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Comprehensive Review and Critical Synthesis of the Literature on Recovery of
Marine Bird Populations from Environmental Perturbations

Draft Final Report

To Restoration & Planning Work Group

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Abstract

The scientific literature pertaining to the ability of marine bird populations to recover from oil spills and other environmental perturbations was reviewed with the aim of considering: (1) the rate, duration and extent of recovery and what response might be expected from various populations, (2) biotic and abiotic influences on the rate, duration and degree of recovery, (3) the influence of management practices on the rate, duration and degree of recovery and (4) how best to monitor the recovery of marine bird populations. The review of the literature, both peer-reviewed and "gray" literature, included seabirds and seaducks, as well as oystercatchers and eagles (if relevant to marine populations). The approach taken was a broad one, to establish the demographic capabilities of marine bird populations to respond to perturbations by reviewing observations on growth and recovery as well as reviewing critical demographic parameters. Some seabirds were characterized by population growth rates of 10 - 13% per year (penguins, albatrosses, petrels, gannets and boobies, skuas, auks) whereas others were characterized by substantially higher growth rates (pelicans, cormorants, gulls); seaducks appeared intermediate between these two groups. Published models of seabird population growth indicate that most species are not capable of growing at much more than 12% per year. The rate of recovery is influenced by the availability of immigrants, the presence of a pool of non-breeders, the abundance of pre-breeders (subadults), and prey availability. Re-establishment of breeding colonies is difficult because recruiting individuals favor high-density colonies and/or their own natal colony. Protection from exploitation and disturbance, management of prey (fish) availability are management practices that can influence rate of recovery; active restoration has not often been attempted. We suggest that, if possible, both total population size and number of breeding pairs be monitored. Otherwise misleading conclusions may be drawn regarding recovery. We advocate that primary demographic parameters be monitored, in order of priority: fledgling production, adult survival and recruitment of offspring. It is very difficult to make quantitative predictions regarding duration (or rate) of recovery without population-specific information on critical demographic parameters.

Introduction

Background and Objectives

A variety of marine birds, waterfowl and other birds were killed or injured as a result of the Exxon Valdez Oil Spill. In order to plan wisely for the restoration of bird populations injured by the spill, it is necessary to consider and estimate the rate, degree, and extent of recovery from oil spill losses. In this review and synthesis we examine studies published in the scientific and "gray" literature pertaining to the recovery of seabird and seaduck species from other oil spills and from other environmental perturbations, both anthropogenic and natural.

Specific goals of the review and synthesis are:

- 1) To consider the rate, duration and degree of recovery of bird populations following disturbance, so as to determine what might be expected, quantitatively and qualitatively, from various populations,
- 2) To consider biotic and abiotic influences on the rate, duration and degree of recovery,
- 3) To consider the influence of management practices on the rate, duration and degree of recovery, including protection of species, protection of habitat, and restoration practices, and
- 4) To consider how best to monitor recovery, if any, of affected species, and how to determine when a population has recovered. The last point also includes consideration of the best indicators to be monitored.

Rationale:

Our review of the literature was wide-ranging. In addition to studies reporting recovery from perturbation, we have also included studies pertaining to the growth of marine bird populations. Information on population growth came from two sources: 1) studies on the basic demographic parameters of a population (production of offspring, survival of offspring to breeding age, survival of adults,

age of first breeding, immigration and emigration), and 2) studies reporting observed changes in total population size or breeding population size.

We had two reasons for adopting this broad, demographic approach. First, the literature on recovery of marine bird populations from perturbations, such as oil spills and other examples of large-scale mortality, is not great, especially in regard to species differences and other influences on rate of recovery. The demography of gulls, cormorants, murres, albatrosses and seaducks are all quite different and so it makes no sense to consider the recovery of a generalized seabird. Secondly, we consider information on the demographic capabilities of seabirds, derived from studies of their growth, to be relevant to the question of how they would respond to a perturbation such as additional mortality or disruption of reproduction. To put it another way, our thesis (and one that has a long tradition in the scientific literature) is that the long-term impact of a perturbation can be predicted knowing the short-term impact coupled with the demographic parameters of the population.

The literature reviewed, presented in the annotated bibliography, can be classified into four groups:

- 1) Studies providing key demographic information enabling one to estimate the intrinsic rate of increase. Either the study provided all necessary information, or the study did so in combination with other studies (which were also included in the literature review).
- 2) Studies reporting recovery (or in some cases, lack of recovery) from a perturbation.
- 3) Studies reporting growth of marine bird populations, for whatever reason. We did not include in the review studies reporting stasis or decline of populations (except for those falling into category 2, above).
- 4) Studies providing other information relevant to the question of recovery, e.g. regarding the role of density dependence.

Scope of the Review:

Taxa included: The literature was searched with regard to all seabirds: penguins, loons (divers), grebes, the Procellariiformes (albatrosses, and the three families of petrels, including shearwaters), the Pelecaniformes (gannets and boobies; pelicans; cormorants and shags; frigatebirds; and tropicbirds), and six families from the Charadriiformes (skuas and jaegers; gulls; terns; skimmers; phalaropes; and alcids [auks]). In addition, we included seaducks (Eider spp., Scaup spp., Scoter spp., *Mergus* and other sawbilled ducks, Oldsquaw, Harlequin Duck, Goldeneye spp., Bufflehead, steamer ducks and Kelp Goose) and Osprey, as well as oystercatchers (most are not marine, but the Black Oystercatcher is) and eagles (if the reference pertained to marine populations). Some taxa were well represented in the literature reviewed, others not at all.

presumably because
none were found

Time period: The period searched emphasized studies published from 1960 on, but quite a few studies published 1940 to 1960 were also included. We reviewed papers obtained by 1 November 1991, with a small number that were received in November and December 1991, principally papers on oystercatchers.

Languages: We emphasized papers published in English, but some foreign language studies were also included.

Geographical regions: No regions were excluded. However, there were few papers from the tropics, and papers from the north temperate regions were the most numerous.

Subject matter: This is discussed in the section, "Rationale," above.

Methods

The literature was systematically searched using computerized bibliographic databases, specifically BIOSIS, Zoological Record, and Wildlife Review, as well as the on-line version of Current Contents. We searched for suitable key words in titles as well as in abstracts.

This approach was supplemented by our own knowledge of relevant papers, studies, etc. and by referring to literature cited by papers already available to us. The systematic, computerized approach was poor at identifying papers in the "gray" literature; for this we relied on our own knowledge or by referring to citations of literature we already had obtained. We emphasized papers that were "readily available", though we did attempt to obtain a number of papers that were not "readily available" (the latter included, e.g. Ph.D. dissertations); some of these were obtained with the assistance of the Alaska Department Fish and Game, others through Inter-Library Loans. In addition colleagues, especially Dr. Joseph Jehl, Jr., and Dr. Eric Woehler were generous in providing references, publications, and reports.

In this way we identified, initially, 313 references, which we then attempted to obtain as detailed above. One of the two co-Principal Investigators (Nur or Ainley) read each article and prepared an abstract. Papers (from among the original 313 that were identified) that were deemed not relevant to the literature review and synthesis were not included in the bibliography; however, papers for which it was not possible to compose an abstract (if no copy of the paper could be obtained in a timely fashion), have been included in the bibliography if they appear to be relevant to the goals of the literature review. At some future date, it would be desirable, we feel, to consult these unannotated references. We deleted older papers from the bibliography if more recent papers superceded them.

The annotations (abstracts) have been written expressly with respect to this project, i.e. they abstract information relevant to the question of recovery of marine bird populations from perturbation. They do not aim to provide a general summary of each article (though that, sometimes, has been accomplished). Instead, the annotated bibliography provides a ready source of information concerning recovery and growth of marine bird populations. It is our hope that the annotated bibliography will provide a useful research tool in and of itself.

Results

General Comments:

We consider that **rate of recovery** is the key parameter of the three mentioned. The **duration** of the recovery will be determined by the **initial impact** of a perturbation (e.g., known or estimated mortality resulting from an oil spill) and the **rate** at which the population can recover. As for **extent of recovery**, we expect that populations will be able to fully recover, eventually, unless the rate of recovery is zero or negative (the latter case, meaning that the situation of a population is worsening rather than ameliorating, subsequent to a perturbation). However, if the time to recovery is fixed (e.g., recovery is measured after 50 years), then the extent of recovery achieved after the fixed period of time will depend on impact and rate of recovery.

