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MODELLING THE SENSITIVITY OF COLONIALLY BREEDING MARINE BIRDS TO OIL SPILLS: GUILLEMOT AND KITTIWAKE POPULATIONS ON THE PRIBILOF ISLANDS, BERING SEA

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SUMMARY

(1) We develop simulation and analytic models to estimate the responses of colonially breeding marine birds to environmental perturbations such as oil spills occurring within the foraging area of the populations.

(2) Short-term impacts are considered through a demographic sub-model, which simulates changes in population size and age structure through a breeding season, and a foraging sub-model, which simulates the daily foraging activities of individuals and estimates their daily energy intake and mortality from direct contact with a spill. The demographic sub-model partitions adults and young into age-states; transfers of individuals between states are produced by immigration, breeding, emigration, growth, and mortality. Survivorship of young is modelled as a function of food delivery rate by the adults. The foraging model generates a distribution of the population at sea in accordance with optimization of individual trip times in relation to projected resource levels in areas surrounding the colony. This distribution is then perturbed by effecting reductions in food supply or direct mortality of adults in areas affected by an oil spill, and the rate of recovery of the population to the optimal distribution and the changes in survival of various age classes projected.

(3) Monte Carlo sensitivity tests indicate that model projections are relatively robust to variations in input values, standard errors of adult survivorship and chick fledging success ranging from 0·03 to 0·21. Other sensitivity tests suggest that the model system is relatively insensitive to variations in the probability of adult death following a spill encounter, but is substantially more sensitive to variations in the rate at which the population responds to the occurrence of a perturbation by adjusting its foraging distribution, and to large changes in the food availability of areas following perturbation.

(4) Applications of the model to populations of guillemots and kittiwakes breeding on the Pribilof Islands in the Bering Sea suggest that guillemot mortality is greatest following perturbations located in shallow inshore areas about the breeding islands, while kittiwakes are less severely affected by localized perturbations but are sensitive to spills occurring over a wider area about the islands. Model explorations employing chronic low-level pollution rather than one-time perturbations suggest that the guillemot population breeding on St George Island could tolerate an overall reduction of 10% in the food supply without suffering a major decline in fledging success, but a reduction of 40% would lead to total reproductive failure in the colony.

(5) We construct three specific scenarios of oil spills to explore the patterns of population mortality and recovery times projected by the models. Kittiwakes seem generally less sensitive to perturbations, especially those occurring in the immediate vicinity of the breeding colonies.

(6) We use a simple population dynamics model in conjunction with the short-term model to estimate the long-term population consequences of both one-time and chronic

perturbations. The effects of varying one-time mortality on guillemots are much more severe if adults rather than first-year birds suffer the mortality. If a given level of one-time mortality is superimposed on a chronic low-level change in survivorship or fecundity, recovery times are markedly longer.

(7) Our analyses are hampered by a lack of field information on several critical model parameters. These features of seabird biology merit closer attention, and their present uncertainty renders our model projections only general rather than precise.

INTRODUCTION

Colonially breeding seabirds are a conspicuous and important element in most marine ecosystems. They often occur in vast concentrations, especially in areas of high productivity. They may have major effects on energy flows in these systems, consuming perhaps 22–27% of the annual production of small pelagic fishes (Wiens & Scott 1975; Furness 1978), and their concentration of nutrients about breeding colonies may have major influences on local patterns of marine nutrient cycling (Tuck 1961; Golovkin 1968). 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 system dynamics will be perturbed increases (Nettleship 1977; Birkhead & 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. Here we develop one approach to predicting the potential impacts of petroleum developments in the vicinity of marine bird colonies by synthesizing aspects of breeding biology, foraging behaviour, demography, and energetics of the birds, using a series of simulation and analytical models.

Our approach is founded upon the following features of marine bird breeding colonies. During the breeding season, seabird populations occupy large colonies along coasts and on nearshore and offshore islands. To obtain the energy required to sustain their own metabolic demands and to feed growing chicks, adults forage more or less radially from the colony, in a typical 'refuging' or 'central place' manner (Hamilton & Watt 1970; Orians & Pearson 1979). The oceanic distribution of foraging birds at various distances from the colony presumably reflects some compromise between the availability and abundance of food in different areas and the energetic (and time) costs associated with foraging there. There is thus a significant spatial component to the pattern of energy demands of breeding seabirds. It follows that if there is a reduction in the availability of food resources in a particular area about the colony, the ability of the birds to adjust their foraging distribution and obtain the energy necessary to survive and to rear young successfully may depend upon both the magnitude of the resource perturbation and its location relative to the colony. Furthermore, perturbations may lead to direct mortality of adults, and this also may vary in accordance with the distribution of the population about the colony.

Intuitively, one would expect a perturbation such as an oil spill or well blowout occurring close to a breeding colony to have a greater impact upon the birds than one occurring at a greater distance from the colony. Determining how much greater that impact might be, however, or how the severity of impact might vary as a function of location relative to the colony, requires an approach based upon more than simple intuition. Such perturbations may have both short-term effects, through direct mortality of adults and/or young, and long-term (multi-year) effects, as the mortality patterns influence

population size, age structure, and growth patterns. Here, we emphasize the development and results of a model of short-term effects. We lack the necessary information to permit a detailed analysis of long-term effects, so these receive limited consideration.

We illustrate our modelling approach by applying it to a preliminary appraisal of the sensitivity to perturbations of colonially breeding seabirds on the Pribilof Islands in the Bering Sea (56°30′N–57°15′N; 169°30′W–170°30′W). This group consists of four islands: St Paul, the smaller nearby Otter and Walrus islands, and St George Island, 64 km to the south-east. The Pribilof group as a whole supports approximately 2·75 million seabirds, about 2·5 million of which nest on St George Island (Hickey & Craighead 1977). The majority of the nesting birds requires cliffs with ledges that are inaccessible to mammalian predators. St George Island has a much larger area of suitable cliff habitat than does St Paul Island. Most of the birds on the Pribilofs are Brünnich's Guillemot (*Uria lomvia* Linnaeus) with approximately 1·6 million birds present, followed by 270 000 least auklets (*Aethia pusilla* Pallas), 240 000 red-legged kittiwakes (*Rissa brevirostris* Bruch), 229 000 common guillemots (*U. aalge* Pontoppidan), 103 000 black-legged kittiwakes (*R. tridactyla* Linnaeus), 75 000 parakeet auklets (*Cyclorrhynchus psittacula* Pallas), 71 000 northern fulmars (*Fulmarus glacialis* Linnaeus), and lesser numbers of horned puffins (*Fratercula corniculata* Naumann), crested auklets (*A. cristatella* Pallas), tufted puffins (*Lunda cirrhata* Pallas), and red-faced cormorants (*Phalacrocorax urile* Gmelin). In aggregate, the Pribilof Islands support one of the largest seabird populations in the Bering Sea, if not the Northern Hemisphere. St George Island is one of four known breeding sites of the red-legged kittiwake, with 88% of the estimated world population of this species (Hunt, Eppley & Drury 1981).

MODEL STRUCTURE

The model of short-term effects of perturbations such as oil spills on seabird colonies involves two interacting sections. One, the demographic submodel, simulates changes in population size and age structure through the course of a single breeding season. Adults of
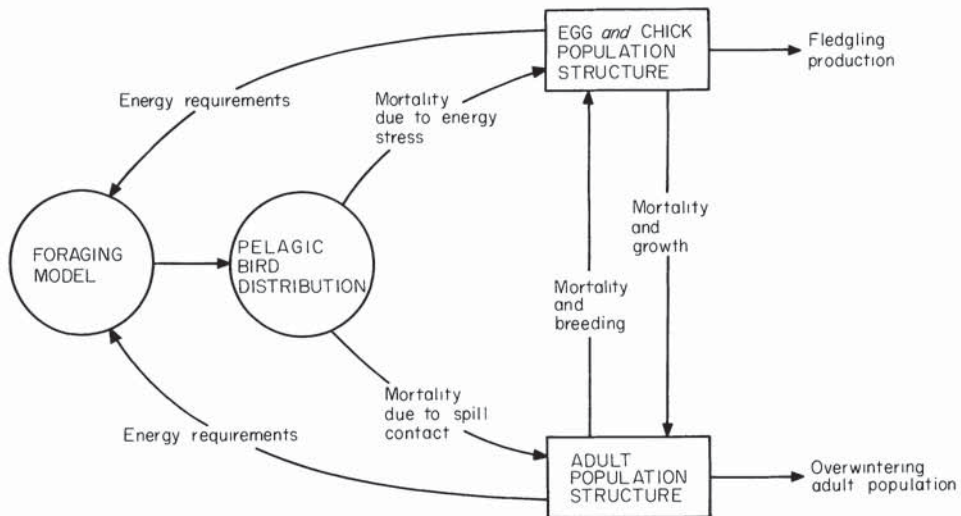

FIG. 1. Generalized flow diagram of the major elements of the short-term model of seabird foraging and population demographics.

a given species arrive at the breeding colony, attempt to raise young (with varying success), and depart at the end of the breeding season. The other submodel simulates the daily foraging activities of colony members and estimates their daily energy intake and their mortality due to direct contact with an oil spill.

The demographic and foraging submodels are interactive (Fig. 1). The demographic submodel determines the size and age composition of a population at a given time, which determine the energy requirements that must be met by the foraging birds. These, together with environmental conditions (primarily food resource distribution), determine the pelagic distribution of the population. This, in turn, affects both the degree to which the birds are successful in meeting energy demands (and thus the patterns of chick growth and survival) and the probability of direct encounter of foraging adults with an oil spill (and thus adult mortality.)

Demographic submodel

In the structuring of the demographic submodel, adults of a given species are partitioned into one of eight mutually exclusive states: (1) not present at the breeding colony; (2) present at the colony but not involved in breeding activities; (3) formation of a clutch initiated, but eggs not yet laid; (4) eggs laid and being incubated; (5) eggs hatched, chick in stage I of development (see below); (6) chick in stage II of development; (7) chick in stage III; and (8) adult dead. The population of young for a given species is partitioned into five sequential states: (1) eggs; (2) chick stage I; (3) chick stage II; (4) chick stage III; (5) fledglings. Chicks (and thus the adults attending them) are considered in three separate stages in order to permit adjustments in chick mortality-rates, chick energy demands, and chick-related adult foraging behaviour that are associated with the rather different phases of normal chick growth. Stage I corresponds to the initial phase of slowly increasing body weight and growth rate of the young, Stage II to the period of rapid weight gain and high growth rate that characterizes chicks of intermediate age, and Stage III to the phase of reduced growth rate as the chick approaches fledging weight: the stages thus correspond to the three major sections of a sigmoidal growth curve.

