SIMULATING THE ROLE OF ENTANGLEMENT IN NORTHERN FUR SEAL, *CALLORHINUS URSINUS*, POPULATION DYNAMICS

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ABSTRACT

A multiage class model treating populations of both male and female fur seals was developed to examine the plausible long-term effect of their entanglement in discarded net debris. The model is based on the data available on age-specific survival and fecundity including data supporting the assumption of density-dependent survival of pups on land and of juveniles up to age 2 at sea. Also included in the model are age-specific and sex-specific harvests for the subadult male harvest as well as other pelagic and land-based commercial and scientific harvests. Entanglement in the model is linked to the observed incidence of subadult males in the harvest (or roundup). Supporting work in model development and parameter estimation has involved evaluation of various attempts to estimate both juvenile survival at sea and the mortality rate due to entanglement. This evaluation work has considered the appropriateness of assumptions and statistical tests used. Model results were evaluated by comparison with survey estimates of pup abundance and of harem bulls on the Pribilof Islands for years when these were available (between 1912 and 1960). Post-1960 survey results were used to examine the plausibility of entanglement mortality estimates in predicting the observed fur seal abundance decline. Sensitivity analysis on the model is used to indicate areas where there is a need for either further data collection or further analysis of existing data.

INTRODUCTION

The marked decline in northern fur seal, *Callorhinus ursinus*, populations on the Pribilof Islands since the mid-1970's has been attributed to a variety of causes, one of the most compelling of which is increased mortality due to seals' entanglement in discarded fishing net

In R. S. Shomura and M. L. Godfrey (editors), Proceedings of the Second International Conference on Marine Debris, 2-7 April 1989, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFSC-154. 1990.

debris (Fowler 1985, 1987) and other flotsam (e.g., packing bands). Although an earlier decline (1957-64) was probably due to pelagic scientific sampling of females at sea and harvest of females on land, later continued declines have not been explicable as being linked to repercussions of this harvest (York and Hartley 1981).

From observations of numbers of subadult male seals in the harvest entangled (about 0.4%), Fowler (1982), using a simple differential equation model and assumptions about the length of time entangled seals survive and the ratio of seals tangled in large (>0.4 kg) versus small (<0.4 kg) debris pieces (the seals entangled in large debris being assumed to die before reaching land), gave predictions for the possible effects of entanglement on the population. These predictions indicated that the entangled seals observed in the harvest could account for annual seal mortalities as high as 17%. Swartzman (1984) expanded Fowler's model to include age classes and density-dependent pup survival on land, as reflected in data from Lander (1981). Swartzman (1984) showed that the age and duration of susceptibility to entanglement can affect the annual mortality rate due to entanglement. The worst case scenarios (i.e., 2 months or less for half the entangled seals to die with only ages 1-3 susceptible to entanglement, or less than 12 months for half the entangled seals to die when all age classes are susceptible to entanglement) result in a long-term elimination of the fur seal population.

We have developed a model to investigate the effect of entanglement on fur seal population dynamics. This model separates male and female populations by age class and separates each age-sex class into entangled and unentangled animals. Sex-specific and age-specific susceptibility to mortality and entanglement mortality rates are also considered. Annual entanglement rate in small (<0.4 kg) debris is grounded in the observed fraction of entangled subadult males in the harvest. In the long-term simulation, harvests of males and scientific samples of females are removed from the population as an amount of seals (rather than as a rate).

The population dynamics of fur seals have been the object of many studies, and several models have been built in this regard. The present model is like many in that it is age-structured. Table 1 gives an overview of these previous models. Current modeling work is motivated by the need to synthesize current entanglement information and by the lack of previous treatment of the male population, no inclusion of male harvests and no previous formal sensitivity analysis having been done on previous models. Also, earlier entanglement models are equilibrium models that, while they were based on the best parameter values available at the time they were constructed, were not evaluated by being compared with historical data on pup estimates and bull counts. Finally, our model brings many of the parameter estimates up to date by including the latest available data. The large number of previous models points to the excellent long-term data base on fur seals, although, as will be shown later, assumptions must be made to fill gaps in the data when long-term model projections are made.

Table 1.--Comparison of northern fur seal population dynamics models (F = female, M = male).

Model	Age range/sex	Years	Harvest	Comments
York and Hartley 1981	2-25/F	1956-79	1956-74F	Juvenile survival higher after 1979.
Smith and Polacheck 1981	3-20/F	Not run	--	Challenged differential M/F juvenile survival.
Eberhardt 1981	1-22/F	1952-77	1952-68F	Density-dependent survival to age 3.
Fowler 1982	Pooled	Equilibrium	None	Entanglement effect with several mortalities.
Swartzman 1984	3-20F	Future, equilibrium	None	Density-dependent survival on land.
Trites 1984	1-25/M&F	1950-80	1956-74F constant M	Leslie model sensitivity analysis.
Reed and French 1987	1-29/M&F	1912-2000	1956-76F constant M	Density-dependent pup and juvenile survival.
Swartzman and Huang	2-18M 2-25F	1911-86	1956-76F Subadult male	Entanglement.

