Density dependence and risk of extinction in a small population of sea otters

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Abstract. Sea otters (*Enhydra lutris* (L.)) were hunted to extinction off the coast of Washington State early in the 20th century. A new population was established by translocations from Alaska in 1969 and 1970, and currently numbers at least 550 animals. A major threat to the population is the ongoing risk of major oil spills in sea otter habitat. We apply population models to census and demographic data in order to evaluate the status of the population. We fit several density dependent models to test for density dependence and determine plausible values for the carrying capacity (K) by comparing model goodness of fit to an exponential model. Model fits were compared using Akaike Information Criterion (AIC). A significant negative relationship was found between the population growth rate and population size ($r^2 = 0.27$, $F = 5.57$, df = 16, $p < 0.05$), suggesting density dependence in Washington state sea otters. Information Criterion statistics suggest that the Beverton–Holt model is the most parsimonious, followed closely by the logistic model. Values of K ranged from 612 to 759 with best-fit parameter estimates for the Beverton–Holt model including 0.26 for r and 612 for K. The latest (2001) population index count (555) puts the population at 87–92% of the estimated carrying capacity, above the suggested range for optimum sustainable population (OSP). Analyses of extinction risk associated with oil spills were based on assumptions of variable spill frequency, and variable mortality rates associated with spills once they occurred. At lower rates of assumed spill frequency, extinction risk was either negligible or was substantial only at the highest assumed mortality rates. At the highest assumed frequency rate (0.5 yr^{-1}), extinction risks were high across the full range of assumed mortality rates. Elasticity analysis was conducted to examine the effects of proportional changes in vital rates on the population growth rate (λ). The elasticity values indicate that the population is most sensitive to changes in survival rates (particularly adult survival).

Introduction

Sea otters once were abundant in coastal regions throughout the North Pacific Rim from northern Japan to central Baja California, Mexico, but were reduced to a number of widely scattered remnant populations during a hunting period between 1741 and 1911 (Kenyon 1969; Rotterman and Simon-Jackson 1988). The reduction of sea otter numbers likely resulted in dramatic changes in prey population dynamics and ecosystems previously occupied by sea otters. The recovery of some sea otter populations, together with reintroductions to previously occupied areas during the 20th century (Jameson et al. 1982), have resulted in pre-exploitation otter

densities in some coastal ecosystems (Gerber and VanBlaricom 1999). Population-level recovery has led to an appreciation for several important patterns: (1) The ecological and evolutionary significance of sea otters as predators; (2) The significant conflicts between sea otters and the shellfish fisheries that emerged while sea otters were absent; (3) The increased likelihood for incidental take of sea otters in net and trap/pot fisheries; (4) The increased interest in hunting of sea otters by Native Americans; and (5) The risk of substantial sea otter mortality associated with the risk of large oil spills in sea otter habitat.

Sea otters were hunted to extinction off Washington state early in the 20th century (Kenyon 1969). A new population was established by translocations from Alaska to the Point Grenville area in 1969, and to the La Push area in 1970. Fifty-nine otters were translocated in total, but at least 16 died in transport or soon after release (Jameson et al. 1982). The newly translocated population likely suffered a decline during the initial post-transplant period, and remained small until the late 1970s (Jameson et al. 1982, 1986; Bowlby et al. 1988; Jameson 1995, 1998). Jameson (1998) has estimated the annual rate of increase for the Washington sea otter population at 21% for the period 1977–1988, and 10–11% since 1989. The sea otter population off Washington numbered at least 550 animals in the summer of 2001. In Washington, coastal habitats currently occupied by sea otters are primarily wilderness areas, administered by the U.S. Fish and Wildlife Service (FWS), the National Park Service, and the Olympic Coast National Marine Sanctuary (OCNMS). Much of the wilderness area has rocky substrata near shore, thought to be a preferred category of habitat for sea otters. It is unclear if and in what direction this population of sea otters will expand their range. Sea otters in both California and Alaska occupy several habitat types, beyond the preferred rocky habitat.

Sea otters are known to be vulnerable to high mortalities when exposed to spilled oil. Significant mortalities were observed following a spill in the Kuril Islands, Russia, in 1965 (Barabash-Nikiforov et al. 1968), and following the *Exxon Valdez* oil spill off southern Alaska in 1989 (e.g., Garrott et al. 1993; Ballachey et al. 1994). The sea otter population in Washington is relatively small. In addition, the population tends to concentrate in a few areas during winter when seasonal storms limit the distribution of canopy-forming kelps that provide important habitat for resting animals. As a result, we suggest that the Washington sea otter population is particularly vulnerable to impacts from oil spills. Even a small spill near a winter aggregation site could cause loss of a significant proportion of the population (Bowlby et al. 1988). In addition, due to the relative inaccessibility of northern Washington coastal areas inhabited by sea otters, oil spill containment and cleanup may be particularly difficult. The risk of oil spills is particularly significant in the Strait of Juan de Fuca, where more than 15 billion gallons of oil are transported as cargo and fuel by more than 10,000 ships that enter and leave the Strait each year. Finally, capturing otters to prevent exposure to oil and treatment of previously oiled animals has historically proven difficult (Siniff et al. 1982; Loughlin 1994). The Washington coast has an unfortunate history regarding oil spills (Bowlby et al. 1988). Over the last several decades, significant spills