Transfer of adults from one state to another occurs in the model structure on a daily basis. Standardized counts of birds at cliff colonies on the Pribilof Islands (S. D. L. Causey-Seigel & R. Squibb, personal observations) suggest that during immigration adults arrive at a roughly constant rate until a maximum population size is attained. The population then remains more or less unchanged until the onset of emigration, during which adults then depart from the colony location at a relatively constant rate. Immigration and emigration are thus defined in the demographic submodel only by their beginning and ending dates. These fluxes of individuals into and out of the breeding colony are considered in relation to an at-sea 'pool' of individuals. During immigration and emigration we assume that the probability of an individual arriving at a colony from the at-sea population or leaving the colony and rejoining the at-sea population is adjusted so that the number of individuals arriving or leaving is constant at a level that produces the appropriate immigration or emigration rates. We assume that during immigration all birds in the at-sea pool eventually arrive at the colony and enter the population as non-breeders; at the end of the breeding season, all birds leave the colony, eventually to rejoin the at-sea population. Mortality during the breeding season, of course, influences the number of individuals involved in these fluxes. We do not consider the spatial location or dynamics of the at-sea populations during the non-breeding season.

Observations on the Pribilof Islands indicate that the rate at which adults initiate

breeding is relatively constant over some discrete time period, usually of short duration, following the completion of immigration. Not all adults, however, initiate clutches. The rate of transfer of individuals from the non-breeding to the breeding state is modelled as a constant increase in the breeding population between the onset and the end of the population breeding period, with a specified maximum proportion of the population actually initiating reproductive activities. Clutches are initiated by individuals after a specified time interval in the breeding state. Adults are returned to the non-breeding segment of the population if their breeding attempt fails due to loss of egg(s), death of the chick(s), or death of the mate, or when the chicks successfully fledge. Adult death is assumed to occur only as a result of direct contact with an oil spill or blowout, and acts on all classes of adults except those not present at the colony. Loss of one or both members of a breeding pair leads to nest failure and egg or chick death; if only one member of a pair is lost, the remaining adult returns to the non-breeding population but remains at the colony location. The adult death rate is calculated in the foraging submodel, and will be described there.

Although chick mortality may occur for a variety of reasons, such as exposure, disease, predation, or starvation, our principal focus is upon the effects of variations in food delivery rate on survivorship. We consider the primary effect of oil spills (or similar perturbations in the foraging area about a colony) on chick survivorship, aside from the loss of one or both parents, to be an increase in mortality resulting from lowered food availability to the foraging adults and, consequently, lowered food delivery rates to the chicks. This source of mortality increases the chick death rate over a baseline level that subsumes other normal causes of death. We employ the foraging submodel to estimate the changes in food delivery rates that accompany habitat alterations in foraging zones. There are few data available to link food delivery rates to chick survivorship in a quantitative or a qualitative manner for any seabirds (Hunt & McLoon 1975; Hunt & Hunt 1976; B. Brown in prep.).

We assume that chick death rate increases as the ratio of average energy delivered to chick metabolic demand decreases. However, the assumption of a linear relationship between these two parameters affecting all birds equally at each time-step tends to lead to an unrealistic threshold effect, in which either virtually all chicks survive or all chicks die. This obviously does not occur in nature, probably because food delivery rates vary widely among breeding pairs. Thus, even when delivery rates are significantly reduced, some chicks may still receive nearly all of their demands and will survive the period of diminished food supply. A realistic model of chick death rate therefore must take into account variance in delivery rates (a function of the length of foraging trips) as well as the relationship between delivery rates and death rate. Our own observations and those of Hunt (1978) indicate that the distribution of trip times can be modelled by fitting an exponential curve of the form $y = \mu e^{\mu x}$, where y is the frequency of trip times, x is the trip time, and μ is the mean trip time. This model takes advantage of the fact that the exponential distribution is a one-parameter curve and requires only mean trip time to model the distribution.

Assuming that the length of one trip is independent of the length of other trips, we then generate the distribution of frequency of total trips per day per breeding pair. The net energy gain for a chick is estimated by subtracting the costs of adult maintenance and foraging from the gross energy uptake of the adults. We assume a linear relationship between the ratio of net chick energy gain to chick metabolic requirement (which will vary, depending on the size of the chick) and the probability of death per day. This function is
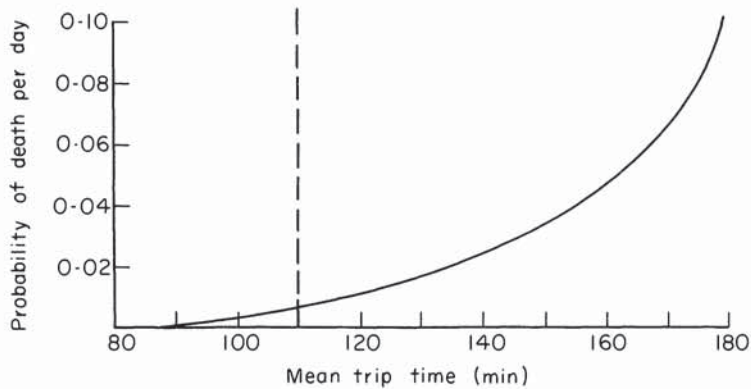
FIG. 2. Chick death rate per day for guillemot chicks of stage I. The dashed line is the observed mean trip time corresponding to an observed chick death rate of 0·005 per day. CDRMAX is set to 0·55.

assumed to vary from a death rate of zero when the ratio is equal to one (i.e. chick demands are balanced by supply), to a value CDRMAX when the ratio is zero. If R is the ratio of net gain to requirement for a chick in a given weight class, P_R is the frequency of R given the distribution of trip times, and D_R is the death rate of chicks in that weight class given R, then the death rate per day of chicks in that weight class is the integral of the product of D_R and P_R from $R = 0$ to $R = 1$. The value of CDRMAX is found by repeatedly running the model under normal (unperturbed) conditions with different initial values of CDRMAX until a value is found that yields a seasonal chick death rate approximating that actually observed. Chick death rate thus varies as a smooth (non-threshold) function of average trip time (Fig. 2). CDRMAX is constant for all chick age classes, but D_R will vary, because chicks in different stages have different metabolic requirements.

State changes of chicks (aside from mortality) occur either as a result of growth or ageing. Chicks hatch a fixed number of days after incubation begins and subsequently enter stage I. Transfer to older chick stages is determined by growth rates, which, within a chick stage, are a function of food delivery rates. The growth increment per day is determined by subtracting metabolic demands from the quantity of energy (food) delivered to the chick, corrected for digestive efficiency and efficiency of growth. Growth rates are not allowed to exceed those found under normal unstressed conditions. Chicks fledge when they achieve a threshold body weight, but if this weight is not achieved by a maximum age, the chicks die without fledging. This approach to chick mortality under stress conditions thus takes into account both the effects of inadequate energy for maintenance and the cumulative effects of inadequate energy for growth.

The variables that are required in the operation of the demographic submodel and the procedures used to estimate them are listed and described in Table 1.

Foraging submodel

In order to assess the influences of environmental perturbations in foraging zones upon these features of seabird demography, we should know the daily movement patterns of individual birds during the breeding season and the spatial and temporal patterns of distribution and availability of food resources in the oceanic area about a colony.

TABLE 1. Listing and description of variables required in the demographic submodel. Variables are listed by the mnemonics used in the submodel programme

Variable mnemonic	Units	Definition	Calculation
Primary input variables			
ADWT	g	Average adult weight	
ARR1[a]	Days	The time of the onset of arrival of the colony. Fixed at 1	
ARRLEN	Days	The length of the period of arrival ('migration') at the colony	
BRDLEN[b]	Days	The length of the (unperturbed) period from onset of breeding to fledging for a breeding pair	
BRDMAX	Days	The maximum proportion of adults engaging in breeding, occurring at BRD2	
CDRMAX	Probability/day	The maximum probability of chick death per day, occurring when the ratio of energy consumed to CHKREQ(I) is zero	
CHKLEN[b]	Days	The length of the (unperturbed) period from hatching to fledging for a chick (or clutch)	
CTPROP(J)[a,b]	Proportion	The proportion of time spent in each of the three chick stages. Fixed at 0·25, 0·50, and 0·25 for stages I, II, and III, respectively	
EDR	Probability/day	Probability of death per day for an egg	
EMGLEN[b]	Days	Length of the period of emigration	
GREF	g/kcal	The conversion factor from kcal (corrected for digestive efficiency) to g for a growing chick	
FW	g	Fledging weight	
HW	g	Hatching weight	
INCLEN	Days	Length of the period of incubation	
NSTAR	Numbers	Population size of breeding colony	
WTPROP(I)[a,b]	Proportion	Proportion of total weight gain from hatching to fledging achieved at the end of each chick stage. Set at 0·125, 0·875, and 1·0, respectively	
Secondary input variables			
ADREQ	kcal/day	Energy required for an adult excluding the cost of foraging and the requirements of a chick	$4\cdot68 * ADWT^{**}0\cdot734$
ARR2	Days	End of the period of immigration	$ARR1 + ARRLEN$
BRD1	Days	Onset of breeding activity, i.e. the initiation of clutches	$ARR2 + 1$
BRD2	Days	End of fledging under normal (unperturbed) conditions	$ARR2 + INCLEN + CHKLEN$
CHKREQ(J)	kcal/day	Metabolic maintenance requirements of a chick at the midpoint of stage j; calculated from the equation of Aschoff & Pohl (1970)	$WTLIM(J) - WTLIM(J-1)/(2^{**}0\cdot734)*4\cdot68$
CMG(J)	g/day	Maximum growth per day of a chick of stage j	$WTLIM(J) - WTLIM(J-1)/BRDLEN * CTPROP(J)$
EMG1	Days	Onset of emigration	$BRD2 + 1$
EMG2	Days	End of emigration	$BRD1 + BRDLEN$
WTLIM(J)	g	Weight at the end of the jth chick stage	$(FW - HW) * CTPROP(J) + FW$

[a] Variable is a fixed parameter.
[b] Variable used for calculation of secondary inputs, but not in itself a model parameter.

Unfortunately, no such data are available for any marine bird species in any habitat. However, three basic sorts of information are commonly available that can be used to approximate both daily movement patterns and food distribution: (1) the observed distributional patterns of birds at sea in colony areas; (2) the length of time that individual birds spend foraging; and (3) the daily energy requirements of breeding seabirds. We can use this information to simulate the pattern of movement and rate of energetic uptake of these birds using a combination of central place and optimal foraging theory. This requires us to make two basic assumptions. First, we must assume that the birds minimize the time spent in gaining the net daily energy requirements for themselves and their chicks; if it is

TABLE 2. Variables employed in the foraging submodel

Variable mnemonic	Description
A_i	Area of the ith sector (km^2)
β	Constant of proportionality between r_i and v_i
C	Energetic cost of foraging; i.e. the difference between the energetic cost of being at sea and the energetic cost of being at rest (kcal)
D_i	Flight distance (linear) between the colony and the centre of the ith sector
E	Daily energy requirement of an adult, including one-half the daily energy requirement of its chick(s) (if appropriate) but excluding the energetic costs of foraging (kcal/day)
K	Maximum load size that can be returned to the colony on a single foraging trip (kcal)
L	Daylength (min sunlight)
N^{*}[a]	Population size
N_i	Density of individuals in the ith sector (number/km^2)
r_i	Rate of energy uptake in sector i (kcal/min)
S	Flight speed (km/min)
T	Expected mean trip time (min)
u_i	Rate of total energetic uptake by all birds foraging in sector i (kcal.km^{-2}.min^{-1})
v_i	Productivity of sector i that is available but not used by foraging birds (kcal.km^{-2}.min^{-1})
W_i	Productivity of the ith sector that is available to foraging birds (kcal.km^{-2}.min^{-1})

[a] NSTAR in Table 1.

impossible to meet these daily requirements, then the birds maximize the energy that they do gain each day. Second, we assume that the rate at which birds assess the productivity (food availability) of the environment is short relative to the actual rate of change in environmental productivity.

