A reanalysis of competing hypotheses for the spread of the California sea otter

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Abstract. From 1938 to 1972, the range of California sea otters (*Enhydra lutris nereis*) expanded with the northern and southern fronts spreading at rates of approximately 1.4 km/yr and 3.1 km/yr, respectively. J. A. Lubina and S. A. Levin proposed the following three factors to explain the large disparity in spread rates: (1) regional differences in dispersal; (2) regional differences in population growth; and (3) advection due to the known presence of a southerly flowing offshore current. While Lubina and Levin used a reaction–diffusion framework to argue for large differences in dispersal, our approach uses a stage-structured integrodifference matrix model to show that relatively minor differences in survival provide a more parsimonious explanation for the disparity in spread rates; especially if the survival rates between the northern and southern groups differ in more than one life stage. The argument is made that many of the present estimates for otter survival rates span intervals wide enough to explain the different spread rates—even more so in the likely case that advection plays at least a minor role in otter movement.

Key words: California sea otter; dispersal distance; elasticity; Enhydra lutris nereis; *integrodifference matrix model; mortality; sensitivity; spread rate; stage-structured model; survival.*

Introduction

In the year 1914, approximately 50 California sea otters (*Enhydra lutris nereis*), believed to be regionally extinct, were discovered near Point Sur, California, USA. Since then, their population has steadily expanded northward and southward along the coast thereby providing the unique simplifying opportunity of being able to model their dynamics and movement using a one-dimensional approach. Since otters can have substantial impacts on shellfisheries, with subsequent effects on kelp beds, invertebrate populations, and fisheries (Estes et al. 1989), understanding the factors associated with their spread has important practical implications.

Beginning in 1938, the California sea otter range grew at a nearly constant rate over essentially homogeneous habitat until both the northern and southern wave fronts encountered habitat discontinuities in 1972–1973 (Lubina and Levin 1988). Using a reaction–diffusion framework, Lubina and Levin (1988) analyzed issues

associated with the spread of the Californian sea otter including potential reasons as to why from 1938 to 1972, the otter population expanding southward tended to do so more than two times faster than the population spreading northward (3.1 km/yr vs. 1.4 km/yr). Their model was of the following form:

$$\frac{\partial n(x,t)}{\partial t} = f[r, n(x,t)] + D\frac{\partial^2 n(x,t)}{\partial x^2} - u\frac{\partial n(x,t)}{\partial x} \quad (1)$$

where $n(x, t)$ is the population density at location x and time t, D is the diffusion constant, u is the advection constant, and $f[r, n(x, t)]$ is the population growth function with intrinsic rate r. Lubina and Levin (1988) noted that if one assumes logistic growth without advection, then the speed of the wave front, c, should asymptotically approach the value specified by

$$c = 2\sqrt{rD}. \quad (2)$$

Lubina and Levin (1988) discussed three factors, not necessarily mutually exclusive, that would explain the difference in spread rate between the two subpopulations of otters. From Eq. 2, it is clear that intrinsic growth rate and diffusivity are two of the factors that may help explain the disparity in spread rates. The third factor discussed by Lubina and Levin (1988) was the effect of advection due to a predominantly southerly flowing current. However, they argued that advection was not likely to have been an important factor since the sea otter range center, which they estimated by the mean of the spatial population distribution, tended to move

only 0.2–0.5 km/yr. Thus, Lubina and Levin's (1988) advection estimates would imply a minimum spread rate northward of $(c - 0.5)$ km/yr and a maximum spread rate southward of $(c + 0.5)$ km/yr: a difference of 1.0 km/yr, which is not large enough to account for the observed disparity in spread rates (i.e., 1.4 vs. 3.1 km/yr). Advection may still have been a partial component, but clearly, other factors had strongly affected the spread rates.

Without discounting the possibility that advection and habitat-dependent growth-rate differences may have also contributed to the observed disparity in spread rates, Lubina and Levin (1988) argued that the disparity was for the most part due to a difference in diffusivity between the northern and southern otters. Assuming that both subpopulations have the same intrinsic growth rate (r), Eq. 2 would imply that $2(rD_S)^{1/2}/2(rD_N)^{1/2} = (3.1/1.4)$, where the subscripts N and S denote the northern and southern otters, respectively. Therefore, Lubina and Levin (1988) essentially argued that the observed 2.2 times greater spread rate to the south (2.2 $\approx 3.1/1.4$) was most likely due to a 4.9 times difference in diffusivity between the two otter subpopulations (since $D_S \approx 4.9 D_N$ from above).

The importance of dispersal in general, and of long-distance dispersal in particular, in determining population spread rates has been repeatedly emphasized by numerous studies (see Hastings et al. 2005 for a recent review). The study by Lubina and Levin (1988) is frequently cited as a classic example of model predictions agreeing with dispersal data (e.g., Shigesada and Kawasaki 1997, Hastings et al. 2005). Lacking any stage-specific demographic data, Lubina and Levin (1988) assumed that all the otters were identical, except for the difference in dispersal capabilities between individuals spreading northward and those spreading southward. However, since 1988, the accumulation of an ample amount of demographic data (Siniff and Ralls 1991, Jameson and Johnson 1993, Riedman et al. 1994, Tinker et al. 2006) and dispersal data (Ralls et al. 1996) allows for a much more detailed examination of the factors that may have controlled historical spread rates of the California sea otter. These studies have suggested that vital rates and dispersal capabilities differ among the life stages of sea otters (see *Methods: Parameterization of the model*), and even more recent studies have shown that vital rates exhibit substantial temporal and spatial variation (Estes et al. 2003, Tinker et al. 2006). The wealth of data acquired since 1988, together with the development of stage-structured population spread models (Neubert and Caswell 2000), enabled us to reexamine the results of Lubina and Levin's (1988) classic paper and to explore differences not readily apparent in their unstructured reaction–diffusion model.

