

## INCORPORATING DIVERSE DATA AND REALISTIC COMPLEXITY INTO DEMOGRAPHIC ESTIMATION PROCEDURES FOR SEA OTTERS

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**Abstract.** Reliable information on historical and current population dynamics is central to understanding patterns of growth and decline in animal populations. We developed a maximum likelihood-based analysis to estimate spatial and temporal trends in age/sex-specific survival rates for the threatened southern sea otter (*Enhydra lutris nereis*), using annual population censuses and the age structure of salvaged carcass collections. We evaluated a wide range of possible spatial and temporal effects and used model averaging to incorporate model uncertainty into the resulting estimates of key vital rates and their variances. We compared these results to current demographic parameters estimated in a telemetry-based study conducted between 2001 and 2004. These results show that survival has decreased substantially from the early 1990s to the present and is generally lowest in the north-central portion of the population's range. The greatest temporal decrease in survival was for adult females, and variation in the survival of this age/sex class is primarily responsible for regulating population growth and driving population trends. Our results can be used to focus future research on southern sea otters by highlighting the life history stages and mortality factors most relevant to conservation. More broadly, we have illustrated how the powerful and relatively straightforward tools of information-theoretic-based model fitting can be used to sort through and parameterize quite complex demographic modeling frameworks.

**Key words:** age-specific survival; age structure; AIC; *Enhydra lutris nereis*; maximum likelihood; model averaging; model uncertainty; southern sea otter; spatially structured demographic model.

### INTRODUCTION

Spatial and temporal variation in population abundance is a universal characteristic of all plant and animal species, and understanding the causes of such variation is a fundamental goal of population biologists (e.g., Caughley 1977). While it is often straightforward to detect changes in the abundance of well-studied species, determining the cause of observed change is generally much more difficult. Populations vary in abundance due to changes in the vital rates of individuals (birth, death, immigration, and emigration), which are shaped by a potentially vast array of biotic and abiotic factors. Nonetheless, understanding the primary causes of spatial and temporal variation of demographic rates is a necessary step in the assessment of population viability (Morris and Doak 2002), and analytical models that incorporate spatial and temporal differences in demographic rates have been important tools in the con-

servation of threatened populations such as the Yellowstone grizzly bear (*Ursus arctos horribilis*) (Eberhardt et al. 1994, Doak 1995, Pease and Mattson 1999) the Northern Spotted Owl (*Strix occidentalis caurina*) (Lande 1991, Forsman 1993), and many other taxa (Beissinger and McCullough 2002).

In spite of these examples, there are few (or no) reliable estimates of vital rates for many endangered or threatened species, especially wide-ranging species such as mammalian carnivores. Direct estimates are difficult and costly to acquire, requiring longitudinal records from marked individuals obtained through tagging, band recovery, or biotelemetry methods (White 1983, Pollock et al. 1990, Lebreton and Gonzalez-Davila 1993). For species with broad geographic ranges and long life spans it is particularly difficult to obtain data from marked individuals over long enough time periods and over sufficiently large areas to form a representative picture of the key demographic drivers of population dynamics. In the few cases where demographic data have been collected over appropriate spatial and temporal scales for large vertebrates, the resulting data sets have provided powerful tools for projecting future

Manuscript received 28 September 2005; revised 31 March 2006; accepted 5 April 2006. Corresponding Editor: D. F. Parkhurst.

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PLATE 1. A southern sea otter (*Enhydra lutris nereis*) near Monterey, California, USA. Photograph courtesy of Sahron Blaziek and the Monterey Bay Aquarium.

population dynamics and/or identifying key life history stages for focusing management efforts (e.g., Eberhardt et al. 1994, Coulson et al. 1999, Pease and Mattson 1999, Milner-Gulland et al. 2000, Schaefer et al. 2001, Walters et al. 2002, Runge et al. 2004). However, for most large species it is either infeasible to initiate large-scale mark-recapture programs, or else mark-recapture programs were not in place when important population dynamics were occurring. In the case of the southern sea otter (*Enhydra lutris nereis*), for example, a telemetry-based study now underway provides estimates of recent demography, but cannot shed light on past population declines.

Given these requirements of mark-recapture studies, it is clearly important to develop alternative methods for inferring demography of populations, making most effective use of whatever data sets are available (Doak and Mills 1994). One alternative method is the indirect estimation of vital rates from population age structure (Caughley 1977). Although the reliability of indirect estimates based on standing age structure has traditionally been restricted by assumptions of constant population size or constant growth rate, several methods using both Bayesian and information-theoretic approaches have been proposed that circumvent these assumptions (e.g., Eberhardt 1988, Wood 1994, Udevitz and Ballachey 1998, Doak and Morris 1999, Miller and Meyer 2000, Nelson et al. 2004, Gross et al. 2005). For many vertebrate species, carcasses can be collected with little effort, and age estimates derived by sectioning of bones or teeth (Matson 1981, Bodkin et al. 1997), making it simpler and more accurate to estimate the

distribution of ages at death than that of living animals. These data, too, can be used to infer vital rates, and this approach was recently used to assess the long-term impact of a major environmental perturbation (the *Exxon Valdez* oil spill) on a population of sea otters in Prince William Sound (Udevitz and Ballachey 1998, Monson et al. 2000a). In addition to age-structure information, simple population counts are commonly available for many populations and can be useful for evaluating alternative hypotheses about demographic variation (Hilborn and Mangel 1997, Morris and Doak 2002), particularly if these counts are structured by developmental stage (e.g., juveniles vs. adults; Pascual and Adkison 1994, Holmes and York 2003), or are used in conjunction with other data.

Southern (or California) sea otters (see Plate 1) are a protected subspecies with "Threatened" status under the Endangered Species Act (USFWS 2003), making the understanding of its population dynamics both interesting and important. In particular, reliable demographic information is needed to guide decision making on management options currently under consideration (G. Sanders, *personal communication*) and to ensure the long-term recovery of this population (USFWS 2003). Although range-wide counts indicate unequivocally that population recovery ceased in the mid 1990s (Estes et al. 2003; also see Fig. 1), it is less clear what specific demographic changes were responsible for the change in population dynamics. Data presented by Estes et al. (2003) indicate that the recent periods of decline in southern sea otters are associated with increased mortality rather than decreased birth rates. Here, we inves-

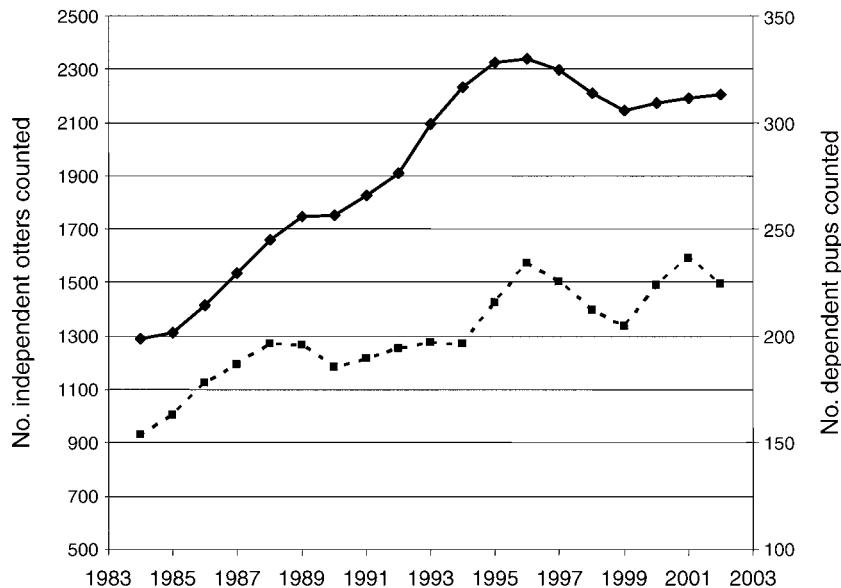


FIG. 1. Annual range-wide counts of southern sea otters, *Enhydra lutris nereis*, conducted between 1984 and 2002. Values represent the three-year running average of the spring counts of independents (solid line) and the average of the spring and fall counts of dependent pups (dashed line).

tigate in greater detail the spatial and temporal changes in age-specific survival rates that halted population growth in the 1990s. To accomplish this, we extend the methodology described by Monson et al. (2000a) to include an assessment of spatial as well as temporal changes in survival, to incorporate other data sources besides carcass age structure (specifically, age-structured population counts) and to more formally incorporate model uncertainty.

California sea otters are somewhat unusual among large carnivores in that there is a deep and broad set of empirical and modeling studies to inform the type of analysis we develop. While this quantity and quality of data is not required for our methods to work, using them in this context allows a more informed evaluation of their reliability and the biological plausibility of the results. In this sense, sea otters provide a useful case study for developing techniques that can be applied to other large, wide-ranging carnivore species for which less information may be available. A particular concern that we discuss in our presentation is how best to constrain the number of alternative model forms to consider. Especially when biological understanding of a population is good, model complexity and hence the number of biologically plausible models that should be considered can rise dramatically. We demonstrate practical approaches for dealing with this challenge.

#### METHODS

##### *Part 1: Estimating past demographic rates (1992–2001)*

Two types of field data were available for the period of interest: population counts and beach-cast carcasses classified by age, sex, and location of recovery. Stand-

ardized, range-wide population counts of the southern sea otter are conducted twice annually: a spring census (early May) provides the primary index of change for this population, while a fall census (early November) is conducted primarily to better estimate pup production rates (Estes and Jameson 1988, Estes et al. 2003). The net results of the survey are uncorrected, minimum counts of independent otters and dependent pups (0–6 months of age [Riedman et al. 1994]). Although no formal correction factor is available to estimate true population size, Estes and Jameson (1988) found the detection probability to be very high (90–95%); therefore, following previous analyses (e.g., Estes et al. 2003, Gerber et al. 2004) we use the uncorrected counts as a proxy for total population size and treat the associated observation error as a parameter to be estimated in the model-fitting process. For independent otters we used 11 spring counts made during the period 1992–2002 (Fig. 1). For dependent pups we used the average of the spring and fall counts made during the same period: due to the continuous nature of reproduction in sea otters (see *Reproduction*), averaging the two pup counts had the effect of reducing sample noise caused by year-to-year variation in the timing of seasonal peaks in pup production.

The California Department of Fish and Game and the Biological Resources Discipline of the U.S. Geological Survey (USGS) have maintained a salvage network to collect beach-cast carcasses of sea otters since 1968. Carcass recovery is largely opportunistic and relies heavily on voluntary public participation (although there are targeted beach walks in certain areas); thus the rate of carcass recovery varies across the range as a function of human population density (Pattison et al.

1997, Estes et al. 2003). In spite of this, a remarkably high proportion (~50%) of all sea otter deaths in California are eventually recovered as beach-cast carcasses (Estes et al. 2003, Gerber et al. 2004). Information about all carcasses, including date of recovery, sex, age class, length, mass, condition, recovery location, and cause of death, is added to a database maintained by U.S. Geological Survey. Since 1992, tooth-age estimates have been collected from all beach-cast carcasses, with the exception of pups (<100 cm total length) and those for which an unbroken premolar could not be obtained. Age at death was estimated by cementum analysis of a single, upper premolar tooth (Bodkin et al. 1997) using consistent methods (Matson 1981), and each age estimate was accompanied by a quality code of A (excellent), B (good), or C (poor). For the current analysis, we used ages from all carcasses collected between January 1992 and December 2001 with estimated age of 1 or more and quality code of A or B, for a total sample size of 742. We excluded 0-year-old carcasses (pups and recently weaned juveniles) because we believe they may be underrepresented in the carcass record (Ames et al. 1983, Pattison et al. 1997, Estes et al. 2003), and thus we implicitly assume that trends in the relative frequency of 1-year-old juvenile carcasses are sufficiently representative of trends for 6–12 month old juveniles. No significant age biases have been found in the representation of older carcasses in previous sea otter studies (Ames et al. 1983, Pattison et al. 1997, Udevitz and Ballachey 1998, Monson et al. 2000a). Based on this fact, and on the high carcass recovery rate overall, we believe this database provides a relatively unbiased index of changes in the frequency distribution of age at death. Note that our analysis depends only on relative age frequencies, not on absolute numbers, and thus any year-to-year variation in the total numbers of carcasses recovered (e.g., Estes et al. 2003) should not influence our model results.

*Overview of modeling approach.*—We use the field data just described to estimate the parameters of a series of alternative models of sea otter demography, with particular emphasis on temporal and spatial changes survival rates. In the course of this model fitting, we also gain the information needed to assess the relative likelihood of each model as a good explanation of patterns in otter demography. Multiple model-fitting frameworks are now commonly used in ecology and wildlife biology, including frequentist methods, maximum likelihood/information theory approaches, and Bayesian modeling. While there are many advocates for each of these general methodologies, the underlying goals of model fitting are usually the same (e.g., Pascual and Kareiva 1996, Stephens et al. 2005), even when the jargon used by different workers to describe similar models and fitting methods diverges. We use a maximum likelihood/information theory framework in this paper, and thus we describe the model structures and fitting

methods in the terminology commonly used in this approach, and in particular to the fitting of demographic models using observations of population size and structure data (e.g., Doak and Morris 1999, Monson et al. 2000a, Holmes and York 2003). Our general approach can be broken into four steps: (1) the construction of alternative functions to predict survival rates by age, sex, time period, and geographic area; (2) the use of these survival rates to construct population projection matrices that predict population growth and structure over the study period; (3) estimation of the parameter values governing the survival rates that result in the best predictions of the observed data, based on maximum likelihood comparisons of the predicted population counts and carcass age structures with the field data; (4) the use of information theory methods (Burnham and Anderson 2002) to select the set of “best” models (those model forms that provide most predictive power and maximum parsimony). We then use this set of models to describe underlying demographic changes over the study period, while accounting for model uncertainty.

