

SIMULATION MODELING OF MARINE BIRD POPULATION ENERGETIC,  
FOOD CONSUMPTION, AND SENSITIVITY TO PERTURBATION

**by**

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## SUMMARY

The objective of our research has been to develop methods of assessing the sensitivity of marine birds in Alaskan waters to petroleum-related environmental perturbations. Our approach has combined field observations and information with various analytic and computer simulation models. This report completes our documentation of the population energy flow patterns, at-sea distributions, and sensitivity to oil spills of the dominant marine bird species breeding at major colonies on Kodiak Island and using the surrounding oceanic areas for foraging. We employed data from 8 major colony locations of breeding Tufted Puffins and Black-legged Kittiwakes, in combination with other information obtained from the seabird literature, to conduct model analyses of the level of mortality of these species that might accompany selected oil-spill scenarios. The model that we used was a simplification of one developed earlier in this research and previously applied to the Pribilof Islands system. In the Kodiak model, we excluded consideration of chick mortality due to death of parents or to diminished growth rate accompanying a shift in parental foraging distributions caused by a spill, and we modeled the spatial distribution of the birds about Kodiak using a system of rectangular coordinates rather than the polar coordinate system employed in the Pribilof analysis. The Kodiak model required 12 parameters, which considered features of population size and distribution, flight speed and trip time, time spent foraging in specific areas and the sizes and locations of those areas, daylength, the probability that adults encountering a spill will suffer mortality, the mortality suffered by birds from a given colony foraging in a given area, and the extent of a simulated oil spill and time required for the affected area to return to an equilibrium following the spill. Spill trajectories were simulated from four launch points at two times of the breeding season, using 50 simulation runs to establish the frequency distributions for each site-season scenario. The results of our modeling indicated that for most scenarios, adult mortality of puffins and kittiwakes was quite low, usually less than 1% of the breeding populations at a given colony. Puffins were somewhat more susceptible than kittiwakes, and spills originating close to a colony generally effected greater mortality than those launched at greater distances, although this was influenced in important ways by the foraging distribution characterizing the birds inhabiting a given colony. For each spill scenario, however, there was a frequency distribution of estimated mortalities that resulted from the influences of the various factors affecting spill trajectory and duration. As a result, some spill scenarios did cause substantial mortality among the breeding birds, although these generally were not likely to occur very often. Monte Carlo analyses indicated that a considerable amount of the variation in the estimates of spill-related mortality of adult puffins and kittiwakes was due to uncertainty in the estimation of various model parameters. This emphasizes the need for good information on those population or colony attributes.

The second part of this report reviews the general status of the information or data base on marine birds and their environments in Alaskan waters that we have found to be necessary to our modeling efforts. From a consideration of a large number of parameters on populations, foraging, energetic, and characteristics of the perturbations themselves, we identify the following as having a high priority for obtaining accurate, colony- or area-specific field data: (1) The size of the colony. (2) The patterns of at-sea distributions of the birds. (3) The trip times of foraging adults. (4) The pattern of age-specific survivorship of the population. (5) The probability that an adult bird encountering an oil spill will suffer mortality. (6) The frequency with which adults shift their foraging distri-

distribution to other areas upon encountering an oil spill. (7) The ways in which a spill may influence resource availability to foraging birds in the affected area. In addition, the following parameters are assigned an intermediate priority: (1) The breeding structure of the population. (2) The foraging pathways of individuals. (3) The metabolic costs of foraging activity. (4) The spatial and temporal patterns of food availability about the Colony. (5) The ways in which changes in food delivery rate to chicks affects their growth rate and survivorship. (6) The distributional dynamics of oil spills.

## PART I. AN ANALYSIS OF KODIAK ISLAND COLONIES

### A. Introduction

Colonially breeding seabirds are a conspicuous and important element of most marine ecosystems. They often occur in vast concentrations, especially in areas of high productivity. They may have major effects on energy flow in these systems, consuming perhaps 22-27% of the annual production of small pelagic fishes (Wiens and Scott 1975, Furness 1978), and their concentration of nutrients about breeding colonies may have major influences on local patterns of marine nutrient cycling (Tuck 1960, Zelickman and Golovkin 1972) or on the contributions of nutrients to adjacent terrestrial systems (Burger et al. 197'8, Smith 1979). As marine ecosystems become subject to increasing demands for human development, especially through activities related to petroleum resources, the probability that the seabirds and their positions in marine trophic dynamics will be disturbed increases (Nettleship 1977, Nisbet 1979, Birkhead and Nettleship 1980). Intelligent management or conservation of marine birds requires some means of anticipating the effects of various perturbations, rather than continued reliance on post facto assessments of development-related mortality.

The objective of our research over the past several years has been to develop methods of assessing the sensitivity of marine birds in Alaskan waters to environmental perturbations such as might accompany petroleum development. The approach has combined the analysis of field observations on the distributions of the birds at sea and on their life history, reproductive, and demographic attributes with simulation modelling of population foraging distributions and demography. This approach was initially developed and applied to colonially breeding seabirds on the Pribilof Islands, Bering Sea (Wiens et al. 1979a, Ford et al. 1981). More recently, we have extended the analysis to the marine birds associated with Kodiak Island and the surrounding waters of the northeast Gulf of Alaska. This report completes the presentation of the results of our investigation of that system.

This research has involved three distinct phases. In the first (Wiens et al. 1979b), we used simulation models to estimate population energy flow patterns for the dominant breeding species in the Kodiak region. We found that Tufted Puffins<sup>1</sup> were the most important consumer species, in terms of their energy demands upon the system. We estimated that the puffin population consumed  $5.90 \times 10^9$  kcal during the course of the breeding season, compared with  $2.12 \times 10^9$  kcal consumed by the Black-legged Kittiwake population and  $1.73 \times 10^9$  kcal consumed by Glaucous-winged Gulls. Total energy demand by these three dominant species was thus estimated to be  $9.75 \times 10^9$  kcal during the breeding season, which converts (following the procedures of Wiens and Scott 1975) to 8,100 metric tons of prey. These values are nearly an order of magnitude less than those we calculated for the Pribilof

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<sup>1</sup>Scientific names of bird species are given in Appendix I.

system (Wiens et al. 1978a). The Kodiak values, however, do not include several major species, such as shearwaters and murre, that do not breed (at least at high densities) on Kodiak but that exploit the nearby waters, so the comparison is of doubtful value.

The second phase of the research involved an analysis of the distributional patterns of the dominant breeding species about Kodiak Island, and a statistical evaluation of the results of seabird censuses in the region (Wiens et al. 1980). Because of the heterogeneity in censusing circumstances and conditions, it was necessary to adjust the raw census values in various ways in order to synthesize the distributional patterns of the birds in the Kodiak area. Our analyses of the distributions of Black-legged Kittiwakes, Glaucous-winged Gulls, murre, Sooty Shearwaters, and Tufted Puffins indicated distinct regions of high and low densities. Some of the high-density areas were probably the result of chance encounters of large aggregations of individuals during censusing, but others were clearly associated with bathymetric features or nearby breeding colonies. In general, the areas around the Semidi and Barren islands, over Portlock North (the eastern end), and South Albatross banks, and the area between the Trinity Islands and Cape Ikolik appeared to be important foraging areas for these species, while Shelikof Strait and the eastern end of North Albatross Bank had consistently low densities, as did the off-shelf areas.

Our statistical analyses of the results of pelagic bird censusing in the Kodiak region was not encouraging. When densities were calculated from censuses in 20 x 20-km blocks of the region around Kodiak, our analyses indicated that only 6% of the area had been surveyed with sufficient intensity to permit the derivation of statistical confidence intervals about the mean density estimates. Of that proportion of blocks, only 3% had been sampled sufficiently enough that the upper confidence limits were within an order of magnitude of the calculated mean, even though the data were pooled over seasons to enhance sample sizes. Thus, while the at-sea censuses available to us at that time were sufficient to permit estimations of densities for the various blocks of ocean about Kodiak, we were generally unable to attach meaningful statistical significance levels to the spatial variations in the densities. Obviously, this lack of statistical validation of the distributional patterns that we (and others) have derived poses a serious constraint on any subsequent efforts to define areas of greater or lesser sensitivity to perturbations.

This report contains the results of the third phase of our research, which has concentrated on employing models to estimate the effects of various petroleum-related perturbation scenarios on mortality of birds associated with breeding colonies on Kodiak Island.

## B. The Data Base

Any modeling analysis is constrained by the nature of the data available as it related to the objectives of the analysis (see Section 11 of this report). Our analysis of the dynamics of the Kodiak seabird systems was constrained by the availability of detailed information on the demography of well-studied colonies and by the quality of the information regarding the distribution of the birds at sea. Partly for this reason, and partly on the basis of the results of our earlier analysis of the Pribilof Islands marine bird system (Ford et al. 1981), we adopted a simplified approach to modeling the Kodiak system. As a result, we required information on basic features of breeding colonies, such as size and location, and on the at-sea

distributions of birds. Colony data were provided for colonies in Sitkalidik Strait and the Chiniak Bight by U.S. Fish and Wildlife Service personnel (Pat Baird, Gerry Sanger, and Pat Gould), and were supplemented with information from the Catalog of Alaskan Seabird Colonies (Sowls et al. 1978). Because little information was available on many of the colonies listed in the catalog, we restricted our consideration to those colonies or colony-groups indicated in Fig. 1 (See also Table 1).

Table 1. Seabird colonies in the Kodiak area used in our modeling analyses (See Fig. 1). Colony names and locations (in parentheses) follow the notation of the Catalog of Alaskan Seabird Colonies (Sowles et al. 1978).

Colony (location)	Numbers of Individuals (x 103)	
	Colonies	Total
<b>TUFTED PUFFIN</b>		
1. Flat Is. (033 002)	30	30
2. Cathedral Is. (034 005)	12	12
3. Ladder Is. (034 007), Ermine Pt. Is. (034 060), Dusk Is. (034 061)	6, 1, 1.5	8.5
4. Gull Pt. (034 010), Long Is. (034 067)	5, 2*2	7.2
5. Chiniak Is & Rks (034 014)	7	7
6. Kekur & Middle Is. (034 015), Svitolak & Utesistoi Is. (034 016), Queer Is. (034 017), Viesoki Is. (034 018), Puffin Is. [1] (034 022), Jug & Kalsin Is. (034 047), Zaimka Is. (034 087), Cliff Is. (034 088), Bird, Kulichkof, Holiday & Popof Is. (034 089), Long Is. & Islets (034 090)	.6, .9, 1.3, 1.8, 1.3, .7, 2.1, .8, .2, 1.7	11.4
7. The Triplets (034 046)	60	60
<b>BLACK-LEGGED KITTIWAKE</b>		
1. Flat Is. (033 002), Jap Bay (033 003)	1, 3	4
2. John Is. (034 003), Middle Triangle (034 050)	3, .4	3.4
3. Cathedral Is. (034 005)	4.1	4.1
4. Inner Right Cape (034 059), Ermine Point Is. (034 060), Dusk Island (034 061)	1.4, 5.5, 1.7	8.6
5. W. Boulder Bay (034 008)	40	40
6. Chiniak Is. & Rks (034 014)	9.8	9.8
7. Kekur & Middle Is. (034 015), Svitolak & Utesistoi Is. (034 016), Viesoki Is. (034 018), Bird, Kulichkof, Holiday & Popof Is. (034 089), Gibson Cove (034 099)	1.2, 2.5, 2.6, .4, .4	7.1
8. Anton Larsen Bay (034 097), N. Barbara Cove Point (034 028), Whale Is. (034 044)	1.5, 2, 4	7*5