Using a model similar to the one presented here, Krkosek et al. (2007) computed the range expansions for the California sea otter between the years 1914 and 1986 for each of four distinct dispersal kernels. However, unlike our analyses, Krkosek et al. (2007) did not allow for the possibility of demographic differences between the northern and southern sea otter groups. Instead, they accounted for the observed disparity in spread rates by fitting different dispersal parameter values to each subpopulation.

The present study addresses whether it is possible to account for the different spread rates between the northern and southern subpopulations without assuming a large asymmetry between parameter values for each group of otters. Our analysis uses a stage-structured integrodifference matrix model, which allows for the incorporation of differences in demography and dispersal among otters in the various life stages. Using the methods of Neubert and Caswell (2000), we calculate asymptotic spread rates during parameter sweeps, and we conduct sensitivity and elasticity analyses of wave speed to changes in both the demographic and dispersal-related matrices. Our results show that minor differences in vital rates between the northern and southern otters can produce a disproportionate difference in spread rate.

METHODS

This section begins with a brief conceptualization of the model including the associated variables and parameters used. The details of the model are then formulated, and a description of the parameterization process is provided based on the available literature. Last, the specific analyses conducted in this study are addressed.

Conceptualization of the model

As mentioned above, a stage-structured integrodifference matrix model gives us the ability to account for demographic and dispersal differences among the various stages of a sea otter development. Our model is comprised of three distinct life stages, pup, juvenile, and adult, which differ from each other in at least one vital rate and/or dispersal parameter (see *Methods: Parameterization of the model*). Several studies indicate that adult mortality is age specific (e.g., Gerber et al. 2004, Tinker et al. 2006), and others have shown that the probability of successfully weaning otter pups increases with mothers' ages both in California (Riedman et al. 1994) and Alaska (Monson and DeGange 1995). Although these detailed data allow for the construction of a much more complicated model with numerous additional stage classes, for the sake of simplicity and to conform with other studies that used a similar approach (e.g., Krkosek et al. 2007), our model is comprised of exactly one adult life stage.

Since the interbirth interval for sea otters has been estimated to be between 342 days (Riedman et al. 1994) and 389 days (Siniff and Ralls 1991), each time step in our model is equivalent to one year. Stage 1 represents otter pups defined to be those individuals in their first year of life. Otters that survive the first year, but are not yet at a reproductive stage are classified as juveniles. The
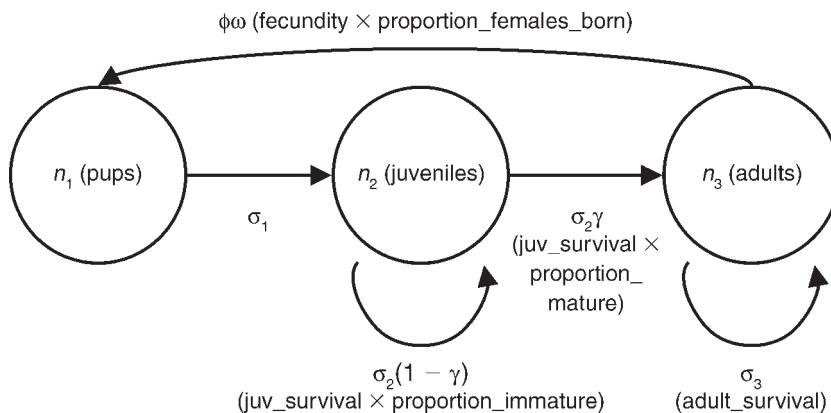
$\phi\omega$ (fecundity $\times$ proportion_females_born)

n_1 (pups) σ_1 n_2 (juveniles) $\sigma_2\gamma$ (juv_survival $\times$ proportion_ mature) n_3 (adults)

$\sigma_2(1-\gamma)$ (juv_survival $\times$ proportion_immature)

σ_3 (adult_survival)

Fɪɢ. 1. Life-cycle graph for the model for the California sea otter (*Enhydra lutris nereis*). See Table 1 for descriptions of the parameters.

third life stage represents reproductive adults. Fig. 1 depicts the life-cycle graph for the model. Survival rates of pups, juveniles, and adults are given by σ_1, σ_2, and σ_3, respectively. The fraction of surviving juveniles that mature into adults each year is equal to γ. Reproduction (by the adult stage only) can occur at a rate of ϕ. Since twinning is extremely rare (Jameson and Johnson 1993), our model assumes that reproducing adult females whelp a single otter pup with the probability of being female represented by the parameter ω. Estimates for all the demographic parameters, except pup survival, are relatively invariant and therefore assumed to be density independent (see *Methods: Parameterization of the model*). While there is evidence that pup survival among Alaska sea otters might be negatively affected by high densities (Monson et al. 2000), since our analyses involve population dynamics near the wave front where densities of the expanding population are low, pup survival is also assumed to be density independent.

Dispersal occurs at every life stage, and those individuals less than four years of age tend to disperse further than adults (Ralls et al. 1996). Therefore, our model incorporates two different dispersal kernels, one for the pups and juveniles, and the other for adults where the standard deviation of the former kernel is greater than the standard deviation of the latter kernel.