resulting from grounding or collision were caused by the vessels *General Meigs* (Clark and Finley 1973), *Nestucca* (Yaroch 1991) and *Tenyo Maru* (Rogne and MacDonald 1993). The *Nestucca* spill in early 1989 was the first North American spill known to cause the death of a sea otter, although numerically significant sea otter mortalities did not occur. In the cases of both the *Nestucca* and the *Tenyo Maru*, only fortuitous current and wind patterns prevented a substantial oiling of Washington's sea otter habitat. Other risks to sea otters off Washington include fishery bycatch, disease, contaminants other than spilled oil, illegal harvest, and habitat modification or loss. There is a possibility of future resumption of traditional tribal harvest of sea otters as well, but no such harvests have been formally proposed. Based on presently available information we regard oil spill risks in sea otter habitat as the primary threat to the continued viability of the Washington sea otter population.

Although the Washington sea otter is legally designated as 'Endangered' by the State (Washington Administrative Code 232-12-014), the population is not listed under the U.S. Endangered Species Act of 1973 (ESA; 16 U.S.C. §§1531-43 [Supp. IV 1974]) as amended. However, the Washington sea otter population is subject to the regulatory provisions of the U.S. Marine Mammal Protection Act of 1972 (MMPA; 16 U.S.C. §§1361-62, 1371-84, & 1401-07 [Supp. IV 1974]) as amended. An important management goal emerging from MMPA is the estimation of Maximum Net Productivity Level (MNPL). MNPL is defined as the population size associated with the maximum value of the first derivative of a function representing population size over time. Under MMPA implementation protocols developed by management agencies in the USA, MNPL sets the lower bound of the 'Optimum Sustainable Population' (OSP). OSP is defined as a range of population sizes based on the population's carrying capacity and ecosystem health (16 U.S.C. 1361 Sec. 2). A population is designated as 'depleted' under the MMPA if it is estimated to be below its MNPL. It is generally accepted that the MNPL of most marine mammals falls between 50% and 80% of carrying capacity (K), most likely occurring between 50 and 70% of K (Taylor and DeMaster 1993; Read and Wade 2000). It is often difficult to assess the status of a particular population relative to MNPL due to difficulty in estimating K. Laidre et al. (2002) used a habitat-based approach to estimate K for Washington sea otters, and reported index estimates of K ranging from 1372 to 2734.

Here we apply several population models to census and demographic data for sea otters in order to evaluate the status of the apparently recovering Washington population. The approach used here incorporates the full range of biological uncertainty in abundance and demographic data to identify a range of plausible estimates of population status. We then used the best available population data to construct population models to estimate the population's risk of extinction and status under the MMPA, in the specific context of population-scale threats associated with oil spills in sea otter habitat. Finally, we used elasticity analyses to determine which life history stages in sea otters might be most sensitive to risk factors, and most responsive to management and conservation measures.

Methods

Estimating carrying capacity using density dependent models

We estimated carrying capacity (K) for sea otters in Washington by fitting census data (USGS, unpublished data) to several density-dependent models. First, we examined census data to determine if density dependence was a likely factor influencing population growth for sea otters in Washington. A simple test was used to examine the relationship between the current population size, N_t and the corresponding value of the population's intrinsic rate of increase (r). Three density dependent models were fit to the census data and the Akaike Information Criterion (AIC) was used to compare the model fits relative to a simple exponential model (Morris and Doak 2002). This approach assumes that K is based on the behavior of the population in its current habitat during the survey period. We fit the census data to each density-dependent model and compared results to the basic exponential model, $N_{t+1}=N_t e^r$, which is density-independent. The first model considered is the commonly used logistic model:

$$N_{t+1} = N_t exp\left[r\left(1 - \frac{N_t}{K}\right)^{\theta}\right]$$

where N is the population size at time t, r is the population's intrinsic rate of increase, K is the population's carrying capacity, and θ is a 'shape parameter' that adjusts the magnitude of the impact of density dependence on the growth rate. In particular, θ permits the inflection point of the growth curve to vary between K/e and K, where e is the base of the natural log. Thus when θ is equal to one, the generalized logistic of the form above collapses to a simple logistic where the growth curve is symmetrical about $N=K/2$ (Gilpin et al. 1976):