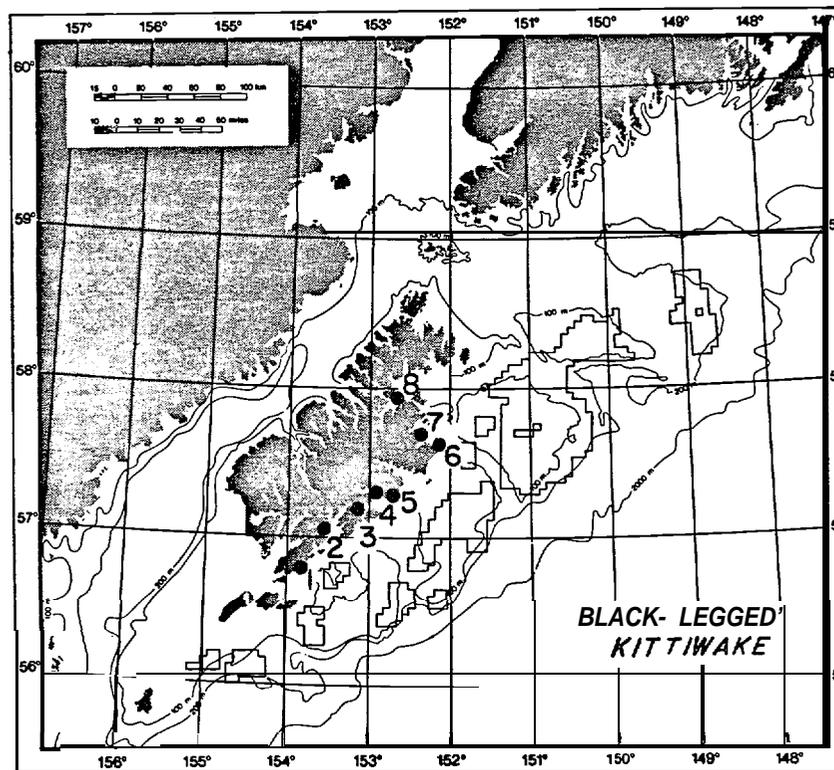
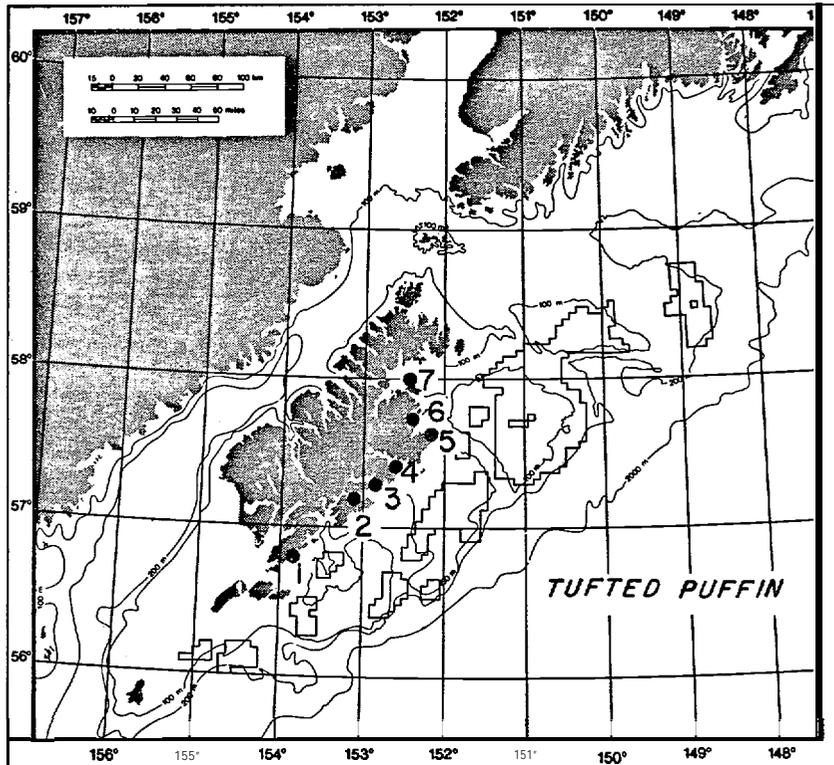


Fig. 1. Locations of colonies of Tufted Puffins (above) and Black-legged Kittiwakes (below) considered in our analysis of oil-spill impacts upon seabird populations. The parameters for these colonies are given in Table 1.

A large array of marine birds species occurs at these colonies and in the waters adjacent to Kodiak Island. Many of these, however, occur at low densities (e.g. Arctic Terns, Pelagic Cormorant), are primarily associated with island groups other than Kodiak itself (e.g. Common and Thick-billed murre), or are not directly associated with the breeding colonies on Kodiak (e.g. Sooty Shearwaters). Accordingly, we restricted our attention to the two major breeding seabirds on Kodiak, Tufted Puffins and Black-legged Kittiwakes. Collectively, these two species contribute roughly 94% of the birds breeding in the Kodiak colonies that we considered.

Information on the distribution of the birds at sea in the areas adjacent to Kodiak was obtained from shipboard and aerial transects conducted by U.S. Fish and Wildlife Service personnel during 1975-1977. These data were included in our earlier analysis of distributional patterns (Wiens et al. 1980). That analysis evaluated distributional patterns by estimating the densities of species in 10 km x 10 km blocks of ocean area. We used the same information to conduct the model analyses reported here, except that distributions were combined into 20 km x 20 km blocks. This change was necessitated by computer limitations: the run time and size of the model increase exponentially with the number of spatial blocks that must be considered. We believe that this slightly coarser spatial scale is appropriate for the sort of spill scenarios we consider.

### C. Model Structure

In the present analyses we have used a modified version of the modeling approach that was employed for the Pribilof Islands (Ford et al. 1982). The Pribilof analysis indicated that the effects of oil spills on mortality of nestling birds had a relatively minor long-term effect on population sizes and recovery rates as compared with adult mortality. We therefore simplified the model approach to consider only adult mortality. While sacrificing some elegance and fine-scale resolution, this approach is more appropriate for systems in which relatively few data on reproductive and demographic parameters of species in specific colonies are available. In addition, we use a rectangular coordinate system to model the spatial distributions of the birds rather than the polar coordinate system employed in the Pribilof model. This change was required by the greater complexity of the Kodiak and mainland coastlines and the larger number of spatially separated colonies that we considered.

The Kodiak model is based upon 12 parameters, which represent three categories: (1) input parameters for which we have a reasonable empirical basis for their values, (2) input values for which we have little or no empirical basis for their estimation and that are part of the Monte Carlo analysis, and (3) values based upon intermediate calculations within the model itself. These parameters may be defined as follows:

#### Category I.--Empirical Input Values

- $C_j$  The population size of a species in colony j.
- $s$  Flight speed (km rein<sup>-1</sup>).
- $A_i$  The area of sector i (km<sup>2</sup>).
- $A'_i$  The area of sector i covered by an oil spill (km<sup>2</sup>).
- $L$  Daylength (rein).
- $'ij$  The mean number of birds from colony j in sector i, where i is a 20 km x 20 km block defined in rectangular coordinates.

## Category 2.--Monte Carlo Input Values

- T Mean trip time (rein).  
p The probability per minute that foraging in a spill region will lead to fatal spill contact ( $rei^{-1}$ ).  
 $\tau$  The time required for an area depleted of birds by spill mortality to return to an equilibrium density of birds.

## Category 3.--Internally Calculated Parameters

- $\bar{v}_{ij}$  The distance from colony j to the midpoint on sector i (km).  
 $\bar{t}_{ij}$  The time spent by birds from colony j foraging in sector i (rein).  
 $\bar{m}_{ij}$  The mortality suffered by colony j in sector i (birds day<sup>-1</sup>).

Our modeling approach is based on the following major assumptions:

Assumption 1.--There exists a foraging distribution of birds at any time that is in a state of "equilibrium." This means that although individuals may shift the focus of the activities from day to day, the density of birds remains constant within a given area. The Pribilof model makes a similar assumption, except that the equilibrium level is determined by the relation between the "food supply" and the absolute number of birds, and when perturbations occur that balance is used to readjust the foraging distribution. In the Kodiak model, equilibrium is determined only by the proportion of a given colony that forages in a given sector (see Figs. 2 and 3). Thus, if the population of a colony were to be halved, the equilibrium number foraging in all sectors would similarly be halved. This means that we do not take into account density-dependent depletion of food supply, as was done in the Pribilof model. The problems with the complexity of the Kodiak area and the data base, however, preclude that sort of analysis in the Kodiak system.

Assumption 2.--The equilibrium proportions of birds in the sectors are constant in time. This, of course, is patently absurd, but it should not affect estimates of mean mortality rates. It does, however, significantly lower estimates of the variability in kill rates, which are of considerable importance. The available data base would need to include far more replication of transects within blocks than it does, or alternatively some sort of a priori stratification (zonation) scheme would be necessary in order to relieve us of this assumption.

Assumption 3.--Birds forage throughout the daytime period.

Assumption 4.--Birds fly in straight-line flight between the colony and their foraging areas. This is a conservative assumption, as it implies that the birds spend the maximum proportion of their time in areas in which they are vulnerable to oil spills.

Assumption 5.--The probability of fatal oil contact is constant per unit time while foraging in the area of the spill.

Additional assumptions will be discussed where appropriate in the following narrative.

Assuming linear flight to and from colony j to the foraging area i, the mean time spent per day foraging in i by birds from j is:

$$\bar{v}_{ij} = (T - 2D_{ij}/S) (L/T)$$

where the first term,  $T - 2D_{ij}/S$ , is the time spent foraging per trip, and  $L/T$  is the number of trips per day. The expected time spent in a spill is the product of  $v_{ij}$  and the proportion of  $i$  that is covered by the spill,  $A_i'/A_i$ . The probability of death per day for birds from  $j$  utilizing  $i$  is:

$$(1 - \rho) \exp (F_{ij}A_i'/A_i)$$

The total number of birds from  $j$  dying in  $i$  per day is the product of the probability of death per day and the number of birds utilizing  $i$ . The number of individual birds utilizing  $i$  will be greater than  $N_{ij}$  because each individual spends only part of its time in  $i$ , and the remainder in transit between  $j$  and  $i$ . The number of individuals is estimated as  $N_{ij}T/(T - 2D_{ij}/S)$ . Thus, if the observed density was 300 birds, trip time was 200 min, and  $(T - 2D_{ij}/S)$  was 10, the number of individuals utilizing  $i$  would be 600 birds.

Total expected mortality is then the product of the daily probability of death and the number of birds at risk:

$$v_{ij} = (1 - \rho) [\exp (F_{ij}A_i'/A_i) | N_{ij}T/(T - 2D_{ij}/S) ] .$$

The new density in  $i$  is thus  $N_{ij} - M_{ij}$ , and the new colony size is  $C_j - \sum_i M_{ij}$ . The following day  $M_{ij}$  is reset, assuming that at equilibrium the proportion of  $j$  that is utilizing  $i$  is the same as that prior to the perturbation. Equilibrium is not achieved in only 1 day, however, but rather roves a fraction  $(1/\tau)$  of the distance from the perturbed value to the equilibrium value. Each day, the total mortality is assessed as  $\sum_j M_{ij}$ .

In order to use this model to estimate the mortality of breeding birds that might be expected from a given oil spill scenario, initial estimates of parameter values must be obtained. In our application of this model to the Kodiak kittiwake and puffin populations, this was accomplished as follows.

$C_j$  - Colony size estimates were based on the values reported in the Alaskan Seabird Colony Catalog (Sowles et al. 1978). These were combined to give a total "colony" value when several nearby colonies were grouped together in our analysis (see Fig. 1 and Table 1).

$S$  - Flight speeds were based upon estimates made by Ford and Heinemann on St. Paul Island in the Pribilofs in 1978 (Wiens et al. 1979a, Ford et al. 1982).

$A_i$  - Sector areas were based upon the gridding scheme that we adopted for this analysis. As each sector was 20 km x 20 km, its area equaled 400 km<sup>2</sup>.

$L$  - Average daylength was assumed to be 900 min; this value was also used in our earlier analyses (Wiens et al. 1979a, Ford et al. 1982).

$v_{ij}$  - The procedures used to calculate the densities of birds at sea from transect survey results were described in detail previously (Wiens et al. 1980). The values obtained in the earlier analysis, which was based upon 10 km x 10 km sectors, were converted to the appropriate values for the 20 km x 20 km sectors used in the present analyses. It was also necessary, however, to estimate the proportion of the birds in each sector that originated from each colony. The estimation of colony-specific foraging distributions was based on the assumption that a given area of water will be dominated by the nearest colony, and that individuals will move the

shortest possible distance to their foraging site. As noted above, minimization of flight time is a conservative assumption. We begin with the estimated values of  $N_i$  and  $C_j$ . An incremental group of birds (i.e. 100) is "released" from each colony. Each group roves to the nearest unoccupied sector relative to its colony. This process is iterated until a given sector is filled (that is, when the sum of the increments is equal to  $N_i$ , the estimated density of birds in the sector). At the next step, the incremental flight of birds is directed to the next nearest sector; this procedure is repeated until all the sectors are filled to their observed densities. The colony-specific foraging distributions generated for each species in this manner are depicted in Figs. 2 and 3).

This approach thus assigns proportions of birds from a colony to sectors in such a way that individual transit time is minimized. This procedure tends to bias the results in the direction of higher mortalities, as birds will spend more of their time foraging (and thus potentially vulnerable to spill contact) than in transit.