The integrodifference model

Mimicking the models presented in Neubert and Caswell (2000), our model takes the following form:

$$\mathbf{n}(x, t+1) = \int_{-\infty}^{\infty} [\mathbf{K}(x-y) \circ \mathbf{B}]\mathbf{n}(y, t)dy \quad (3)$$

where $\mathbf{n}(x, t)$ is the vector of the otter population level at location x and time t; $\mathbf{B}$ is the population projection matrix; and $\mathbf{K}(x-y)$ is the matrix of dispersal kernels in which each entry $k_{ij}(x, y)$ specifies the probability that an individual having made the transition from stage j to stage i moves from location y to location x. Note that the symbol "∘" represents element-by-element multipli-

cation of matrices, also known as the Hadamard product (i.e., the ijth element of $\mathbf{K} \circ \mathbf{B} = k_{ij}b_{ij}$). Using dispersal kernels that are functions of $(x - y)$ implicitly assumes that the environment in spatially homogeneous, and that the probability of dispersal from y to x only depends on the distance between the two locations.

Based on the demographic parameters listed in the previous section, and the fact that we chose to model the dynamics of only female otters (with fecundity now $\phi\omega$), the matrix of demographic transitions is given by

$$\mathbf{B} = \begin{bmatrix} 0 & 0 & \phi\omega \\ \sigma_1 & \sigma_2(1-\gamma) & 0 \\ 0 & \sigma_2\gamma & \sigma_3 \end{bmatrix}. \quad (4)$$

In a study involving California sea otters, Ralls et al. (1996) found that many individual otters tended to remain in the same area for extended periods and then suddenly move great distances over a relatively short timeframe. Therefore, the Laplace dispersal kernel is a good choice to model otter movement. Compared to modeling movement as a diffusion-based process, which essentially assumes a Gaussian distribution, the Laplace dispersal kernel allows for a larger portion of individuals to either move a very short distance or move very far away. Consequently, the Laplace distribution has a higher peak and fatter tails compared to the normal distribution with the same standard deviation. Based on the data from Ralls et al. (1996), such a distribution more accurately depicts the actual movements of otters.

Let kernel k_1 represent the movement of pups and juveniles, and let a second kernel, k_2 represent the movement of adults, which in general, do not disperse as far as the other two life stages. Based on the information mentioned above, the dispersal matrix $\mathbf{K}$ is then given by

$$\mathbf{K} = \begin{bmatrix} \delta(x) & \delta(x) & k_1 \\ k_1 & k_1 & \delta(x) \\ \delta(x) & k_2 & k_2 \end{bmatrix} \quad (5)$$

where $\delta(x)$ is the Dirac delta function representing those transitions for which there is no dispersal, and where

TABLE 1. Parameter descriptions and their default values for the model for the California sea otter (*Enhydra lutris nereis*).

Parameter	Description	Default value
ϕ	adult fecundity	0.90
ω	proportion of females born	0.50
σ_1	pup survival (at low densities)	0.70
σ_2	juvenile survival	0.78
σ_3	adult survival	0.90
γ	juvenile maturation	0.33
ρ_2	standard deviation of adult dispersal kernel	6.20 km
ρ_1	standard deviation of pup/juvenile dispersal kernel	1.5×6.20 km
β	relative difference in dispersal capabilities (ρ_1/ρ_2)	1.5

$$k_i(x) = \frac{1}{2\alpha_i} e^{-|x|/\alpha_i} \qquad i = 1, 2. \qquad (6)$$

The standard deviation for the Laplace distribution is $2^{1/2}\alpha_i$, henceforth denoted by ρ_i. Since pups and juveniles tend to disperse further than adults (Ralls et al. 1996), $\rho_1 = \beta\rho_2$ with $\beta > 1$.

Parameterization of the model

The parameterization of our model was based on the rich body of demographic and, to a lesser extent, dispersal-related literature that has accumulated since Lubina and Levin's publication in 1988. When available, parameter values were estimated based on data for the California sea otter with estimates from studies conducted elsewhere (mainly Alaska) otherwise. The following is a discussion of the available data. Table 1 summarizes our findings with a list of the default parameter values.

Fecundity among otter populations appears to be surprisingly invariant to location and density (Monson et al. 2000). Values in the literature range from 0.85 to 0.94 (Siniff and Ralls 1991, Jameson and Johnson 1993, Riedman et al. 1994). The default value for our model is $\phi = 0.90$. Fetal sex ratios range from an approximate 1:1 ratio (i.e., 50% females) observed by Kenyon (1969) to a sample collected by Bodkin et al. (1993) demonstrating significant female bias with a ratio of 17:32 (65% females). While our default value for the proportion of females born is $\omega = 0.5$, our analysis includes calculated spread rates for values of ω up to 0.65.

