Exxon Valdez Oil Spill
Restoration Project Final Report

Nearshore Synthesis: Sea Otters and Sea Ducks - Modeling Amendment

Restoration Project 10100808
Final Report

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<u>Study History</u>: Sea otters suffered heavy losses from the direct effects of the *Exxon Valdez* oil spill (EVOS), with an estimated several thousand animals dying within a few months of the spill. Subsequently, based on various post-spill studies, the potential for long-term chronic effects on sea otters and other nearshore species became evident. For sea otters, population models have provided one approach to evaluating chronic injury.

Initially, Monson et al. (2000) used simple population models fit to the age distributions of beach cast sea otters to examine post-spill survival rates. This analysis suggested that through 1998, survival rates in the western Prince William Sound (PWS) population had generally declined since the EVOS and that these declines were stratified by age and time since the spill. In more recent efforts, the population models were updated by using the age distribution and survey data through 2005 in conjunction with time-varying *source-sink* population models to estimate the number of sea otters at risk and potentially lost due to chronic effects from the spill. With the *source-sink* model dynamics, a portion of the western PWS population is constrained to have a stable or declining population trajectory (the "*sink*" population, which is that part of the population with deleterious oil spill effects and declining numbers), and the remaining western PWS population is considered to be the "*source*".

In the more recent modeling work (Monson 2009), the most supportable models suggest continued depression of survival rates for the *sink* population, with numbers stable from 1990 to 2005 at approximately 350 individuals. Total chronic loss estimates include nearly 600 animals attributable to direct mortality with another 400 lost from reduced reproductive potential. However, there also were reasonably supportable models that indicate the *sink* population has declined through time with initially over 600 individuals at risk, but dropping below 100 individuals by 1995 and below 10 by 2001. Model-averaged predictions also indicate the *source* population would be growing at ~16% per year if not for loss of emigrants to the *sink* population, and the *sink* population would be declining at ~14% per year if not for the addition of immigrants from the *source*.

We undertook the current work to incorporate 4 additional years of data into updated models. Ages-at-death (based on recovery of otter carcasses), and ages of live animals (based on data from captured otters), are available for 2006-2008, and aerial survey data of population abundance for 2007-2009. Further, the aerial survey results from 2007-2009 indicate that sea otter abundance in the most heavily oiled areas of western PWS is now increasing, which is a distinct change from previous years. We reran the population models to determine the effects of incorporating the most recent years of data (2006-2009); to see if the sea otter survival rate is returning to a prespill pattern, and to elucidate the factors related to the *sink* and *source* populations that would explain the recent increase in otter numbers.

Abstract: Over twenty years ago, the *Exxon Valdez* oil tanker spilled 42 million L of crude oil into the waters of Prince William Sound, Alaska. At the time of the spill, the sea otter (*Enhydra lutris*) population inhabiting the spill area suffered substantial acute injuries and loss. Subsequent research has resulted in one of the best-studied species responses to an oil spill in history. However, the question remains – is the spill still influencing the Prince William Sound sea otter population? Here we fit time-varying population models to data for the sea otter population of western Prince William Sound, Alaska, to quantify the duration and extent of mortality effects from the spill. We hypothesize that the patchy nature of residual oil left in the environment has created a *source-sink* population dynamic. We fit models using the age distributions of both living and dying animals, and estimates of sea otter population size to predict the number of sea otters in the hypothesized *sink* population and the number lost to this *sink* due to chronic exposure to residual oil. Our results suggest, the *sink* population has remained at approximately 800 individuals (95% CI 635 - 840) between 1990 and 2009, during which time prime-age survival remained 2-6% below prespill levels. This reduced survival led to chronic losses of ~500 to 900 animals over the past two decades, which is similar in magnitude to the number of sea otter deaths documented in Prince William Sound during the acute phase of the spill. However, the unaffected *source* population appears to be counterbalancing these losses, with the model indicating the sea otter population increased from ~ 2000 individuals in 1990 to nearly 3000 in 2009. The most optimistic interpretation of our results suggesting mortality effects dissipated between 2005 and 2007. Our results suggest that residual oil can continue to affect wildlife populations on time scales much longer than previously believed, and that cumulative chronic effects can be as significant as acute effects. Further, *source-sink* population dynamics represent a plausible explanation for the slow recovery observed in the spill-affected western Prince William Sound sea otter population.

Key Words: Prince William Sound Alaska, USA; sea otter; *Enhydra lutris*; oil spills; mortality; *source-sink* models; AIC; information theoretic; likelihood; ecological risk assessment.

Project Data: Data will be kept in digital format (MS Excel) at the USGS Alaska Science Center, Anchorage, Alaska.

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Could residual oil from the *Exxon Valdez* spill create a long-term population "*sink*" for sea otters in Alaska?

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Abstract. Over twenty years ago, the *Exxon Valdez* oil tanker spilled 42 million L of crude oil into the waters of Prince William Sound, Alaska. At the time of the spill, the sea otter (*Enhydra lutris*) population inhabiting the spill area suffered substantial acute injuries and loss. Subsequent research has resulted in one of the best-studied species responses to an oil spill in history. However, the question remains – is the spill still influencing the Prince William Sound sea otter population? Here we fit time-varying population models to data for the sea otter population of western Prince William Sound, Alaska, to quantify the duration and extent of mortality effects from the spill. We hypothesize that the patchy nature of residual oil left in the environment has created a *source*-*sink* population dynamic. We fit models using the age distributions of both living and dying animals, and estimates of sea otter population size to predict the number of sea otters in the hypothesized *sink* population and the number lost to this *sink* due to chronic exposure to residual oil. Our results suggest, the *sink* population has remained at approximately 800 individuals (95% CI 635 - 840) between 1990 and 2009, during which time prime-age survival remained 2-6% below prespill levels. This reduced survival led to chronic losses of ~500 to 900 animals over the past two decades, which is similar in magnitude to the number of sea otter deaths documented in Prince William Sound during the acute phase of the spill. However, the unaffected *source* population appears to be counterbalancing these losses, with the model indicating the sea otter population increased from ~ 2000 individuals in 1990 to nearly 3000 in 2009. The most optimistic interpretation of our results suggesting mortality effects dissipated between 2005 and 2007. Our results suggest that residual oil can continue to affect wildlife populations on time scales much longer than previously believed, and that cumulative chronic effects can be as significant as acute effects.

Further, *source-sink* population dynamics represent a plausible explanation for the slow recovery observed in the spill-affected western Prince William Sound sea otter population.

Key words: Prince William Sound Alaska, USA; sea otter; Enhydra lutris; oil spills; mortality; source-sink models; AIC; information theoretic; likelihood; ecological risk assessment.

INTRODUCTION

On 24 March 1989, the tanker vessel *Exxon Valdez* ran aground on Bligh Reef in northeastern Prince William Sound, Alaska, spilling an estimated 42 million L of Prudhoe Bay crude oil (Spies et al. 1996). At that time, this spill was the largest recorded accidental release of oil into U.S. waters. Oil spread by current and winds in a southwesterly direction, leaving a heavy layer on numerous beaches within western PWS (WPWS) before exiting Montague Strait and other passages at the south-west corner of the Sound (Fig. 1). Islands in the central portion of WPWS were in the direct path of the moving oil and not far from the source, making contamination of these islands particularly heavy. The Knight Island Complex (Fig. 1) included some of the heaviest oiled habitat in WPWS. Oil eventually covered over 26,000 km^2 of water in WPWS and the Gulf of Alaska and coated over 1,900 km of coastline (Morris and Loughlin 1994, Spies et al. 1996).

At the time of the *Exxon Valdez* oil spill (*EVOS*), toxicological studies generally examined immediate, acute effects on wildlife populations. In the case of the *EVOS*, acute effects were dramatic, and spill response personnel recovered thousands of dead or injured birds and mammals in the first few months following the spill (Piatt et al. 1990, Garrott et al. 1993). One of the more severely affected inhabitants of WPWS included sea otters (*Enhydra lutris*), which are a species highly susceptible to oil related injuries and death (Costa and Kooyman 1982, Siniff et al. 1982, Williams et al. 1988). At the time of the spill, sea otters suffered lung, liver and kidney damage due to acute oil exposure via inhalation, consumption, and external contact (Lipscomb et al. 1993, Lipscomb et al. 1994, Rebar et al. 1995). By September 1989, nearly 1,000 dead otters had been recovered in the spill area (Ballachey et al. 1994), with total immediate mortality due to the spill potentially higher, but difficult to quantify (Garrott et al. 1993, DeGange et al. 1994, Loughlin et al. 1996, Garshelis 1997).

After the spill, initial studies focused on damage assessment, followed by a series of longer-term studies designed to assess the recovery status of the WPWS ecosystem as a whole (Bodkin et al. 2002, Esler et al. 2002, Golet et al. 2002, Bowyer et al. 2003). These studies led to the recognition that relatively unweathered and toxic residual hydrocarbons remained in the environment long after the spill (Short et al. 2004, Short et al. 2006, Short et al. 2007, Li and Boufadel 2010). Sea otters and other nearhsore benthic-feeding organisms forage in intertidal soft sediment habitats where reservoirs of oil contamination remain (Wolfe et al. 1994, Short and Bobcock 1996, Hayes and Michel 1999, Short et al. 2004, Short et al. 2006, Short et al. 2007). This creates the potential for continued exposure to hydrocarbons while digging for prey and ingestion of oil while grooming and eating contaminated infaunal and epifaunal prey. Peterson et al. (2003) summarized numerous studies that concluded that long-term exposure has resulted in effects to benthic feeding predators including sea otters (Esler et al 2000, Fukuyama et al. 2000, Trust et al. 2000, Dean et al. 2002, Bodkin et al. 2002, Esler et al. 2002, Golet et al. 2002, Jewett et al. 2002, Peterson and Holland-Bartels 2002). Negative survival effects on the sea otter population are consequential because their foraging activities can have profound effects on nearshore community structure (Estes and Palmisano 1974, Estes and Duggins 1995, Estes et al. 1998, Springer et al. 2003).

Monson et al. (2000a) quantified the long-term survival effects of the *EVOS* on sea otters in WPWS, using population models fit to the age distributions of beach-cast sea otter carcasses collected each spring. They found that from 1989 to 1998, survival rates in the WPWS population had declined, and that the magnitude of the decline depended on the age-class of animals and the time since the spill. The strongest patterns included reduced survival of younger age classes and normal survival of older adults within the first three years following the spill, and improving survival of younger age classes (< 9 yrs) and decreasing survival for older animals (> 9 yrs) over the first decade following the spill (Fig. 2a and 2b). Negative survival effects were not limited to animals alive at the time of the spill (i.e. individuals that potentially survived acute exposure) suggesting that chronic exposure to residual contaminants in the environment was not trivial. Other evidence that these patterns of survival were caused by lingering oil include low juvenile survival rates of marked otters following the spill (Monnett and Rotterman 1995, Ballachey et al. 2003), and the discovery in other nearshore species of elevated biomarker activity associated with hydrocarbon exposure (Esler et al. 2002, Golet et al. 2002, Jewett et al. 2002, Boyer et al. 2003, Esler et al. 2010, Ricca et al. 2010).

