simulate colony structure. For some species, this may be important to minimize predation. Furthermore, Coulson (1968) recognized the importance of spatial dispersion in relation to center-edge effects and productivity in kittiwakes. Others (e.g., Birkhead 1977) have shown how birds at the edge of colonies were more likely to suffer predation than birds in the interior. Spear (1993) also demonstrated that when the spatial structure of a murre colony fails (in this case due to El Niño), all pairs were likely to suffer predation by gulls. Restoration activities that attract birds to the colony center, while simultaneously providing some degree of protection on the edge, might be most effective if predation is limiting population recovery. Unfortunately, little is known about mechanisms that might attract birds to one area or another within a colony.

Metapopulation Dynamics: Sources and Sinks

The importance of "sources" and "sinks" in relation to vertebrate population dynamics has only recently been recognized (Pulliam 1988, Pulliam and Dunning 1994). Buckley and Downer (1992) have investigated some aspects of this phenomenon in seabirds. A sink population is one in which the current local production of recruits is less than the mortality of established individuals, and therefore the population is not currently self-sustaining; it can be sustained only by immigration from other, currently more productive populations. A source population is productive enough so that an excess of potential recruits is produced relative to mortality. This can lead to growth of the source population and emigration of recruits to other, possibly sink, populations. A network of source and sink populations can be joined by immigrants and emigrants; this may be referred to as a "metapopulation" or "network of populations." An important implication of the source-sink paradigm is that population dynamics cannot be understood at the level of a single population or colony (which may be either a source or sink) but rather must be approached at the level of the entire network or landscape of populations. Pulliam and colleagues further demonstrated that a single source (i.e., "mother") 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 relation to conservation and restoration efforts for seabirds, projects should be directed at (1) maintaining the dynamics of source populations and (2) altering the dynamics of sink populations. If sink populations can be manipulated to the point where they also produce excess recruits, the overall stability and persistence of seabird metapopulations will be improved. Moreover, efforts directed at current sink populations without regard for the current local source population may be doomed to failure.

Habitat Selection

Seabirds select colony sites based upon a number of factors: climatic characteristics, oceanographic conditions of local foraging grounds, and habitat features (reviewed by Buckley and Buckley 1980 and Kaiser and Forbes 1992). Much information on suitability of nesting and foraging habitat can

be obtained from the presence and activities of conspecifics and other breeding seabirds (Kharitonov and Siegel-Causey 1988, Reed and Dobson 1993).

Once a colony has been formed, population growth and recovery may be facilitated by providing artificial nest sites (e.g., nest boxes or nesting ledges). This type of effort will be most effective if nest sites are limited and other factors (e.g., food availability) are not currently limiting the population. In general, seabird populations are not usually limited by a lack of available nest sites (Furness and Birkhead 1984, Birkhead and Furness 1985, Cairns 1989, Croxall and Rothery 1991), although in some species evidence in support of a "habitat saturation" hypothesis of population regulation is compelling (Manuwal 1974a, Potts *et al.* 1980, Duffy 1983, Porter and Coulson 1987, Coulson 1991). Aside from placing nest boxes for cavity- and burrow-dwelling seabirds, habitat manipulations have not been regularly attempted in the Northern Hemisphere, presumably because it is expensive, except where direct economic benefits have been realized (e.g., nesting platforms constructed for guano harvest in Peru and Africa). Furthermore, this type of restoration requires data on species-specific habitat use (e.g., Bédard 1969b, Grant and Nettleship 1971, Nettleship 1972, Manuwal 1974a, Birkhead 1977, Vermeer *et al.* 1979, Gaston and Nettleship 1981, Birkhead and Nettleship 1987). However, detailed habitat information is exceedingly rare. Moreover, the value of artificial habitat, including nest boxes, as a restoration tool has not been adequately evaluated. Although nest boxes will be used by a variety of crevice-nesting seabirds, including procellariids and alcids (Ainley and Boekelheide 1990, Hester and Sydeman 1995, Podolsky and Kress 1989b), an evaluation of artificial habitat use through time and comparisons of the demography of pairs nesting in or on artificial structures versus natural ones is needed.

CONCLUSIONS

In general, a great deal more basic life history research is needed to answer some fundamental questions pertaining to seabird ecology and restoration. Life history and demographic analyses have high priority in terms of seabird restoration, as well as in assessing the impacts of oil pollution on seabird populations (Wiens *et al.* 1984). In particular, analyses of demographic parameters can be used to understand population dynamics and quantify the potential results of differing restoration options (Burgman *et al.* 1993). We recommend increased attention to life history characteristics in seabirds that appear to be crucial for understanding population dynamics. *Demographic parameters that appear to be most important in promoting population growth include adult survival, juvenile and subadult survival, and the breeding probability of first-time breeders.*

The status of a population and the success of restoration efforts ultimately depends upon the subadult, prebreeder population as well as on the size and status of breeding populations. Nonbreeding individuals make up as much as 45% of all seabird populations. Consequently, greater effort to monitor prebreeder population size and to identify dispersal and recruitment characteristics, as critical demographic processes, is recommended. This work will be challenging because nonbreeding individuals are difficult to monitor or study. Nonetheless, some fine examples of this work are available (Harris and Wanless 1991, Coulson and de Méergnies 1992).

Specific questions concerning recruitment that require investigation in relation to many, if not most, restoration programs include the following.

- (1) What proportion of young recruit into natal colonies/locations?
- (2) If emigration occurs, what is the typical range of gene flow?
- (3) Which factors are responsible for differences in philopatry and emigration, and are there individual-, cohort-, year-, and colony-specific effects?
- (4) How do young birds select the colony sites to which they emigrate?
- (5) What behaviors by conspecifics are attractive to recruits, and what behaviors are practiced by recruits during dispersal?

Molecular genetic (e.g., mtDNA and microsatellite) analyses may be an effective means of addressing some of these issues, which, in the past, have been addressed only through long-term banding and monitoring studies (see Chapter 3a). Meanwhile, it is also important to recognize that individual colonies and populations may not be isolated, and that information about metapopulation and source-sink dynamics is needed in order to understand and predict the dynamics of seabirds and to plan restoration. Many population models have neglected the important effects of emigration (Dauchin and Monnat 1992, Nur *et al.* 1994, Beissinger 1995, but see Buckley and Downer 1992). In order to succeed, restoration programs must evaluate and incorporate dispersal.

From the standpoint of both life history and behavioral ecology, a great deal more could be learned concerning the role of density-dependence. A review of the minimum group size required to establish a breeding colony (as well as the size needed for successful reproduction) would be an excellent way to initiate such investigations. Additionally, a related question that needs to be answered is: what are the minimum viable population sizes for colonial seabird species? One way to investigate this question would be to consider the effect of density on reproductive success and evaluate whether the relationship appears to be monotonic, a step-function, or a parabola. With regard to the Allee effect, some factors that appear to affect surface-nesting seabirds (e.g., predation) would appear to promote threshold or step-function colony-size relationships. However, even seabirds that are protected from aerial predators may require a critical mass in order to stimulate mating and territorial behavior. For example, nocturnal alcids and petrels may use vocalizations to communicate between conspecifics (Podolsky and Kress 1989b). Restoration ecology of seabirds would benefit from empirical data establishing the conditions when these density-dependent effects may occur. Moreover, minimum viable population or colony size represents a metric for evaluating the effectiveness of restoration activities. Certainly, any restoration project that fails to generate a minimum viable population size for a given population or colony should be considered unsuccessful.