Using data based exclusively on the California sea otter, Siniff and Ralls (1991) found that female juveniles had survival rates that ranged from 0.75 to 0.80, while the survival rates for female adults ranged from 0.89 to 0.91. Default values of $\sigma_2 = 0.78$ and $\sigma_3 = 0.90$ are therefore certainly reasonable. As perhaps the principal demographic mechanism of population regulation in sea otters (Monson and DeGange 1995, Monson et al. 2000), pup survival varied significantly in the literature. Based on data from two sea otter populations in Alaska, Monson et al. (2000) found that weaning success was nearly 50% lower within a population at equilibrium (0.52) vs. an expanding population (0.94). In the California sea otter, survival to weaning probabilities seemingly ranged from 0.46 to 0.65 (Siniff and Ralls 1991, Riedman et al. 1994). However, none of the California studies took into account potential density-dependent effects. Since our analyses only involve population dynamics at the leading edge of each wave front where densities are low, our default value is $\sigma_1 = 0.70$, thereby assuming relatively high pup survival at low densities. This assumption only applies for the years covered by our study (i.e., 1938–1972), at the end of which the subpopulations encountered their respective habitat discontinuities (i.e., Monterey and Morro Bays) with subsequent data suggesting that comparatively higher mortality rates occur in these areas (J. Estes, *personal communication*).

Although some females in Alaska start reproducing in their third year of life (Bodkin et al. 1993, Monson and DeGange 1995), 70% of females within a study of California sea otters did not reproduce before their fifth year of life (Jameson and Johnson 1993). Based on these data, our default juvenile maturation rate is $\gamma = 0.33$. That is to say, each year one-third of all female juveniles move into the adult life stage (assuming that there is an equal proportion of juvenile otters in their second, third, and fourth years of life).

In a study involving California sea otters, Ralls et al. (1996) found that juvenile females ranged over distances that were up to twice the range of distances for adult females. Therefore, it is reasonable to assume a $\beta = 1.5$-fold difference between the standard deviations of the juvenile/pup and adult dispersal kernels (i.e., $\rho_1 = 1.5\rho_2$). The default value for ρ_2 was derived by matching model predictions to the population range expansion. Recall that the spread rates for the northern and southern subpopulations from 1938 to 1972 were 1.4 km/yr and 3.1 km/yr, respectively. Our default value of $\rho_2 = 6.20$ km gives rise to an overall spread rate of 2.25 km/yr, thereby splitting the difference between the northern and southern spread rates (assuming default values for the remaining parameters). This value falls well within the range estimated by Krkosek (2007). The next section includes a discussion of the methods used to calculate spread rates.

Calculation of wave speeds and sensitivity/elasticity analyses

Our analyses are based on methods developed by Neubert and Caswell (2000) who were the first to

TABLE 2. Parameter values that will account for the various calculated differences in intrinsic spread rate (in km/yr) between the northern (N) and southern (S) subpopulations of California sea otters, assuming advection constants of 0.0, 0.2, or 0.5 km/yr, thereby resulting in the observed spread rates from 1938 to 1972 (i.e., 1.4 km/yr northward and 3.1 km/yr southward).

Parameter	North	South	Increase (%)	λ_N	λ_S
Advection = 0.0, intrinsic_spread_rate_northward = 1.4, intrinsic_spread_rate_southward = 3.1					
pup_survival (σ_1)	0.518	0.987	90.5	1.0185	1.0859
juv_survival (σ_2)	0.668	0.912	36.5	1.0189	1.0840
adult_survival (σ_3)	0.856	0.961	12.3	1.0172	1.0916
fractional change of all σ_i	−0.031	0.045	na	1.0182	1.0890
dispersal (ρ_2)	3.847	8.535	121.9	1.0475	1.0475
Advection = 0.2, intrinsic_spread_rate_northward = 1.6, intrinsic_spread_rate_southward = 2.9					
pup_survival (σ_1)	0.554	0.907	63.7	1.0246	1.0758
juv_survival (σ_2)	0.692	0.879	27.0	1.0248	1.0743
adult_survival (σ_3)	0.865	0.946	9.4	1.0233	1.0798
fractional change of all σ_i	−0.025	0.033	na	1.0239	1.0777
dispersal (ρ_2)	4.397	7.985	81.6	1.0475	1.0475
Advection = 0.5, intrinsic_spread_rate_northward = 1.9, intrinsic_spread_rate_southward = 2.6					
pup_survival (σ_1)	0.610	0.798	30.8	1.0336	1.0613
juv_survival (σ_2)	0.728	0.831	14.1	1.0337	1.0608
adult_survival (σ_3)	0.879	0.922	4.9	1.0329	1.0624
fractional change of all σ_i	−0.015	0.016	na	1.0333	1.0616
dispersal (ρ_2)	5.225	7.085	35.6	1.0475	1.0475

Notes: Recall that a nonzero advection constant is associated with a southerly flowing current, which means that the observed spread rate northward (1.4 km/yr) equals the intrinsic spread rate northward minus the advection constant while the observed spread rate southward (3.1 km/yr) equals the intrinsic spread rate southward plus the advection constant. One parameter was varied at a time (using default values for the remaining parameters), except for the rows labeled "fractional change of all σ_i," which represent across-the-board fractional changes in survival. For example, a fractional change of −0.03 (respectively, 0.03) refers to a 3% decrease (respectively, increase) in the default survival parameter values for each of the three life stages. To help gauge the relative magnitude for each of the gaps in parameter values, the table includes a column that provides the percentage increase required to go from the northern to the southern parameter value. Note that with all three advection scenarios, the disparity in spread rates result from comparatively smaller percentage changes in survival vs. dispersal. Also calculated was the associated population growth measure, λ, for each subpopulation (i.e., the dominant eigenvalue of matrix **B** in Eq. 4). The abbreviation "na" stands for "not applicable."

calculate the wave front speed for stage-structured models and to derive associated formulas for evaluating the sensitivity and elasticity of wave speed to changes in parameter values. Their work relied upon the linear conjecture (van den Bosch et al. 1990, Mollison 1991), which states that the asymptotic wave speed for an unstructured model of spatial spread is the same as that computed from its linearization at low population densities, assuming (1) an individual's reproduction in an "occupied" environment is always less than its reproduction in a "virgin" environment (i.e., no Allee effect), and (2) the influence of an individual on the environment far from its (present) position is negligible. While the linear conjecture has yet to be proved or disproved, it has received much support and provided a foundation for additional research including the work of Neubert and Caswell (2000) who extended the use of the linear conjecture to stage-structured models.

