

Exxon Valdez Oil Spill
Restoration Project Final Report

A Population Model for Sea Otters in Western Prince William Sound

Restoration Project 93043-3
Sea Otter Demographics

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Study History: Restoration Project 93043, *Sea Otter Population Demographics in Areas Affected by the Exxon Valdez Oil Spill*, was initiated in 1993. The population model reported herein was one of three components. The other two components were aerial surveys (reported separately, *1993 Trial Aerial Survey of Sea Otters in Prince William Sound, Alaska*, by J. Bodkin and M. Udevitz) and mortality patterns (reported separately, as part of NRDA MM6 Report, *Age Distributions of Sea Otters Found Dead in Prince William Sound, Alaska, Following the Exxon Valdez Oil spill*, by D. Monson and B. Ballachey).

Abstract: A large portion of the western Prince William Sound (PWS) sea otter population was killed by the *Exxon Valdez* oil spill in March 1989, but little is known about the dynamics of this population before the spill or the rate at which the population can be expected to recover. We estimated age-specific reproductive and survival rates for the western PWS population before the spill based on examinations of reproductive tracts and the age structure of carcasses collected in 1989. We developed a new technique for estimating survival rates that uses age-structure and age-at-death data, and does not require the assumption of a stable age structure. A Leslie 2-sex projection matrix was used to integrate these estimates with other available information on the western PWS sea otter population and to project its potential recovery. Because of the lack of data for estimating juvenile survival rates, we considered a series of 4 potential scenarios. The population was projected to decrease slightly during the first year under all of the scenarios and then begin increasing, achieving maximum rates of increase ranging from 10% to 14% per year and recovering to its estimated 1985 population size in 10 to 23 years. Projected population sizes during the first few years after the spill are in broad agreement with estimates based on boat surveys in 1990, 1991 and 1993. Although it probably is not possible to fully quantify the uncertainty associated with the projected population trajectories, we recognize that the amount of uncertainty is likely to be large. This uncertainty is reflected to some extent by the disparity between the projected recovery times under the various scenarios.

Key Words: age structure, *Enhydra lutris*, *Exxon Valdez*, oil spill, population model, reproduction, sea otter, survival.

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EXECUTIVE SUMMARY

A large portion of the western Prince William Sound (PWS) sea otter population was killed by the *Exxon Valdez* oil spill in March 1989, but little is known about the dynamics of this population before the spill or the rate at which the population can be expected to recover. We estimated age-specific reproductive and survival rates for the western PWS population before the spill based on examinations of reproductive tracts and the age structure of carcasses collected in 1989. We developed a new technique for estimating survival rates that uses age-structure and age-at-death data, and does not require the assumption of a stable age structure. A Leslie 2-sex projection matrix was used to integrate these estimates with other available information on the western PWS sea otter population and to project its potential recovery. Because of the lack of data for estimating juvenile survival rates, we considered a series of 4 potential scenarios. The population was projected to decrease slightly during the first year under all of the scenarios and then begin increasing, achieving maximum rates of increase ranging from 10% to 14% per year and recovering to its estimated 1985 population size in 10 to 23 years. Projected population sizes during the first few years after the spill are in broad agreement with estimates based on boat surveys in 1990, 1991 and 1993. Although it probably is not possible to fully quantify the uncertainty associated with the projected population trajectories, we recognize that the amount of uncertainty is likely to be large. This uncertainty is reflected to some extent by the disparity between the projected recovery times under the various scenarios.

INTRODUCTION

The *Exxon Valdez* oil spill in March 1989 resulted in lethal and sublethal exposure of sea otters to oil. The most severe effects on sea otters were in western Prince William Sound (PWS), where an estimated 2,650 otters were killed (Garrott et al. 1993). An unknown additional number of otters received sublethal exposures that may have reduced their subsequent survivorships or reproductive rates (Ballachey et al. 1994). Current research and management is directed at restoration of resources damaged by the oil spill, but the rate at which the western PWS sea otter population can be expected to recover is unknown.

Little is known about the dynamics of the western PWS sea otter population before the spill. A small population in south-western PWS was one of the few remnant populations that survived following the extensive eighteenth and nineteenth century fur harvests (Lensink 1962). This population began increasing in the early part of this century and then began expanding rapidly to the north and east beginning about 1950, with the last areas of favorable habitat in eastern PWS being occupied by about 1980 (Garshelis et al. 1984). The western portion of PWS is generally considered to have been occupied at or near carrying capacity for some years preceding the oil spill, with the population size either constant (Johnson 1987) or growing very slowly (Garrott et al. 1993). There is some evidence to suggest that the western PWS population structure was relatively stable from at least 1976 through 1989 (Monson and Ballachey 1995). There is a very limited amount of information about survival rates of pups (Garshelis and Garshelis 1987) and weanlings (Monnett 1988) from before the oil spill. There are no published estimates of adult survival rates from that period. Jameson and Johnson (1993) have suggested that reproductive rates were probably comparable to estimated rates in the Aleutian Islands and in California.

A number of studies were initiated after the spill to assess damages and monitor recovery of the western PWS sea otter population (Ballachey et al. 1994). There were extensive collections of beach cast carcasses (DeGange and Lensink 1990, Doroff et al. 1993) that provided data for estimating reproductive rates (Bodkin et al. 1993) and age structures (Monson and Ballachey 1995). Telemetry-based studies provided direct estimates of survival and reproductive rates for certain components of the population (Rotterman and Monnett 1991, Monnett and Rotterman 1992, NBS unpubl. data). Boat-based surveys were used to estimate the size of the population in 1989, 1990, 1991, and 1993 (Burn 1994, Agler et al. 1994).

OBJECTIVES

This report presents the modeling component of Restoration Project #93043, Sea Otter Demographics and Habitat Use. The objectives of this component were to 1) estimate age specific reproductive and survival rates for the western PWS sea otter population based on the beach cast carcass collections in 1989, and 2) develop a model to integrate these estimates with other available information and project recovery of the western PWS sea otter population.

METHODS

Data Collection

Sea otter carcasses were collected throughout the oil spill zone as part of the oil spill response effort (DeGange and Lensink 1990, Doroff et al. 1993). Five hundred and eight sea otter carcasses were collected in western Prince William Sound between 30 March and 30 August 1989 (Figure 1). Personnel at the collection centers attempted to record, among other things, location and date of collection, sex, lactational status, and extent of decomposition for each carcass. Female reproductive tracts were removed and examined to determine reproductive status. Teeth (premolar, when available) were extracted for age determination.

Time of death (before or after the oil spill) was estimated for each carcass based on the extent of decomposition and the degree to which skeletal remains were dried or bleached. Evidence of lactation or the presence of a fetus, embryo, or corpus luteum in the reproductive tract was used to identify females that could have produced a pup between 1 October 1988 and 30 September 1989 (Bodkin et al. 1993).

Ages at the time of death were estimated from decalcified, longitudinal tooth sections (Garshelis 1984, Pietz et al. 1988). Up to 4 sections were prepared from each tooth and examined by Matson's Laboratories (Box 308, Milltown, MT). Age determination was based on the assumption that a cementum annulus was deposited each winter after an otter had its permanent teeth. Otters with deciduous teeth were assumed to be less than 6 months old. Otters were grouped into age classes with age class 0 corresponding to ages less than 6 months (no permanent teeth), age class 1 corresponding to ages ranging from 6 to 18 months (permanent teeth, no annulus), age class 2 corresponding to ages ranging from 18 to 30 months (permanent teeth, 1 annulus), and so on.

Reproductive Rates

Estimation of reproductive rates was based on the 148 carcasses examined by Bodkin et al. (1993) that came from western Prince William Sound. Of these, 143 were a subset of the known-age females used for estimating the age and sex structure of the population (see below). The other 5 carcasses were known-age females that died at a rehabilitation center. Bodkin et al. (1993) reported results for these and an additional 28 carcasses that came from outside Prince William Sound.

Age specific reproductive rates were estimated as the proportions of pregnant or lactating females in each age class (ages 2 - 16). These estimates were then smoothed by fitting the observed proportions to the proportional hazards model used by Eberhardt and Siniff (1988). The form of this model was

$$m_x = m(A,B)m(D,E),$$

where m_x is the reproductive rate (including male and female offspring) for age class x ,

$$m(A,B) = A(1 - \exp[-B(x-2)])$$

is a function that describes the rate at which reproductive rates increase with age for young otters,

$$m(D,E)=\exp[-D(\exp[Ex]-1)]$$

is a function that describes the rate at which reproductive rates decrease with age for old otters, and A, B, D, and E are parameters to be estimated (Eberhardt and Siniff 1988). Parameters were estimated by the method of least squares.

Structure of Ages-at-death

We used all carcasses classified as dying before the spill with known sex and age > 1 (n = 29) to estimate the structure of natural mortality that occurred during the year preceding the oil spill. Carcasses in age classes 0 and 1 were not considered because smaller beach cast carcasses tend to persist for shorter periods of time and are therefore less likely to be recovered (Bodkin and Jameson 1991). The proportion of deaths in each age and sex class of the population was estimated by its respective proportion in the carcass sample.

Population Age Structure

We used all carcasses classified as dying after the oil spill with known sex and age > 0 (n = 344) to estimate the structure of the population just before the spill. We included age class 1 carcasses because collections began almost immediately after the spill so it was not likely that any size related differences in carcass persistence would have had time to affect recovery probabilities. This assumption was tested based on a comparison of recoveries of lactating females and dependent pups (see below).

The proportion of age class 0 otters in the age structure could not be estimated from the recovered age class 0 carcasses because this class was defined to include otters that were not yet born (actual ages between -6 and +6 months). Therefore, the number of age class 0 otters corresponding to the collected carcasses was estimated as

$$N_0 = \sum_{x=1}^{25} N_x m_x ,$$

where N_x is the number of recovered carcasses of females in age class x and m_x is the estimated reproductive rate for age class x. We assumed a 1:1 sex ratio for age class 0 otters based on the observed sex ratio of sea otters born in rehabilitation centers during the summer of 1989 (8 males, 9 females, USFWS unpublished data). The proportion of otters in each age and sex class of the population was estimated by its respective proportion in the carcass sample, with the estimated numbers of age class 0 otters substituted for the observed numbers.

Relative Recovery Rates

An approximate test of the hypothesis that carcass size did not affect carcass recovery rate of otters that died after the spill was based on a comparison of the proportions of recovered dependent pups and lactating females. We assumed that if either member of a mother-pup pair was killed by the spill, then both were likely to have been killed. Under this assumption, if recovery rates did not depend on carcass size, then the proportion of dependent pups should approximately equal the proportion of lactating females in the recovered carcass sample. The proportion of dependent pups could be obtained directly as the proportion of recovered carcasses in age class 0. The proportion of lactating females had to be estimated because some carcasses had unknown sex or lactational status.

