Appendix A

OREGON SEA OTTER POPULATION MODEL (ORSO, VERSION 1.0), USER INTERFACE APP

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INTRODUCTION/CONTEXT

The Oregon Sea Otter Population Model (ORSO; Version 1.0[1]) has been developed as a user-friendly interface for community members and managers to explore possible sea otter recovery patterns after a reintroduction. The model can contribute to responsible stewardship of sea otters and other nearshore marine resources. ORSO's overall goal is to anticipate the approximate magnitude of expected population growth and spread of sea otters in coastal Oregon in the foreseeable future under different scenarios of translocation or reintroduction. This information will help in evaluating management options and anticipating ecological and socioeconomic impacts in a spatially and temporally explicit way. However, experience from prior reintroductions has demonstrated that it is extremely difficult to predict where translocated animals will settle, how many will remain following release, and how soon population growth will commence. Therefore, this model is not intended to predict specific outcomes but rather to explore a range of outcomes that may be most likely given an extensive scope of model inputs and assumptions.

METHODS

Overview

ORSO has been developed using information from published reports and previous examples of sea otter introductions, population recovery, and range expansion in the northeast Pacific. In particular, data collected from areas of sea otter recovery in California, Washington, and Southeast (SE) Alaska can be used to inform our expectations for sea otter colonization and recovery in Oregon. The distinct habitats and differing historical contexts of these neighboring populations preclude a direct translation of expected dynamics; however, the data from studies of these populations can be used as the basis for developing a predictive model tailored to Oregon's habitat configuration.

1 See https://nhydra.shinyapps.io/ORSO_app/.

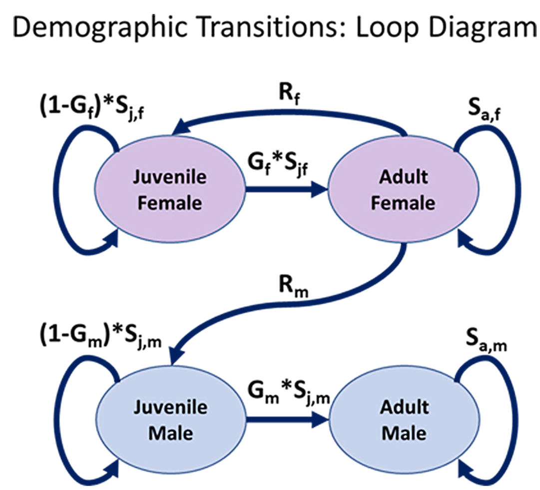
Spatially structured population models have been constructed for other sea otter populations in North America and have proved effective at predicting patterns of population recovery and range expansion in diverse habitats (Udevitz et al. 1996, Monson et al. 2000a, Tinker et al. 2008, USFWS [U.S. Fish and Wildlife Service] 2013, Tinker 2015, Tinker et al. 2019a, Tinker et al. 2021). By building on these previously published model designs and incorporating locally relevant data on sea otter vital rates, movements, habitat quality, and environmental parameters, it should be possible to define realistic boundaries for the expected patterns of population abundance and distributional changes over time. These patterns can then be used as a basis for designing an appropriate monitoring design for sea otters and the habitats they are expected to affect as change occurs over time. Such a model can also be used to combine and integrate information on habitat impacts and sea otter monitoring data over time, allowing projection updates and modifications to monitoring methods; in essence, ORSO aims to be a quantitative tool for conducting adaptive management.

Using data from comparable sea otter populations and geographic areas, primarily California (but augmented by data and models from SE Alaska and Washington), we developed a spatially explicit, simulation-based population model for evaluating a range of realistic scenarios of sea otter reintroduction to Oregon. ORSO incorporates demographic structure (age and sex), density-dependent variation in vital rates, habitat-based variation in population growth potential, dispersal and immigration, and a spatial diffusion approach to model range expansion over time.

Demographic Processes

As with previous sea otter models (Tinker 2015), the core of ORSO is a stage-structured projection matrix describing demographic transitions and thus population growth over time (Caswell 2001). The projection matrix is used to model transitions among four age/sex classes (c = 1:4): (1) juvenile females (weaning to three years old), (2) adult females (three to 20 years), (3) juvenile males (weaning to three years), and (4) adult males (three to 20 years). Transition probabilities are described by three parameters: stage-specific annual survival (S), *adult female reproductive output* (R, defined as the probability an adult female gives birth to and successfully weans a male or female pup into the juvenile age class), and the *growth transition parameter* (G, the probability that juveniles advance to the adult age class, conditional upon survival). These demographic transitions can be visualized as a loop diagram (Figure A.1). Survival rates are age- and sex-dependent and are assumed to vary stochastically and as a function of population density (Siniff and Ralls 1991, Eberhardt and Schneider 1994, Monson et al. 2000b, Tinker et al. 2006).

Figure A.1. Loop diagram of demographic transitions for sea otters in a population model.



Reproductive contributions to juvenile stages by adult females are assumed to reflect a 50:50 sex ratio at birth and are estimated as

$$R_{f/m} = S_{a,f} \cdot \tfrac{1}{2} b \cdot w \tag{1}$$

where b is the birth rate (held constant at 0.98; Tinker et al. 2006) and w is the weaning success rate, which is stochastic and density-dependent (Monson et al. 2000b). Note that Equation 1 also reflects the fact that pup survival is conditional upon adult female survival. Growth transitions for each sex are calculated using the standard equation for fixed-duration age classes (Caswell 2001):

$$G_{f/m} = \left(\frac{\left(S_{j,f/m}/\lambda\right)^{T} - \left(S_{j,f/m}/\lambda\right)^{T-1}}{\left(S_{j,f/m}/\lambda\right)^{T} - 1} \right) \tag{2}$$

where T is the stage duration for juveniles (2.5 years) and λ is the annual rate of population growth associated with a specified matrix parameterization. Combining all parameters into matrix form, we estimate annual population dynamics using matrix multiplication (Caswell 2001):

$$\begin{pmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \\ n_{4,t+1} \end{pmatrix} = \begin{pmatrix} \left(1-G_f\right)S_{j,f} & R_f & 0 & 0 \\ G_f \cdot S_{j,f} & S_{a,f} & 0 & 0 \\ 0 & R_m & \left(1-G_m\right)S_{j,m} & 0 \\ 0 & 0 & G_m \cdot S_{j,m} & S_{a,m} \end{pmatrix} \times \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \end{pmatrix} \tag{3}$$

In Equation 3, the population vector $n_{c,t}$ tracks the abundance of otters in each age/sex class in year t of a model simulation. At low population abundance (defined as $\Sigma\, n_{c,t} < 50$), we adjust Equation 3 to account for demographic stochasticity, as described elsewhere (Morris and Doak 2002).

Parameterization of vital rates was based on published data for sea otter populations in California, Alaska, and Washington (Siniff and Ralls 1991, Monson and Degange 1995, Garshelis 1997, Gerber et al. 2004, Tinker et al. 2006, Laidre et al. 2009, Tinker et al. 2017, Tinker et al. 2021). Results from past work have suggested that much of the variation in age-specific survival and weaning success is explained by density with respect to carrying capacity (K), although individual variation and random year-to-year variation (i.e., environmental stochasticity) can also be important (Staedler 2011, Miller et al. 2020). Accordingly, following methods used in other simulation models (Gerber et al. 2004, Bodkin and Ballachey 2010), we sampled from the survivorship schedules reported for populations at varying densities (ranging from low-density, rapidly growing populations to high-density populations at K) to inform our model. We collapsed all age-structured data down to the age/sex classes using geometric averaging of the annual rates for year classes in each age class, and we accounted for uncertainty by drawing from *Beta* distributions, with means and variances corresponding to the published data sets. Resampling from these distributions, we created a table of 1000 sets of vital rates (survival, birth rates, and weaning success rates), reflecting the full range of potential demographic schedules for sea otter populations having biologically feasible growth rates ($0.90 < \lambda < 1.22$). We calculated the value of λ associated with each set of vital rates (using standard matrix algebraic methods; Caswell 2001) to facilitate the use of these vital rates for parameterizing model simulations while allowing for both environmental stochasticity and density dependence. Specifically, in year t of a simulation, we calculate the expected growth rate using a stochastic theta-logistic model:

$$\lambda_t = e^{r_{\max}\left(1-\left[N_{t-1}/K\right]^{\theta}\right)+\varepsilon_t} \tag{4}$$

where r_{max} is the maximum instantaneous growth rate for sea otters ($r_{max} = 0.2$; Estes 1990), N_{t-1} represents the total abundance of otters in the previous year of the simulation ($N_{t-1} = \Sigma n_{c,t-1}$), K is the local carrying capacity or abundance at equilibrium (see the "Estimating K and Habitat Effects" section), Θ allows for nonlinear effects of density-dependence, and ε represents the effect of environmental stochasticity. Furthermore, ε_t is drawn randomly from a normal distribution with a mean of 0 and standard deviation σ, a user-specified parameter where $0 < \sigma < 0.2$ (Tinker et al. 2021). Having calculated λ_t, we then randomly draw a set of vital rates after filtering the table to just those sets with associated λ equal to our computed λ_t, and we use these to parameterize Equation 3 in year t of the simulation. We note that demographic processes are expected to be different during the years immediately following a reintroduction as a new population becomes established. Thus we allow for modified dynamics during this establishment phase, as described below (see the Establishment Phase section).

Spatial Processes

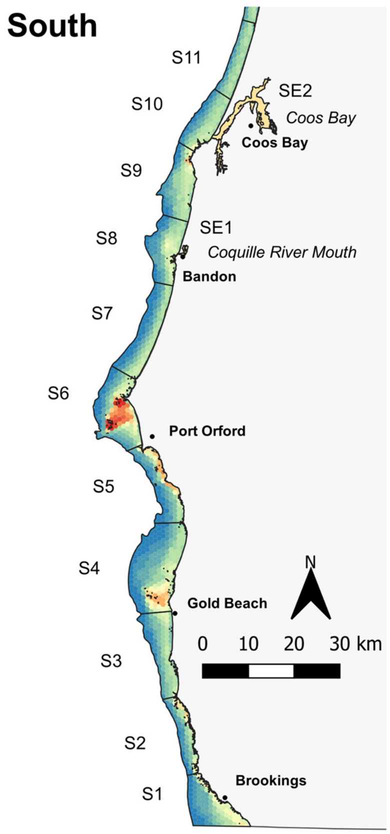
The processes of population dynamics and regulation (as described by Equations 3 and 4) occur at relatively small scales in sea otter populations, resulting in potentially divergent population trends and densities at different locations within a regional population (e.g., Laidre et al. 2001, Bodkin et al. 2002, Tinker et al. 2017). To accommodate this demographic structure, previous modeling efforts have divided regional populations into subpopulations and tracked demographic processes within each subpopulation, as well as the movement of animals between subpopulations (Tinker 2015). The use of spatially structured models facilitates the incorporation of range expansion, as new subsections of habitat can be sequentially added into the model to reflect a population's expansion along a coastline (Tinker et al. 2008). Range expansion has also been modeled effectively as a continuous process using diffusion models (Lubina and Levin 1988, Williams et al. 2017); however, to increase computational efficiency and parameter estimation, continuous diffusion dynamics can be approximated within a discretized matrix model by incorporating key features and predictions (e.g., the asymptotic invasion speed of the frontal edge of a population). Discretization can be especially effective if the population is divided into relatively small subsections such that demographic processes vary between subsections but can be assumed to be approximately homogeneous within sections.