The sensitivities and elasticities of spread rate to changes in the demographic matrix **B** and the dispersal matrix **K** were evaluated using Eqs. 26–29 of Neubert and Caswell (2000) noting that a typographical error in Eq. 29 was corrected in Eq. 8 of Caswell et al. (2003). Following the steps listed in Table 1 from Neubert and Caswell (2000), wave speeds were calculated while performing single parameter sweeps, holding all but one of the parameters constant, and assuming one of three levels of advection corresponding to the estimates

provided by Lubina and Levin (1988) (i.e., 0.0, 0.2, and 0.5 km/yr).

It is important to note that our model satisfies each of the following four assumptions from page 1616 of Neubert and Caswell (2000), which allows us to use the methods described therein: (1) the demographic matrix **B** is nonnegative and primitive (as are most population projection matrices); (2) the largest eigenvalue for matrix **B** at low density must be greater than one (1.0475 in our case); (3) the vital rates (i.e., entries in matrix **B**) must not be positively affected by an increase in population density; and (4) each dispersal kernel must have a moment-generating function (in our case, $1/(1 - \alpha_i^2 t^2)$, where $i = 1, 2$).

Results

Table 2 summarizes the survival- and dispersal-related parameter values required to account for the northern and southern spread rates under three different advection scenarios: no advection, a southerly advection effect of 0.2 km/yr, and finally an advection effect of 0.5 km/yr (corresponding to the estimated range of advection constants provided by Lubina and Levin [1988] in their model). Table 2 also contains the calculated population growth measure λ (i.e., the dominant eigenvalue of matrix **B** in Eq. 4) associated with each parameter value. For the default demographic parameter values of Table 1, $\lambda = 1.0475$ corresponding to an intrinsic growth rate
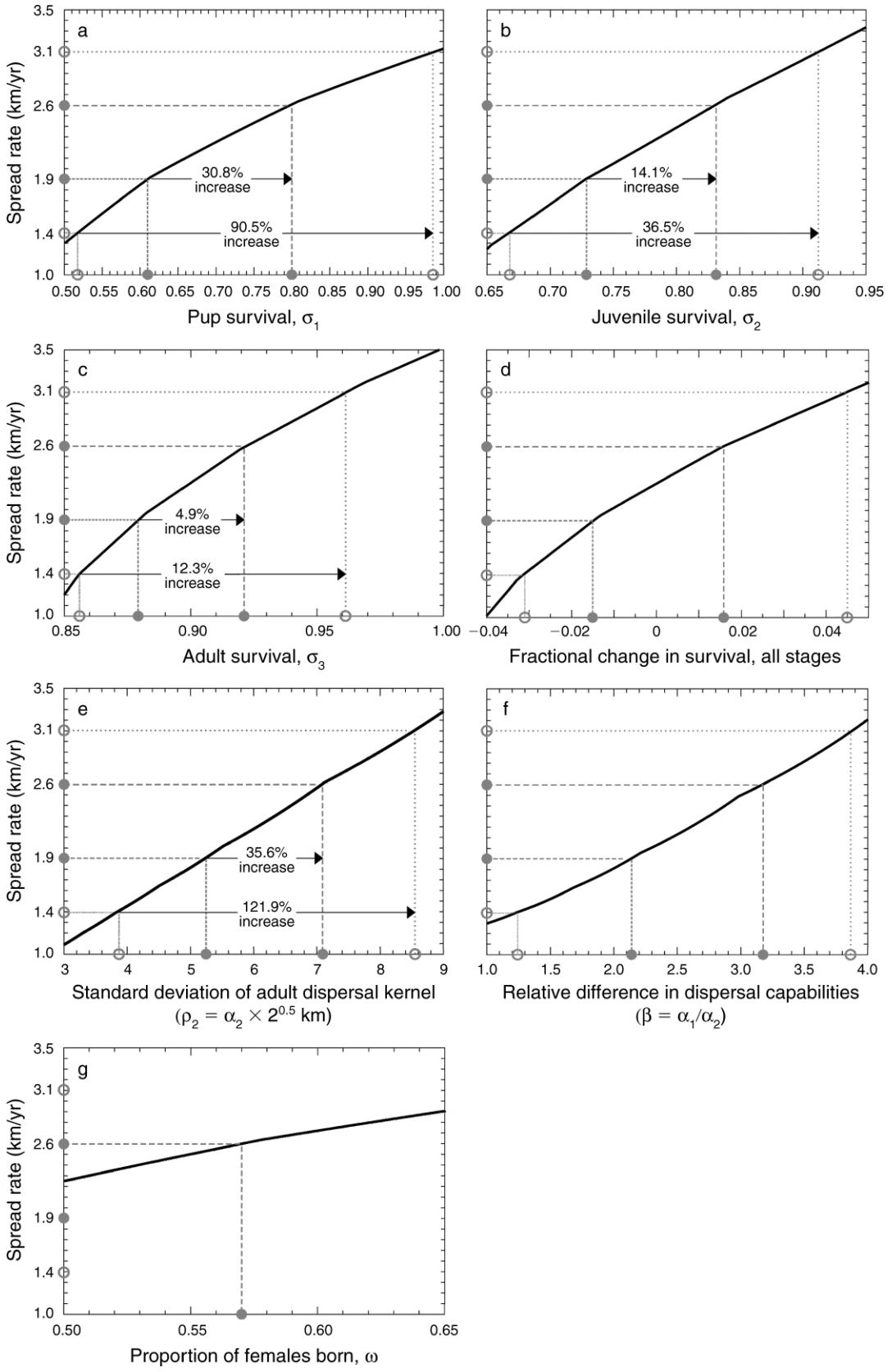
of ~4.6% ($= \ln \lambda$), which is in close agreement with the 5% population growth rates reported for California sea otter populations between the years 1938 and 1972 (Estes 1990).