Given the current state of our knowledge of seabird foraging behaviour, it is not possible to verify these assumptions. Data available for some bird species, however, indicate that birds may be capable of practising varying degrees of time minimization or energy maximization in their daily foraging (Krebs & Davies 1978; Orians & Pearson 1979). Examination of the at-sea distribution of seabirds (see Fig. 7) shows that their movements are markedly non-random, and it seems reasonable to assume that this strong deviation from random behaviour is in the direction of optimality. We thus believe that we can use optimal foraging theory to provide the basis for a model that in its general form responds realistically to perturbations, and that this is the most appropriate modelling paradigm to follow, given the limitations of the available data. Below we briefly explore the projections of model analyses when this assumption of optimality in foraging is relaxed.

The variables employed in the foraging submodel are listed and described in Table 2. Following a description of the submodel structure, we describe how some of these variables are derived, using a specific example.

Within the framework we have outlined above, the optimal strategy for a foraging seabird is to maximize its rate of energy uptake—in other words, to minimize the time spent in capturing a maximum load of K kilocalories of food. We consider the breeding colony as a point in the centre of an area of surrounding ocean that may be used for foraging. This foraging area is divided into radial sections separated by 45° (or some other appropriate angle). Concentric annuli encircling the central point at set distance intervals from the point then define sectors (the area enclosed between two adjacent radii extending from the colony and two adjacent concentric rings about the colony equals one sector). Given this spatial framework, the expected trip time, T, for a bird foraging in some sector i is

$$T = K/r_i + 2D_i/S, \tag{1}$$

where D_i is the distance to the centre of the ith sector, S is the flight speed, and r_i is the rate of food uptake while foraging in sector i. The term K/r_i is the time required to capture a full load of food while in sector i, and D_i/S is the time required to return from sector i to the colony. Note that the optimality assumption requires that a maximum load of food be captured before an individual returns, because returning with anything less would be a waste of the cost of travel. Optimality also requires that birds should tend to go to sectors in which T is minimized. If $T_i < T_j$ (where i and j are different sectors), birds should go to sector i in preference to sector j. This will continue until sector i is sufficiently depleted relative to sector j that $T_i = T_j$. Therefore, when equilibrium is achieved, T is equal for all sectors.

In order to make use of the fact that T is constant under equilibrium optimal foraging conditions, it is necessary to know the relationship between N_i, the density of birds hunting in sector i, and r_i, the average individual energy uptake rate in sector i. Solving (1) for r_i, we obtain:

$$r_i = K/(T - 2D_i/S). \tag{2}$$

The rate at which all birds are removing energy per unit area from sector i, u_i, is the product of N_i and r_i,

$$u_i = N_i r_i = N_i K/(T - 2D_i/S). \tag{3}$$

The rate at which energy is located and consumed will be a function of the rate at which energy is made available in the environment. Because energy already consumed by other birds in sector i, u_i, is not available to a subsequently foraging individual, the rate of uptake of an individual bird, r_i, must be a function of the unutilized production, v_i. If the rate at which prey items are located increases approximately linearly with increasing density of prey, we can state that

$$r_i = \beta v_i, \tag{4}$$

where β is a constant of proportionality that relates the rate of food uptake to the available productivity of a given region. Substituting for r_i from eqn (2) into (4) and solving for v_i yields

$$v_i = r_i/\beta = K/\beta(T - 2D_i/S). \tag{5}$$

The productivity per unit area of sector i, W_i, is the sum of the utilized production, u_i, and the unutilized production, v_i:

$$W_i = u_i + v_i. \tag{6}$$

Substituting from (3) and (5),

$$\dot{W_i} = (N_i + 1/\beta)r_i = [N_i + 1/\beta][K/(T - 2D_i/S)]. \tag{7}$$

Solving for r_i,

$$r_i = W_i/(N_i + 1/\beta). \tag{8}$$

From (8) it is apparent that r_i decreases with increasing density of foraging birds, asymptotically approaching zero as N_i tends to infinity, and reaching a maximum value of βW_i at $N_i = 0$. At equilibrium, all r_i at a given distance are equal (Fig. 3), and there is a value of N_i specified for each sector.

To find the optimal trip time and the optimal bird density for each sector, we must be

able to estimate the net daily gain (in kcal) of an individual, G, given a trip time, T. If we initially assume that T is known, then we can solve (7) for N_i:

$$N_i = W_i(T - 2D_i/S)/K - 1/\beta. \qquad (9)$$

The sum of the products of N_i and A_i for all sectors, $\sum N_i A_i$, is the total number of birds foraging at any instant in time. The ratio of $\sum N_i A_i$ to N^*, the total population size, is the proportion of the colony that is foraging at a given time for a particular value of T; it is also the proportion of time that an individual bird spends at sea. This ratio must be $\leqslant 1$, or $\leqslant 0\cdot 5$ for birds such as guillemots in which one or the other parent remains with the chick or egg over most of the breeding period. Knowing T and the proportion of time spent at sea, we can calculate the net gain per day, G, as a function of T. The total net energetic gain of a bird in the course of the day is the product of the rate of net energy gain while foraging and the time spent foraging. The net rate of gain per unit time on a foraging trip is the load size divided by the trip time, K/T, less the added cost of foraging, C, where C is the increment of energy expenditure per unit time over standard metabolism. The net gain per day is the product of the net rate of gain while foraging, the proportion of time spent foraging, and daylength, L:

$$G = (K/T - C) \left(\sum N_i A_i/N^* \right) L. \qquad (10)$$

To find the optimal trip time, we search for the value of T such that

$G = E$ and T is minimal, or
$G < E$ and G is maximized,

where E is the maximum amount of energy that can be utilized per day.

To carry out the optimization, we select an initial value for T and distribute birds starting from the colony and working outward using eqn. 9. When $\sum N_i A_i/N^*$ reaches its maximum value (i.e. the maximum proportion of the colony is foraging) or $G = E$, this procedure is stopped. This process is then carried out for alternative values of T, $T + \Delta T$, and $T - \Delta T$, where ΔT is some arbitrary time increment. Of these three possible values (T,
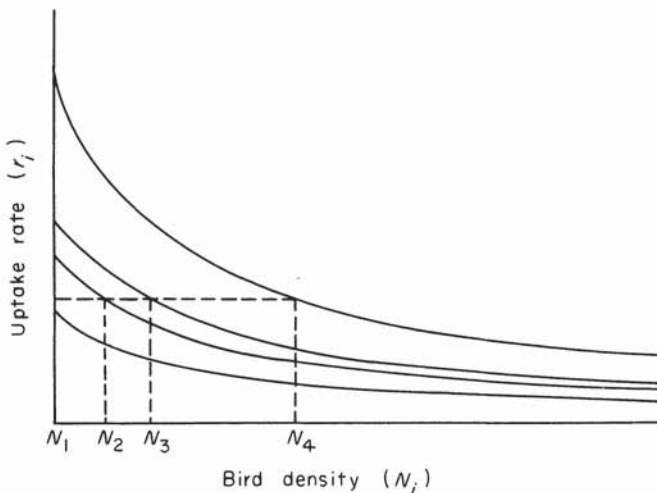

FIG. 3. The functions used to relate uptake (r_i, in kcal min^{-1}) to densities of birds (N_i) in the foraging submodel.

$T + \Delta T$, and $T - \Delta T$), we select the smallest value such that $G = E$, or, if $G < E$ in all cases, we select the value that maximizes G. This value is used to replace T and the process is iterated until no improvement can be found by modifying T by $\pm \Delta T$. We then decrement ΔT and repeat the procedure until again no further improvement can be made by changing T. When ΔT has reached a predefined minimum (0·5 min), the process is stopped.

The optimization is more complex when all of the birds in the population do not have the same constants for eqns 9 and 10. The load size, K, in eqn 9 is different for birds with and without chicks, as birds with chicks carry an additional quantity of food for feeding their young beyond what they can themselves assimilate; guillemots, for example, normally carry a single fish as a load for their chick. The daily energy requirement, E, will also vary among different classes of birds. Obviously, the daily energy requirement of an adult with a chick nearly ready to fledge will be much greater than that of a non-breeding or incubating adult. These differences complicate the calculation of foraging equilibrium because we must deal with two types of trips, those with and without added loading for chicks, and different energy demands associated with adults with chicks in varying stages of development.

To solve this more complex optimization problem, we first select two values for trip times, T_1 and T_2, corresponding to adults without and with chicks, respectively. Birds are distributed in accordance with eqn 9 as before, except that each sector is assigned to adults of type 1 or type 2 depending on which class will reduce the food supply in that sector to the lowest level. Thus, if, for sector i, $K_1/(T_1 - 2D_i/S) < K_2/(T_2 - 2D_i/S)$ (see eqn 2), sector i will be assigned to type 1, birds without chicks. This is continued until the maximum proportion of each type is foraging or until the total energy demands of all the birds of both types are satisfied. The trip time for type 1 birds, T_1, is then incremented by $\pm \Delta T$ as described above while holding T_2 constant, and the preferred value of T_1 is selected as described above. The process is then repeated for birds of type 2, selecting the preferred value of $T_2 - \Delta T$. T_2, and $T_2 + \Delta T$ while holding T_1 constant. The algorithm proceeds in this manner through successive decrements of ΔT as before until no further improvements can be made by either type, and the process is then terminated.

Once the optimal values of T are found, the distribution of birds is then specified and is used for estimating the effects of environmental perturbations such as oil spills. T_2 is used as input to the chick death rate submodel, and G is calculated from eqn 10 and used as input to the demographic submodel for determining chick growth rates.

Modelling the primary effects of an oil spill requires that we know three additional parameters: (1) the probability of death per unit time of a bird encountering a spill (ρ); (2) the rate at which a population of foraging birds tracks or responds to environmental changes (τ); and (3) the proportion by which the productivity (W) of the perturbed region is lowered, Δ. The probability of death can be estimated from descriptions of oiled birds available in the literature (e.g. Bourne, Parrack & Potts 1967; Bourne 1968; Holmes & Cornshaw 1974; Vermeer & Vermeer 1975; King & Sanger 1979; P. G. Conners & S. Gellman personal communication), although actual mortality probabilities are not available. The second and third parameters are currently unknown and until pertinent data can be collected they must be approximated by intuition.