In the following sections we explain in detail each of these four steps. We also note that, while for many species it is most reasonable to estimate temporal changes in demography as stochastic variation around mean values, this approach is not consistent with known sea otter biology, for which populations typically show extraordinarily little effect of random interannual variability (Eberhardt and Siniff 1988, Siniff and Ralls 1991, Monson et al. 2000a, b). Thus, we confine our modeling to deterministic approaches, while we consider a wide range of temporal and spatial patterns in demography. All model programming and associated statistical analyses were conducted using the MATLAB programming language (MathWorks, Natick, Massachusetts, USA).

*Model structure.*—The projection matrix models we use classify otters by age, sex, and geographic region, and allow temporal change in rates in one of two general patterns. In each year, this results in an age-classified Leslie matrix (Leslie 1945) for otters of each sex in each region. We formulated our matrices in terms of 20 discrete age classes (age  $x = 1, 2, \dots, 20$ ), with the time-step set to one year. This simplifies presentation of results and corresponds to the discrete age scores resulting from the tooth cementum analysis and the annual population counts; it is also consistent with previous formulations of sea otter demographic models (e.g., Eberhardt and Siniff 1988, Eberhardt 1995, Udevitz and Ballachey 1998, Monson et al. 2000a, Gerber et al. 2004). We note, however, that sea otters actually reproduce throughout the year, and so our discrete matrices represent an approximation to a birth-flow population. Specifically, we assume that a “typical” individual entering the first age class ( $x = 1$ ) is a recently weaned juvenile of 6 months, and thus the survival rate for  $x = 1$  actually corresponds to the probability of surviving from 6 months to 18 months of age, while

survival for  $x = 2$  corresponds to the probability of surviving from 1.5 years to 2.5 years of age, and so on.

We did not consider immigration or emigration between geographic regions in this model. The challenge in making these models is thus to construct a reasonable range of possible forms for survival and reproductive rates.

**Reproduction.**—While reproduction in sea otters occurs throughout the year, reproduction is effectively an annual event at the level of the individual: gestation lasts approximately 6 months, followed by the birth of a single offspring that is dependent on exclusive maternal care for a period of ~6 months, resulting in a maximum average reproductive output of one weaned offspring per female, per year (Wendell et al. 1984, Jameson and Johnson 1993), a fact that facilitates matrix discretization. The age of first reproduction reported for southern sea otters ranges from 2 to 5 years of age, with most females having produced their first pup by age 4 (Sinha et al. 1966, Jameson and Johnson 1993, Riedman et al. 1994). The annual probability of a mature female sea otter producing an independent juvenile is the product of two vital rates, the annual birth rate ( $b$ ) and the weaning success rate ( $w$ , defined as the probability that an offspring will be successfully reared from birth to weaning at 6 months, conditional upon survival of the mother). Published estimates of  $b$  for southern sea otters range from 0.88 to 1.07, depending on the method of calculation (Siniff and Ralls 1991, Eberhardt and Schneider 1994, Riedman et al. 1994, Eberhardt 1995), but the accumulating weight of evidence suggests that  $b$  is relatively invariant within and between sea otter populations (Monson et al. 2000b). In contrast,  $w$  can vary as a function of female age (Riedman et al. 1994) or body condition (Monson et al. 2000b). Examination of our own telemetry-based data (Appendix), together with the results of previous analyses (Estes et al. 2003, Tinker 2004), suggested that neither birth rate nor pup survival have changed measurably in southern sea otters over the past two decades: we thus treat age-specific reproductive rate ( $b_x$ ) and weaning success rate ( $w_x$ ) as fixed for the purpose of our current analyses. We set the age of first reproduction to 2.5 years (Monson et al. 2000b),  $b_x$  to a constant value of 0.98, and modeled  $w_x$  as a continuous function of age:

$$w_x = -1.231x^{-0.4845} + 1.0922. \tag{1}$$

Eq. 1 was empirically derived from our telemetry-based data set (see *Methods: Part 2* and Appendix), leads to a success rate that increases asymptotically with the mother’s age, and has a population-wide average of ~0.56, consistent with previous studies (Siniff and Ralls 1991, Eberhardt and Schneider 1994, Riedman et al. 1994, Eberhardt 1995).

**Survival.**—The probability that a single sea otter (age  $x$ , sex  $y$ , located within geographic area  $g$ ) would survive from year  $t$  to year  $t + 1$  was estimated using a logit function of the following form:

TABLE 1. A summary of the general functional forms used to model survival rates.

Main effect	Component	Functional form
Age	$f_x$	$f_x = x\theta_1 + x^2\theta_2 + x^3\theta_3 + \frac{\theta_4}{x}$
Sex	$f_y$	$f_y = y\theta_5 + xy\theta_6$
Time	$f_t^1$	$f_t^1 = t\theta_7 + tx\theta_8 + ty\theta_9 + txy\theta_{10}$
	or $f_t^2$	$f_t^2 = A\theta_7 + Ax\theta_8 + Ay\theta_9 + Axy\theta_{10}$
Location	$f_g$	$f_g = B\theta_{11} + Bx\theta_{12} + By\theta_{13} + Bt\theta_{14} + Bxyt\theta_{15}$

*Notes:* For all equations,  $\theta_1, \theta_2, \theta_3$ , etc., indicate fitted parameters. Functions shown are for a model with all interaction terms and for a linear time effect in  $f_t^1$ , a categorical time effect with one time break in  $f_t^2$ , and a categorical spatial effect with one geographical division in  $f_g$ . Parameters  $A$  and  $B$  represent switch variables and are used to control the categorical effects of time and location, respectively. By taking values of either 0 or 1, they can “switch on” other fitted parameters in certain time periods or regions. Other model forms that were used featured subsets of the interaction terms shown and included both second- and third-order effects in  $f_t^1$ , up to three discrete time periods in  $f_t^2$ , and between zero and three geographical divisions in  $f_g$ .

$$s_{x,y,t,g} = \frac{\exp(f_{x,y,t,g})}{1 + \exp(f_{x,y,t,g})} \tag{2}$$

where the linear function  $f_{x,y,t,g}$  specifies the effects of age ( $x$ ), sex ( $y$ ), time ( $t$ ), and location ( $g$ ). We considered a range of possible main effects and interactions between the main effects: this resulted in a large number of alternate models, all of which were biologically reasonable and reflect important differences in hypothesized mortality patterns. Table 1 summarizes the general forms that we used to construct  $f_{x,y,t,g}$  functions. Below, we discuss the four basic components of  $f_{x,y,t,g}$  in terms of age, sex, time, and location effects,  $f_x, f_y, f_t$ , and  $f_g$ , respectively, which sum to  $f_{x,y,t,g}$ . Although each of these subfunctions can include many interaction effects, this breakdown facilitates description of the model forms used.

1. **Age effects.**—The function we use to model age-specific variation in survival,  $f_x$ , is a third-order polynomial function plus an additional term,  $\theta_4/x$ , that allows greater flexibility in fitting juvenile survival. Like the competing-risks function that has previously been used to model otter survivorship (Siler 1979, Eberhardt 1985), this function can generate the “inverted U” shaped survival curve, typical of large mammals (Caughley 1977), but does so with fewer parameters (Tinker 2004).

2. **Sex effects.**—We incorporated male–female differences in survival using a simple additive main effect and an interaction between age and sex (Table 1).

3. **Temporal changes.**—To allow for temporal changes in age- and sex-specific survival, we used one of two functions (Table 1):  $f_t^1$  was used to model smoothly changing survival rates, while  $f_t^2$  was used to model discrete time effects. As shown in Table 1,  $f_t^1$  allows for a linear time effect. However, by adding additional

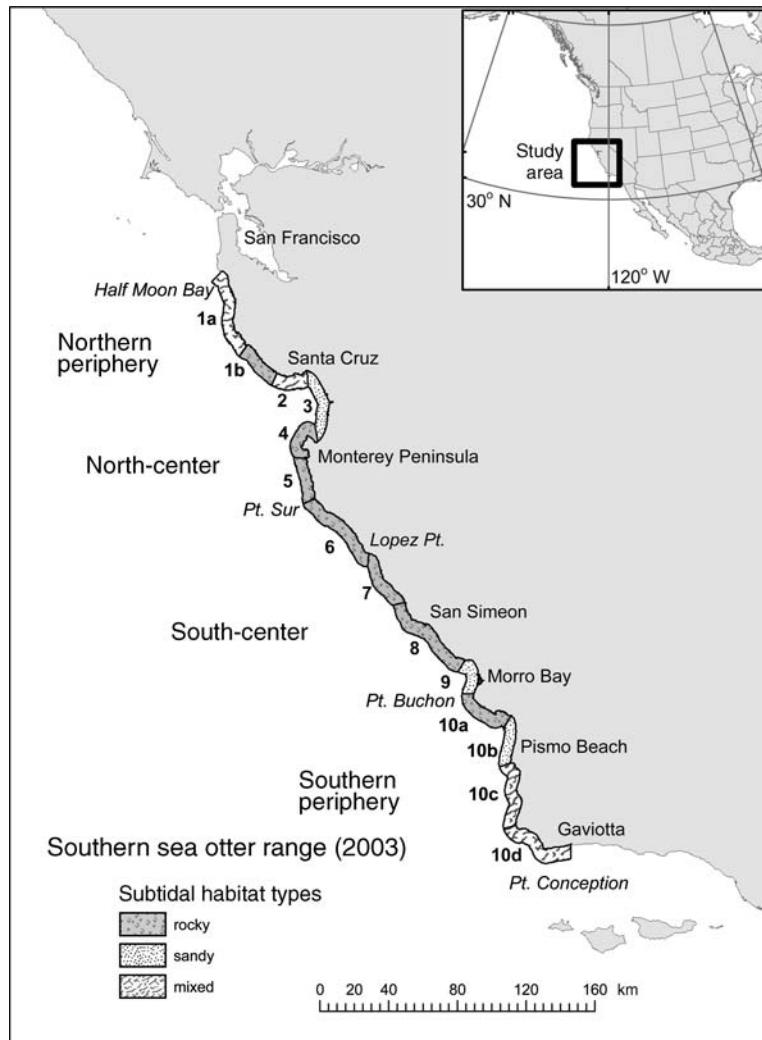


FIG. 2. Range of the southern sea otter along the mainland coast of California (range limits based on 2003 survey data) divided into 14 sections of similar subtidal habitat (Laidre et al. 2001). These sections were used as fundamental geographical units for our analysis of spatial variation in demography, although the northern-most units (1a and 1b) and the southern-most units (10a–d) were collapsed into sections 1 and 10, respectively, in order to achieve sufficient carcass sample sizes for each of the 10 remaining coastline sections.

parameters we also evaluated second- and third-order time effects. In contrast to the continuous temporal changes allowed by  $f_t^1$ , function  $f_t^2$  allows steady rates for variable numbers of years followed by a discrete breakpoint, at which new rates apply. In the version of  $f_t^2$  shown in Table 1,  $A$  is a switch variable,  $A = 0$  if  $t < \theta_t$ ,  $A = 1$  if  $t \geq \theta_t$ , and  $\theta_t$  is a fitted parameter that specifies the temporal breakpoint in survival probabilities. We also evaluated models with zero or two temporal breakpoints. Both  $f_t^1$  and  $f_t^2$  allow for interactions between time, age, and sex.

4. *Spatial variation.*—We incorporated spatial variation in survival by defining discrete geographic areas: specifically, we divided the sea otter's range in California into different regions within which demographic rates were assumed to be constant, but between which rates

were allowed to vary. The locations of boundaries between groups, and the actual number of groupings, were treated as unknowns to be determined by maximum likelihood analysis. To make this fitting manageable, we first divided the current range of the southern sea otter into 10 contiguous coastline segments (Fig. 2), corresponding to areas of similar benthic habitat type (Laidre et al. 2001), with each roughly equal to the annual home range of a single adult female sea otter (Ralls et al. 1996). Spatial groups ( $g$ ) were next defined as combinations of one or more of these coastline segments with similar demographic rates. We did not require that all coastline segments within a demographic group be geographically contiguous: for example, assuming only two group levels ( $g = 1$  or  $2$ , and assuming the first segment is always set to 1), 3 of the

TABLE 2. Sample demographic classification schemes for 10 contiguous coastline segments spanning the entire range of the southern sea otter.

Classification scheme	Coastline segment									
	1	2	3	4	5	6	7	8	9	10
i	1	1	1	1	1	2	2	2	2	2
ii	1	2	2	2	2	2	2	2	2	2
iii	1	2	2	2	2	1	1	1	1	1

Notes: In each of the three examples (i–iii), the numbers listed for each segment indicate their assignments to spatial groups, where groups were defined as combinations of one or more of these coastline segments with similar demographic rates. Only two group levels are shown here; however, our model allowed for up to four group levels.

512 possible ways to classify the 10 coastline segments are shown in Table 2.

