Chapter 3. Population and Demographic Considerations

M. Tim Tinker

While there are multiple reasons that resource managers may decide to reintroduce a wildlife species to a habitat from which it has been extirpated, the success of such an action will ultimately be determined in part on the performance of the population after the reintroduction. The key metrics of performance are thus evaluated at the population-level rather than the individual-level, or according to IUCN/SSC Guidelines:

"Conservation translocation is the deliberate movement of organisms from one site for release in another. It must be intended to yield a measurable conservation benefit at the levels of a population, species or ecosystem, and not only provide benefit to translocated individuals." (IUCN 2013). As a conservation tool, reintroductions are intended to restore viable populations of the focal species within their former ranges, and specifically to habitats from which they have previously been extirpated (Seddon et al. 2007). Given these underlying goals, a fundamental requirement for evaluating the feasibility of a reintroduction program is a realistic assessment of population and demographic considerations. If a proposed reintroduction is unlikely to result in a viable population within the recipient habitat, then it does not meet the most basic conservation criteria. Likewise, if the net impacts of the proposed reintroduction to overall species viability are likely to be negative (or not measurably positive), it cannot be considered successful from a conservation perspective. While these population and demographic considerations represent just one component of a broader suite of issues to be considered prior to initiating a reintroduction, including socioeconomic, political and organizational considerations (Reading et al. 2002), it is nonetheless a necessary step to examine carefully the likely population-level consequences of reintroduction. We consider these consequences with respect to the source populations, the recipient population (i.e., the prospective population that managers wish to establish), and the species overall.

Impacts of Reintroduction to Source Populations

For any wildlife reintroduction program, individuals must be taken from some source population for translocation to the new habitat. Because the removal of individuals will necessarily cause a reduction in population size, the question is not whether a source population will be negatively affected, but rather if these negative effects will be statistically or biologically significant. In the case of an Oregon reintroduction, there are several possible source populations (see Chapter 9 of this report), and the impacts are likely to vary among these potential sources. We consider three potential source populations here: SE Alaska, California, and aquarium-rehabilitated stranded juvenile sea otters from California. We selected these three populations because of the availability of recently completed population analyses that allow us to make a quantitative assessment of the impacts of removing animals from each of these sources. We do not explicitly consider a fourth possible source population, Washington, because a comparable population model is not available at this time; however, given the similarity in population sizes we believe the results from the California analysis will be relevant and provide guidance for potential use of the Washington population as a source. We note that a population model for Washington is currently in review at a journal (Hale et al. in review) and should be available soon for use in a similar assessment.

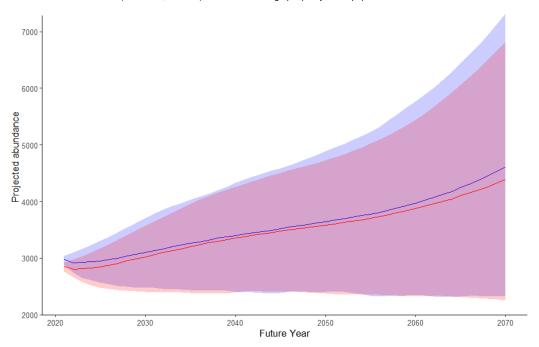
In SE Alaska, translocations of sea otters to multiple locations in the 1960s and 70s successfully established a growing meta-population which has now increased to over 25,000 animals (Esslinger and

Bodkin 2009, Tinker et al. 2019). A spatially-structured population model was recently developed for sea otters in this region (Tinker et al. 2019), and this model was then adapted for the purpose of evaluating the population impacts of Native Alaska subsistence harvest on sea otters (Raymond et al. 2019). Because the removal of sea otters for the purpose of translocating to a different region (Oregon) is, demographically speaking, identical to the lethal removal of animals during a harvest, we can use the results of these analyses to evaluate the demographic consequences of using SE Alaska as a source population for an Oregon reintroduction. The key results from the harvest impacts study were that the demographic consequences of harvest was negligible when annual removals were less than 10% of local population size (Raymond et al. 2019). For example, in the Maurelle Islands over 100 otters were frequently harvested in a single year, but because of the high number of otters in the Maurelle Islands this harvest rate represented less than 5% of the population, and effects on population trends were negligible. In Sitka Sound, harvest levels prior to 2005 were <10% in most years, and this level had only minor effects on population growth; however, after 2005 the annual harvest rate increased and levels frequently exceeded 10% of the local population (and sometimes >25%) resulting in substantial population impacts, with a >50% decline in abundance. These results highlight two important points: 1) the consequences to a source population of removing animals for the purpose of translocation should be assessed at a local scale (i.e., within 20-60 km of the site of capture) rather than at a regional scale; and 2) removals of animals that approach or exceed 10% of the local population are likely to have population-level consequences, but removals of less than this level may be sustainable. If we assume that 100 animals were to be captured for translocation to Oregon, there are several sub-regional population segments in SE Alaska identified by Tinker et al (2019) that could sustain this level of removal with minimal impacts (i.e., 100 animals would represent <<10% of local abundance), including Icy Straits and Glacier Bay in northern SE Alaska, or the Maurelle Islands, northwest Prince of Wales Island, and Kuiu Island in southern SE Alaska.