Monson et al. (2000a) assumed mortality was spatially homogeneous affecting the entire WPWS sea otter population, and that changes in survival rates through time were monotonic and could not return to “normal” any time after the spill. These assumptions may not be appropriate given the observed patterns of population change (Fig. 2a and 2b), and the locations of residual oil. In reality, residual oil was limited to geographically scattered locations within only a few areas of WPWS (Wolfe et al. 1994, Short and Bobcock 1996, Hayes and Michel 1999, Short et al. 2004, Short et al. 2006, Short et al. 2007), and thus the entire WPWS sea otter population could not be equally exposed to residual contaminants.

Support for heterogeneous exposure levels and mortality effects include diverging population trends between heavily oiled areas, and areas with little or no residual oil. For example, during post spill damage assessment studies, the Knight Island complex (Fig. 1) was chosen as a study site because it received heavy oiling in 1989, and the area continued to hold considerable amounts of oil on scattered beaches 20 years after the spill (Short et al. 2007). Acute sea otter mortality at the time of the spill approached 90% in this area (Bodkin et al. 1993), and consistent with the most supported predictions of Monson et al. (2000a), sea otter numbers remained reduced in this area through at least 2005 (Bodkin et al. 2002, USGS unpublished data). The reduced sea otter densities in this area allowed prey populations to increase and by the mid-1990’s, prey biomass per otter was approximately four times higher in the northern Knight Island complex than in a non-affected area where the population had been increasing since the spill (Dean et al. 2002). Thus, the lack of growth in the Knight Island complex sea otter population was not due to limited food resources, and instead was potentially due to the demographic effects suggested by Monson et al. (2000a). In contrast, over the two decades since the spill, sea otter numbers increased in WPWS as a whole (Fig. 2) and within unoiled areas in particular even while prey resources were less plentiful than in the Knight Island complex (Dean et al. 2002, Bodkin et al. 2002).

Monson et al. (2000a) concluded that the diverging population trends of otters in oiled and unoiled areas occurred because chronic oil effects influenced only the subset of the population residing in the most heavily oiled areas. Clearly, the WPWS population was recovering; however, presumably, this oil-affected sub-population was acting as a population *sink* (Pulliam 1988, Pulliam and Danielson 1991, Dunning et al. 1992) where chronic exposure continued to remove some unknown number of individuals from local oil affected areas, and thus constraining recovery of the larger WPWS population to some unknown extent.

Here we explicitly look for long-term heterogeneous effects of the 1989 *EVOS* in Prince William Sound by modeling the WPWS sea otter population as two sub-populations in a *source-sink* frame work, and explore the hypothesis that the spill created oil-affected "*sink*" and non-affected "*source*" sub-populations. Similar to Monson et al. (2000a), our analyses utilize age-at-death data acquired from beach cast carcasses. In addition, we incorporate sea otter population survey data for WPWS and the age distributions of live captured animals residing in both oiled and unoiled areas (see Bodkin et al. 2002 for survey and capture details). We use time-varying, age-specific demographic models to predict changes in sea otter survival rates in the hypothesized source and sink sub-populations. We fit these models by iteratively changing survival rates in both sub-populations away from prespill, baseline values (Udevitz et al. 1996, Udevitz et al. 1998) until the predicted age-distributions of both living and dead animals and trends in population numbers best matches observed values. The "best fit" model parameter values are determined by calculating negative log-likelihood values based on the difference between the observed and predicted values (Burnham and Anderson 2002). These methods allow us to identify the most likely ways in which the spill has influenced the demography of the hypothesized sink population (Doak and Morris 1999, Tinker et al. 2006), thus providing additional insight into the magnitude and persistence of potential chronic effects of the *EVOS* on WPWS sea otters. Our goals included 1) estimating the size of the hypothesized sink population relative to the total WPWS population, 2) estimating the number of animals lost to the sink population since the *EVOS*, and 3) explicitly looking for a point in time when survival rates in the sink subpopulation may have returned to normal, or at least changed in some way relative to the mortality patterns demonstrated immediately after the spill. Our methods also illustrate the flexibility and complexity that a source-sink model structure provides to simple population models, and their utility in assessments of environmental impacts on populations subject to non-uniformly distributed stressors.

METHODS

Observations

We collected three types of empirical data relating to the status of the Prince William Sound sea otter population: (1) annual carcass collections in oiled areas to determine the age structure of winter mortality, (2) nearly annual aerial surveys to estimate population size of the WPWS population as a whole and an oiled and unoiled subarea, and (3) nearly annual captures of live sea otters in both an oiled and unoiled area to monitor population health and indices of exposure from which we also estimated the age structure of the living populations. Carcass collections from 1976 through 1998 have been described (Monson et al. 2000a), and similar collections continued through 2008. Green Island (Fig. 1) was the site of prespill collections, and we continued to collect carcasses there through 2008. In 1990 and 1991, carcasses were collected opportunistically by beach clean-up and monitoring crews throughout the spill area. Beginning in 1996, in addition to the Green Island collections, we systematically collected carcasses on or near shorelines throughout WPWS that received heavy oiling in 1989, including areas where residual oil was found through at least 2008 (Fig. 1, Short et al. 2004, Short et al. 2006, USGS unpubl. data). Because sex of dead animals often was not determined, we combined the sexes when examining age-at-death distributions. We collected the skull when present, and we removed a tooth (preferentially a premolar) for age analysis, although we identified pups by open skull sutures and deciduous teeth. Longitudinal sections of each tooth were decalcified for cementum annuli readings, generally providing age estimates ±1 year (Bodkin et al. 1997). Matson's Laboratory (Box 308, Milltown, MT 59851) sectioned and aged all teeth.

We estimated the total population size in WPWS from aerial surveys conducted each year from 1993 (the first year they were conducted) to 2009 (Bodkin and Udevitz 1999, Bodkin et al. 2002). We obtained age-distribution information for the living population by capturing animals at both an unoiled site on the northwest coast of Montague Island and within the oiled Knight Island complex (Fig. 1). We captured animals each summer from 1996-1998 and then again from 2001-2008. Capture and handling methods included tangle nets and diver-operated traps (Ames et al. 1983). Sea otters were sedated (Monson et al. 2001), and body measurements taken and blood drawn to measure body condition and health of the individuals. For each independent otter, we extracted a premolar for age determination (Bodkin et al. 1997). On the rare occasions when a tooth age was not determined (tooth not available or broken), we used an estimated age at capture, based on tooth wear, morphometrics, and coloration. Following reversal from anesthesia, we released sea otters in the same vicinity as captured.

Model Construction

We constructed source-sink population models using two sub-population matrices (i.e., a source and a sink sub-population) connected by emigration/immigration. Within each sub-population, survival rates varied independently via their own time-varying age- and sex-structured demographic models. Table 1 shows the number of parameters and functional form of each component of the population models. Table 2 describes how the various model components were put together to form the four categories of model architecture examined in this manuscript. We initialized each model using baseline age and sex-specific survival estimates from smoothed maximum likelihood analyses of ages-at-death based on prespill carcasses collections (Udevitz et al. 1996, Udevitz et al. 1998). Baseline survival rates were then modified in postspill years using the same functional forms described by Monson et al. (2000a) (i.e., logistic and modified logistic) plus the complementary log-log form (cloglog), which has similar but more flexible structure than the logistic function (Table 1). Based on the observed population growth in unoiled portions of WPWS, we assumed the spill did not negatively affect source population survival rates, thus source population survival rates were only modeled using the modified logistic function, which allows survival rates ≥ prespill values and lambda (λ) ≥ 1. In contrast, the sink population had sufficient resources to fuel population growth but did not increase (Dean et al 2002), so we assumed that the mortality effects of the spill would be negative, and changes to age-specific survival must be ≤ prespill values. The logistic and cloglog functional forms only allow modifications that are ≤ baseline rates, so we modeled survival in the sink population with one of these two functional forms (i.e., potential $\lambda \leq 1$). This model structure (potential for $\lambda \geq 1$ in the source population and $\lambda \leq 1$ in the sink population) allows this potential dichotomy between the growth potential in the source population with the negative survival effects expected in the sink population.

We also modeled movement of individuals to connect the source and sink populations, but did so in a simple way, commensurate with the data available to fit the model. In the model, the sink population is constrained to a constant size in a given time step, $j = 1$ year. If changes to the sink population survival rates produced a population decline over the time-step, at the end of the time-step "immigrants" were moved from the source population into the sink population to counter the loss. Young animals and particularly males are the most likely to emigrate (Kenyon 1969, Garshelis et al. 1984, Riedman and Estes 1990), thus immigrants were drawn from the youngest age classes of the source population (50% 1 yr-olds and 50% 2 yr-olds) with most drawn from the male pool of these age-classes (75% male and 25% female). We define direct chronic losses as the number of immigrants required to maintain the sink population within time-steps. However, if survival rate changes in the sink population produced population growth within a time-step, the model allowed emigrants to leave the sink population for the source population and reduce the estimate of chronic loss.

We explicitly examined the possibility that negative spill effects were dissipating through time. To do this, we added features allowing sink population survival rates to return to prespill "baseline" values. We hypothesized that a return to prespill survival rates could happen in two ways. First, age-specific survival rates in the sink population could begin to improve at some point in time. To accommodate this, we created models that allowed a secondary change in sink population survival rates at some year postspill (j_{shift}) by using two unlinked sink population survival functions each fit independently before and after year j_{shift}. We looked for the most likely year when sink population survival trends may have changed by examining j_{shift} over the range from 5 to 18 years postspill (Table 1). Secondly, if the sink population itself simply declined through time until the number of negatively affected individuals became small (e.g., because oil contamination declined with time through weathering processes), then only the source population survival rates would be in effect and these presumably would be ≥ prespill values. This possibility is modeled by allowing the sink population size to begin at a new start value at the beginning of each time-step, although within each time-step size is still required to remain stationary (i.e., the source population still provides emigrants at the end of each time-step to bring the sink population size back to its start value). From one time-step to the next, the rate of the sink population decline was controlled by a four parameter sigmoid function (Table 1).