In order to construct an approximate statistical test, we further assumed that for the sample of $N_1 = 407$ recovered carcasses,

$$(f,m,d) \sim \text{multinomial}(N_1, P_f, P_m, P_d),$$

where f = the number of independent females, m = the number of independent males, and d = the number of dependent pups. The number of independent otters with unknown sex is $N_1 - f - m - d$. We assumed that for the sample of $N_2 = 148$ females examined to determine reproductive status,

$$l \sim \text{binomial}(N_2, P_l),$$

where l = the number of females that were lactating. Finally, we assumed that distributions of (f,m,d) and l were approximately independent. The assumption of independence is not strictly valid because most of the N_2 examined females were a subset of the N_1 recovered carcasses. However, we do not expect that this form of dependence would greatly affect the test. Under these distributional assumptions the joint likelihood for (f,m,d,l) is proportional to

$$P_f^f P_m^m P_d^d (1 - P_f - P_m - P_d)^{N_1 - f - m - d} P_l^l (1 - P_l)^{N_2 - l}. \quad (1)$$

The proportion of lactating females out of the N_1 carcasses is

$$P_l^* = P_l \left(P_f + \frac{P_f(1 - P_f - P_m - P_d)}{P_f + P_m} \right).$$

Under the assumption that carcass size did not affect recovery probability, the proportions of lactating females and dependent pups out of the N_1 recovered carcasses will be the same, so that

$$P_l = \frac{P_d}{P_f + \frac{P_f(1 - P_f - P_m - P_d)}{P_f + P_m}}. \quad (2)$$

We obtained maximum likelihood estimates of P_f , P_m , P_d , P_l , and P_l^* based on the likelihood (1) with and without the constraint (2) and used the likelihood ratio to test the assumption represented by that constraint.

Survival Rates

Basic relations.-- The relations between survival rates, age structure, and structure of ages-at-death are well known for populations with stable age structures (e.g., Tanner 1978). The standard expressions for these relations in birth pulse populations are

$$s_x = \frac{c_{x+1}\lambda}{c_x}, \quad x=0, \dots, m, \quad (3)$$

and

$$s_x = 1 - \frac{d_x \lambda^x}{\sum_{i=x}^m d_i \lambda^i}, \quad x=0, \dots, m, \quad (4)$$

where

- s_x = the annual survival rate for individuals in age class x ,
- λ = the finite rate of increase for the population,
- c_x = the proportion of live individuals in age class x at the time of a birth pulse,
- d_x = the proportion of annual deaths in age class x , and
- m = the maximum attainable age.

Equations (3) and (4) rely on the assumption of a stable age structure and the resulting constancy of the parameters over time. If the population growth rate is known and an unbiased estimate of the age structure is available, then equation (3) can be used to obtain unbiased estimates of the survival rates. Likewise, if the population growth rate is known and an unbiased estimate of the structure of ages-at-death is available, then equation (4) can be used to obtain unbiased estimates of the survival rates. Age specific survival rate estimates obtained from (3) or (4) will usually require some form of smoothing (Tanner 1978).

We are not aware of any previously developed techniques for estimating survival rates from age structure and age-at-death data in cases where age structures are not stable. To develop the necessary relations we allow all of the parameters to depend on time. Let t index the annual birth pulses,

- $N_x(t)$ = the number of live individuals in age class x at time t ,
- $c_x(t)$ = the proportion of live individuals in age class x at time t ,
- $s_x(t)$ = the proportion of live individuals in age class x at time t that survive to time $t+1$ (when they will be in age class $x+1$),
- $F_x(t+1)$ = the number of live individuals in age class x at time t that die before time $t+1$,
- $d_x(t+1)$ = the proportion of individuals dying between times t and $t+1$ that were in age class x , and

$\lambda(t)$ = the finite rate of increase for the population between times t and $t+1$.

Finally, let

$$N(t) = \sum_{i=0}^m N_i(t)$$

be the total number of live individuals at time t and let

$$F(t+1) = \sum_{i=0}^m F_i(t+1)$$

be the total number of live individuals at time t that died before time $t+1$. We consider ages $x=0, \dots, m$, where m is the maximum attainable age so that $s_m=0$ and $c_{m+1}=0$.

Now, by definition we have

$$c_x(t)N(t)s_x(t) = c_{x+1}(t+1)N(t+1), \quad x=0, \dots, m$$

and

$$N(t+1) = \lambda(t)N(t)$$

so that

$$s_x(t) = \frac{c_{x+1}(t+1)\lambda(t)}{c_x(t)}, \quad x=0, \dots, m. \quad (5)$$

Also by definition, we have

$$F_x(t+1) = c_x(t)N(t)[1-s_x(t)], \quad x=0, \dots, m,$$

so that

$$\begin{aligned} d_x(t+1) &= \frac{F_x(t+1)}{F(t+1)} \\ &= \frac{c_x(t)[1-s_x(t)]}{\sum_{i=0}^m \{c_i(t)[1-s_i(t)]\}}, \quad x=0, \dots, m. \end{aligned} \quad (6)$$

If the age structure is stable, then $c_x(t+1)=c_x(t)$ and this identity can be used to derive equations (3) and (4) from equations (5) and (6). However, equations (5) and (6) can also be solved directly for $s_x(t)$ and $c_x(t)$ without any assumptions about stability to give

$$c_x(t) = c_{x+1}(t+1)\lambda(t) + d_x(t+1)(1 - \lambda(t)[1 - c_0(t+1)])$$

and

$$s_x(t) = \frac{c_{x+1}(t+1)\lambda(t)}{c_{x+1}(t+1)\lambda(t) + d_x(t+1)(1 - \lambda(t)[1 - c_0(t+1)])}, \quad x = 0, \dots, m. \quad (7)$$

If the population growth rate is known and unbiased estimates of the age structure and the structure of ages-at-death are available, then equation (7) can be used to obtain unbiased estimates of the survival rates. Because the age structure is not assumed to be stable, the survival rates are not assumed to be constant. The estimated survival rates apply only to the period between t and $t+1$.

If data for age classes less than or equal to some value z are not available or not reliable (as in our case, where $z=1$ for the structure of ages-at-death data), then the proportions can be based on only age classes $> z$ with

$$c_x(t) = \frac{N_x(t)}{\sum_{i=z+1}^m N_i(t)},$$

$$d_x(t) = \frac{F_x(t)}{\sum_{i=z+1}^m F_i(t)}, \quad x=z+1, \dots, m,$$

and all of the relations discussed in this section will still hold. In this case, however, $\lambda(t)$ represents the finite growth rate only for age classes $> z$ rather than for the whole population. If the age structure is stable, the finite growth rates for the population and any subsets of age classes will be the same.

Estimation.-- We obtained 3 separate sets of survival rate estimates based on 3 different combinations of the age-structure and age-at-death data sets and associated assumptions. The first set of estimates was based only on the estimated age structure at the time of the spill (age classes 0 - 25) and the following assumptions:

1. Reproduction could be approximated as an annual birth pulse occurring at the time of the spill.
2. The population was not increasing or decreasing ($\lambda = 1$).
3. The population had a stable age structure.

Survival rates were estimated separately for males and females according to equation (3) with $\lambda = 1$. The second set of estimates was based on the same set of assumptions, but using only the estimated structure of ages-at-death during the year preceding the spill (age classes 2 - 25). Survival rates were estimated separately for males and females according to equation (4) with $\lambda = 1$. For the final set of estimates, we relaxed the assumption of a stable age structure and used both the estimated age structure and the estimated structure of

ages-at-death. Survival rates were estimated separately for males and females according to equation (7) with $\lambda = 1$.

Smoothing.-- Eberhardt and Siniff (1988) used a proportional hazards model (Eberhardt 1985, Siler 1979) to smooth survivorship estimates based on age structure data. We adapted their basic approach to provide a consistent method for smoothing survival rate estimates obtained according to any of the above methods. Our approach consisted of transforming survival rate estimates into l_x values that are formally equivalent to survivorship rates, smoothing these by fitting to the proportional hazards model used by Eberhardt and Siniff (1988), and then back-transforming the smoothed l_x values to obtain smoothed survival rate estimates.

Survival rate estimates obtained from (3), (4), or (7) were transformed according to

$$l_0 = 1 ,$$

$$l_x = \prod_{i=0}^{x-1} s_i(t) , \quad x=1, \dots, 26. \tag{8}$$

When the survival rates in (8) are based on equation (3) or (4) under the assumption of a stable age structure, then the l_x values can be interpreted in the conventional sense as survivorship rates. Survivorship rates cannot be expressed as a function of the $s_x(t)$ at a single time t when survival rates are not constant over time. Thus, when the survival rates in (8) are based on equation (7), the l_x values will not generally be equivalent to survivorships. However, equation (8) still defines a one-to-one transformation of the s_x , $x=0, \dots, k$ if $s_x > 0$ for all $x \leq k$. The resulting l_x values form a nonincreasing function of x that can be smoothed by fitting to the proportional hazards model used by Eberhardt and Siniff (1988).

The form of the proportional hazards model was

$$l_x = l(A,B)l(G)l(D,E),$$

where

$$l(A,B) = A(1-\exp[-Bx])$$

is a function describing the initial rapid decrease in survivorship with age for juvenile otters,

$$l(G) = \exp[-Gx]$$

is a function describing the constant decrease in survivorship with age for prime-aged adults,

$$l(D,E) = \exp[-D(\exp[Ex]-1)]$$

is a function describing the accelerated decrease in survivorship with age for senescent otters, and A , B , G , D , and E are parameters to be estimated (Eberhardt and Siniff 1988).

Parameters were estimated by the method of least squares. In cases where survival rates were not estimated for the youngest age classes, we set $l(A, B) = 1$ and did not attempt to fit the initial phase of the survivorship model. Otherwise, if the least squares estimate of B was greater than 10, the value of B was set to 10 and B was no longer treated as an unknown parameter. Values of $B \geq 10$ result in $l(A, B)$ being essentially constant for $x > 0$. Finally, if we were unable to obtain convergence and a nonsingular jacobian, then we set $l(D, E) = 1$ and attempted to fit the reduced model that did not include a senescence effect.