We constructed models with up to four spatial groups and all possible permutations of coastline segments within each group. As described above for  $f_t^2$ , we used switch variables ( $B$ ) in  $f_g$  to model geographic grouping effects (Table 1). For the version of  $f_g$  shown in Table 1, there are two groups ( $B = 1$  if  $g = 2$ , and  $B = 0$  if  $g = 1$ ) and interactions of area with age, sex, and time. By adding additional switch variables (and thus additional fitted parameters), we allowed for up to four grouping levels. The location of each spatial breakpoint was also a fitted parameter: thus example i in Table 2 would require one additional parameter (specifying the breakpoint between coastline segments 5 and 6), while example iii in Table 2 would require two additional parameters (specifying breakpoints between coastline segments 1 and 2 and between coastline segments 5 and 6).

*Matrix projection and maximum likelihood analysis.*— Altogether, the subfunctions shown in Table 1 can be substantially modified by adding or removing individual terms, resulting in models with and without certain main and interaction effects, as well as different numbers of spatial and geographic groupings. Each unique  $f_{x,y,t,g}$  function was used to create a series of annual projection matrices that together represent a hypothetical model of demographic variation in the southern sea otter between 1992 and 2001. For each model  $i$  ( $i = 1$  to  $I$ , where  $I$  is the total model count) these projections are also a function of the particular set of parameter values,  $j$ , used, and we will therefore denote a unique projection model as  $M_{i,j}$ .

To initialize the model in year 1992 we used a population vector made from the product of the observed 1992 population count (independents + dependent pups) and the stationary age distribution (SAD) associated with the matrix transition probabilities at  $t = 1$ . The model start-point is thus assumed to be immediately precensus, or early May. (This is of course somewhat arbitrary because reproduction is continuous.) We used the SAD in the absence of any better estimates of age structure and in light of the fact that population growth had been relatively constant for many years prior to the study period (at  $\lambda = 1.05$ ;

see Fig. 1 and Estes et al. 2003), presumably allowing the age structure to stabilize. Each model generates three types of predictions that are used in maximum likelihood calculations. First is the age/sex frequency distribution of carcasses, which is a straightforward result of the series of matrices and the starting conditions. Somewhat more complex to estimate are the number of independent and dependent animals in the population. The number of older animals predicted in each year is simply the product of each year’s projection matrix and the previous population vector. However, annual census data also tracks dependent pups, and, combined with continuous reproduction, this results in the need to separately estimate dependent pups (those under 6 months age) and independent pups (those between 6 and 12 months age). We estimate the average probability that a female of age, year, and location  $x$ ,  $t$ , and  $g$ , respectively, will produce an independent pup of sex  $y$  as

$$R_{x,t,g \rightarrow y}^1 = \frac{1}{2} \left[ \frac{b_x}{2} w_{x,t,g}(s_{x,0,t,g})^{3/4} (s_{1,y,t,g})^{1/4} \right]. \tag{3}$$

This result assumes that half of the reproductive females in the population will give birth within the first six months of the year, and a typical female from this group must survive for three-quarters of the year if her pup is to be weaned successfully, while the weaned pup must then survive for the remaining one-quarter of the year as an independent juvenile. A pup sex ratio of 1:1 is also assumed. For the remaining reproductive females (those that pup in the second six months of the year) our estimate of the production of dependent pups of sex  $y$  is

$$R_{x,t,g \rightarrow y}^2 = \frac{1}{2} \left\{ \frac{b_x}{2} s_{x,0,t,g} \frac{1}{6} \sum_{m=1}^6 w_x^{0.32 \ln[(m-0.5)/6] + 1} \right\} \tag{4}$$

where  $m$  represents pup age, in months, and the total dependency period is assumed to be six months. This result is based on similar logic to Eq. 3, and also incorporates the declining probability of pup mortality through the weaning period (see the Appendix for further explanation of how this function was derived). The sum of Eqs. 3 and 4 was used to parameterize the first row of the projection matrix, that is, the expected contribution of a female of age  $x$  in location  $g$  at time  $t$  to the first age class of sex  $y$  at time  $t + 1$ , while the product of Eq. 4 and the population vector at time  $t$  (summed across all female ages and for pups of both sexes) is the expected number of dependent pups that would be alive during the census at  $t + 1$ .

With the estimates of living and dying animals estimated from these results, we can calculate the relative likelihood of each model form and also the single “most likely” set of parameter values for each model  $M_i$ , given the observed data sets. Specifically, we want to evaluate the relative likelihood ( $\ell$ ) of obtaining the observed counts of independent otters ( $N^{\text{obs}}$ ), dependent pups ( $P^{\text{obs}}$ ), and carcass age distributions

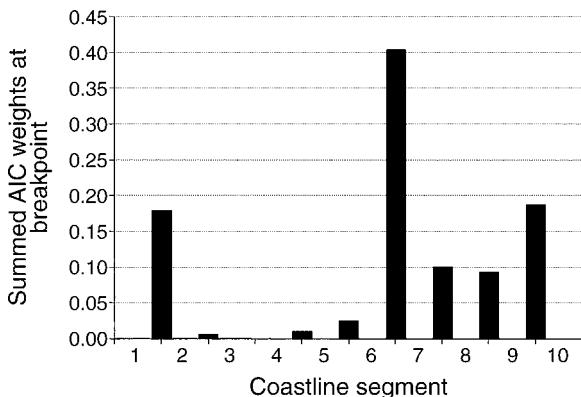


FIG. 3. The relative degree of model support for all potential arrangements of 10 coastline segments into areas of similar demography. Summed AIC weights ( $\alpha_i$  values) are shown at each potential breakpoint: the three best-supported breakpoint locations (between segments 1 and 2, segments 6 and 7, and segments 9 and 10) together account for 76% of the summed AIC weights.

( $C^{obs}$ ), given the expected counts ( $N^{exp}$  and  $P^{exp}$ ) and carcass age-frequency distributions ( $D^{exp}$ ) predicted by a model  $M_{i,j}$ . We estimated the likelihood of an observed carcass age/sex distribution in a given year and location using multinomial probabilities (Hilborn and Mangel 1997, Doak and Morris 1999):

$$\ell(C_{y,t,g}^{obs} | M_{i,j}) = \frac{\left(\sum_{x=1}^{20} C_x\right)!}{C_1!C_2! \dots C_{20}!} d_1^{C_1} d_2^{C_2} \dots d_{20}^{C_{20}} \quad (5)$$

where  $C_x$  is the observed number of carcasses and  $d_x$  is the expected proportion of carcasses in age class  $x$  for a given year, location, and sex class. (Note that we have dropped the additional subscripts from the right side of the equation in the interest of brevity.) To calculate the relative likelihood of observed population counts, we assumed that the deviations between observed and expected counts of independents and pups were primarily due to observer error, rather than process error, and that the deviations were normally distributed (Hilborn and Mangel 1997):

$$\ell(N_{t,g}^{obs} | M_{i,j}) = \frac{1}{\sqrt{2\pi\sigma_N^2}} \exp\left[-\frac{(N^{obs} - N^{exp})^2}{2\sigma_N^2}\right] \quad (6)$$

$$\ell(P_{t,g}^{obs} | M_{i,j}) = \frac{1}{\sqrt{2\pi\sigma_P^2}} \exp\left[-\frac{(P^{obs} - P^{exp})^2}{2\sigma_P^2}\right]. \quad (7)$$

The variance terms  $\sigma_N^2$  and  $\sigma_P^2$  have the effect of weighting the contribution of the two data sets according to their relative variability, and were treated as additional fitted parameters following Pascual et al. (1997). As was the case for the carcass data, likelihoods of independent and dependent otters were solved separately for each year and coastline segment.

The net likelihood of  $M_{i,j}$  is equivalent to the combined likelihood of obtaining the observed carcass age distributions and population counts across all years and spatial groupings, and is thus the product each of these three likelihood values over all time periods and spatial groupings and both sexes. Following standard practice, we converted all likelihood values to negative log-likelihoods [ $L = -\log(\ell)$ ], and instead calculated the sum of the associated  $L$  values (Hilborn and Mangel 1997). The maximum likelihood solution for the best parameter estimates for model  $M_i$  was obtained by minimizing the total  $L$ . Model fits were performed using TOMLAB, an optimization toolbox for MATLAB (Holmström 1999); in particular, we used the “gblsolve” function, a box-bounded, nonlinear global search routine, and iterative searches were performed using a large number of randomly selected starting points to ensure that global minima were found (Holmström 1999).

*Model comparisons.*—We used information theory criteria to compare and select models, and to formally account for model uncertainty in our final, overall estimates of demographic parameters (Chatfield 1995, Burnham and Anderson 2002). For each model form,  $M_i$ , we calculated an associated AIC value (Akaike 1973),  $AIC_i = 2L_{i,min} + 2n_i$ , where  $L_{i,min}$  is the minimum negative log-likelihood value and  $n_i$  is the number of fitted parameters for model  $M_i$ . The AIC value provides an unbiased method for comparing both nested and nonnested model forms, penalizing models with large numbers of parameters (Akaike 1973). The best-supported model, given the data at hand, has the lowest associated AIC value,  $AIC_{min}$ , but other models may also have considerable support as measured by  $\Delta_i = AIC_i - AIC_{min}$  and Akaike weights,  $\alpha_i$ , which represent a measure of the relative level of support for model  $i$  (Burnham and Anderson 2002).

The large number of possible spatial grouping permutations that could be included in our model formulation presented a severe computational challenge. Rather than finding maximum likelihood solutions for every possible combination of functional form and spatial grouping scheme, we used an iterative selection approach to limit the number of grouping schemes considered. First, using the saturated model form of  $f_x$ ,  $f_y, f_i^1$ , and  $f_g$  (Table 1), we conducted maximum likelihood analysis for all possible permutations of spatial grouping schemes with 2–4 group levels. We then summed  $\alpha_i$  values across all models that included each of the 9 possible breakpoints (i.e., the 9 boundaries between the 10 coastline sections), and used  $\alpha_i$  sums as an indication of the relative support for each breakpoint. The three breakpoints with most support each had >15% of the summed  $\alpha_i$ , for a total of 76.9%, while all other breakpoints had <10% (Fig. 3). We conducted all subsequent analyses using the 15 spatial grouping schemes that included all or a subset of these three breakpoints (i.e., ranging from 1 to 4 grouping levels).

The total number of alternate models thus evaluated was 2075, which included all combinations of the 15 spatial groupings and biologically plausible formulations of  $f_{x,y,t,g}$ .

Following estimation of the maximum likelihood parameters for each of these models, we limited further consideration to the subset of  $Z$  models having  $\Delta_i$  values below a cutoff value,  $\Delta_{\text{crit}}$ , which we set initially to 10 (Burnham and Anderson 2002). For each of the  $Z$  best models,  $M_i$ , we generated the variance-covariance matrix for the  $n_i$  model parameters. While this matrix may be estimated during maximum likelihood function optimization as the negative inverse of the Hessian (Lebreton and Gonzalez-Davila 1993), we instead used the central difference approximation to estimate the second derivatives of  $L_i$  with respect to the  $n_i$  parameters, providing a more reliable (though computationally intensive) set of variance-covariance estimates (White and Burnham 1999). We then used the multivariate delta method (Oehlert 1992) to derive from this matrix the variance estimates associated with model-specific survival rates. Finally, model-averaged estimates of the mean and unconditional sampling variance in survival rates were calculated following Eqs. 4.1 and 4.9 in Burnham and Anderson (2002). We evaluated the effect of including more or fewer models by varying  $\Delta_{\text{crit}}$ . Decreasing  $\Delta_{\text{crit}}$  to include fewer models resulted in changes to at least some model-averaged estimates, while increasing  $\Delta_{\text{crit}}$  to include more models produced no significant changes (i.e., all estimates stabilized to two decimal points); we therefore retained the initial  $\Delta_{\text{crit}}$  value of 10.

*Presentation of results.*—As a graphical evaluation of the goodness of fit of the model estimates of demographic rates we generated quantile-quantile plots (Q-Q plots, Doksum and Sievers 1976) of expected vs. observed carcass age-class distributions for each spatial grouping and for three separate time periods (1992–1994, 1995–1997, and 1998–2001). We excluded carcasses >12 years of age from this analysis because so few were predicted or recovered. We also compared the matrix projection of population growth with the observed population counts for the period 1992–2001. Graphical comparisons of expected and observed population dynamics were made for the population as a whole and for three major geographic subdivisions: ordered from north to south, these were (1) the northern half of the range (Half Moon Bay to Lopez Pt.); (2) the south-center of the range (Lopez Pt. to Pt. Buchon); and (3) the southern periphery of the range (Pt. Buchon to Gaviotta; Fig. 2).

Although we calculated demographic rates and their unconditional variance estimates for 20 age classes, for presentation purposes we collapsed these 20 estimates into four broader categories corresponding to descriptive life stages, which simplifies the presentation and facilitates comparisons with telemetry-based estimates: juveniles (first year postweaning), subadults (1.5–3.5

years of age), prime-age adults (3.5–9.5 years of age), and old adults (9.5–19.5 years of age). For each life stage,  $a$ , model-averaged estimates for survival rates ( $\hat{S}_a$ ) were calculated by taking the arithmetic means of the survival rates of the constituent year classes, weighted by the stable age distribution. Variances for each life stage were calculated from the age-class variances using the multivariate Delta method (Oehlert 1992) and assuming that the survival estimates for each age class within a life stage were perfectly correlated. We calculated 95% unconditional confidence intervals for all estimates of survival rates using a logit-based “back transform” method (Burnham and Anderson 2002).