When appropriately adjusted, each of the parameters in Table 2 can alone account for the difference in spread rate between the northern and southern otters. However, the required magnitude of change varies greatly among the parameters. For example, from Table 2, under the no advection scenario, the standard deviation of the adult dispersal kernel for the southern subpopulation needs to be 121.9% higher than that of the northern otters in order to account for the larger spread rate southward. However, with assumed advection constants of 0.2 km/yr and 0.5 km/yr, substantially smaller increases of 81.6% and 35.6% are required. For the same three advection scenarios, the required increases for each of the survival parameters are: pup survival 90.5%, 63.7%, and 30.8%; juvenile survival 36.5%, 27.0%, and 14.1%; and adult survival 12.3%, 9.4%, and 4.9%. We also calculated the fractional change in the default survival values required to account for the differences in spread rate for each of the advection scenarios. For example, assuming no advection, the northern spread rate of 1.4 km/yr is obtained by an across-the-board decrease of 3.1% in the default survival rates (i.e., multiplying each of the three default survival rates by 0.969), while the southern spread rate of 3.1 km/yr requires an across-the-board increase of 4.5% to each of the default survival rates. If advection plays a role in dispersal, the required changes in survival are even smaller: −2.5% (north) and 3.3% (south) assuming an advection constant of 0.2 km/yr; and −1.5% (north) and 1.6% (south) assuming an advection constant of 0.5 km/yr.

Fig. 2 provides graphical representations of the degree to which spread rate is affected by changes in survival, dispersal distance, and proportion of females born. For example, Fig. 2d gives a visual representation of the considerable effect that a simultaneous fractional change in survival rates has on spread rate, while the graphs depicted in Fig. 2e, f depict how spread rate is much less so affected by changes in the dispersal-related parameters. Fig. 2g depicts the likely interval over which the proportion of females spans (Kenyon 1969, Bodkin et al. 1993), which is not broad enough to account for the large disparity in spread rates between the northern and southern subpopulations of sea otters. Similarly, Table 3

shows that spread rate has relatively little dependence on juvenile maturation rate (i.e., first year of reproduction).

Based on our sensitivity and elasticity analyses, the most pronounced changes in wave front speed should come from changes in adult survival (Fig. 3), which is further substantiated by the data in Table 2 and Fig. 2c, where it is seen that compared to other model parameters (Fig. 2a, b, e, f, g), the disparity in spread rate can be accounted for by disproportionately small changes in adult survival. Our sensitivity and elasticity results are in agreement with similar analyses conducted by Gerber et al. (2004). Their results showed that the California sea otter population growth rate is more sensitive to changes in survival than growth or reproduction, and specifically that the growth rate is more sensitive to adult (4–12 years) survival than to any of the younger life stages.

Due to some uncertainty as to which dispersal kernel might best represent otter movement, our model was rerun assuming Gaussian dispersal, the results of which differ negligibly from those obtained when dispersal is Laplacian (compare Table 2 with Appendix A: Table A1). To allow for the possibility that California sea otters might reproduce earlier than age four, we also present results assuming age three as the first year of reproduction. As is the case under the default conditions, spread rate is most affected by changes in survival instead of dispersal (compare Table 2 with Appendix A: Table A2). However, the ranges of survival rates required to account for the disparity of spread rates are, in general, wider when otters are assumed to reproduce earlier.

DISCUSSION

Between the years 1938 and 1972, California sea otters spread northward and southward along the coast at surprisingly different rates. Lubina and Levin (1988) modeled the spread using a reaction-diffusion approach and they proposed three hypotheses to explain the disparity in spread rates: an advection hypothesis, a population growth hypothesis, and a dispersal hypothesis. They suggested advection as a potential factor due to the presence of a southerly flowing current throughout the range of the California sea otter. The other two hypotheses stem from Equation 2 ($c = 2(rD)^{1/2}$), which represents the asymptotic wave speed for their model and involves measures of population growth (r) and diffusivity (D). Lubina and Levin (1988) argued that the

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FIG. 2. Calculated spread rates, without advection, as a function of (a) pup survival, (b) juvenile survival, (c) adult survival, (d) fractional change in survival, (e) the standard deviation of the adult dispersal kernel, (f) the relative difference between the standard deviations of the pup/juvenile vs. adult dispersal kernels, and (g) the proportion of females born. For (d), a fractional change of 0.03 refers to a 3% increase in the default survival parameter values for each of the three life stages. For (a–e) and (g), all the remaining parameters have their default values. The same is true for (f), except for the standard deviation of the adult dispersal kernel, which is assumed to be 4.20 km so that the calculated spread rates span the interval of observed spread rates. The open circles along the horizontal axes correspond to the measurements that would account for the northern (1.4 km/yr) and the southern (3.1 km/yr) spread rates assuming the advection constant is 0.0 km/yr, while the closed circles correspond to the measurements that would account for the northern (1.9 km/yr) and the southern (2.6 km/yr) spread rates assuming the advection constant is 0.5 km/yr.