$$N_{t+1} = N_t exp\left[r\left(1 - \frac{N_t}{K}\right)\right]$$

Compared to the theta-logistic model that exhibits a 'humped' relationship between density and recruitment such that total recruitment declines at high densities, the Beverton–Holt model includes an asymptotic relationship between density and recruitment (Beverton and Holt 1957):

$$N_{t+1} = \frac{e^r K N_t}{e^r K N_t - N_t + K}$$

We used estimates of population parameters (r, K, θ) for the best-fit models to determine OSP levels and the status of the current population. More complicated models can often achieve a better fit than simpler models simply by adding additional parameters (e.g., K, θ). However, this increased fit comes at the cost of increased uncertainty, as each additional parameter must be estimated. To address this issue, we used AIC statistics to compare the fit of the models with different

parameters. The method allows comparison of the likelihood of the model (how likely it is to explain the observed data) with the number of parameters using the following relationship:

$$\text{AIC}_c = -2logL_{max} + \frac{2pq}{q - p - 1}$$

where L_{max} is the likelihood, p is the number of parameters in the model, and q is the number of data points available. The model with the lowest AIC value is the most parsimonious and the best description of the data. Models are most easily compared using Akaike weights, which convert the AIC value of each model into a probability.

Computer simulation to estimate extinction risk for a density-dependent population model

To estimate extinction risk for sea otters in Washington, we used a simulation model to predict the size of the population at 1-year intervals, starting with the current population size. We assume here that oil spills constitute the primary extinction risk for sea otters off Washington, and we do not consider other possible risk factors in our analysis. The model relies on parameter estimates from our density-dependent models and empirical data on the effects of catastrophic oil spills. Oil spill risk was incorporated using estimates of frequency and intensity provided by Bonnell et al. (1996) and French (2000). Bonnell et al. (1996) reported that the frequency of occurrence ranged from 0.13 to 0.19, based on analyses of tanker spills in U.S. waters between 1974 and 1989, and intensity (mortality if the spill occurs) ranged from 0 to 50% based on different distances from the spill (Bonnell et al. 1996). French (2000) reported values for frequency ranging from 0.10 to 0.50 for small and large spills, and intensity values ranging from 23 to 42%. Thus, to incorporate the full range of plausible oil spill effects, our simulations (described below) incorporate three scenarios for frequency (0.10, 0.19, 0.50). For each of these three frequencies, we consider four ranges for intensity (0–0.5, 0.25–0.5, 0.25–0.75, 0.5–0.75). In other words, for a given frequency of occurrence, a spill could cause a 0–50% mortality, a 25–50% mortality, and so on.

To examine the effects of an oil spill on extinction risk for Washington sea otters, we simulated population growth using the logistic model, with the parameters determined by the model fitting analysis described above. The variance estimates are used to add stochasticity in annual growth rates. After calculating annual growth rates, the model makes a random draw to determine if an oil spill occurs (based on frequencies described above). Should the spill occur, the level of mortality caused by the spill was chosen from a range of values, such as 0–50% mortality, with a uniform distribution. A large number of population trajectories (30,000) were run, each with an independent annual chance of catastrophe. The number of populations remaining extant each year were tabulated. For each of the three scenarios for frequency, we recorded the cumulative probability of extinction for each of the four ranges of potential mortality.
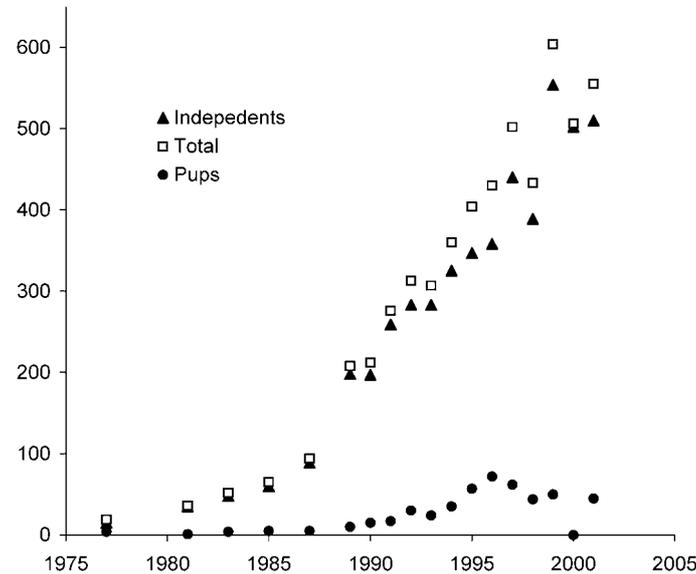
Figure 1. Abundance estimates of sea otters from 1977 to 2001. These data represent counts made during annual summer (July) surveys (USGS, unpublished data).