We collated information on rate of recovery from reports of observed population growth, whether or not that growth was in response to an identified perturbation. In some cases, seabird populations grew because areas were newly colonized or because additional food sources became available (e.g., fishery refuse for gulls). Some papers did not report the reason for population growth, e.g. whether or not the growth represented recovery from a perturbation, and in some cases this was probably not known. Other papers included speculation on reasons for

population growth without firmly establishing the antecedent factors and influences.

Rate, duration and extent of recovery:

Observed rates of population growth are presented in Table 1, grouped by taxonomic family. We have calculated exponential growth rates, for time periods where the population was observed to grow. This is equivalent to assuming that the growth rate of a population was constant during the period considered; in many cases this assumption was supported. Where population growth could be divided into two or more periods, one period in which growth was rapid and others in which growth was slow, we have separated the phases. At the same time, we have tried to avoid including data on growth of very small, incipient populations, for two reasons: 1) there is greater sampling error associated with the dynamics of very small populations, and 2) there is greater likelihood that changes in the size of small colonies represents immigration and emigration, as compared to either very large colonies or populations of entire regions, in which immigration and emigration play a smaller role. We included reference to immigration if a researcher thought it was an important factor. We also excluded cases in which the population showed no growth, very slow growth (less than 1% per year) or even decline. We stress that our objective in this exercise was not to characterize all possible population trajectories, but to characterize recovery or the potential for recovery of marine bird populations. The rationale was that if, for instance, a species is often observed to grow at a rate of 13% per year but is rarely observed to grow at a faster rate, then this indicates that a perturbed population (e.g. subject to large-scale mortality) can grow at this rate, but not that a perturbed population will grow (recover) at that rate.

The data collected in Table 1 present a great diversity of results. Nevertheless, some generalizations are possible. The first is that different taxa display characteristically different growth rates. In other words, though there is no rate of

growth that characterizes all marine birds, species or groups of species (genera or families) do exhibit characteristic rates of growth. *Larus* gulls are clearly capable of sustaining growth rates of 12-13% per year. In fact, Herring Gulls on the Isle of May did so for sixty-five years (Duncan 1978), until a program of gull control was instituted. However, the Emperor Penguin does not appear to be able to sustain such growth rates: no population has been observed to grow at more than 10% per year. Other species groups growing at 12% or less per year include the petrels and skuas. Table 2 summarizes life history characteristics of seabirds (by family) in relation to "typically observed" growth rates. To provide an objective criterion for comparing "typical" rates of growing populations, we present in Table 2 the median observed growth rate and the upper quartile growth rate (derived from Table 1, excluding populations growing at less than 1% per year). As a preliminary estimate of what a recovering population is capable of achieving we put forward the upper quartile statistic.

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In general, species groups can be divided into one of two classifications: upper quartile growth rate 19% or more (pelicans, cormorants, and gulls) or upper quartile growth rate 13% or less (penguins, albatrosses, shearwaters, boobies, skuas, terns, and auks), with seaducks intermediate (15% upper quartile). The "fast" growing species are characterized by laying a clutch of more than one egg. The "slowly" growing species either are characterized by a clutch of one or a clutch of two eggs in which only one chick is successfully reared (penguins and skuas). Terns are exceptional in that their clutch size is three yet the upper quartile growth rate is only 10%.

It would be overly simplistic to expect that much of the variation in observed maximal growth rates could be attributed to a single life-history (or demographic) trait. However, the other two life-history traits, age of first breeding and adult survival rate, do not demonstrate a strong correlation with observed population growth rates. Albatrosses, for example, have the latest age of first breeding, but

do not show the lowest rate of population growth. Nevertheless there does seem to be a trend for early age of first breeding to be associated with faster population growth, as might be expected. Adult survival tends to correlate negatively with population growth, contrary to any simplistic views of population dynamics. This is probably because adult survival tends to be negatively correlated with fecundity (Ricklefs 1973); a partial correlation analysis assessing the correlation of adult survival with growth rate, after adjusting for the effect of fecundity, would be valuable. A key demographic parameter which has not been included in this analysis, owing to a lack of published data, concerns survivorship of young after fledging.

We stress that there are strong limitations on what we may conclude from the data in Table 1. Results indicate what growth rates are possible, and plausible; they provide an envelope of possibilities. However, they do not allow predictions of what growth rate will actually occur. Predicting growth rate appears to be an elusive goal. The key demographic parameters determining population growth rate are not easy to obtain and, in particular, are not species-constant and are not even population-constant. For example, during a period of stasis of the Skomer Common Murre population (in the mid 1970/s), adult survival and fledging success (and possibly, survival of immatures) were lower than they were during a period of positive growth (in the mid-late 1980/s) (Hatchwell & Birkhead 1991). Knowledge of the demographic parameters of the Skomer population in the 1970/s would not have allowed adequate prediction of population behavior in the mid 1980/s. Similarly, adult survival of Atlantic Puffins on the Isle of May was high (96%) while the population was expanding (1973-1981), but was considerably lower during the period of stasis and decline in the 1980/s (Harris 1991).

It was also apparent that growth rates often vary with time, depending on the phase of growth or recovery. Soon after the perturbation, growth is often high (approaching or even exceeding the maximum intrinsic rate of growth), but later

much lower rates of growth are observed. This pattern is characteristic of colonization (or recolonization). For example Northern Fulmars grew at 16.0% per year soon after colonizing Great Britain (1879-1901), at 10.0% between 1909 and 1939 and at 6.5% between 1939 and 1969 (Evans 1984).

The temporal and spatial scale of the perturbation influences recovery. Where short-term, localized mortality has occurred, populations often respond and recover rapidly in a few years, owing to a pool of immigrants and subadults who were elsewhere when the mortality occurs. A classic example is provided by European Shags breeding in NE Britain. Shags breeding on Farne Island were subjected to a red tide in 1968 and the breeding population crashed, from 350 pairs to 75 pairs (Potts et al. 1980). However, within 6 years, the population had recovered its original number, as a result of both immigration from nearby populations (not affected by the red tide) and of recruitment of additional individuals into the breeding population (who otherwise were non-breeding owing to lack of adequate breeding site). Another classic example is offered by the Peruvian "guano birds" (pelicans, boobies and cormorants). In former years there was such a large "floating" population, precluded from breeding by lack of a breeding site, that in spite of large-scale mortality due to lack of food (brought about by El Niño events), once the food web was re-established breeding populations returned to pre-El Niño levels (Murphy 1936, Tovar et al. 1987). As is often the case, it was impossible to quantify the total population and track its trends.

Conversely, where there is long-term pervasive mortality recovery starts slowly and requires decades to complete. For example for King Penguins on Macquarie Island, who^{ick} had been hunted to the point of near-extinction, recovery took about 80 years (Rounsevell & Copson 1982). However in the first 20 years following the cessation of hunting the population showed no growth. The Macquarie Island is very isolated and thus no immigration was possible and all growth was intrinsic.

A strong influence on observed population growth rate is immigration and emigration, the former being especially important among growing populations, and the latter likely important among shrinking populations (see below). The results in Table 1 provide inferences about immigration, in that unusually rapid growth implicates immigration. More specifically, observed growth exceeding the demographic capabilities of a population implies that immigrants are contributing to this growth. In Table 3 we list studies in which predicted population growth rates (based on demographic models), were compared with observed population growth rates. Cases where the observed growth rate exceeds the projected growth rate (for that species or that population) suggest immigration as a factor. Another example (not in Table 3) is provided by Ainley et al. (1990), who estimated a negative growth rate for a population of skuas, but data on banded birds indicated that immigration resulted in a stable population. Note, however, that growth rates less than the predicted maximal growth rate do not imply the absence of immigration.

Table 3 gives us reason to believe that immigration is implicated in the growth of certain populations (e.g. Atlantic Puffins on the Isle of May; Harris 1983). What is most striking about the results in Table 3, however, is that no population model predicted a growth rate of more than 12%, except for a model of Harris (1983) in which he allowed adult survival to be 100%, an exercise of theoretical value only, and a model by Kosinski & Podolsky (1979) in which fecundity and mortality of a kittiwake colony ^{e/c} was assumed to reflect observed values for "center" individuals only (no "edge" individuals included, whose fecundity and mortality are lower). Even in these two instances, projected growth rate was only 14 to 14.9%. Yet Table 1 provides numerous examples of observed growth rates exceeding 14.9%, not to mention 12%. Two conclusions should be considered: (1) The populations represented in Table 3 are a biased sample of those in Table 1, i.e. biologists have not studied rapidly growing populations in sufficient detail to construct models of their growth, or (2) A large number of populations listed in Table 1 are rapidly

growing because of immigration rather than intrinsic growth. We have no reason to favor conclusion (1) and so are led to conclude that growth rates much in the excess of 12 to 15% reflect, to a great extent, immigration.