$A'_i$  - The area of a sector covered by a spill in a given scenario was derived from the results of the spill trajectory analysis, which is described below.

T - Although some data on trip times of individuals from nest sites to foraging areas and back were available for both Tufted Puffins and Black-legged Kittiwakes from the Sitkalidik Strait colony, we were unable to use them. Our estimates of time spent moving between colonies and foraging areas based upon the distributional data indicated minimal transit times that were 2-3 times greater than the total trip times observed for both species. We therefore concluded that these data were not representative, and based our estimates of trip times on our experience on the Pribilof Islands. Using estimates of mean minimal transit times, we assumed that birds spent 30-70% of their foraging trips in transit; we used 50% as our best approximate ion.

For this input parameter (and for  $p$  and  $-c$ ), however, we do not have a firm empirical base from which to estimate values. This does not mean that we know nothing about them, but it does imply that what we do know is perhaps best described as an "educated guess." There are several alternative approaches to dealing with this uncertainty. First, we could simply make our "best guess" for a parameter value, and use that. This has the disadvantage that we lose sight of the potential variability in the outcome due to our uncertainty, and it thus ignores the problem of sensitivity. Another approach would be to estimate the upper and lower limits of possible values for the parameter. The model could then be run repeatedly (Monte Carloed) using different parameter values selected from a uniform distribution of possible values, where the endpoints of the uniform distribution are defined by the upper and lower limits of our guesses. This technique is an improvement in that it does not mask the variability in the outcome due to uncertainty, but it perhaps has the disadvantage of overemphasizing the extreme possible values. Our approach is to use a triangular ("house top") probability density function in which the peak is the "best guess" and the endpoints are the estimated maximum and minimum parameter values (Fig. 4). This approach preserves the potential variability in the estimated parameter values without losing sight of the fact that, by definition, the "best guess" is the most likely value. Thus, in determining values for trip time, we conducted Monte Carlo runs using a house-top distribution in which the range of reasonable values (30-70% of the mean transit time) defined the endpoints of the distribution and 50% of the mean transit time was the mode.

$p$  - The probability of fatal spill contact per minute was varied in the same manner as T, using 0.0 and 0.00264 as the range and 0.002 as the "best guess." These values were based upon the analyses of Wiens et al. (1979a).

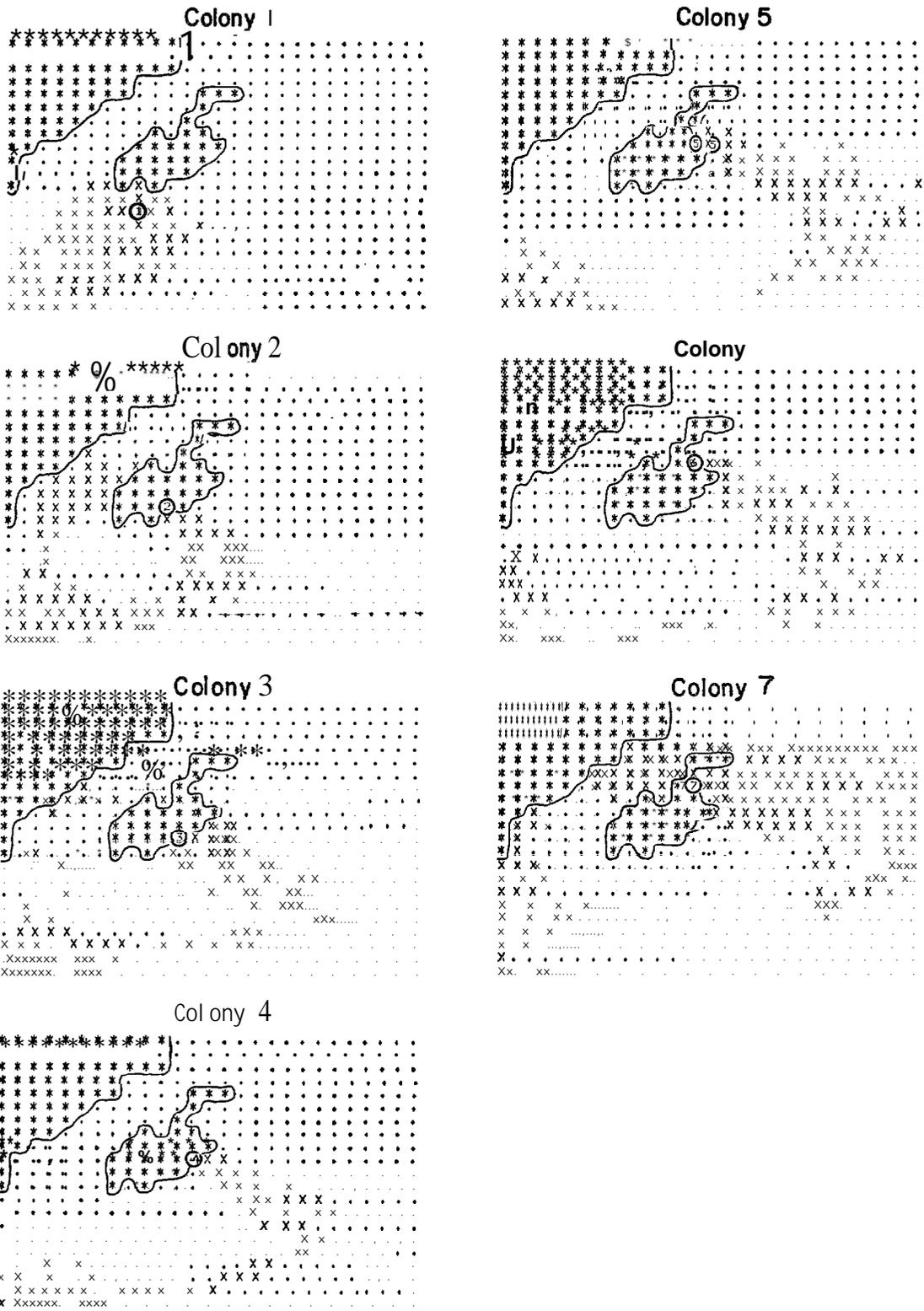


Fig. 2. Projected foraging distributions for individuals breeding in each of the Tufted Puffin colony locations shown in Fig. 1. In these computer-generated plottings, the stars represent grid blocks located on the mainland (upper left corner) or Kodiak Island (center) ; Xs represent grid blocks in which foraging occurred, and dots represent grid blocks in which little or no foraging by birds from a specified colony occurred. See text for derivation of these maps.

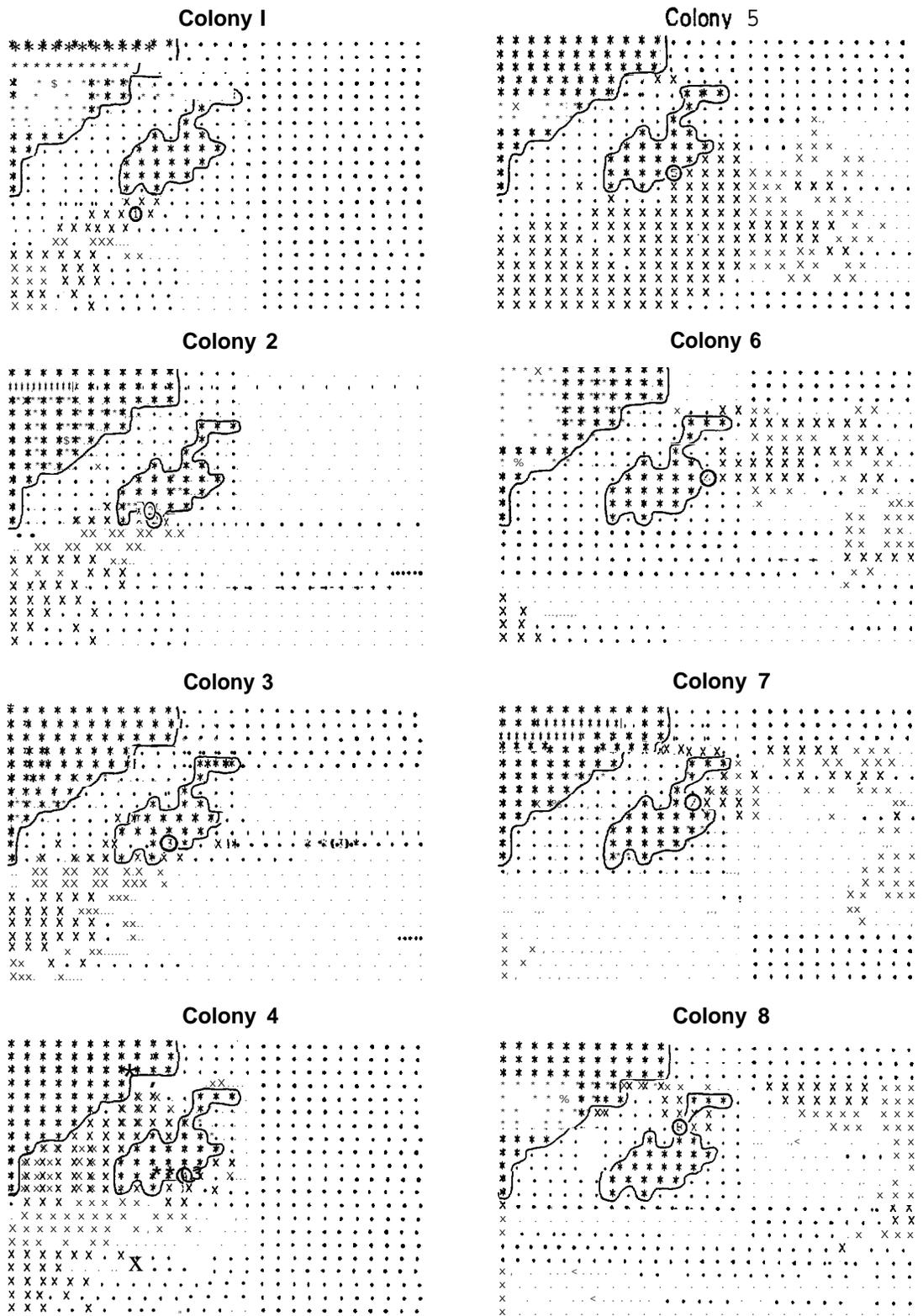


Fig. 3. Projected foraging distributions for individuals breeding in each of the Black-legged Kittiwake colony locations shown in Fig. 1. See Fig. 2 for explanation.

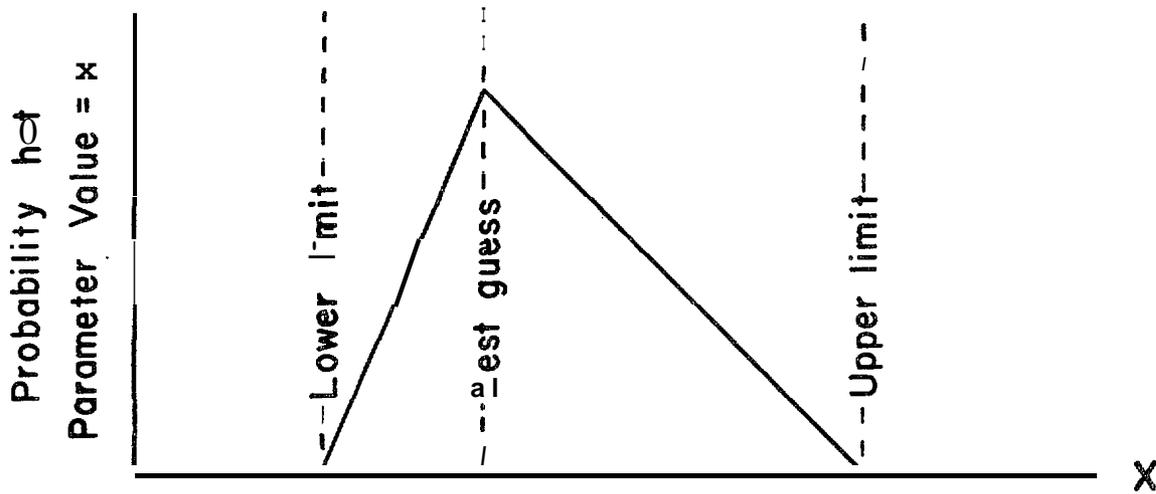


Fig. 4. The "housetop" distribution of parameter values employed in sensitivity tests. "X" represents a range in parameter values, with lower and upper limits, and a "best guess" value determined from field data, literature reports, or intuition. The curve gives the probability distribution of values from which individual parameter values were randomly drawn in Monte Carlo simulations, as described in the text.