At each time step in the model analysis, a distribution of foraging birds is calculated. If a sector contains an oil slick (or is otherwise perturbed), birds of the type utilizing that sector suffer mortality proportional to the area of the sector covered by the slick. The probability per day that an adult of class j (determined on the basis of load size and energy requirements) will contact a spill in sector i and die is calculated from O_i and N_{ij}, where O_i

is the area covered by the slick in i, and N_{ij} is the density of birds of class j foraging in i. The average time spent on each trip foraging in i will be $(T_j - 2D_i/S)$. The average number of trips will be the net energy requirement divided by the net gain per trip, $E_j/(K_j - CT_j)$ (providing that this value does not exceed the maximum length of time the bird can be away from the nest). The total time spent foraging in i by a bird of class j, F_{ij}, is

$$F_{ij} = [E_j/(K_j - CT_j)]\,(T_j - 2D_i/S). \tag{11}$$

If ρ is the probability of death per unit time while foraging in the vicinity of a spill, then the probability of death per day for a bird of class j foraging in that area is $[1 - (1 - \rho)^{F_{ij}}]$. The total number of birds of type j that die per day while foraging in sector i is then:

$$N_{ij}\,O_i[1 - (1 - \rho)^{F_{ij}}]. \tag{12}$$

At the next time step, each adult class is reduced by the number of birds dying in the polluted sector, and a new equilibrium distribution is generated. We do not assume, however, that equilibrium is necessarily achieved in only one time step. The new distribution is the weighted average of the previous distribution and the new equilibrium distribution. The weighting factor, τ, determines the number of days, $1/\tau$, required for the population to move from one equilibrium to the next.

Estimation of foraging submodel parameters

To illustrate how the major parameters employed in the foraging submodel are estimated or derived, we relate the submodel to the two guillemot species and the two kittiwake species breeding on the Pribilof Islands. The dynamics of these populations will also form the foundation for preliminary applications of our models, as detailed below.

β

Given a subset of the total number of sectors within which it is reasonable to assume that total productivity (W_i) is not simply a function of distance from the colony (island), we can use eqn (9) to estimate β. Rearranging eqn (9), we find that bird density, N_i, is a linear function of distance, provided that W_i does not change systematically with distance:

$$N_i = (-2W_i/SK)\,D_i + TW_i/K - 1/\beta. \tag{13}$$

We regress bird density on distance for each sector to derive the equation

$$N = mD + b. \tag{14}$$

We then solve for β as a function of the constants of the linear regression line, m and b.

In calculating β using actual distributional data for birds at sea, the assumption that W_i is independent of distance from the island is at times rather obviously violated. For guillemots about the Pribilofs, for example, exceptionally high densities are present in some of the relatively shallow inshore waters around St George (see Fig. 7). These high-density regions may be associated with demersal feeding or with euphausiid swarms at the surface near tide rips, and as such their high densities are related in part to nearness to the island. These sectors were not used in the calculation of the regression equations, and thence of β. Finding an appropriate subset of distance-independent W_i sectors for kittiwakes is somewhat more difficult. They appear to localize much of their feeding activity along the continental shelf break south and west of St George (see Fig. 8). Thus W_i increases (at least

to the south-west) as D_i increases. We therefore used only those sectors that lie along the region of the shelf break for estimating β for kittiwakes.

C

The incremental cost of foraging is a composite of the cost of flight, the cost of diving, and the cost of sitting on the sea surface, and it depends upon the relative proportions of time spent by a species in each of these three activities. As precise time budget information is not available for foraging birds at sea, we estimated this parameter using our experience and the derivations of King (1974). The cost of foraging does not include the underlying metabolic costs that would have been required had the bird remained at the colony.

E_j

The daily energetic requirement of a nonactive bird at thermoneutrality is calculated from the equation of Aschoff & Pohl (1970):

$$\text{kcal/day} = (1 \cdot 3)\,(3 \cdot 6)\,(\text{Weight})^{0 \cdot 734}.$$

This is incremented by one-half the energy requirements of a chick (or chicks) of the mean weight of stage j plus the growth requirement for stage j, assuming a growth efficiency of $0 \cdot 75$ (Ricklefs 1974) and a digestive efficiency of $0 \cdot 75$ (Wiens & Innis 1974).

K

The maximum load of food that can be returned to the colony on one foraging trip is assumed to be the total requirement of an adult (including both resting and foraging costs) plus one-half of the maintenance and growth requirements of a chick of stage j, divided by the mean number of trips per day. Energy requirements are corrected for a digestive efficiency of $0 \cdot 75$ (Wiens & Innis 1974).

N^*

Estimates of total population sizes of colonially breeding seabirds are difficult to obtain, either because the extent of the colony itself or the numbers of non-breeding individuals foraging near the colony are unknown. To some degree, the isolation of the Pribilof Islands from other colonial nesting areas reduced such problems. To obtain values of N^* for our analyses, we used the values of Hickey & Craighead (1977), which were derived from counts of birds inhabiting subsamples of the cliff nesting areas on the Pribilofs.

N_i

Determination of the densities of individuals in each sector requires rather complete and precise estimates of the pelagic distributional patterns of individuals in the vicinity of a breeding colony. For the Pribilof analyses, we employed the data obtained on shipboard transects by Hunt for 1975–1977. The derived density estimates were corrected for total population size and time spent foraging so that the sum of all birds observed at sea divided by the time spent foraging was equal to the total population size.

S

Flight speeds may be obtained by monitoring the time required for birds flying in a straight line to pass between two points separated by a known distance. We obtained such estimates for guillemots and kittiwakes during studies on St Paul in 1978.

T

Mean trip time may be calculated by observing specific nest sites in a colony and determining the time between departure on a foraging trip and return of individuals to those nest sites. Such measures necessarily assume that flight to a foraging sector is direct and that once a bird arrives at a sector it initiates foraging immediately. Our estimates of trip times were calculated from the data of Hunt (1977) and R. Squibb (personal communication).

W_i

One of the most difficult tasks in the development of this foraging submodel is finding a way to estimate the distribution of food resources available to foraging birds. To estimate this parameter directly would require a detailed knowledge of the abundance of fish and invertebrate prey over an area extending nearly 200 km from the breeding colony (in the case of the Pribilofs). Data of this sort are not available, and to obtain them would require enormous effort and expenditures. An alternative method would be to use telemetry to determine the success rates of individuals foraging in different areas, and then use this as an indirect measure of prey abundance. This approach has the advantages of being both less difficult and probably more accurate, as it is more likely to measure the density of available prey, which is potentially quite different from the absolute density of prey. Because neither of these approaches was open to us in our analysis of the Pribilof colonies, we resorted to a third method of estimating W_i that requires knowledge only of bird distributions and the assumption that the formulation of the foraging submodel is a substantially correct interpretation of the birds' behaviour. We thus use the distribution of N_i to tell us what the distribution of W_i must be in order to satisfy eqn (9). Knowing K, T, and S, and having estimated β, we can solve eqn (9) for each W_i given N_i and D_i (because K and T vary with adult type, we use weighted averages based on the estimated proportions of birds in each adult class). This has the advantage of guaranteeing consistency between observed and modelled foraging distributions under unperturbed conditions, but makes it impossible to double-check the validity of the foraging submodel.

SENSITIVITY TESTS

A complex simulation model such as we present here involves large numbers of input parameters, many of which must be based on data with high variances, small sample sizes, or in some cases educated guesswork. These parameters often involve synergistic interactions, so that perturbing only one variable at a time can give a misleading impression of model stability. For this analysis, we have used a Monte Carlo simulation in which each input variable (see Tables 1 and 2) was simultaneously perturbed for each of a series of model runs. The variation in output values of adult survivorship and number of chicks fledged was used as an index of model stability. As the actual distributions of most of the input parameters are even more difficult to obtain than average values, we drew perturbed values from a triangular or 'housetop' probability distribution defined by the range and most likely value of each parameter (see O'Neill 1979).

Five runs were made for the St George guillemot population based on three oil spill scenarios (A, B, and C, described in detail below). All input parameters except three relating directly to the interaction between foraging birds and oil slicks were varied simultaneously by randomly drawing values from triangular probability distributions of each parameter. The three parameters that were excluded from this portion of the analysis

were τ, the rate of environmental tracking, ρ, the probability of death on encountering a spill, and $\varDelta$, the reduction in food supply of the perturbed region.

Table 3 gives the results of the Monte Carlo sensitivity analysis for the remaining primary inputs. Standard errors range from 0·03 to 0·21 except for fledging success for scenario C. The relatively large standard error in this case (0·79) results from the small number of chicks fledged on any model run (see scenario C, below).

The three parameters excluded from these analyses, τ, ρ, and $\varDelta$, were approximated by educated guessing because no data are available that can be used to estimate them either directly or indirectly. The probability of death following a spill encounter (ρ) is unknown for any seabird species. We chose conservative values for this parameter in our model analyses (1·0 for guillemots, 0·5 for kittiwakes). Guillemots were considered to be more susceptible than kittiwakes because they spend more time sitting on the surface and diving. Within what we consider to be a reasonable range of values for this parameter (the stippled region of Fig. 4), model results are relatively insensitive to the precise value of ρ, varying only by about 25%. This insensitivity, however, results in part from our basic assumption that no learning takes place on the part of birds that have encountered a spill. This is a convervative assumption that cannot be verified until spill encounters can be described in more detail than is currently available.

The rate of environmental tracking, τ, determines the rate at which new birds enter a polluted region and encounter a spill. The value of τ could only be measured by detailed monitoring of the movement patterns of individual birds, information that we lack. We

TABLE 3. Results of Monte Carlo sensitivity tests of short-term model input parameters (see text). The values are standard errors for values of adult survivorship and numbers of chicks fledged for five Monte Carlo simulation runs using the conditions of scenarios A, B, and C (see below and Figs 12–16)

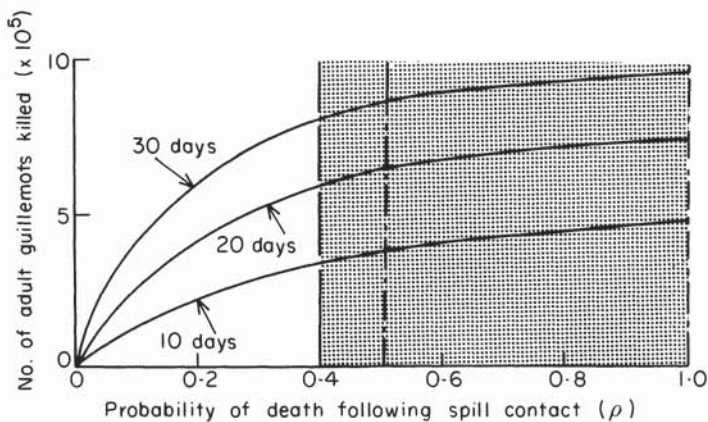| Scenario	Adult survivorship	Chicks fledged
A	0·16	0·04
B	0·21	0·04
C	0·03	0·79

FIG. 4. The number of adult guillemots killed by a 1000-km² offshore oil spill simulated with persistence times of 10, 20, and 30 days. The impact of the spill is plotted as a function of ρ, the probability of death following spill encounter. Dashed lines indicate values used in model runs; 0·5 for kittiwakes and 1·0 for guillemots. The stippled region corresponds to what we consider a reasonable range of values of ρ.

used what we consider to be a relatively rapid rate of environmental tracking, 5 days for both guillemots and kittiwakes. More rapid tracking rates lead to higher kills from oil spills because new individuals move more rapidly into the spill region to replace those that have died (Fig. 5). Within the range of reasonable values for this parameter, however, the model is more sensitive to τ than to ρ, varying by as much as 50% for reasonable values of τ.