Identifying critical life stages using demographic models

In addition to analyzing census data with density dependent models, we used demographic models (*sensu* Caswell 2001) to determine which aspects of life history would be most sensitive to management. Demographic data are sparse for Washington State sea otters, so a range of data were compiled from other populations of sea otters (Table 2, Gerber et al. 2004). To encompass uncertainty in vital rates for sea otters, matrices were constructed using high, average, and low estimates from reported rates in the available data. We then analyzed these matrices to obtain values of λ and generated elasticity matrices to illustrate the relative impact of changes in each parameter on λ. Our demographic models are all age-based Leslie matrices, and thus require values for the following age- or stage-specific vital rates: fecundity (number of female offspring produced per female per year, assuming a 1:1 sex ratio at birth), weaning success rate (probability that a female pup survives from birth to weaning), juvenile survival (the juvenile age class begins after weaning, at about 6 months, and extends to about 24 months), sub-adult survival (the sub-adult age class included 2–3 year olds), adult survival (4–12 year olds) and old-adult (13–20 year olds) survival. The first rows of the population matrices consist of age-specific reproduction, defined as the age-specific probability of producing a 1-year-old female offspring (calculated as the product of fecundity, weaning success rate, and the square root of the annual juvenile survival rate; Gerber et al. 2004). We refer to these products as *reproductive rates* throughout
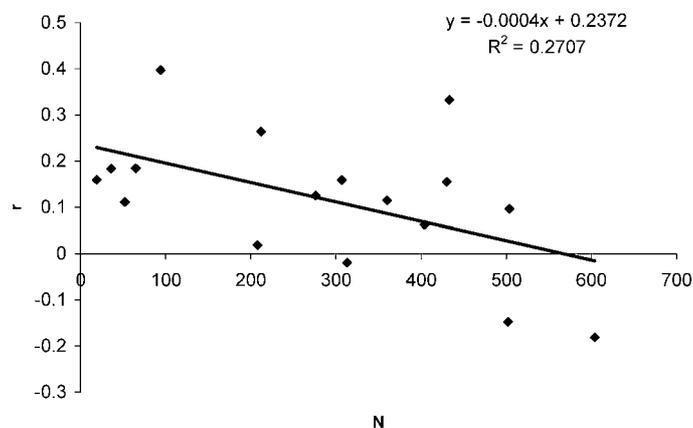
Figure 2. Population size versus growth rate *r*, $\ln(N_t/N_{t+1})$. Growth rates decline significantly as population size increases, suggesting that negative density dependence is a relevant factor in sea otter population dynamics.

Table 1. Best-fit parameters and sum squared error for each type of model. The OSP is calculated as 50–80% of the carrying capacity (*K*) suggested by each model. Low AIC values indicate more parsimonious models. Akaike weights represent the probability of each model being the best description of population dynamics.

	r	*K*	Sum squared error	OSP (50–80%)	AIC_c	Akaike weights
Exponential	0.13		298,723		189.34	0.012
Logistic	0.25	621.4	17,079	310–497	182.19	0.432
Theta-logistic	0.23	759.46 ($\theta = 1.16$)	16,375	379–607	184.79	0.117
Beverton–Holt	0.26	612.48	17,049	306–489	182.16	0.439

the paper. We assumed that 20 years was the maximum attainable life span of otters in this population. While all of our models are *age-based*, we report results in terms of the *stage-specific* survival and reproductive parameters for juvenile, sub-adult, adult and old-adult otters that are used to formulate the age-specific elements of the population matrices.

Results

Estimating carrying capacity using density dependent models

We found a negative correlation between population growth rate and population size ($r^2 = 0.27$, $F = 5.57$, df = 16, $p < 0.05$), suggesting that growth rates do decline to some extent as population sizes increase (Figure 2). AIC statistics suggest that the Beverton–Holt model is the best-fit model, followed closely by the logistic
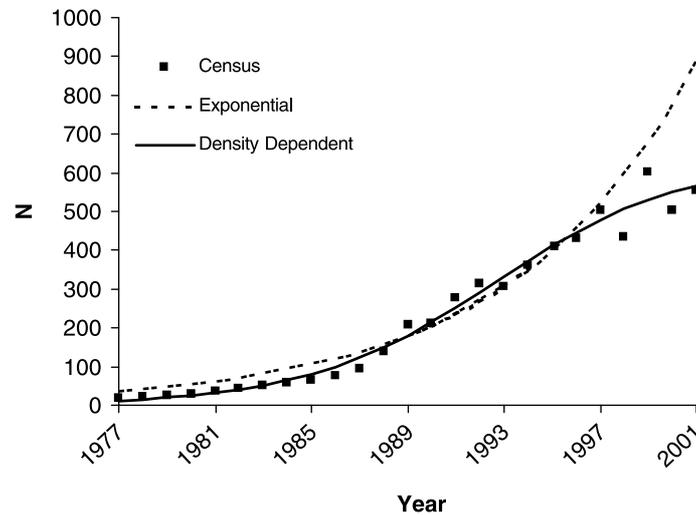
Figure 3. Comparison of best-fit logistic model to exponential model.