MODEL DOCUMENTATION

The model consists of 24 female and 18 male age classes. Populations in each modeled age class are updated by age-specific and sex-specific survival. Sex-specific and year-specific harvests on either (or both) land and sea are also removed from the proper age-sex classes each year. Pup numbers are computed from the adult female population based on age-specific fecundities. Running the model consists of solving a set of differential equations (one for each age-sex class) using the Runge-Kutta method with a time step of 0.25 years. The model is run from 1911 to 1986. The 0.25 time step was chosen to fit with the time period that pups are on land in the Pribilof Islands (3 months), allowing computation of pup survival on land to occur over a single time step. Survival of juveniles from the time they leave land to age 2 is also modeled as a density-dependent factor

based on regression analysis of pup counts and male survival estimates (data provided in Lander 1981). Entanglement rate depends on a year-specific susceptibility (based on the observed proportion of entangled subadult males in the harvest each year), an age-specific relative susceptibility factor, and the ratio of seals entangled in large to seals entangled in small debris parameter. Additionally, there are age-specific and sex-specific entanglement mortality and escapement (from entanglement) rates. Animals entangled in large debris (>0.4 kg) are assumed to die rapidly (at the same rate at which they are entangled).

A mnemonic notation is used to describe model equations (Swartzman and Kaluzny 1987). The first digit of a variable name denotes the variable type, with x used for state variables, k for parameters, g for intermediate variables, and z for driving variables (unaffected by system behavior and read in from a driver data file). The following letters are descriptive mnemonics such as mrt for mortality or n for numbers. Several parameters are numerically subscripted (e.g., k_1) rather than having a mnemonic name. This was done for parameters that were not easily made mnemonical.

The model is a series of differential equations for the rate of change of female and male seals by age class, with entangled seals (in small net debris) separated from unentangled seals.

$$\frac{dxn_{ij}(t)}{dt} = -(gent_i(t)+kmrt_{ij}+gmrtlg_{ij}(t))xn_{ij}(t)+kesc_{ij}xent_{ij}(t) \qquad (1)$$

where j = 1 for male and 2 for female

i is an age index (1-24 for female; 1-18 for male. These denote ages 2-25 and 2-19 for females and males, respectively)

xn_{ij} = number of unentangled seals in age class i of sex j

$gent_i$ = entanglement rate in small debris for age i seals (yr^{-1})

$kmrt_{ij}$ = natural mortality rate for age i sex j seals (yr^{-1})

$gmrtlg_{ij}$ = entanglement rate in large debris for age i sex j seals (yr^{-1})

$xent_{ij}$ = number of entangled seals in age class i of sex j

$kesc_{ij}$ = rate of escapement from entanglement for age i sex j seals (yr^{-1}).

Population dynamics of entangled seals are:

$$\frac{dxent_{ij}(t)}{dt} = -(kmrtent_{ij}+kmrt_{ij}+gmrtlg_{ij}(t)+kesc_{ij})xent_{ij}(t)$$

$$+gent_i(t)xn_{ij}(t) \qquad (2)$$

where $kmrtent_{ij}$ = entanglement mortality rate for seals entangled in small debris (yr^{-1}).

These equations account for the possibility of entangled seals escaping as reported by Scordino and Fisher (1983), Fowler (1987), and Fowler et al. 1990).

In addition to these continuous time equations there are also discrete time equations that update the population at set times of the year.

- The pupping time (i.e., early July), when pups are produced, ages of the populations are updated, and harvests of subadult males (and pelagic harvests, if any) are taken;

- The time pups leave land, when the density-dependent number of surviving pups is computed.

The number of pups produced in any year are computed from age-specific fecundity

$$xpup(t) = \sum_{i=1}^{24} kfec_i xn_{i2}(t) \tag{3}$$

where $kfec_i$ = age-specific fecundity including the influence of age-specific maturity.

At the time pupping occurs, the model updates time, ages the seals by 1 year, and removes seals by harvest for that year (harvest includes the subadult male commercial harvest, any harvest of females, and any scientific samples taken that year).

$$xn_{ij}(t+1) = xn_{(i-1)j}(t) - zharv_{ij}(t+1) \tag{4}$$

where $zharv_{ij}(t)$ = the total harvest and samples of age-sex class ij in year t (data entry).

Harvests are most commonly applied to the annual subadult males on the Pribilof Islands, but involved females between 1956 and 1968 and research samples including a variety of age-sex classes in many years. Analogous harvest equations exist for entangled male and female animals (there is a data file for entangled seals as well as for unentangled seals from the harvest statistics).