In California, a recent habitat-based estimate of sea otter carrying capacity (Tinker et al. 2021), combined with a comprehensive analysis of sea otter mortality patterns (Miller et al. 2020), has allowed for the development of a spatially structured integrated population model (IPM) for southern sea otters (Tinker et al. in press). The IPM model can be used to assess the population-level impacts of variation in cause-specific mortality, as well as reintroductions or removals of animals from specific locations within the range of sea otters in California. We therefore used this model to evaluate the impacts of a hypothetical removal of animals for translocation to Oregon. As with the SE Alaska model, we evaluated spatially explicit scenarios of the removal of up to 100 individuals. Specifically, we ran 50-year simulations of population dynamics in California, with 100 animals removed from one or more coastal segments in year 1 of the simulation, and we the assessed how much this removal would reduce population growth over the next 50 years as compared to an identical simulation without the removal. We found that a removal from the northern range periphery (the coastal area between Santa Cruz and Pigeon Pt) would result in a 4.9% reduction in projected abundance after 50 years (Figure 3.1a). In contrast, a similar removal of 100 sea otters from the range center (between Monterey and San Simeon), where local abundance is high and approximately at carrying capacity (K), resulted in only a 0.8% reduction in projected abundance after 50 years (Figure 3.1b). The first scenario resulted in greater impacts to the source population for two reasons: 1) the northern periphery is well below K and thus the removals would delay local recovery far more than would removals from an area already near K; and 2) a removal of animals near the range edge would tend to reduce or delay the potential for future range expansion into new habitats, while removal of animals from the range center would have no such effect.

A) Projected Trend, baseline (blue) vs alternative scenario (red)

Remove 100 otters (60 female, 40 male) from northern range periphery of CA population.



B) Projected Trend, baseline (blue) vs alternative scenario (red)

Remove 100 otters (60 female, 40 male) from range center of CA population.

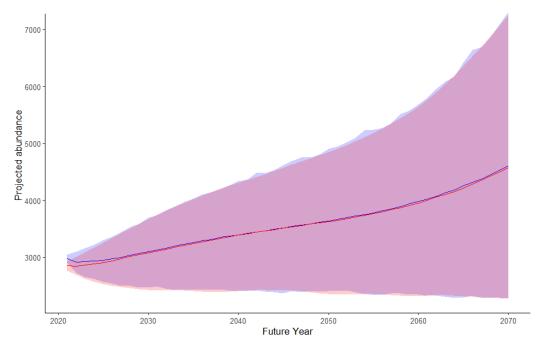


Figure 3.1. Population simulation results for an IPM model evaluated with and without the removal of animals for use in a translocation to Oregon. The blue line shows the baseline projected trend, while the red line shows the projected trend under the "alternative scenario" with 100 sea otters removed in year 1 of the simulation A) from the northern range periphery and B) from the range center.

Thus, when considering where sea otters might be taken from California (if it were to be used as a source population), it is important to consider local population status – areas near to K will be more resilient to removals than areas well below K – as well as the potential implications for future range expansion. Removing animals from areas near the edge of the range may be inadvisable, as it could have greater impacts on future recovery by reducing or delaying range expansion into new habitats.