In the case of ORSO, because range expansion was one of the key features we wished to address, we divided the region of interest (all coastal areas of Oregon) into 42 coastal sections, each spanning approximately 15 km of the outer coastline and/or encompassing a single coastal estuary (Figure A.2). Annual intrinsic dynamics (changes in abundance due to births and deaths) are modeled for each coastal section using Equations 3 and 4; however, each of these subpopulations is embedded within a range-wide meta-population that allows for the dispersal of animals between occupied sections. Range expansion of the meta-population along the coast is incorporated into the model by allowing unoccupied sections to be "colonized" by animals from neighboring occupied sections, with the rate of new sections' colonization constrained to maintain a prespecified rate of the population front's advancement along the coast (henceforth v, the asymptotic frontal wave speed, measured in km/year; Figure A.3). We treat v as a user-specified parameter, noting that a realistic range of values based on previous studies is 1–5 km/year (Lubina and Levin 1988, Tinker et al. 2008).

The dispersal of sea otters between coastal sections is modeled and tracked separately for each age/sex class in ORSO, reflecting the different mobility and dispersal capability of sea otters of different ages and sex (Jameson 1989, Tarjan and Tinker 2016, Breed et al. 2017). We used previously collected data from radio-tagged sea otters to estimate probabilities that otters of each age/sex class emigrate from coastal section i to coastal section j in a given year. To account for occasional (but potentially important) long-distance dispersal, we did not restrict dispersal to adjacent cells only; rather, we used the empirical distribution of annual dispersal distances to parameterize this step. For each tagged animal and each year of monitoring, we computed the *net annual linear displacement* (NLD; Tarjan and Tinker 2016), defined as the number of kilometers between an animal's location at the start of the year and its location at the end of the year in terms of the swimmable distance along the coast.[2] We used maximum likelihood methods to fit exponential distributions to NLD data collected from otters of each age/sex class (implemented using the "fitdistr" library in the "R" software application). We then used the fitted exponential distributions to calculate the cumulative distribution function (CDF) values at z_i, defined as the average distance from the centroid to the boundary of each coastal section i: These computed CDF values correspond to the mean probability of remaining within coastal section i for an otter of a specified age/sex class (Tinker et al. 2008), the inverse of which represents $\delta_{c,i}$, the per capita probability of emigration from section i for an otter of class c.

2 The distinction of swimmable distance is important: We used swimmable distances as opposed to Euclidean distances because of the complex coastal topography of sea otter habitats and the fact that sea otters cannot travel overland. For the purpose of calculating NLD, and for all other distance calculations described in the methods, we used a Least Cost Paths function (implemented using the "gdistance" package in the "R" software application), which estimates the shortest distance between two points while accounting for the "costs" of moving through different habitat classes that might be encountered between the points. By assigning a prohibitively high "cost" to moving overland, we ensure that the Least Coast Path distance is the shortest distance through water only.

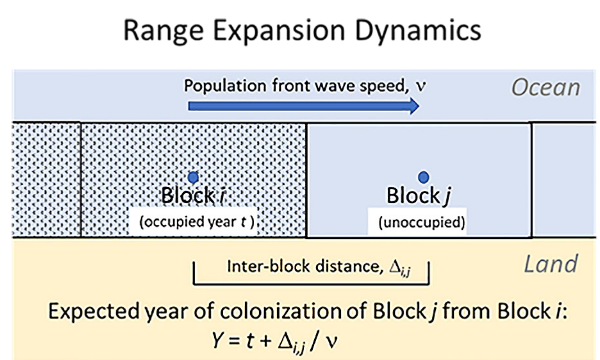
Figure A.2. Results of a habitat-based model of sea otter *K* to the Oregon coast (Kone et al. 2021).



Note. This figure is the same as Figure 3.4 in Chapter 3. It illustrates the spatial configuration of coastal habitat in Oregon used for population modeling. Coastal habitat sections (labeled polygons) show the basic geographic unit for modeling demographic processes, while the colored spatial grids within these polygons show the relative expected density at *K* based on a previously developed model of habitat-density relationships (Kone et al. 2021, Tinker et al. 2021).

The actual number of otters of class *c* emigrating from section *i* in year *t* ($d_{c,i,t}$) was randomly drawn from a Poisson distribution with rate parameter $n_{c,i,t} \cdot \delta_{c,i}$. To determine where emigrating otters dispersed to, we first computed the swimmable distances between all pairwise combinations of section centroids, and for each pairwise distance ($\Delta_{i,j}$), we used the fitted exponential functions to calculate the probability density function (PDF) values at $x = \Delta_{i,j}$. Then during each year of a model simulation, we identified the set of all other currently occupied sections ($j = 1,2... J, j \neq i$), rescaled the PDF values such that $\Sigma PDF_{i,j} = 1$, and then drew randomly from a multinomial distribution with probability parameters $PDF_{i,j}$ to determine which coastal section *j* would "receive" the emigrating otters. In this way, emigration was treated probabilistically and not deterministically so that each iteration of the simulation model results in different dispersal outcomes. We note that spatial processes (dispersal and range expansion) are expected to differ during the post-introduction establishment phase, and thus, we allow for modified spatial dynamics during this period, as described below (see the upcoming Establishment Phase section).

Figure A.3. Schematic drawing illustrating how the model incorporates range expansion of a sea otter population from occupied habitat into unoccupied habitat.



Estimating *K* and Habitat Effects

Carrying capacity (*K*) is defined as the population size that can be supported in a specified environment over the long term, and this equilibrium abundance is generally dictated by some limiting resource (i.e., prey, nesting sites, refuge habitat). In sea otters, *K* is thought to be primarily determined by prey resource abundance and productivity. Equilibrium abundances of sea otter populations have been found to be highly variable, with local densities ranging from 0.5 sea otters per square kilometer of *benthic habitat* (defined as a benthic substrate between the low tide line and the 40-m depth contour) to over 20 sea otters per square kilometer.

Previous studies have found that the density at *K* varies as a function of certain habitat features (presumably because these habitat features are proxies for prey productivity). However, the precise nature of these relationships varies across regions (e.g., Laidre et al. 2001, Laidre et al. 2002, Burn et al. 2003, Gregr et al. 2008, Tinker et al. 2021). In California, areas of rocky substrate were found to support higher densities than areas of unconsolidated sediment (Laidre et al. 2001), while in Vancouver Island, it was areas of complex coastline that supported higher densities (Gregr et al. 2008). And in SE Alaska, some of the highest densities were supported in soft-sediment bays (Esslinger and Bodkin 2009). Given this variation, it is difficult to predict which habitat types in Oregon will eventually support high or low densities of sea otters. However, given the proximity to California and the general similarity of habitat types between these regions, we believe California habitat-density relationships provide the best starting point for predicting these relationships in Oregon. Therefore, a recently developed model predicting local *K* as a function of biotic and abiotic habitat variables (Tinker et al. 2021) has been applied to the equivalent spatial layers of habitat variables in Oregon to project potential *K* at fine scales throughout the state (Kone et al. 2021).

We use this projected *K* data layer to parameterize ORSO, interpolating projected equilibrium densities from Kone et al. (2021) at each cell *h* of a hexagonal grid laid over the study area (Figure A.2). The absolute number of otters expected within the grid cell *h* at *K* is calculated as the product of the expected equilibrium density (K_h^d) and the area of that cell (A_h). Summing this product over all habitat cells contained within coastal section *i* (h = 1, 2, ... H_i) gives the expected abundance at *K* for that section (used for Equation 4). Dividing by A_i (the total area of habitat in section *i*) gives the mean expected density at *K* for coastal section *i*:

$$K_i^d = \frac{1}{A_i} \sum_{h=1}^{H_i} K_h^d \cdot A_h \qquad (5)$$

Establishment Phase

Previous sea otter translocations and reintroductions have shown that the years immediately after reintroduction can be a period of great uncertainty (Jameson et al. 1982, Bodkin et al. 1999, Carswell 2008, Bodkin 2015). During this population *establishment phase*, there is limited population growth and often a significant decline in abundance, associated with elevated mortality and the dispersal of a substantial proportion of animals away from the release site. Otters that disperse from the introduction site may settle at other areas of suitable habitat within the region (as occurred in SE Alaska), return to their former home ranges if possible (as occurred at San Nicolas Island), or move entirely out of the region (as was suspected of having occurred for some animals in the Oregon translocation, believed to have moved north to join the Washington or British Columbia populations). Notably, in all cases, there is likely to be significant mortality for both dispersing and non-dispersing animals. Thus, the "typical" patterns of density-dependent population growth, dispersal, and range expansion, described in the previous sections, only emerge after this establishment phase, which may extend for five to 20 years after the initial translocation (Jameson et al. 1982, Bodkin et al. 1999, Carswell 2008, Bodkin 2015).

To model establishment phase dynamics, we define several additional parameters and associated functions. The first of these is *E*, the expected duration of the establishment phase itself (in units of years). For all years where $t \leq E$, we adjust the baseline age and sex-specific survival rates ($S_{c,t}$, the random survival rates selected based on the solution to Equation 4) such that the mean growth rate (λ) is forced to 1 (i.e., no net growth on average) but with default levels of environmental stochasticity. We next define parameter *M*, the mean excess annual mortality rate during the establishment phase: This parameter, assumed to occur within the range of $0 < M < 0.5$, is used to further adjust stage-specific annual survival (*S*) rates during the establishment phase, thereby allowing for negative growth rates:

$$S'_{c,t} = S_{c,t} \cdot (1 - m_t), \quad where\ m_t \sim Beta(\alpha, \beta \mid M) \tag{6}$$

In Equation 6, the annual excess mortality rate (m_t) is drawn from a *Beta* distribution with parameters α and β, which are set so as to create a 0–1 bounded distribution with a mean of *M* and coefficient of variance of 0.25, a level of variation consistent with previously published demographic schedules (Gerber et al. 2004, Tinker et al. 2019b). The modified stochastic survival rates ($S'_{c,t}$) are used to parameterize the population projection matrix **P** (Equations 1–3) for each year during the establishment phase. Thus, if we define the initial population vector of introduced animals as $n_{c,0}$ (where $N_0 = \Sigma\, n_{c,0}$), then the survivors in Year 1 are calculated via matrix multiplication as $n_{c,1} = \mathbf{P}_0 * n_{c,0}$.