model (Table 1). The exponential model, on the other hand, is far less suitable (Figure 3). It has only a 0.1% chance of being the most suitable model, as compared to 0.43% for both the Beverton–Holt model and the logistic model. Therefore it is likely that negative density dependence is, in fact, playing a role in the population dynamics and is an important factor in predicting future growth. The different forms of density dependence used in the model provided similar results, suggesting *K* values from 612 to 621. Given the latest (2001) population index count of 555, the population is at 87–92% of the carrying capacity of currently occupied habitat, which is likely above MNPL and within the suggested range for OSP.

Computer simulation to extinction risk for a density-dependent population model

For all assumed frequencies of occurrence, the increased risk of extinction due to oil spills depends largely upon the assumed intensity and subsequent effects on mortality (Figure 4). For the 0.10 frequency scenario, the extinction risk was negligible unless mortality rates could reach levels as high as 75%. In the worst case, there was an 80% risk of extinction by 200 years. For the 0.19 frequency scenario, low intensity, such as the range between 0 and 50% had very little influence on risk of extinction; high intensity (especially that ranging up to 75%) would result in a 97% chance of extinction in 100 years. For the 0.50 frequency scenario, extinction risks were quite high. If mortality ranged from 0 to 50%, there was about a 60% risk of extinction in 100 years. In all cases of higher mortality, extinction was virtually guaranteed in 60 years, and could occur in as few as 20
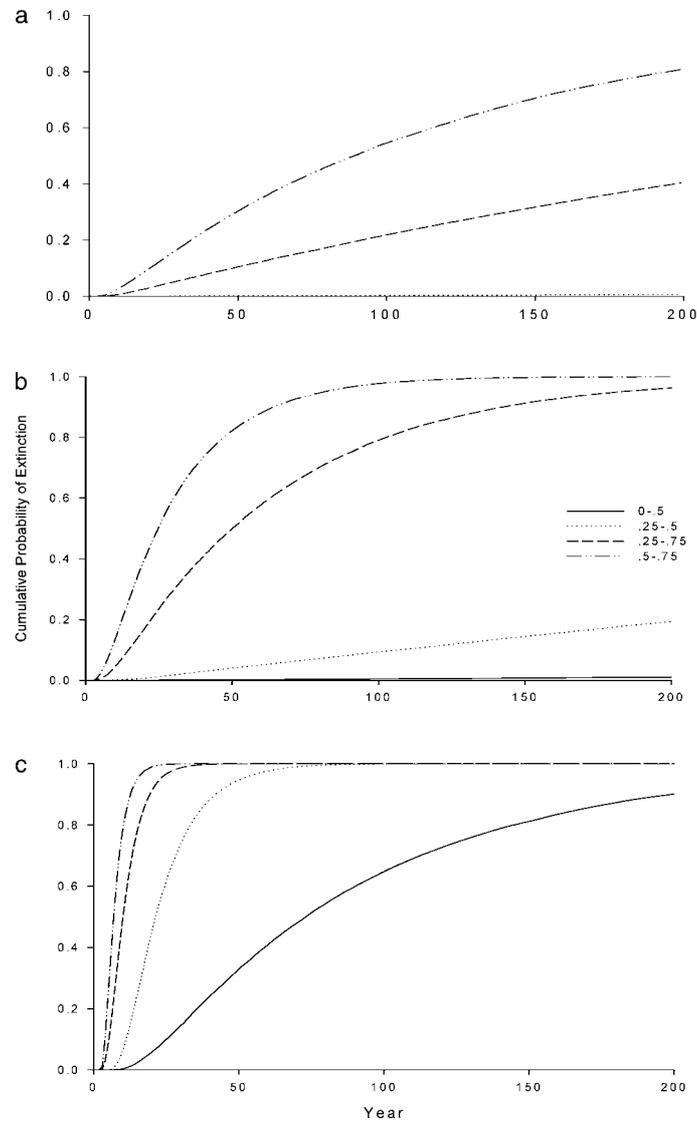
Figure 4. Cumulative probability of extinction in the presence of catastrophic oil spills for assumed probability of a spill occurring is (a) 0.10, (b) 0.19, and (c) 0.50 and four different ranges for intensity. For each of these three frequencies, we consider four ranges for intensity (0–0.5, 0.25–0.5, 0.25–0.75, 0.5–0.75). Mortality caused by the spill is determined by random draws from the uniform distribution given for the four specified ranges.

years. In general, the frequency of oil spills has a strong effect on the viability of the population, especially for oil spills of high frequency and intensity (i.e., that result in high mortality rates).