The survival of 1-year-old and 2-year-old seals is treated somewhat differently from the survival of older seals. The natural mortality of seals between age 3 months (the time pups leave land) and age 2 is computed by the density-dependent function

$$gmrt_{mj}(t) = kfmrt_j \frac{-\log_e \left[\frac{ks_1(xpup(t-m+0.25)-ks_2)}{(xpup(t-m+0.25)-ks_3)} \right]}{1.75} \tag{5}$$

Here m denotes age class (1 or 2) and j sex class. The 0.25 year (3 months) adjusts time back to the time pups leave land. The ratio of female to male mortality rates is $kfmrt_2$, and $kfmrt_1 = 1$. The total number of pups leaving land (male + female) in the year for which we are computing mortality rate (m = 1) or in the previous year (m = 2) is $xpup(t-m+0.25)$. Instead of $kmrt_{mj}$, $gmrt_{mj}(t)$ is used in equations (1) and (2) for age classes 1 and 2 to denote that these are intermediate variables rather than parameters. The natural logarithm and 1.75 are used to convert the fraction of seals surviving to age 2 (excluding entanglement) to a rate. A mortality rate must be used instead of a fraction surviving (which is what we estimate from the primary data source) because entanglement mortality may also be incurred by these younger seals. We noted earlier that the model considers age classes beginning with age 2 seals. As such, the above computations for age class 1 seals are not included in the part of the code that deals with the seal age classes, but as a separate calculation. Age class 1 animals are excluded from the model because very little is known about survival rates of pups after they leave land and estimates are based solely on the male juveniles that begin showing up in the Pribilofs at age 2.

At the time pups leave land (at 3 months of age), the model computes the number of pups leaving according to a density-dependent function (Swartzman 1984) and divides them into male and female groups assuming a 1:1 sex ratio.

$$xpup_j(t+0.25) = \tfrac{1}{2}k_1(1.0 - k_2 e^{-k_3 xpup(t)}) \tag{6}$$

Parameters are k_1, k_2, and k_3 in this density-dependent relationship. The seal entanglement rate is assumed to be age, sex, and time specific. A year-specific driving variable, zprop(t), the proportion of entangled subadult males observed in the harvest, is multiplied by an age-specific and sex-specific variable:

$$gent_i(t) = zprop(t) k_4 \cdot e^{-k_5 \cdot i} \tag{7}$$

Here k_4 is the ratio of entanglement rate for pups to the proportion of subadult males in the harvest entangled in small debris, and k_5 is a parameter controlling the age susceptibility of seals to entanglement. Entanglement is represented as an exponential function of age, with youngest seals being most susceptible. The parameter k_5 controls the rate of decline of entanglement susceptibility with age. Setting $k_5 = 0.0$ makes all ages equally susceptible. As a way of simplifying sensitivity analysis, this function was used to represent age changes in susceptibility to entanglement by a single parameter, rather than a vector of parameters. The entanglement rate of age i seals in large debris is equal to $k_6 \cdot gent_i$. The model assumes that seals entangled in large debris die rapidly enough

for the mortality rate to be equal to the entanglement rate. Thus, the entanglement rate in large debris is equated to a mortality rate $gmrtlg_{ij}$ (as shown in equations 1 and 2). The parameter k_6 is the ratio of entanglement in large versus small debris.

The mortality rate of seals entangled in small debris $kmrtent_{ij}$ was for convenience also modeled as a function of age and sex. As with entanglement rate, an exponential function was used because it gives flexibility in the change of entanglement mortality with age. The equation is:

$$kmrtent_{ij} = kentl_j e^{-kent2_j \cdot i} \tag{8}$$

Here $kent2_j$ is a sex-specific parameter for changes in the mortality rate of entangled seals with age. It is analogous to k_5. The mortality rate for age 0 seals (i.e., pups) is $kentl_j$.

Model Parameters

Parameter values used in this model are given in Table 2, along with sources of data. A calibration process was used to improve the fit between the model and data. It consisted of changing selected parameters to produce agreement with pup counts on the Pribilof Islands. During calibration, parameters were constrained to be changed only within "reasonable" limits ("reasonable" depending upon the accuracy of the parameter estimate).

The parameters k_1, k_2, and k_3 were estimated using a nonlinear regression based on equation (6) of estimates of pups born against estimates of pups leaving the Pribilof Islands. The regression gave estimates of $k_1 = 1.06 \times 10^6$, $k_2 = 1.007$, and $k_3 = 1.04 \times 10^{-6}$. When the model was run with best estimates for these and other parameters (see Table 2), the fit from 1911 to 1950, the period of population growth, was very poor. We had ascertained earlier (Swartzman 1984) that the population behavior was very sensitive to these parameters (i.e., k_1, k_2, and k_3). This being so, we used bootstrap resampling to obtain estimates of the variance of each parameter (by redoing the regression with different resamples) and then "searched" the parameter space (1,000 Monte Carlo runs) to see which combinations of parameter values provided the best fit to the data during the population growth period. This experiment produced the values for k_1, k_2, and k_3 given in Table 2.

Model-Data Comparison

Our initial desire for this model was to have it replicate the female fur seal population abundance. Any model unable to do that must be judged insufficient for investigating the effect of entanglement on fur seal population dynamics. Figure 1 compares the model to pup numbers and bulls (for the model this includes all bulls 7 years or older), which are the only long-term data available. The vertical dashed lines in Figure 1 show (from left to right) the year pelagic sampling of females began, the year entanglement began, the year commercial pelagic harvest ended, and the year all female sampling ended (both scientific sampling and commercial harvests).

Table 2.--Parameter values and data sources for northern fur seal population dynamics model.