The most complex source-sink models (Table 2; models 3d and 4d) allowed age (*i*), time (*j*), and age*time specific changes in survival in both the source population ($S_{i,j\text{-}source}$ [intercept + 3 parameters = 4 parameters]) and in the sink population before and after j_{shift} ($S_{i,j\text{-}sink1}$ [4 parameters] + $S_{i,j\text{-}sink2}$ [4 parameters] + Y [1 parameter] = 9 parameters), and allow the sink population size to change through time (N_j [4 parameters]) for a total of 17 parameters. In addition, all models used one additional parameter to estimate the most likely 1990 WPWS population size (N_0). A large number of less complex source-sink models could be formed within this framework by leaving out various interactions and main effects, but we only fit the subset of 12 possible model forms, which reflected our judgment of the most biologically plausible alternate descriptions of the population (Table 2). Models numbered 1 and 2 modify sink population survival rate with one set of parameter values while models numbered 3 and 4 use a second set of parameter values to produce a secondary trend in sink population survival rates after the year j_{shift}. Models with “a” or “c” subscripts held the sink population constant over time, while “b” and “d” models allowed it to change. Models with “a” or “b” subscripts exclude the age*time interactions in all survival functions while “c” and “d” models include the interaction in all survival functions. For example, the simplest models (Table 2; models 1a and 2a) left out the age*time interactions in both source and sink population survival functions [-2 parameters], did not have a secondary sink population survival function or j_{shift} parameter [-5 parameters], and kept the sink population stationary over time [-3 parameters], for a total of 18 - 10 = 8 parameters. Models 1c and 2c added the age*time interactions [+2 parameters], and progressively more complex models utilized the functions that modified sink population size and post-j_{shift} sink population survival rates (Table 2).

Model Fitting

We fit source-sink models by comparing their predictions to four empirical data sets: 1) the ages-at-death of otters dying in the sink population (based on carcass collections from within oiled areas of WPWS), 2) the size of the WPWS sea otter population each year since the *EVOS* (based on aerial survey data), 3) the age distribution of the living females captured within an oil-affected area and 4) the age distribution of the living females captured within an unoiled area of WPWS. We calculated the minimum negative log-likelihood (-*L*) values for each data set, and took the sum as the total -*L* estimate for each model (Hilborn and Mangel 1997, Hobbs and Hilborn 2006, Tinker et al. 2006). Relative negative log-likelihoods from each year’s age-at-death distributions were estimated using multinomial probabilities for observer error (Hilborn and Mangel 1997, Doak and Morris 1999), and the sum of yearly -*L* values became -*L*1.

$$-L1 = \sum_{j=1}^{20}\sum_{i=1}^{20} N_{i,j} * \log P_{i,j} \tag{1}$$

where $N_{i,j}$ is the number of carcasses of age i collected in year j and $P_{i,j}$ is the relative frequency of carcasses of age i predicted to be produced in year j by a particular model. Age 0 animals (pups) were removed when calculating relative frequencies and not used in the calculation of $-L1$ as they tend to be underrepresented in carcass collections because their small size allows them to be easily removed by scavengers (Bodkin and Jameson 1991).

The population survey-based $-L$ ($-L2$) is the sum of the survey $-L$s:

$$-L2 = \sum_{j=1}^{20} \log \sigma_j + \frac{1}{2}\log 2\pi + \frac{(N_{obs,j} - N_{exp,j})^2}{2(\sigma^2_j)} \tag{2}$$

where σ^2_j is the estimated survey variance from the WPWS survey data in year j, $N_{obs,j}$ is the point estimate for the WPWS population in year j, and $N_{exp,j}$ is the population size predicted with a particular model in year j (Hilborn and Mangel 1997).

Negative log-likelihoods from each year's living female age distributions in both the sink and source population ($-L3$ and $-L4$ respectively) were estimated similar to the age-at-death $-L$ using multinomial probabilities for observer error.

$$-L3 \; and \; -L4 = \sum_{j=1}^{20}\sum_{i=1}^{20} N_{i,j} * \log P_{i,j} \tag{3}$$

where $N_{i,j}$ is the number of females of age i captured in year j from either the oiled ($-L3$) or unoiled ($-L4$) area and $P_{i,j}$ is the relative frequency of females of age i predicted to be living in year j in either the oiled ($-L3$) or unoiled ($-L4$) area by a particular model. We removed age 0 otters (pups) when calculating relative frequencies and did not use them in the calculation of $-L3$

or -*L*4 because they are again expected to be underrepresented, as females with small pups tended to avoid net capture, and were sometimes avoided during diving captures.

For each model, we solved for the parameter values that minimize the total negative log-likelihood ($-L_{\text{total}} = -L1 + -L2 + -L3 + -L4$), and then used Akaike's Information Criterion (AIC), $\text{delta}_{\text{AIC}}$ and Akaike weights (w_i) for model selection (Burnham and Anderson 2002, Johnson and Omland 2004). We determined one-dimensional 95% likelihood profile confidence intervals for each parameter in the model by holding all but one parameter at a time at their "best" estimated value, and then varying the parameter of interest to arrive at a delta $-L_{\text{total}}$ of +1.92 (Burnham and Anderson 2002). However, several predictions of the model (e.g., the chronic loss estimate and source and sink population lambda values) are based on the interactions of multiple parameters in the model and their values are less certain. We looked at uncertainty in these predictions by choosing random parameter values for each parameter in the model, and determining the $-L_{\text{total}}$ value and resulting predictions using these random parameter values. We repeated this procedure 10,000 times and likelihood profile estimates for each prediction could then be determined (Burnham and Anderson 2002). We limited the range of randomly selected values to within the 95% likelihood profile confidence intervals for each parameter to increase the number of outcomes within a reasonably close $-L_{\text{total}}$ to the original best estimate (i.e., delta $-L_{\text{total}} \leq 5$).

We estimated maximum likelihood parameter values for each model using algorithms that explored the entire constrained parameter space. Minimizations were performed in MATLAB (The Mathworks, Inc., Natick, Massachusetts) using the optimization toolbox TOMLAB (Holmström 1999). We first used the ''glcfast'' function, with the results of this routine used as start values for the “snopt” function, a sequential quadratic programming algorithm for large-scale linear or non-linear optimizations (Gill et al. 1984, Gill et al. 2005). We performed iterative searches using a large number of randomly selected starting points and parameter bounds values to ensure that global minima were identified (Holmström 1999). Fitting these complex, non-linear models to multiple data sets added challenges to finding the “best” parameter estimates, and required use of constraints on some parameters and fitting penalties (Reklaitis et al. 1983) to enforce those constraints, which eliminate the possibility of converging on mathematically possible but biologically unreasonable parameter values. For example, we did not use 0 age animals (dependent pups) in the age-at-death distributions so pup survival could vary between 0 and 1 without affecting the -*L* values. The modifier function used to control source population survival rates allowed changes within this entire range. However, even though mathematically possible, a survival rate of 0 or 1 is not biologically reasonable. Thus, we put limits to source population survival rates and when these limits were exceeded, a penalty of 1was added to the -*L* value. The limits for 0 age survival were determined from empirical estimates obtained from both stable, equilibrium populations (lower limit) and growing, non-food limited populations (upper limit) (Monson et al. 1995, Monson et al. 2000b). In addition, we enforced a sink population change in models that allowed it to avoid having the fitting algorithm settle on a small, insignificant population change biologically indistinguishable from models that held the sink population constant. In this case, if the sink population size did not decline by at least 100 over 20 years we added 10 to the -*L* value, and if it did not decline by at least 250 an additional penalty was added, which was inversely proportional to the size of the change (i.e. the greater the change, the less the penalty). This created a constrained parameter space within which reasonable changes to population survival rates and population sizes could vary.

After identifying the best model forms and most likely parameter values, we used Kolmogorov-Smirnov (K-S) tests (Sokal and Rohlf 1995) to determine the goodness-of-fit between the predicted and observed age-at-death distributions summed over two postspill periods (before and after j_{shift}). We assessed the predicted population trends graphically by plotting the predicted and observed values.

Model application

We had three goals when constructing these models. The first was to estimate the size of the hypothesized sink population, which was an explicit parameter in the model. The second was to estimate chronic losses that have occurred in the sink population since the *EVOS*. We assumed the number of immigrants from the source population required to maintain the sink population each year represented direct losses to the sink population, with the sum of these immigrants over all years equaling total chronic loss. In addition, at each time step we calculated λ for each sub-population given the modeled survival rates based on the dominant eigenvalue of each population matrix. Lambda values changed each year as survival rates changed through time, however we only contrast λ values for each sub population at the end of 2009, assuming the estimated survival rates at that time persist into the future. After finding the best-fit parameter values for each model, we applied them to each population, but “disconnected” them by removing the emigration/immigration link, allowing the source population to grow as if the direct losses had not occurred. We then interpreted the difference in the size of the source population in 2009 between linked and unlinked models as a second estimate of total chronic loss that also includes the reproductive potential of the direct losses. We subtracted the direct losses estimated by the linked models with this second estimate of chronic loss found by comparing linked and unlinked models to estimate the magnitude of lost reproductive potential that occurred due to direct losses. Our third goal was to look for an “end-point” when spill effects may have decreased to negligible levels. We looked at this in two ways: 1) is there evidence that survival rates are returning to normal in the sink population? And/or 2) is the size of sink population declining through time?

We used model-averaging methods to arrive at predictions of key parameters over all models fit (Burnham and Anderson 2002). However, the overwhelming support for a single model rendered these results nearly identical to those for the best model, and we concentrate on these results in our presentation.

RESULTS

Observations

We recovered 157 sea otter carcasses during prespill collections from 1976 to 1985, and another 58 carcasses in 1989 that were deemed prespill mortalities (total = 215). From 1990 to 1998, we recovered 245 carcasses, which were the basis for data used in Monson et al. (2000a). From 1999 to 2008, we recovered another 285 carcasses. The proportion of prime-age (2 - 8 yr-old) animals in the 1999-2008 collection was high compared to prespill collections (0.39 vs. 0.20) and was higher than the proportion observed in the 1990-1998 collection (0.31; Fig. 3).

Most importantly, the difference between the prespill and 1999 to 2008 age distributions do not suggest a return to prespill demographic rates in the second decade following the spill.

We conducted aerial sea otter surveys nearly annually between 1993 and 2009. Growth in the WPWS sea otter population began sometime between 1997 and 2003, with potentially the most rapid increase apparent in 2008 and 2009 (Fig. 2). In contrast, the number of animals residing in the oiled northern Knight Island study area was stable (but below prespill numbers) until 2001 when it declined until at least 2005, with no population growth evident until 2007 (Bodkin et al 2002, USGS unpublished data). Population size in the Knight Island area averaged approximately 65 animals over the 20 postspill years, however, we assume this area represents the population trend in the hypothesized sink population, but not the size of the entire sink population, and we did not use these surveys in $-L_{\text{total}}$ calculations.

We captured 158 otters in the oiled northern Knight Island complex between 1996 and 2008. Of these, we recaptured 42 individuals 1 to 3 times for a total or 60 recaptures. We captured 201 otters in the unoiled Montague Island area during this same time. Of these, we recaptured six individuals just one time. For the purposes of determining the age-distribution of living animals each year, we assumed recaptured individuals resided in their respective areas for all intervening years between initial capture and their last recapture.