The constant Δ determines the extent to which a region impacted by an oil spill loses its attractiveness (i.e. the amount the density of food is diminished) to foraging birds. For most of the analyses reported here, we have assumed that there is no reduction in attractiveness ($\Delta = 0$). This assumption was made because there are no data available that indicate otherwise, and the assumption of unchanged attraction is conservative in the sense that the higher the degree of attractiveness, the more adults will be killed and the more severely the population will be affected. If foraging birds to some extent avoid slick areas or the slick itself, however, this immediately lowers the perceived food supply, and the adult kill rate will be lowered while the chick death rate is raised. This is because in the model structure a high loss rate of adults (and the concomitant loss of their chicks if they are breeding) eases competition for food resources, thereby increasing delivery rates and decreasing the loss of chicks due to causes other than parental death. If adults avoid a region normally utilized for foraging, on the other hand, delivery rates will decrease and chick death rates due to causes other than adult death will rise. These effects are illustrated in Fig. 6, where both adult death and chick death are plotted for scenario C for guillemots for varying values of Δ. Within the range of Δ values of 0·0–0·5, adult death rate and chick death rates due to parental death or other causes remain relatively constant. Between values of Δ of 0·5 and 1·0, however, adult death rates and total chick death rate decline steeply, although chick death rate not due to adult death approximately doubles. In general, chick death due to parental loss is much more significant than chick loss due to increased foraging time. Note also that scenario C involves probably the most extensive loss of foraging areas that is likely to occur for guillemots as a result of a single major spill; under most other possible spill scenarios, the relative importance of chick death due to decreased food supply would be less.
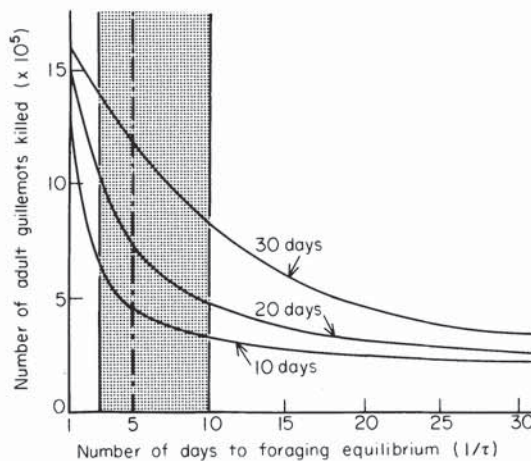

FIG. 5. The number of adult guillemots killed by a 1000-km² offshore oil spill simulated with persistence times of 10, 20, and 30 days. The impact of the spill is plotted as a function of $1/\tau$, the number of days required for the population to reach a new equilibrium foraging distribution following perturbation. Stippled region and dashed lines as in Fig. 4.
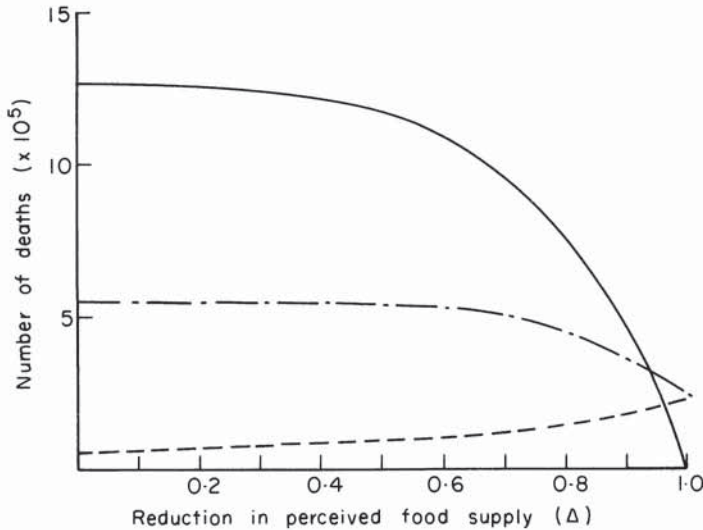
FIG. 6. The number of adult and chick guillemots dying as a consequence of various levels of reduction in the apparent food supplies following an oil spill covering 1680 km² and persisting for 30 days (scenario C; see below and Fig. 16). ——, adult death; —·—, total chick death; ———, chick death not due to adult death.

MODEL ANALYSES

Here we employ some of the colonially breeding seabirds that occur on the Pribilof Islands as examples of the sorts of results that this model provides. Because these analyses were conducted using data gathered during the first phases of studies on these islands, their results should be considered as general qualitative indications of the potential impacts of perturbations rather than precise, definitive predictions.

Our analysis of the potential impacts of oil development has concentrated on the area around St George, because of its overall importance. We have conducted model analyses for the two guillemot species and the two kittiwake species, which we considered to be the most appropriate and important species. Guillemots and kittiwakes constitute the major portion of the breeding avifauna of the Pribilofs; the red-legged kittiwakes breeding there represent most of the world's population of this species, and guillemots, while abundant at many locations in northern oceans, are especially vulnerable to oiling (Brown *et al.* 1975). We lacked adequate field data to extend the analysis to any other species breeding on these islands, but the results of these analyses may be qualitatively applicable to at least some of the unanalysed species.

Guillemots and kittiwakes are distributed in the waters about St George and St Paul in a distinctly non-random fashion. Guillemot densities are highest relatively close to the islands (Fig. 7), although, as noted previously, there are major density concentrations in the relatively shallow waters directly east of St George and to the south-east of St Paul. Generally, guillemot densities at sea are low at distances greater than 60 km from the breeding island. The distributional pattern of kittiwakes, on the other hand, is strikingly different from that of guillemots (Fig. 8). Kittiwake densities are generally rather low in the areas immediately adjacent to breeding colonies, and instead are concentrated in sectors generally lying in the region of the continental shelf break to the south-west and south of St
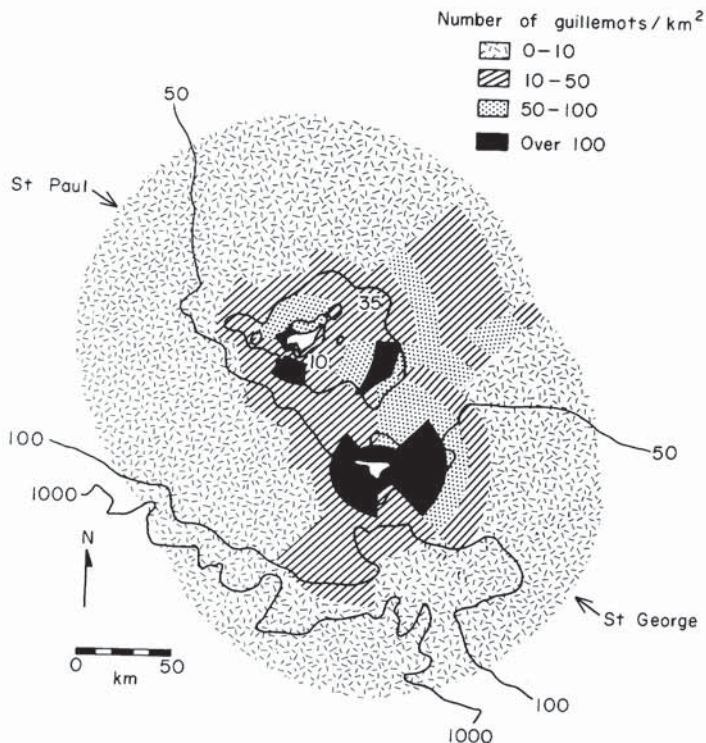
FIG. 7. The oceanic distribution of guillemot densities (birds km^{-2}) by sectors out to 120 km
from St Paul (above) and St George (below). Densities in sectors with no sampling effort were
extrapolated from the densities in adjacent sectors. The contours indicate depth (m).

George. This concentration is primarily of red-legged kittiwakes that forage for myctophid
fish, midwater fish that are found in the shelf slope and oceanic waters and that come to
the surface at night. These fish comprise a major portion of the kittiwake's diet (Hunt,
Eppley & Drury 1981). The distributional patterns of the two kittiwake species are
generally similar, although red-legged kittiwakes exhibit a tendency to occur at greater
densities than black-legged kittiwakes in the sectors relatively close to and south-east of St
George.

Using these distributional patterns as a foundation, and employing values from the
initial phases of studies of these species conducted on the Pribilof colonies to specify input
parameters, we examined the potential effects of oil spills on guillemots and kittiwakes by
calculating the kill rate of adults per km^2 for spills occurring in each sector defined by
radials of 45° and annuli 12 km in width for guillemots and 16 km for kittiwakes. The kill
rate is the number of adults killed per day per km^2 on the first day of a spill occurring at
the peak of the breeding season when the energy requirements of adults and chicks are at
their maximum (designated as mid-July for kittiwakes and mid-August for guillemots). As
an index of sensitivity, it has the advantages that it is not dependent on the size or duration
of the spill and is a conservative estimator because it is made at the peak of foraging
activity and on the first day of the spill, when the kill rate will be maximal.

The distribution of kill rates for guillemots around St George (Fig. 9) is generally similar
to the distribution of densities shown in Fig. 7. Kill rates are highest in the shallow inshore
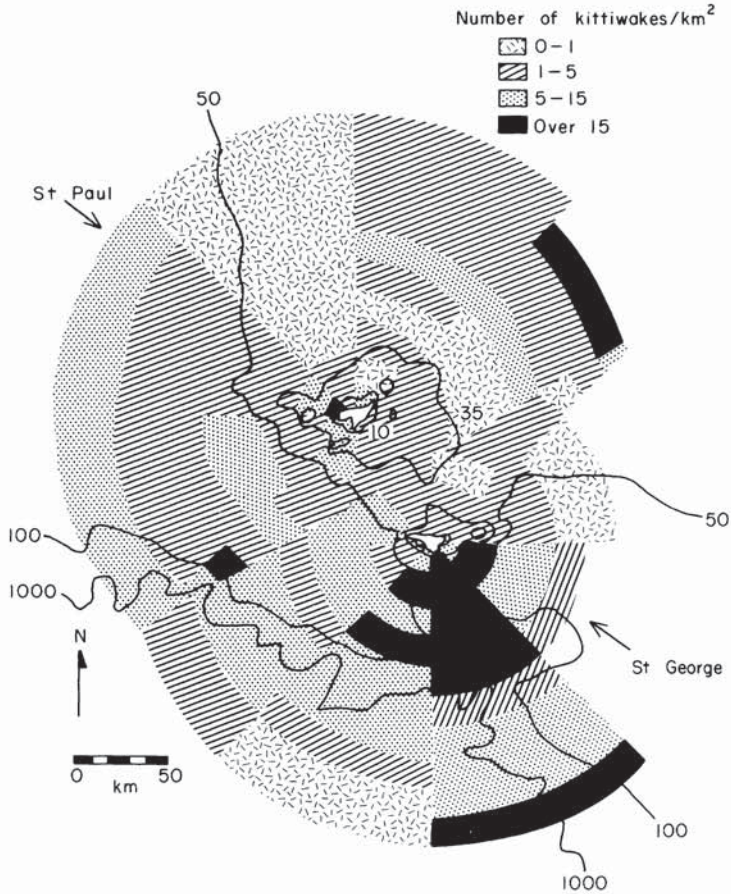
Number of kittiwakes/km^2

◌ 0–1
▨ 1–5
▨ 5–15
■ Over 15

50

St Paul

50

35

10

100

1000

N

0   km   50

St George

50

100

1000

FIG. 8. The oceanic distribution of kittiwakes (densities in birds km^{-2}) by sectors out to 160 km from St Paul and St George. Blank sectors received no sampling effort, and the available data do not permit extrapolation from adjacent sectors.

feeding areas around the island, reaching values as high as 1031·6 adults dying per km^2 per day. This analysis assumes that there is no change in attractiveness of these areas and that the probability of an ultimately fatal spill contact (ρ) of a bird utilizing these regions is 0·002, or about 0·50 per day. The sensitivity drops off rapidly around 24 km and is negligible beyond 60 km. Kittiwakes, on the other hand, have much lower maximum kill rates than guillemots (Fig. 10) because their population size is smaller, they disperse over a larger area, and they do not tend to aggregate as densely.