#### *Part 2: Estimating recent demographic rates (2001–2004)*

Between October 2000 and September 2003 we captured and radio-tagged 115 adult sea otters as part of a long-term telemetry-based study of southern sea otters. By estimating age-, sex-, and location-specific survival rates from these data, we provide another point of comparison for the maximum likelihood estimates derived from carcass age-structure and census data (*Part 1*). To maximize statistical power for one life stage, and based on indications from the carcass record that decreased adult survival might be largely responsible for the faltering recovery of the population as a whole (Estes et al. 2003), we intentionally biased our sampling to capture mostly adults. Consequently, our sample sizes were too low to present mark-recapture survival data for juveniles or subadults.

In general, capture and instrumentation of study animals followed methods described for previous telemetry-based studies of sea otters (McClenaghan and Ames 1976, Williams and Siniff 1983, Siniff and Ralls 1991, Monson et al. 2001). We partitioned our sampling effort into three study areas: 30 females and 13 males were captured at Monterey peninsula (north-center of range), 35 females and 12 males were captured at San Simeon (south-center of range) and 25 males were captured at Pt. Conception (southern periphery of range; Fig. 2). At Pt. Conception we did not capture females because only males currently utilize this southernmost portion of the range. All study animals were monitored by ground-based and/or aerial-based radio telemetry (following methods described by Siniff and Ralls 1991) for a minimum of two years, or until they died or disappeared. Abdominally implanted VHF radios were equipped with thermal monitors that allowed us to record internal body temperature and/or to detect mortality whenever the animal was in radio contact; mortality was assumed when body core temperature dropped below 35°C, and the carcass was retrieved for necropsy whenever possible. Daily relocation of study animals was conducted by ground-based radio-trackers in San Simeon and Monterey, while animals at Pt. Conception (as well as animals that went missing from the San Simeon and Monterey study areas) were relocated every two weeks using a Cessna plane

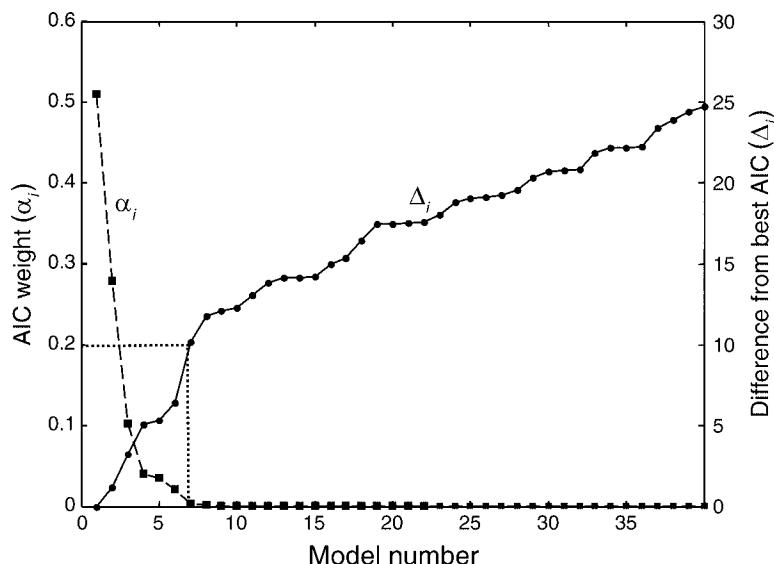


FIG. 4. Profiles of  $\alpha_i$  values (left axis, dashed line) and  $\Delta_i$  values (right axis, solid line) for the 40 models with  $\Delta_i \leq 25$ . Including models with  $\Delta_i > 10$  in the analyses had no effect on model-averaged survival estimates, so only the six models with  $\Delta_i \leq 10$  (indicated by the dotted line) were used for estimating model-averaged vital rates.

equipped with ATS radio-tracking equipment. Results from a previous study (that utilized identical instrumentation [Siniff and Ralls 1991]) suggested that the VHF transmitters were generally reliable for two years postdeployment, and based on deployments from the current study with precisely known radio transmitter life spans ( $N = 25$ , mean = 756 days, 95% CL = 629–886 days), there appeared to be a negligible failure rate for the first 18 months postdeployment. Consequently, we restrict our analyses to the first two years of data for all animals, and treat all permanent disappearances within 18 months of deployment as presumptive mortalities. Data for animals that permanently disappeared after 18 months of deployment were deleted prior to analysis. In total, 8 of 41 mortalities (20%) were presumptive and the remaining 33 were confirmed (i.e., carcasses were recovered).

Estimates of reproductive parameters were calculated from marked study animals as described in the Appendix. We estimated survival rates from the radio-telemetry relocation data using the Kaplan-Meier method, which allows for staggered entry of study animals (Pollock et al. 1989, Bunck et al. 1995). Daily and biweekly relocation data were collapsed to monthly intervals prior to analysis, with all animals being classified each month as alive, dead, or missing. Using a monthly time-step greatly reduced the number of animals that were not located (and thus censored from the risk group [Bunck et al. 1995]) for a given interval, and, for a long-lived species such as sea otters, a finer temporal resolution was considered unnecessary (Sorensen and Powell 1998). Study animals were first added to the risk group in the month they were captured (if they were captured during the first half of the month) or

in the subsequent month (if they were captured during the second half of the month [Pollock et al. 1989]). We evaluated a range of model forms in our estimation of survival, ranging from the simplest (no variation in survival rates) to more complex models that allowed for location effects (i.e., study area), sex, and time effects, and all possible interactions. We did not allow for an age effect because all study animals included in the analysis were considered to belong to a single life stage (adults). Temporal effects evaluated included both annual (corresponding to calendar year) and seasonal effects, where seasons were defined as winter (January–April), summer (May–August), and fall (September–December). Kaplan-Meier estimates of monthly survival and associated variances (Pollock et al. 1989) were converted to seasonal and annual survival probabilities and variances using the Delta method (Oehlert 1992). Parameters were estimated using maximum likelihood techniques, with calculations performed using Program MARK (White and Burnham 1999). For each model form evaluated, we calculated negative log-likelihoods, AIC values, and Akaike weights ( $\alpha_i$ ) and used these to select the best-supported suite of models, limiting consideration to models having  $\Delta_i$  values below 10. We used model averaging to incorporate model uncertainty into the final estimates (refer to methods for *Part 1*, and Burnham and Anderson 2002).

All estimates reported in the text are followed by 95% confidence intervals ( $CI_{0.95}$ ) and the error bars in figures represent  $\pm$  one standard error (unless otherwise indicated). With the exception of the birth rate and weaning success rate estimates derived from telemetry data (Appendix), model-averaged estimates are reported throughout, and confidence intervals and standard

TABLE 3. Maximum likelihood analysis of carcass distributions and population counts, 1992–2001: summary of six model forms having greatest support ( $\Delta_i \leq 10$ ).

Model support		Model description†			
AIC	$\alpha_i$	Sex effect	Location effect	Time effect	Interactions between main effects
4592.6	0.516	$\delta < \text{♀}$	north < center < south	categorical with two levels, 1992–1994 > 1995–2001	location–age: lower juvenile survival in north age–sex: senescence earlier for males
4593.8	0.283	$\delta < \text{♀}$	north < center < south	categorical with two levels, 1992–1994 > 1995–2001	location–age: lower juvenile survival in north
4595.8	0.104	$\delta < \text{♀}$	north < center < south	categorical with three levels, 1992–1994 > 1995–1997 < 1995–1997 < 1998–2001	location–age: lower juvenile survival in north time–age: post-1994 decrease greater for old animals
4597.7	0.040	$\delta < \text{♀}$	north < center < south	categorical with two levels, 1992–1994 > 1995–2001	location–age: lower juvenile survival in north age–sex: senescence earlier for males time–sex: post-1994 decrease greater for females
4597.9	0.036	$\delta < \text{♀}$	north < center < south	categorical with two levels, 1992–1994 > 1995–2001	location–age: lower juvenile survival in north time–sex: post-1994 decrease greater for females
4599.0	0.021	$\delta < \text{♀}$	north < center < south	continuous decrease in survival over time (linear)	location–age: lower juvenile survival in north age–sex: senescence earlier for males time–age: temporal decrease greater for old animals time–sex: temporal decrease greater for females

Notes: Note that all six of the best models shared the same spatial grouping configuration: breakpoints between coastline segments 6 and 7, and between 9 and 10, divided the range into three demographic regions (north, center, and south). Interactions between the location effect and other main effects varied between models, as indicated in the far right column.

† Qualitative impacts of model parameters on survival estimates.

errors reflect unconditional sampling variances. The relative degree of support for specific model effects is represented by the summed AIC weights ( $\Sigma\alpha_i$ ) of all model forms in which the effect was present.

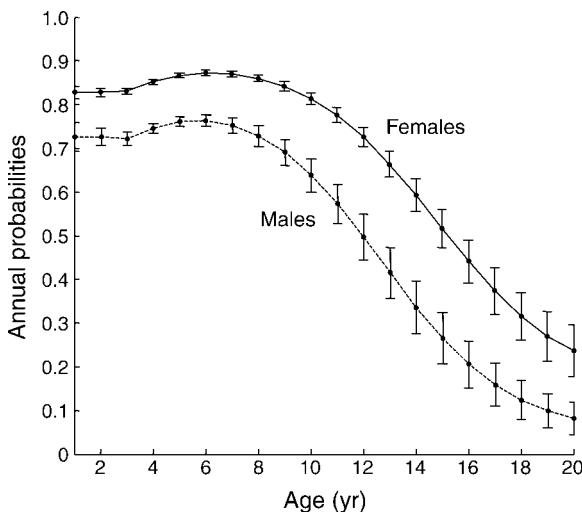


FIG. 5. Age-specific schedule of annual survival rates for females (solid line) and males (dashed line). Model-averaged estimates and their standard errors are shown for 2001 in the north-center of the range.

RESULTS

Part 1: Past demographic rates (1992–2001)

There were six model forms having  $\Delta_i \leq 10$  (Fig. 4, Table 3). The model-averaged estimates of age-specific vital rates lead to a survival schedule that is consistent with previous models (Siniff and Ralls 1988). Annual survival was relatively low for juveniles, increased to a maximum for animals aged 4–7 years, and then decreased gradually for older adults (Fig. 5). Female survival was higher than that of males at all ages, and an age–sex interaction was present in three of the best-fit models ( $\Sigma\alpha_i = 0.58$ ), resulting in an slightly accelerated decline in survival with age for males as compared to females: such a pattern is consistent with the female-biased sex ratio reported for southern sea otters (Jameson 1989). Three of the models ( $\Sigma\alpha_i = 0.10$ ) included a time–sex interaction, such that the temporal decrease in survival was greater for females than for males; in general, however, the model results indicated similar temporal and spatial trends in survival for males and females, and because changes in male survival rates have little effect on population growth, especially for non-monogamous species such as the sea otter, we report all further results for females only.

TABLE 4. Maximum likelihood model-averaged estimates of annual survival rates for 1992–2001, derived from carcass distributions and population counts.

Group and year	Northern half of range			South-center of range			Southern periphery of range		
	Mean	SE	95% CL	Mean	SE	95% CL	Mean	SE	95% CL
Females									
Juvenile									
1992	0.858	0.008	0.841, 0.873	0.890	0.008	0.873, 0.905	0.905	0.019	0.861, 0.936
2001	0.828	0.015	0.797, 0.855	0.866	0.014	0.835, 0.892	0.884	0.017	0.845, 0.913
Subadult									
1992	0.859	0.005	0.849, 0.869	0.888	0.004	0.880, 0.896	0.903	0.012	0.877, 0.924
2001	0.829	0.008	0.813, 0.844	0.863	0.008	0.847, 0.878	0.881	0.013	0.854, 0.904
Adult									
1992	0.888	0.006	0.877, 0.899	0.890	0.005	0.879, 0.900	0.905	0.010	0.884, 0.922
2001	0.861	0.007	0.846, 0.875	0.862	0.006	0.849, 0.875	0.880	0.011	0.857, 0.900
Old adult									
1992	0.757	0.032	0.690, 0.814	0.714	0.028	0.657, 0.765	0.737	0.032	0.669, 0.795
2001	0.714	0.040	0.631, 0.785	0.668	0.032	0.603, 0.728	0.694	0.038	0.616, 0.763
Males									
Juvenile									
1992	0.771	0.026	0.717, 0.817	0.819	0.025	0.764, 0.863	0.842	0.028	0.778, 0.890
2001	0.727	0.033	0.658, 0.786	0.781	0.023	0.734, 0.822	0.808	0.021	0.762, 0.846
Subadult									
1992	0.770	0.015	0.738, 0.798	0.813	0.014	0.785, 0.839	0.836	0.020	0.794, 0.871
2001	0.725	0.017	0.690, 0.758	0.774	0.013	0.748, 0.799	0.801	0.016	0.767, 0.831
Adult									
1992	0.792	0.012	0.768, 0.815	0.798	0.014	0.768, 0.824	0.822	0.017	0.785, 0.853
2001	0.747	0.018	0.710, 0.780	0.754	0.018	0.717, 0.788	0.781	0.021	0.738, 0.819
Old adult									
1992	0.618	0.056	0.504, 0.721	0.564	0.044	0.478, 0.647	0.594	0.050	0.493, 0.688
2001	0.562	0.049	0.465, 0.654	0.507	0.036	0.436, 0.577	0.538	0.043	0.454, 0.621

Notes: Results shown are means, standard errors (SE), and 95% confidence limits.