For those otters that survive the initial reintroduction, we assume that a substantial number will disperse a significant distance away from the reintroduction site. We define φ as the expected probability of dispersal away from the reintroduction site during the establishment phase ($0 < \varphi < 1$) and calculate the actual number of dispersers (D^*) as a random binomial variable:

$$D^* \sim Binomial(N_1, \varphi) \tag{7}$$

where N_1 is the number of individuals that survived the initial translocation. The stage structure of the dispersals is assigned randomly using a multinomial distribution with probabilities corresponding to the stage structure of $n_{c,1}$. Several lines of evidence suggest that the probability of post-introduction dispersal (φ) may be affected by one or more covariates, including the age structure of the introduced population and the release site habitat. Specifically, in the case of the San Nicolas translocation, it was observed that younger animals (subadults) were more likely to remain at the release sites than adults, with the latter more likely to attempt to return to their original home ranges (Carswell 2008). It has also been suggested that otters introduced into estuarine habitats may be more likely to remain resident (Hughes et al. 2019, Becker et al. 2020), and this may be especially true if enclosures are set up to retain some animals until they become familiar with estuarine prey and substrates. We therefore included two additional parameters to account for these potential covariates: We define ω as the expected ratio of dispersal probability for subadults relative to adults ($0 < \omega < 1$) and ψ as the expected ratio of dispersal probability for otters in estuaries relative to outer coast habitats ($0 < \psi < 1$). If we define φ as the probability of dispersal for a group of adults in an outer-coast environment, then the realized dispersal probability for a given section (φ_i') is calculated as

$$\varphi_i' = \varphi \cdot \left(R_{Ad,i} + \omega \cdot (1 - R_{Ad,i})\right) \cdot ((1 - Est_i) + \psi \cdot (Est_i)) \tag{8}$$

where $R_{Ad,i}$ is the ratio of adults to subadults introduced to section i, and Est_i is a switch variable that indicates whether section i is an estuary ($Est_i = 1$) or outer coast ($Est_i = 0$).

To allow for the likelihood that a significant proportion of the animals dispersing from the reintroduction site will either die or move outside of the study region (i.e., outside of coastal Oregon, possibly joining the Washington or California populations), we define parameter Ω as the loss rate for dispersing animals. The remaining dispersers, calculated as $D^*(1 - \Omega)$, are assumed to settle in one of the other coastal sections (Figure A.2), which is selected randomly from a multinomial distribution with parameters proportional to the mean *K* densities of each section (Equation 5), thereby assuming that the dispersers are more likely to settle in an area of higher-quality habitat.

An ORSO user may adjust all the above-described parameters to explore assumptions about the establishment phase and its implications for the success of a proposed reintroduction. We note that setting parameters to values close to their defaults ($E = 10$, $M = 0.15$, $\varphi = 0.9$, $\omega = 0.5$, $\psi = 0.5$, $\Omega = 0.7$) will produce dynamics that match, on average, the observed population dynamics at San Nicolas Island during the three decades after that translocation (see Table 2.1 in Chapter 2 for details).

Model Simulations

Having developed and parameterized ORSO as described in the previous sections, we use this model to conduct simulations of sea otter population dynamics in Oregon for a newly established population. Simulations are run to evaluate population growth and range expansion under different reintroduction scenarios and under varying sets of assumptions about population dynamics, as reflected by different combinations of user-specified parameters. See Table A.1 for a complete list of user-specified parameters, definitions, and suggested values. A stepwise description of model parameterization and dynamics ("pseudo-code") is as follows:

1. Select coastal sections for reintroducing sea otters and specify the numbers of animals ($N_{0,i}$) to be introduced to each section, both during the initial translocation year and, optionally, as "supplemental" additions of more otters in subsequent years ($O_{i,t}$). The age/sex composition of introduced otters is also specified: $R_{Ad,i}$ is the ratio of adults to subadults, and $R_{F,i}$ is the ratio of females to males.
2. Adjust the expected values of other parameters to investigate their effects. Parameters that can be adjusted include the maximum population growth rate (r_{max}), the environmental stochasticity in growth rates (σ), the functional shape of density-dependence (Θ), the asymptotic wave speed for population range expansion (v), the number of years required for the population to become established (E), the excess annual mortality rate during the establishment phase (M), the probability of dispersal for adults post-introduction (φ), the dispersal probability adjustment for subadults relative to adults (ω), the dispersal probability adjustment for otters in estuaries (ψ), and the proportion of dispersers lost (Ω).
3. Iterate a large number of simulations (which ORSO calls "*reps*"), each one describing "*Nyrs*" years of population dynamics. Both *reps* and *Nyrs* are user-adjustable; the default is 100 *reps* of 25 years.
4. Step through the processes of population dynamics for $t = 1, 2, \ldots$ *Nyrs*. For each year of each simulation, the model conducts the following steps:
   a. During the establishment phase ($t \leq E$), calculate the proportion of animals that disperse away from the release site (accounting for age and estuary effects), stochastically choose a target coastal section for these dispersers, and move the dispersers to that location, accounting for losses due to death and emigration out of coastal Oregon.
   b. If the establishment phase is complete ($t > E$), determine any new sections that have become occupied since the previous time step: A section is eligible to be colonized depending on its distance to a neighboring occupied section, the number of years the neighboring section has been occupied, and the value of v, as illustrated in Figure A.3.
   c. For all sections occupied at time t, calculate intrinsic population growth rates (Equation 4). Draw random sets of vital rates corresponding to $\lambda_{i,t}$ and use them to parameterize projection matrix $\mathbf{P}_{i,t}$ following Equation 3. If the establishment phase is ongoing ($t \leq E$), adjust rates accordingly based on parameter M (Equation 6). To account for spatial autocorrelation in environmental stochasticity, values of $\varepsilon_{i,t}$ are drawn from a multivariate normal distribution, with a mean of 0 and covariance matrix adjusted (using standard auto-regressive methods) to produce standard deviation σ and correlation across neighboring sections of 0.8 (Gelfand and Vounatsou 2003).
   d. If the establishment phase is complete ($t > E$), draw randomly from a Poisson distribution (with rate parameters $n_{c,i,t} \cdot \delta_{c,i}$) to determine how many (if any) otters of each age/sex class disperse from section i ($d_{c,i,t}$).
   e. Draw randomly from a multinomial distribution (with probability vector $PDF_{i,j}$) to determine which occupied sections will receive the dispersers from section i.
   f. Calculate the stage-specific change in abundance for section i in year t as

$$n_{c,i,t} = \mathbf{P}_{i,t} \cdot n_{c,i,t-1} - d_{c,i,t} + \sum_{j} a_{c,j,i,t} + o_{c,i,t} \qquad (9)$$

where $d_{c,i,t}$ represents the dispersal of animals out of section i in year t, $a_{c,j,i,t}$ represents otters dispersing into section i from any other occupied section j in year t, and $o_{c,i,t}$ represents additional supplemental otters introduced to section i (the numbers of these supplemental otters, age/sex, and number of years that otters are added are all adjustable parameters).

5. Tabulate the abundance of otters in each section for each year of each model simulation.
6. Downscale estimated densities to the scale of 1-km^2 habitat cells by spatial interpolation between section centroids, weighted by the habitat suitability index of each cell (Equation 5).
7. Summarize results graphically and in tables.

The complete "R" code used to run ORSO, as well as the associated data files needed to parameterize it, are available upon request (email ttinker@nhydra.com).

The user-specified parameters can be varied independently to produce an enormous range of different dynamics, allowing users to create and explore highly customized scenarios. For illustrative purposes, we present results for a "typical" scenario, using values provided in Table A.1.

SIMULATION RESULTS: SAMPLE SCENARIO

The ORSO model simulations can produce a broad range of projected patterns of growth and range expansion, appropriately reflecting the large amount of uncertainty about the future after a reintroduction event. The outcome after 25 years (in terms of the magnitude of growth and extent/pattern of range spread) depends upon the reintroduction scenario and the various assumptions implicit in the user-specified parameters (Table A.1). For areas of Oregon that do become occupied, the model predicts fine-scale spatial variation in sea otter densities after 25 years, explained in part by the length of time a particular area is occupied and in part by the suitability of the local habitat (Figure A.2).

Table A.1. Default values for user-specified parameters.

User parameter	Default value	Explanation
reps	100	Number of replications for population simulations
Nyrs	25	Number of years to project population dynamics
Intro_Sections	NA	Coastal section(s) for reintroduction
$N_{0,i}$	50	Number of otters introduced to each specified coastal section
O_i	3	Number of otters (annually) in supplemental introductions to section i
Nyrs_add	5	Number of years for supplementary introductions
$R_{F,i}$	.6	Proportion of introduced animals that are female
$R_{Ad,i}$	.25	Proportion of introduced animals that are adult
E	10	Expected years before the population becomes fully established (i.e., before "normal" population growth and range expansion begins)
M	.15	Mean excess annual mortality rate during the establishment phase
φ	.7	Probability of dispersal (for adults) in the establishment phase
ω	.5	Dispersal probability adjustment for subadults relative to adults
ψ	.5	Dispersal probability adjustment for otters in estuaries
Ω	.75	Proportion of post-introduction dispersers lost (i.e., die or move out of study area)
v	2	Asymptotic wave speed of range expansion, km/yr, minimum
rr_{max}	0.18	Maximum instantaneous rate of growth: default r_{max} = 0.2 (Note: exp(0.2) = 1.22 or 22% per year)
σ	0.1	Environmental stochasticity (std. deviation in log-lambda)
Θ	0.9	Theta parameter for the theta-logistic model; for the standard Ricker model, theta = 1; for delayed onset of D-D effects, use theta > 1

Note. NA = not applicable.