Table 2. Summary of published estimates for sea otter vital rates, and the range of values used for the current analyses (Gerber et al. 2004).

| Source	Age of sexual maturity	Annual birth rate	Pup survival (weaning success)	Juvenile survival (0–1 year)	Sub-adult survival (2–3 years)	Adult survival (4–12 years)	Old adult survival (13–20 years)	Lambda
Siniff and Ralls (1991)								
Female:	3	Low: 0.90 High: 0.94	Low: 0.46 High: 0.58	Low: 0.75 ± 0.145 High: 0.80		Low: 0.89 ± 0.088 High: 0.91		1.05
Male:	6			Low: 0.85 ± 0.179 High: 0.88		Low: 0.52 ± 0.167 High: 0.61		
Riedman et al. (1994)	3	Age 3–6: 0.90 Age 7–20: 1.07	Mother age 3–6: 0.40 Mother age 7–10: 0.75 Mother age 11–14: 1.0					
Eberhardt and Schneider (1994)	4–5	Low: 0.890 High: 0.898						
Jameson and Johnson (1993)	3	Low: 0.87 High: 0.90						
Current study, minimum values	3	Age 3: 0.60 Age 4–6: 0.90 Age 7–20: 1.05	Mother age 3–6: 0.40 Mother age 7–10: 0.70 Mother age 11–20: 0.8	0.50	0.70	0.84	0.80	0.92
Current study, maximum values	3	Age 3: 0.60 Age 4–6: 0.90 Age 7–20: 1.05	Mother age 3–6: 0.70 Mother age 7–10: 0.95 Mother age 11–20: 1.0	0.90	0.95	0.98	0.98	1.17
Current study, intermediate values	3	Age 3: 0.60 Age 4–6: 0.90 Age 7–20: 1.05	Mother age 3–6: 0.55 Mother age 7–10: 0.83 Mother age 11–20: 0.9	0.70	0.83	0.91	0.89	1.05
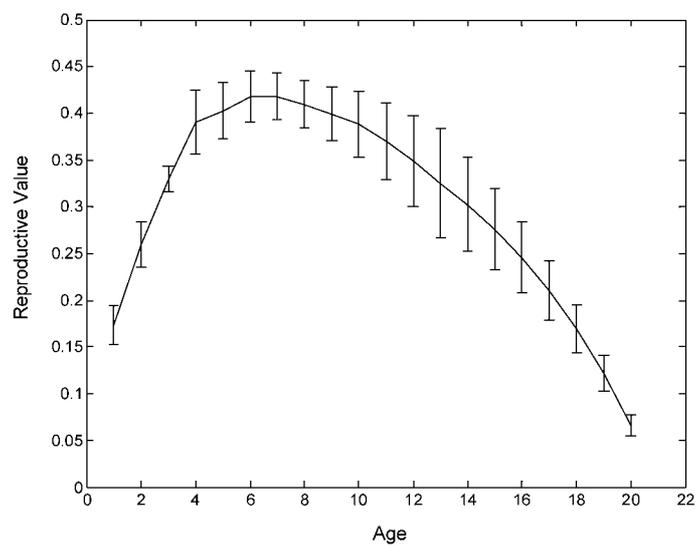
Figure 5. Mean reproductive value vector (*v*) for replicate Leslie matrices. For each replicate matrix, vital rates were selected as uniform random variables from within the range of possible values. Error bars indicate 1 standard deviation above and below the mean.
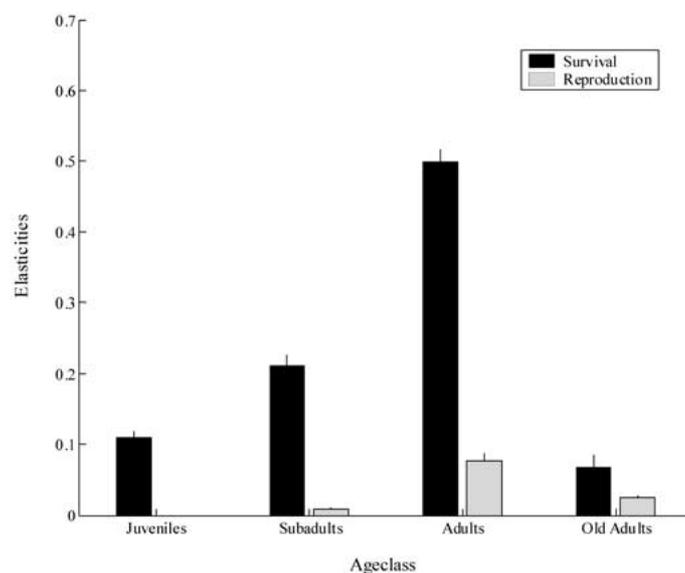

Figure 6. Elasticities of λ to changes in age-specific survival and reproduction values for all entries into the population projection matrix. Mean elasticities are shown, plus 1 standard deviation, for replicate matrices in which vital rates were selected as uniform random variables from within the range of possible values.