$\tau$  - Values for this parameter were also estimated using Monte Carlo procedures. Time to equilibrium was estimated to range between 1 and 10 days, with 5 days being the "best guess" (Wiens et al. 1979a).

Spill trajectories.---Model runs were made using output from the USGS spill trajectory model (W. Samuels, pers. comm.). Spill trajectories were provided in the form of point locations at 3-h time steps, starting from four different spill launch points distributed evenly through the lease tract on a north-south gradient (Fig. 5)\* The trajectory model is stochastic, so we used 10 sample trajectories per launch point. Because wind and current vectors vary on a seasonal basis, we used two sets of trajectories, one for spring and another for summer. Thus, there were 4 (launch points) x 2 (seasons) = 8 scenarios. For each launch point-season scenario, there were 10 trajectories simulated.

We assumed that each spill was a circular area of 50 km<sup>2</sup>; this defined the parameter value for  $A_i$ , the area of sector  $i$  covered by a spill. Spills were assumed to persist without change until they hit land, moved beyond the geographic limits of the model, or had been in existence for 30 days.

To evaluate the sensitivity of the model to our estimates of the values of the parameters  $T$ ,  $p$ , and  $\tau$ , we also varied these in a Monte Carlo fashion. For each of the 80 (4 x 2 x 10) trajectories, we made five model runs using different values of  $T$ ,  $p$ , and  $\tau$  that were selected at random from the previously described distributions of parameter values. Thus, each launch point-season scenario entailed a total of 10 x 5 = 50 simulation runs. Each of the frequency distributions that we present below (Figs. 6 and 7) is this based upon five versions of 10 possible trajectories.

#### D. Results

The estimated mortality of adults accompanying each of the spill scenarios depicted in Fig. 5 is given in Tables 2 and 3. Several features are apparent. First, the mortality rates are generally quite low, usually less than 1% of the birds estimated to be present at a colony. Second, mortality of Tufted Puffins is generally greater than that of Black-legged Kittiwakes for a given spill scenario. This is a consequence of the differences in the foraging distributions of the species, as kittiwakes forage over a border area about a colony (Figs. 2 and 3), and the probability of individual encounter with oil in a restricted spill is thus less for kittiwakes than for puffins. Third, the proportion of a colony suffering mortality is generally a function of the distance from the colony to the spill launch point, but this is influenced in important ways by the pattern of foraging distribution of the birds associated with a colony. Thus, for Tufted Puffins, birds from colony 1 suffer little mortality in any of the spill scenarios, even though two launch points (A10 and A11) are not far from the colony. Colony 2 is most strongly affected by spill A11 in spring, while colony 3, located not far away, is most sensitive to spills originating from point A7, especially during summer. A glance at Fig. 2 indicates that these differences are associated with the foraging distribution patterns assigned to birds from these two colonies. Colony 4, with a foraging distribution similar to that of colony 3, is likewise most sensitive to spills from point A7. Colonies 5 and 6 are most strongly affected by summer spills from A3, but are influenced only slightly less by spring spills from A7. Colony 7 is by far the most sensitive of the puffin colonies, suffering in excess of 10% mortality for spring and summer spills originating at point A3, and mortality greater than that of any other colony with spring and summer spills from A7 and spring A10 spills. The wide foraging distribution of birds assigned to this colony (Fig. 2) is at least

**Table 2.** Mean mortality (numbers of adults killed) of Tufted Puffins by colony and oil-spill scenario. Percentages of total colony population are given in parentheses.

Spill Scenario	Colony (size)						
	1 (30,000)	2 (12,000)	3 (8,500)	4 (7,000)	5 (7,000)	6 (11,500)	7 (6,000)
A3 Spring	12 (0.04)	6 (0.05)	9 (0.11)	7 (0.10)	16 (0.23)	26 (0.23)	650 (10.83)
A3 Summer	0 (0.00)	21 (0.18)	54 (0.64)	55 (0.79)	132 (1.89)	218 (1.90)	762 (12.70)
A7 Spring	41 (0.14)	130 (1.08)	149 (1.75)	90 (1.29)	88 (1.26)	142 (1.23)	279 (4.65)
A7 Summer	24 (0.08)	88 (0.73)	176 (2.07)	140 (2.00)	40 (0.57)	71 (0.62)	179 (2.98)
A10 Spring	229 (0.76)	140 (1.17)	46 (0.54)	27 (0.39)	15 (0.21)	19 (0.17)	130 (2.17)
A10 Summer	120 (0.40)	15 (0.13)	40 (0.47)	39 (0.56)	23 (0.33)	33 (0.29)	76 (1.27)
A11 Spring	150 (0.50)	171 (1.43)	42 (0.49)	17 (0.24)	0 (0.00)	10 (0.09)	0 (0.00)
All Summer	348 (1.16)	127 (1.06)	33 (0.39)	3 (0.04)	0 (0.00)	2 (0.02)	0 (0.00)

Table 3. Mean mortality (numbers of adults killed) of Black-legged Kittiwakes by colony and oil-spill scenario, Percentages of total colony population are given in parentheses.

Spill Scenario	Colony (size)							
	1 (4,000)	2 (3,500)	3 (4,000)	4 (8,500)	5 (40,000)	6 (10,000)	7 (7,000)	8 (7,500)
A3 Spring	0 (0.00)	0 (0.00)	1 (0.03)	0 (0.00)	57 (0.14)	138 (1.38)	58 (0.83)	42 (0.56)
A3 Summer	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	144 (0.36)	10 (1.00)	20 (0.29)	20 (0.27)
A7 Spring	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	194 (0.48)	3 (0.03)	0 (0.00)	0 (0.00)
A7 Summer	2 (0.05)	0 (0.00)	2 (0.05)	5 (0.06)	202 (0.51)	27 (0.27)	8 (0.11)	0 (0.00)
A10 Spring	0 (0.00)	0 (0.00)	4 (0.10)	22 (0.26)	340 (0.85)	18 (0.18)	0 (0.00)	0 (0.00)
A10 Summer	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.02)	101 (0.25)	8 (0.08)	7 (0.10)	0 (0.00)
All Spring	1 (0.03)	0 (0.00)	6 (0.15)	0 (0.04)	134 (0.09)	0 (0.00)	0 (0.00)	0 (0.00)
All Summer	7 (0.18)	1 (0.03)	14 (0.35)	8 (0.09)	196 (0.49)	0 (0.00)	0 (0.00)	0 (0.00)

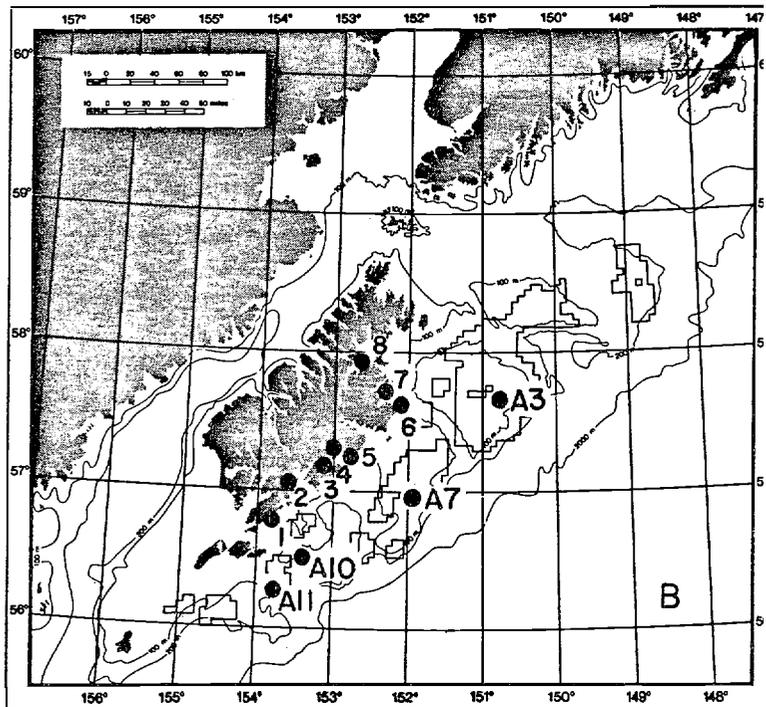
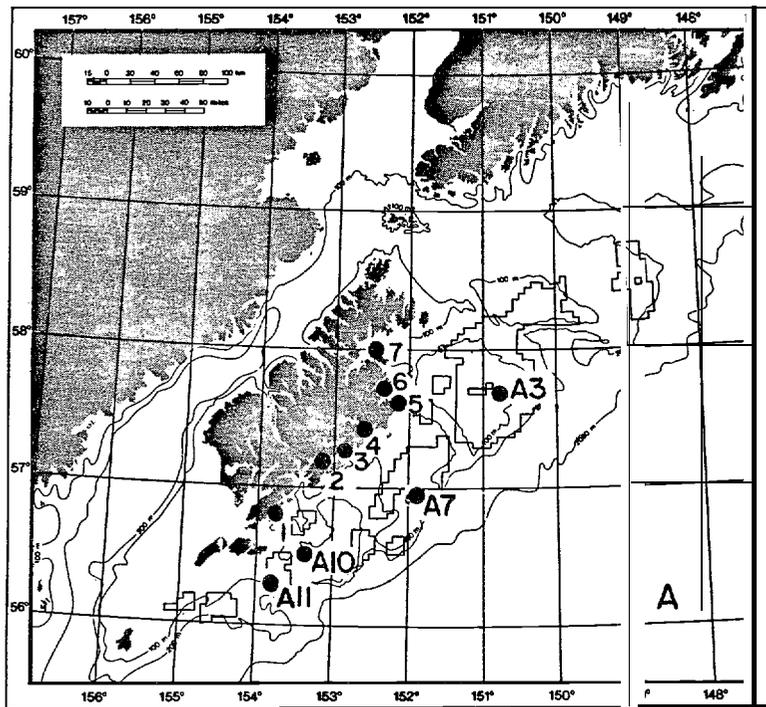


Fig. 5. Launch points for oil spills (A3-Ail) in relation to the locations of Tufted Puffin (A) and Black-legged Kittiwake (B) colonies considered in our analyses.

partly responsible for these mortality patterns. For Black-legged Kittiwakes, the only spill scenarios that effected in excess of 1% mortality were spring and summer spills from A3 for colony 6.

These figures relate to the effects of the different spill scenarios on specific breeding colonies. If we instead ask what degree of mortality of puffins and kittiwakes from all of these colonies is associated with each of the spill scenarios, we find that in only one situation (spring runs of spills from launch point A7 on puffins) is the overall mortality in excess of 1% of the breeding population (Table 4). In general, then, none of these spill scenarios seems to exert a powerful direct effect on survivorship of breeding birds in these colonies, given the constraints and assumptions of our modeling approach. One must remember, however, that even small alterations in annual survivorship of adults can affect the age-structure of a population, and increase its susceptibility to devastating long-term effects of one-time perturbations of greater magnitude (Wiens et al. 1979a, Ford et al. 1982).

The values presented in Tables 2-4 all represent average mortalities associated with the 50 runs of each spill scenario. Although these are instructive in a general sense, they may be somewhat misleading, in that they do not consider the fact that the mortality accompanying some runs may be substantially greater than that associated with others. In Figs. 6 and 7 we present the frequency distributions of total mortalities of the two species (summed over all colonies) for the 50 runs of each spill scenario. For some (e.g. A3 spring and A7 summer for puffins), the mortality estimates are more or less normally distributed about the mean. For others, however, the distributions are distinctly skewed. Scenarios A10 and (especially) All exhibit frequency distributions with a preponderance of low or zero-mortality values. Others, such as A3 summer and A7 spring, contain a substantial number of individual runs predicting rather high mortalities for each species, even though the overall average mortalities accompanying these scenarios are not especially great (Table 4). Thus, on this basis, we attribute somewhat greater potential impact to spills originating from the areas of points A3 and A7, at least some of the time.

One important source of variation in our estimates of spill-associated mortality is that associated with our uncertainty in the values of the parameters  $T$ ,  $\rho$ , and  $\tau$ , which were Monte Carloed in our simulation runs. In an attempt to assess the proportion of the variance in our estimates of mortality that is associated with this parameter uncertainty, we conducted an ANOVA of the 50 simulated runs for each scenario, for each of the two species. Table 5 presents the proportion of the variance in estimated mortalities attributed to parameter uncertainty in the model. The apparent importance of this variation (and thus in the precision with which we estimate the values of  $T$ ,  $\rho$ , and  $\tau$ ) varies considerably, but is seemingly substantial for spring spills at launch point A3 and summer spills from points A7 and All for puffins, and for spring and summer spills from A7 and spring spills from A3 and A10 for kittiwakes. These are not generally those spill scenarios that accounted for the greatest proportionate mortality of the species (Table 4), perhaps alleviating somewhat our concern about the need for accuracy in the estimation of these parameters. Nonetheless, they may contribute substantially to the variation in our estimates of the mortality potentially associated with given spill events.