Running model simulations with "typical" values for user-specified parameters (Table A.1) revealed that an initial translocation of 50 otters to Coastal Section S6 (assuming 60% female and 25% adult), with supplemental additions of three juveniles per year for five years, could grow to a population of approximately 78 sea otters after 25 years (Figures A.4 and A.5), although there is considerable uncertainty around this value (between 17 and 190 otters within a confidence interval [CI] of 95%). Range expansion over this period is projected to be limited to the southern portion of the Oregon coast (Coastal Sections S1–S11; Figures A.5 and A.6). This fairly low rate of growth and range spread reflects a population establishment phase of 10 years, as well as a relatively low diffusion rate (v = 2 km/year), which is comparable to the rate of range spread observed for California and Washington State (Tinker et al. 2008, Laidre et al. 2009). We note that changing the user-specified parameters can lead to considerably different projections of both population growth and range expansion.

Figure A.4. Map of coastal Oregon showing projected sea otter abundance and distribution after 25 years.

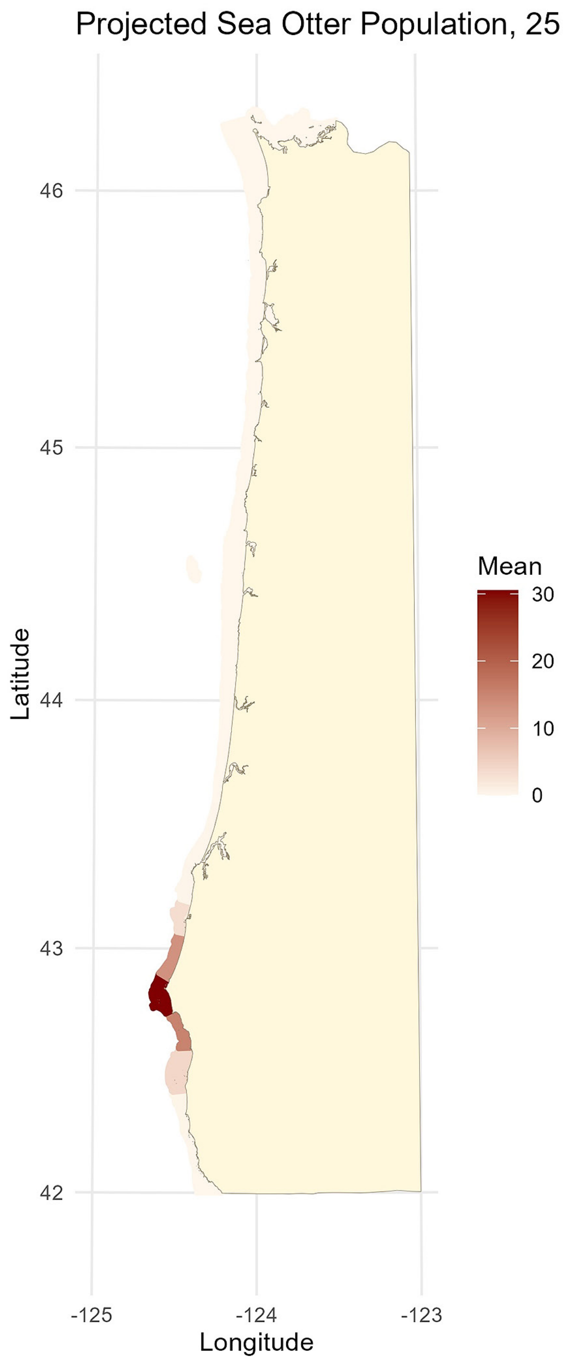
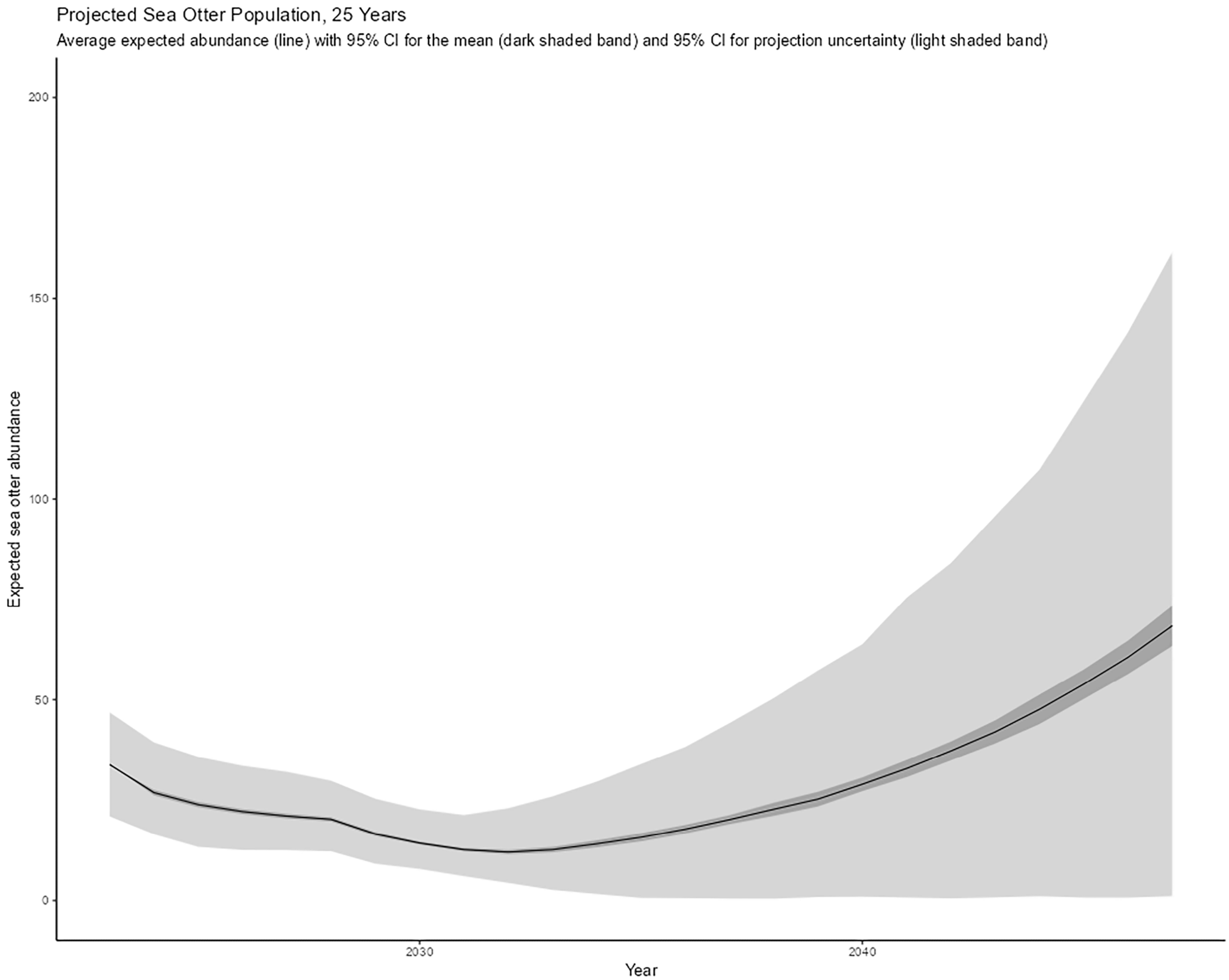


Figure A.5. Results from model simulations of sea otter population dynamics over 25 years in coastal Oregon, showing projected population trends.



Note. The light gray band shows the 95% CI for simulations; the dark gray band shows the 95% CI for the mean.

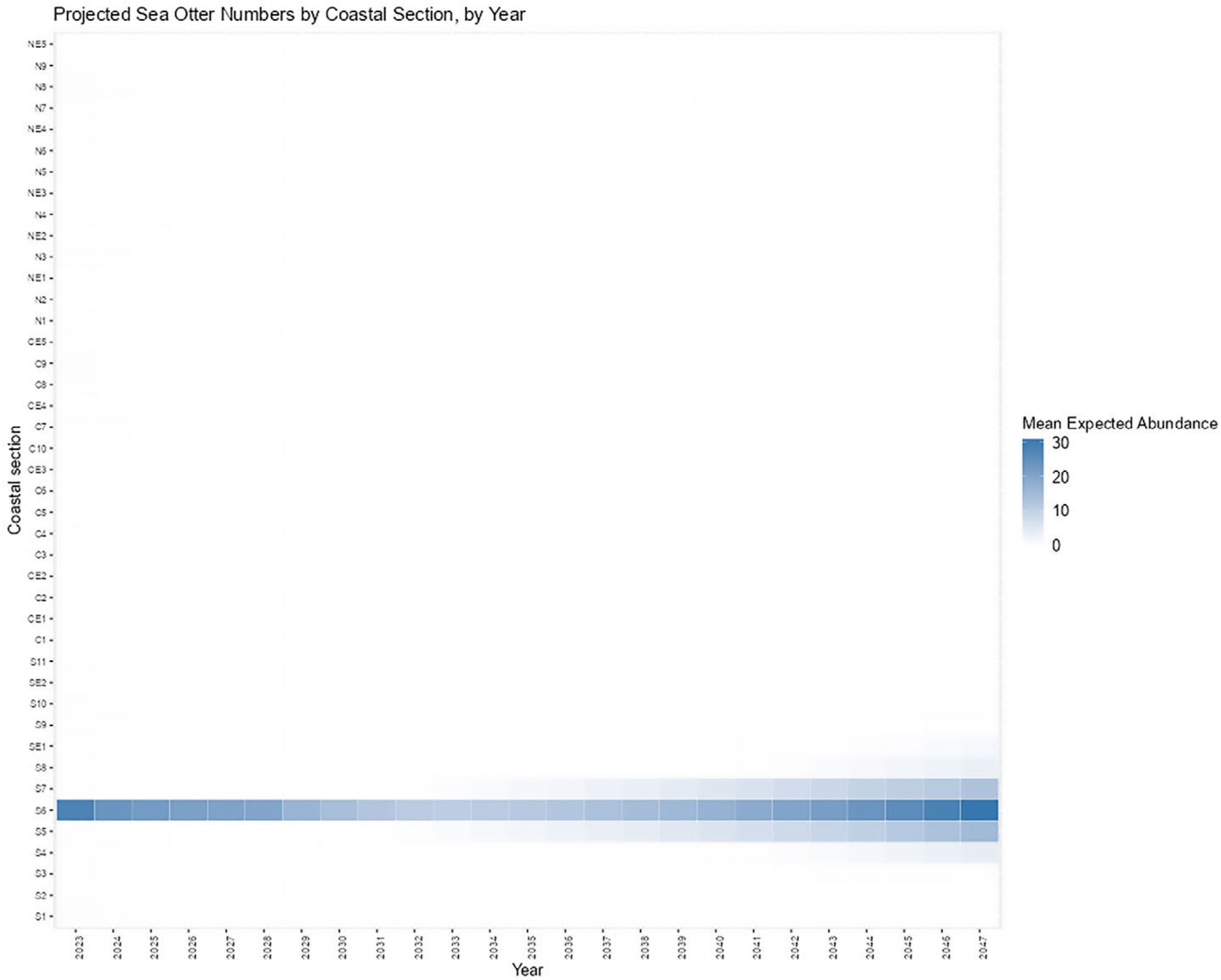
COMPONENTS OF THE ORSO APP

Overview

The web-based ORSO app is organized into several panels, which the user can navigate by clicking any of the three selection tabs embedded in the title bar at the top of the screen, as shown in Figure A.7 as items (a), (b), and (c). The panel that is active by default when the app is opened is **Setup Model Simulations**, while the other two panels (**Model Output GRAPHS** and **Model Output TABLES**) can be accessed by the user to view model results AFTER having run simulations.