Parameter	Definition	Value	Estimate source
k_1	Maximum land pup survival	728451	Regression; Lander (1981) calibration.
k_2	Density-dependent land pup survival	0.982037	Regression; Lander (1981) calibration.
k_3	Density-dependent land survival exponent	1.609502e-6	Regression; Lander (1981) calibration.
k_4	Ratio of age 0 seal entanglement to fraction of entangled subadult males	5	Fowler (1982) calibration.
k_5	Change of entanglement with age	0.35	Calibration.
k_6	Ratio of large to small net entanglement rates	15	Fowler (1984) calibration.
$kent1_1$	Entanglement mortality rate for younger males	0.8	Fowler (1982).
$kent1_2$	Entanglement mortality rate for younger females	0.8	Fowler (1982).
$kent2_1$	Entanglement mortality age effect for males	0.35	Calibration.
$kent2_2$	Entanglement mortality age effect for females	0.35	Calibration.
$kfmrt_2$	Ratio of young female to male mortality rate	0.6	Chapman (1964) calibration.
ks_1	Density-dependent survival to age 2	0.5428	Regression; Lander (1981).
ks_2	Density-dependent sea survival parameter	0.7643	Regression; Lander (1981).
ks_3	Density-dependent sea survival parameter	0.7372	Regression; Lander (1981).
Male seals (age-class-specific)			
$kmrt_{11}$	Seal mortality rate	--	Lander (1981).
$kesc_{11}$	Age-specific escapement from entanglement	0.0008	Calibration.
Female seals (age-class-specific)			
$kmrt_{12}$	Seal mortality rate	--	Lander (1981).
$kesc_{12}$	Age-specific escapement from entanglement	0.0008	Calibration.
$kfec_1$	Age-specific fecundity	--	York and Hartley (1981).

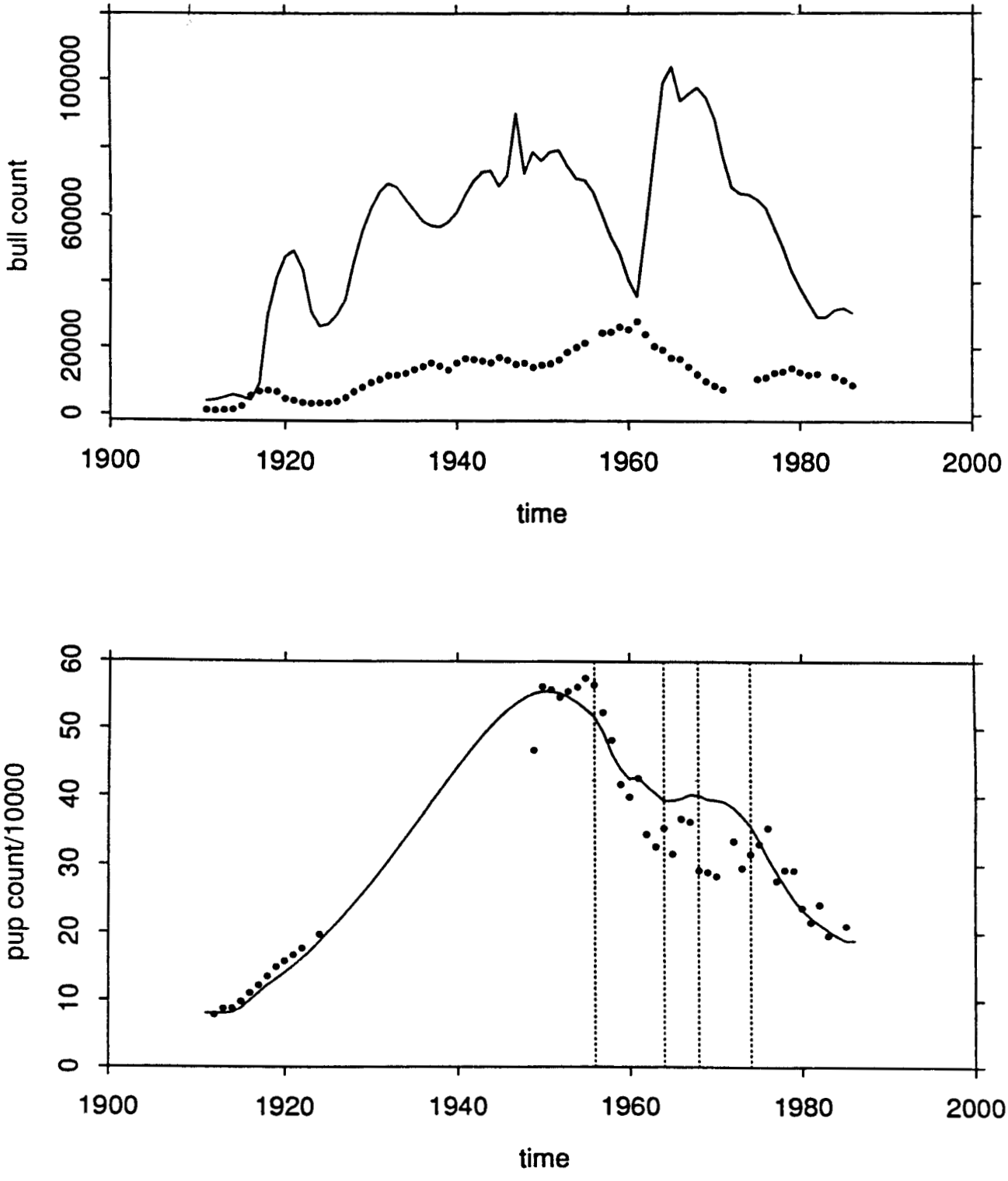

Figure 1.--Model-data comparison between pup and bull counts, 1911-86.