Predicted non-zero survivorships from the fitted model were then back transformed to obtain the smoothed survival rate estimates

$$s_x = \frac{l_{x+1}}{l_x}, \quad x=0, \dots, 25.$$

RESULTS

Reproductive Rates

Positive reproductive rates estimates were obtained for age classes 3 through 16, with estimates of 0.6 or greater for ages greater than 3 (Figure 2). Least square estimates of the parameters in the smoothing function were

$$\begin{aligned} A &= 0.907955 \\ B &= 0.544397 \\ T &= 16.056893 \\ S &= 0.064483 \end{aligned}$$

where $D = \exp[-T/S]$ and $E = 1/S$. This gave smoothed reproductive rate estimates that increased from 0 at age 2 up to a high of 0.91 at age 15 and then decreased back to 0 by age 17 (Figure 2).

Structure of Ages-at-death

Female sea otters accounted for an estimated 79% (23/29) of the natural mortality in age classes ≥ 2 during the year preceding the oil spill (Figure 3). An estimated 70% (19/23) of the female mortality and 83% (5/6) of the male mortality was in age classes 8 - 16. 13% (3/23) of the female mortality occurred in age classes 19 and above, with 2 of the female carcasses (9%) in age class 21. No male carcasses were recovered in age classes greater than 15 (Figure 3).

Population Age Structure

The estimated population structure at the time of the oil spill consisted of 26% (120/464) age class 0 otters and 35% (164/464) age class 1 - 3 otters, with the remaining 39% in age classes 4 - 17 (Figure 4). We estimated that 57% (265/464) of the population was female (Figure 4).

Relative Recovery Rates

Without assuming equal recovery rates, we estimated that 5.4% of the 407 recovered carcasses of otters that died after the spill were dependent pups and 5.7% were lactating females (Table 1). The difference in these proportions was not significant (likelihood ratio test, $\chi^2 = 0.03$, $df=1$, $P=0.86$). Under the assumption that the proportions of dependent pups and lactating females were equal, we estimated that each of these subclasses comprised 5.6% of the recoverable population (Table 1). These results suggest that, of the otters that died after the spill and were recovered, most were probably recovered before any size related differences in persistence could affect recovery rates.

Survival Rates

Survival rates estimated from age structure data were quite variable, with 7 of the female and 6 of the male age classes having estimated rates greater than 1 (Figures 5A and 6A). An estimate greater than 1 results whenever the proportion of individuals in an age class is greater than the proportion in the next youngest age class. The fitted smoothing functions indicated sharp initial increases in survival rates from age 0 to 1 followed by nearly constant rates of about 0.93 for females and 0.79 for males up to at least age 10 (Table 2, Figures 5A and 6A). Smoothed survival rate estimates then decreased to 0 by age 18 for females. We were not able to fit a term for a senescent phase to the male data (Table 2).

Survival rates estimated from ages-at-death data were somewhat less variable (Figures 5B and 6B). This was due, at least in part, to the fact that these estimates cannot exceed 1. However, survival rate estimates will equal 1 for each age class with no recovered carcasses if there is an older age class for which some carcasses were recovered. In many cases, the absence of any carcasses in an age class probably only resulted from the small total number of carcasses recovered. There were 12 female age classes with recovered carcasses that provided survival rate estimates less than 1. There were only 6 male age classes with any recovered carcasses and each of these had just 1 carcass. We did not attempt to fit the initial phase of the smoothing function to these data because we only considered age classes 2 and above. We were able to fit the constant as well as the senescent phase of the function to both male and female ages-at-death (Table 2). Smoothed survival rates for age class 2 (0.98 for females and 0.97 for males) were higher than the corresponding smoothed estimates based on age structure data. Smoothed female rates remained above 0.95 through age 6 and then declined to 0.20 by age 25 (Figure 5B). Smoothed male rates remained above 0.95 through age 4 and then declined relatively rapidly to below 0.10 by age 19 (Figure 6B).

As might be expected, survival rates estimated from both the age structure and ages-at-death data were somewhat in between the estimates obtained from either data set by itself (Figures 5C and 6C). Age classes that had survival rate estimates equal to 1 when

based on only ages-at-death data also had estimates equal to 1 when based on both data sets. This reduced some of the variability in the estimated rates, but also nullified any information the age structure data could have provided for those age classes. Once again, we did not attempt to fit the initial phase of the smoothing function to these data because we only considered age classes 2 and above. We were able to fit both remaining phases of the function to the female data (Table 2), resulting in smoothed survival rate estimates starting at 0.95 for age class 2 and decreasing to less than 0.10 by age 18 (Table 3, Figure 5C). Smoothed survival rate estimates for males were a constant 0.86 for age classes 2 and above (Table 3, Figure 6C). We were not able to fit the senescent phase of the smoothing function to the male data (Table 2).

DISCUSSION

Reproductive Rates

Our estimates of age-specific reproductive rates assumed that mortality of otters and recovery and selection of carcasses for examination were independent of reproductive status within each age class, and that there was no bias in determining the age class or reproductive status of each examined carcass. These are the same assumptions used by Bodkin et al. (1993), who considered them to be reasonable based on the extent of the oil spill and evaluations of the selection, aging and examination techniques. Our unsmoothed estimates are similar to those obtained by Bodkin et al. (1993), but are more variable because we did not combine any age classes. We note that our age class i corresponds to age class $i+1$, $i=0, \dots, 25$ as defined by Bodkin et al. (1993).

The smoothing function fit the observed reproductive rates quite well (Figure 2). However, the onset and form of senescence were entirely determined by the observed rate for age 16 (0.60, based on only 5 examined otters) and the lack of any data for older age classes. Lack of data for these older age classes was a result of their apparent rarity in the population. Assuming a reproductive rate of 0 for age classes > 16 will not have much effect on overall population dynamics if the number of females in those age classes is negligible.

Jameson and Johnson (1993) estimated a minimum annual reproductive rate of 0.64 for mature females based on observations of 49 tagged otters near Green Island during 1975-84. They considered this estimate to be a minimum because the otters were observed infrequently and they suggested that the true rate may have been close to the value of 0.88 obtained from examination of reproductive tracts of mature females collected by Kenyon (1969) at Amchitka Island. Based on comparisons from the Aleutian Islands, Prince William Sound, and California, Jameson and Johnson (1993) concluded that annual reproductive rates of 0.85 to 0.90 were typical for mature females (age > 4) regardless of population status. Weighting our smoothed reproductive rate estimates by the estimated proportions in age classes > 4 gives an overall reproductive rate estimate of 0.85 for mature females, which is consistent with the conclusions of Jameson and Johnson (1993). This estimate is higher than estimates obtained after the oil spill by Monnett and Rotterman (1992). Their telemetry-based estimates of reproductive rates for mature females in western PWS were 0.58 (21/36) during 1990 and 0.78 (29/37) during 1991. These estimates may be lower than

ours, at least in part, because Monnett and Rotterman (1992) did not instrument otters that were in advanced stages of pregnancy when captured and they may not have detected pups that died within the first few days after birth. Also, our estimates are partly based on detected pregnancies, some of which may not have resulted in live births.

Structure of Ages-at-death

Our estimate of the structure of natural mortality that occurred during the year preceding the oil spill assumed that 1) there was no age or sex related bias in recovery of carcasses of otters that died during the year preceding the spill, 2) there was no age or sex related bias in determining time of death for recovered carcasses, and 3) there was no bias in determining sex or age class for recovered carcasses. The most likely bias that could have affected recovery of carcasses is related to carcass size (Bodkin and Jameson 1991). We reduced the potential for this bias by not considering the 2 age classes with the smallest carcasses. Almost all adult sea otter mortality in PWS occurs during the winter (Johnson 1987, Monnett 1988), so that the adult carcasses on beaches in early spring should be representative of total annual adult carcass deposition. The potential for violations of assumptions (2) and (3) was reduced by not including any carcasses without clear determinations of time of death, sex and tooth-based age.

Our estimated structure of ages-at-death is broadly consistent with patterns observed previously for this region (Johnson 1987). Monson and Ballachey (1995) were not able to detect significant differences among age distributions from annual collections of beach-cast carcasses in western PWS during 1976 through 1984 and during the oil spill response in 1989 (carcasses classified as dying before the spill). This result is consistent with the assumption of a stable population structure during this period, but annual sample sizes and, therefore, the power to detect differences were quite low.

Population Age Structure

Our estimate of the population structure at the time of the spill assumed that 1) there was no age or sex related bias in mortality due to the oil spill, 2) there was no age or sex related bias in determining time of death for recovered carcasses, 3) there was no age or sex related bias in recovery of carcasses of otters that died after the spill, 4) otters classified as dying after the oil spill died as a result of the oil spill, 5) our smoothed estimates of age-specific reproductive rates were unbiased, and 6) the sex ratio of age class 0 was 1:1 at the birth pulse.

It is not known whether there was any age or sex related bias in oil spill mortality. All age and sex classes (ages < 14) were represented in the recovered carcass sample. Oil related mortality is not likely to be biased with respect to fitness of individuals in the path of an oil spill (Piatt et al. 1990). However, age and sex related differences in behavior and spatial distribution (Garshelis et al. 1984, Riedman and Estes 1990) may have resulted in an age or sex related bias in exposure and subsequent mortality of sea otters. Oiled areas in western PWS were primarily breeding areas, occupied by territorial males and adult females. Geographic information system plots of recovery locations gave no indication of any age or sex related segregation within the oil spill area.

Assumptions (2) and (3) were also required for estimating the structure of ages-at-death and were discussed above. In this case, however, we were able to test the assumption of no size related bias in carcass recovery and found it to be valid even for age class 0 otters. Assumption (4) was not likely to be seriously violated because the vast majority of the carcasses were recovered shortly after the spill and almost all natural adult mortality occurs during the winter.

Assumptions (5) and (6) were required for estimating the proportion of age class 0 otters in the population. The smoothed reproductive rate estimates appear reasonable, as discussed above. Our assumed 1:1 sex ratio for age class 0 is consistent with the observed ratios for pups born at rehabilitation centers (9 female : 8 male), recovered dependent pups with known sex that died after the oil spill (9 female : 10 male), and dependent pups captured with tangle nets and dip nets in 1992 (17 female : 18 male, NBS unpubl. data). Other efforts to capture dependent pups in western Prince William Sound have resulted in lower proportions of females (15 female : 20 male, Monnett 1988; 14 female : 25 male, Rotterman and Monnett 1991). The proportion of females in the sample of recovered fetal sea otters was higher than our assumed value for age class 0 (32 female : 17 male, Bodkin et al. 1993). It may be that sea otter sex ratios generally favor females at conception (Bodkin et al. 1993), but males have higher survival rates than females in utero, and perhaps as neonates (Monnett 1988), so that sex ratios of dependent pups tend to favor males. Our assumption of a 1:1 sex ratio was probably reasonable because we approximated reproduction with birth-pulse dynamics and estimated numbers in age class 0 based on pregnant and lactating females at the time of the pulse.