Because rate of recovery tends to be higher where the perturbation is less extensive (in time and space), the recovery duration increases in a more-than-proportional manner with an increase in the severity of the perturbation. To provide a yardstick to assess recovery durations, we note that if a population has been knocked down to one-half its previous size, it will require 7 to 8 years to recover to its former size at a growth rate of 10% per year, 5 to 6 years to recover to its former size if the population growth rate is 13% per year, and about 4 years to recover if its growth rate is 19% per year.

Influences on recovery rates, biotic and abiotic

Immigration and emigration:

Immigration, or its absence, plays an important role in the recovery process. Where there are unaffected populations nearby, this allows the possibility that immigrants will help restore population number (see European Shags, above). 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, or to put it another way, site tenacity is low. In general, seabird species show a considerable amount of dispersal at the juvenile stage, post-fledging. Dispersal during the juvenile stage may or may not lead to effective dispersal among breeding individuals. Harris (1991) 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, then, that many puffins returned to their natal colony to breed should not be taken to imply that puffins are constrained to do so. In sum, the potential for immigration depends

on both the species and its tendency to disperse, and on the population substructure, i.e. the availability of nearby colonies to serve as a source of additional breeders. This potential has, in fact, been tested "experimentally" by culling Herring Gulls (Coulson 1991).

Many seabirds are specifically attracted to extant seabird colonies. Coulson found that small colonies were the most attractive to Black-legged Kittiwakes seeking to breed, whereas Birkhead (1977) found that Common Murres were most attracted to high-density subcolonies, but were most likely to settle in medium-density subcolonies (since high-density subcolonies had few vacancies). Heubeck et al. (1986) 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 are poor. Furthermore, extinction or near-extinction of a breeding colony, as a result of a perturbation, may make it hard to reestablish that colony.

Variation in rate: role of density dependence.

There is little consensus regarding the evidence for density-dependent population regulation in seabirds (Birkhead & Furness 1985). In some cases, nest sites appear limiting. However, population regulation by way of food limitation is not well supported. Instead, food has a direct effect (not necessarily dependent on density) on reproductive success and perhaps survival, too, (Croxall & Rothery 1991). This contrasts with the commonly-held view, among the lay public, that events reducing population number, e.g. oil spills, are "good" for the population. Evidence from murres indicates, if anything, the opposite relationship: reduction in density decreases reproductive success, by making their colonies more susceptible to predation (Hudson 1985). It is not a simple matter, however, too large a colony can act to lower reproductive success (Hunt et al. 1986).

The importance of food availability:

In general, population dynamics of seabirds tracks food availability more than any other ecological factor (Furness & Monaghan 1987). For example, when predatory fish were heavily fished in the North Sea, sand lance (*Ammodytes*; their prey) bloomed, and numbers of many seabird species increased, but when numbers of sand lance crashed (a result of a switch in target species of the fisheries), so too did the reproductive success of seabirds and with that population numbers. Decline in North Sea herring stocks was associated with decline in kittiwake reproductive success (chicks fledged per pair) and a decline in population growth rate (Coulson & Thomas 1985). The Peruvian seabirds represent another example: overfishing of anchoveta caused a dramatic decline in baseline numbers of boobies and cormorants and in the ability of these seabirds to recover from El Niño events (Tovar et al 1987).

Pool of non- or pre-breeders.

Mortality of breeders can lead to the recruitment into the breeding population of individuals who otherwise would not breed (e.g. if they were previously excluded from obtaining nest sites). An example is provided by European Shags, not just at Farne Island (Potts et al. 1980), discussed above, but also on the Isle of May (Aebischer 1986). The recruitment of individuals who had not yet begun breeding at the time of the perturbation (i.e. pre-breeders) can also hasten recovery. However, we should consider that individuals recruiting^{ed} early in the recovery process (i.e. at an earlier age than they might otherwise do) are not available to recruit later in the recovery process. Furthermore, recruitment of individuals who had previously^{ed} been pre-breeders can lead to a spurious recovery, a good example of which is provided by Cory's Shearwaters breeding on Selvagem Grande Island (Mougin & Roux 1987). The population had been decimated by poaching up through 1976. Between 1977 and 1986 the number of breeders increased dramatically, fivefold, to 25000. At the same time, the number of sub-adults dropped correspondingly (as those who had been pre-breeders entered the

breeding population). The result was that the total population of Cory's Shearwaters did not increase at all during this time. If only breeders had been monitored (common practice for seabirds), a dramatic recovery would have been implicated. An alternative example is that of the Peruvian guano birds mentioned above.

Influence of management practices

The most common, effective management practice promoting recovery of seabirds is protection: protection from eggging, hunting, and from disturbance. Scores of species have benefited from protection, including Common Murres on the Farallones (Ainley & Boekelheide 1990), King Penguins on MacQuarie Island (Rousevell & Copson 1982) and Laysan Albatrosses on Midway Island (Rice & Kenyon 1962).

A second means of promoting recovery concerns effective management of prey availability, specifically fish. As pointed out above, availability and abundance of fish is a prime determinant of seabird population growth. Recovery of Peruvian guano birds (especially Peruvian Booby and Guanay Cormorant) was strongly affected by the anchoveta fishing industry. For example, since 1963 the population number of guano birds has been inversely correlated with the anchoveta catch. Fishery activity in the Gulf of Alaska area has great potential to impact recovery of seabirds.

A third means of promoting recovery is through active restoration. One such success story is that of the Atlantic Puffin, reintroduced to Maine by obtaining chicks from Newfoundland, artificially rearing chicks in burrows in Maine, and releasing them there (Kress and Nettleship 1988). The investigators provided puffin decoys in an effort to encourage puffins to breed at the release site. Restoration efforts have not been commonly pursued. They are affected by all the

processes reviewed above and certainly require large, local source populations and a propensity to emigrate.

Overview and Discussion and Conclusions

We first consider the question, ¹¹How to monitor seabird recovery? ¹¹ After discussing a definition of recovery, we consider which parameters should be monitored, and how this should be carried out.

Defining recovery:

Monitoring recovery of seabirds from perturbation requires adopting a definition of recovery, in particular defining a suitable endpoint. This endpoint could be: (1) return of the population to what it was before the perturbation or (2) return of the population to what it would have been had the population not been perturbed. The second definition is of greater value but it is always difficult to establish what might have been. Use of the first definition is thus more practical, but the problem is that the environment may be deteriorating (making it impossible for a species to return to its previous state) or improving. Ford et al. (1982) use a third criterion of recovery, return of the population to a stable age structure, but a drawback of this criterion is that, in practice, due to a fluctuating marine environment (Ainley & Boekelheide 1990) many populations never achieve or maintain a stable age structure.

What to Monitor: Population Size.

There is no disagreement among biologists that monitoring population size is of great importance, but there are different ways to enumerate a population. The first question is whether to enumerate the entire population or just the breeding portion. If the latter, then one can count nest-sites, defended territories, breeding pairs, nest-sites with eggs, etc., as appropriate. In murre studies it is common practice to count all adult individuals at a colony and then translate that number

into the number of breeding pairs by using a correction factor, based on study plots which establish the ratio of adults to breeding sites. In any case, in most seabirds, it is the breeding population that is enumerated. This approach has some drawbacks: (1) The proportion of individuals attempting to breed often varies among years (Ainley & Boekelheide 1990, Ainley et al. 1990), and (2) the demographic health of a population depends on the number of juveniles, subadults, and non-breeding adults, too, and not just the number of breeding adults (see Peruvian guano bird example, above). We have also already mentioned the example of Cory's Shearwaters on Selvagem Grande Island, in which the breeding population appeared to recover dramatically, whereas the total population did not increase at all. However, counting the entire population (irrespective of breeding status) has its drawbacks: (1) Non-breeders are often not present at a seabird colony, and only return to the colony for breeding or prior to obtaining a breeding territory, and (2) the reproductive capacity of a population depends on the number of breeding pairs not the total population size. It would be of greatest value to monitor both breeding numbers and total population size.

The importance of monitoring additional demographic parameters:

We stress that effective monitoring of seabird species requires more than merely enumerating population size. Knowledge of the primary demographic parameters (fledgling production, adult survival, juvenile survival, proportion of breeders among adults) is of critical value in effective monitoring and management. Population size can give some insight into the status of a species, but does not provide insight into causes of population decline or growth. In addition, population size shows considerable time-lag in revealing problems affecting a species. For example if the only effect of a perturbation is to reduce fledgling success to nil, the size of the breeding population will not demonstrate adverse effects for several years to come (i.e., until that fledgling class would have recruited).