Source-Sink Models

Source-sink model 4a produced the best fit (AIC = 4411.0, $w_i = 0.996$) with very little support for any other model (Table 3). The model-averaged results are essentially the same as for model 4a because of the overwhelming support for this model (Table 4). Model 4a suggests the most likely WPWS population size in the spring of 1990 one year after the *EVOS* was ~2000 animals (Table 4), which is in close agreement to the empirical estimates that averaged 1991 (± 606) otters living in the oiled areas of WPWS in the summer of 1990 (Burn 1994), and covers most of our WPWS survey area. More importantly, the model suggests a stable sink population size of ~800 animals (Table 4, Fig. 4). The model further suggests juvenile (0 to 2 yrs old) survival rates within the sink population were severely reduced in 1990 but improved to near prespill levels by 1994, while prime-age animals (with the exception of 2 yr olds) initially had near normal survival rates, from 1990 to 1993, after which their survival rates declined and remained 2-9% below prespill values for the next 20 years (Fig. 4). Under the scenario portrayed by this model, the sink population is predicted to experience an average of 110 (range 90 to 120) mortalities per year (excluding pup mortalities), with 35 to 45 of these deaths considered "premature" by prespill baseline survival rate standards (i.e. they would not have occurred had prespill survival rates been applied to the sink population). These premature losses result in a cumulative loss estimate of ~735 animals since the spring of 1990 (Table 4). We collected an average of 20 (range 6 to 47) non-pup carcasses per year in spill affected areas (i.e., ~10%-40% of available). As the model architecture moves mostly males (75% of immigrants) into the sink population to replace these losses, the lost reproductive potential in the source population is minimal and estimated to be < 50 individuals over the same 20-year period (Table 4). If in reality a higher proportion of female immigrants replaced these losses, the lost reproductive potential of the source population would be higher. In contrast, the model suggests that survival rates in the source population were above prespill levels for juveniles and essentially unchanged for prime-age animals (the most demographically important age group) throughout the 20 years post spill (Fig. 4). This dichotomy in prime-age survival rates between the source and sink population results in a source population that would be growing by 4% per year in 2009 when, at the same time, the sink population would be declining by 5% (Table 4). Clearly, the growth potential of the source population was more than enough to counter the losses in the sink population such that by 2009, the model predicts the entire WPWS should have grown by ~1000 animals to an estimated ~3000 individuals. This prediction is below the actual 2009 empirical WPWS population estimate of nearly 4000 otters, although it is within the survey confidence intervals (Fig. 4).

The spring 1990 WPWS population size was an explicit parameter (N_0) in the model and thus it is straightforward to estimate a one-dimensional 95% likelihood profile confidence interval around this value (1888 to 2167 animals; Table 5). The sink population size is also an explicit parameter value (CI = 635 to 839; Table 5); however, this parameter has a fairly large effect on predictions of chronic loss, which is influenced by the results of nearly all the other parameter values. Using the results from 10,000 iterations of randomly selected parameter values, the Akaike weighted average WPWS population estimate in 1990 was 2017, the sink population was 792 individuals and the weighted average premature loss estimate from 1990 to 2009 was 676 otters. In Fig. 5a, we plotted the predicted sink population size against the corresponding model averaged chronic loss estimate for the 10,000 iterations of randomly selected parameter values. This plot shows the positive correlation between predicted sink population size and the corresponding predicted chronic loss estimate. Fig. 5b illustrates the confidence intervals around the 2009 λ estimates for the source and sink populations based on the 10,000 iterations of randomly selected parameter values, and indicates a higher degree of certainty regarding the predicted population trajectory within each subpopulation. Fig. 5b also indicates several iterations produced $-L_{\text{total}}$ values slightly lower than the “best” estimate from the fitting routines, indicating there are combinations of parameter values that would produce a slightly better fit than those presented in Table 5. However, we did not keep track of the randomly chosen values, and they would have been within the 95% confidence intervals of the original parameter estimates and would not have changed the quantitative or qualitative results significantly.

Goodness-of-fit

The population trajectories predicted by the source-sink models match the observed population trend in WPWS with the exception that the abundance estimates from surveys indicate population growth in WPWS may have accelerated to higher than predicted levels in 2008 and 2009 (Fig. 4). The predicted sink population age-at-death distributions were not significantly different from the observed distributions for either the 1990-1993 or the 1994-2008 periods (Fig. 6, K-S test, $D \leq 0.10$, $P > 0.05$). It may be that some portion of the carcasses in our collections originated from the source population. If this is true, the predicted age distribution from the combined mortalities of both the source and sink populations should match our observed distribution. However, the combined distribution predicted for the 1994-2008 period (weighted by predicted total number of deaths in each subpopulation) differed significantly from the observed distribution (K-S test, $D > 0.09$, $P < 0.05$) suggesting we did not collect significant numbers of “source” population carcasses.

DISCUSSION

Monson et al. (2000a) identified significant long-term mortality effects within the spill affected WPWS sea otter population. The magnitude of these mortality effects would have reduced the WPWS sea otter population to a fraction of its original number within 5 years post spill had they been affecting the entire population. Instead, the population as a whole demonstrated slow but steady growth, while a subpopulation of otters inhabiting one of the most heavily oiled areas remained at reduced numbers for at least 15 years following the spill despite having ample prey resources for population growth. These conflicting outcomes suggested a portion of the WPWS population was acting as a sink (Pulliam 1988, Pulliam and Danielson 1991). Population sinks can be created by a variety of anthropogenic mechanisms including habitat fragmentation or restructuring (Naranjo and Bodmer, 2007, Smith and Person 2007, Feeley and Terborgh 2008, Lees and Peres 2008, Hawlena et al. 2010, Heinrichs et al. 2010, Schaub et al. 2010), and these sinks can represent a significant threat to population persistence depending upon the life-history characteristics of the species (Lees and Peres 2008). Here we have explored the possibility that habitat degradation created by residual contaminants in the environment created a population sink for sea otters in WPWS. The distribution of residual oil in WPWS is patchy, but where protected from the "cleaning" action of storms, subsurface oil has persisted in a concentrated, relatively unweathered state for at least 20 years (Irvine et al. 1999, Short et al. 2004, Irvine et al. 2006, Short et al. 2006, Short et al. 2007, Short et al. 2008). Because of this patchy distribution, it is reasonable to expect that oil exposure levels for nearshore predators such as the sea otter will be heterogeneous as oiled habitats will not be equally available to all individuals in the population, nor will exposure necessarily be equal among individuals with access to oiled habitats (Estes et al. 2003, Tinker et al. 2007, Tinker et al. 2008).

Here we modeled the WPWS sea otter population as two sub-populations in a source-sink framework. The model outcomes suggest chronic exposure resulted in small reductions in prime-age survival in the sink population. The model also suggests a fairly constant number of sea otters experienced lower survival from 1990 to 2009, and this number comprised ~40% of the WPWS population in 1990 but only ~20-25% of the WPWS population in 2009 due to growth in the source population. Reductions in survival within the sink population appear to have resulted in the cumulative loss of approximately 500-900 animals since 1990, which is of a similar magnitude to the number of acute phase losses documented within WPWS at the time of the spill. Emigrants from the source population moving into and replacing these losses in the sink population would result in additional lost reproductive potential within the source population; however, if most of the emigrants were males as this model's architecture currently dictates, this effect would be minimal.

Most importantly, we found no indication from this model that mortality effects of the spill have dissipated through time, with estimates of absolute numbers of animals lost annually predicted to be nearly constant from 1994 to 2009. This finding confirms assertions that residual contamination from oil spills can affect wildlife populations far longer than previously believed (Peterson et al. 2003, Bejarano and Michel 2010), and that the magnitude of losses due to chronic effects can be as great as acute phase losses. Our most optimistic time-line for the end of oil related mortality effects comes from comparisons of the predicted and observed sea otter population sizes. The most recent sea otter survey results suggest the WPWS population may have grown more rapidly than predicted by the model starting sometime between 2006 and 2008. If true, it could be a sign that mortality effects were finally dissipating sometime between 2005 and 2007. Consistent with this interpretation, the northern Knight Island population finally appeared to experience positive population growth between 2007 and 2009 when the model indicates it should still be declining. Both the magnitude and duration of the mortality effects suggested by our model are similar to those documented in Harlequin ducks, another nearshore predator of the WPWS system (Esler and Iverson 2010, Iverson and Esler 2010).

These model outcomes are conservative in one particular way – they did not include animals lost in a “secondary mortality event” the first winter following the spill (Burn 1994). Boat-based survey data suggest a secondary spill-related mortality event occurred, with the loss of several hundred animals during the first winter following the spill. This first postspill winter mortality pulse has generally been overlooked. Garshelis and Johnson (2001) questioned the occurrence of this secondary mortality event. We suggest that while the magnitude of population decline between fall 1989 and spring 1990 is uncertain, its occurrence is plausible. These losses likely reflected those animals with relatively severe sub lethal oil exposures that were unable to withstand the stressful conditions of winter. This “delayed” mortality pulse in sea otters is perhaps similar to a delayed mortality event observed for marine iguanas (*Amblyrhychus cristatus*) on the Galapagos island of Santa Fe the year following an oil spill there (Wikelski et al. 2002). Regardless, this study considers the potential for spill-related losses after this first winter’s mortality event, which likely removed some compromised animals that had survived the initial months of the spill.

Presumably, sea otters continue to be exposed to oil primarily by digging in oiled sediments.

Sea otters occupying the Knight Island area specifically, utilized intertidal habitats for, on average, nearly 15% of their feeding dives, and at peak times in the spring, for up to 45% of feeding dives (USGS, unpublished data). This translates into an individual otter digging several thousand to over 20,000 intertidal pits each year. The population of sea otters inhabiting northern Knight Island averaged ~65 individuals over the past 20 years (USGS unpublished data), and collectively they dug an estimated 200,000 pits per year or ~4 million pits over the past two decades. Any physical disturbance to lower intertidal sediments will expose sub-surface oil and enhance microbial biodegradation, and sea otters with their physical digging of pits in the intertidal may be the most effective mitigation process that has been active continuously in the area for the last 20 plus years.