All of the well-supported models indicated that survival rates were variable over both space and time (Table 3). The general nature of the spatial effect was similar for all of the best-fit models: survival was lowest in the north and center of the range and highest in the southern periphery of the range south of Pt. Buchon. Survival rates decreased in all areas between 1992 and 2001 (Table 4), and all but one of the best-fit models ( $\Sigma\alpha_i = 0.98$ ) included this time effect as a sudden decrease in survival after 1994. Because models with a categorical time effect were penalized for having an additional parameter ( $\theta_t$ , the location of the temporal break), the strong support for a sudden drop in survival in the mid 1990s (as opposed to a gradual decline over the 1990s) is unlikely to be spurious.

The spatial and temporal trends in survival were similar but not identical for all age/sex classes: for example, all of the well-supported models included interactions between age and location, with much lower juvenile and subadult survival in the north half of the range (Fig. 6). Two of the best-fit models ( $\Sigma\alpha_i = 0.13$ ) also included a time–age interaction, such that older animals experienced a greater decrease in survival after 1994 than juveniles or subadults. The greatest temporal decrease in survival (proportionally) was thus experi-

enced by old adults; however, given the age-specific patterns of matrix elasticity values (Fig. 7), decreased survival of prime-age adults and subadults likely contributed most to the observed change in population growth over the 1990s (Gerber et al. 2004).

There was a relatively good match between predicted and observed carcass age distributions over space and time (Fig. 8), indicating that the model did well at fitting vital rates to the carcass age-structure data set. Slight deviations from linearity in the Q–Q plots were seen for the 1992–1994 period, when the fewest carcasses were available, but these deviations were not sufficient to suggest any pervasive or consistent pattern of non-linearity. Model projections also resulted in a predicted pattern of population growth that corresponded relatively well with those observed (Fig. 9A). Interestingly, there was greater disparity between expected and observed counts when plotted separately for the three major geographic regions (Fig. 9B–D). The greatest disparities were between expected and observed counts in the south-center and southern periphery of the range. However, annual discrepancies were negatively correlated for these two regions ( $\rho = -0.60$ ), suggesting that these disparities may reflect the movement of animals between regions.

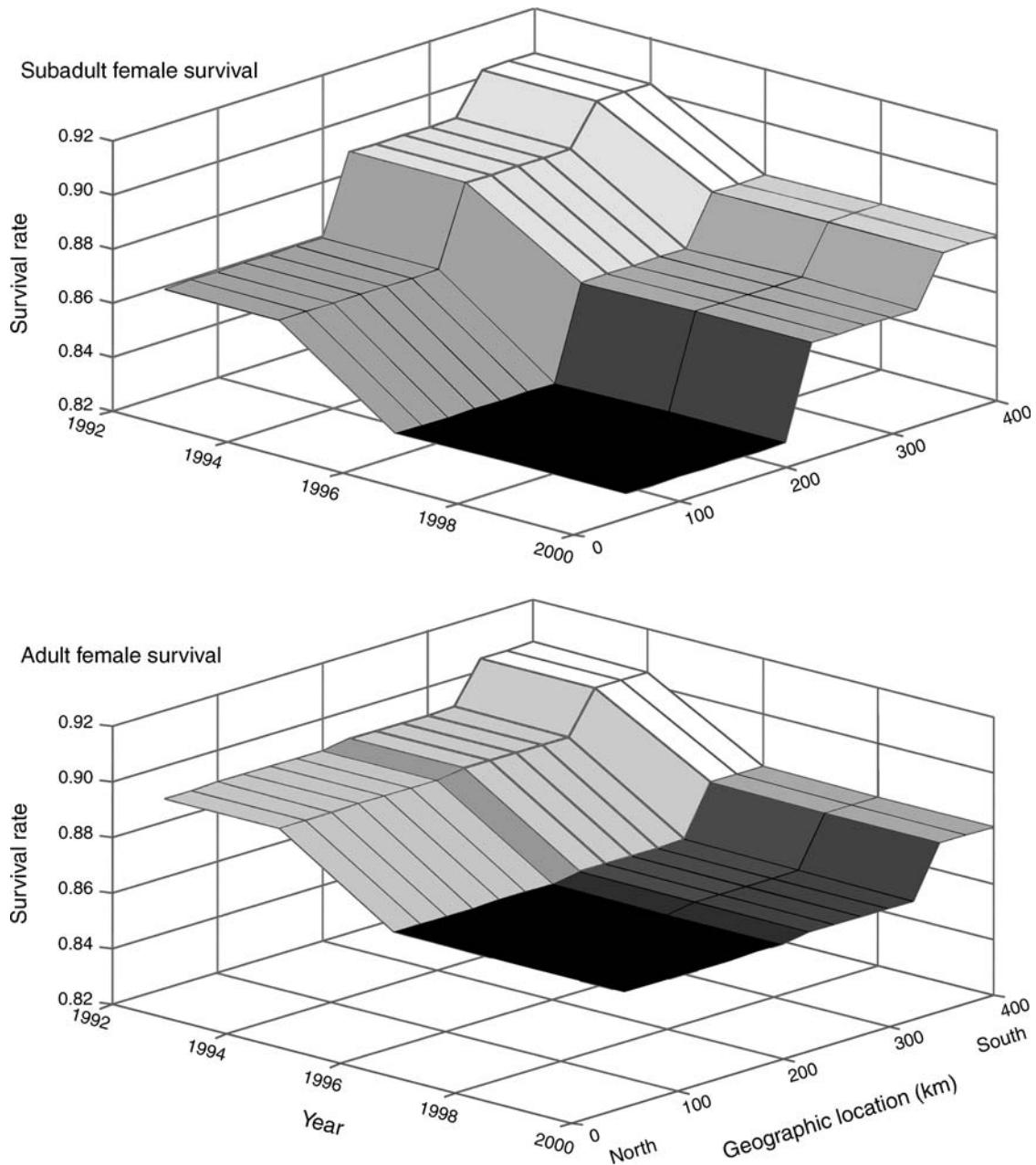


FIG. 6. Spatial and temporal variation in survival rates are plotted for subadult females (top) and adult females (bottom). The two horizontal axes are time (in yearly increments, 1992–2000) and geographic location within the range, measured along the 10-m bathymetric contour that parallels the coast, from Santa Cruz in the north (0) to Pt. Conception in the south (400). The vertical axis is the model-averaged annual rate of survival for the indicated life stage. The three-dimensional surfaces are shaded to indicate relief, with darker shades of gray corresponding to lower survival rates; lines on the surfaces represent 25-km intervals.

#### *Part 2: Recent demographic rates (2001–2004)*

Maximum likelihood estimation of recent survival rates (using radio telemetry data) resulted in 10 model forms having  $\Delta_i \leq 10$  (Table 5). The two best-supported models ( $\Sigma\alpha_i = 0.71$ ) included both a location effect and a seasonal effect, but no variation due to sex or study year. There was overwhelming model support ( $\Sigma\alpha_i = 0.80$ ) for a difference in survival between the center of

the range (Monterey and San Simeon study areas) and the Pt. Conception study area, but very little support ( $\Sigma\alpha_i = 0.02$ ) for a difference between Monterey and San Simeon. Animals from Pt. Conception experienced higher survival than animals from the center of the range (Table 6), consistent with the spatial patterns reported in *Part 1* (Fig. 6). In the Monterey and San Simeon study areas, survival during the summer months

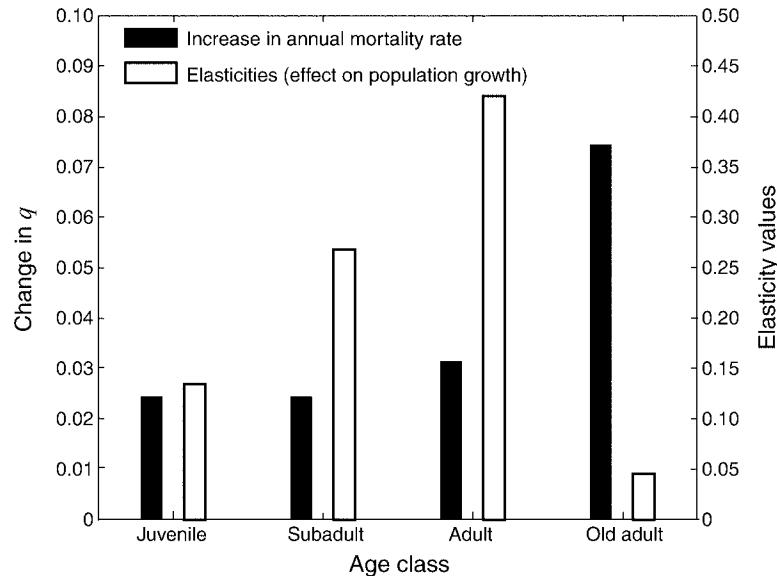


FIG. 7. Increase in annual mortality rates ( $q = 1 - S_a$ ) between 1992 and 2001 (solid bars) and corresponding survival elasticity values (open bars) for four female life stages: juveniles, subadults, adults, and old adults. Elasticity values (Caswell 2001) provide estimates of the relative effect of changes in vital rates for population growth and were derived algebraically from the 1992 matrix and summed for each life stage.

(May–August) was lower than the rest of the year ( $\Sigma\alpha_i = 0.75$ ); this trend was not evident in the Pt. Conception study area, where summer survival rates were either identical ( $\Sigma\alpha_i = 0.42$ ) or slightly higher ( $\Sigma\alpha_i = 0.54$ ) than fall and winter survival rates.

The recent survival rates reported here for adult females are lower than the estimates reported from the 1980s (Table 6), even though both studies used identical methodologies and spanned the same geographical range. In contrast, the trend for males is an increase in survival since the 1980s. Combining the recent survival estimates and the 1980s estimates (both derived from mark–recapture data) with the estimates for the 1990s (derived from carcass age-distributions and census counts; *Part I*) provides a consistent and comprehensive picture of temporal variation in adult female survival (Fig. 10).

#### DISCUSSION

In this paper we have described in detail an extension of an existing technique (Doak and Morris 1999, Monson et al. 2000a) that allows for incorporation of multiple sources of demographic information (carcass age distributions and population counts), and for assessment of spatial as well as temporal variation in survival for the threatened southern sea otter. Perhaps more importantly, our general approach to incorporating uncertainty may be applicable to other threatened populations for which there are many possible demographic scenarios to consider, but limited data for analysis and insufficient a priori information with which to identify a few clearly most plausible scenarios. Animal populations are influenced by an almost infinite

assortment of deterministic and stochastic forces that together affect demographic processes in often complex ways. The vast majority of these forces lead to demographic variation that is immeasurably small and can thus be safely ignored by biologists wishing to model populations to evaluate their viability or select among management options. Statistical hypothesis-testing techniques and model selection criteria are typically used by biologists to reject insignificant effects or to select the most parsimonious model or hypothesis (Hilborn and Mangel 1997, Burnham and Anderson 2002). Unfortunately, in most systems there is considerable uncertainty underlying every component of the analysis, and the risks of a wrong decision resulting from such uncertainty are very rarely taken into account (Burgman et al. 1993, Chatfield 1995). At least when dealing with a data-rich system such as ours, we agree with Pascual et al. (1997) that a reasonable way of dealing with this uncertainty is to evaluate many alternative models, and then use formal techniques for incorporating the uncertainty into parameter estimates (Chatfield 1995, Burnham and Anderson 2002). Although this may entail sacrificing a certain degree of heuristic simplicity, it provides a rigorous way to advance understanding of the complex dynamics that are questions of biological interest in such systems.

We emphasize that we are using an information theoretic approach in an exploratory way here; we are not hypothesis testing or striving for a model that is generally applicable to all situations. The most recognized and definitive reference on information theory and model selection written for ecologists (Burnham and Anderson 2002) is very clear on the dangers of “data