When active, the **Setup Model Simulations** panel is itself divided into two main sections: a sidebar panel at left (Figure A.7d), where the user can adjust various parameters and run the simulations, and an information panel at right (Figure A.7e), which shows a map of Oregon with coastal sea otter habitat (the nearshore zone out to 60 m of depth, plus estuaries) divided into 42 numbered coastal sections. These coastal sections represent the main spatial units for

Figure A.6. Results from model simulations of sea otter population dynamics in coastal Oregon, showing a heatmap of mean expected abundance by coastal section over a 25-year period.



Note. Refer to Figure A.2 for the locations and boundaries of each coastal section.

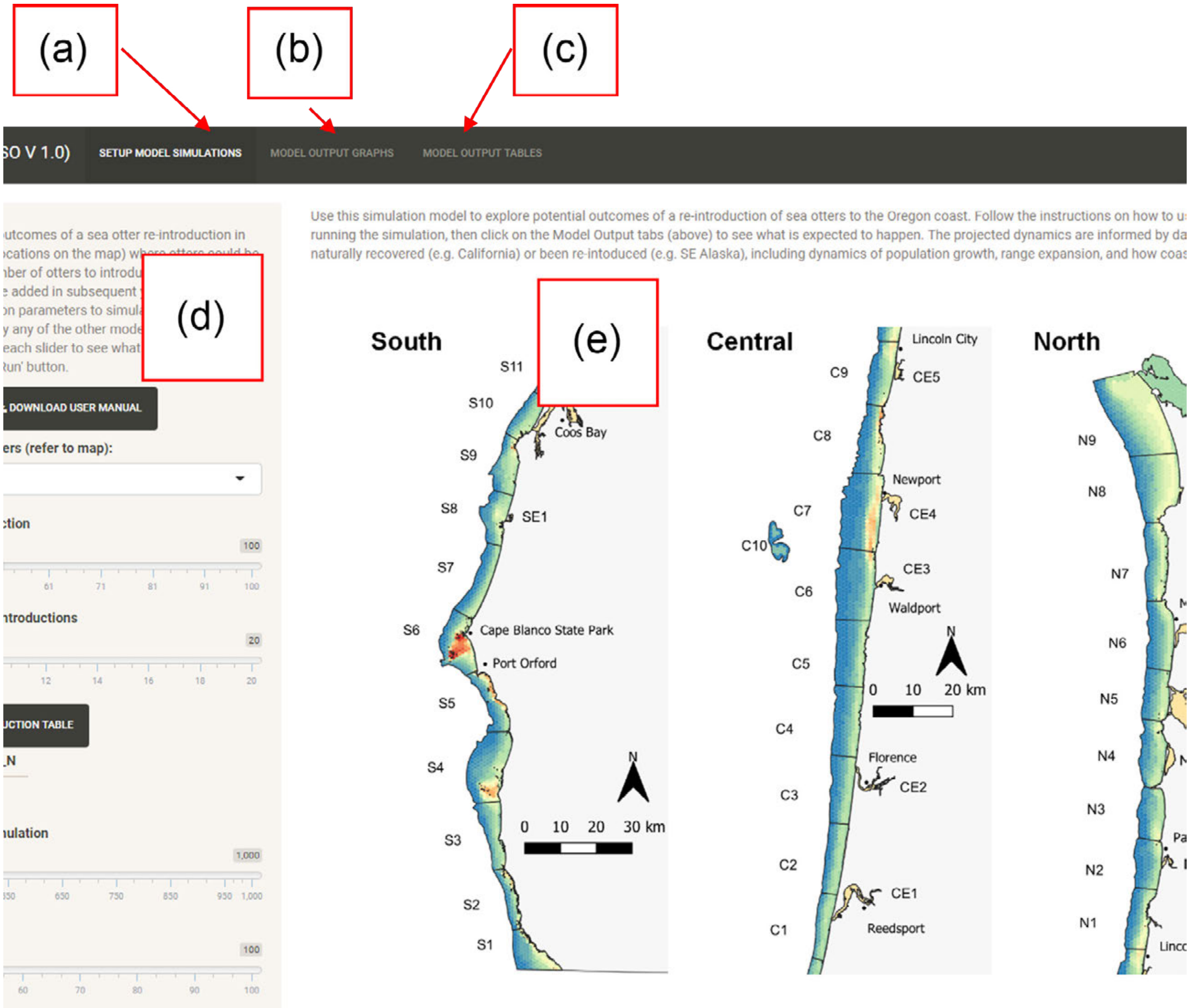
tracking sea otter abundance and distribution over time: The map allows the user to see the location of specific sections, as needed, to initiate simulations and interpret model results.

Setup Model Simulations Panel

At the top left of the sidebar panel are some simple instructions to guide the user and two large buttons: **Run Simulations Now and Download User Manual** (Figure A.8).

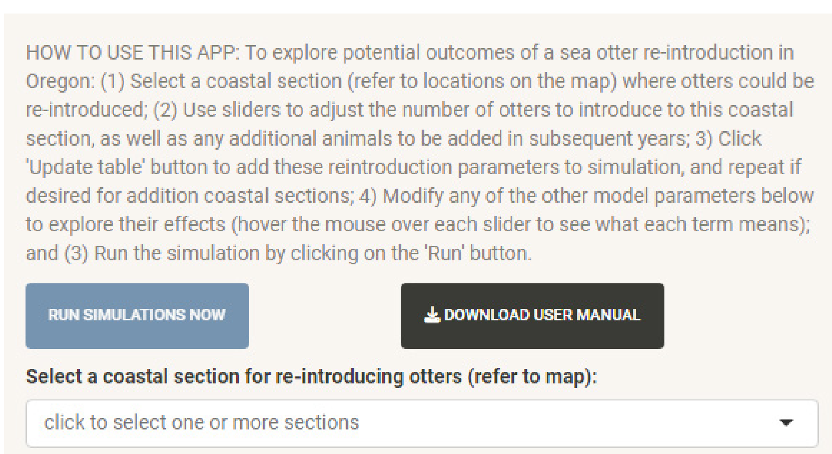
The **Download User Manual** button at right allows the user to download the same manual presented here, in Appendix A, at any time. The **Run Simulations Now** button at left is ORSO's primary action button, used to run a set of simulations. However, this button should only be clicked **AFTER** having first selected one or more coastal sections under consideration for a sea otter reintroduction and setting the user-adjustable parameters in the sidebar panel that describe the reintroduction details and control the underlying assumptions about the nature of population growth and range expansion. A description of each user-adjustable parameter will appear when the user moves the cursor over

Figure A.7. Three tabs in ORSO's title bar to select viewing panels.



Note. (a) The **Setup Model Simulations** selection tab in ORSO's title bar. (b) The **Model Output GRAPHS** selection tab. (c) The **Model Output TABLES** selection tab. (d) The sidebar panel in **Setup Model Simulations**, which allows a user to adjust parameters and run simulations. (e) The information panel in **Setup Model Simulations** with a map of Oregon divided into 42 numbered coastal sections.

Figure A.8. Buttons in the left sidebar panel of **Setup Model Simulations**.

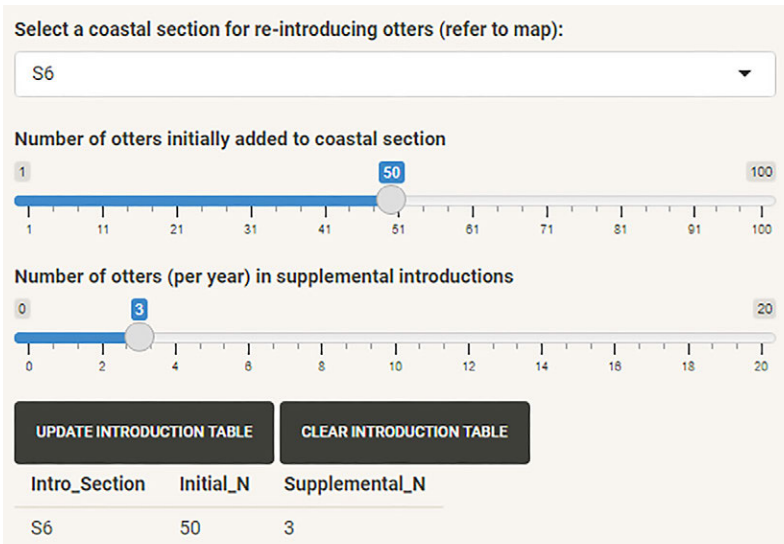


the parameter's name, and default values for each parameter are set based on data from other sea otter populations. These user-parameter adjustment controls are illustrated and explained below:

Select Coastal Sections for Reintroduction and Numbers of Otters to Be Added

Clicking on the selection box labeled **Select a coastal section for re-introducing otters** (Figure A.9) at top reveals a drop-down list of the 42 coastal sections (whose geographic locations can be viewed on the map at right), from which the user can select a coastal section where sea otters are to be introduced. Next, the two sliders below the selection box can be used to adjust the number of otters in the initial translocation event, as well as (optionally) the annual number of animals added to this section as part of supplementary introductions in subsequent years. Clicking on the **Update Introduction Table** button will add these user selections to a parameter table below the button. The user can then repeat this process (if desired) to specify additional coastal sections and associated translocation parameters and add those to the parameter table. To clear the table and start again at any time, click on the **Clear Introduction Table** button.

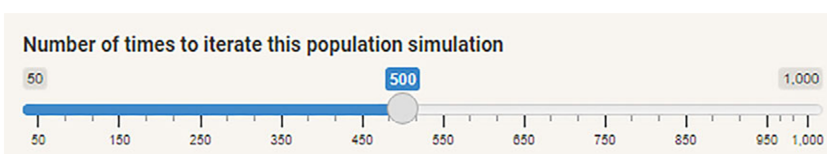
Figure A.9. ORSO controls to select coastal sections and numbers of otters for a reintroduction



Adjust Number of Iterations

This slider control (Figure A.10) is used to increase or decrease the number of simulation iterations: that is, the number of times a population simulation is replicated with random draws of all appropriate stochastic parameters. Increasing the number of replications of a simulation improves the precision of model predictions but will take longer to run. At least 100 iterations are suggested.