The estimated age structures for both sexes included a large number of age classes with higher proportions of individuals than the next youngest age classes. This suggests either very poor precision in estimating the age structure, violation of one or more of the assumptions about age bias, or that the population structure was not stable. Because of the relatively large sample size for estimating age structure and the other considerations discussed above, it seems most likely that the age structure was not stable at the time of the spill.

Survival Rates

Our estimates of age-specific survival rates were based on some or all of the following assumptions.

- 1) The estimated structure of ages-at-death was unbiased.
- 2) The estimated population age structure was unbiased.
- 3) The annual growth rate for either the whole population or for age classes > 1 was $\lambda=1$ during the year preceding the oil spill.
- 4) The population age structure was stable at the time of the spill.

Assumptions (1) and (2) were discussed above. There are no data for directly assessing assumption (3). If the population was actually growing during the year preceding the spill, then our estimated survival rates would be negatively biased. We expect that any such bias would be small because it is widely believed that if the population was growing, its

growth rate was small (Garrott et al. 1993). As discussed above, the assumption of a stable age structure was not likely to have been true.

The traditional survival rate estimates based on equations (3) and (4) rely on the assumption of age structure stability. The estimates based on equation (7) are the only ones that do not rely on the assumption of age structure stability and therefore are probably the most appropriate for this case. The estimates based on equation (7) do rely on assumptions (1), (2), and (3). We were not able to obtain estimates of survival rates for age classes 0 and 1 based on equation (7) because of the possible size bias in recovery of otters that died before the spill. The quality of the estimates was also limited by the small overall sample size of ages-at-death data. This was particularly true for males ($n=6$). Lack of age structure data for age classes > 16 for females and 17 for males may have prevented the fitting of a realistic form for senescence in the smoothing function. The actual form of senescence may not be important to overall population dynamics, however, if the older age classes are a negligible portion of the population.

There are no published estimates of survival rates for PWS sea otters in age classes > 1 from before the spill. Garshelis and Garshelis (1987) observed survival rates of 0.60 ($n=5$) for female and 0.33 ($n=3$) for male pups that were tagged near Green Island while dependent and then followed approximately 1 month after independence. This pup category may correspond most closely with the last 3 to 6 months of our age class 0, but the weanings were considered atypical (Garshelis and Garshelis 1987). Monnett (1988) estimated annual survival rates of 0.34 for female and 0.21 for male weanling sea otters based on telemetry data from eastern and western PWS during 1984-87, under the assumption that otters died on the day their carcasses were found and that missing otters were dead. This weanling category may approximately correspond to our age class 1.

Rotterman and Monnett (1991), Monnett and Rotterman (1992) and NBS (unpubl. data) provided telemetry-based estimates of survival rates for certain segments of the western PWS population during time periods after the oil spill. Monnett and Rotterman (1992) estimated a 10 month survival rate of 0.96 for adult females during 1990-91 based on the assumption that missing otters were dead. Weighting our smoothed survival rate estimates from equation (7) by the estimated proportions in each age class gives an overall estimate of 0.86 for females in age classes ≥ 2 . The overall survival rate estimated by Monnett and Rotterman (1992) may have been greater than ours because their sample of otters may have included a higher proportion in the prime age classes. We estimated survival rates of 0.95 for female age classes 2 through 4 and rates > 0.90 for age classes 2 through 9.

All of the other estimates of survival rates in western PWS after the spill are for otters in age classes ≤ 1 . Monnett and Rotterman (1992) estimated 2 month survival rates for dependent pups, both sexes combined, to be 0.76 in 1990 and 0.97 in 1991. This dependent pup category corresponds approximately to months 7 and 8 of our age class 0. Rotterman and Monnett (1991) estimated 8 month survival rates of 0.08 for male and 0.21 for female weanling sea otters during 1991 based on the assumption that missing otters were dead. These rates appear to be extremely low and may be a result of chronic oil effects (Rotterman and Monnett 1991). This weanling category approximately corresponds to the first 8 months of our age class 1. NBS (unpubl. data) estimated 15 month survival rates of 0.59 for females and 0.47 for males monitored from 3 months of age during 1992-93, based on the assumption that missing otters were dead. This 1.5 year weanling category most closely corresponds to our age class 1.

MODEL

We used a Leslie-type 2-sex projection matrix (Caswell 1989) to integrate the available information on western PWS sea otter population dynamics and to project its potential recovery following the oil spill. We assumed that there was no emigration from or immigration to western PWS, which is largely consistent with telemetry data from after the spill (Monnett and Rotterman 1992b, NBS unpubl. data). The model approximated the reproductive cycle with an annual birth pulse occurring at the anniversary of the oil spill. This date is close to when most pups are born in this population (Garshelis et al. 1984). Parameter values used with the model are given in Tables 3 and 4. Fecundity values were obtained from our smoothed reproductive rate estimates (Figure 2) and the assumption of a 1:1 sex ratio for age class 0. Based on the conclusions of Jameson and Johnson (1993), we assumed that reproductive rates remained constant and were not affected by the oil spill or the status of the population. Survival rates for age classes 2 - 20 for females and 2 - 17 for males were the smoothed estimates from equation (7) (Figures 5C and 6C). We set survival rates for males in age classes 18 - 20 equal to 0, because no carcasses in age classes greater than 17 were recovered and there were insufficient data for fitting the senescent phase of the smoothing function. Based on the relatively high survival rate for adult females observed by Monnett and Rotterman (1992a) during 1990-91, we assumed that adult survival rates also remained constant and were not affected by the oil spill or the status of the population.

Following Eberhardt and Siniff (1988), we assumed that the most likely parameters to be affected by the oil spill or population status would be survival rates for the youngest age classes. Telemetry data suggest that there may have been an initial depression in survival rates for age class 1 (Rotterman and Monnett 1991), followed by increases in survival rates for age classes 0 and 1 in the first few years after the spill (Monnett and Rotterman 1992a, Rotterman and Monnett 1991, NBS unpubl. data). We allowed survival rates for age classes 0 and 1 to vary over time, and used telemetry-based estimates of those rates in the years for which they were available.

We assumed that if survival rates were perturbed from equilibrium levels, then density dependent processes would eventually cause them to return toward equilibrium levels. Density dependence was modeled separately for males and females with a generalized logistic function (Taylor and DeMaster 1993). The general form of this function is

$$s_N = s_c + (s_m - s_c) \left(1 - \left(\frac{N}{N_c} \right)^\theta \right)$$

where s_N is the survival rate when the population is size N , N_c is the population size at equilibrium, s_c is the survival rate at equilibrium, and s_m is the maximum survival rate (the theoretical rate when $N=0$). Here, we set $N_c=5808$, which was the estimated population size in 1985 (Garrott et al. 1993). The parameter θ controls the shape of the function. Following Eberhardt and Siniff (1988), we used a relatively large value of θ ($\theta=9$) so the effect of density dependence would not be evident until the population came close to its equilibrium size (Figure 7). Nine was the largest value for θ that consistently resulted in stationary trajectories rather than limit cycles in our model projections.

Because of the lack of data for estimating survival rates of age class 0 and 1 otters in most years, we considered a series of 4 potential scenarios (Table 4). In all of the scenarios, we used the telemetry-based estimates of survival rates for age class 1 otters in 1990-91 (Rotterman and Monnett 1991) and 1992-93 (NBS unpubl. data). We used the mean of the 1990-91 and 1992-93 estimates for age class 1 otters in 1991-92. Based on the extremely low survival rate observed for age class 1 otters in 1990-91 (Rotterman and Monnett 1991), we assumed that there was no survival of age class 0 or 1 otters in 1989-90.

In scenarios 3 and 4, we used the telemetry-based estimates for age class 0 otters in 1990-91 and 1991-92 reported by Monnett and Rotterman (1992a). These values are likely to be overestimates of the actual survival rates because they account for mortality only during the first 2 months after the neonatal period. The rate of 0.97 for 1991-92 (Monnett and Rotterman 1992a) is higher than rates observed for any other populations in Alaska (Monnett and Rotterman 1992a; Monson 1995; Monson and DeGange 1995) or California (Loughlin 1981; Siniff and Ralls 1991; Jameson and Johnson 1993; Riedman et al. 1994). We assumed that in 1992-93, survival rates for age class 0 otters began a density dependent decrease to equilibrium values, and survival rates for age class 1 otters increased to our estimated rate for prime age adults and then began a density dependent decrease to equilibrium values (Table 4, Figure 7). It is unlikely that survival rates for age class 1 otters could actually be as high as those of prime-aged adults. The assumed survival rates for age classes 0 and 1 in these scenarios probably can be best viewed as upper limits for the actual rates that potentially could occur in this population. The differences between scenarios 3 and 4 are the assumed values for the equilibrium survival rates (see below).

In scenarios 1 and 2, we again assumed that survival rates for age class 0 increased to their maximum level in 1991-92 and then began a density dependent decrease to their equilibrium values (Table 4, Figure 7). However, we used a lower, telemetry-based estimate of the age class 0 survival rate from Kodiak (0.83; Monson and DeGange 1995) for the maximum rate. Kodiak provides an example of an increasing sea otter population in recently occupied, prime habitat (Monson and DeGange 1995) with survival rates that are probably close to the maximum for the species. The rate reported by Monson and DeGange (1995) accounts for mortality during the first 5 months after the neonatal period. We obtained a survival rate of 0.65 for age class 0 in 1990-91 by assuming the same proportional reduction from the 1990-91 rate reported by Monnett and Rotterman (1992a) as effectively assumed for the 1991-92 rate (i.e., $0.65/0.76=0.83/0.97$). We assumed that survival rates for age class 1 were at their equilibrium values in 1993-94 and that they remained at that level throughout the recovery period (Table 4, Figure 7). Given the other parameters in the model, this is the most conservative assumption that can be made about age class 1 survival rates that will still allow the population to eventually recover. The differences between scenarios 1 and 2 are in the assumed values for the equilibrium survival rates.

There were no data for directly estimating equilibrium survival rates in the western PWS population. However, given values for the other parameters in the model and an assumed equilibrium value for the survival rate of either age class 0 or age class 1 females, the equilibrium value of the other female survival rate can be derived numerically. We used this approach to derive equilibrium survival rates based on two different sets of assumptions. In the first set (equilibrium assumption A), we assumed that the observed age class 1 survival rates of 0.59 for females and 0.47 for males in 1992-93 (NBS unpubl. data) were the equilibrium survival rates for this population. This results in an equilibrium survival rate of

0.56 for age class 0 females. We assumed that the survival rate for age class 0 males was the same as for age class 0 females. Scenarios 1 and 3 were based on equilibrium assumption A (Table 4, Figure 7).