#### E. Discussion

As the modeling approach we have followed in treating spill-related mortality of seabirds in the Kodiak system is a simplification and extension of that employed in

Table 4. Mean mortality (number of adults killed) of Tufted Puffins and Black-legged Kittiwakes for all colonies combined, by spill launch point.

Spill Origin	Tufted Puffin		Black-legged Kittiwake	
	Spring	Summer	Spring	Summer
A3	725 (0.88)	347 (0.42)	296 (0.35)	284 (0.45)
A7	<b>991</b> <b>(1.21)</b>	<b>718</b> <b>(0.88)</b>	<b>430</b> <b>(0.51)</b>	<b>245</b> <b>(0.29)</b>
A10	599 (0.73)	345 (0.42)	386 (0.46)	118 (0.14)
Al 1	<b>288</b> <b>(0.35)</b>	<b>512</b> <b>(0.62)</b>	<b>145</b> <b>(0.17)</b>	<b>228</b> <b>(0.27)</b>

Table 5. Proportion of the variance in number of individuals killed that is attributable to uncertainty in the model parameters. See text for explanation.

Spill Scenario	Tufted Puffin	Black-legged Kittiwake
A3 Spring	0.46	0.23
A3 Summer	0.15	<b>0.11</b>
A7 Spring	0.11	0*35
A7 Summer	0.24	0.39
A10 Spring	0.13	0.33
A10 Summer	0.04	0.05
All Spring	0.17	0.07
Al 1 Summer	0.29	0.12

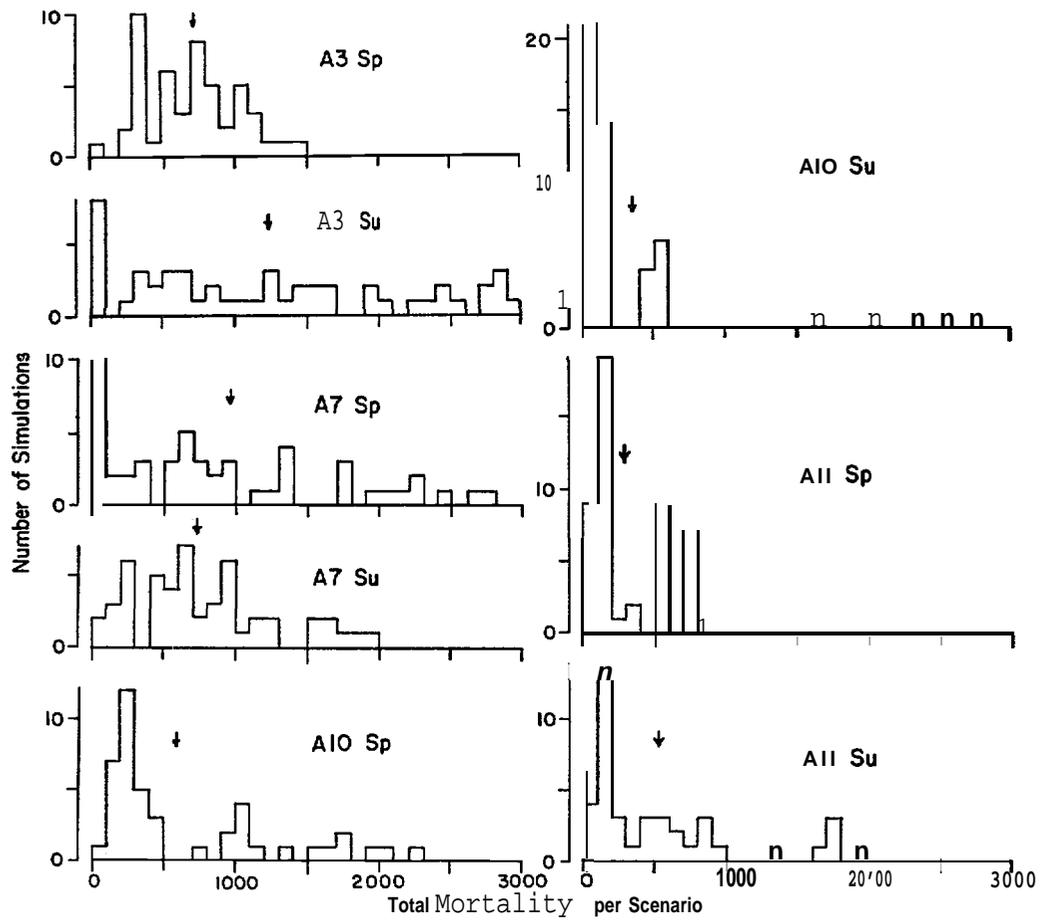


Fig. 6. Frequency distributions of Tufted Puffin adult mortality (number of individuals killed) associated with 50 simulations of each of 8 oil-spill scenarios. The arrow indicates the average mortality. See text for description of the procedures.

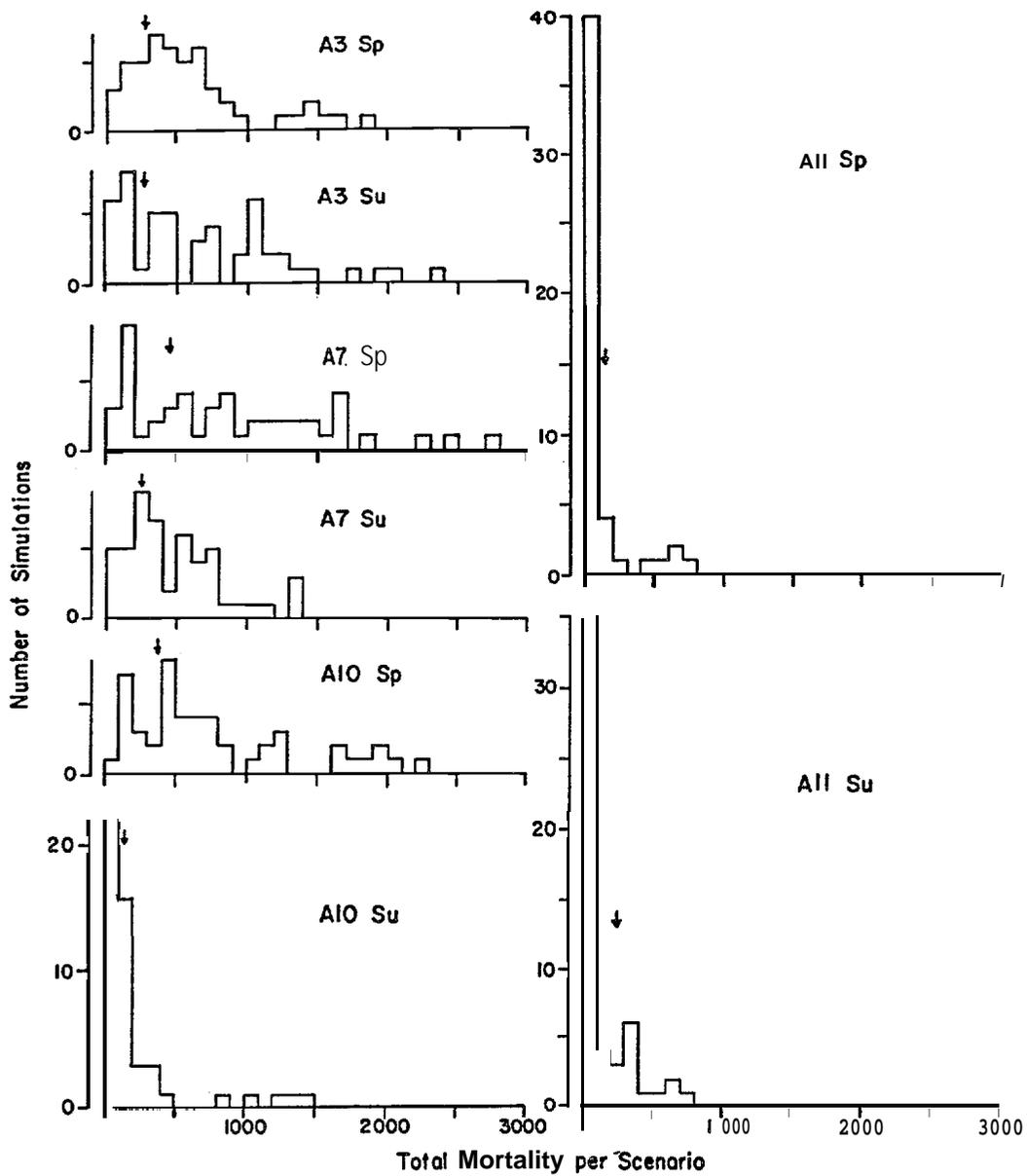


Fig. 7. Frequency distributions of Black-legged Kittiwake adult mortality (number of individuals killed) associated with 50 simulations of each of 8 oil-spill scenarios. The arrow indicates the average mortality. See text for description of the procedures.

our earlier analysis of the Pribilof Islands system, it seems appropriate to compare the models and their results. The model we developed for the Pribilofs could almost be considered an art form, in that it represented an attempt to portray the actual form of biological patterns, and incorporated a good deal of elegance. The slimmness of the data base from Kodiak for many of the parameters of that model precluded its direct application to the Kodiak system, and therefore a simplified modeling approach was necessary. In a sense, however, the Pribilof model represented a necessary ontogenetic stage in our modeling development, as we were able to employ the results of analyses using that model to determine which functions could be dispensed with or modified considerably with minimal effects on the overall model predictions. It was on the basis of the Pribilof results, for example, that we felt justified in omitting the chick growth/survivorship features of the Pribilof model in developing the Kodiak model. We thus assumed that chick mortality results from adult mortality, not from food deficiency of the young. Given these and other simplifying assumptions that we have made in its development (see above), the Kodiak model seems to provide a reasonable approach to producing general projections of the mortality that might accompany specific spill scenarios, although it lacks some of the biological richness of the Pribilof model. Both approaches, of course, are constrained by our inability to verify the model estimations directly, by comparing model projections against the mortality patterns accompanying actual spills. Until controlled spill experiments and attendant monitorings of the accompanying mortality of marine birds are undertaken, our projections must remain in the realm of educated (albeit sophisticated) guesses.

PART II. ASSESSING THE SENSITIVITY OF MARINE BIRDS TO OIL SPILLS:  
INFORMATION GAPS AND PRIORITIES

A. Introduction

Industrialized societies are demonstrating an increasing dependence on and demand for petroleum. As these demands grow, it is inevitable that perturbations of the marine systems that are used for producing or transporting petroleum will increase in frequency and magnitude. As such seepages, spills, blowouts, wrecks, and the like are likely to have major repercussions on the biota of marine systems, it is imperative that we be able to predict their consequences and plan petroleum-related activities and development accordingly. Unfortunately, at present we seem largely restricted to after-the-fact assessments of damage once the perturbations have occurred, and while these may lead to some understanding of the dynamics and consequences of oil pollution in oceanic systems, they do not provide much guidance in developing means to minimize such effects.

We have recently attempted to approach the problem of predicting the effects of petroleum-related perturbations on colonially breeding marine birds through the development of mathematical models (Ford et al. 1982). This exercise led us to consider the existing information on marine birds, their activities, and their resources from a perspective that is not commonplace. In the process, we became aware of gaps in the available information, sampling problems, and inefficiencies in the approach of most studies of marine birds that severely constrained our attempts to structure realistic and intelligent models. Because we believe that these problems are likely to thwart any attempts to develop a priori means of assessing petroleum-related perturbation effects, and because some of the problems and deficiencies might be reduced if field investigations were more cognizant of them, we believe that a discussion of the difficulties that we have encountered is warranted. In this paper we will briefly describe our modeling approach, indicate the sorts of

data that are required in the model structure and the problems associated with obtaining reliable information on each, and assign provisional priorities to our information needs.