The direct mortality of oiled adult birds is not the only way in which a seabird population might be impacted by development. It is also possible that the effects of oil or other pollutants on food organisms, lingering effects of a single massive spill, or the development of an extensive fishery could lower the breeding success of a colony by decreasing the food supply, thereby decreasing the delivery rate of food to chicks. We examined such a possibility for the St George guillemot population by first assuming that specific spill scenarios resulted in the destruction of the food supply in the impacted region without directly affecting the survivorship of adults. The effect of spills of moderately large
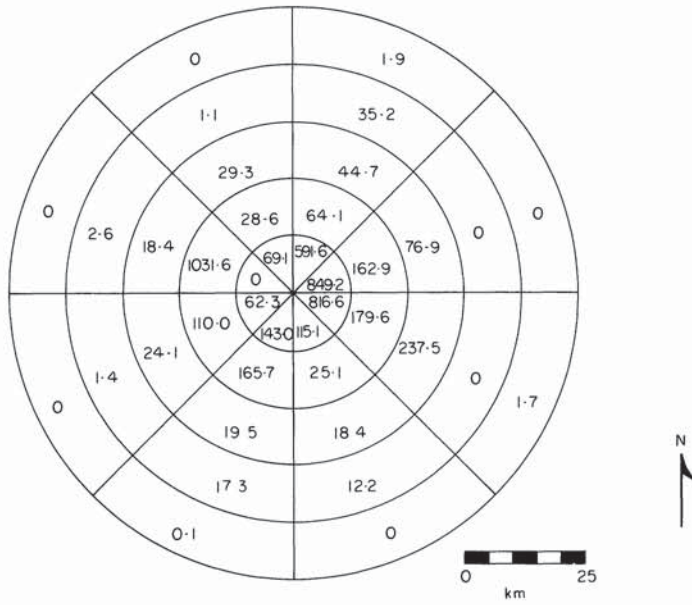
FIG. 9. Number of adult guillemots killed per day per km² on the first day of an oil spill occurring in each sector around St George Island. We assume that birds do not avoid the spill and that the probability of death per minute for a bird foraging in the perturbed region is 0·002 (or about 0·5 per day). Annuli are spaced at 12-km intervals.
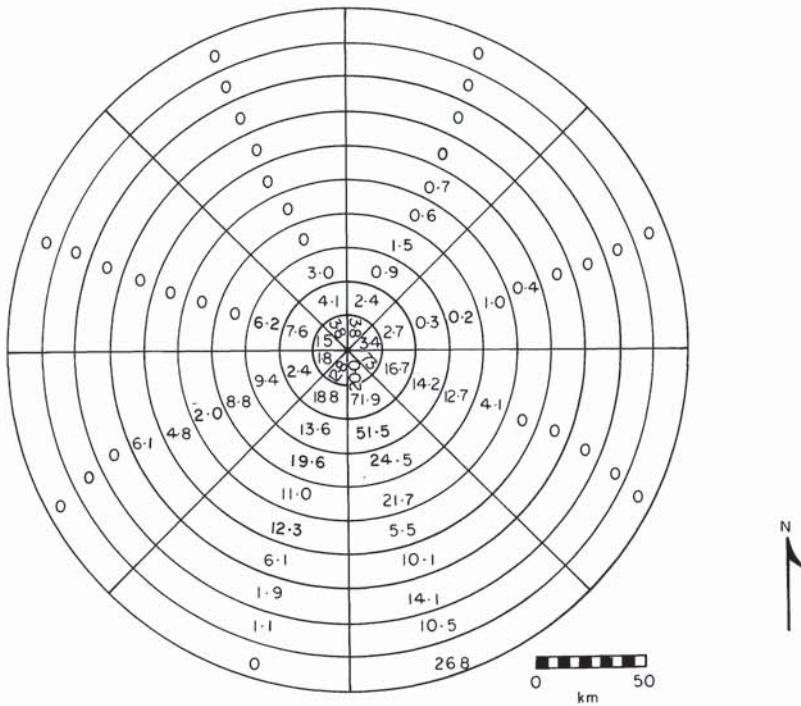

FIG. 10. Number of adult kittiwakes killed per day per km² on the first day of an oil spill occurring in each sector around St George Island. Assumptions as in Fig. 9. Annuli are spaced at 16-km intervals.
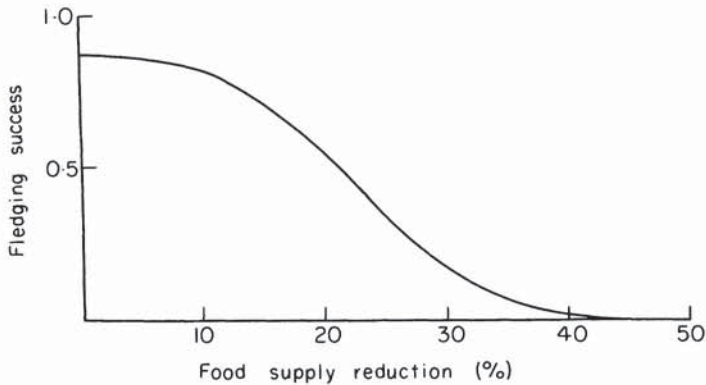
FIG. 11. Model estimation of the degree of reduction in fledging success of guillemots breeding on St George Island following region-wide reductions of food supplies by varying proportions.

dimensions (see scenarios A and B below) was found to be relatively small, resulting in a decrease in fledging success of several percent. A worst case scenario (see scenario C below) in which a very large spill destroyed most of the inshore feeding grounds, however, resulted in a reduction of the ratio of chicks hatched to chicks fledged from 0·86 to 0·46.

Because single spills are unlikely to cover areas of sufficient size and importance to affect trip times severely, we also examined the effect of a regional reduction in food supply by lowering the productivity (W) in all sectors by a set proportion. Such an effect might be produced by chronic large-scale pollution or the development of a previously unexploited fishery. Model results indicate that the St George guillemot population could tolerate an overall reduction in food supply of about 10% (Fig. 11) without a major decline in fledging success, but fledging success drops off steeply between a reduction of 10% and 30%. An overall reduction in food supply of 40% or more results in total colony failure. Variations in food supply of this magnitude occur naturally, and it is also possible to envisage a development scenario that could lead to such a rapid change in productivity (e.g. the anchovetta fishery in Peru).

OIL SPILL SCENARIOS

One of our objectives in developing these models was to provide a management tool for evaluating the potential effects of specific oil development policies on seabirds. Scenarios that project the consequences of specific perturbation events may be especially useful for this. Here we present three examples of the sorts of analyses that our models can provide, using oil spill scenarios and their projected impacts on the guillemots and kittiwakes breeding on St George Island. Although we believe that the oil spill magnitudes, trajectories, and persistence used for these scenarios are realistic, they are not based upon actual studies of oil spill dynamics in these oceanic areas.

Spill scenario A

In this scenario (Fig. 12) we consider a spill of approximately 1000 barrels originating 24 km east of St George that originates on 22 June and persists until 7 July. The spill moves to the north-west, partly encircling the island; its maximum extent is 455 km². This situation thus models a moderate-sized spill that occurs in the middle of the breeding season near the colony and is carried inshore by currents. Guillemots are strongly affected by this perturbation because this region is one of their principal feeding grounds. The model estimates suggest that such a spill scenario would lead to the death of approximately 627 500 adult guillemots (39% of the adult population); the fledgling production would be reduced by 69%. The effect of these reductions upon the seasonal age structure of the population is shown in Fig. 13, which contrasts the population structure under these spill conditions with that normally found. Given these changes in survivorship and analysing them with a preliminary version of a model of long-term effects (see below), we estimate that a population suffering this sort of perturbation would require roughly two decades to recover to a stable age distribution. Kittiwake populations are less severely depressed by this perturbation, largely because their activities are not concentrated in areas close to the breeding island. We estimate a reduction of 15% in the adult kittiwake population (42 500 adults killed directly) and a loss of 27% of the normal fledgling production.
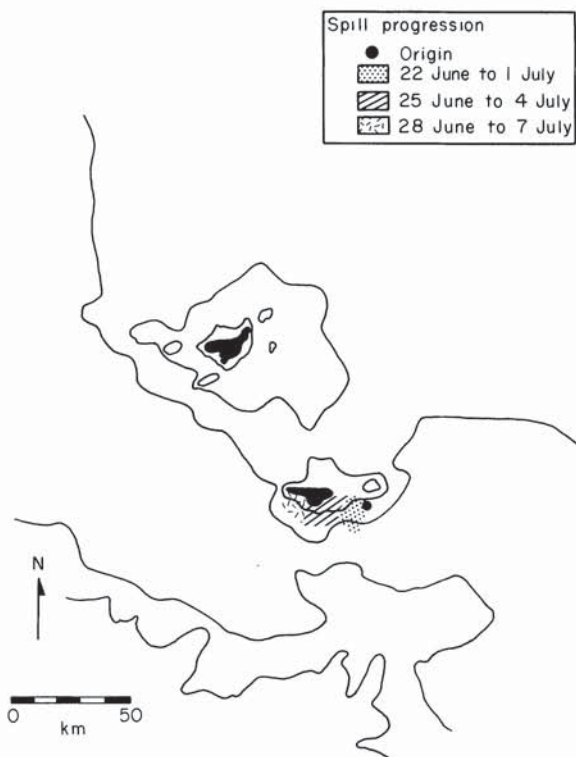