Of the primary demographic parameters that could be monitored we list the following, in order of their value and/or practicality:

- (1) Fledgling production (by which we include also the parameter fledging success, i.e. proportion of eggs which successfully fledge). We place this parameter first because it is relatively easy to monitor and much evidence indicates that it is an important determinant of population change (Croxall & Rothery 1991). An additional advantage is that it can be used to predict the health of a population several years in advance, as pointed out above. Finally, fledgling production may provide a good index of food availability for that species, and thus serve as a more general monitoring tool, i.e, a means of monitoring a species' prey base (Ainley & Boekelheide 1990).
- (2) Adult survival. There is increasing evidence that population change among seabirds is associated with changes in adult survival (Coulson & Thomas 1985, Harris 1991, Hatchwell & Birkhead 1991). However, monitoring adult survival is more difficult than monitoring fledgling production. For one, monitoring adult survival requires banding individuals, which is itself disturbing to the colony. Secondly, small differences in adult survival can have important implications for population dynamics, but can require excessively large sample sizes to determine the magnitude (or even the existence) of such differences. For example, a change in adult survival rate, from 0.96 to 0.92, which implies a doubling of adult mortality, would require a total sample size of over 1000 individuals to establish statistical significance (at the 0.05 level) with a probability (i.e. power) of 80%.
- (3) Survival to breeding age and/or probability of recruitment into the population. This parameter is undoubtedly of importance in the growth and decline of seabird populations but is more difficult to study than fledging production or adult survival. In fact, only a handful of seabird studies have obtained good information on this parameter. One problem is that investigators must wait three, five, or even ten years for a single cohort to recruit; a second problem is that juveniles often disperse, and may or may not return to their natal colony to breed.
- (4) Proportion of the adult population that breeds. This parameter does not seem

responsible for long-term changes in population size, though it may be responsible for short-term changes in breeding number (and thus fledgling production).

Remarks on Monitoring Alaskan Common Murres following the *Exxon Valdez* Oil Spill:

Common and Thick-billed Murres appeared to have been strongly impacted by the *Exxon Valdez* spill, not just with regard to mortality of adults and subadults but also with regard to reproductive success, which was near zero for affected colonies in 1989 and 1990, and not much greater in 1991 (Nysewander & Dippel 1991). We wish to point out that the dramatic reduction in reproductive success (fledgling production) observed at these colonies was unprecedented: we know of no other case where murre reproductive success (or that of any alcid species) was affected over such a large scale, in space and time. Nysewander & Dippel (1991) attributed the reproductive failure, proximally, to a lack of reproductive synchrony. We wish to correct the impression that the Farallon Common Murre population experienced a similar reproductive failure associated with a population crash between 1982 and 1986 (cf. Nysewander & Dippel 1991). In the first place, reproductive failure on the Farallons was short-lived, in 1983 alone, and this failure could be directly attributed to the El Niño of 1982/83, itself an unprecedented environmental perturbation affecting food availability for breeding birds, rather than being attributed to the effects of gill-net mortality (Ainley & Boekelheide 1990). In 1984 reproductive success was reduced, but not dramatically so; by 1985, fledgling production was normal. Secondly, there was no lack of reproductive synchrony in 1983 or 1984. Instead, in those two years, there was a low proportion of breeders among individuals at the colony. This leads us to suggest that a similar phenomenon has occurred at oil-impacted colonies in Alaska. That is, it is not that adults are breeding asynchronously in affected colonies but rather that adults have been less likely to breed at all. If reproductive asynchrony is suspected we suggest that it be quantified. It would also be helpful to study chick diet throughout the breeding season in these colonies and compare that to chick diet at unaffected colonies. Reproductive

asynchrony may be coming about because prey abundance and availability has become de-synchronized rather than as a result of an intrinsic, social mechanism. We suggest that late-breeding birds be monitored at unaffected colonies to facilitate comparisons with birds breeding at affected colonies (who have been breeding late). Our final recommendation is that oil-impacted colonies be studied as thoroughly as possible, not just fledgling production and chick diet (see above), but also adult survival, age of first breeding, and recruitment of offspring.

Recovery and non-recovery:

It is easier to find studies documenting a recovery, to whatever degree and at whatever that rate might be, than it is to find reports discussing the lack of recovery. A more rigorous approach to finding information that may instruct us in the recovery process might be to consider major incidents (as reported in the literature) and then follow each one up, leading either to recovery or not.

Unfortunately, this would be very hit or miss (many incidents have not been followed up and it would be hard to track those that have), and we feel this approach would not yield a large number of studies. By keying in on recoveries, in our search, we bias our selection to cases where recovery has occurred. This bias was partly compensated by our inclusion of studies that described growth of populations regardless of whether a perturbation occurred. An additional bias may exist if investigators are less likely to report a non-recovery than they are to report a recovery. Finally, we remark that short-term impact of oil spills are commonly reported in the literature, but the long-term impact is rarely reported, often due to a short-fall in funding. We wish to encourage investigators to redress the balance.

We earlier pointed out that the duration of recovery is set by the impact of the perturbation coupled with the rate of recovery. However, the true impact of a perturbation is not often known: it is difficult to assess mortality and sub-lethal

effects are often overlooked. As a result, predicting duration of recovery is very inexact, and this is complicated further by the fact that measuring the duration depends on the definition of recovery used.

One conclusion of our review is that one cannot, with much confidence, predict the rate, duration, or even extent of recovery of a marine bird population, simply on the basis of knowing the short-term impact of a perturbation. Statements such as "Populations should fully recover in 20-70 yr" (Piatt et al. 1990:395) are suspect unless based on studies of affected populations. Moreover, making an accurate prediction requires the availability of current estimates of all the critical demographic parameters of that population. Such parameter estimates are difficult to obtain for avian populations in general, and for seabirds may be impossible to obtain, for example, due to limited access to breeding colonies for observation and banding. The problem is that these demographic parameters vary among populations and, even within a population, they vary with time. For example, intensive study of the Skomer (Wales) Common Murre population indicated that during a period of growth (in the mid-1980's, which represented recovery from a population crash in 1969/70), fledging success and adult survival increased compared to values during a period of stasis, about a decade earlier (Hatchwell & Birkhead 1991). However, survival and recruitment probability of offspring during the mid-1980's were not at that time known. Using parameter estimates for survival to breeding age, collected during the 1970's, produced a projected rate that did not match the observed population growth rate. Hatchwell and Birkhead inferred that survival to breeding age was about 50% greater during the 1980's than during the 1970's. If so, projected population growth rates matched observed rates. In other words, even in a relatively well-studied population, growth (i.e. recovery) rates, instead of being predicted by our knowledge of demographic parameters, are being used, retrospectively, to fill in our knowledge of these parameters.

There ^{are} is also substantial differences among populations in their demographic parameters, e.g. Common Murre populations on Skomer Island (Wales), Isle of Canna (Scotland) and Semidi Islands (Alaska) all differ in one or more primary demographic parameters (Birkhead & Hudson 1977, Swann & Ramsey 1983, Nysewander & Dippel 1991). It is questionable, therefore, whether one can construct a useful population model that "borrows" parameter estimates from one population to apply to a divergent population, as was done by Murphy et al. (1985).

The difficulty biologists and managers face is not just of quantitatively predicting a recovery trajectory, but even of qualitatively predicting it. Why a population recovers or does not recover is a question, in practice, not easily answered. For example, Common Murres on the Farallon Islands were recovering well during the 1970's and early 1980's from the effects of disturbance and chronic oil pollution (Ainley & Boekelheide 1990). Between 1982 and 1986, however, they were subjected to heavy mortality from gill-nets, a severe El Niño, and two oil spills (Takekawa et al. 1991). Though these perturbations did not extend beyond 1986, the murre population has yet to show any signs of recovery, even by 1991 in spite of high breeding success (PRBO, unpublished). A second example of the elusiveness of predicting population recovery also concerns Common Murres, those of Skomer Island. After heavy winter mortality in 1969/70, the murre population dropped substantially. Between 1970 and 1972 the population recovered only 50% of its losses; between 1972 and 1979 there was no further population recovery. However, between 1979 and 1988 the murre breeding population increased by 85-90%. Hatchwell & Birkhead (1991) offered no explanation for the pattern of recovery and non-recovery.