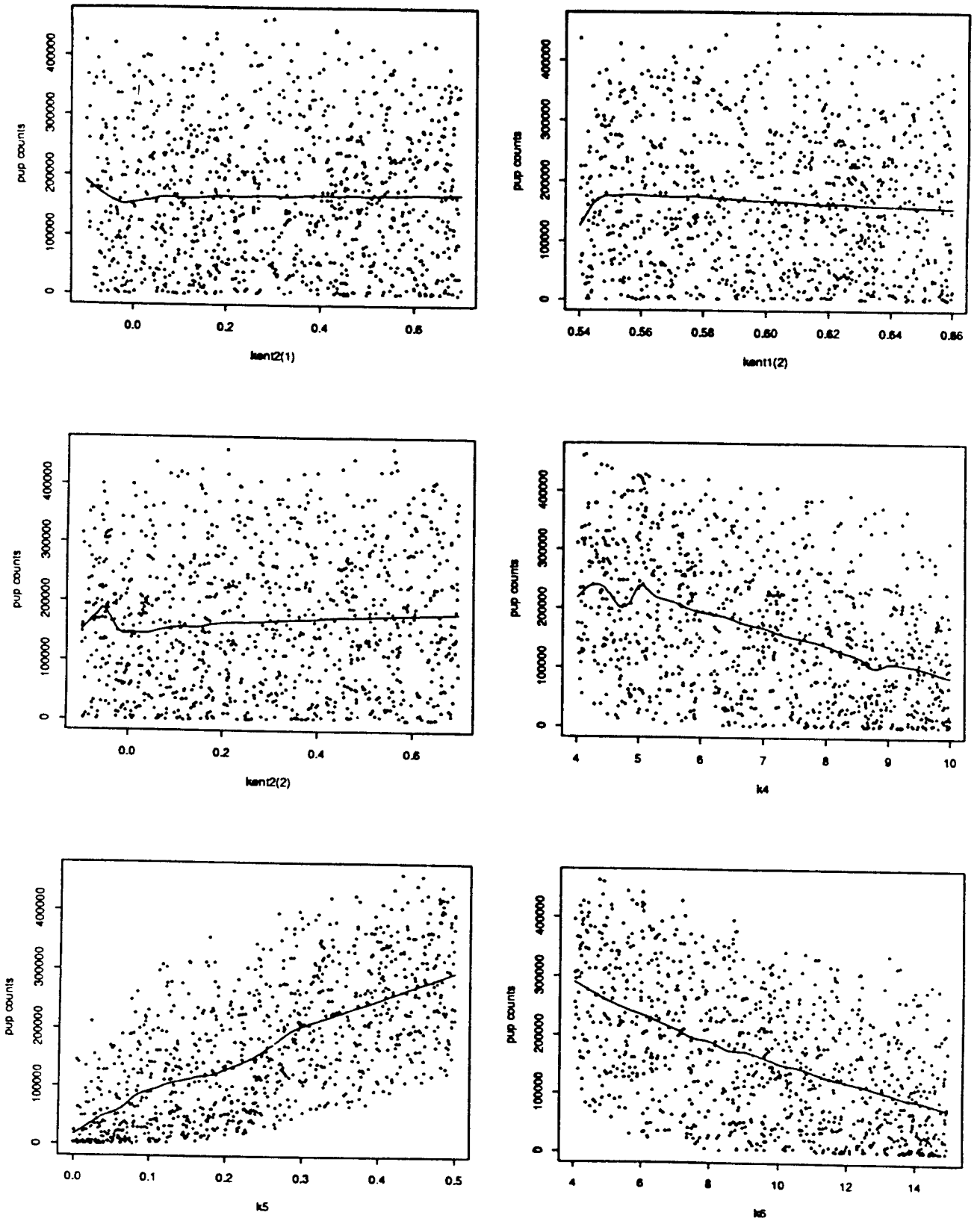

Figure 2.--Sensitivity of 1986 pup counts to entanglement parameters.

Although the fit to the pups appears credible, the bull counts are overestimated by the model. Through many runs of the model adjusting male parameters (the female population is unaffected by these changes), it became apparent that in order for the model not to seriously underestimate the number of bulls during the late 1950's and early 1960's (a period of large subadult male harvests), bull counts in the model during the earlier period need to be significantly higher than reported counts. The possibility that the model was in error was minimized by our checking the calculations and also observing that the bull counts do not appear to respond to marked annual changes in harvests, especially during the 1940's. Possible explanations for this model-data disparity (remember that during this period the model appears to fit pup counts well) are that (1) the actual number of bulls is much higher than the number of territorial bull counted both with females (harem bulls) and as "idle bulls," (2) the pup estimates during this period are in error and pup numbers were actually significantly higher than those obtained by the tagging estimates made in the 1950's (Chapman 1973), or (3) that estimated survival parameters for males are in error.