Large-scale anthropogenic contamination events like the *EVOS* will almost never affect all individuals in a population equally because long-term, chronic exposure levels will be heterogeneous. This heterogeneity stems from the likely patchy distribution of residual contaminants, and the mobility and spatial distribution of individuals of various species. Even where all individuals have equal access to contaminated habitats, exposure levels will vary with individual habitat use and prey preferences (Estes et al. 2003, Tinker et al. 2007, Tinker et al. 2008). This heterogeneity in exposure levels is an important consideration as it helps explain why detecting chronic effects, and linking them to contamination events can be so difficult. Variable exposure levels leads to variable health effects ranging from none to subclinical to clinical and even death. It is only the final two stages that direct connections are easily made between health and contaminants in the environment. However, the probability of sampling clinically sick animals in the wild is low as individual residence time within this stage is likely short. Furthermore, in remote areas, the probability of capturing sick animals or finding fresh dead animals also is extremely low. However, we can use the record left behind by the dying animals in the form of the age-distribution at death to inform demographic models. By incorporating additional data sets in the fitting process such as information on the living population age structure and population trend, we can examine more detailed and complex candidate models. Future environmental catastrophes are inevitable, as demonstrated by the “Deepwater Horizon” oilrig explosion April 20, 2010 in the Gulf of Mexico. The lessons learned from the *EVOS*, and the potential for the creation of areas that become population sinks that limit the recovery of endangered or otherwise important species, should be at the forefront of planning for research into the potential long-term effects of this or any other future wide-spread contamination event.

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Table 1. Functions used in source-sink models: Modeled survival rates ($M_{i,j}$) were found by modifying baseline sea otter survival rates ($R_{i,j}$) where i=age and j=year. The sink population survival rates were estimated by modifying baseline rates with the logistic or complementary log-log function while source population survival rates were estimated by modifying baseline rates with a modified logistic function. Models also estimated the sink population size at the beginning of each time step (N_j), which was either a constant value through time or was allowed to decline via a sigmoid function. In the most complex models, the sink population utilized a second survival function, which took effect in the year j_{shift}. All models used various combinations of these functions to form unique families of models (Table 2). At a minimum, each model uses 1) a source population survival modifier function $S_{i,j,source}$ (modified logistic function with or without $i*j$ interaction), 2) a sink population survival modifier function $S_{i,j,sink1}$ (logistic or cloglog function with or without $i*j$ interaction), 3) a sink population size modifier function $N_{sink,j}$ (constant or sigmoidal function) and 4) an intercept term that estimates WPWS population size in 1990 (N_0). The most complex models add 5) a second sink population survival modifier function $S_{i,j,sink2}$ (logistic or cloglog function with or without $i*j$ interaction) and 6) a parameter to estimate the most likely year (j_{shift}) the secondary sink population survival function should be applied.

Main effect	Functional form	link	Model calculation
1) [1]survival rates	[2]$Logit(S_{i,j}) = \theta_1 + \theta_2*i + \theta_3*j + \theta_4*(i*j)$ or [2]$Cloglog(S_{i,j}) = \theta_1 + \theta_2*i + \theta_3*j + \theta_4*(i*j)$ and [3]$Mod.\ logistic(S_{i,j}) = \theta_5 + \theta_6*i + \theta_7*j + \theta_8*(i*j)$	$\text{logit}(\alpha) = \ln[\alpha/1\text{-}\alpha]$ $\text{Cloglog}(\alpha) = \ln[-\ln(1\text{-}\alpha)]$ $\text{logit}(\alpha) = \ln[\alpha/1\text{-}\alpha]$	$M_{i,j} = R_{i,sex}*Logit(S_{i,j})$ $M_{i,j} = R_{i,sex}*cloglog(S_{i,j})$ $M_{i,j} = Logit(S_{i,j})^{(\ln(Ri,sex)/\ln(1/2))}$
2) sink population size	$y_0+\theta_9/(1 + \exp(-(j-x_0)/\theta_{10})$ or θ_9	sigmoidal decline constant	$N_j = y_0+\theta_9/(1 + \exp(-(j-x_0)/\theta_{10})$ or $N_j = \theta_9$
3) shift year	θ_{13}(range 5 - 18)	constant	$j_{\text{shift}} = 20\text{-} \theta_{13}$
4) WPWS population size (1990)	θ_{14}	constant	$N_0 = \theta_{14}$

[1] models contained two or three survival functions each; an initial sink population survival function, a source population survival function, and a subset of models utilize an additional sink population survival function, which takes effect after some point in time (j_{shift}).

[2] sink population survival rates are always modified using either the logistic or cloglog function. In a subset of models, a second survival function (θ_{15}, θ_{16}, θ_{17}, and θ_{18}) takes effect after some point in time (j_{shift}), and the same function (logistic or cloglog) is always used to modify survival rates in both time periods.

[3] source population survival rates are always modified using the modified logistic function.

Table 2. Description of source-sink (models 1 - 4) models used to examine post *EVOS* changes in sea otter survival in WPWS. Models include two population matrices connected by immigration of 1-2 yr-olds (1:2 = 50:50) of both sexes (M:F = 75:25). Models 1 and 2 modify sink population survival rates with one set of parameter values (single trend) while

models 3 and 4 use independent parameter estimates to modify sink population survival rates before and after year j_{shift} (two survival trends). Models 1 and 3 use the logistic function to modify sink population survival rates while models 2 and 4 use the cloglog function to modify sink population survival rates. The sink population is held constant in “a” and “c” models, but allowed to change at the beginning of each time-step in “b” and “d” models. Survival functions for “a” and “b” models do not include age*time interaction terms (i.e., $S_{i,j} = \theta_1 + \theta_2 * i + \theta_3 * j$) while survival functions for “c” and “d” models do include the age*time interaction (i.e., $S_{i,j} = \theta_1 + \theta_2 * i + \theta_3 * j + \theta_4 * (i * j)$).

Model number	**Survival modifier function**	**Sink pop. survival functions**	**Sink population size**	**$S_{i,j}$ includes $i*j$ interaction**	**# model parameters**
1a, 1c	*source* = mod. logistic *sink* = logistic	one	stationary	a = no, c = yes	a = 8, c = 10
1b, 1d	*source* = mod. logistic *sink* = logistic	one	sigmoid decline	b = no, d = yes	b = 11, d = 13
2a, 2c	*source* = mod. logistic *sink* = cloglog	one	stationary	a = no, c = yes	a = 8, c = 10
2b, 2d	*source* = mod. logistic *sink* = cloglog	one	sigmoid decline	b = no, d = yes	b = 11, d = 13
3a, 3c	*source* = mod. logistic *sink1* = logistic, *sink2* = logistic	two	stationary	a = no, c = yes	a = 12, c = 15
3b, 3d	*source* = mod. logistic *sink1* = logistic, *sink2* = logistic	two	sigmoid decline	b = no, d = yes	b = 15, d = 18
4a, 4c	*source* = mod. logistic *sink1* = cloglog, *sink2* = cloglog	two	stationary	a = no, c = yes	a = 12, c = 15
4b, 4d	*source* = mod. logistic *sink1* = cloglog, *sink2* = cloglog	two	sigmoid decline	b = no, d = yes	b = 15, d = 18

Table 3. Relative support for 16 source-sink models fit to $-L_{\text{total}}$ along with likelihood values for “null” model (no change to baseline survival rates) and best-fit parameter values for the logistic and modified logistic model from Monson et al. (2000a) assuming a 1990 WPWS sea otter population size of 2230.

		-L					Based on total -L		
Model	parms	total	Age-at-death	wpws survey	KNI live	MON live	AIC_i	Δ_i	w_i
“null” 2000	1	3188.5	1728.1	132.6	981.4	346.3	6379.0	+	*
logistic[1]	5	2900.5	1263.9	495.1	796.9	344.7	5810.9	+	*
mod. logistic[1]	5	6623.3	4724.0	761.0	773.4	364.9	13256.5	+	*
1a	8	2205.9	1041.3	117.7	707.8	339.0	4427.9	13.8	*
1b	11	2207.4	1038.6	118.2	709.6	341.0	4436.8	22.7	*
1c	10	2215.3	1046.4	117.5	713.1	338.2	4450.5	36.4	*
1d	13	2203.1	1038.6	117.6	708.7	338.2	4432.2	18.1	*
2a	8	2205.1	1038.9	117.9	709.4	339.0	4426.2	12.1	0.001
2b	11	2201.9	1037.6	117.1	708.0	339.1	4425.7	11.6	0.001
2c	10	2214.1	1047.7	118.3	710.0	338.1	4448.2	34.1	*
2d	13	2213.2	1053.1	117.7	704.7	337.7	4452.5	38.4	*
3a	12	2199.4	1036.7	118.0	705.7	339.0	4422.8	8.7	0.003
3b	15	2208.7	1044.5	119.1	703.0	342.1	4447.3	33.2	*
3c	15	2203.0	1038.5	120.4	701.1	343.0	4436.1	22.0	*
3d	18	2220.2	1042.1	118.3	721.3	338.5	4476.4	62.3	*
4a	12	2193.5	1038.3	117.8	698.3	339.1	4411.0	0.0	0.996
4b	15	2207.1	1045.3	117.5	702.6	341.7	4444.2	30.1	*
4c	15	2207.2	1040.6	117.8	711.4	337.5	4444.3	30.2	*
4d	18	2224.3	1037.3	116.8	726.7	343.5	4484.6	70.5	*

[+] $\Delta_i > 1000$

[*] $w_i < 0.001$

[1] Likelihood values obtained by applying model parameter values from Monson et al. (2000a) to entire WPWS population and assuming 1990 population size of 2000 to calculate WPWS survey -*L* (see also Fig. 2).

Table 4. Individual predictions for 16 evaluated source-sink models (* $w_i < 0.001$). Gray shading denotes model groupings where Akaike weights will sum to 1 (i.e., w_i^1 = contrast all models, w_i^2 = contrast stationary N_{sink} or changing N_{sink} models, and w_i^3 = contrast single sink population survival trend models or models that allow a secondary sink population survival trend). Cumulative Akaike weights for stationary vs. changing sink population models are listed at the bottom of the w_i^2 column, and Cumulative Akaike weights for single survival trend models vs. models that allow a secondary sink survival trend are listed at the bottom of the w_i^3 column.