The case of the Peruvian guano birds and the collapse of the anchoveta fishery provides an example in which the degree of recovery can be attributed to a biological factor: fish availability (Tovar et al. 1987). El Niño events in 1957, 1965,

and 1972 each caused a crash of Peruvian Boobies and Guanay Cormorants, followed by recovery of population number. Over-fishing of the anchoveta, a key prey species, however, caused each subsequent recovery to be weaker than the preceding. That is, the carrying capacity of the environment had changed between the time of the population crash and the time of the recovery. This same phenomenon may explain why the Farallon murre populations in the 20th century have never come close to recovering their mid-19th century population numbers (Ainley & Lewis 1974). Thus, for some species, the answer to the question, "How long until recovery?" is "Never", at least if recovery is defined as return to pre-perturbation numbers.

Critique of the Review by Baker et al.

We conclude the discussion by considering the arguments by Baker, et al. (1990) in their paper, "Natural recovery of cold water marine environments after an oil spill", with regard to birds. We emphasize the paper of Baker et al. for two reasons: (1) It purports to be a review of studies concerning the recovery of marine populations, including seabirds, from oil spills, and thus its subject matter is similar to our own literature review. (2) Baker et al.'s review was intended to draw inferences about the expected consequences of the *Exxon Valdez* oil spill on marine populations, an objective which is coincident with that of the Restoration & Planning Work Group in requesting this study.

Baker et al. make several points that we wish to take issue with. First, they state that "there is no reason to suppose that, from a biological point of view, this mortality [as a result of oil slicks] is damaging to seabird populations" (p. 23). On the contrary, there is certainly good reason, from a biological point of view, to think that such mortality is damaging, unless the mortality from oiling is compensated by a reduction in mortality from other sources. There is no good basis for supposing that oiling mortality is of that nature. What evidence there is from marine birds suggests the opposite. For example, Hudson (1985) argues

that, for auks, mortality from an oil spill will endanger a population, because reproductive success often declines as colony size declines (as might happen after a spill). The field reports from the 1989 - 1991 breeding seasons (Nysewander & Dippel 1991) indicate that the deleterious effects of the *Exxon Valdez* oil spill on murre reproductive success may have been much more severe than even Hudson anticipated. Whether compensatory mortality is a real phenomenon is a subject of discussion in the duck literature where there has been argument concerning the role of hunting in population regulation. Many studies have provided evidence that hunting mortality is compensatory, while a comparable number have produced evidence that hunting mortality is additive, non-compensatory (Nichols 1991). Therefore no facile argument regarding compensatory mortality can be made. Baker et al. (1990) present no evidence that oil spill mortality is compensated.

Secondly, Baker et al. (1990) state, "Arctic and sub-Arctic seabirds also suffer heavy mortality from natural causes and from fishery practices." This argument, to our mind, indicates why oil spill mortality is so critical. It is because Arctic and sub-Arctic seabirds suffer from high mortality from other causes, that the additional mortality resulting from oil spills could be critical. Heavy mortality from natural causes can hardly meliorate mortality from oil spills. As for mortality stemming from fishery practices, at best one can say that fisheries should share the blame for declines (or lack of recovery) of seabird populations.

Some of Baker et al.'s arguments are irrelevant, e.g. "Many animals overproduce young, often on a colossal scale, and nearly all of them die before reaching the age of reproduction." Besides the fact that many seabird species do not "overproduce" young, what matters is whether or not increased mortality is detrimental to the population or not. In fact, seabirds are characterized by some of the lowest reproductive rates among vertebrates (Lack 1966).

A fourth point, and this is probably the key argument of Baker et al., is that even "auks, which because of their very low reproductive rate might be expected not to be able to make good these losses, have sustained their population." This argument is fallacious on two grounds. First, what holds for the auks of Great Britain and the North Sea may not hold for Alaskan auks. Baker et al. admit that auk colonies are much larger in the Arctic than they are further south, and yet there is good evidence that the ability of auks to rear young is diminished at the uppermost levels of colony size (Hunt et al. 1986). Therefore even if auks in Great Britain are able to sustain their number, in the face of oiling, this tells us nothing about the ability of Alaskan auks to maintain theirs. Baker et al.'s argument also collapses because British and North Sea auks have been declining in recent years, not increasing or maintaining their numbers. In the 1970's, in spite of well-publicized oil-related mortalities, auk numbers in Britain were indeed increasing but by the 1980's were not, and in fact were declining; in Norway they were declining during both decades (Harris 1991, Lloyd et al. 1991). This widespread decline of auk numbers is not likely a result of oiling, but rather of changes in food availability, but this does not absolve the oil industry. The impact of an oil spill on an increasing population is indeed transient, but the impact of an oil spill on a declining or otherwise static population is essentially permanent.

The fifth point of Baker et al. is that a reservoir of non-breeding individuals exists which can be tapped to make good mortality of breeders. This may be the case in some species (e.g. European Shag, Armstrong et al. 1978) but is not widespread. What is more likely is that an individual which loses a mate, can replace it, but often at the price of reduced reproductive success in the first year or two (Manuwal 1972, Emslie and Sydeman in press). In contrast, a crash in the population size of Common Murres on the Farallon Islands between 1982 and 1986, has not resulted in a shift toward earlier age of first-breeding (PRBO unpublished).

Finally, we note that between 1969 (when efforts were first made to monitor the effects of oil spills on seabirds) and the present, the British Isles have not suffered an oil spill killing large numbers of seabirds, comparable to the number affected by the *Exxon Valdez* oil spill. Therefore the conclusion that British seabird populations have been able to tolerate oil spills, with only transient effects, even if correct, is of little value in assessing the impact of a catastrophic oil spill, such as that of the *Exxon Valdez*.

Literature Review. Marine Birds

TABLE 1. Summary of exponential growth rates (percent increase per annum) in various seabird populations.

Species	Area (No.Sites)	Rate	Period	Chronology	Cause	Source
PENGUINS						
<i>Aptenodytes forsteri</i>	Amanda Bay	7.1	1961-87	G		Woehler ms
	C.Washington	9.5	1968-86	G		
	Franklin I	5.8	1964-83	G		
	Haswell I	2.3	1962-70	G		
	Kloa Pt.	5.0	1977-85	G		
	Taylor Glacier	6.7	1980-88	G		
<i>A. patagonicus</i>	Crozet I (2)	10.2	1962-86	Rec,Late	E	Jouventin & Weimirskirch 1990
	Heard I	24.0	1963-71	Rec,In	E	Budd 1974
		18.1	1969-88	Rec	E	Woehler 1991
	N Spit Bay	23.4	1969-80	Rec	E	Gales & Pemberton 1988
	S Spit Bay	10.6	1969-88	Rec	E	Gales & Pemberton 1988
	Kerguelan I (2)	6.7	1963-86		E	Jouventin & Weimirskirch 1990
	MacQuarie I	9.1	1930-80	Rec,All	E	Rousevell & Copson 1982
	South Georgia I	5.6	1925-80	G,All	E	Croxall et al. 1984
		17.3	1978-85	Rec,Late	E	Woehler ms
<i>Eudyptes chrysolophus</i>	Kerguelan I	0.7	1963-80	G	F	Jouventin & Weimirskirch 1990
<i>Megadyptes antipodes</i>	Otago Peninsula	12.2	1942-52	G	E,Im	Richdale 1957
<i>Pygoscelis adeliae</i>	Ardley I	8.5	1980-84	G		Woehler ms
	Aviation I	7.4	1961-85	G		
	Buckle I (3)	3.8	1973-84	G		
	C.Denison	11.8	1974-82	G		
	Joubin Is (4)	4.6	1984-90	G		
	Haswell I	2.3	1912-62	G,All		Pryor 1968
	Hope Bay	2.2	1945-63	G,Late	F	Conroy 1974
	Peterman I	18.0	1982-88	Col,In		Woehler ms
	Pt.Geologie	1.7	1958-84	G	C	Thomas 1986
	Pr.Olav Coast (3)	3.4	1972-81	G		Woehler ms
	Ross Sea (20)	8.5		G	C	Taylor et al. 1990
	C.Bird	4.6	1967-87	G	C	K.Wilson 1990
		8.7	1981-87	G		Woehler ms
	C.Hallett	1.3	1967-88	Rec,All	D	
		9.8	1981-87	G	C	
	Beaufort I	9.2	1963-87	G		Taylor et al. 1990
		5.7	1981-87	G	C	Woehler ms
	C.Royds	5.2	1966-87	G	C	Taylor et al. 1990
		10.0	1980-87	G		Taylor & Wilson 1990
	C.Crozier	7.7	1970-87	G		Woehler ms
	Unger I	27.1	1980-85	Col,In		
	Sentry Rk	42.8	1980-85	Col,In		
	Duke of York I	16.8	1982-88	G		
	Downshire Cliffs	3.5	1982-88	G		
	C.Wheatstone	2.7	1964-87	G		
	Coulman I (4)	2.4	1964-88	G		
	Wood Bay	4.1	1981-89	G		
	Inexpressible I	3.0	1963-87	G		
	Franklin I (2)	2.1	1981-86	G		
	Sabrina I	5.6	1978-84	G		
	Signy I	2.8	1957-82	G	F	Croxall et al. 1984
	Syowa Coast (10)	9.9	1975-82	G		Woehler ms
	Windmill Is. (14)	4.6	1961-89	G	C	Woehler et al. 1991
<i>P. antarctica</i>	Cuerville I	24.9	1971-88	Col,In		Woehler ms
	Deception I (5)	20.0	1953-66	G,In	F	Conroy 1974
	(7)	3.5	1967-87	G,Late		Woehler ms
	Georges Pt	18.9	1984-88	Col,In		
	Heywood I	6.7	1966-87	G		
	Harmony Pt	4.5	1972-87	G		
	Joubin I	6.2	1984-90	Col,In		
	Livingston I (3)	14.0	1957-65	G,In	F	Conroy 1974
	(4)	1.0	1965-87	G,Late		Woehler ms
	Nameless I	11.4	1984-90	Col,In		
	Seal I	11.3	1970-88	G		
	Signy I	6.6	1957-82	G	F	Croxall et al. 1984
	Tupinier I	5.4	1969-90	G		Woehler ms
<i>P. papua</i>	Livingston I (3)	17.9	1957-65	G	F	Conroy 1974
	Harmony Pt	6.4	1957-65	G	F	
	Heard I	1.9	1954-87	Rec	E	Woehler 1991