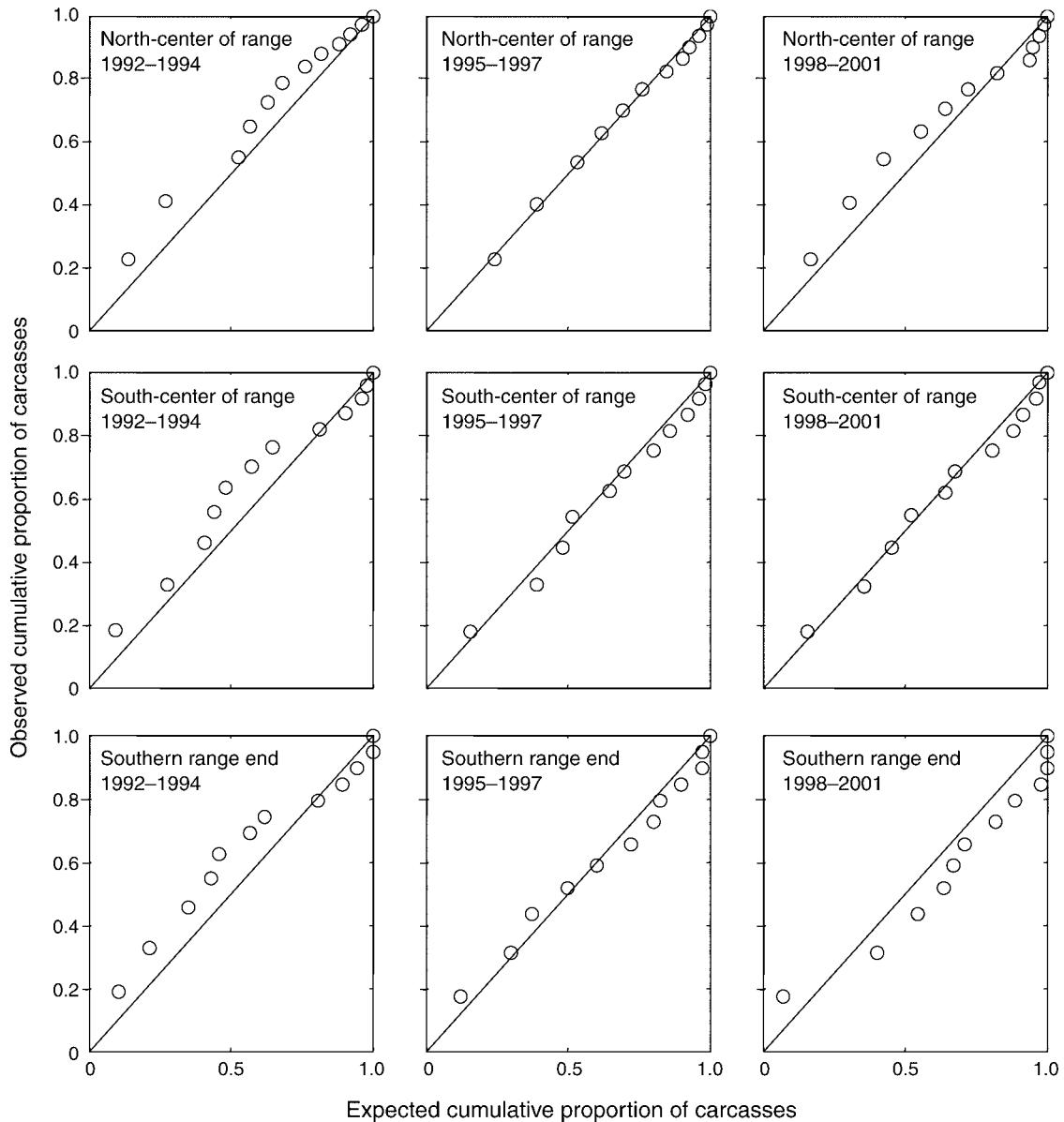


FIG. 8. Quantile–quantile (Q–Q) plots of predicted carcass age class distributions for nine spatial/temporal groupings of the historical data. Each subplot shows the cumulative proportion of observed vs. expected carcasses in the first 12 age classes: the degree of conformity to a linear relationship with slope of 1 (represented as a diagonal line) indicates the relative goodness of fit of the model.

dredging,” a term that is somewhat vague but could be taken to refer to any approach other than consideration of a relatively small, exclusive set of alternative hypotheses (e.g., a model with compared with one without a time effect) that are not modified once model fitting commences. While we did not modify our suite of model forms, our methodological approach (as described in *Part 1*) clearly violates Burnham and Anderson’s maxim because we consider such a large suite of possible model forms. However, this number of model forms is nearly unavoidable if both temporal and spatial variation are to be included in a structured

demographic model. We propose that if one can properly account for model uncertainty (i.e., using model averaged estimates and unconditional variances [sensu Burnham and Anderson 2002]), then a maximum likelihood approach used in this exploratory way can be an appropriate first step towards the elucidation of key demographic processes and spatial/temporal patterns of variation that can be targeted by further data collection and subsequent analyses. The approach we suggest can focus future attention on a smaller number of well-supported, testable hypotheses about factors underlying

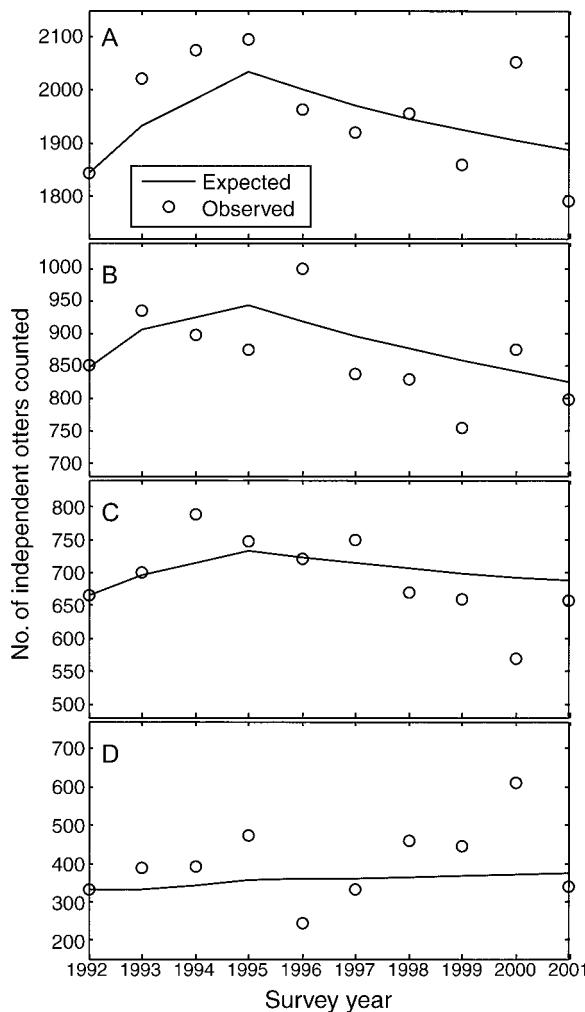


FIG. 9. Expected trends in population abundance (number of independent sea otters) between 1993 and 2001, as predicted by matrix projections using the maximum likelihood estimated vital rates. Observed counts of independents are plotted for comparison. Data are shown (A) for the population as a whole, and also for three major geographic subdivisions of the range: (B) the north (Half Moon Bay–Lopez Pt.); (C) the south-center (Lopez Pt.–Pt. Buchon); and (D) the southern range end (south of Pt. Buchon).

observed trends, while helping to divert attention away from other, less important factors.

With respect to conservation of the southern sea otter, the pertinent conclusions that can be drawn from the analyses presented here are that age-specific survival schedules vary considerably across the geographic range of this population (Fig. 6), and mean survival rates (particularly survival of prime-aged adult females) decreased quite suddenly after 1994 (Fig. 10). In contrast to variation in survival rates, it appears that reproduction (birth rates and weaning success) have remained fairly constant (Estes et al. 2003, Tinker 2004). We must add the caveat that our model could not detect trends in mortality of very young juveniles because 0-year-old

carcasses were excluded from analysis, due to known recovery bias. Thus the potential role of variation in early postweaning survival as a contributing factor to population dynamics (e.g., see Ballachey et al. 2003) is impossible to directly assess with currently available data, and may be underrepresented. This uncertainty should be addressed in future field studies; however, we believe it is unlikely that survival rates of 6-month juveniles would exhibit spatial or temporal trends that were substantially different from that of 12-month-old juveniles. The concordance between independent estimates of adult survival (Fig. 10) further suggests that the age-specific patterns implicated by our analysis are not spurious, and provides strong support for the temporal and spatial patterns indicated by both methodologies.

The spatial and temporal trends described here can be used to focus future research on those factors most likely to drive population changes; in particular, factors that impact survival of adult females in the center of the range are of greatest concern. A number of recently identified diseases in southern sea otters, including protozoal encephalitis and idiopathic cardiomyopathy, appear to be responsible for a considerable proportion of the mortality of adult females within the center of the range (Thomas and Cole 1996, Miller et al. 2002, Kreuder et al. 2003), and the proximate and ultimate causes of these diseases should be the subject of further research. Another major source of mortality for young animals is acanthocephalan peritonitis, caused by heavy intestinal loads of thorny-headed worms (Mayer et al. 2003); the incidence of this disease is particularly high in the north-center of the range, especially Monterey Bay (Kreuder et al. 2003, Mayer et al. 2003). This geographic distribution matches the model prediction of relatively lower juvenile and subadult survival in the north half of the range, and thus provides us with one possible explanation for the observed spatial pattern. We emphasize that the methodological approach described here does not directly test the relative importance of specific factors that may be affecting survival (e.g., diseases, contaminants, fishing gear entanglement); however, our results can now be incorporated into sensitivity analyses that do so (e.g., Kreuder et al. 2003, Gerber et al. 2004).

Some of the patterns that emerged from these analyses raise more questions than they answer. For instance, the seasonal variation in survival rates of telemetered animals (Table 5) is perplexing, especially considering that the observed pattern, lower survival in the summer, seems to be the opposite of that described for sea otters in Alaska and Russia (e.g., Kenyon 1969, e.g., Bodkin et al. 2000). This pattern is consistent, however, with the reported increase in beach-cast carcasses retrieved in summer months during periods of population decline in California (Estes et al. 2003). One explanation for this pattern might be increased incidence of disease in summer, possibly associated with some seasonally driven environmental factor (e.g., warm water algal

TABLE 5. Maximum likelihood analysis of mark–resight survival data, 2001–2003: summary of 10 model forms having greatest support ( $\Delta_i \leq 10$ ).

Model support		Model description				
AIC	$\alpha_i$	Sex effect	Spatial variation†	Yearly variation	Seasonal variation	Season–location interaction
254.3	0.541	no	(1 = 2) < 3	no	summer < winter and fall in areas 1 and 2	summer > winter and fall in area 3
256.6	0.172	no	(1 = 2) < 3	no	summer < winter and fall in areas 1 and 2	no seasonal variation in area 3
257.7	0.097	no	no	no	no	no
259.3	0.043	no	(1 = 2) < 3	no	no	no
259.5	0.040	♂ > ♀	no	no	no	no
259.9	0.032	no	no	no	summer < winter and fall	no
260.1	0.029	no	no	2003 < 2001 and 2002	no	no
260.9	0.020	no	2 < 1 < 3	no	no	no
261.3	0.016	♂ > ♀	(1 = 2) < 3	no	no	no
263.3	0.006	no	(1 = 2) < 3	2003 < 2001 and 2002	no	no

† Spatial variation effect allows for different survival estimates in three study areas: 1, Monterey; 2, San Simeon; 3, Pt. Conception.

blooms or terrestrial run-off patterns). Another potential explanation for a seasonal trend in survival relates to female reproductive status: because there is a higher frequency of pup births in the winter, there must be a corresponding midsummer peak in the number of females having recently weaned pups. Females generally lose mass throughout the pup dependency period (Monson et al. 2000b), and individuals that are otherwise nutritionally stressed are probably at their poorest body condition immediately postweaning, at which time they are also generally in estrus and may experience repeated mating interactions with males. The interaction of all these stress factors may cause a midsummer peak in female mortality; the problem with this explanation is that the seasonal variation in survival appears to affect males equally. A third explanation (not mutually exclusive of the others) pertains to diet profitability. Seasonal variation in the nutritional and/or energy composition of some sea otter prey species is known to occur (related to prey reproductive cycles, e.g., Watt et al. 2000), and may lead to seasonal peaks in the degree of nutritional or energetic stress experienced by some individuals. All of these possible explanations

represent testable hypotheses, and further data will be needed to properly evaluate their relative importance. It is worth noting, however, that the latter two explanations can be encompassed by a broader hypothesis of density-dependent population regulation. The seasonal decrease in survival was observed for animals at the center of the range, where recolonization occurred earliest, densities are highest, and where it might be expected that females would be in poor body condition and thus subject to stress-related mortality associated with pup weaning and/or variation in prey profitability. At the same time, simple density-dependent mechanisms are difficult to reconcile with the sudden decrease in survival in the mid-1990s, especially in light of the fact that density in the center of the range had been nearly constant for some time.

Incorporating the estimated demographic rates into a projection matrix predicted dynamics that were consistent with observed trends for the population as a whole between 1993 and 2001 (Fig. 9A). However, the poorer fit between expected and observed counts within each geographic region (Fig. 9B–D) was surprising, since the logit functions we used allow sufficient flexibility to fit even complex patterns of spatial and temporal variation. To some degree this failure to closely track year-to-year variation in observed counts reflects the constraining effects of the continuous functions fit to the carcass age-structure data, which will tend to predict gradual changes in population numbers rather than vacillating, short-term variations, regardless of patterns in the population counts that are simultaneously fit with the models. Another contributing cause of the discrepancies is highlighted by the negatively correlated discrepancies in adjoining areas, suggesting that some of the variation in counts at the regional level reflects movement of animals between regions, a process not accounted for in our current projection matrix. It is likely that this type of regional redistribution primarily involves males and not

TABLE 6. Maximum likelihood model-averaged estimates of annual survival rates for adult sea otters, derived from telemetry data.

Sex/study group	Mean	SE	95% CL
Females			
1984–1986, center of range†	0.91	0.088	...
2001–2003, Monterey peninsula	0.832	0.059	0.683, 0.917
2001–2003, San Simeon	0.831	0.060	0.682, 0.916
Males			
1984–1986, center of range†	0.61	0.167	...
2001–2003, Monterey peninsula	0.833	0.060	0.683, 0.918
2001–2003, San Simeon	0.833	0.060	0.681, 0.918
2001–2003, Pt. Conception	0.864	0.095	0.567, 0.956

† Estimates reported by Siniff and Ralls (1991).