The second set of assumptions (equilibrium assumption B) is based on the observed survival rate of 0.47 for age class 0 sea otters at Amchitka, Alaska (Monson et al. In prep.). The Amchitka population is the only other Alaskan sea otter population which is thought to be at equilibrium and for which we have pre-weaning survival data. The telemetry-based estimate from Amchitka (Monson et al. In prep.) is similar to the estimate of 0.46 (Siniff and Ralls 1991), but somewhat lower than the estimate of 0.60 (Riedman et al. 1994) for the California population, which also appears to be close to equilibrium. However, dynamics of California and Alaska populations may not be generally comparable (Bodkin et al. 1995; Estes et al. 1995). Given the other parameters in our model, an equilibrium survival rate of 0.47 for age class 0 females results in an equilibrium rate of 0.70 for age class 1 females. As in equilibrium assumption A, we assumed that age class 0 survival rates were the same for males and females. We obtained the equilibrium survival rate of 0.56 for age class 1 males by assuming the same proportional increase from the observed 1992-93 male rate (NBS unpubl. data) as effectively assumed for females (i.e., $0.56/0.47=0.70/0.59$). Scenarios 2 and 4 were based on equilibrium assumption B (Table 4, Figure 7).

We used the model to project a separate population recovery trajectory based on each of the 4 scenarios. For each scenario, the model was initiated with our estimate of the population structure at the time of the spill (Figure 4) and the total population size of 3,898 otters estimated to remain after the spill by Garrott et al. (1993). We then incremented the population annually at the anniversary of the spill with a projection matrix parameterized according to Table 3 and the appropriate column of Table 4. In all of the scenarios, there was a projected decrease to a population size of 3,234 otters after the first year (Figure 8). The initial decrease was due to the assumption of no survival for juvenile otters in the first year. The population was projected to begin increasing after the first year in all of the scenarios, with maximum rates of increase of 10% per year in scenarios 1 and 2 and 14% per year in scenarios 3 and 4. The projected times required to recover to the estimated 1985 population size of 5808 otters (Garrott et al. 1993) were 23 years in scenario 1, 16 years in scenario 2, and 10 years in scenarios 3 and 4 (Figure 8). Projected recovery times were more sensitive to assumptions about maximum survival rates than assumptions about equilibrium survival rates over the range of scenarios we considered.

The equilibrium survival rates are the rates required for the population to maintain a constant size. We assume that annual survival and reproductive rates fluctuated around their equilibrium values in the years preceding the spill (i.e., mean annual survival rates were the equilibrium values) because the population was maintaining its size during that period. If none of the survival or reproductive rates increased above their equilibrium values following the spill, then the population would not recover to its previous size. Recovery, in our model, is driven by the possibility that survival rates for age classes 0 and 1 can exceed their equilibrium values. All of the scenarios we considered assume that survival rates for age class 0 exceeded their equilibrium values by 1990-91 and that survival rates for age class 1 reached or exceeded their equilibrium values by 1993-94. Once all of the survival rates reach or exceed their equilibrium values, the population will continue to increase as long as the survival rate for at least one age class remains above its equilibrium value.

Scenarios 3 and 4 are highly optimistic with respect to survival rates for both age classes 0 and 1. The rate of recovery under these scenarios probably represents the maximum that could occur considering the available data. Scenarios 1 and 2 are more conservative but probably still somewhat optimistic with respect to survival rates for age class 0. This is because these rates still do not include fetal or neonatal mortality. Also, it is not known whether the western PWS habitat could have recovered to the point where it could support survival rates equivalent to those at Kodiak so quickly. However, other factors such as predation rates may also differ between the two areas. On the other hand, scenarios 1 and 2 are quite conservative with respect to survival rates for age class 1. Because they combine somewhat optimistic assumptions for age class 0 with conservative assumptions for age class 1, the projected recovery rates for scenarios 1 and 2 are probably more realistic than those for scenarios 3 and 4.

The assumption that adult survival rates were not affected by the spill may also be somewhat optimistic. This assumption was used in all 4 scenarios and is consistent with the available telemetry data (Monnett and Rotterman 1992a). However, age distributions of beach-cast carcasses collected in 1990 and 1991 suggest that adult mortality may have been relatively high in those years (Monson and Ballachey 1995). Given the pathologies observed in oiled otters dying in 1989 (Lipscomb et al. 1994) and patterns generally observed in laboratory studies of toxic effects, it is possible that sub-lethal effects of oil exposure could have reduced survival of adult sea otters for some period of time after the spill.

All of the scenarios we considered indicated that the population would decrease during the first year after the spill and then begin a relatively steady increase to its equilibrium size. Agler et al. (1994) were not able to detect any trend in the western PWS sea otter population size based on their analysis of the boat-based surveys conducted from 1989 through 1993. This may be due, at least in part, to the large amount of variability associated with each of the survey estimates (Table 5). The model projections under all of the scenarios are well within the 95% confidence intervals of the population estimates from all of the boat-based surveys conducted after the spill if they are adjusted for detectability following Garrott et al. (1993) (Table 5).

We believe that the model presented here provides a reasonable structure for approximating the dynamics of the western PWS sea otter population. However, we want to stress that there is considerable uncertainty associated with the various assumptions used to estimate parameters and with the estimation of the parameters, given the assumptions. It might be possible to use bootstrap (Efron 1982) or Bayesian (Raftery et al. 1995) approaches to quantify some of this uncertainty. Of most concern, though, is that beyond 1993, there are no data for estimating the model parameters and their values must be based purely on assumptions about how future values are likely to relate to past estimates. In addition to assuming a particular form for this relationship, all the scenarios assume that the relationship will remain unperturbed throughout the recovery period. The uncertainty associated with these assumptions is partially evident in the disparity between projected recovery times under the various scenarios. These projections might best be viewed as benchmarks, indicating how the population is likely to recover, given the available data and selected sets of assumptions. The potential for recovery under alternative sets of assumptions could be roughly evaluated by comparison to the sets of assumptions we have considered. Continued monitoring would be required to determine how the population vital rates actually change

after 1993. Updated (or improved) estimates of survival rates, reproductive rates and population size should be incorporated into the model as they become available.

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Table 1. Maximum likelihood estimates of proportions of otters in sample subclasses.

Sample subclass	Proportions of lactating females and dependent pups assumed equal	
	No	Yes
Of 407 recovered carcasses		
Independent females	0.523	0.522
Independent males	0.354	0.354
Independent unknown sex	0.069	0.068
Dependent pups	0.054	0.056
Independent lactating females ^a	0.057	0.056
Of 143 examined independent females		
Lactating	0.101	0.099
Non-lactating	0.899	0.901
-2 ln(L) ^b	950.448	950.478

^a These include the proportion of known females estimated to be lactating and the portion of unknown sex estimated to be lactating females.

^b $L = (P_f)^f (P_m)^m (P_d)^d (1 - P_f - P_m - P_d)^{1-f-m-d} (P_l)^l (1 - P_l)^{1-l}$. See text for symbol definitions. Difference in proportions of lactating females and dependent pups not significant (likelihood ratio test, $\chi^2 = 0.03$, $df = 1$, $P = 0.86$).

Table 2. Least squares estimates of parameters in smoothing functions for survival rates.

Source of survival rate estimates	Parameter ^a				
	A	B	exp(-G)	T	S
Female					
Age structure	0.94	10 ^b	0.92	16.38	0.87
Ages-at-death	-c-	-c-	1	11.45	5.54
Age structure & Ages-at-death	-c-	-c-	0.95	12.31	2.18
Male					
Age structure	0.39	10 ^b	0.79	-d-	-d-
Ages-at-death	-c-	-c-	0.98	10.03	3.25
Age structure & Ages-at-death	-c-	-c-	0.86	-d-	-d-

^a $D = \exp(-T/S)$, $E = 1/S$.

^b Least squares estimate of B was greater than 10, so B was set equal to 10 and no longer treated as a parameter.

^c Parameters for initial phase of smoothing function not estimated because only age classes 2 and above were considered.

^d Parameters for senescent phase of smoothing function not estimated because unable to obtain convergence and nonsingular jacobian.

Table 3. Parameter values used for projecting recovery of the western PWS sea otter population following the *Exxon Valdez* oil spill in March 1989.

Age class	Parameters		
	Fecundity	Female Survival	Male Survival
0	0.00	*	*
1	0.00	*	*
2	0.00	0.95	0.86
3	0.38	0.95	0.86
4	0.60	0.95	0.86
5	0.73	0.94	0.86
6	0.81	0.94	0.86
7	0.85	0.93	0.86
8	0.87	0.92	0.86
9	0.89	0.90	0.86
10	0.90	0.88	0.86
11	0.90	0.84	0.86
12	0.90	0.78	0.86
13	0.91	0.69	0.86
14	0.91	0.57	0.86
15	0.91	0.43	0.86
16	0.60	0.27	0.86
17	0.00	0.13	0.86
18	0.00	0.04	0.00
19	0.00	0.01	0.00
20	0.00	0.00	0.00

* See Table 4 for survival rates of age class 0 and 1 otters.

Table 4. Survival rates used for age classes 0 and 1 in projecting recovery of the western PWS sea otter population under 4 potential scenarios following the *Exxon Valdez* oil spill in March 1989.

Age	Year	Scenario			
		1	2	3	4
0	1989-90	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
	1990-91	0.65/0.65	0.65/0.65	0.76/0.76	0.76/0.76
	1991-92	0.83/0.83	0.83/0.83	0.97/0.97	0.97/0.97
	equilib. ^a	0.56/0.56	0.47/0.47	0.56/0.56	0.47/0.47
1	1989-90	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
	1990-91	0.21/0.08	0.21/0.08	0.21/0.08	0.21/0.08
	1991-92	0.40/0.28	0.40/0.28	0.40/0.28	0.40/0.28
	1992-93	0.59/0.47	0.59/0.47	0.59/0.47	0.59/0.47
	1993-94	0.59/0.47	0.70/0.56	0.95/0.86	0.95/0.86
	equilib. ^b	0.59/0.47	0.70/0.56	0.59/0.47	0.70/0.56

^a Survival rates assumed to begin density dependent decrease to equilibrium values after 1991-92 in all scenarios.

^b Survival rates assumed to remain constant after reaching equilibrium values in 1992-93 (scenario 1) or 1993-94 (scenario 2). Survival rates assumed to begin density dependent decrease to equilibrium values after 1993-94 in scenarios 3 and 4.

Table 5. Estimates of the western PWS sea otter population size derived from boat-based surveys and from model-based projections.