Table 1 (continued)
Literature Review: Marine Birds

	Peterman I	11.2	1982-88	G		Woehler ms
	Port Lockroy (2)	12.5	1984-88	G		
	Pr. Edward I (14)	12.6	1974-84	G		
	Thule I	20.2	1966-79	G		
	Yankee Harbour	19.9	1957-65	G	F	Conroy 1974
<i>Spheniscus magellanicus</i>	Pen. Valdes	3.0	1978-87	G,Late		Boersma et al. 1990
GREBES						
<i>Podiceps cristatus</i>	Netherlands	4.4	1966-83	Rec?	E?	Camphuysen 1989
ALBATROSS						
<i>Diomedea albatrus</i>	Torishima I	6.6	1956-82	Rec,In	E,	Hasegawa & DeGange 1982
<i>D. immutabilis</i>	Laysan	5.3	1911-57	Rec	E,H	Rice & Kenyon 1962
	Lisianski I	10.4	1923-57	Rec	E,H	
	Midway I	27	1900-45	Rec,In	E,H	
		4.0	1945-58	Late		
		4.7	1958-73	Rec,Late	E,H	Fisher 1975
<i>D. melanophrys</i>	Heard I	4.3	1954-87	Rec,Late	E,D	Woehler 1991
<i>D. nigripes</i>	Laysan	8.7	1911-57	Rec	E,H	Rice & Kenyon 1962
	Lisianski I	3.0	1923-57	Rec	E,H	
	Midway I	27	1900-45	Rec,In	E,H	
	Torishima I	13.2	1964-82	Rec,In	E,Im	Hasegawa 1984
PETRELS						
<i>Fulmarus antarcticus</i>	Pt. Geologie	6.0	1955-84	G		Thomas 1986
<i>F. glacialis</i>	Funk I	11.0	1959-80	G,All	F	Kirkham & Montevecchi 1982
	NE Atlantic	7.0	1952-80	G,Late	F	Ollason & Dunnet 1983
	Great Britain	16.0	1879-'01	G/Col,In		Evans 1984b
		10.0	1909-39	G,Mid		
		6.5	1939-69	G,Late		
	Eynhallow I	6.0	1953-70	G		Dunnet et al 1979
	Shetland Is	10.3	1878-'59	Col,All	F	Fisher 1966
	Orkney Is	4.6				
	Isle of Man	8.6	1969-86	G		Lloyd et al 1991
	Norway	10.0	1920-47	Col	Im	Brun 1979
	Runde	5.3	1947-81	G,Late		Barrett & Vader 1984
	SW Norway	10.2	1950-79	Col,All	F	Toft 1983
	Ydre Kitsigsut	12.1	1971-83	G,Late		Evans 1984a
<i>Puffinus diomedea</i>	Selvaen Grde I	1.2	1980s	Rec,In	E	Mougin et al. 1987
<i>P. tenuirostris</i>	Fisher I	6.0	1972-80	Rec,In	E	Serventy & Currey 1984
PELECANIFORMS						
<i>Pelecanus occidentalis</i>	Anacapa I	37.0	1973-80	Rec	P,F,Im	Anderson & Gress 1983
	Coronado I	8.6	1920-35	Rec,All	E	Jehl 1973
		24.0	1971-80	Rec	P,F,Im	Anderson & Gress 1983
	No. Carolina	46.8	1977-83	Rec,In		Clapp & Buckley 1984
	So. Carolina	18.7	1978-82	Rec,In		
<i>Phalacrocorax aristotelis</i>	Farne Is	9.0	1910-65	Rec,All	E	Potts 1969
		11.0	1930-65	G,In	E	Armstrong et al. 1978
		40.0	1968-74	Rec,In	Im	
	Isle of May	7.7	1900-53	Rec,All	E	Potts 1969
		15.6	1962-83	G	E	Aebischer 1986
	N E England	11.1	1969-86	Rec,All	Red Tide	Lloyd et al 1991
	SW Norway	6.8	1950-79	G		Toft 1983
<i>Ph. atriceps</i>	Arthur Harbor	17.6	1973-87	G		Ainley & Sanders 1988
	Heard I	3.5	1951-85	Rec	D	Woehler 1991
	South Orkney Is	2.0	1960-87	G		Cobley 1989
<i>Ph. auritus</i>	Anacapa I	25.0	1973-80	Rec	P,F,Im	Anderson & Gress 1983
	Br. Columbia	8.6	1959-83	G	E	Vermeer & Sealy 1984
	Mandarte I	10.8	1927-83	G	E	
	Farallon I	20.7	1972-82	Rec,All	E	Ainley & Boekelheide 1990
		70.0	1983-86	Rec,All	E	
	Great Lakes	21.5	1970-80	Rec,In	P	Bloekpol & Scharf 1990
		38.4	1980-87	Rec,Late		
	Maine	24.2	1934-45	G,In	E	Buckley & Buckley 1984
		1.6	1972-77	G,Late		Milton & Austin-Smith 1983
	New England	21.0	1930-45	G Im		Drury 1973/4
	Nova Scotia	9.4	1927-71	G,In	E	
		10.2	1971-82	G,Late	E,Im	
	St. Lawrence R	3.0	1963-80	G,Late	E	
	Texas	24.4	1949-75	G,All	E,Im	Morrison et al. 1983
<i>Ph. bougainvillii</i>	Peru	50.0	1953-57	Rec	F	Tovar et al. 1987
		10.0	1959-64	Rec	F	