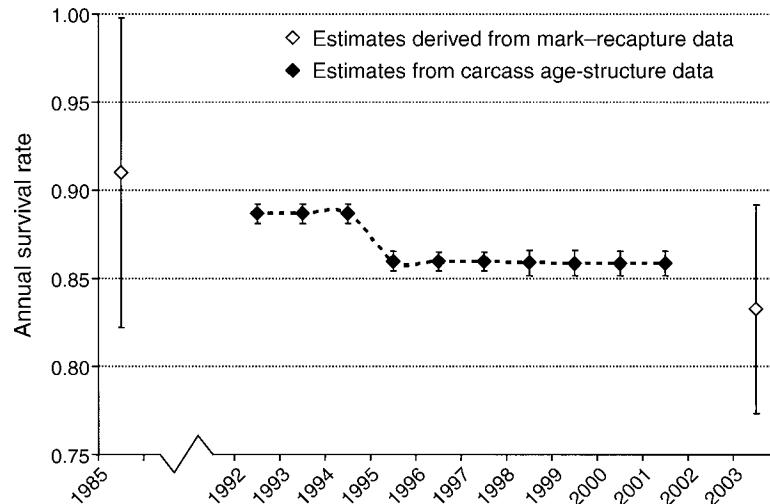


FIG. 10. Synthesis of survival estimates derived from two independent analyses and three data sets, summarizing the inferred temporal changes in adult female survival in the center of the range. The 1985 estimate is that reported by Siniff and Ralls (1991). Error bars indicate  $\pm$ SE.

females, as males are more mobile than females (Ralls et al. 1996), and long-distance seasonal movements by some males between the south and center of the range have been reported (Jameson 1989, Tinker 2004). Movement between subpopulations could (and should) be included in future analyses and management considerations, and data from ongoing telemetry studies (U.S. Geological Survey, *unpublished data*) and previous studies of this population (Ralls et al. 1996) can be used to parameterize individual movement rates.

The modeling of populations is at its heart an effort to assemble disparate sources of information into a coherent whole. If the data we relied on to construct models, especially demographic models, were simple, then comparatively simplistic statistical models would be sufficient to understand these data and formulate predictions from them. Unfortunately, highly complex and fragmented data sets are far more common for most wildlife populations, and it is thus surprising that more attention has not been paid to the use of multiple data sources and the uncertainties inherent in their use. Nowhere is this more true than in the realm of demographic modeling. While there is increasing concern about these issues (e.g., Chatfield 1995, Hilborn and Mangel 1997, Burnham and Anderson 2002, Buckland et al. 2004), flexible tools with which to unite multiple data sources and to select the most appropriate model forms are still limited, as are examples of their use (Pascual et al. 1997, Link et al. 2002, but see Holmes and York 2003, Kauffman et al. 2004, Rivot et al. 2004). Here, we have illustrated how the powerful and relatively straightforward tools of information-theoretic-based model fitting (Burnham and Anderson 2002) can be used to sort through and parameterize quite complex demographic modeling frameworks. We have paid particular attention to the estimation of parameter

uncertainty because in our system, as for most, a clear understanding of the uncertainties in spatial and temporal trends is of key importance. While all circumstances will not allow the use of the type of unified model selection process that we have employed here, when it is possible, we believe that Burnham and Anderson's (2002) approach yields benefits that more than offset its added complexity.

#### ACKNOWLEDGMENTS

We are grateful to the dozens of researchers and volunteers who collected sea otter carcasses and contributed to field work: thank you in particular to J. Ames, M. Harris, and M. Kenner for carcass recovery and live otter captures, and to C. Alfano, G. Bentall, B. Cummings, J. Hill, A. Kage, C. Lin, T. Nicholson, K. Sanchez, J. Stewart, and B. Van Wagenen for collection of radio telemetry data. Primary support for fieldwork activities was provided by a grant from the Minerals Management Service (MMS Cooperative Agreement 14-35-0001-31063), and by funding from the U.S. Geological Survey (Western Ecological Research Center and Alaska Science Center), California Department of Fish and Game, and the Monterey Bay Aquarium. Additional support for analysis was provided by a grant from "Friends of the Sea Otter" and NSF DEB-0087078 and USDA 2002-00610 to D. F. Doak. The manuscript benefited greatly from constructive suggestions by M. Runge and an anonymous reviewer.

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## APPENDIX

Estimation of reproduction parameters from radio-tagged sea otters in central California (*Ecological Archives* A016-074-A1).

## **Appendix A: Estimation of reproduction parameters from radio-tagged sea otters in central California**

As with many other previously published studies of sea otter reproduction (Siniff and Ralls 1991, Eberhardt and Schneider 1994, Riedman et al. 1994, Monson et al. 2000), we used longitudinal records of observational data from marked individual females to estimate of reproductive parameters. Because females with small pups (less than 8 weeks of age) tend to rest and swim on their backs carrying their pups on their abdomens, frequent visual re-sights of marked females provides a reliable means of detecting pup births and pre-mature deaths. Older pups can swim and feed independently and may even resemble independent juveniles superficially, however they are always associated closely with their mothers and their behavior (including frequent suckling behavior, maternal food sharing and grooming, and play behavior) easily identifies them as dependant pups to an experienced observer; consequently, the age at weaning can also be determined with precision so long as visual observations are frequent enough. In the current study, shore-based or boat-based observers were often able to visually locate female study animals after their initial detection by radio-telemetry (see methods, Part 2). Visual re-sightings were made 5–7 times per week for females in the San Simeon study area, and these frequent re-sights allowed for reliable estimates of reproductive parameters (birth rates and weaning success rates). Visual re-sightings were less frequent in the Monterey study area (1–2 per week generally, but interspersed with longer periods without visual re-sights for some animals), and so these data were not used for estimating reproductive parameters due to the potential of missing pups that died soon after birth, and thus under-estimating birth rates (Eberhardt and Schneider 1994).

We calculated mean birth rate using the “direct method” (*sensu* Eberhardt and Schneider 1994):

$$\bar{b} = \frac{1}{K} \sum_{k=1}^K b_k \left( \frac{365}{N_k} \right) \quad 1$$

where  $K$  is the total number of females monitored for at least 365 days,  $b_k$  is the number of observed births observed for female  $k$ , and  $N_k$  is the number of days female  $k$  was monitored. We limited analysis to adult females that were monitored continuously for a minimum of 365 days ( $N=26$ , Table A1) to avoid biasing estimates (Eberhardt and Schneider 1994). The average monitoring period was 648 days per female, for a total of 16,840 monitoring days, and 45 pups were produced within this period. Although pups were produced year-round, the frequency of pup births was higher between September and February ( $n = 35$ ) than between March and August ( $n = 10$ ). Solving equation 1 using these data resulted in an estimate of  $b = 0.98$  ( $\pm 0.055$ ,  $CI_{95} = 0.87-1.09$ ), a value entirely consistent with previous estimates for this population (Siniff and Ralls 1991, Eberhardt and Schneider 1994, Riedman et al. 1994).

In order to test for a relationship between birth rate and mother’s age, we used a sub-set of females for which tooth-age estimates provided relatively precise age estimates ( $\pm 1$  year) and who produced two or more pups during the time of monitoring. We then plotted inter-birth interval (the inverse of birth rate) against mothers’ age for all consecutive pairs of pups born to these females for which the weaning date (or date of pup-loss) of the first pup and the birth date of the subsequent pup were known within  $\pm 7$  days ( $n = 24$  pairs; Figure A1). No significant relationship between mothers’ age and inter-birth interval was evident from this analysis (least-squares linear regression  $F = 0.025$ ,  $P = 0.875$ ). We therefore use an age-independent value of 0.98 to parameterize age-specific birth rate in the population matrix model (see Methods, Part 1).

We analyzed weaning success as a binomial variable, with individual weaning success for each female calculated as the proportion of pups produced during the study that were weaned successfully. In most cases pup death or successful weaning was confirmed by direct observation; however, in cases where the outcome was un-confirmed (i.e. a female was observed with a pup on one re-location and without the pup on the subsequent re-location, but neither the weaned pup nor a pup carcass could be found) we assumed that those pups with a dependency period of 150 days or more were weaned successfully, while those with a dependency period of under 150 days had died (Siniff and Ralls 1991, Riedman et al. 1994). We then estimated the population weaning rate as the average individual success rate across all females (N=27, Table A1). The result of this analysis was a mean weaning success rate of 0.56 ( $\pm 0.090$ ,  $CI_{95} = 0.38\text{--}0.74$ ), virtually identical to the value of 0.57 reported from the late 1980's (Siniff and Ralls 1991).

The results of previous studies of reproduction in sea otters indicate a functional relationship between female age and reproductive success (Siniff and Ralls 1991, Riedman et al. 1994, Monson et al. 2000). We tested for such a relationship in our current data set by fitting a smoothing function to age-specific weaning success ( $w_x$ , where  $x$  is the mother's age, in years). For this analysis we used data from 21 females with precise age estimates ( $\pm 1$  year), and treated each of their pups (N=35) as an independent data point with a success score equal to 1 (pup weaned successfully) or 0 (confirmed or assumed failure to wean successfully). These data are summarized in Table A2. We then evaluated 8 different smoothing functions, including a constant rate (i.e. age-independent) as well as linear, exponential, power, rational and logistic functions, the latter models including both simple and higher-order age effects (Table A3). We fit the models using maximum likelihood methods, assuming binomial probabilities (Hilborn and

Mangel 1997), and models were then ranked based on their associated AIC values and Akaike weights (Burnham and Anderson 2002). We also evaluated the goodness of fit for each model using  $R^2$  values. Because the Akaike weights and  $R^2$  values were fairly similar across a range of the model forms evaluated (Table A3), we used all 8 functions to calculate model-averaged estimates of age-specific weaning success and 95% unconditional confidence intervals, following Burnham and Anderson (2002). The resulting model-averaged point estimates increased smoothly and asymptotically with age, and were well-approximated ( $R^2 = 0.999$ ) by the function:

$$w_x = \theta_1 \cdot x^{\theta_2} + \theta_3 \quad 2$$

where  $\theta_1$ ,  $\theta_2$  and  $\theta_3$  were fitted parameters:  $\theta_1 = -1.231$ ,  $\theta_2 = -0.4845$  and  $\theta_3 = 1.0922$  (Figure A2). Equation 2 was therefore used to parameterize age-specific weaning success probability in the population matrix model (see Methods, Part 1).

The probability of sea otter pup mortality during the 6 month dependency period has been found in previous studies to be highest during the first weeks and months of lactation (Monson et al. 2000). This trend was also evident in the current study, based on 18 recorded pup deaths (Figure A3). To predict the relative probability of pup mortality as a cumulative function of its age (days since birth) we fit a simple log-linear function to the pup age-at-death data (Figure A3). We then used the resulting function to estimate  $S_{p(d)}$ , the probability of pup survival until day “ $d$ ” of the 180 day dependency period, as:

$$S_{p(d)} = w^{0.32 \cdot \ln(d/180) + 1} \quad 3$$

where  $w$  is the overall weaning success rate for the female in question. Equation 3 is useful because it offers a more precise means of predicting the proportion of pups expected to be alive

at a given point in time than would be achieved by assuming a constant rate of pup mortality throughout the dependency period. Specifically, our discrete matrix model (see Methods, Part 1) approximates a birth flow population by assuming that reproductive females can be divided into two groups: those that reproduce early in the year (during the first 6 months), and those that reproduce late in the year (during the second 6 months). In the case of early females, all pups produced will either be dead or independent juveniles by the time of the census at year  $t+1$ ; in the case of late females, all pups produced will either be dead or still dependent. For a “typical” late reproducing female, the probability that a pup is still alive to be counted at the time of the census depends on both the number of days elapsed since the pups’ birth and the cumulative likelihood of pup mortality within that period. Unfortunately, calculating this probability for a typical female whose pup is born 3 months before the survey (the simplest approach for a birth-flow approximation) would provide a biased estimate for the group as a whole because the instantaneous pup mortality rate varies as a function of pup age. To account for this, we further sub-divided late reproducing females into 6 sub-groups, based on the month of their pups’ birth, and for each sub-group we used equation 3 to estimate the probability of pup survival at the time of census. The arithmetic mean of these estimates provides a less biased estimate of the “average” probability of a pup surviving to be counted during the census, and we used this value to generate the expected annual counts of dependent pups for each matrix parameterization (see Methods, Part 1).

Table A1. Reproductive data collected for female sea otters at the San Simeon study site, showing estimates of individual rates of annual pup production (for those animals monitored for at least 1 year) and weaning success.