## B. Model Structure

The models we have developed (Ford et al. 1982, Part I of this report) predict the mortality that might be expected in colonially breeding seabirds (murre, puffin, and kittiwake) if a portion of the ocean area about the breeding colony were to experience a pollution event (a spill, in the examples we have considered). Such mortality may be of two kinds: direct mortality of adults caused by their encounter with the spill, and indirect mortality of offspring caused by the death of their parent(s) or by diminished growth, a consequence of the redistribution of foraging birds away from the spill area and the accompanying decrease in their rate of food delivery to the young. These mortality effects are expressed through the operation of a demographic submodel, which projects the number of individuals present in each of several age classes of a population at any point in time as a consequence of immigration, reproduction, emigration, growth, and mortality. Survivorship of the young is modeled as a function of the food (energy) delivery rate of the adults in relation to the energy demands of the chicks at given phases of their growth.

Food delivery rates and direct mortality via spill encounter by adults are projected through a foraging submodel. This submodel derives a distribution of birds from the population in the ocean area about the colony by considering daily movement patterns of foraging birds in relation to projected resource levels in various areas. Using optimality assumptions, we presume that birds will forage so as to minimize the length of time spent in foraging trips (trip time). Trip time may then be considered as a function of the distance from the colony to the foraging area, flight speed, the rate of food capture while foraging, and the overall energy demands (adult + young) that must be satisfied on a daily basis. Breeding individuals thus must obtain more food while foraging than adults without young, as they must balance both their own and their chicks' energy demands. Food capture rate is assumed to decline with increasing density of birds present in an area, as greater densities should lead to either localized depletion of food resources or interference, increasing the birds' search time. The spatial distribution of individuals at sea under conditions of optimal foraging (minimal trip time) should thus reflect a compromise between seeking out areas of high resource abundance and avoiding areas of high densities of foraging birds.

The effects of oil spill perturbations are then modeled by effecting a reduction in food supply and a proportionate direct mortality of adults in areas affected by the spill. Birds that do not suffer direct mortality must shift their foraging to other areas, and because the previous distribution was defined as optimal, this shift will lead to a reduction in foraging efficiency (greater costs of foraging associated with reduced prey capture rates in the new area) and an increase in trip time. This, in turn, will reduce the rate of food delivery to the young, affecting their growth rate and leading to mortality of the young if the growth rate falls below survival levels.

These submodels predict the short-term consequences of a specified perturbation for populations of breeding seabirds. Because the perturbation effects mortality of individuals, however, there will in addition be long-term results, as the mortality will reduce population density and alter the age structure of the population. In

another model, we evaluate these long-term effects by using the mortality rates projected from the short-term model as inputs to a simple set of population dynamics algorithms. Given information on the age-dependence and density-dependence of fecundity, mortality, and emigration and immigration rates in an unperturbed population, we can project the length of time required for a population to return to an equilibrium age structure and size following a spill event, or the magnitude of perturbation beyond which the population is unlikely to be able to recover and will suffer local extinction.

### c. Information Needs

This modeling approach provides general predictions of the likely response of marine bird colonies to perturbations in the oceanic areas about the colony. The models are built upon details of the biology of the species, and as such, they are realistic and potentially quite useful. The predictions that emerge however, are limited in their accuracy by the levels of precision and accuracy of our knowledge of the basic biological parameters on which the models are founded. Unfortunately, there are some dismaying gaps in our knowledge of these systems, and some problems in the use of the information that does exist. These indicate that conventional field studies of marine birds have not addressed some important aspects of seabird biology and have perhaps addressed others incorrectly. We therefore discuss the information requirements of our modeling approach and the status of the information that is available to fill our needs. In Table 6 we summarize the status of available information for the critical model parameters for two Alaskan situations that we have modeled, and for the seabird literature in general.

Table 6. Estimations of the quality and availability of data for various parameters of seabird biology required to model the sensitivity of populations to oil spills, and an importance rank (research priority) for each.

Parameter	Quality of Data <sup>a</sup>			Importance rank <sup>b</sup>
	Pribilof Islands	Kodiak Island	In literature	
Population (colony) size	3	2	1-3	3
Time of occupancy	3	2	1-4	1
Population age structure and % breeding	1	0	0-2	2
At-sea densities	2	1	1	3
Food availability in foraging areas	1	0	0-1	2
Reproductive phenology	4	3	2-4	1

Table 6 continued

Parameter	Quality of Data <sup>a</sup>			Importance rank <sup>b</sup>
	Pribilof Islands	Kodiak Island	In literature	
Reproductive success	4	3	1-4	1
Chick growth rate	4	3	0-4	1
Body weight	4	4	2-3	1
Probability of death on spill encounter	0	0	1	3
Age-specific fecundity and survivorship	0	0	1-2	3
Foraging trip time	2	1	0-2	3
Foraging activity budget and flight path	0	0	0	2
Perturbation tracking	0	0	0	3
Metabolic rate	0	0	2	1
Thermoneutral zone	0	0	1	1
Digestive efficiency	0	0	1	1
Chick growth efficiency	0	0	1	1
Foraging (flight) cost	0	0	1	2
Flight speed	2	0	2	1
Food load size	2	0	0-2	1
Chick response to food deprivation	1	0	0	2
Foraging rate as a function of resource density	0	0	0	3
Oil spill dynamics	0	1	1	2
Changes in food availability due to perturbation	0	0	0	3

<sup>a</sup> 0 = absent, 1 = poor, 2 = marginal, 3 = good, 4 = excellent

<sup>b</sup> 1 = low, 2 = intermediate, 3 = high

## 1. Population Parameters

Population size and density---In order to initiate any consideration of the possible impacts of oil development on colonially breeding seabirds, it is necessary to know the size of the colony, when it is occupied, the age structure of the population (especially the proportion of the population that is actually involved in breeding activities), the density of birds at sea in defined areas, and the temporal variations in this at-sea distribution. General approximations of the sizes of breeding colonies have been developed for some areas (e.g. Sowles et al. 1978, U.S. Fish and Wildlife Service 1980), and these often provide a workable estimate of colony size. For many of the species, these estimates are derived from "cliff counts," in which the number of individuals of a species occupying breeding sites on a designated area of cliff-face is counted directly or from photographs, and that count extrapolated to the total area of cliff-face available in an area. Such sampling "is rarely done in a systematic fashion, however, and there may be substantial errors involved in extrapolating from a few counts to a total colony estimate, because of the difficulty of assessing the total area of suitable cliff habitat that is available to the birds or that is actually occupied by the colony (see Lloyd 1975). Further, such cliff counts cannot be used to obtain accurate estimates of the densities of burrow- or crevice-nesting species (e.g. storm-petrels, auklets, puffins, guillemots).

If cliff counts are taken frequently, they may provide information on the seasonal flux of colony size, but generally this is not done. Thus, the initial arrivals and departures of birds at the colony at the onset and termination of the breeding season are often missed because observers are present only during the peak of breeding activities. In our modeling exercises, we have been forced to assume that no birds are present in the area prior to the onset of immigration to the colony in the spring or following the completion of emigration in late summer, an assumption we know to be false for some species. We have also assumed that the immigration and emigration rates are constant between initiation and completion of these phases, and that the population size remains unchanged during the period between the completion of immigration and the initiation of emigration. Cliff counts conducted on the Pribilof Islands by S.D.L. Causey-Siegel and R. Squibb (pers. comm.) suggest that the rate of arrival of birds during immigration may indeed be relatively constant, but otherwise we have no data available to test these assumptions for the seabird systems we have studied.

In order to estimate the potential reproductive output of a colony and the way in which it may be affected by perturbations, information on the proportion of the population that is actually breeding is required. In most seabird species maturation is delayed, and a proportion of the birds using the waters adjacent to colonies may not be reproductively active. In some species, age-dependent plumage changes provide a way to index population age structure and at least separate subadult individuals from adults. In other species, however, plumage does not differentiate age classes; moreover, a significant portion of adult birds may not participate in breeding in a given year, for various reasons. Age-structure data were not available for any of the Alaskan populations that we studied (Table 1). Such data are available, however, for Atlantic populations of murre and Black-legged Kittiwakes (Tuck 1961, Coulson and Weller 1976, Birkhead 1977, Weller and Coulson 1977). These can be used as estimates of the values for the Alaskan populations, although the only justification for doing this is that the data relate to the same species that we studied. Interpopulational differences in other parameters, however, cast doubt on the precision of this procedure (see below). Unfortunately,

information on the age structure or breeding status of individuals in populations is difficult to obtain, usually requiring marking studies. Resightings of marked individuals at sea are not likely to be obtained in sufficient quantity to permit anything beyond a coarse estimate of the proportion of the at-sea population that is affiliated with a breeding colony.

At the foundation of any attempt to predict perturbation impacts on marine birds is an accurate knowledge of the distributions of the populations at sea, as this will influence the **liklihood** that birds will encounter a spill in a given area. Considerable effort has been devoted to determining the distributional patterns of marine birds at sea (e.g. **Summerhayes et al. 1974**, **Brown et al. 197'5**, **Lensink and Bartonek 19'76**, **Lensink et al. 1976**, **Gould 1977**, **Harrison 1977**, **Lensink et al. 1978**, **Nettleship and Gaston 1978**, **Pocklington 1979**, **Brown 1980**, **Hunt et al. in press**). Generally, these estimates are derived from shipboard or aerial transects that are run through specified areas. As such, the procedures suffer from all of the problems that are inherent in line transect population census methods (**Wiens et al. 1978b**, **Burnham et al. 1980**), which are aggravated by the fact that movements of the ship or aircraft are not generally linear and thus determination of the area actually sampled by a transect is subject to error. Our analysis of transect densities derived from aerial and ship transects in the Kodiak region of the Gulf of Alaska (**Wiens et al. 1980**) indicate that the probability of detecting no birds is always greater for aerial transects than for ship transects, and that for **most** species the mean/variance ratio is consistently higher for the aerial transects. These discrepancies hinder attempts to combine aerial and ship transects in any straight-forward manner, although if both types of transects **are** available for some areas one may be standardized against the other to obtain at least relative consistency.

Observation conditions (e.g. visibility, attentiveness of observers) also **may** vary substantially among transects. If one adds to this the between-observer variation that **is** inevitable **when many** different individuals record observations on different transects, the variability attributable to sampling error of the transect counts becomes substantial. Further variation is introduced because the area of concern about breeding colonies is usually far too large to permit adequate sampling of the entire region in a short period of time. Surveys are often taken on an opportunistic basis as ship-time becomes available, and some areas **may** be surveyed frequently while others receive little or no attention. In particular, close inshore areas **may** be neglected because ships generally avoid them; such areas, however, may be important foraging zones for many of the less pelagic colonial seabirds (e.g. **guillemots**, glaucous-winged gulls, terns, cormorants). Thus, even in intensive studies such as those that are part of the OCSEAP, censusing is unevenly distributed over areas of ocean and through time.

The censuses that are available for estimation of at-sea densities thus exhibit substantial heterogeneity in time, area, and **method** of sampling. As a consequence, some degree of pooling of transect samples over space and time is **necessary**, and this inevitably is accompanied by a loss of resolution in the at-sea density distribution patterns that emerge. In our analysis of the perturbation sensitivity of populations breeding at several colonies on Kodiak Island, we were compelled to combine survey data collected at different times of year to produce **overall** annual density distribution patterns in spite of our knowledge that the pattern varied considerably during the year. Spatially, the frequency of surveys taken in the major ocean areas about the island was sufficient to permit us to consider distributions in 10 km x 10 km blocks, although we found it necessary to develop **means** of weighting the density estimates in relation to the number and location of transects

run through a given area (Wiens et al. 1980). Even with such broad lumping of transect data, however, some critical portions of time and space were still not represented, necessitating extrapolations to derive density/distribution estimates.

Information on the at-sea distributional patterns of marine birds is thus confounded by variability. Some of this is a consequence of the methods and observers, some a result of the patchy distribution of sampling effort in different areas at different times. Most of the variation, however, is due to the birds themselves. Many species are distributed in a distinctly aggregated fashion, presumably in response to oceanographic and/or resource conditions. Densities of a given species may vary over 3-4 orders of magnitude during time intervals of hours or days and distances of only 5-10 km. As a consequence, the frequency distributions of transect densities are extraordinarily skewed--very low densities per transect are most common, but densities orders of magnitude higher occur with regularity. This means that standard statistical approaches to establishing confidence limits to the density estimates for given blocks of ocean or for testing for differences in densities between areas are invalid unless sample sizes are extremely large (which, as noted above, they generally are not). In our work with seabird distributions in Alaskan waters, we were compelled to develop new statistical procedures for estimating confidence limits, based upon the gamma distribution (Wiens et al. 1980, Ford and Qualls ma). Our applications of this procedure to the transect density estimates for the areas adjacent to Kodiak Island (employing coarser 20 km x 20 km blocks of area and combining surveys over the year) indicated that our confidence in any estimates of Kodiak area seabird densities is quite low. There are two basic problems. First, within the area we considered (approximately 90,000 km<sup>2</sup>), only 3-6% of the area was sampled with sufficient intensity to provide any estimate of density confidence limits, despite our generous lumping procedures. Second, if a block was sampled sufficiently to provide confidence intervals, only 30-80% of these blocks (depending on species) yielded confidence limits such that the observed mean density and the upper confidence limits were within an order of magnitude of each other. The problem was most severe with shearwaters because of their highly skewed abundance distributions in the transects, but the more important foraging areas appeared to show more severely skewed distributions for all species, so that our confidence in the density estimates was often lowest where it was most important. These conclusions are quite discouraging, especially when one considers the fact that we were employing data sets generated in a rather massive transect sampling program (OCSEAP).