Table 1. (continued)
Literature Review: Marine Birds

		1.2	1966-72	Rec	F	
		8.2	1974-82	Rec	F	
Ph. carbo	France	4.0	1968-83	G	E	Evans 1984b
	NW Overijssel	17.0	1930-40	Rec, In	E	Veldkamp 1986
		12.0	1970-86		P	
	Nova Scotia	10.3	1940-72	Col, All		Erskine 1972
	Nova Scotia	3.8	1971-82	G, Late	E	Milton & Austin-Smith 1983
	Scotland	4.0	1905-83	G	E	Evans 1984b
	Dublin Co.	7.8	1969-86	G		Lloyd et al 1991
Ph. olivaceous	Texas	32.0	1967-75	Rec, In	E, Im	Morrison et al. 1983
Ph. pelagicus	Bare Pt	8.8	1959-83	G	E	Vermeer & Sealy 1984
	Farallon I	16.3	1976-81	Rec, All		Ainley & Boekelheide 1990
	Mandarte I	4.7	1915-83	G	E	Vermeer & Sealy 1984
Sula bassanna	Bird Rks	1.0	1967-73	G, Late	E, F	Nettleship 1976
	Bonaventure I	3.6	1919-76	G	E	Brown & Nettleship 1984
		2.2	1961-73	G	E, F	Nettleship 1976
		9.9	1961-66	G		
	Funk I	19.3	1936-72	G, All	E, F, Im	Kirkham & Montevecchi 1982
		3.0	1959-72	G, Late	E, F	Nettleship 1976
	Great Britain	3.0	1900-83	G		Evans 1984b
	Grassholm I	20.3	1914-24	Rec, In	E	Fisher & Vevers 1944
	Grassholm I	7.8	1924-1939	Rec, Mid	E	Fisher & Vevers 1944
	Bass Rock	6.3	1969-86	G		Lloyd et al 1991
	Runde	8.4	1969-74	G, Late		Brun 1979
		7.5	1969-82	G, Late		Barrett & Vader 1984
	Skarvklakken	38.4	1969-82	Col, In	Im	Barrett & Vader 1984
	Syltefjord	14.5	1969-74	Col, In		Brun 1979
		18.3	1969-82	Col, In		Barrett & Vader 1984
S. capensis	Algoa Bay	3.6	1956-74	G, Late	E, D	Randall & Ross 1979
S. serrator	Colville	4.9	1928-47	G		
	Hawkes Bay	2.5	1931-46	G		
	Hawkes Bay	2.5	1879-'03	Col, In		Fleming & Wodzicki 1952
S. variegata	Peru	10.0	1953-57	Rec	F	Tovar et al. 1987
		8.0	1959-64	Rec	F	
		7.8	1966-72	Rec	F	
		1.0	1974-82	Rec	F	
SKUAS						
Catharacta skua	Foula	3.3	1880-1963	Rec	E	Parslow 1967
	Orkney	9.3	1915-63	Rec	E	
	Orkney	9.4	1974-84	Rec, Late		Lloyd et al 1991
	Shetland	7.0	1900-70	G	E	Evans 1984b
C. maccormicki	Arthur Harbor	7.6	1974-87	G		Ainley & Sanders 1988
	McMurdo Snd (9)	1-15	1957-83	G, All	F, Im	Ainley et al. 1986
	Pt. Geologie	2.7	1966-81	G, All	F	Jouventin et al. 1984
Stercorarius parasiticus	Fair Isle	11.6		Rec	E	Parslow 1967
		3.7	1962-73	G	E	O'Donald & Davis 1975
	Orkney Is	9.4	1969-86	G, In		Lloyd et al 1991
GULLS						
Larus argentatus	Berlengas I	3.2	1939-81	G, Late	F	Barcena et al. 1984
	E Canada	13.1	1925-35	G, All	F, H	Lewis 1927
	Funk I	5.9	1956-80	G, All	F	Kirkham & Montevecchi 1982
	E U.S.	4.5	1900-70	G	F	Nisbet 1978
	Lk Huron/Mich.	12.3	1960-65	G, All	F, H	Ludwig 1966
	Muskeget I	9.2	1925-40	G, In	F	Kadlec & Drury 1968
	Thatcher I	92.0	1959-66	G, All	F, Im	
	New England	9.8	1938-42	G		Drury & Kadlec 1974
	New England	4.2	1900-40	G		Drury 1963
	Great Britain	12.8	1930-70	G, All	F	Chabrzyk & Coulson 1976
	Skokholm I	10.2	1959-69	G		Harris 1970
	Skomer I	10.8	1962-69	G		Harris 1970
	Isle of May	12.0	1907-70	G, All	F	
	Walney I	17.0	1904-64	Col, All	E, F, Im	Parslow 1967
	Suffolk Co.	7.0	1973-86	G		Lloyd et al 1991
	German					
	Wadden Sea	5.7	1966-82	Rec, All	P	Becker 1991
	Holland	12.1	1930-38	G	F	Morzer Bryuns 1958
		5.3	1947-54	G	C	
	Scania, Sweden	4.7	1947-76	G	E	Mathiasson 1980
	Sisargas I	5.1	1948-81	G, Late	F	Barcena et al. 1984
	SW Finland	8.7	1943-80	G	F	Berman 1982
	SW Norway	3.6	1950-79	G	F	Toft 1983
L. a. heuglini	Meda I	4.4	1961-82	G	F, E	De Juana 1984
L. atricilla	Jamaica Bay	84.6	1979-84	Col, In	Im	Buckley & Buckley 1984
L. auduonii	Cabrera Is	14.1	1974-82	G, In	F, E	De Juana 1984

Table 1. (continued)
Literature Review: Marine Birds

L. californicus	Chafarinas I	8.5	1966-83	G/Col, In	F, E, Im	De Juana et al. 1984
	Columbretes I	20.2	1974-82	Col, In	F, E	De Juana 1984
	Western U.S.	2.0	1920-80	G, All	F, H	Conover 1983
	Lahontan Lk	7.0	1941-83	G, All	F	Jehl et al. 1991
	Mono Lk	4.6	1916-76	Rec, All	E	Winkler & Shuford 1988
L. delawarensis		15.1	1950-76	G, Late	H	Jehl et al. 1984
	Pyramid Lk	19.5	1927-60	Rec, All	E, F	Jehl et al. 1991
	San Fran. Bay	80.0	1980-89	Col, In	F, Im	Ainley & Hunt 1990
	Stillwater	17.6	1950-77	Col, All	F, H	Jehl et al. 1991
	E Canada	2.4	1925-35	G, All	H	Lewis 1937
	Maritime Prov	20.9	1972-86	G, Late	F, Im	Lock 1988
	New Foundland	11.2	1940-80	G, All	F, Im	
	St. Lawrence R	7.6	1945-67	G, All	F, H	Ludwig 1974
	Lk Erie	23.6	1945-67	G, All	F, H	
		19.1	1976-84	G, Late	F, H	Bloekpol & Scharf 1990
	Lk Huron	22.1	1930-45	G, In	F, H	Ludwig 1974
		8.4	1945-67	G, Mid	F, H	
		10.1	1976-84	G, Late	F, H	Bloekpol & Scharf 1990
	Lk Michigan	17.3	1945-67	G, All	F, H	Ludwig 1974
		11.3	1976-84	G, Late	F, H	Bloekpol & Scharf 1990
L. dominicanus	Lk Ontario	14.4	1930-45	G, In	F, H	Ludwig 1974
		22.2	1945-67	G, Mid	F, H	
		9.5	1976-84	G, Late	F, H	Bloekpol & Scharf 1990
	Lk Superior	11.3	1976-84	G, Late	F, H	
	Western U.S.	6.0	1920-80	G, All	F, H	Conover 1983
L. fuscus	Lk Wainono	33.0	1969-77	G, All	F, H, Im	Pierce 1980
L. glaucescens	New England	14.8	1941-65	G		Drury 1973/74
	Spain (2)	77.8	1973-81	Col, In	F, Im	Barcena et al. 1984
	SW Norway	3.7	1950-79	G	F	Toft 1983
	Skokholm	20.6	1960-69	G Im?		Harris 1970
	Walney I	29.0	1930-66	Rec, All	E, F, Im	Parslow 1967
L. marina	NW Washington(7)	2.0	1963-70	G, Late	F	Reid 1988
	Colville I	3.0	1963-75	G	F	Amlaner et al. 1977
	Protection I	5.9	1976-84	G, Late	F	Reid 1988
	SW Br. Columbia(4)	4.0	1900-60	G	F	Reid 1988
	Mandarte I	4.7	1915-60	G	F	Vermeer & Sealy 1984
	Mitlenatch I	3.6	1922-75	G		
	E Canada	6.2	1925-35	G, All	F, H	Lewis 1937
	E U.S.	17.0	1926-65	Col, All	F, Im	Nisbet 1978
	New England	18.7	1930-65	G, In	F	Buckley & Buckley 1984
		2.0	1965-77	G, Late	F	
L. occidentalis	England/Wales	15.0	1880-1930	G, In	E, F	Parslow 1967
		1.4	1930-56	G, Late	E, F	
	Funk I	17.1	1956-80	G, All	E, F	Kirkham & Montevecchi 1982
	Isles of Scilly	1.5	1930-66	G, Late	E, F	
	SW Norway	1.7	1950-79	G	F	Toft 1983
	Alcatraz I	7.7	1982-88	G, Late	F	Boarman 1989
	Santa Barbara I	19.0	1980-84	G	F, Im	Ainley & Hunt 1990
	Lk Tasserssuaq	52.0	1971-80	Col, In		Evans 1984a
	England/Wales	11.2	1938-58	G	E, F	Parslow 1967
	Lancashire	8.3	1969-86	G		Lloyd et al 1991
Rissa tridactyla	Berlengas I	20.1	1975-81	Col, In		Barcena et al. 1984
	E Canada	15.7	1970-83	Col, All	F	Lock 1987
	Germany	30.0	1952-62	G, In	F	Evans 1984b
		19.5	1972-82	G, Late		
	Great Britain	3.5	1900-69	G, All	E, F	Coulson 1983
		1.0	1969-79	G, Late	E, F	
	Shetland Island	7.2	1977-83	G		Heubeck et al 1986
	Humberside	6.4	1969-86	G		Lloyd et al 1991
	SW Norway	7.4	1950-79	G		Toft 1983
		8.6	1956-79	G, All		Munkejord & Folkedal 1981
TERNS	Kjor	38.9	1956-63	G, In		
	Urter	28.7	1973-80	Col, In		
	W Greenland	9.0	1965-74	G	F	Evans 1984a
	Long I	14	1924-72	Rec, All	E, Im	Nisbet 1973
	Loir/Allier Val	1.5	1905-80	G		Evans 1984b
	Massachusetts	10.2	1923-50	Rec, All	E, Im	Nisbet 1973
		5.5	1890-1946	Rec, All	E	
	St. arctica	3.4	1925-35	G, All	H	Lewis 1937
	St. caspia	4.0	1960-65	G, All	F	Ludwig 1966
St. dougalli	Lk Huron/Mich	2.6	1980-87	G, Late	F	Bloekpol & Scharf 1990
	Lk Huron	2.6	1980-87	G, Late		
	Lk Michigan	3.8	1976-87	G, Mid		
	Lk Ontario	28.7	1976-87	G		
	Pacific US	2.6	1960-80	G		Gill & Mewaldt 1983
	Massachusetts	1.4	1872-1938	Rec, All	E	Nisbet 1973