Year	Boat-based survey estimates		Model-based projections			
	Unadjusted ±95% C.I.	Adjusted ^e ±95% C.I.	Scenario 1	Scenario 2	Scenario 3	Scenario 4
1989	2709±884 ^a	3898±1272	3898	3898	3898	3898
1990	1991±606 ^b	2865±871	3234	3234	3234	3234
1991	2149±976 ^c	3092±1404	3560	3560	3671	3671
1993	1525±1560 ^d	2194±2245	3486	3644	3883	3883

^a Based on June, July, and August surveys (Garrott et al. 1993).

^b Based on June, July, and August surveys (Burn 1994).

^c Based on July survey (Burn 1994).

^d Based on July survey (Agler et al. 1994).

^e Adjusted for detectability following Garrott et al. (1993). Approximate variance obtained by multiplying the unadjusted variance by the square of the correction factor. This results in an underestimate of the variance (and the confidence interval) because it does not account for the error in estimating the correction factor.

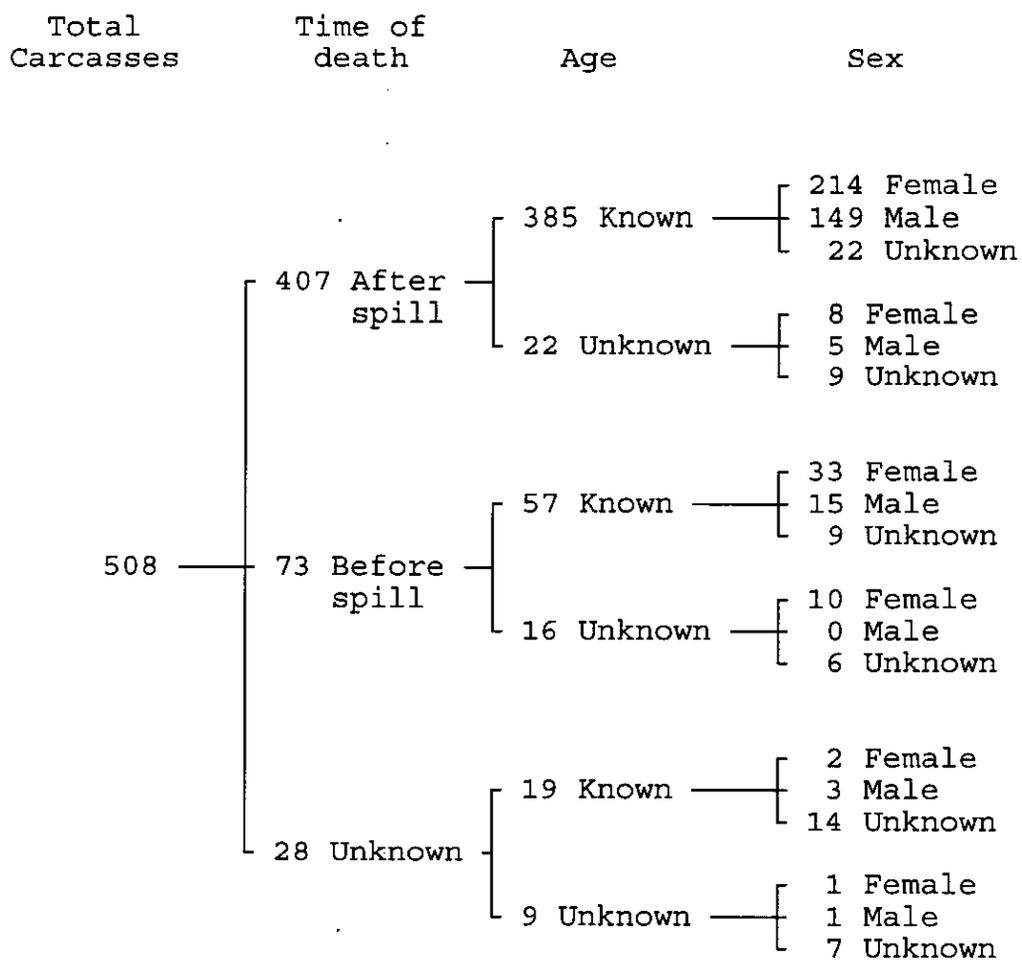


Figure 1. Sea otter carcasses collected in Prince William Sound between 30 March and 15 September 1989. Carcasses with unknown ages are all in age classes >0.

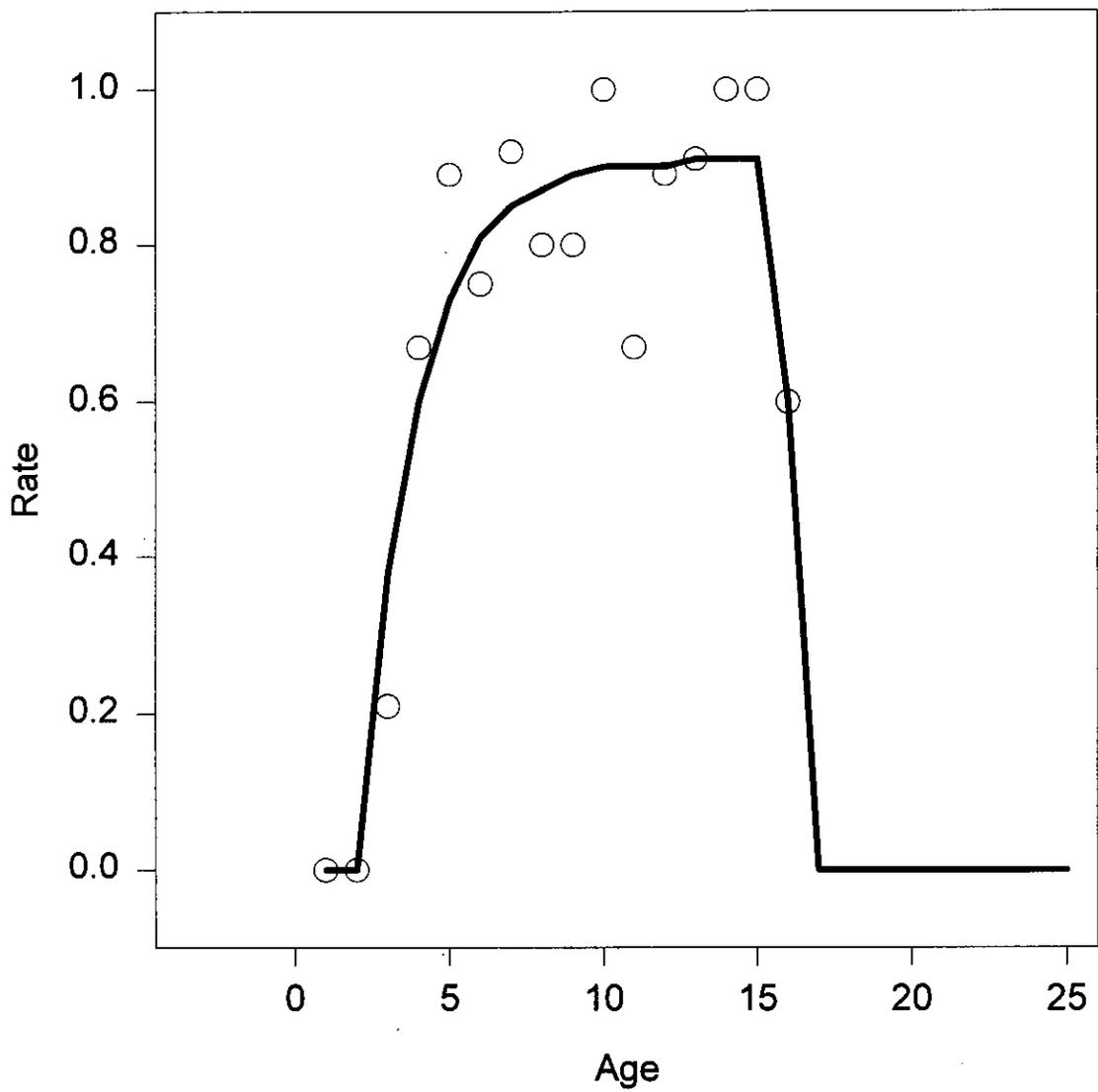


Figure 2. Observed and smoothed reproductive rate estimates for female sea otters at the time of the spill.

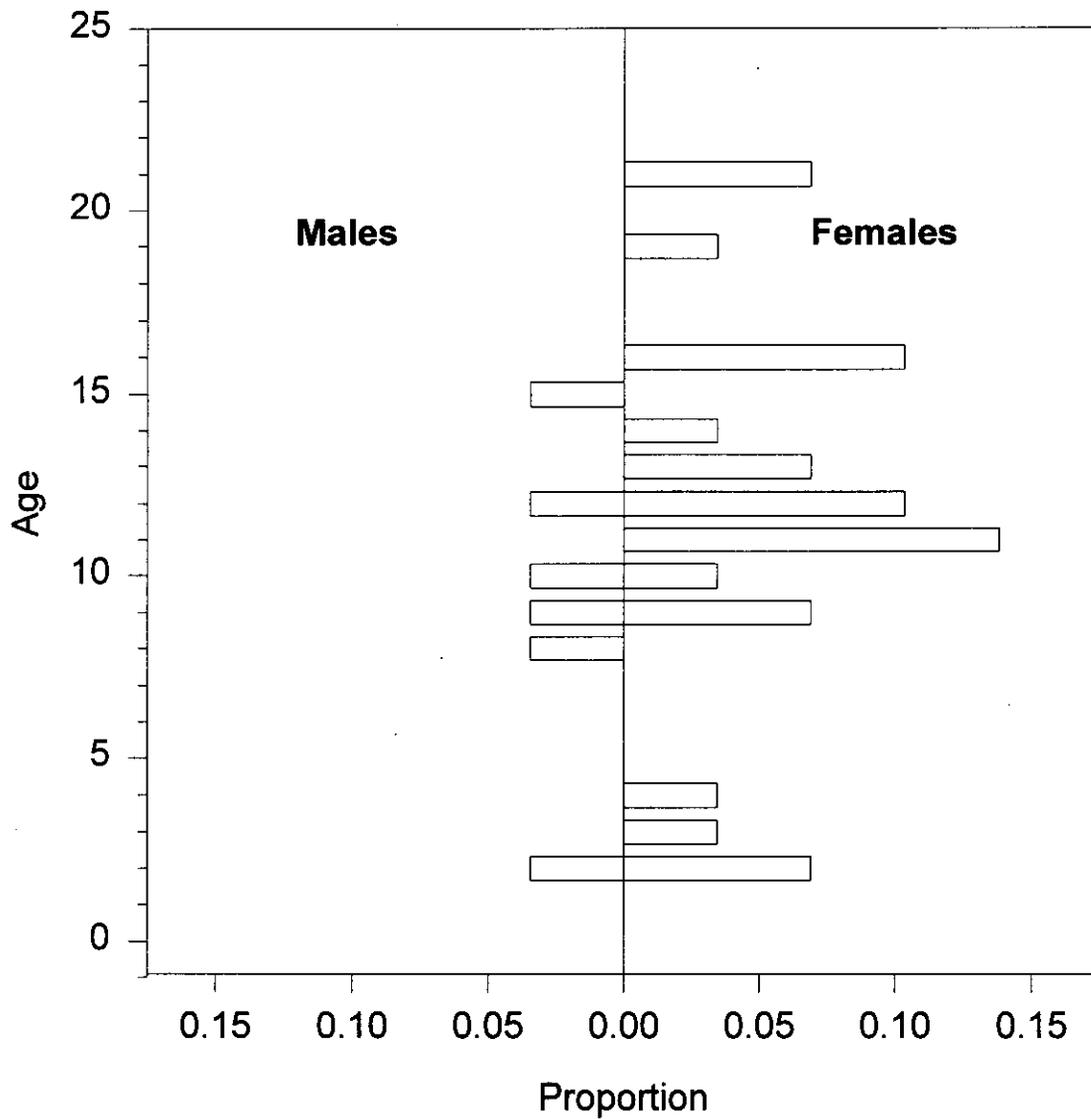


Figure 3. Estimated structure of natural mortality for age classes 2 and above during the year preceding the spill. Numbers in each age and sex class are expressed as proportions of the total number of deaths in age classes 2 and above.