Reproduction and survivorship.--Operation of models to assess the proximate effects of perturbations on populations and the long-term effects on the recovery or persistence of the population requires a variety of demographic data. Fortunately, some aspects of the reproductive biology of populations are easily studied and are often included in conventional breeding biology investigations. Other parameters, however, are difficult to measure or are generally ignored in seabird studies. Our modeling exercises suggest that some of these may be critical to predicting the population consequences of perturbations.

Perhaps the most readily available data concern the timing of reproduction in the populations occupying a given colony. If a colony has received any on-site study at all, it is likely that information on the onset of incubation, the distribution of breeding attempts among individuals in the population, the mean and variance of hatching dates, and the timing of fledging of young will be available, at least in the form of coarse phenological measures. When colonies do receive close study, aspects of reproductive success are often a primary focus, and thus

data on the average hatching success of eggs laid and the average fledging success of young hatched are frequently available, perhaps accompanied by variance measures for these parameters. These data are most easily obtained for open-nesting species, can be gathered with considerable effort for cavity or burrow nesters (e.g. Hunt et al. in press), and are extremely difficult to obtain for species that nest in deep crevices. Information on the breeding success of populations is thus likely to vary substantially among species. Obviously, accurate information on both the timing and success of reproductive efforts in local populations under "normal" conditions is essential if we are to predict the effects of perturbations occurring at various times through the breeding season with any degree of accuracy.

In one of the **models** we developed (Ford et al. 1982), indirect mortality of young in response to an oil spill is effected by a reduction in the rate at which adults deliver food to them, and thence in the rate at which the young grow. In order to assess such effects, we **must** know how young grow under normal circumstances. Growth studies have been especially fashionable in seabirds because their patterns and rates of growth and maturation differ so markedly from the typical passerine patterns (e.g. Ricklefs 1973, 1979), and there is thus a **moderate** amount of information available in the literature. Growth rates **may** therefore be available for **most** of the species at a given colony, although colony- or area-specific growth rates for the populations are likely to be available only if populations in the area have been subjected to intensive breeding-biology studies. Between-colony or between-year differences in growth rates of chicks of a given species may sometimes be substantial (e.g. Mahoney and Threlfall 1981, Hunt et al. in press). In addition, the disparity **among** species of different nesting habits noted above is likely to be even **more** extreme for growth data than for success measures,

Unfortunately, obtaining accurate measures of the reproductive success or chick growth rates for populations requires fairly intensive field study, especially for those species nesting in burrows or crevices. The activities of investigators about the colonies or the nest sites disturbs the breeding birds, and the **more** intensive the studies, the greater this disturbance effect **may** be. Several studies have documented the degree to which even **moderate** levels of investigator activity about breeding colonies **may** depress reproductive success (e.g. Ellison and Cleary 1978, Tremblay and Ellison 1979, Lenington 1979, Duffy 1979, Ellison 1979). We are thus confronted with the paradox that the **more** effort we put into obtaining really precise measures of reproductive success or chick growth rates, the less natural and accurate those **values** are likely to be.

Information on normal body weights of adults is usually (but, regrettably, not always) gathered when collections **are** made for dietary studies or other purposes. Such information is required in **any** model that attempts to evaluate perturbation effects through estimation of individual or population **energy** demands (see below). If energetic analyses are to be employed to gauge the effects of varying food delivery **rates** on chicks, then additional weight data **must** be available for eggs, chicks at **hatching**, and fledglings. Such data are usually not obtained unless growth studies are conducted, and even then egg weights are often not recorded.

In our **models**, the sole source of adult mortality accompanying oil spills is the direct death of birds that encounter a spill while at sea. We can **model** the probability of a bird encountering a spill by relating the at-sea distribution patterns and the foraging dynamics of the birds to the specific area occupied by a **spill**. We do not know the details of individual behavioral responses to spills or oil slicks (e.g. attraction vs. repulsion), however, and such behaviors would influence the

probabilities of spill encounter calculated solely from distributional information. In addition, however, we must know the probability that a bird encountering a spill will actually suffer mortality. No direct measures of this parameter are available, and in our modelling exercises to date we have been forced to estimate values from descriptions of oiled birds available in the literature (e.g. Bourne et al. 1967, Bourne 1968, Holmes and Cornshaw 1974, Vermeer and Vermeer 1975, King and Sanger 1979).

The remaining features of reproduction and survivorship that are required relate to attempts to translate the proximate, short-term effects of perturbations into predictions of the long-term population consequences of those effects. To do this, any realistically structured model requires information on the patterns of age-specific fecundity and survivorship in the population, as these are the basic features of demography upon which life-table analyses are built. Moreover, if one has reason to believe that any degree of density-dependence influences these population processes, the magnitude of these density-dependent effects must be determined. Such information is difficult to obtain, as it generally requires long-term investigations. A few such studies have been conducted on seabirds in the North Atlantic (murre, Tuck 1960; Black-legged Kittiwakes, Coulson and White 1959, Coulson and Wooller 1976, Wooller and Coulson 1977; Gannets, Nelson 1978; Fulmars, Dunnet et al. 1979; Shags, Potts et al. 1980), but no information of this sort exists for any of the North Pacific breeding species. In the absence of other data, one is tempted to apply the information from Atlantic populations to Pacific populations of the same species. For kittiwakes, this is obviously inappropriate, as the fecundity reported for the two populations differs considerably (Coulson and White 1959, Coulson and Weller 1976, Wooller and Coulson 1977, Wiens et al. 1979a), and incorporation of the Atlantic values into a life-table model for the Pacific populations yields rates of change in population size from current levels that are unrealistic (Wiens et al. 1979a). Given the magnitudes of inter- and even intracolony variations in reproductive parameters that may occur for many seabirds (e.g. Harris 1980, Mahoney and Threlfall 1981, Birkhead and Nettleship 1981, Hunt et al, in press), such extrapolations may be generally suspect.

## 2. Foraging Parameters

The modeling approach that we have followed places heavy emphasis upon features of the foraging behavior of the birds. This is because birds generally use the oceanic areas where pollution is most likely to occur primarily for feeding, and as breeding birds are restricted to using areas within range of the breeding colony, their options for responding to a perturbation will be rather limited. The key variable that we have employed in structuring our models is trip time, which includes the time taken by a foraging adult to travel from the colony to a foraging location, the time spent in searching for and capturing prey sufficient to make a load for the return trip, and the time taken to return to the colony. Information on trip times is rarely gathered in seabird studies (but see Pearson 1968), even in those that devote considerable effort to documenting the various reproductive parameters (e.g. Birkhead 1977). When trip time has been determined, it has usually been obtained from only a few individual birds at one colony (or one location within a colony), on just a few days. The slimness of this data base makes it impossible to model the temporal dynamics of foraging patterns without making some assumptions (e.g. the optimality of foraging; see Norberg 1981), which are largely untested. It seems surprising that trip time information is often not gathered in association with continuous observations of colony sections (as in some cliff counts) or nest

sites. Possibly this is because the importance of information on trip times has not generally been realized.

Our use of trip time in the **models** is based upon two important assumptions. One is that the allocation of time to activities during a trip is optimal, that is, once the birds arrive in the foraging area they spend their time foraging at the maximum efficiency in relation to resource availability. This assumption requires testing, and the information that would provide the test is basic activity-budget data taken from birds at sea. How **much** of the time spent in a foraging area is actually spent in foraging? How **much** is spent "resting" or "loafing"? How does foraging success rate (and thus the time spent in foraging activities) relate to resource density? No information on any of these aspects of foraging behavior is available for any of the Alaskan populations, and data on dive times and success rates obtained in studies elsewhere (e.g. Stonehouse 1967, Scott 1973) provide **only** part of the requisite information.

The second assumption of our trip time calculations is that birds use the shortest, most **direct** flight path between the colony and the foraging area at sea. This, of course, presumes that a foraging individual knows precisely the location of its destination when it leaves the colony, and that decisions to change foraging locations are made with little time expenditure in searching for new areas. We know very little of the actual flight paths of foraging birds, although radio-tracking of tagged individuals could supply this information rather easily, at least for those species that forage relatively close to the colony.

When an area used for foraging by birds from a colony suffers an oil spill, we expect that the individuals that do not suffer direct mortality from the **spill** will adjust their foraging distribution to avoid the polluted area. It is unlikely that this response will be instantaneous, however, as birds that have been foraging in a traditional feeding area **may** exhibit some reluctance to leave it and forage elsewhere, especially if the spill is not massive. There **will** thus be a lag time in the response to a **spill**, and it **may** require several days for a population to adjust its at-sea foraging distribution to a new optimum dictated by the perturbation event. Because no studies of the proximate response of seabird populations to oil spills have been conducted, information on this "tracking" parameter is completely lacking, and intuition provides relatively little guidance. This is the sort of parameter that is generally not even defined **unless one** undertakes a **modeling exercise**, such as ours.

### 3. Energetic Parameters

Our modeling approach relies upon estimates of the balance between the **energy** demands of adults and chicks and the availability of energy (food) in various foraging areas to project perturbation-related alterations in the foraging patterns of adults and the growth rates and survival of young. Previous attempts to model the energetic patterns of seabird **populations** (e.g. Wiens and Scott 1975, **Furness 1978**) have followed the basic procedure of determining individual metabolic energy demands as they are **modified** by various environmental or behavioral factors, converting these to population-wide estimates, and then converting the energy demand values into estimates of food consumption rates. The derivation of such estimates is dependent upon knowledge of the values of several basic energetic parameters, and these also figure in the energetic calculations we have employed in assessing spill impacts.

The foundation of the energetic estimations is some procedure for deriving the metabolic rate of individuals on a daily basis, unadjusted for activities such as foraging. In our earlier modeling of seabird energetic (Wiens and Scott 1975, Wiens et al. 1978a), we used the equations presented by Kendeigh et al. (1977), which project daily existence energy requirements for nonpasserines as functions of body weight, ambient temperature, and photoperiod. Because it provides estimates of similar accuracy but requires less input information, we used the equation of Aschoff and Pohl (1970) for the daily energy requirement of a nonactive bird at thermoneutrality in our more recent models. Such general equations must be used to estimate metabolic rates because so few seabirds have been studied directly (but see Johnson and West 1975). Use of the Aschoff-Pohl equation required that we establish that the birds we studied were normally at thermoneutrality. This assumption seems justified for seabirds; Johnson and West (1975) reported a lower critical temperature for murrelets of 4.5°C, and the sea-surface temperatures recorded in the Bering Sea during the May-August breeding period rarely fall below that level (Wiens et al. 1978c). Use of this equation instead of the Kendeigh et al. equations also assumes that the effects of photoperiod are unimportant. The influences of photoperiods at high latitudes on metabolic rates are generally unstudied, although a series of sensitivity tests we performed on the estimates of seabird energy demands derived using the Kendeigh et al. equations indicated that small variations in photoperiod had relatively little effect on the overall energy requirements (Wiens et al. 1978c). In the absence of species-specific metabolic studies of seabirds, use of the Aschoff-Pohl equation thus seems justified, although the energy requirement estimates derived may not be very precise. As they are used in the models primarily to predict the magnitude of change accompanying a perturbation, however, their primary value is as a relative rather than an absolute measure, and for this they are probably quite suitable.