TABLE 3. Effect of juvenile maturation rate on spread rate.

Year of first reproduction	Juvenile years	Juvenile maturation rate	Spread rate (km/yr)
6	2–5	0.25	1.88
5	2–4	0.33 (default)	2.25
4	2–3	0.50	2.72
3	2	1.00	3.27

Note: Assuming an extreme interval of juvenile maturation rates from 0.25 to 1.00 cannot account for the observed difference in spread rates between the northern (1.4 km/yr) and southern (3.1 km/yr) subpopulations of California sea otters (using default values for the remaining parameters). The maturation rates are based on the assumption that there is an equal proportion of otters in each of the specified juvenile years.

observed 2.2 times greater spread rate to the south was most likely due to dispersal differences between the two subpopulations, which according to Eq. 2, corresponds to a 4.9 times difference in diffusion constants.

To conclusively test whether the different spread rates were more so due to differences in population growth vs. dispersal, one would need to separately characterize the northern and southern California sea otters with region-specific vital rates and dispersal distance data. However, in the absence of such information, a stage-structured integrodifference matrix model allowed us to investigate whether minor differences in stage-specific parameter values could account for the large disparity in spread rates, perhaps providing a more parsimonious explanation than the large differences in diffusivity for which Lubina and Levin (1988) argued.

Krkosek et al. (2007) used a stage-structured integrodifference matrix model of California sea otter spread from 1914 to 1986 to conclude that fat exponentially unbounded dispersal kernels best match range expansion data, thereby implying an overall accelerating invasion rate. However, if they had limited their analysis to the years 1938–1972 when the expansion rate was essentially linear, then perhaps the Laplace kernel used in our model would have provided the best fit. Another point of contrast comes with the fact that their analyses, much like those conducted by Lubina and Levin (1988), were constrained by the assumption that there were no demographic differences between the northern and southern otters.

Using the methods of Neubert and Caswell (2000), our analyses show that when appropriately adjusted, each survival- and dispersal-related parameter can account for the difference in spread rate between the northern and southern otters and that the required magnitude of change varies greatly among the parameters. For example, if one assumes no advection and that the northern and southern sea otters share identical vital rates, then the standard deviation of the adult dispersal kernel for the southern subpopulation needs to be 121.9% greater than that of the northern otters in order to account for the larger spread rate southward (Table 2 and Fig. 2e). However, assuming such a large asymmetry between the two groups remains an unsatisfying explanation. On the other hand, if one assumes that the difference between the northern and southern sea otters
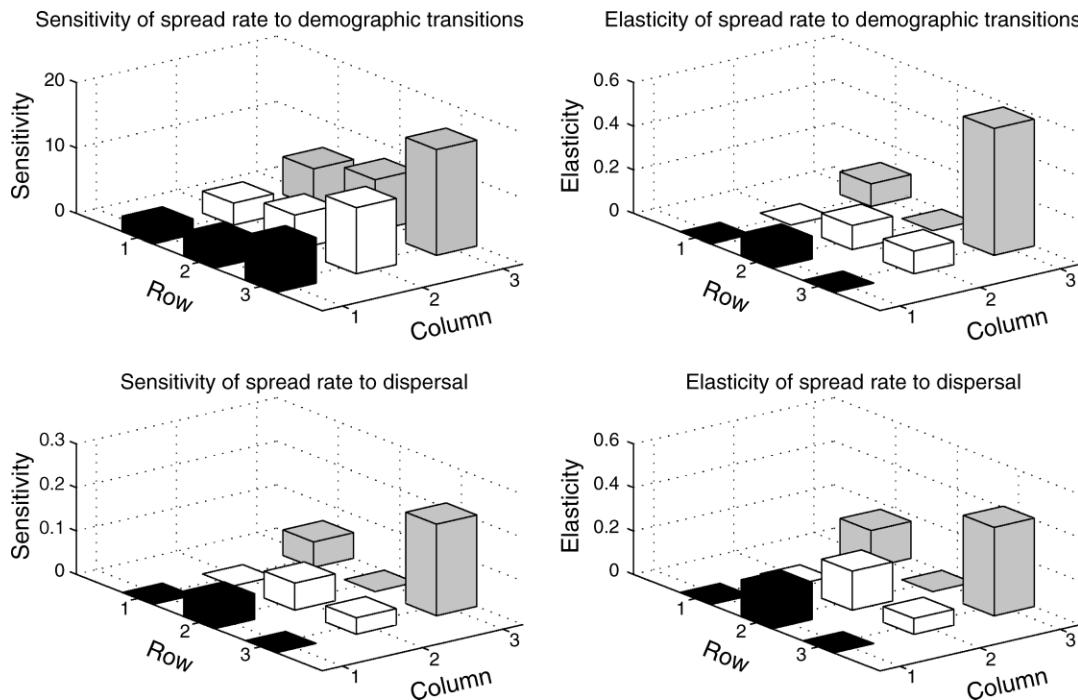

FIG. 3. Calculated measures for the sensitivity and elasticity of spread rate to changes in the entries of the demographic matrix **B** (Eq. 4) and the dispersal matrix **K** (Eq. 5). All elasticities were rescaled to sum to 1. The results indicate that the most pronounced effect on spread rate should come from changes in adult survival.

is in survival instead of dispersal, then significantly smaller increases are required (Table 2 and Fig. 2a–c).