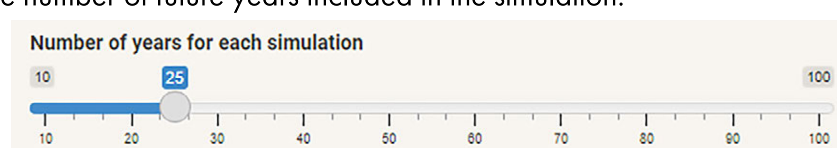
Figure A.10. Change the number of simulation iterations.



Adjust Number of Years

This slider control (Figure A.11) is used to increase or decrease the number of years into the future the simulation is run. Increasing the number of years (*N*) can provide insights into conditions farther in the future, but results become less reliable the farther ahead in time the model is projected.

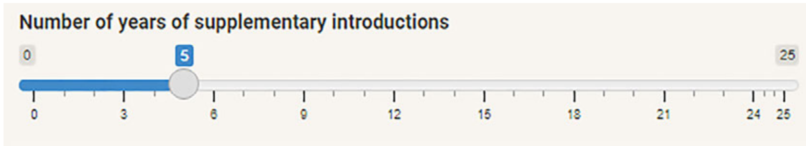
Figure A.11. Change the number of future years included in the simulation.



Adjust Number of Years That Supplemental Introductions Occur

This slider control (Figure A.12) is used to increase or decrease the number of years after the initial translocation event in which additional otters may be added to the initial reintroduction site (supplemental reintroductions). Adding more otters could potentially improve the success of the reintroduction by stabilizing the population during the establishment phase. These additional otters could be wild otters or juvenile rehabilitated otters from captivity.

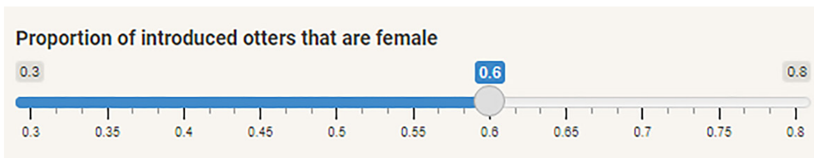
Figure A.12. Change the years between the initial translocation and supplemental reintroduction(s).



Adjust Sex Ratio of Reintroduced Otters

This slider control (Figure A.13) allows the user to specify the proportion of introduced otters that are female. Including a higher proportion of females can increase the potential for growth, though there must be at least some adult males for reproduction to occur.

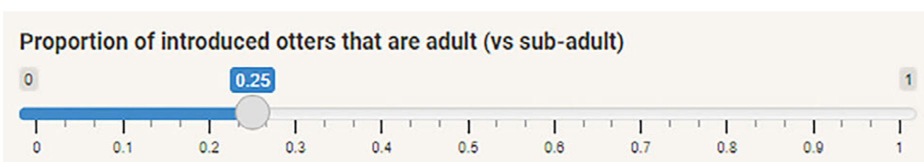
Figure A.13. Specify how many introduced otters are female.



Adjust Age Composition of Reintroduced Otters

This slider control (Figure A.14) allows the user to specify the proportion of introduced otters that are adult (vs. subadult or juvenile). Only adult sea otters produce pups, so introducing adults can hasten reproduction. However, in past translocations, it has been found that subadults may be more likely to successfully "take to" their new habitat, so a higher ratio of subadults may improve success.

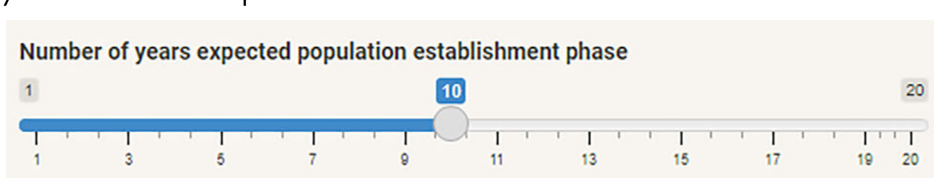
Figure A.14. Specify how many introduced otters are adults.



Adjust Duration of Population Establishment Phase

Newly established sea otter populations often experience an initial period of reduced growth and limited range expansion as the population becomes established. This establishment period has varied from five to 15 years in previous reintroductions and natural return events. This slider control (Figure A.15) allows the user to set the expected duration of this phase. In addition to reduced survival rates and range expansion during the establishment period, the user can specify the probability of post-introduction dispersal away from the release site.

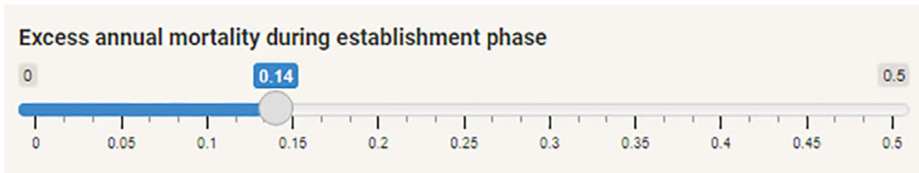
Figure A.15. Specify the establishment phase's duration.



Adjust Excess Mortality During Establishment

During the establishment phase of an introduced population, there may be higher than average levels of mortality as the introduced animals become accustomed to their new habitat. In past translocations, excess annual mortality rates of 10%–25% (expressed as 0.1–0.25 in the ORSO interface slider) have caused translocated populations to decline substantially during the establishment phase. This slider control (Figure A.16) allows the user to set the establishment phase's anticipated excess mortality rate.

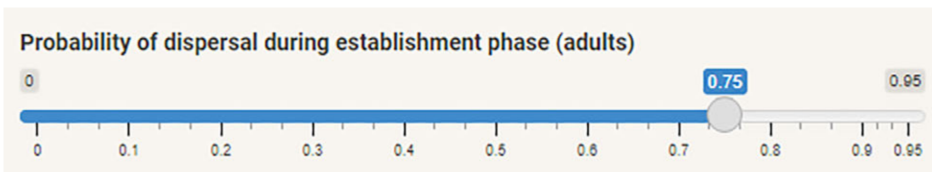
Figure A.16. Specify the establishment phase's anticipated mortality rate.



Adjust Probability of Dispersal During Establishment Phase for Adults

In several previous sea otter translocations, a substantial proportion of the introduced animals moved a significant distance away from the introduction site during the establishment phase. The details and destinations of post-release dispersal are impossible to predict, but the user can set the mean expected proportion of otters to disperse (Figure A.17).

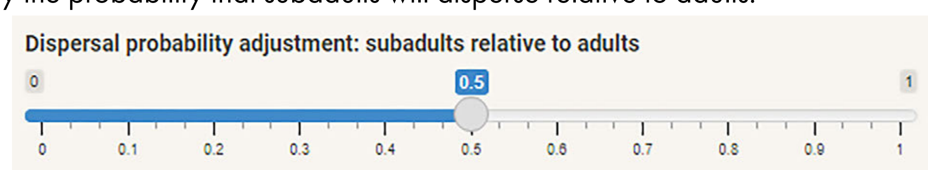
Figure A.17. Specify the number of otters (adults) expected to disperse during the establishment phase.



Adjust Probability of Dispersal During Establishment Phase for Subadults

In previous sea otter translocations, it has been observed that subadult animals may be less likely to disperse than adults (i.e., more likely to remain near the introduction site). This parameter (Figure A.18) adjusts the likelihood of dispersal for subadults compared to adults: A value of 0.25 would mean that subadults are one-quarter as likely to disperse as adults.

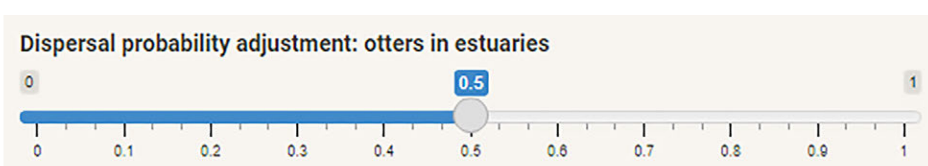
Figure A.18. Specify the probability that subadults will disperse relative to adults.



Adjust Probability of Dispersal During Establishment Phase for Otters in Estuaries

Based on several lines of evidence, it has been suggested that otters reintroduced to estuaries may be less likely to disperse (i.e., more likely to remain near release sites) than otters added to outer coast habitats. This parameter (Figure A.19) adjusts the likelihood of dispersal for estuaries compared to open coast: A value of 0.25 means otters in estuaries are one-quarter as likely to disperse post-introduction.

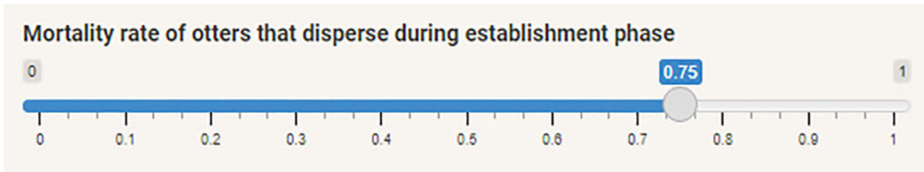
Figure A.19. Specify the probability that otters reintroduced to estuaries will disperse relative to those in outer coast habitats.



Adjust Mortality Rate for Otters That Disperse During Establishment Phase

The fates of otters that disperse away from a reintroduction site are hard to determine in most cases. In some reintroductions, there appears to have been high levels of mortality for dispersers. In others, there is emigration to a different region altogether. This parameter (Figure A.20) sets the expected loss rate for the dispersers: that is, the proportion of the dispersing group that dies (or moves entirely out of the study area and is effectively lost to the Oregon meta-population).

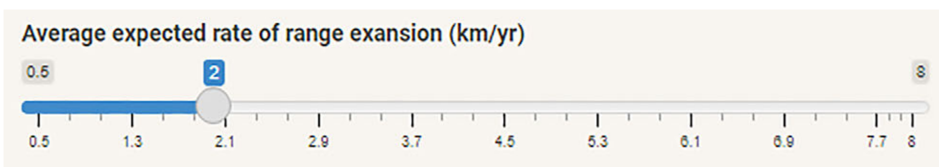
Figure A.20. Specify the mortality rate for otters that disperse during establishment.