Model	1990 N_{PWS}	1990 N_{sink}	2009 N_{sink}	λ_{source}	λ_{sink}	total loss to sink population	lost reproductive potential	Year 2nd trend begins	Akaike weights		
									w_i^1	w_i^2	w_i^3
1a	2003	719 (0.36)	719 (0.18)	1.04	0.92	683	32	.	*	*	0.157
1b	2241	1817 (0.81)	1529 (0.39)	1.17	0.89	1181	927	.	*	0.004	0.002
1c	2196	973 (0.44)	973 (0.25)	1.05	1.00	377	12	.	*	*	*
1d	2279	402 (0.18)	299 (0.08)	1.04	0.95	213	0	.	*	0.038	0.018
2a	2000	895 (0.45)	895 (0.23)	1.05	0.90	692	36	.	0.001	0.001	0.364
2b	2221	471 (0.21)	32 (0.01)	1.05	0.67	2	0	.	0.001	0.958	0.459
2c	2016	863 (0.43)	863 (0.22)	1.01	1.00	370	0	.	*	*	*
2d	2000	216 (0.11)	103 (0.03)	1.02	0.97	96	0	.	*	*	*
3a	2013	891 (0.44)	891 (0.23)	1.06	0.91	893	131	1991	0.003		0.003
3b	2154	1305 (0.61)	1050 (0.27)	1.11	1.00	622	578	1998	*	*	*
3c	2000	238 (0.12)	238 (0.06)	1.10	0.97	202	36	1995	*	*	*
3d	2167	1330 (0.61)	1124 (0.28)	1.04	0.81	1040	326	2004	*	*	*
4a	2000	803 (0.40)	803 (0.20)	1.04	0.95	735	46	1994	0.996	0.997	0.997
4b	2334	339 (0.15)	131 (0.03)	1.04	0.99	89	0	1992	*	*	*
4c	2000	890 (0.45)	890 (0.22)	1.05	0.87	382	0	2000	*	*	*
4d	2341	1708 (0.73)	1104 (0.28)	1.19	0.52	1383	1903	1991	*	*	*
model avg.	**2001**	**803 (0.40)**	**803 (0.20)**	**1.04**	**0.95**	**735**	**46**	**1994**	**cum. w_i**	**stationary 0.999** **changing 0.001**	**single 0.001** **secondary 0.999**

Table 5. Parameter estimates and one-dimensional 95% likelihood profile confidence intervals for the single best-fit source-sink model. Numbers in parenthesis are actual numbers produced when using the corresponding parameter value.

	Sink population survival (1)			Source population survival			N_{sink}	j_{shift}	N_0	Sink population survival (2)		
Parameter	θ_1	θ_2	θ_3	θ_5	θ_6	θ_7	θ_9	θ_{13}	θ_{14}	θ_{15}	θ_{16}	θ_{17}
Estimate	-0.552	0.376	0.593	0.745	-0.001	-0.104	-0.34 (803)	15 (1994)	2000	1.712	-0.011	-0.078
Lower CI	-0.940	0.195	0.335	0.690	-0.017	-0.122	-0.77 (635)	16 (1993)	1888	1.630	-0.019	-0.090
Upper CI	0.140	0.925	*	0.813	-0.001	-0.083	-0.17 (839)	13 (1996)	2167	1.845	0.0004	-0.063

*no upper CI as beyond after a small increase in -L_{total} it remains the same with increased values of θ_3.

Fig. 1. Map of Prince William Sound and the trajectory of oil from the 1989 *Exxon Valdez* oil spill. Carcasses were collected in oiled portions of WPWS with systematic collections at Green Island and opportunistic collections at Naked Island, the northern Knight Island complex and other islands and passages south of Knight Island. Aerial surveys of WPWS included all waters west of Montague Island including the western shore of Montague Island.

Fig. 2a. Predicted age-specific survival rates (lower half of figure) and resulting population change for 20yrs post-spill (upper half of figure) using the logistic model and parameter estimates from Monson et al. 2000a, and applied to the entire WPWS sea otter population (i.e., homogenous population effect). X-axis is age in yrs for the survival rate (lower) graph and year postspill for the population (upper) graph. Note modeled population change (solid black line) relative to actual aerial survey estimates (black X's).

Fig. 2b. Predicted age-specific survival rates (lower half of figure) and resulting population change for 20 yrs post-spill (upper half of figure) using the modified logistic model and parameter estimates from Monson et al. 2000a, and applied to the entire WPWS sea otter population (i.e., homogenous population effect). X-axis is age in yrs for the survival rate (lower) graph and year postspill for the population (upper) graph. Note modeled population change (solid black line) relative to actual aerial survey estimates (black X's).

Fig. 3. Observed age distribution of sea otters found dead on WPWS beaches from 1976 to 2008. Numbers in parentheses are the total number of carcasses in each

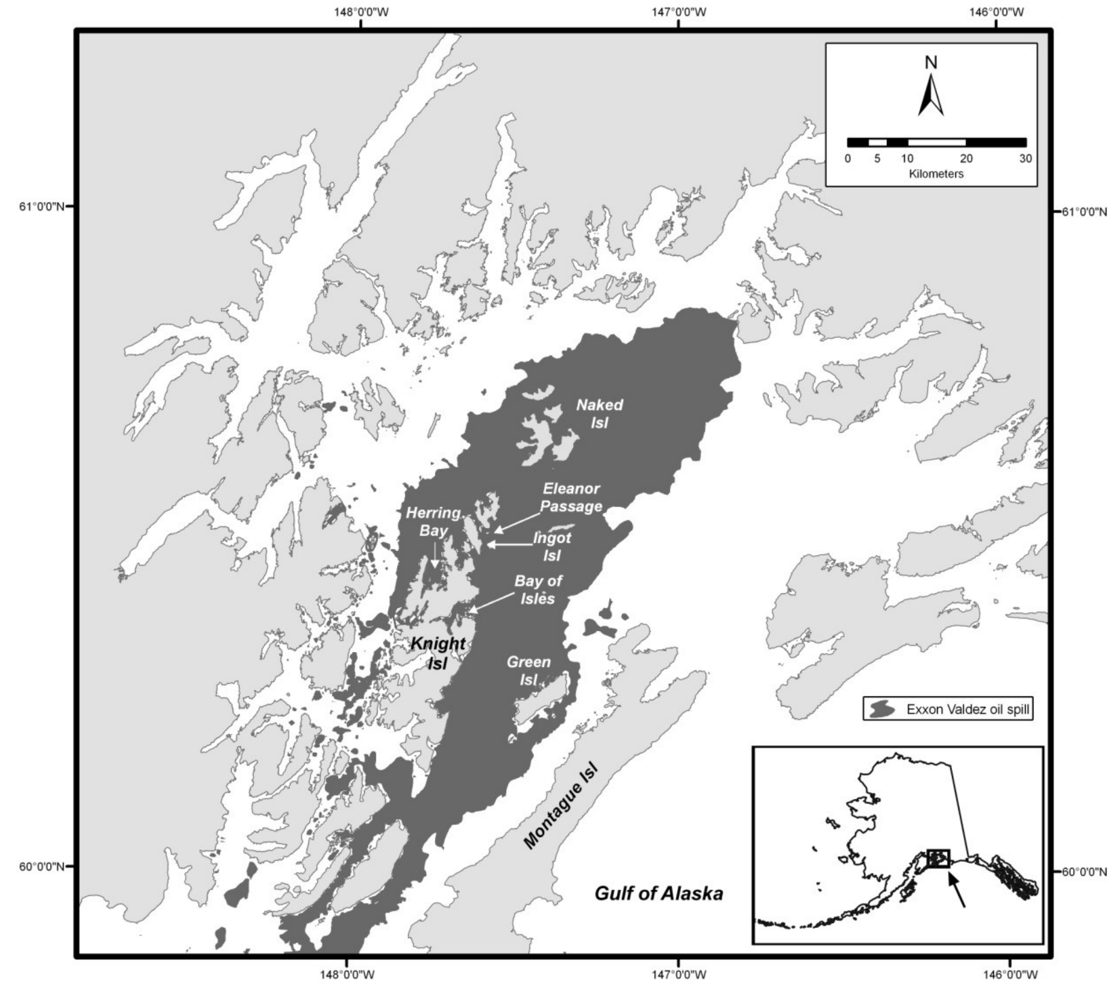
distribution, and age class 2 to 8 years is considered “prime-age”. Postspill age distributions are separated by those previously presented in Monson et al. (2000a) and additional carcasses collected since that time. Yearly age-specific distributions are the basis for the -*L*1 value.

Fig. 4. The top half of the figure illustrates the predicted population trajectories of the best source-sink model (4a) compared with empirical population estimates for WPWS. The thick black lines represent the predicted size of the entire WPWS sea otter population (i.e., source + sink) while the thin gray lines indicate the predicted source and sink population sizes. The lower half of the graph illustrates the age-specific survival estimates (solid lines represent sink population survival rates while broken lines represent the source population survival rates). Black lines indicate 1990 survival rates with subsequent years becoming gray.

Fig. 5a. Sink population sizes and corresponding predicted chronic loss values derived from 10,000 predictions of the best source-sink model (4a) using random values of all parameter estimates chosen from within the 95% likelihood profile confidence intervals of each parameter value. Here, we plot sink population size (within its 95% CI range) against the corresponding model averaged chronic loss estimates for each give population size value. Symbol colors are shaded based on Akaike weights for each giving sink population size value (lighter gray = lower, less likely values, darker gray to black = higher, more likely values), and the solid line is the regression through these points weighted by the Akaike weight values.

Fig. 5b. Likelihood profile intervals for estimates of lambda in the source and sink populations in 2009 based on the best source-sink model (4a). Each point derived from the $-L_{total}$ values from 10,000 predictions of the best source-sink model (4a) using random values of all parameter estimates chosen from within the likelihood profile confidence intervals of each parameter value. The horizontal line represents the 95% likelihood profile confidence interval (delta $-L_{total} \leq 1.9205$). The yellow Xs represent the single best estimates from the original model fitting. (note: the yellow Xs are not at delta $-L_{total} = 0$ indicating the 10,000 iterations found a few solutions with slightly improved fit.

Fig. 6. Observed vs. predicted age-at-death distributions in the sink population for the best source-sink model (4a) for the initial (1990 to 1993) and secondary (1994 to 2008) post spill survival periods. The predicted distributions were not statistically different from the observed distribution in either period (K-S tests, $P > 0.05$ for both).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Knight Isl
Green Isl
Exxon Valdez oil spill
Montague Isl
Gulf of Alaska
60°0'0"N
60°0'0"N
148°0'0"W
147°0'0"W
146°0'0"W

Fig. 1.