If the first alternative is true, then many mature bulls, especially the younger ones (e.g., ages 7 and 8), are at sea much of the time and do not show up in the bull counts. If the model's bull predictions are to be believed, there must have been a very large pool of idle bulls in some years that spent either little or no time on land in the Pribilof Islands. Furthermore, the size of this pool has changed over time, being large in the 1930's and 1940's, small around 1960, large again in late 1960's, and now being drastically reduced.

SIMULATING THE EFFECT OF ENTANGLEMENT ON FUR SEAL POPULATIONS

The fit between model and data in Figure 1 was based on a calibration, where entanglement parameters were selected to best fit the population trajectory for pups after 1960. As recorded in Table 2, several of these entanglement parameters are based on limited data and others are simply based on achieving a fit of the model to the data. This is true of the age specificity of both entanglement rate and mortality rate of entangled seals, which has not been studied in the field. The ratio of the rate of seals entangled in large versus small debris is based only on the relative incidence of these two kinds of debris in land and pelagic surveys (Fowler 1987). Also, no studies have been devised to estimate susceptibility of seals to entanglement in debris. Therefore, it is to be expected that our uncertainty about the values of these parameters is great.

To investigate the sensitivity of model predictions of pups and adult males in 1986 (chosen as a measure of model performance that directly relates to the effect of entanglement) to changes in entanglement-related parameters, we performed a Monte Carlo sensitivity experiment. Parameter values were sampled from a uniform distribution over the range of values judged to be reasonable (within our expectation of what the parameter values may be). Our choice is, of course, somewhat subjective. It is to be expected that our range of acceptable parameter values will narrow considerably as a result of this experiment. This method of using a sensi-

tivity study to narrow the tolerance limits on parameter values by choosing combinations giving realistic model behavior was devised by Hornberger and Spear (1981).

Because we are primarily interested in sensitivity of the seal population to entanglement, we restricted our sensitivity study to parameters directly related to entanglement. These include parameters k_4-k_6, relating to the entanglement rate in both large and small debris and the change over age in susceptibility to entanglement; $kent1_j$ and $kent2_j$, the entanglement mortality rates for males and females and how they change with age; and $kesc_{ij}$, the age-specific and sex-specific rates of escape from entanglement. The pup and bull populations predicted by the model in 1986 were used as an output variable for comparing sensitivity runs. From Figure 1 it is seen that the population consistently declines after 1960, the year entanglement mortality begins to take effect, and therefore the 1986 value is a measure of the degree of decline (all sensitivity runs are at the same population level in 1960 because they differ only in entanglement-related parameters).

Initial results indicated that the escape-from-entanglement parameters $kesc_i$ are significantly less influential than the other parameters. Therefore the Monte Carlo runs were restricted to the other seven parameters. Table 3 gives the values and ranges used for each parameter in the sensitivity study. Due to uncertainty about the parameter values, we chose to sample parameter values from uniform distributions.

Ranges of parameters were set as follows: $kent1_j$, the age 0 small debris entanglement mortality rate, was set to a range of 10% on either side of the baseline run estimate value of 0.6. Considerable effort has been devoted to estimating the mortality rate of entangled seals, both through observation of marked entangled animals and by looking at the age distribution of entangled versus unentangled seals in the subadult male harvest (Fowler 1987). As such, a modest range of variability was assumed. Three parameters control the age distribution of entanglement effects. Parameter $kent2_j$ is the exponent controlling the age distribution of entanglement mortality for male ($j = 1$) and female ($j = 2$) seals, and k_5 is the same for entanglement rate (no sex distinction here). Baseline estimate for each of these parameters was 0.35. Little is known about how susceptibility to entanglement changes with age, except that significantly more young seals are observed entangled in debris on the Pribilof Islands. Having k_5 of 0.35 makes 0-age seals 20 times as susceptible to entanglement as 8-year-olds. A range of 0 (no difference in age susceptibility) to 0.5 (ratio of 55 in age 0 to age 8 susceptibility) seemed adequate to cover the plausible range of values. For kent2 and kent4 a wider range, from -0.1 (older animals die more rapidly when entangled) to 0.7, was chosen, reflecting our having no data on how long animals at different ages survive when entangled.

The last two sensitivity parameters, k_4 and k_6, are not well known. For k_6, the ratio of entanglement rates in large to small debris, Fowler (1984) estimated a value of 5 based on the ratio of large to small debris in beach surveys on Amchitka (Merrell 1980) and the Pribilof Islands.

Table 3.--Parameter values and ranges for sensitivity analysis.