Demographic model

Using the intermediate values of reported demographic rates for sea otters (Table 2) resulted in an expected rate of annual growth of 5% per year ($\lambda = 1.05$; Gerber et al. 2004). Selecting all rates as random variables between the lower and upper allowable values resulted in a distribution of growth rates ranging between $\lambda = 0.94$ and $\lambda = 1.15$ (95% confidence limits to the mean = 1.00–1.09). These rates of growth correspond fairly well to minimum and maximum values reported for sea otters in the literature (Riedman et al. 1994). The vector of reproductive values was relatively consistent for all matrix replications (Figure 4): juvenile and sub-adult females had very low reproductive values, with maximum values occurring for adult females between 6 and 8 years of age and then declining rapidly for older animals. The elasticities obtained for sea otters indicate that the population is far more sensitive (*sensu* Caswell 2001) to changes in survival than growth or reproduction, and more sensitive to adult survival than to sub-adult or juvenile survival (Figure 6; Gerber et al. 2004).

Conclusions and discussion

Extinction risk and catastrophic oil spills

The risk of extinction for sea otters in Washington is low in the absence of catastrophic oil spills. Under the assumption that oil spills are the primary risk factor for continued survival of sea otters off Washington, we found that extinction risk increased sharply with oil spill intensity. Because sea otters lack an insulative blubber layer and rely entirely on their fur and the air entrapped therein for protection from heat loss, they are particularly vulnerable to oil spills. The greater metabolic requirements caused by increased thermal conductance of oiled fur may result in thermal stress leading to hypothermia (Costa and Kooyman 1982; Siniff et al. 1982; Williams et al. 1988; Geraci and Williams 1990). Both the probability of occurrence (frequency) and intensity of oil spills in Washington are highly uncertain. Thus, it is difficult to provide a precise estimate of extinction risk associated with oil spill risk for sea otters off Washington. The greatest ongoing potential for oil spill risks along the U.S. west coast comes from vessel traffic (e.g., Townsend and Glazer 1994; Bonnell et al. 1996). Tankship transport of petroleum products through the Strait of Juan de Fuca (both crude oil and refined materials) averages 616,000 bbl/day (Washington Department of Ecology 1997). Offshore oil and gas exploration and development off the coast also may pose serious threats to Washington's sea otter population. Alteration of tanker traffic patterns is a strategy for reducing oil spill risk to vulnerable coastal wildlife habitats, such as those of sea otters (e.g., Benz 1996; Saunders 1996; VanBlaricom 1996). Similarly, reduction or elimination of marine oil development activities may occur if there is a general perception that such development will increase the risk of detrimental effects on vulnerable wildlife. Recent changes in coastal tankship traffic patterns, with large

vessels traveling farther offshore, may improve the margin of safety, but substantial risks remain. Nevertheless, the tankship industry associates significant costs with alteration of normal activities to facilitate reduction of oil spill risks (e.g., Townsend and Glazer 1994). Thus, the industry likely would incur increased costs if operational patterns were modified in favor of a conservative approach to oil spill risk management for the benefit of Washington's sea otters. Increased operational costs may result in political opposition to modification of shipping patterns, with consequent difficulties in reducing the risks of oil spills to sea otters.

Estimating carrying capacity for current and future habitat

Washington sea otters presently occur off remote, largely wilderness portions of the Olympic Peninsula. The present range extends from Kalaloch to Cape Flattery, with centers of abundance in the vicinity of Destruction Island, Cape Alava, Ozette and Bodelteh Islands, and Makah Bay. Alternative estimates of carrying capacity reported for this population are based on the potential of currently unoccupied habitat to support specific densities of sea otters. James Dobbins Associates (1984) estimated a potential carrying capacity of 1280–2560 sea otters in Washington based on the assumption that sea otter range would eventually extend from Destruction Island to Observatory Point (west of Port Angeles, approximately at the midpoint of SJDF) with a standard density of eight otters per square mile. Laidre et al. (2002) used a similar approach to James Dobbin Associates (1984); however, sea otter densities were stratified by three habitat types and differences in potential offshore habitat used. Index estimates of K, directly relating to the index counts used to monitor the population, were reported as 1372 (CV 0.13)–2734 (CV 0.13). MNPL was assumed to fall at 60% of K (Demaster et al. 1996). It is important to note that although the two habitat estimates are substantially higher than what is reported here, these approaches incorporate a fundamental difference in estimating carrying capacity. Habitat-based methods assume that sea otters will re-occupy all or a portion of their historical range, and consequently extrapolate a density to obtain a potential number of sea otters that could be supported in the Washington environment, given that the population disperses in some direction from currently occupied habitat. Laidre et al. (2002) reported that approximately 800–1000 sea otters could be supported by the currently occupied rocky habitat. This estimate of K for a section of the coast, although higher, is the best comparison with our estimates of K (approximately 600).