Female	Days Monitored	Pups born	Annual Pup Production	Success Rate
1	269	1	N/A	0
2	366	1	0.99726776	1
3	425	1	0.858823529	1
4	483	2	1.511387164	0
5	483	1	0.755693582	0
6	483	1	0.755693582	0
7	484	1	0.754132231	1
8	484	2	1.508264463	0
9	498	1	0.732931727	1
10	520	1	0.701923077	0
11	545	2	1.339449541	0
12	584	2	1.24893071	1
13	585	2	1.246797609	0.5
14	681	1	0.535976505	1
15	684	2	1.067251462	0.5
16	684	2	1.067251462	0
17	685	2	1.065693431	0
18	686	2	1.064139942	1
19	687	1	0.531295488	1
20	690	2	1.057971014	1
21	772	2	0.945595855	1
22	774	2	0.943152455	1
23	778	3	1.407455013	1
24	831	1	0.439229844	0
25	854	2	0.854800937	0.5
26	1047	3	1.045845272	0.66667
27	1047	3	1.045845272	1

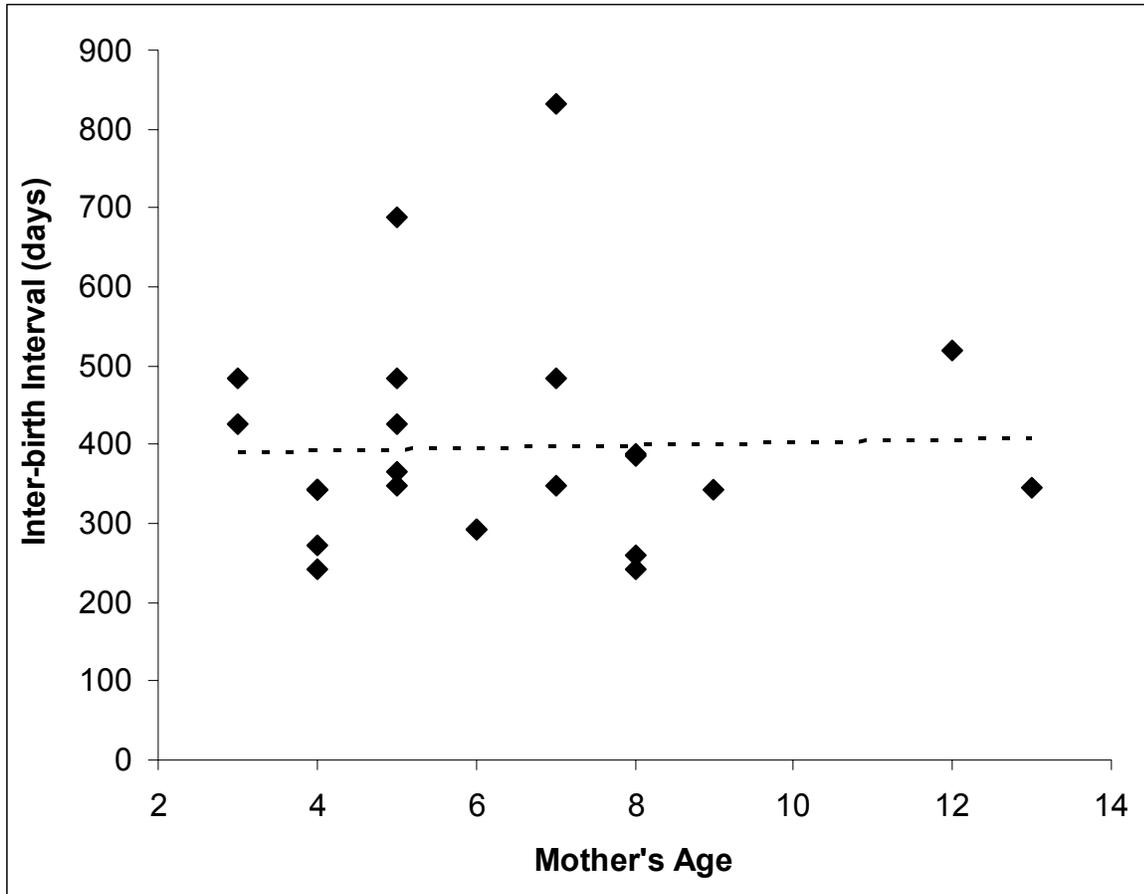
Table A2. Weaning success data collected from 21 female sea otters of “known age” (age estimate based on tooth-section analysis, assumed accuracy +/- 1 year) at the San Simeon study site. Each record corresponds to a single pup born to one of the females (note that some females are represented by more than one pup). The first column shows the mothers’ age at the time of pup birth, and the second column indicates whether or not the pup was weaned successfully: a success score of 0 indicates pup death prior to weaning, while a score of 1 indicates successful weaning (see text for further explanation).

Age of mother (years)	Weaning Success score
3	0
3.2	0
3.4	1
3.7	0
3.7	1
3.9	0
4.4	0
4.6	1
4.7	0
4.7	1
4.9	0
4.9	1
5.5	0
5.5	1
5.6	0
5.7	1
5.8	0
5.8	1
6.4	1
6.7	0
6.7	1
6.8	1
7	1
7.7	1
7.7	0

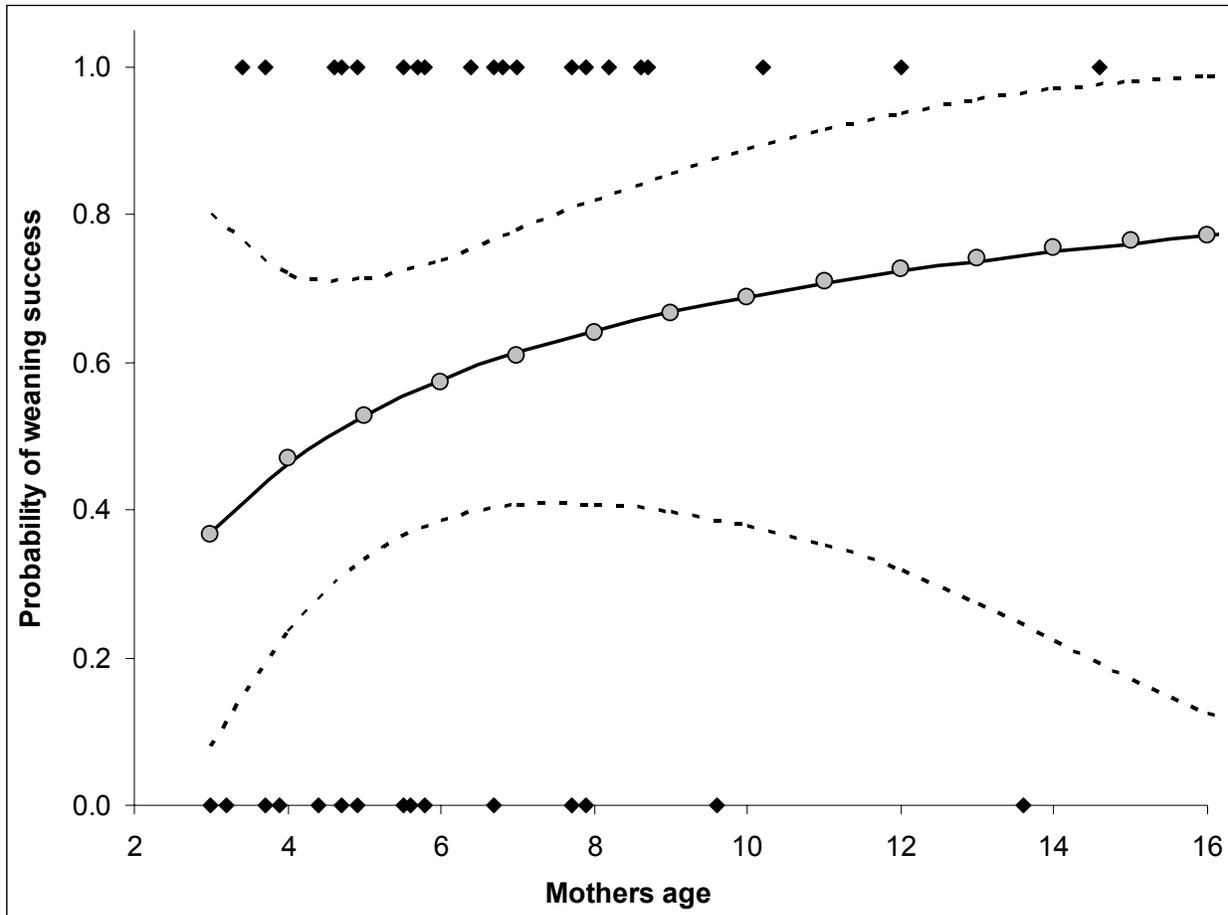
7.9	1
7.9	0
8.2	1
8.6	1
8.7	1
9.6	0
10.2	1
12	1
13.6	0
14.6	1

Table A3. Model fitting results for 8 different smoothing functions fit to age-specific weaning success data (see Table A2). Models are ranked in order of ascending AIC values, with the most parsimonious model at top. The goodness of fit for each model is also provided (measured as R<sup>2</sup> values) and AIC weights indicate the relative level of support for each model.

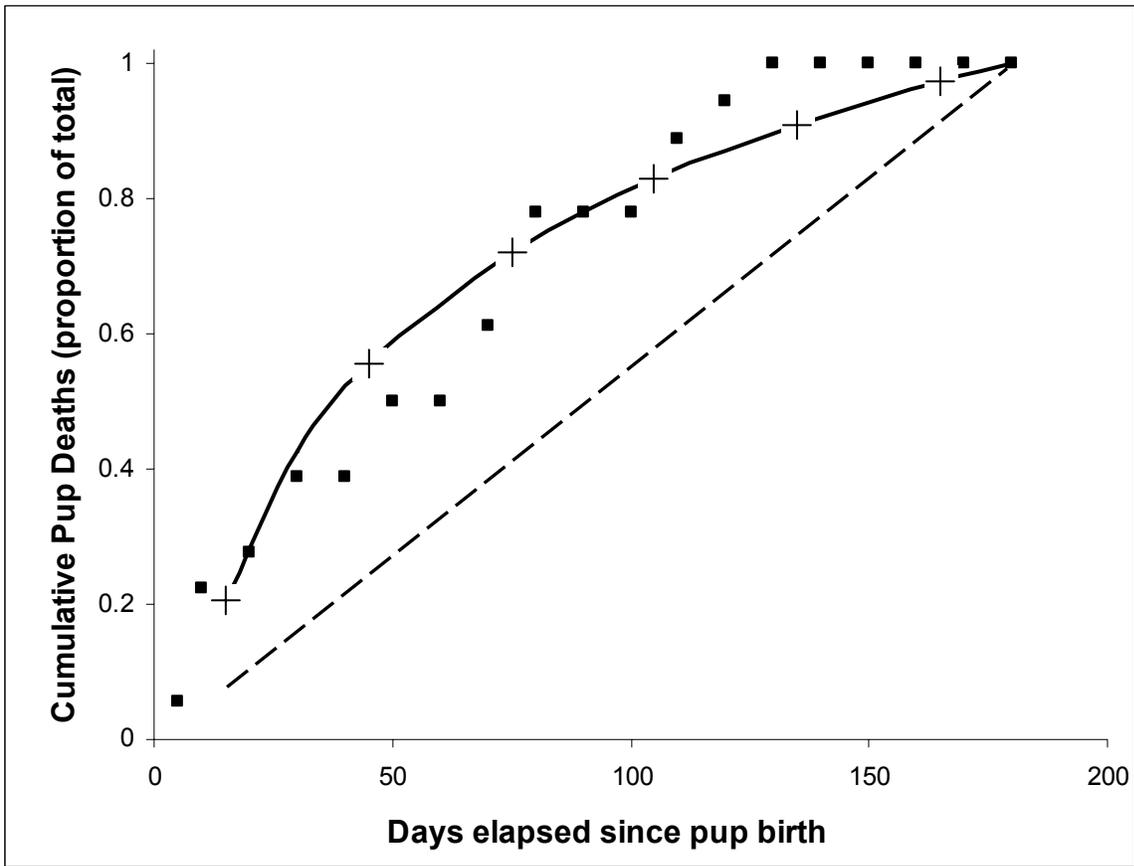
Model Name	Model Form	Number of Parameters	– Log Likelihood	AIC value	R <sup>2</sup> value	AIC weight
Rational 1	$w_x = \frac{(\theta_1 \cdot x + \theta_2)}{x}$	2	22.6195	49.239	0.0730	0.20562
Constant	$w_x = \theta_1$	1	23.9018	49.8036	< 0.0001	0.155048
Power	$w_x = \theta_1 \cdot x^{\theta_2}$	2	23.047	50.094	0.0517	0.134093
Logit 1	$w_x = \frac{e^{(\theta_1 \cdot x + \theta_2)}}{1 + e^{(\theta_1 \cdot x + \theta_2)}}$	2	23.192	50.384	0.0488	0.115993
Linear	$w_x = \theta_1 \cdot x + \theta_2$	2	23.2424	50.4848	0.0418	0.110292
Exponential	$w_x = \theta_1 \cdot e^{(\theta_2 \cdot x)}$	2	23.3332	50.6664	0.0348	0.100719
Rational 2	$w_x = \frac{(\theta_1 \cdot x + \theta_2)}{(x + \theta_3)}$	3	22.3751	50.7502	0.0792	0.096586
Logit 2	$w_x = \frac{e^{(\theta_1 \cdot x^2 + \theta_2 \cdot x + \theta_3)}}{1 + e^{(\theta_1 \cdot x^2 + \theta_2 \cdot x + \theta_3)}}$	3	22.5431	51.0862	0.0764	0.081649



**Figure A1** Inter-birth interval plotted against mothers' age for all pairs of pups for which the weaning date (or date of pup-loss) of the first pup and the birth date of the subsequent pup (produced by the same female) were known to within +/- 7 days. The dashed line represents the best-fit linear least-squares trend line fit to the data (the slope was not significantly different from 0,  $P = 0.875$ ).



**Figure A2** Weaning success probability as a function of female age (in years). Actual weaning success data is plotted as filled diamonds (1 = successfully weaned pup, 0 = pup death), circles indicate the model-averaged, maximum-likelihood predicted values for females aged 3 to 19 years, and dashed lines indicate the unconditional 95% confidence intervals around the model-averaged predictions. The solid line represents a power function fit to the model-averaged point estimates; this function was used to parameterize weaning success rates in the population matrix model.



**Figure A3** Cumulative proportion of recorded pup deaths as a function of pup age (expressed as days elapsed since pup birth, with 180 days representing a “typical” 6 month dependency period). Observed data for 18 pups are shown as filled squares, while lines indicate the cumulative proportion of total pup deaths expected at a given point of the dependency period if the probability of pup mortality was constant over time (dashed line) or initially high and declining over time (solid line) as described by the log-linear function  $f(x) = 0.32 \cdot \ln(x/180) + 1$ . Crosses indicate the expected cumulative proportion of pup mortality at each month of lactation as predicted by the log-linear function.

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