Parameter	Monte Carlo distribution	Best estimate
$kent1_1$	U(0.54, 0.66)	0.6
$kent2_1$	U(-0.1, 0.7)	0.35
$kent1_2$	U(0.54, 0.66)	0.6
$kent2_2$	U(-0.1, 0.7)	0.35
k_4	U(4, 10)	5
k_6	U(4, 15)	15

However, our baseline estimate, which resulted in a reasonable model-data fit, was 15. We therefore chose a range of 4 to 15, putting our estimate at the high end in deference to Fowler's more data-based measure. Parameter k_4 represents the ratio of entanglement rate in small debris for 0-age seals to the fraction of observed subadult male seals entangled on the Pribilof Islands. The latter is the only data-based time series on annual entanglement available. Estimating k_4 is like trying to assess the size of an iceberg from the part above water. There is a lot unknown below the surface. For a range of values, we blanketed our baseline estimate, 5, by 4 and 10, the relatively high lower bound being due to results of preliminary experiments with the model that showed low values of k_4 leading to an overprediction of pup abundance (too weak an effect of entanglement). One caveat of the calibration approach to parameter estimation in this case is that we are assuming entanglement to be the sole cause of the additional mortality since 1960. If, in fact, there are other yet-undiscovered causes, then entanglement parameter values estimated here would be biased. This is to be borne in mind during the discussion of the sensitivity analysis, which examines parameter ranges that lead to realistic behavior, assuming that all sources of mortality are accounted for in the model (either through harvest, sampling, entanglement, or natural mortality, or through density-dependent juvenile survival).

SENSITIVITY ANALYSIS RESULTS

Figure 2 shows results of the sensitivity study for six of the parameters plotted against pup numbers. Results are omitted for $kent1_1$, which is similar to $kent1_2$. A smooth using supersmoother (Friedman and Stuetzle 1982) was fit to each plot. The three entanglement susceptibility parameters appear to have a stronger effect on 1986 pup numbers than the entanglement mortality parameters. Low values of k_5 (no age-specific or weak age-specific entanglement susceptibility) appear to lead to low 1986 pup predictions.

To get a sense of which parameter combinations led to realistic predictions, we extracted those runs (of the 1,000 runs made) that gave 1986 pup estimates between 170,000 and 200,000 (the baseline run gave 189,000 pups in 1986, close to the pup count estimate for that year).

Figure 3 illustrates which combinations of parameters give realistic model behavior. The first three plots show the entanglement rate parameters against each other for pup numbers within this range, including a super-smooth fit of the resulting scatterplots. The next three plots show each of these parameters' values against pup numbers (for the latter restricted between 170,000 and 200,000 pups). These indicate that over the range of "realistic" pup numbers, none of these parameters has a significant effect on pup numbers (there is no significant slope to the smooths). From the first three plots we deduce that k_4 and k_5 are inversely related to each other, and k_5 and k_6 are inversely related to each other. This can be interpreted to mean that there cannot be a low value of k_5 and a high value of k_4 (and contrariwise a high value of k_5 precludes a low value of k_4). This information is useful because it sets limits of parameter combinations leading to realistic behavior. Furthermore, if more information becomes available concerning any one of these parameters it further delimits the possible values of the other parameters. For example, if observation of entangled animals at sea would indicate that seals are more susceptible to entanglement in large debris than the ratio of large to small debris in beach surveys would indicate (implying a value of k_6 near the upper end of the 4 to 15 range used here), then the entanglement rate needs to be age-specific, with older animals significantly less susceptible to entanglement than younger animals. Significant benefit for research direction can be derived from these results, because they suggest that improved estimates of entanglement rates in small debris can be obtained by seemingly unrelated (and potentially less expensive) then the studies such as finding out about age-related susceptibility to entanglement.

Another interesting result of this sensitivity study is that entanglement rates are much more important for population survival than is entanglement mortality. Another way of saying this is that the rate at which seals enter the entangled animal pool is more important to long-term population trends than the rate at which they die once they are in it. Assuming mortality rate much larger than the rate of escape from entanglement assures that most animals entering the entangled pool will die before they can leave their mark on future generations through reproduction.

ENTANGLEMENT QUESTIONS AND RESEARCH

The model can be used to explore recovery scenarios such as how the population would respond to removing entanglement or reducing it. However, such an exercise is unnecessary. Except for short-term effects, the response to removing entanglement can be observed in Figure 1 in the model's pup counts during the upward cycle starting around 1923. Intermediate entanglement rates would result in less rapid recovery rates. The actual rate of recovery depends on the specific entanglement rates and combinations of parameters. These include the entanglement parameters (k_4-k_6) as well as the non-entanglement-related parameters that were calibrated to fit time traces from 1915 to 1960 pup counts.