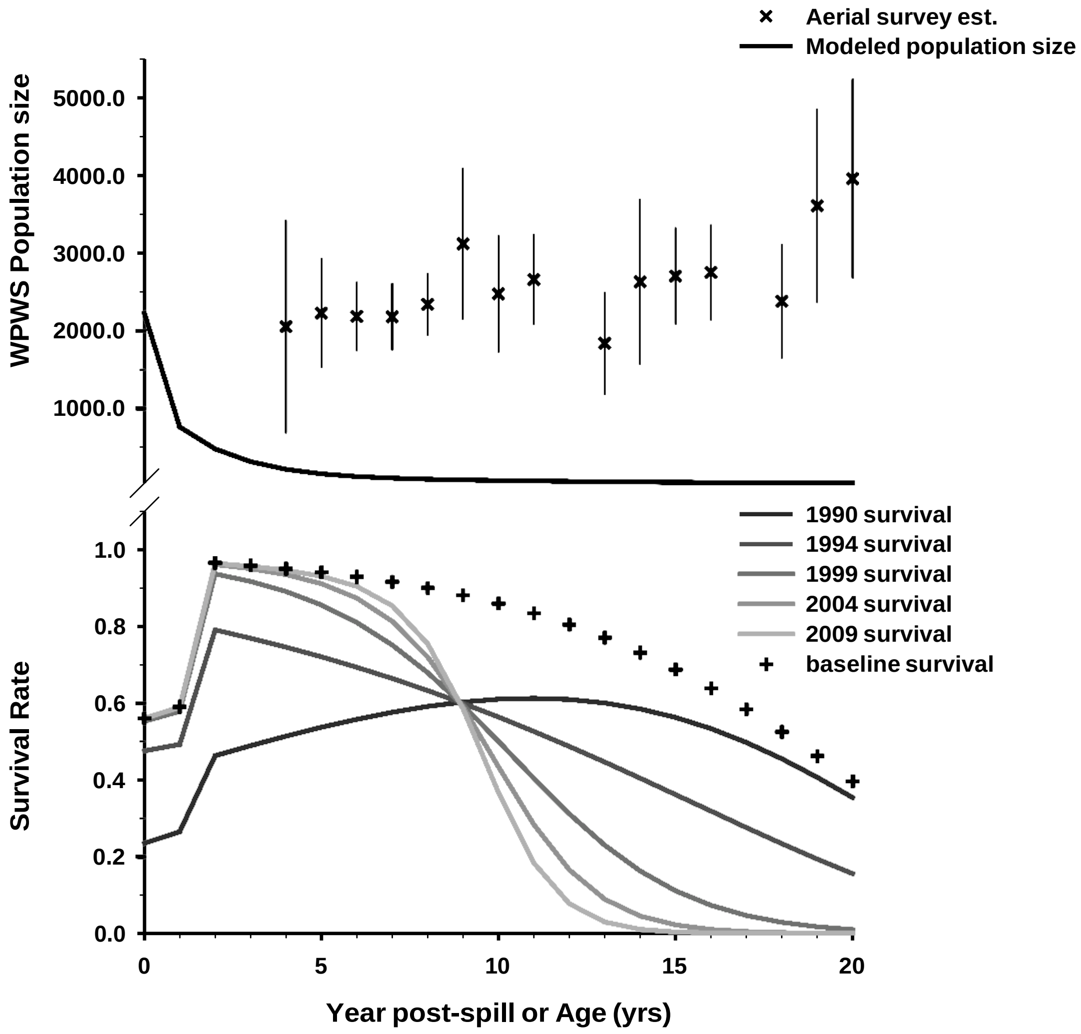
× Aerial survey est.
Modeled population size
WPWS Population size
5000.0
4000.0
3000.0
2000.0
1000.0
1990 survival
1994 survival
1999 survival
2004 survival
2009 survival
+ baseline survival
Survival Rate
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
Year post-spill or Age (yrs)

Fig. 2a.

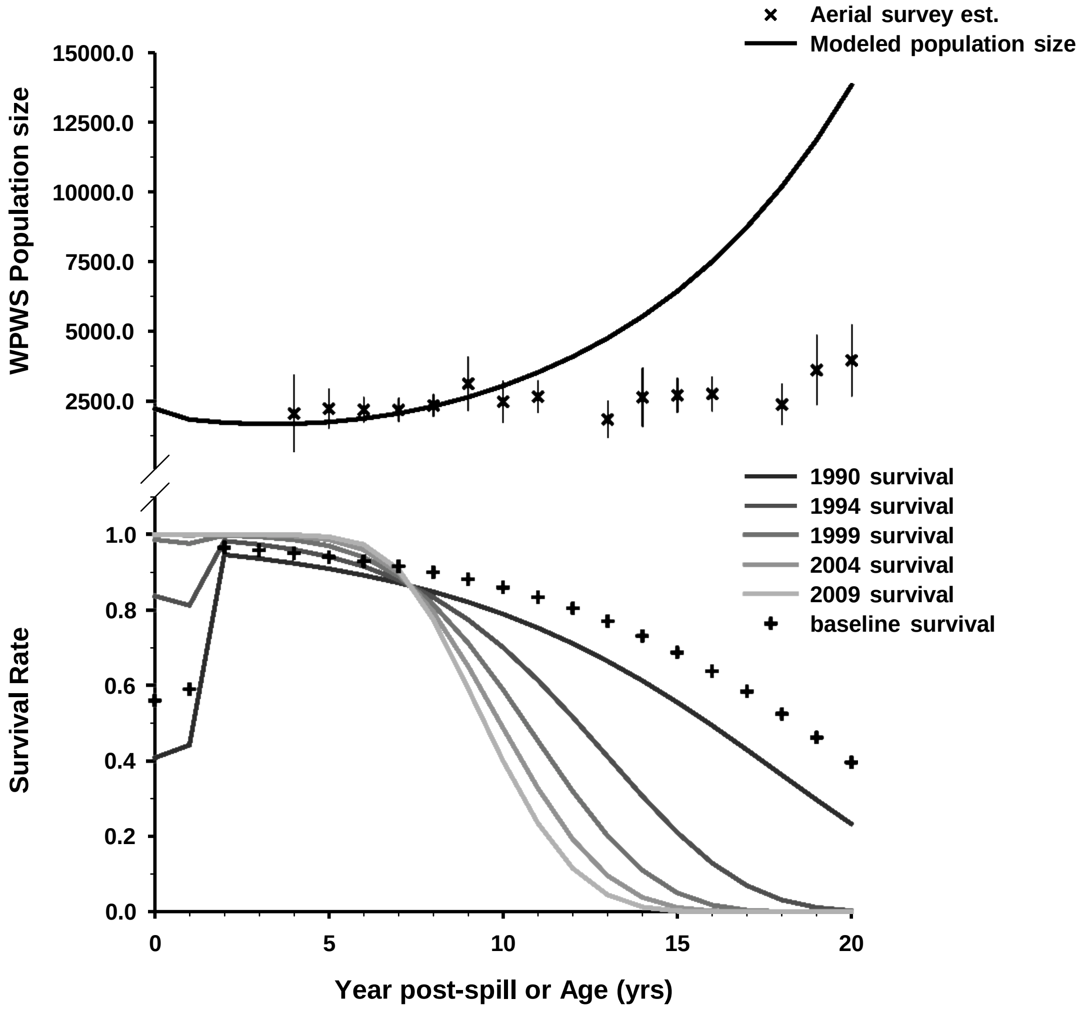
× Aerial survey est.
Modeled population size
WPWS Population size
15000.0
12500.0
10000.0
7500.0
5000.0
2500.0
1990 survival
1994 survival
1999 survival
2004 survival
2009 survival
✚ baseline survival
Survival Rate
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
Year post-spill or Age (yrs)

Fig. 2b.

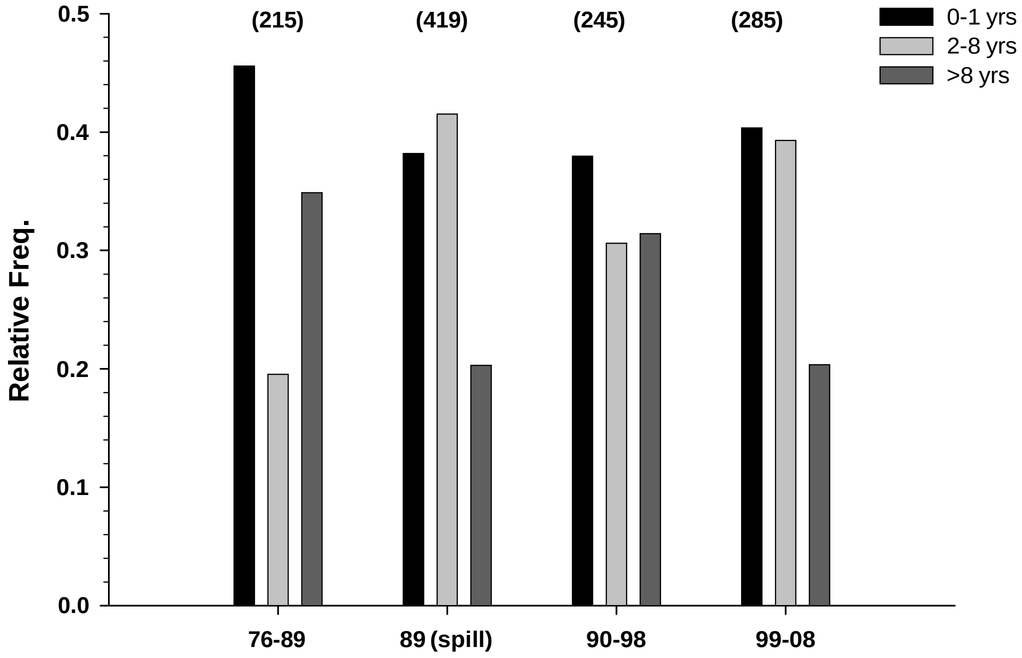
0.5
0.4
0.3
0.2
0.1
0.0
Relative Freq.
(215)
(419)
(245)
(285)
0-1 yrs
2-8 yrs
>8 yrs
76-89
89 (spill)
90-98
99-08

Fig. 3.