Table 1. (continued)
Literature Review: Marine Birds

St. hirundo		4.0	1885-1920	Rec,All	E	
	Great Lakes	2.3	1900-60	Rec,All	E	Bloekpol & Scharf 1990
	Maine	4.3	1900-40	Rec,All	E	Nisbet 1973
	Shetland I	6.1	1969-86	G		Lloyd et al 1991
St. sandvicensis	Angholmarna	14.0	1945-76			Mathiasson 1980
	Foteviken	30.7	1939-52			
	Maklappen	20.4	1912-38	Rec,All	E,Im	
	SE Britain	3.2	1920-64	G	E	Parslow 1967
St. paradisaea	Shetland	6.1	1969-86	G		Lloyd et al 1991
	Krunnit Is	9.1	1963-73	Rec	D	Helle et al 1988
St. paradisaea	German					
hirundo	Wadden Sea	5.7	1968-82	Rec,In	P	Becker 1991
ALCIDS						
Alca torda	Hornoy	9.0	1967-80	G		Barrett & Vader 1984
	Orkney Is	7.6	1976-85	G		Benh et al 1987
Cephus grylle	E Canada	10.1	1925-35	Rec,All	H	Lewis 1937
	New England	6.8	1931-45	G		Drury 1973/4
	SW Norway	0.9	1950-79	G		Toft 1983
Cerorhinca						
monocerata	Cleland I	19.2	1967-88	Col,All		Rodway 1990
	Farallon I	56.4	1972-82	Rec,All	P,E,Im	Ainley & Boekelheide 1990
Fratercula arctica	E Canada	2.6	1925-35	Rec,All	H	Lewis 1937
	Mantinius Rk	4.7	1937-77	Rec,All		Buckley & Buckley 1984
	Hornoy	30.3	1967-80	G		Barrett & Vader 1984
	SW Norway	1.8	1950-79	G		Toft 1983
	Farne I	12.2	1969-75	G		Harris 1983
	NE Britain	9.1	1969-1979	G		Harris 1983
	Isle of May	19.0	1973-81	G Im		Harris 1991
F. cirrhata	Farallon I	6.4	1971-82	Rec,All	P	Ainley & Boekelheide 1990
Ptychoramphus						
aleuticus	Farallon I	5.0	1870-1920	Rec,All	F	Ainley & Lewis 1972
Uria aalge	E Canada	5.4	1925-35	Rec,All	H	Lewis 1937
	Funk I	10.8	1936-1972	Rec,All	E	Kirkham & Montevecchi 1982
	Farallon I	7.9	1972-82	Rec,All	E	Ainley & Boekelheide 1990
	Hornoy	36.4	1974-82	G		Barrett & Vader 1984
	Humberside	7.0	1972-76	G		Stowe 1982
	Isle of Cana	c.13	1973-82	G		Swann & Ramsey 1983
	Skomer I	6.6	1977-88	Rec,All		Hatchwell & Birkhead 1991
	Farne I	13.0	1970-85	G		Harris 1991
DUCKS						
Somateria						
mollissima	Baltic	10.3	1969-81	G	E,F	Stjernberg 1982
	New England	15.2	1949-72	G		Drury 1973/4
	E. Canada	5.7	1925-35	G	E,H	Lewis 1937
	Great Britain	3.9	1958-82	Rec	E	Coulson 1984
	Scania	5.1	1947-76	Rec	E,H	Mathiasson 1980
	Netherlands	14.8	1968-76	Rec	P	Camphuysen 1989
Histrionicus						
histrionicus	E U.S.	23.7		G,All	H,Im	Vickery 1988
OSPREY/EAGLES						
Pandion						
haliaetus	New England	c. 9	1976-81	Rec	P	Spitzer et al. 1985
OYSTERCATCHERS						
Haematopus						
ostralegus	Rottumeroog,NL	7.5	1960-88	Rec,All	P	Nolet, 1988
	Germany	5	14 yrs	G		Schnakenwinkel, 1970

Rec=recovery from population decline; duration: In=initial period, Mid=middle period, Late=late period;
G=growth of established population, All=entire period

Factors involved: E=relaxation from exploitation, F=enhanced food supply, D=relaxation from disturbance, H=habitat improvement, Im=immigration, P=lessening of pollution

Table 2. Comparison of Life History Traits and Population Growth Rates

	<u>Life History Traits</u>			<u>Growth Rates (%)</u>		
	Fecundity	Age First Breeding	Adult Survival (%)	Median	Upper Quartile	N= Sample Size
Penguins						
<u>Aptenodytes</u> spp.	1	3-4	82-95	9	11	15
Other penguins	1.7-2	2.5	c.85	7	12	56
Adelie				5	9	33
non-Adelie				11	16	23
Grebes				(4)	-	1
Albatrosses	1	7-9	92-96	7	12	11
Petrels & Shearwaters	1	4-6	90-96	7	12	11
Pelicans	3	2	c.80	19	24	5
Gannets & Boobies	1	4	c.94	8	10	23
Cormorants/Shags	3	2	c.83	10	21	39
Skuas	2	3-4	78-94	8	9	9
Gulls						
Larus argentatus	2.4-3	3-4	91-93	9	12	23
Other Larus	2.5-2.9	2-4	80-87	11	19	53
non-Larus spp.	2	3	87	9	20	13
Terns	3	2	c.91	4	10	22
Auks	1-1.8	3	83-96	9	13	23
Seaducks	8-10	1-2	54-72	10	15	5
Eagles/Osprey	2.9	3	85	(9)	-	1
Oystercatchers	4	4	87-91	6	-	2

Table 3. Comparison of Projected and Observed Population Growth Rates

Species	Population Growth Rate (%)		Reference
	<u>Projected</u>	<u>Observed</u>	
Northern Fulmar	7	6	Ollason & Dunnet, 1978
Cory's Shearwater	1.2	0.0	Mougin et al. 1987
European Shag	11.0	11.0	Potts et al. 1980
Great Skua	8.9	7	Furness 1978
Arctic Skua	4.0	3.7	O'Donald & Davis, 1975
Herring Gull	11-12	10-11	Harris 1970
Herring Gull	4.7-6.5	9.2	Kadlec & Drury, 1968
Herring Gull	9.5	24.4	Brown 1976
Herring Gull	5	5	Samuels & Ladino, 1983
Glaucous-winged gull	5.1	2-6	Reid, 1988
Black-legged Kittiwake	4.7-14.9	14.6	Kosinski & Podolsky, 1979
Black-legged Kittiwake	4	4	Porter & Coulson 1982
Common Tern	3	5-6	Samuels & Ladino, 1983
Atlantic Puffin	9-14	19-22	Harris 1983
Common Murre	1-6.6	6.6	Hatchwell & Birkhead 1991
Common Murre	8	8-10	Nur & Ainley, unpublished