More important than recovery scenarios are dominant questions suggested by the model concerning entanglement. These are:

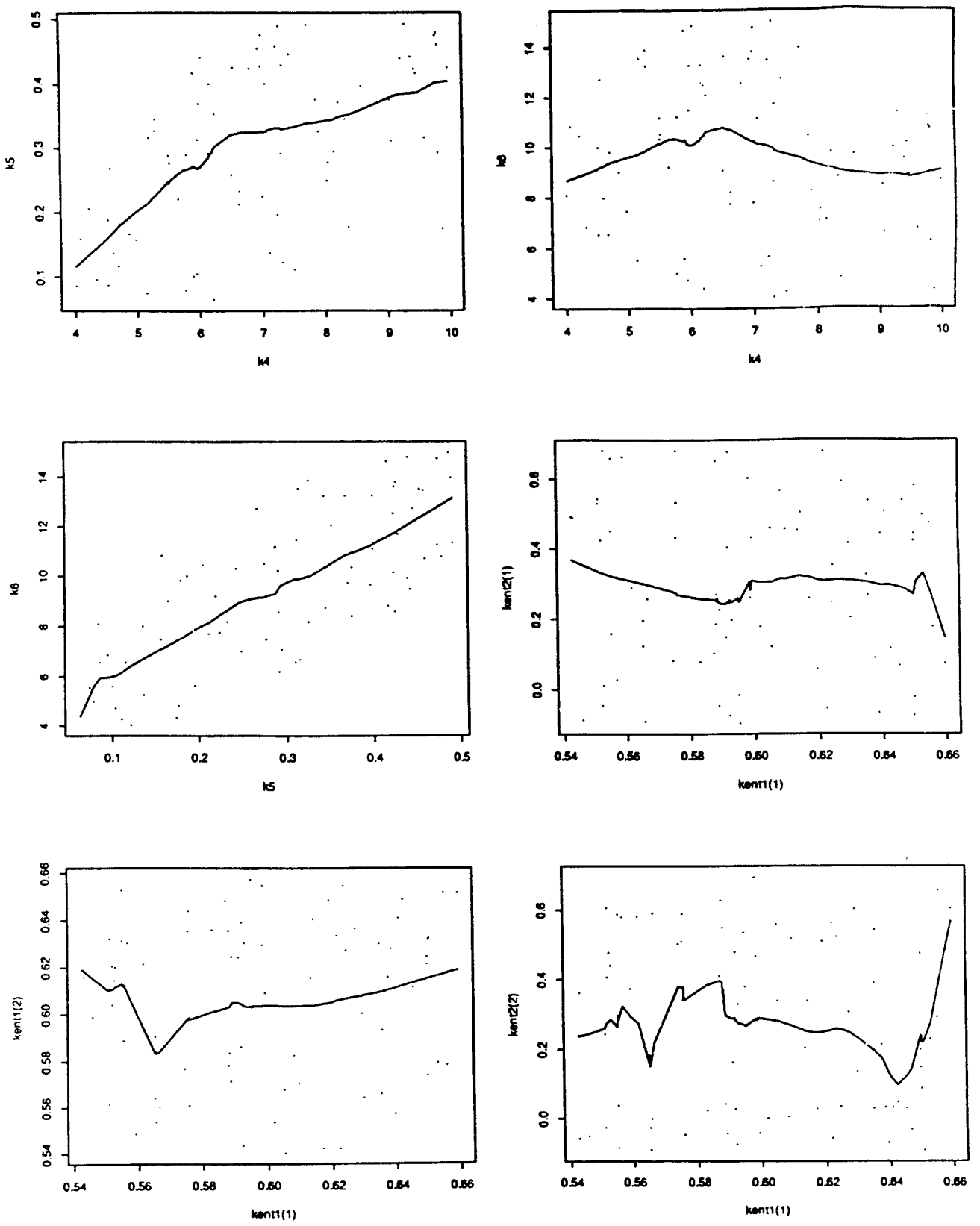

Figure 3.--Parameter interaction for 1986 pups and bulls close to nominal run levels.

1. What is the rate of entanglement in small debris and how is this influenced by debris abundance and distribution?

2. Are there age differences in susceptibility to entanglement and if so how can we measure them?

3. How relatively susceptible are seals to entanglement in large versus small debris?

This modeling exercise has demonstrated that, within the degree of uncertainty that we can answer the above three questions, entanglement is a plausible explanation for the decline in Pribilof Island fur seal populations since the late 1960's. The model's representation of male abundance has raised some questions about using the idle and harem bull counts as an index of total adult male abundance. At the very least, large fluctuations in male harvest are not reflected by subsequent appropriately large changes in bull counts. At the most, a variable, potentially large fraction of the mature males either may not be resident on the Pribilof Islands during the summer or may be resident for only part of the summer. Finally, the modeling has defined the research questions that can help reduce uncertainty about the possible past and future effects of entanglement on seal populations. The first question, about entanglement susceptibility, requires increased (and preferably simultaneous) observation of entangled seals and debris at sea and the development of a debris encounter probability estimate and an estimate of the probability of a seal's being entangled given that it has encountered debris (Ribic and Swartzman 1990). The second question requires taking a closer look at the age-sex distribution of entangled seals on land and perhaps conducting tank experiments on a larger scale than previously done. The third question requires observation of entangled animals at sea and development of statistical methods for estimation based on very infrequent encounters. Research around both the first and third questions may benefit from additional models designed to test various assumptions made in doing the estimates. For example, a Monte Carlo seal-debris encounter model, coupled with further transect observations might help clarify what the probability of entanglement is, given an encounter at sea.

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