Adjust Rate of Range Expansion

This slider control (Figure A.21) allows the user to adjust the expected rate at which the growing population spreads into new habitat. The distribution of the initial sea otter population will likely be limited to a relatively small area(s) of the coast where sea otters are introduced. As the population grows, its distribution (range of occupancy) will spread outwards along the coastline, encompassing more area. The *rate of range expansion* is measured as the speed at which the frontal edge of the population moves along the coastline (see Figure A.3, several pages earlier in this appendix). In other populations, this range expansion speed has varied from 1 to 5 km/year.

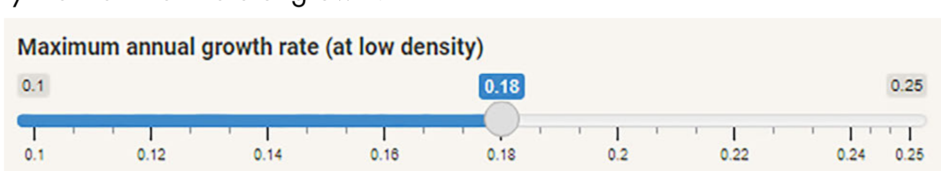
Figure A.21. Specify the rate of range expansion.



Adjust Maximum Rate of Growth

Sea otter populations tend to show the highest rate of growth at low densities: As local abundance increases, the growth rate slows until it eventually reaches 0 when population abundance reaches *K*. This slider control (Figure A.22) allows the user to adjust the maximum rate of growth (at low densities): In most sea otter populations, this value is between 0.15 and 0.20.

Figure A.22. Specify the maximum rate of growth.



Adjust Environmental Stochasticity

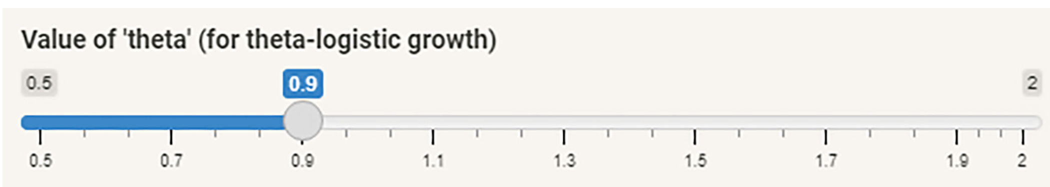
The average rate of growth for a reestablishing sea otter population in a given area can be predicted as a function of the local density with respect to *K*. However, year-to-year variation in environmental conditions and prey population dynamics can lead to unpredictable deviations in the growth rate, referred to as *environmental stochasticity*. This slider control (Figure A.23) can be used to adjust the degree of annual variation in growth rates: Typical values are 0.05–0.15.

Figure A.23. Specify the maximum rate of growth.

Adjust the Theta Parameter for Theta-Logistic Growth

The average rate of growth for a reestablishing a sea otter population in a given area can be predicted as a function of the local density with respect to *K*. One of the parameters of this function is *theta*, which determines the nature of the onset of reduced growth rates at higher densities: Theta values less than 1 lead to the onset of reduced growth rates at fairly low densities, while theta values greater than 1 mean that significant reductions in growth occur only at higher densities. This slider control (Figure A.24) can be used to adjust theta: Typical values reported for marine mammals are between 0.8 and 2, and a recent study in California reported a value of close to 0.9 for southern sea otters.

Figure A.24. Define the nature of the onset of a reduced growth rate (i.e., theta).



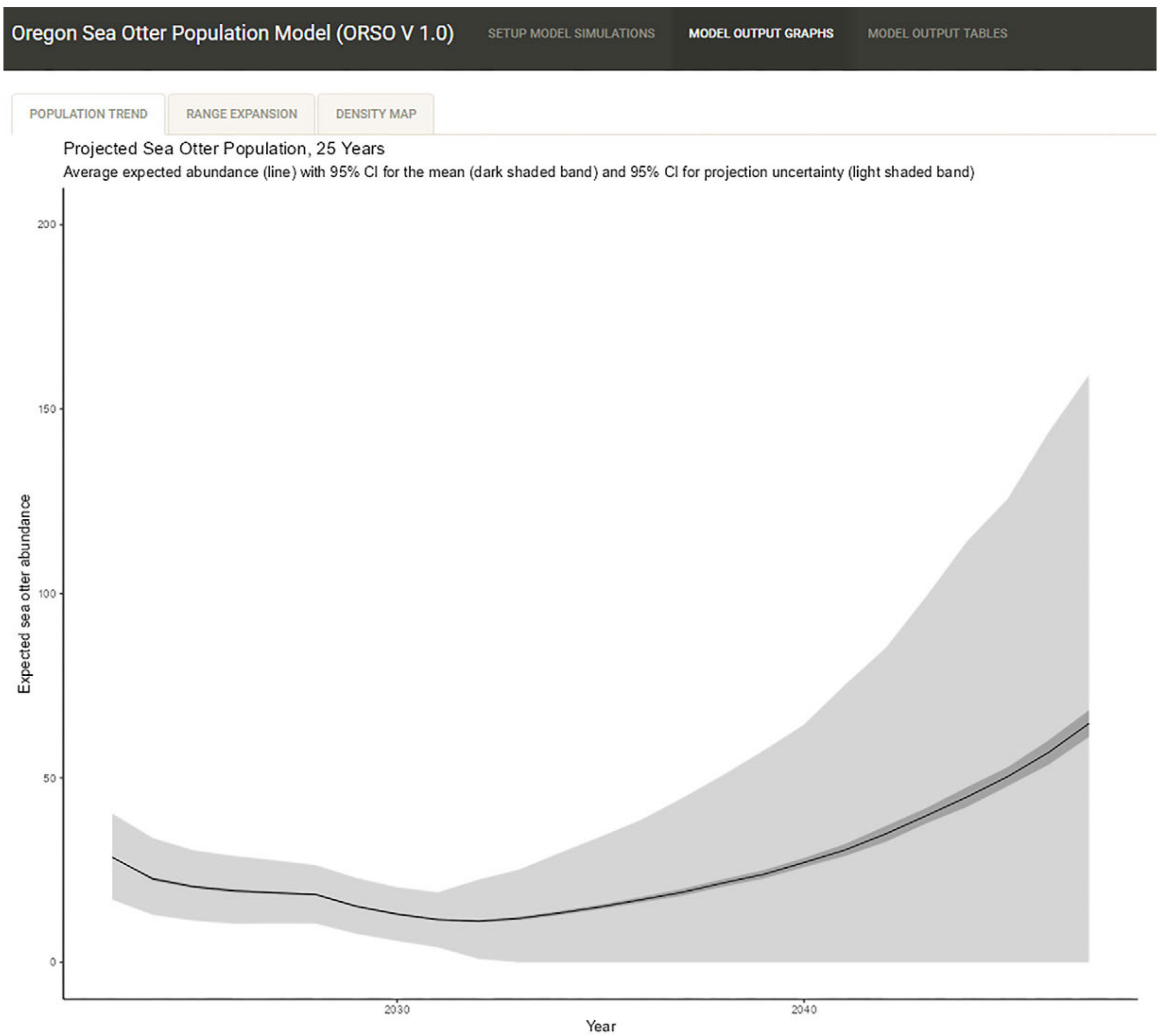
Model Output GRAPHS Panel

After setting up and running simulations, the user can navigate to the **Model Output GRAPHS** panel to view graphical results from model simulations. Three separate graphs can be viewed, and the user can move between them by selecting one of the three graph selection tabs just below the title bar.

Population Trend Graph

This plot shows the projected abundance over time of sea otters in Oregon based on results from the simulation model (THE EXAMPLE SHOWN IN FIGURE A.25 IS FOR ILLUSTRATIVE PURPOSES ONLY). The horizontal axis represents years into the future, while the vertical axis represents the expected total number of sea otters in a given year. Uncertainty about model results is calculated based on the distribution of results from stochastic iterations of the simulation. The solid black line represents the average abundance trend (i.e., averaged across all iterations), the dark gray band shows the 95% CI for the mean trend (i.e., uncertainty about the true average), and the light gray band shows the 95% CI for the full distribution of results (i.e., uncertainty about the range of possible outcomes).

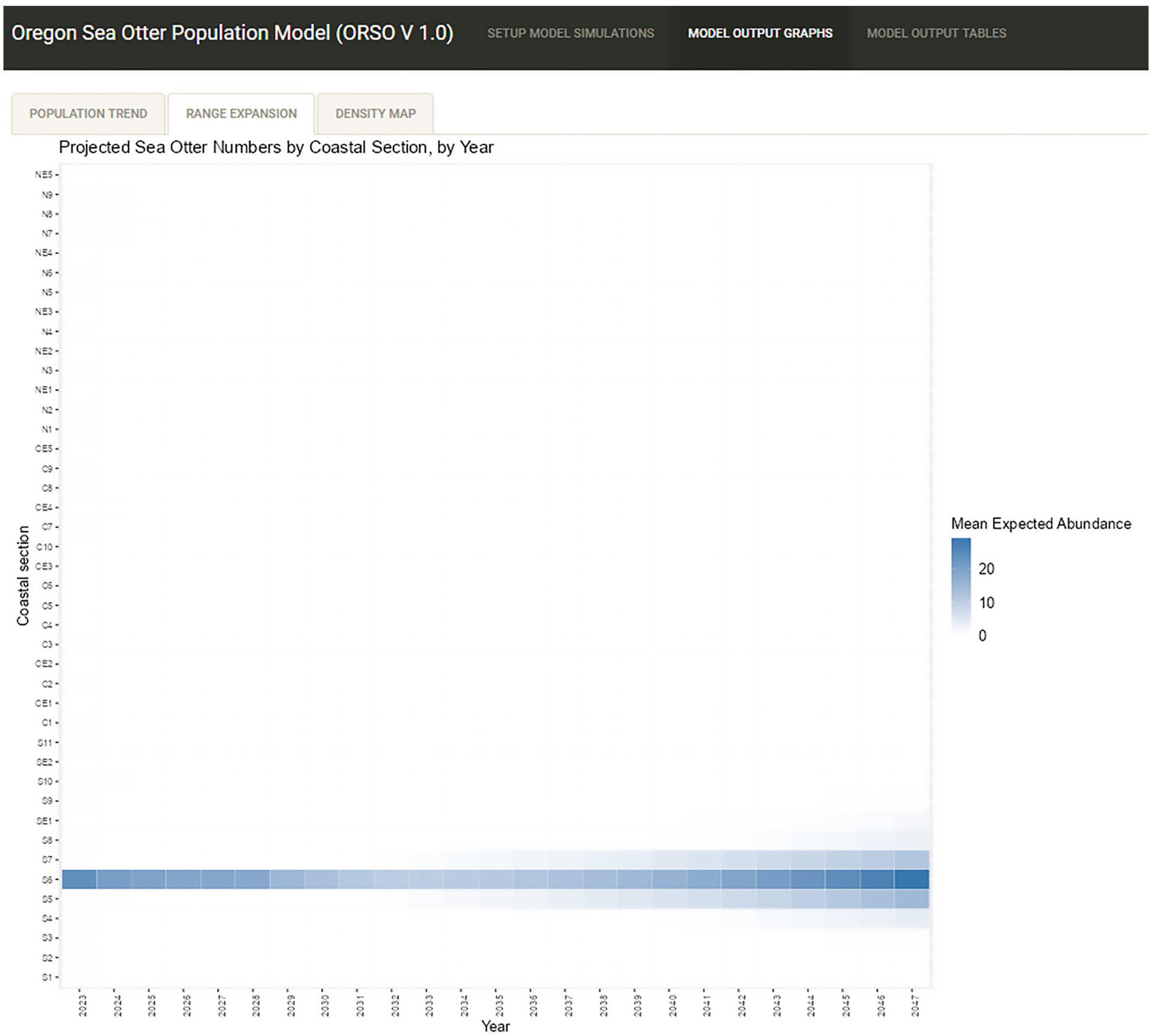
Figure A.25. An example of a population trend graph generated from ORSO simulations.