In contrast to the habitat-based approaches, the method of estimating K used here does not explicitly take into consideration the quality of habitat. By focusing solely on population dynamics, this method removes the level of guesswork involved in deciding what constitutes good habitat, or in making comparisons between ranges. The trade-off is that our population models assume that density dependence and environmental variation are the primary determinants of population growth. Additionally, our estimate of K applies to currently occupied habitat, and does not apply to potential future habitat. As with any model, the accuracy depends upon the

quality of the data, and the ability to forecast future growth or decline of a population depends upon the shape of the model and the behavior of the data to date. It is reasonable to expect that the approach based on population history is less conservative than habitat-based approaches because we assume we have accounted for all factors affecting population growth. Both approaches to estimating K address different aspects of the population's status, and are dependent on a series of different assumptions whose respective accuracies ultimately are unknown.
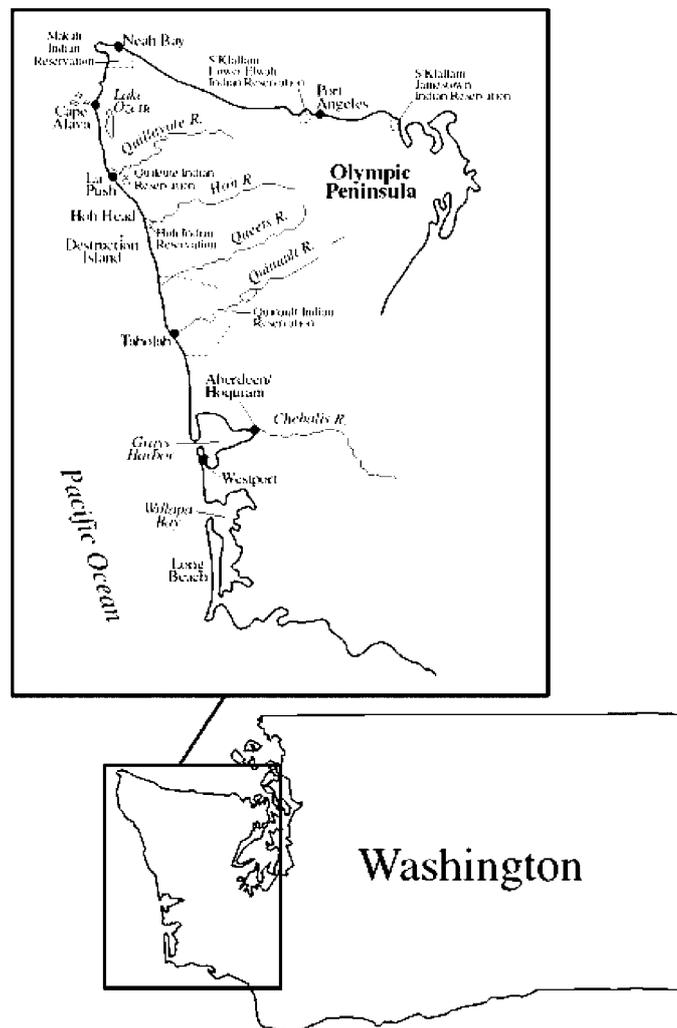

Figure 7. Olympic Peninsula of Washington State; locations of Tribes likely to be affected by increasing sea otter population.

It is not currently possible to predict the direction, rate, or extent of future expansion by the sea otter population off Washington. This information can dramatically change estimates of K and would certainly change the estimates reported here. Otters may move east along the south shore of SJDF, north across the mouth of SJDF to Vancouver Island, Canada, or south towards sandy coastal estuaries once occupied by the historical population (Figure 7).

It is important to note that our population model represents the dynamics exhibited by the population in its current habitat; if the population were to expand into unoccupied habitat our results would represent an underestimate of K for Washington sea otters. More broadly, comparing results to habitat-based models illustrates the importance of considering both population trend and habitat data in assessing population status. The 'true' carrying capacity, if it could be determined, most likely lies somewhere in between the conservative model estimates and the more optimistic habitat-based approaches. Continued population monitoring will help determine if growth rates decline as population increases, and future work on telemetry and dispersal will indicate the suitability of potential habitats. Finally, an important next step in modeling work will be to examine the effect of emigration to unoccupied habitats on estimates of K using spatial logistic and matrix population models.

Acknowledgements

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