Our work demonstrates that relatively minor differences in survival, especially among adults, can have marked effects on the spread rate of sea otters. To see why this is not unexpected, it is important to note that, as was the case in the examples provided in Neubert and Caswell (2000), the sensitivities and elasticities of spread rate to changes in the elements of demographic matrix **B** (in Eq. 4) are highly correlated with the associated sensitivities and elasticities of population growth rate λ (see Appendix B: Figs. B1 and B2). Furthermore, the growth rates for long-lived populations tend to be most sensitive to the least variable survival parameter (Pfister 1998), which is that of adults in the case of the California sea otter. Therefore, one would expect that minor changes in adult survival would result in disproportionate changes in population growth and consequently spread rate.

However, the disproportionate effects of adult survival on spread rate do not discount the effects that survival rates in the younger life stages might also have on spread rate. For example, as mentioned in the *Methods* section, pup survival appears to be the most highly variable parameter among sea otter populations. Therefore, despite the relative insensitivity in our model to this particular parameter (Fig. 2a and Fig. 3), the natural variation in pup survival may nonetheless contribute significantly to differences in spread rate.

If the northern and southern sea otter groups are assumed to have proportional differences in survival rates in more than one life stage, then the required differences in any one life stage are extremely small. For instance, in the presence of an advection effect of 0.5 km/yr, the 2.2-fold difference in spread rate is accounted for when the northern and southern subpopulations have survival rates that are only 1.5% lower and 1.6% higher, respectively, than the default values for our model (see Table 2 and Fig. 2d for the corresponding results).

Based on the above discussion, our analyses clearly lend support to the hypothesis that the disparity in spread rates between the northern and southern otters is most likely due to different intrinsic growth rates. Many of the estimates within the literature for otter survival rates span intervals wide enough on either side of our default parameter values to account for the different spread rates, especially in the likely case that advection plays at least a minor role in otter movement.

In light of evidence that strong surf conditions influence mortality rates in Alaska sea otters (Kenyon 1969), Lubina and Levin (1988) speculate that the rough winter surf in Northern California may adversely affect foraging among juveniles. In addition, Jameson and Johnson (1993) have suggested that inclement weather is probably the most important cause of pup mortality in the California sea otter population. Since our results show that spread rate responds strongly to across-the-board changes in survival, it would be interesting to investigate whether, in general, the California sea otter experienced more severe weather while expanding northward vs. southward between the years 1938 and 1972.

Even though Lubina and Levin (1988) argue that dispersal differences were responsible for the disparity in spread rates, they mention that habitat-dependent mortality constitutes the major competing hypothesis, and that it is quite reasonable to assume differences exist in both factors: dispersal and mortality. We also suspect that no single hypothesis accounts for such a large disparity in spread rates. However, we contend that our results demonstrate that the difference in spread rate was due, for the most part, to minor differences in survival rates instead of large differences in dispersal capabilities. Recent results from Tinker et al. (2006) indicate that our claim is indeed very plausible. They found that vital rates among the California sea otter exhibited substantial spatial (and temporal) variation from 1992–2001. In particular, survival, especially among juveniles and subadults, was lowest in the northern range and highest toward the southern extent. However, since the analyses from Tinker et al. (2006) were based on data collected after the period that modeled here (i.e., 1938–1972), their applicability regarding our results should be treated cautiously.

The research presented here provides some direction for future work. For example, since many of the current parameter estimates for our model span intervals large enough to account for the observed disparity in spread rates, future data collection efforts need to include enough data to tease apart what may likely be very minor differences in demography between the northern and southern California sea otters. In a broader context, the methods from Neubert and Caswell (2000), and our surprising results regarding the sensitivity of spread rate to survival, also have potential implications regarding the spread of invasive species. It is important that future research emphasize not only the dispersal-related traits of an invading species, but its demographic characteristics as well (e.g., Neubert and Parker 2004, Buckley et al. 2005).

A disproportional increase in spread rates due to long-distance dispersal events has been repeatedly predicted by many models of population spread (Kot et al. 1996, Higgins and Richardson 1999, Clark et al. 2003, Hastings et al. 2005), and the existence of such elusive events has been assumed in order to account for otherwise unexplained fast spread rates (e.g., Cain et al. 1998, Clark et al. 1998, Powell and Zimmermann 2004). Using a stage-structured model, Caswell et al. (2003) found that differences in spread rates among bird species were most likely due to differences in the tail of the dispersal. It is quite possible that such long-distance dispersal events, if they occurred among the California sea otter, were not adequately represented by our choice of a Laplace dispersal kernel. However, long-distance dispersal events, which are highly stochastic, are unlikely

to account for the persistent difference in spread rates between the northern and southern sea otter populations over nearly three decades.

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APPENDIX A

Model results assuming Gaussian dispersal (instead of Laplacian dispersal), along with model results assuming age 3 as the first year of reproduction (instead of age 4) (*Ecological Archives* E090-176-A1).

APPENDIX B

Correlation between the sensitivities (respectively elasticities) of spread rate and population growth rate λ to changes in the demographic transitions found in matrix **B** (Eq. 4) (*Ecological Archives* E090-176-A2).