Range Expansion Graph

This heatmap graph shows the average projected abundance and spatial distribution of sea otters over time (THE EXAMPLE SHOWN IN FIGURE A.26 IS FOR ILLUSTRATIVE PURPOSES ONLY). Each grid cell represents a coastal section (vertical axis), as defined by the map on the front page, on a given year (horizontal axis). The shading of the grid cells indicates the relative abundance of sea otters (darker colors = more otters, white cells = no otters). The increase from left to right in the number and intensity of shaded cells illustrates the spatiotemporal patterns of range expansion. On the left-hand side of the heatmap (Year 1), the spatial distribution is constrained by the starting conditions (density = 0 at all but the section(s) where sea otters are introduced). As one moves from left to right across the heatmap (i.e., moving forward through time), the changes in density and distribution reflect the rates of population growth and range expansion.

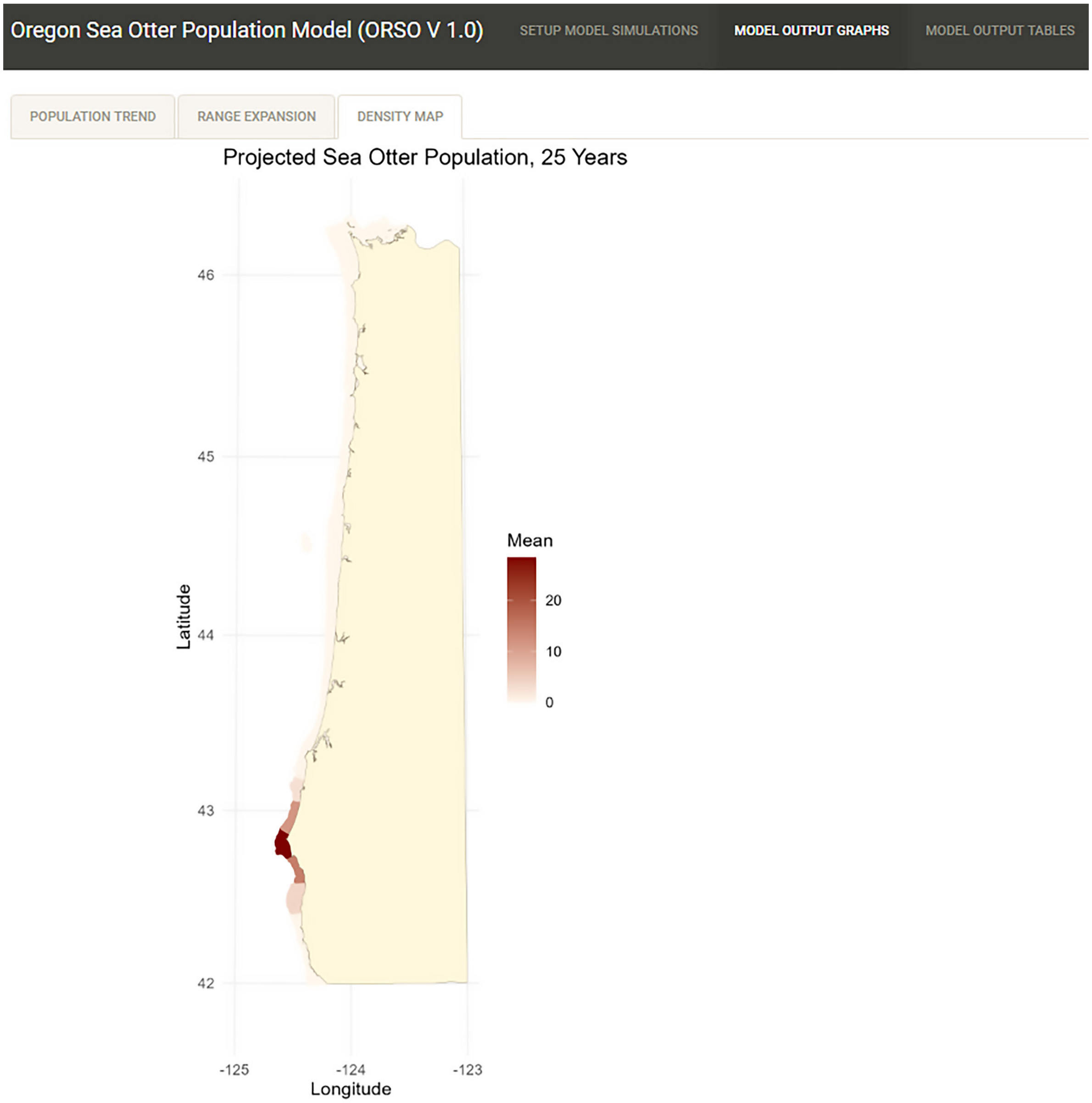
Figure A.26. An example of a range expansion heatmap graph generated from ORSO simulations.



Density Map

This map of coastal Oregon shows the average projected abundance and distribution of sea otters at the end of the simulation period (THE EXAMPLE SHOWN IN FIGURE A.27 IS FOR ILLUSTRATIVE PURPOSES ONLY). The mean expected number of sea otters in each coastal section (for the specified reintroduction scenario) is illustrated by the shading of the nearshore habitat zone, with darker shades of red-brown indicating higher abundances of sea otters.

Figure A.27. An example of a range expansion heatmap graph generated from ORSO simulations.



Model Output TABLES Panel

The results of the simulation model can also be viewed in tabular form. After setting up and running simulations, the user can navigate to the **Model Output TABLES** panel, where two standardized tables can be viewed and/or downloaded as *.csv files: one for abundance by year (Table A.2) and the other for abundance by coastal section in the final year (Table A.3).

Table A.2 summarizes the total projected abundance across all of coastal Oregon for each year of the simulation and includes six metrics: (1) average projected abundance, (2) lower bound of the 95% CI for the distribution of projected abundance estimates, (3) upper bound of the 95% CI for the distribution of projected abundance estimates, (4) estimation uncertainty expressed by the standard error (SE) of the mean projected abundance (ORSO uses the abbreviation SE to mean "standard error" though it means "southeast" in the rest of this study), (5) lower bound of the 95% CI for the average expected abundance, and (6) upper bound of the 95% CI for the average expected abundance.

Table A.2. Projected sea otter abundance by year.

Oregon Sea Otter Population Model (ORSO V 1.0) SETUP MODEL SIMULATIONS MODEL OUTPUT GRAPHS MODEL OUTPUT TABLES

TABLE 1: PROJECTED SEA OTTER ABUNDANCE BY YEAR TABLE 2: PROJECTED ABUNDANCE BY COASTAL SECTION IN FINAL YEAR

DOWNLOAD TABLE 1

Year	Average Number	Lower Estimate (CI)	Upper Estimate (CI)	Estimation Uncertainty (SE)	Lower 95% CI for the Mean	Upper 95% CI for the Mean
2021.00	21.81	4.16	42.90	0.00	21.81	21.81
2022.00	21.62	5.81	40.04	0.39	20.86	22.38
2023.00	22.81	7.66	41.17	0.39	22.05	23.57
2024.00	24.61	9.30	42.80	0.44	23.75	25.47
2025.00	26.35	11.36	46.31	0.44	25.49	27.20
2026.00	28.59	13.02	49.71	0.44	27.74	29.45

Note. In this table only, SE = standard error. CI = confidence interval.

Table A.3 summarizes the projected abundance and density in each coastal section in the simulation's final year. Columns include the (1) area of benthic habitat in each section (km2), (2) average projected number of sea otters, (3) lower bound of the 95% CI for the distribution of projected abundance estimates, (4) upper bound of the 95% CI for the distribution of projected abundance estimates, (5) average density (number of sea otters/km^2), (6) lower bound of the 95% CI for the distribution of projected density estimates, and (7) upper bound of the 95% CI for the distribution of projected density estimates.

Table A.3. Projected sea otter abundance by coastal section in the final year.

Oregon Sea Otter Population Model (ORSO V 1.0) SETUP MODEL SIMULATIONS MODEL OUTPUT GRAPHS MODEL OUTPUT TABLES

TABLE 1: PROJECTED SEA OTTER ABUNDANCE BY YEAR TABLE 2: PROJECTED ABUNDANCE BY COASTAL SECTION IN FINAL YEAR

DOWNLOAD TABLE 2

Coastal Section	Area (km2)	Year	Average Number	Lower Estimate (CI)	Upper Estimate (CI)	Density (#/km2)	Lower Density Est.(#/km2)	Upper Density Est.(#/km2)
S1	86.97	2045.00	0.09	0.00	0.00	0.00	0.00	0.00
S2	55.32	2045.00	0.10	0.00	0.00	0.00	0.00	0.00
S3	90.69	2045.00	0.09	0.00	0.00	0.00	0.00	0.00
S4	181.74	2045.00	13.11	0.00	30.00	0.07	0.00	0.17
S5	82.00	2045.00	44.95	13.00	94.00	0.54	0.16	1.15
S6	123.91	2045.00	91.54	29.00	191.00	0.73	0.23	1.54
S7	100.98	2045.00	35.90	10.00	72.00	0.35	0.10	0.71
S8	87.37	2045.00	9.51	0.00	23.00	0.11	0.00	0.26
S9	88.00	2045.00	0.54	0.00	4.00	0.00	0.00	0.05
S10	71.63	2045.00	0.23	0.00	0.00	0.00	0.00	0.00

In addition to viewing the tables, they can also be downloaded as *.csv files by clicking on the download buttons above each table.

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