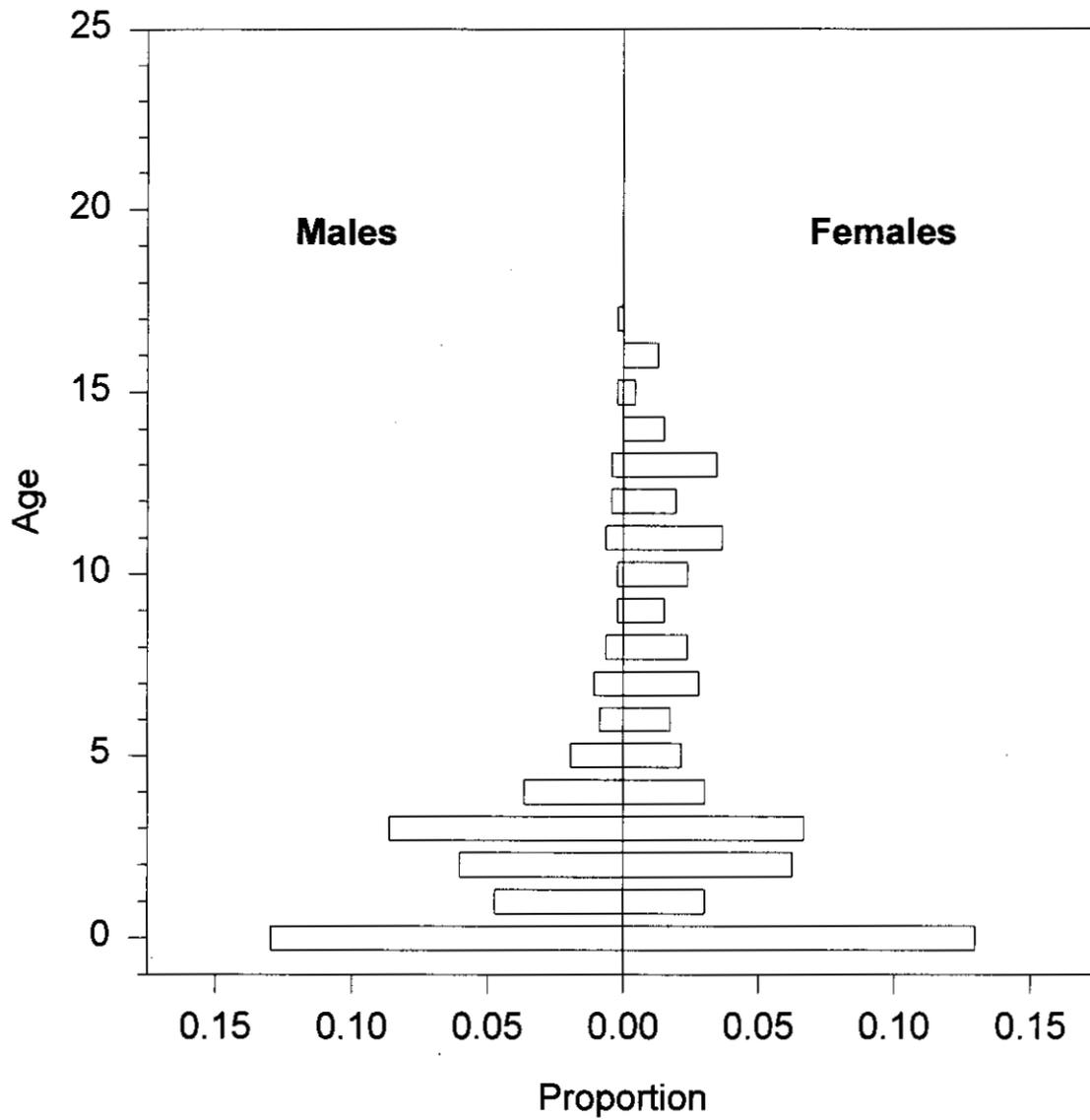


Figure 4. Estimated population structure at the time of the spill. Numbers in each age and sex class are expressed as proportions of the total population size.

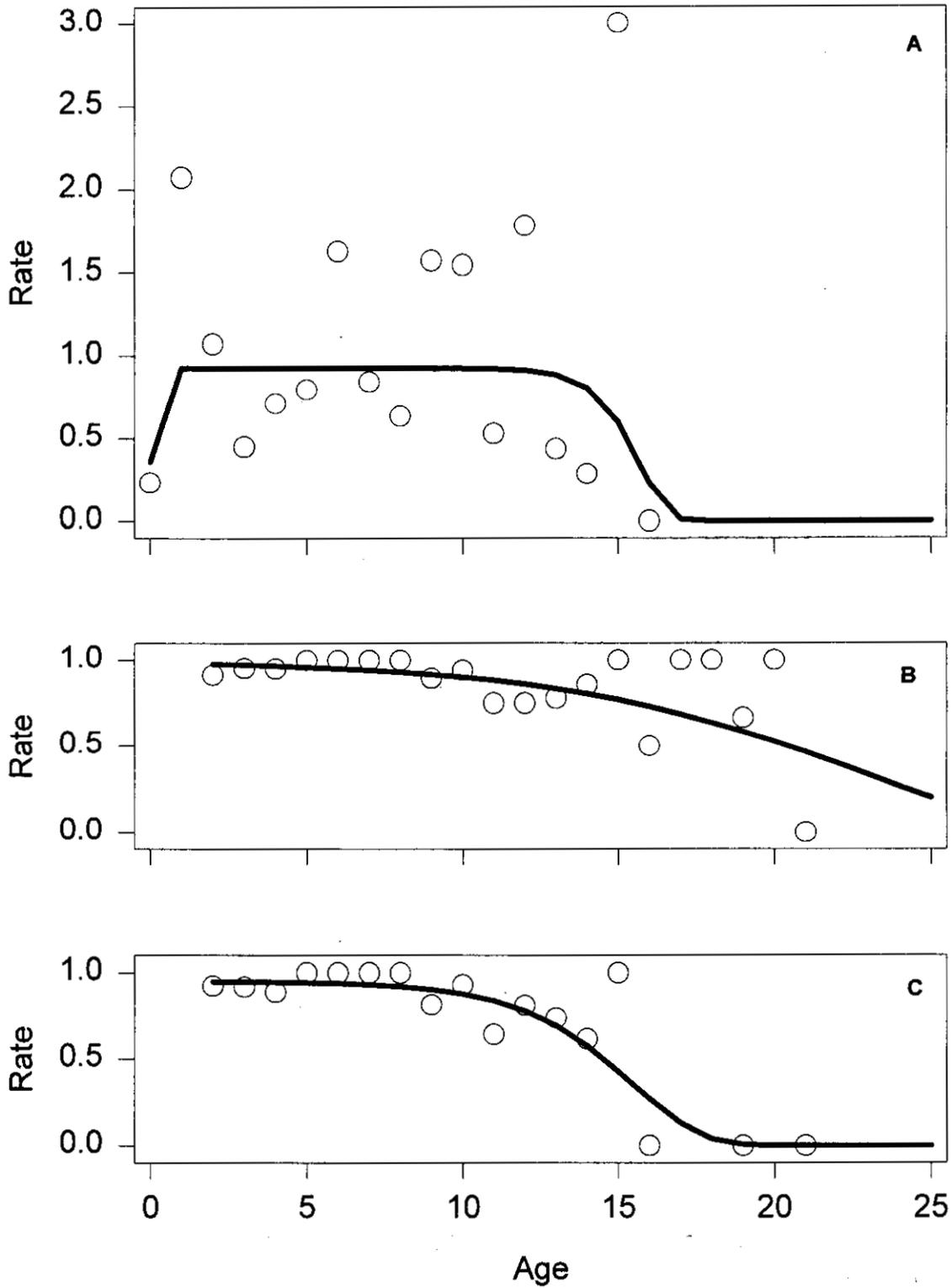


Figure 5. Estimated and smoothed survival rates for female sea otters: A) based on age structure data, B) based on ages-at-death data, C) based on age structure and ages-at death data.