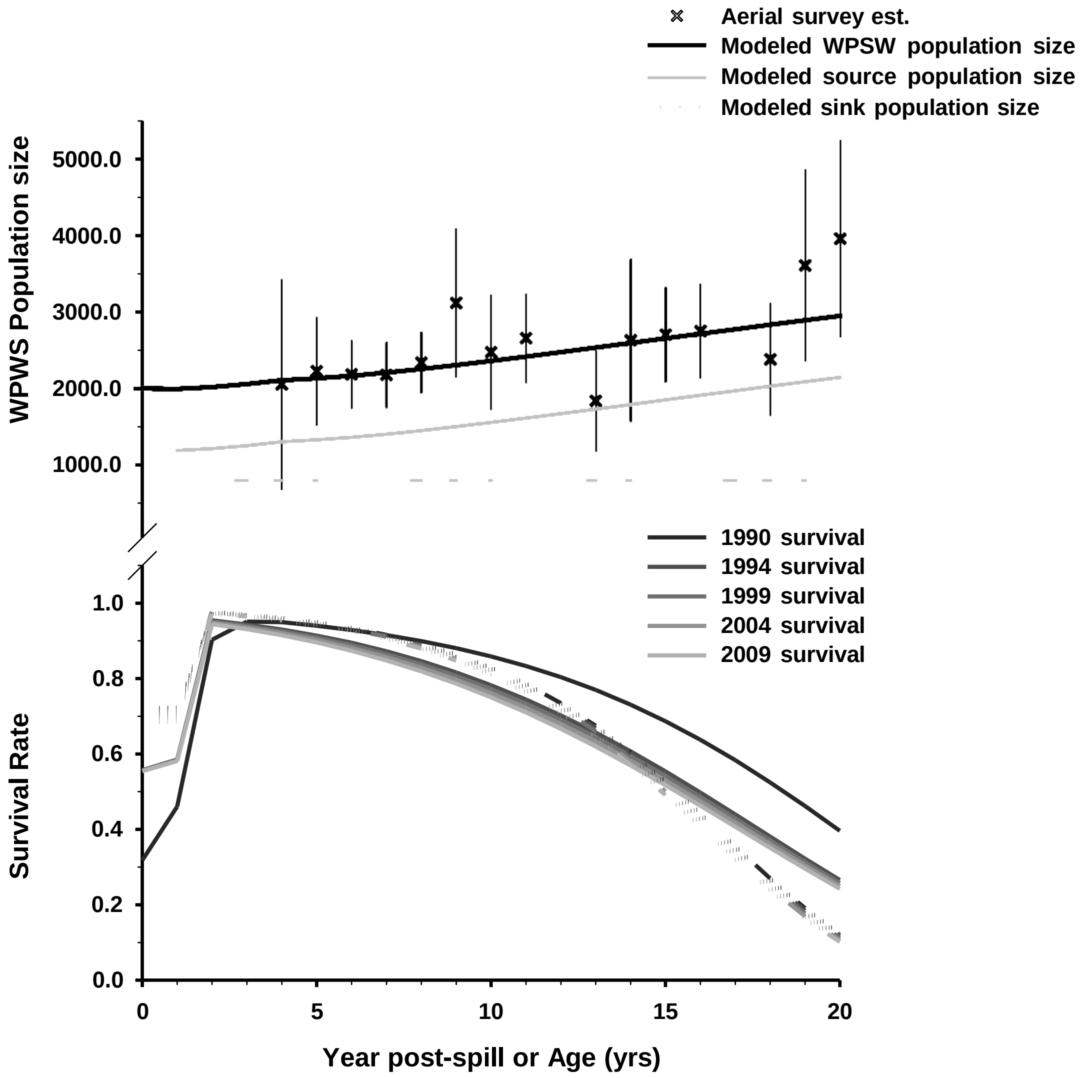
Aerial survey est.
Modeled WPSW population size
Modeled source population size
Modeled sink population size
WPWS Population size
5000.0
4000.0
3000.0
2000.0
1000.0
1990 survival
1994 survival
1999 survival
2004 survival
2009 survival
Survival Rate
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
Year post-spill or Age (yrs)

Fig. 4.

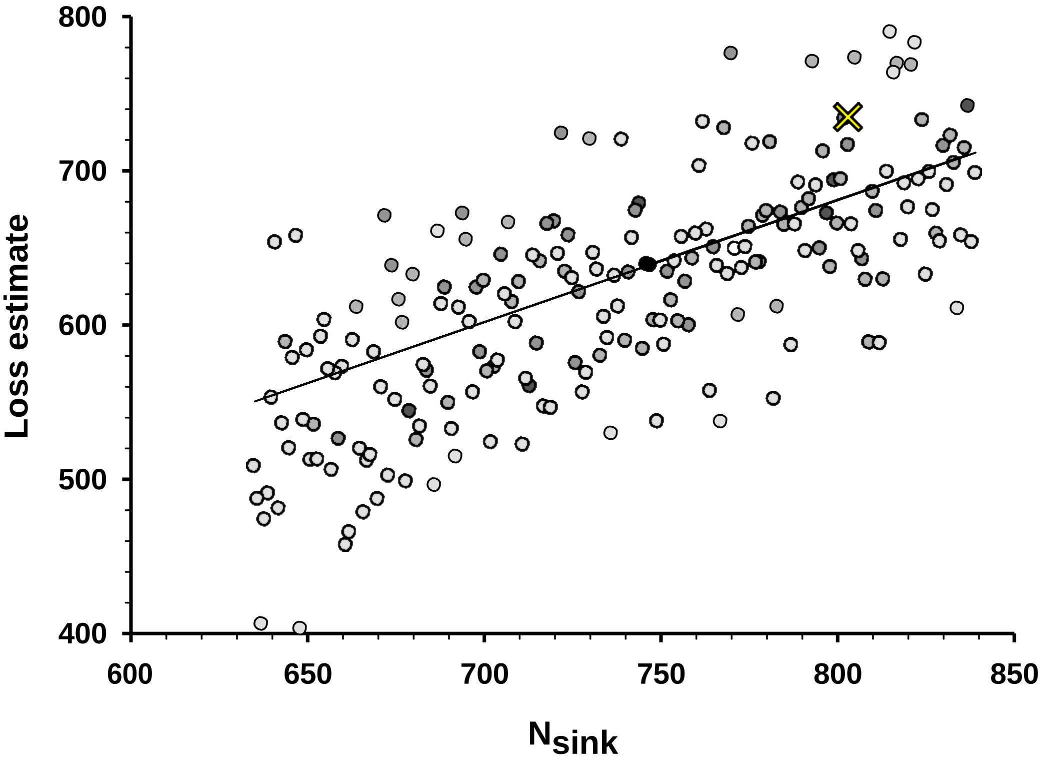
800
700
600
500
400
Loss estimate
600
650
700
750
800
850
N_{sink}

Fig. 5a.

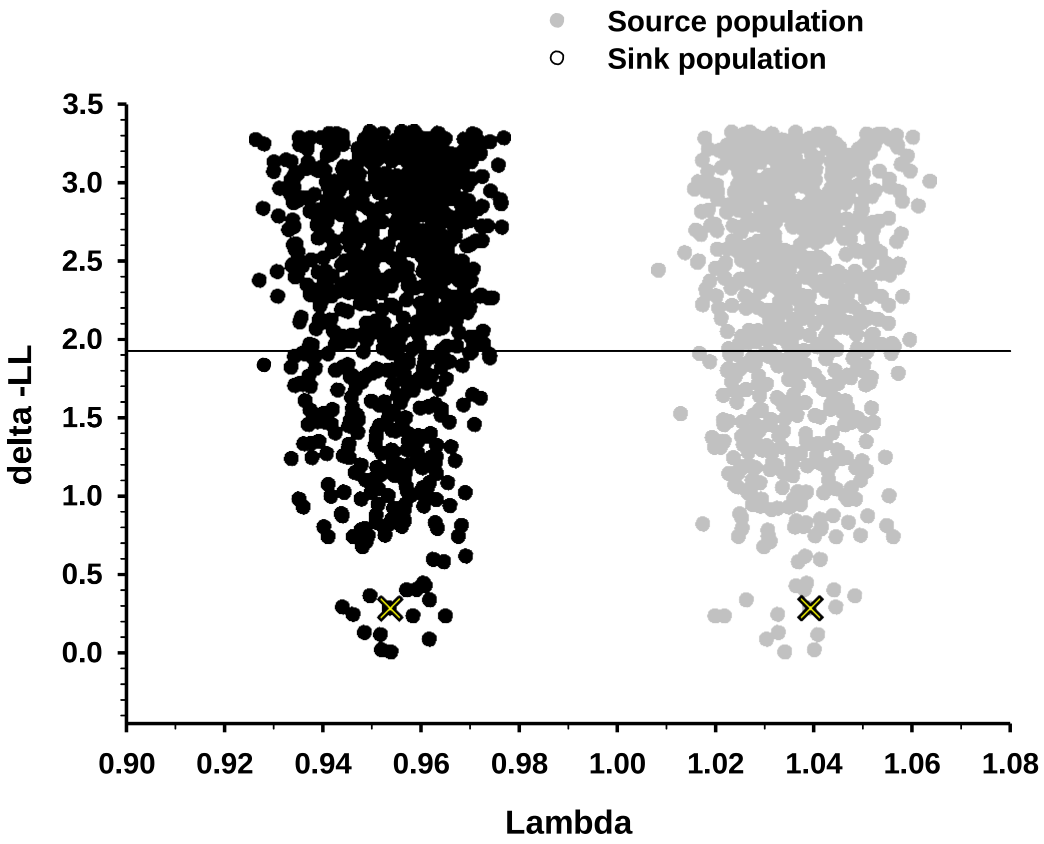
● Source population
○ Sink population
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
delta -LL
0.90
0.92
0.94
0.96
0.98
1.00
1.02
1.04
1.06
1.08
Lambda

Fig. 5b.

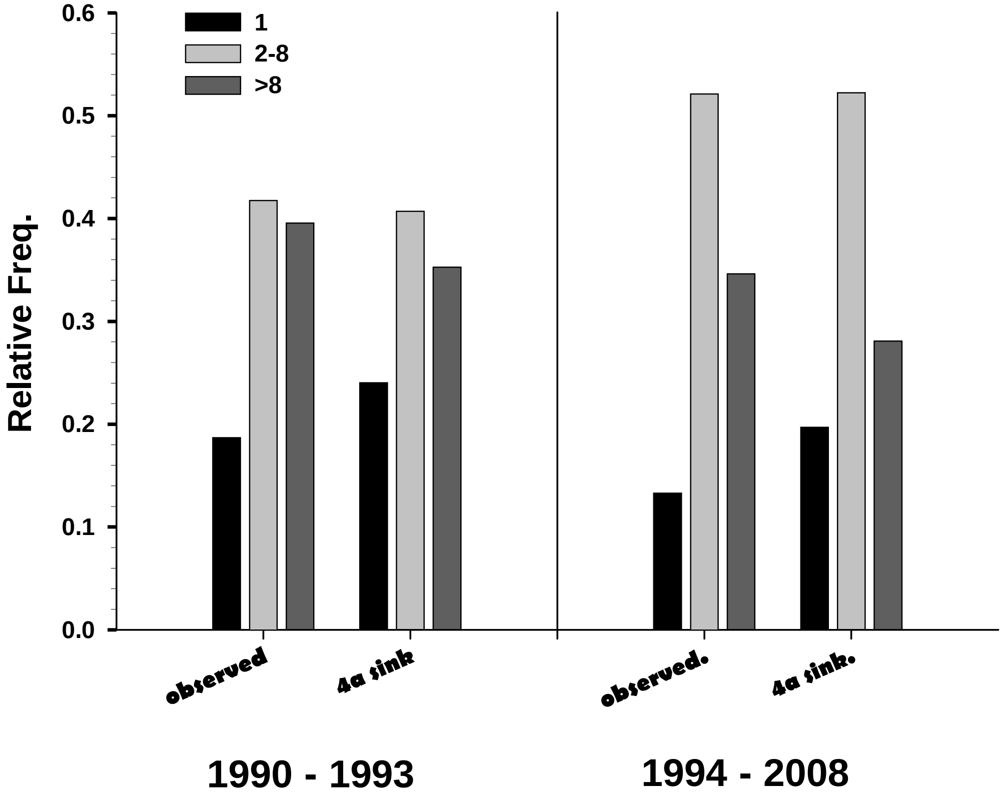
Relative Freq.
0.0
0.1
0.2
0.3
0.4
0.5
0.6
1
2-8
>8
observed
4a sink
observed.
4a sink.
1990 - 1993
1994 - 2008

Fig. 6.