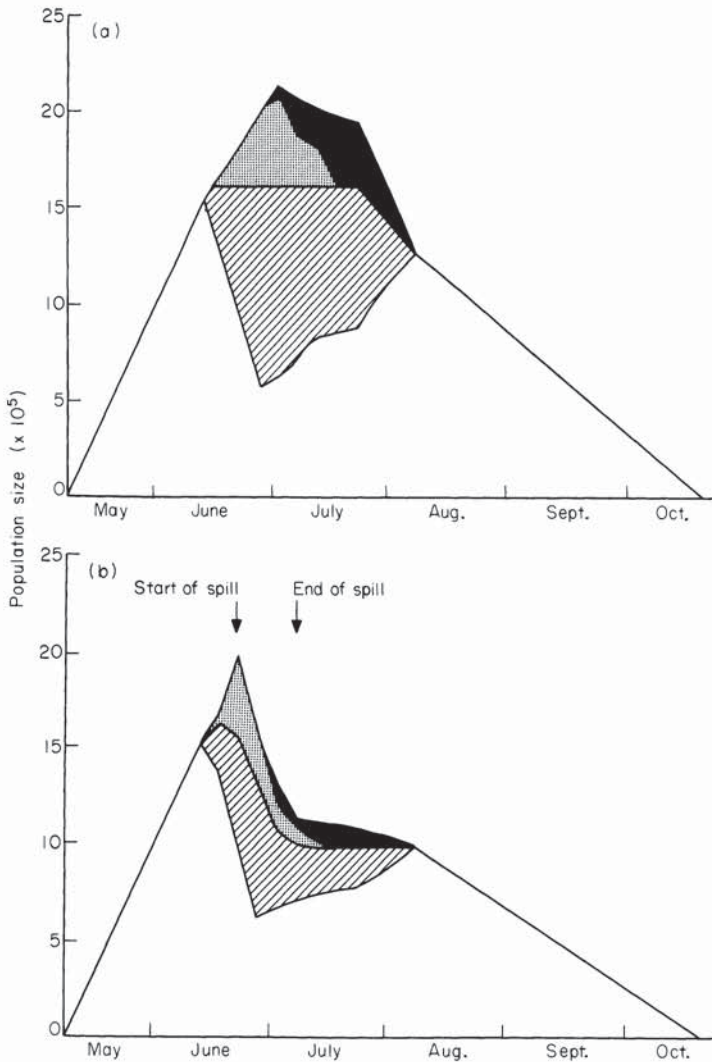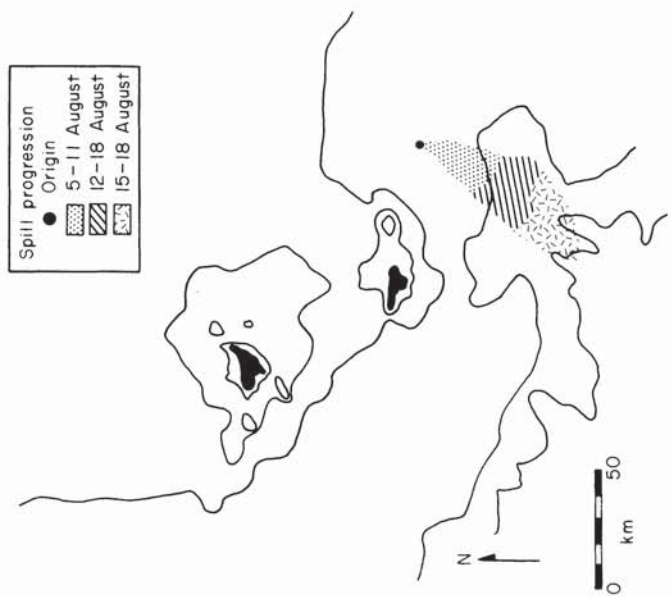FIG. 12. Oil-spill progression for scenario A.

FIG. 13. Model projections of age structure and phenology of the St George guillemot population during a normal year (a) and under the conditions of spill scenario A (b). The width of each band is equal to the number of individuals in that category. ▩, eggs; ■, chicks; ▨, breeding adults; □, non-breeding adults

Spill scenario B

In this scenario (Fig. 14) a relatively large spill of approximately 3500 barrels occurs late in the breeding season (5–18 August) 60 km south-east of St George and drifts south-west with prevailing winds across the shelf break, covering a maximum area of 1498 km². Because this region is an important feeding area for kittiwakes but beyond the normal distance flown by guillemots, kittiwakes suffer greater disruption of population structure. For guillemots we estimate that such a spill would result in mortality of 6% of the adult
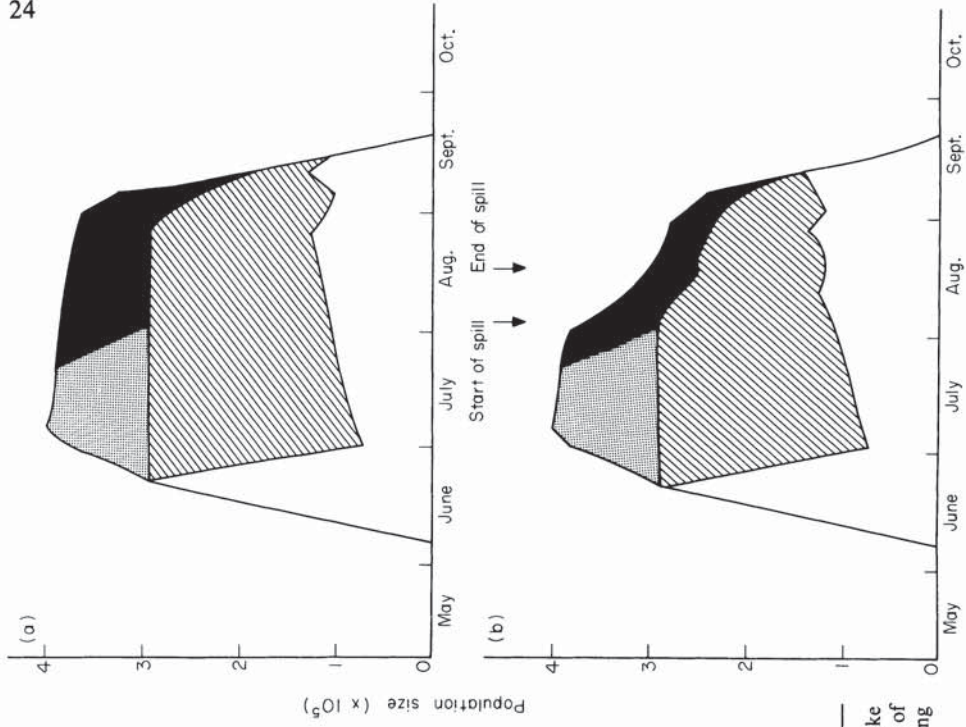
Fig. 15. Model projections of age structure and phenology of the St George kittiwake population during a normal year (a) and under conditions of spill scenario B (b). The width of each band is equal to the number of individuals in that category. ▨, eggs; ■, chicks; ▨, breeding adults; ☐, non-breeding adults.

Fig. 14. Oil-spill progression for scenario B.

population (93 600 birds) and a reduction in the fledgling population of 14%; approximately 2 yr might be required for a recovery to a stable age distribution. For kittiwakes, on the other hand, this spill would lead to the death of 41 460 adults (14% of the population) and a reduction of offspring production of 28%. The temporal patterns of these effects upon kittiwake population structure in relation to a normal year are shown in Fig. 15.

Spill scenario C

In this scenario we consider a large spill (approximately 4000 barrels) that occurs during the middle of the breeding season (27 June–27 July). It originates 24 km west of St George (Fig. 16) and is carried south and west around the island by inshore currents. It covers a maximum area of 1680 km², much of it in one of the principal guillemot foraging areas. This results in a 68% mortality of adult guillemots (1 094 000 birds killed) and a reduction in fledgling production of 96%. Under these circumstances the population is severely depressed, and recovery to a stable age distribution might take as long as four decades. The adult population of kittiwakes, on the other hand, is reduced by only 10% (28 200 birds), fledgling production by 15%.
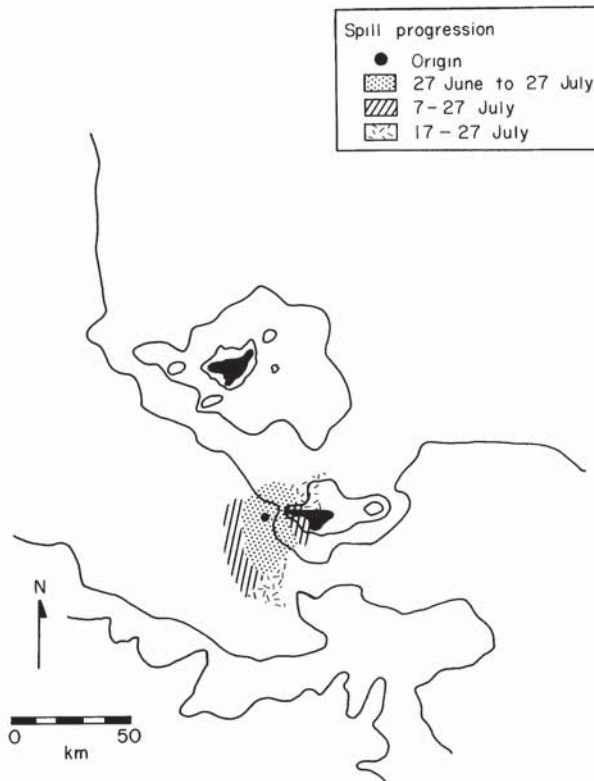

FIG. 16. Oil-spill progression for spill scenario C.

LONG-TERM EFFECTS

When considering the potential impacts of localized and sporadic perturbations such as oil spills, or of chronic low-level pollution and/or colony disturbance associated with oil resource development, it is important to estimate the long-term effects of such perturbations upon the structure and stability of the population. In addition to the short-term effects considered above, there are two components of the long-term effects of perturbations on the persistence or stability of a population, the time to recovery, and the minimum perturbation magnitude necessary to make recovery impossible (extinction point). Localized one-time perturbations may cause mortality in one or several age classes of a population, which will then be followed by a period of population growth until the population recovers to its original size and age distribution; if severe, such perturbations may lead to extinction. Chronic low-level pollution or disturbance may produce permanent changes in the survivorship and fecundity schedules of a population, which can alter the recovery time and extinction point for one-time perturbations. Attempts to model the dynamics of seabird responses should include consideration of these long-term effects.

Our efforts to develop such long-term models of seabird population dynamics, however, have been severely hampered by a lack of data for the most basic and essential parameters. For example, to develop a model of long-term population effects that is really useful, one needs information on (1) age-specific fecundity and survivorship and their variances; (2) the form of density-dependence of fecundity and survivorship; (3) the amount of emigration and immigration, their variances, and their dependence on density; and (4) the extent to which non-breeding adults and subadults may buffer the population from the effects of mortality among breeding birds. For the Pribilof seabirds that we have considered, data are available only on average fecundity and its variance. Values for age-specific survivorship of the two guillemot species are available for several populations in the North Atlantic (Mead 1974; Birkhead & Hudson 1977). As fecundity rates for these populations are similar to those for the Pribilof populations, we might provisionally expect the survivorship patterns from the North Atlantic to be similar to those of the Pribilof populations. No data on the other population dynamics parameters are available for guillemots. Some information on age-specific survivorship, intercolony movement, and dependence of fecundity and survivorship on density is available for one population of black-legged kittiwakes in the British Isles (Coulson & White 1959; Coulson & Wooller 1976; Wooller & Coulson 1977; Kosinski & Podolsky 1979), but it would be inappropriate to apply these data to the Pribilof populations, because Coulson's colony is very small, it is in an unnatural location, and the fecundity rates are not at all similar. We therefore report here only preliminary results from our analyses of the guillemots.