The estimates of daily individual energy requirements derived from this (or some other) equation must be adjusted for several costs in order to determine the actual energy demands that are placed upon the environment (and that thus will be affected by alterations in resource availability or energy capture rate associated with perturbations). One such cost is that associated with the inefficiency of the digestive process; an individual must consume somewhat more food than that dictated by its metabolic energy demands alone, as not all of it will be digested and made available for metabolic action. For a wide variety of avian species and food types, digestive efficiency is close to 70% (Ricklefs 1974). Little direct information is available on the efficiency with which various seabirds process food, although data from Sooty Shearwaters (L. Krasnow, pers. comm.) suggest that birds feeding on fish and squid may have a digestive efficiency as high as 80%. Beyond this cost, chicks have the additional cost of converting food input into new tissue during growth. Again, no information on the value of growth efficiency is available for seabird species, and we must resort to using the general value of 75% provided by Ricklefs (1974).

A basic premise of the approach that we have taken to predicting responses to perturbations is that a disruption of foraging areas will force feeding birds to fly farther from the colony to obtain food, and that the indirect consequences of the perturbation will thus be mediated through the increased costs in time and energy spent in foraging. In terms of energetic, this means that we must have some means of adjusting the nonactive metabolic energy requirements for the additional costs of activities such as foraging. Unfortunately, little is known of the degree to which activity elevates energy demands in any birds (King 1973, 1974; Tucker 1974; Pennycuik 1975, Rayner 1979, Walsberg 1980, Norberg 1981), much less seabirds. In

previous work with passerine, we have used a value of 0.25 times existence energy demands to adjust for the additional costs of free-living activity (Wiens and Innis 1974, Wiens and Scott 1975). In the absence of additional data, a similar value would seem appropriate for seabirds, although this is really little more than an educated guess. This is unfortunate, as foraging costs are distance-dependent, and thus would seem to be important to predicting space-dependent perturbation impacts.

Other parameters, while not specifically energetic, relate to these energy-based calculations. Thus, in order to evaluate the additional time costs associated with a shift in foraging area accompanying an oil spill, we must know the average straight-line flight speed of each species. Such information is not generally gathered in colony studies, although it is not especially difficult to obtain. Some estimates for seabirds have been published (e.g. Meinertzhagen 1955) ; in our modeling we used these values, as modified by our own observations of murre and kittiwakes on the Pribilof Islands. Another important parameter is load size, the quantity of food (or energy) that an adult carries back to the colony on a foraging trip to feed the young. This value, combined with the frequency of feeding trips per day and the energetic features of the young, will determine the growth patterns of the young and their survivorship probability. For species such as murre that carry a single prey item on each trip, load size may be estimated by recording the type and size of prey when it is brought to the young, and then converting to biomass or energy by comparison with voucher specimens of the prey types. For species that bring multiple items per trip, or that carry back partially digested food in the crop or stomach (e.g. auklets, gulls, fulmar), estimation of load size is much more difficult.

In our model (as in nature), a reduction in food delivery rate to the young is reflected by a reduction of their growth rate. At some point this growth reduction becomes debilitating and the probability of mortality of the chicks increases dramatically. A few studies (e.g. Birkhead 1977, 1978; Harris 1978, Braun and Hunt ms) have investigated the degree to which growth is reduced under conditions of reduced food delivery. The effects of such reduced growth rate on survivorship may be cumulative: a chick may be able to tolerate a day or two of reduced growth and still fledge on schedule (albeit at a below-average weight), but several successive days of depressed growth may affect the chick so that fledging weight is abnormally low or fledging is delayed, decreasing survivorship (but see Hedgren 1981). Information on the growth dynamics of seabirds under different food-delivery regimes could be obtained from carefully controlled feeding trials or deprivation experiments, but few such studies have been conducted.

Finally, in order to assess the foraging dynamics of birds during the time that they are present in a foraging area, we should know the food capture rate as a function of the density or availability of the resource. While some information on the dive success rates of foraging seabirds is available (e.g. Scott 1973), this does not serve to relate the success rates to resource availability (which was not measured in these studies). Indeed, no information of this sort exists for foraging seabirds. Not only would we require data on prey capture success rates, but on the resource densities in various areas of the ocean about the colony, the rates of depletion of these resources as a function of prey uptake by the birds, and the temporal dynamics of these parameters.

#### 4. Perturbation Parameters

When the effects of an oil-related perturbation of a marine system are considered after the fact, determining the physical features of the event (e.g. its composition, size, distribution, duration) is generally rather straightforward and of high priority. If one instead wishes to predict these effects a priori, determination of spill parameters and dynamics are **much more** difficult (see Audunson 1980). In our initial modeling efforts we developed several spill scenarios arbitrarily, using information regarding oil spills available in the literature to make these fairly realistic. A **much more** accurate and powerful approach involves using data on ocean current patterns, surface conditions, and wind flows to predict the trajectories likely to be followed by surface oil launched (i.e. spilled) from a specified point at sea. Such a model has been developed by W. Samuels and his colleagues (pers. comm.). Because the trajectories for any given spill event are probabilistic, varying with the patterns of currents, wind conditions, and so on, we have used the spill trajectory model to generate spill scenarios for our impact analyses by conducting multiple spill model runs for each launch point at a given time. This yields estimates of the probability of spill encounter for various areas located about the spill source. When combined with the estimations of spill effects on the birds that are generated from our models, this enables us to predict the possible effects of a given spill scenario in a probabilistic fashion. Unfortunately, such spill trajectory models are available for relatively few ocean areas, although the Samuels et al. model is equipped to analyze spill characteristics for any area for which the requisite measures of physical features of the ocean area are available. These are **much more** likely to be available than are the many biological parameters that we have discussed above.

#### D. DISCUSSION: PARAMETER PRIORITIES

The approach that we have advocated to generating predictions of the possible impacts of oil developments and perturbations upon colonially breeding marine birds requires information on a substantial number of parameters of seabird biology. The data base available for some of these parameters is reasonably good (Table 6). This is especially true of those measures that pertain directly to the reproductive biology of individuals, such as clutch sizes, reproductive success, or breeding phenology. For many of the parameters, however, little or no information is available, and the preceding text reads like an inventory of what we do not know about seabird biology.

Does this mean that our approach, or any attempt to predict seabird responses to perturbations based on knowledge of their biology, is doomed to failure, and that we must continue to be content with post facto assessments? Perhaps not. Perhaps intelligent and reasonably accurate predictions can be generated without precise knowledge of the values of all of the parameters for a given colony. In our modelling we have often been forced to use general species-specific values of parameters rather than population-specific values, and in some instances we have resorted to approximating values for a species from literature values from other species in other areas in the absence of any more specific data. For those parameters lacking any sort of quantitative data base, we have derived educated guesses of "reasonable" values from our own intuition or that of other seabird workers.

In an attempt to justify the use of all these approximations, and to evaluate the possible effects of errors in their estimation on the output or predictions of

our models, we have conducted several sensitivity tests of the parameters and the models (Wiens et al. 1978c, 1980; Ford et al. 1982). In one exercise, we systematically varied the estimated values of parameters relating to the breeding structure of the population, photoperiod length (as it might influence daily energy demands), and the degree to which metabolism is elevated by activity (i.e. foraging). These sensitivity tests indicated that variations in the first two parameters had relatively minor consequences on the values of model output, but the variations in the costs of foraging activity over a reasonable range of values produced variations in model output on the order of  $\pm 10\%$  (Wiens et al. 1978c).

A more robust and thorough approach to sensitivity analysis involves the use of Monte Carlo simulations, in which each of the input variables to the model is simultaneously drawn at random from a specified probability distribution of values of the variable. We conducted such sensitivity tests on multiple runs of our model of seabird dynamics in the Pribilof Islands system (Ford et al. 1982), using most of the variables that we have described above. We used variations in the model output values of adult survivorship and number of chicks fledged as an index of the sensitivity of model predictions to variations in parameter values. Standard errors of the model predictions ranged from 0.03 to 0.21 for most oil-spill scenarios, suggesting that our ability to generate predictions of perturbation consequences using this approach was relatively insensitive to reasonable variations in the values of most input parameters. This implies that general, qualitatively reasonable estimates of values for many of the parameters we have discussed may be quite satisfactory for generating reasonable predictions of perturbation effects.

Three model parameters were not included in these sensitivity tests: the probability of adult death associated with spill encounter ( $p$ ), the rate of population response ("tracking") to the occurrence of a spill ( $\tau$ ), and the amount of change in food availability in a foraging area due to a perturbation ( $A$ ). A separate set of sensitivity tests in which these parameters were varied over the range of reasonable values indicated that variations in  $p$  produced variations in model output on the order of  $\pm 25\%$ , while similar variations in the values of  $\tau$  altered model predictions by as much as  $\pm 50\%$ ; large variations in  $A$  produced substantial changes in model output. These parameters (especially  $\tau$  and  $A$ ), then, seem to require some accuracy in their estimation.

Other indications of the relative importance of various sets of parameters can be gained directly from the model output, especially when considered in the context of the long-term population consequences of perturbation events. Thus, the likelihood that a perturbation will seriously impair the capacity of a population to return to equilibrium is greater if the adult age class rather than the chick age class suffers the greatest mortality. If chronic, low-level pollution reduces average fecundity and/or survivorship of adults by only a few percent, the ability of the population to then recover from a one-time, large-scale oil spill may be drastically affected; effects on survivorship are more important than those on fecundity (Ford et al. 1982). Collectively, these results point to the relatively greater importance of factors influencing survivorship than reproduction or fecundity, and to the relative unimportance of the chicks in comparison to adults.

Overall, then, our experiences in developing these models, in assembling parameter values, and in conducting sensitivity tests lead us to define several variables as critical to attempts to generate predictions of oil-spill impacts on marine birds (Table 6). We may consider these in two priority categories.

I. Intermediate priority

A. The breeding structure of the population, in particular the proportion of the at-sea "pool" of birds that is not breeding and not associated with a given colony.

B. The foraging pathways of individuals. We have assumed straight-line flight in our models, but if individuals move about in the foraging areas or take a wandering course to or from the colony, the proportion of the foraging trip during which a bird will be vulnerable to spill contact will be diminished.

C. The metabolic costs associated with foraging activity, especially flight.

D. The spatial and temporal patterns of food availability in the areas about a colony (as these play a major role in setting the distributional patterns of the birds).

E. The manners in which changes in food delivery rates to chicks affect the growth rates and survival probabilities of the chicks.

F. The distributional dynamics of oil spills in specific areas.

11. High priority

A. The size of a breeding colony.

B. The patterns of at-sea distributions of birds associated with a given colony under normal conditions, including estimates of their spatial and temporal variability.

C. The distribution of trip times of adults foraging under normal conditions.

D. The normal pattern of age-specific survivorship characteristic of a population.

E. The probability that an adult encountering an oil spill will suffer mortality.

F. The frequency with which individual members of the population shift their foraging region, which determines the rate at which "naive" birds encounter the spill area.

G. The manner in which a spill influences resource availability and thus the potential rate of prey capture by birds that forage in the spill area.

Gathering information on these parameters will not be easy, and it is discouraging (although not entirely unexpected) that those parameters that seem most critical to producing accurate predictions are generally the most difficult to measure or estimate. Conversely, if we continue to measure with considerable precision the various parameters of reproductive biology that are readily obtained in typical colony studies, this may contribute rather little in our ability to form predictive models of the dynamics of seabirds and oil spills. It is our hope that, by drawing attention to the relative importance of these parameters, and by specifying those that seem most important, individuals or groups involved in seabird research may redirect some of their efforts to exploring some of these difficult, but essential, parameters.

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APPENDIX A. Scientific Names of Bird Species

Fulmar	<u>Fulmaris glacialis</u>
Sooty Shearwater	<u>Puffinus griseus</u>
Gannet	<u>Morus bassanus</u>
Shag	<u>Phalacrocorax aristotelis</u>
Pelagic Cormorant	<u>Phalacrocorax pelagicus</u>
Glaucous-winged Gull	<u>Larus glaucescens</u>
Black-legged Kittiwake	<u>Rissa tridactyla</u>
Arctic Tern	<u>Sterna paradisaea</u>
Common Murre	<u>Uris aalge</u>
Thick-billed Murre	<u>Uris lomvia</u>
Tufted Puffin	<u>Lunda cirrhata</u>

APPENDIX B. Publications

- Wiens, J.A. 1979. Summarizing remarks, Part II. Pp. 259-261 in Shorebirds in marine environments (F.A. Pitelka, Ed.). Studies Avian Biol. No. 2
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- Wiens, J.A., R.G. Ford, and D. Heinemann. (in preparation). Assessing the sensitivity of marine birds to oil spills: information gaps and priorities.
- Heinemann, D., R.G. Ford, and J.A. Wiens. (in preparation). Confidence and the estimation of numbers of pelagic marine birds.
- Ford, R.G., and C. Quails. (in preparation). Estimation of confidence limits by the gamma distribution.