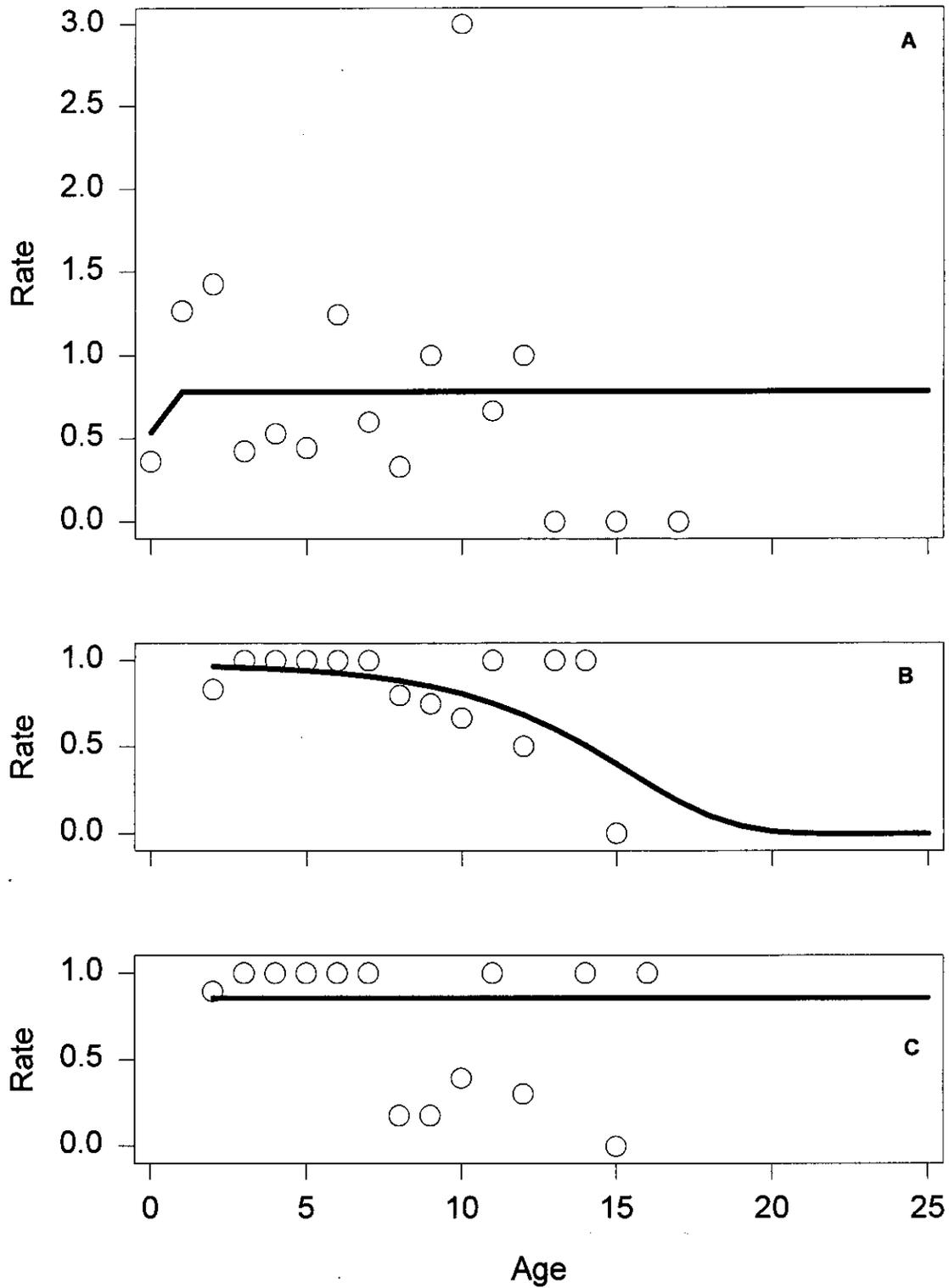


Figure 6. Estimated and smoothed survival rates for male sea otters: A) based on age structure data, B) based on ages-at-death data, C) based on age structure and ages-at death data.

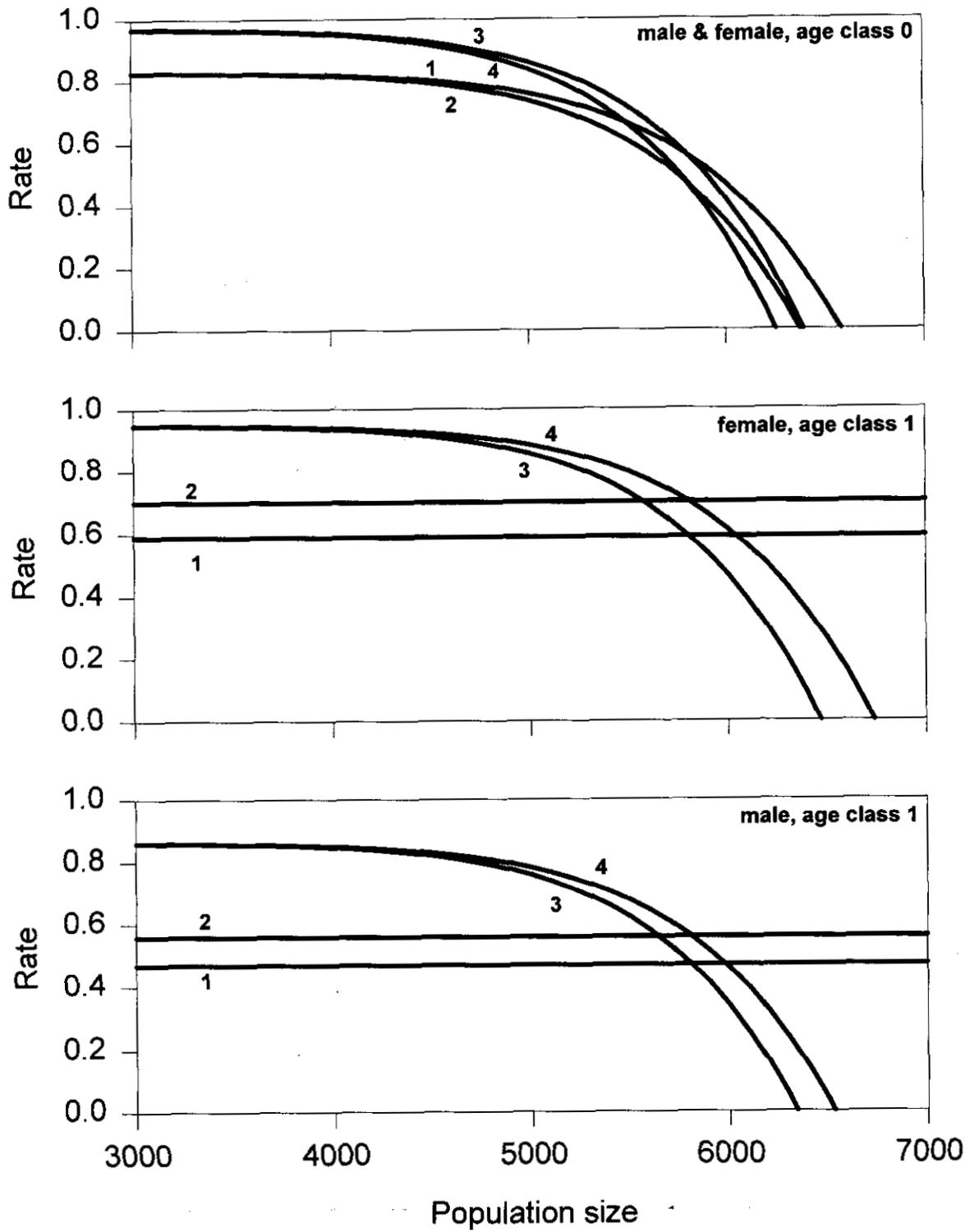


Figure 7. Relation of juvenile sea otter survival rates to population size under 4 different model scenarios.

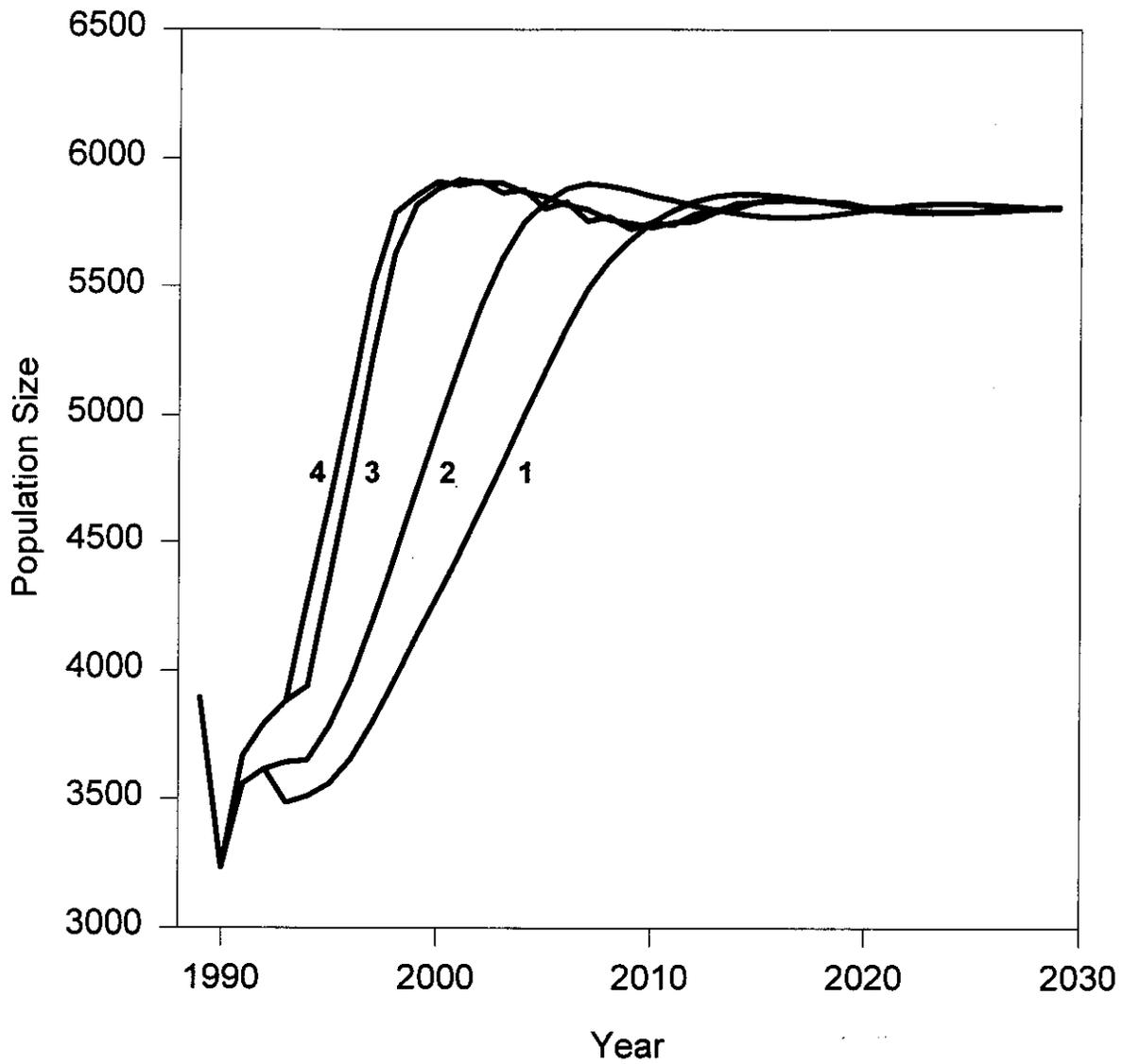


Figure 8. Four scenarios for projected recovery of the western Prince William Sound sea otter population following the *Exxon Valdez* oil spill in March 1989.