To explore the potential long-term effects of oil development on guillemot populations in the Pribilof Islands, we considered two important one-time mortality scenarios. The first occurs when adults are killed due to oil contamination and the second when chicks die of starvation due to a reduction in the rate of energy (food) delivery that occurs when adults are forced to make longer foraging trips to avoid areas contaminated by oil; the effect of most other scenarios of one-time mortality is quite similar to one of these two scenarios. Because we lacked data relating guillemot survivorship or fecundity rates to population density, we used a density-independent model in these preliminary analyses. Model estimations of recovery time following one-time mortality episodes of varying intensities on different age classes indicated that recovery time is longest with adult mortality and shortest following first-year mortality (Fig. 17). Note that complete breeding failure in one
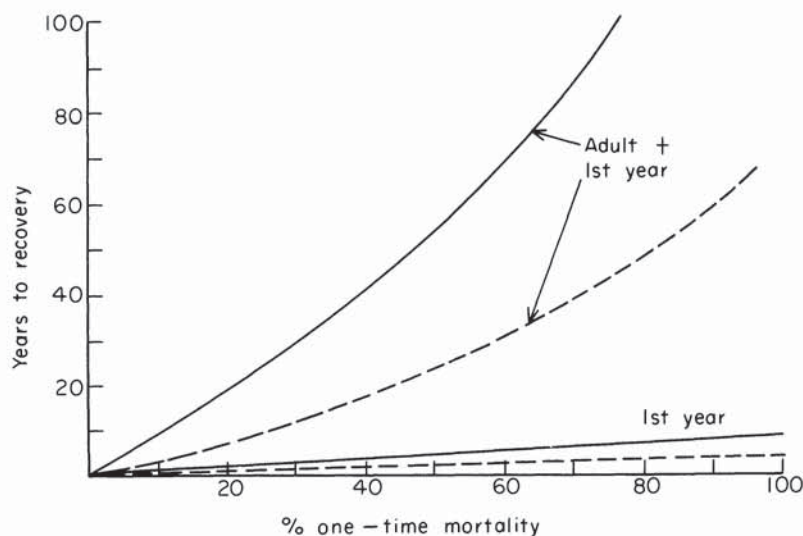
FIG. 17. Time to recovery of a stable age distribution and the original population size as a function of one-time mortality for adult and first-year Common (——) and Brünnich's guillemots (–––).

year may have a lesser effect than a 5% one-time die-off of adults. The differences in recovery times between common and Brünnich's guillemot reflect the difference in their annual rates of population increase (1% and 2%, respectively), which is primarily due to the higher fecundity of Brünnich's guillemot on the Pribilofs. The extreme sensitivity to adult mortality and insensitivity to first-year mortality are of course to be expected for species with high adult survival rates, as is the case with guillemots (Birkhead & Hudson 1977). This result is probably generally applicable to large seabirds breeding on the Pribilofs.

We modelled chronic low-level effects by changing the fecundity or survival rates of a population by a specified amount and then determining the time to recovery following an episode of one-time adult mortality. A very small decrease in fecundity (Fig. 18) or in adult survival (Fig. 19) produces large increases in recovery time. As might be expected, recovery time proved to be largely insensitive to changes in first-year survival rates. Figure 19 shows the projected change in survivorship that will lead to population extinction. Were we able to consider density-dependent influences, however, this threshold would probably be lowered and the curves flattened, as chronic changes in survivorship that produced a negative annual rate of population growth would probably be offset by an increase in fecundity and perhaps some rebound in survivorship when the population reached a lower density. In general, much larger changes in fecundity are needed to produce a similar effect (Fig. 18).

It seems likely that the seabird populations breeding in the Pribilofs would be somewhat buffered from such chronic or one-time perturbations by density-dependent changes in population parameters, immigration, or recruitment from the pool of non-breeding adults. These preliminary model analyses of long-term effects are thus quite simplistic. Because the natural fecundity rates of the birds are low and extremely variable, however, even these preliminary model estimates may have some bearing on reality, for even small decreases in the fecundity or survivorship rates due to chronic pollution or colony disturbance may
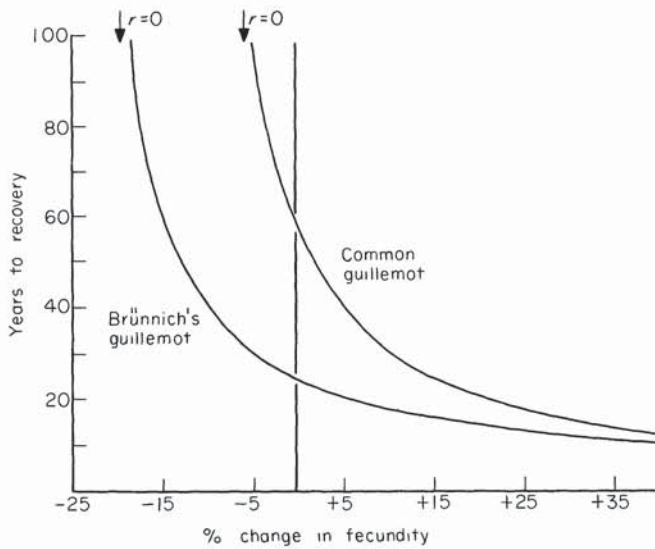
FIG. 18. Time to recovery as a function of long-term changes in mean fecundity rate, at 50% one-time adult and chick mortality, of Common and Brünnich's guillemots, assuming density-independent survival and fecundity schedules.
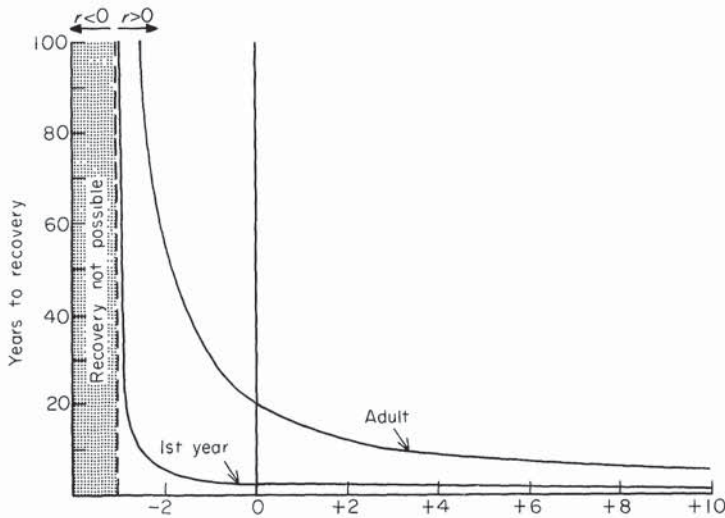

FIG. 19. Time to recovery as a function of long-term change in the mean survival rate of adult and first-year age classes of Brünnich's guillemot, given a 50% one-time mortality pulse.

have profound influences, by substantially increasing the vulnerability of the populations to single one-time perturbation events and the probability of extinction.

CONCLUSIONS

There are many ways to model biological processes, ranging from theoretical to purely analytical and predictive, from general to quite specific. Our approach to modelling the

dynamics of colonial seabird systems and their responses to perturbations has been to emphasize predictive power at the expense of theoretical elegance, and to stress applicability to populations of marine birds such as gulls and alcids rather than to seek algorithms that may be generally applicable to all birds. This does not mean, of course, that the models we have developed are purely mechanistic and devoid of theory—to the contrary, the foraging submodel relies heavily on concepts of optimal foraging, and the long-term model is a simple application of standard population demography theory to this specific situation. We believe such a blend of mechanism and theory is essential to the development of models of systems in which good information is available on some aspects but not others: those areas that are clearly understood and that are supported with solid field data are perhaps best modelled mechanistically, while features of a system for which we have few data and only a general understanding are more suitably structured using theoretical or conceptual approaches. We believe that one of the contributions of our modelling exercise is to point out how various modelling approaches (e.g. optimization, simulation, life-table) may be integrated into a functionally valid attack upon a particular biological system.

All models that attempt to describe complex biological systems or processes are of course oversimplifications (Cowardin & Johnson 1979), and there is always a danger that the model may be so oversimplified as to be naïve, incomplete, or misleading. These dangers are of especial consequence when a model has potential management applications, as does ours. In such situations, the possibility that the model is structured incorrectly or incorporates functions that are based upon erroneous assumptions is of particular concern. We believe that by structuring a fairly detailed model, some of the inaccuracies that can arise from the use of very general functions are avoided. The sensitivity tests of our model suggest that even if our input values are not precisely correct, or even if the structure of the model functions ignores some sources of variation, the predicted patterns of response of populations to perturbations still generally hold—the model seems to be fairly robust.

This should not lead one to believe, however, that the model provides highly accurate projections of the changes in population features accompanying a given perturbation scenario. It does not. The model projections must be regarded as first-level estimates, likely to be correct in a relative sense (e.g. guillemots are more sensitive than kittiwakes) or as approximations of magnitudes of response (e.g. the recovery time of guillemots associated with scenario C is more likely to be close to 40 yr than to 5 yr or 100 yr). In a system such as this, the major constraint on our ability to develop models that provide highly accurate and realistic predictions is the inadequacy of the data base upon which we must build model functions and from which we must draw input values. One of the values of a modelling approach to a system is the identification of information gaps, some of which may not be apparent from conventional field studies alone. Such gaps represent important limitations on the applicability of this model, and they should be primary candidates to receive careful attention in future studies of colonial seabird populations. The critical deficiencies are the lack of information on (1) the size of the pool of nonbreeding birds within a population—these birds do not directly contribute to colony reproduction during a given year, although they may act as a buffer to density variations in the breeding population; they may nonetheless be affected by perturbations, and a reduction in their survivorship may influence the long-term dynamics of the population; (2) the movement patterns of individuals as they forage—we have assumed that movement to foraging areas is straight-line flight, but individuals undoubtedly move about in foraging areas, and this will functionally enlarge the value of D; (3) the spatial and temporal distribution and

availability of food to foraging birds in various areas about a breeding colony; (4) the relationships between the rate of delivery of food to chicks of various ages and their growth rates and survival probabilities; (5) the degree of density-dependence in various population parameters; (6) the probability that an individual will die as a result of a direct encounter with an oil spill—or, more precisely, the mortality probabilities associated with encounters of various spill types by individuals of various breeding status; (7) the age-specific mortality schedules characterizing local populations under 'normal' conditions; (8) what we have called the 'tracking rate' (τ), the rate at which a population responds to a perturbation and regains an equilibrium at-sea distribution; and (9) the effect of a spill on the short-term availability of food (Δ). Of all these data gaps, our simulations indicate that the last four are by far the most important. None of these features is likely to be easy to measure, and some would probably require rather massive logistical support. Still, these are all critical features of seabird biology, and if we are to develop effective means of managing their populations in the face of increasing human demands upon the systems they inhabit, such features can no longer be ignored.

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