A third potential source of animals for reintroduction to Oregon are juvenile animals in California that strand as pups, and are then rescued, rehabilitated and reared by "surrogate" mother sea otters in captivity (Nicholson et al. 2007). These rehabilitated juvenile animals have already been demonstrated to have potential to enhance population recovery in areas of low abundance (Estes and Tinker 2017, Mayer et al. 2019), and it has been suggested that similar methods might allow these animals to be used to establish a new population in California or Oregon (Mayer et al. 2019, Becker et al. 2020). A key advantage of this approach would be that the wild population in California would not be impacted at all, since the stranded animals are already effectively disconnected (demographically) from the wild population. Thus, at first glance this potential source population would seem to be ideal in terms of not negatively impacting a wild population. However, it is also true that the rehabilitated captive juvenile population is a highly limited resource: currently there are only a small number of animals that are successfully rescued, rehabilitated and available for release to a new area each year. If these animals were to be used as a source population for Oregon reintroduction, that would prohibit their use for establishment of new population centers within unoccupied habitats in California (or at least would reduce the numbers of animals available for reintroductions within California). Population simulations using the IPM have shown that the re-establishment of new population centers in un-occupied areas of California using rehabilitated animals could potentially have substantial impacts on future population growth, with projected increases of up to 50% (as compared to simulations without reintroductions) for a population established in the Channel Islands, and up to 100% for a population successfully established in San Francisco Bay (Tinker et al. in press). These projections are based on a great many assumptions (most importantly, that the establishment of new populations using rehabilitated animals would be successful) and thus should be interpreted cautiously. Nonetheless, these results do demonstrate that the use of rehabilitated sea otters for reintroduction in Oregon would come with a hidden opportunity cost: because they represent a limited resource, their use for reintroduction in one area will preclude their use in other areas, and thus the potential benefits (and costs) of this strategy should really be considered regionally, in both Oregon and California.

Impacts of Reintroduction to Recipient Population

In previous sea otter reintroduction efforts, the viability of the translocated populations has often been uncertain during the decades after reintroduction: a previous translocation to Oregon eventually resulted in failure (Jameson et al. 1982), and other translocated populations (such as San Nicolas Island in California) have dropped to very low population sizes before eventually beginning to increase (see Chapter 2 of this report for a more detailed review). Therefore, a realistic assessment of the likely viability of a proposed reintroduction, as well as an understanding of the factors that are likely to affect viability, is an important requirement for a feasibility study.

To help in our assessment of the likely viability of reintroduced sea otters in Oregon, we have developed an Oregon sea otter population model (ORSO). This model features a user-friendly interface, to help community members, stakeholders and managers explore possible sea otter recovery patterns after introduction. Full details of the rationale, analytical methods, and results of this model are provided in

Appendix XX. The ORSO model is intended to contribute to responsible stewardship of sea otters and other nearshore marine resources, by helping to anticipate the approximate magnitude of expected population growth and range spread of sea otters in coastal Oregon in the foreseeable future, under different scenarios of translocation/reintroduction. This information can help in evaluating management options and anticipating ecological and socio-economic impacts in a spatially and temporally explicit way. We caution, however, that experience from prior reintroductions demonstrates the difficulty in predicting where translocated animals will settle, how many will remain following release and how soon population growth will commence. The ORSO model is therefore not intended to predict specific outcomes, but rather to explore a range of outcomes that may be most likely, given an extensive range of model inputs and assumptions.

The ORSO model was developed using information from published reports and previous examples of sea otter introductions, population recovery and range expansion in the northeast Pacific. Data collected from areas of sea otter recovery in California, Washington and SE Alaska were 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 that is tailored to the habitat configuration of 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 uses a spatial diffusion approach to model range expansion over time. The model structure and parameterization is based on similar models constructed for other sea otter populations in North America that have proved effective at predicting patterns of population recovery and range expansion in diverse habitats (Udevitz et al. 1996, Monson et al. 2000, Tinker et al. 2008, USFWS 2013, Tinker 2015, Tinker et al. 2019, 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, we believe it is possible to define realistic boundaries for the expected patterns of population abundance and distributional changes over time.

Previous translocations and reintroductions of sea otters 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 the population establishment phase there is generally limited population growth, and often a significant decline in abundance, associated with elevated mortality and dispersal of a substantial proportion of animals away from the release site. The likelihood of post-release dispersal is thought to be high, but may be less for younger sea otters that have not yet formed strong attachments to a specific home range (Carswell 2008), and releasing sea otters in estuaries may allow for better retention of animals near the release site (Mayer et al. 2019, Becker et al. 2020). Otters that do disperse from the introduction site may settle in 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 to have occurred for some animals in the Oregon translocation, believed to have moved north to join the Washington or BC populations), though 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 only emerge after this establishment phase, which may extend for 5-20 years after the initial translocation (Jameson et al. 1982, Bodkin et al. 1999, Carswell 2008, Bodkin 2015). The ORSO model accounts for these establishment phase dynamics and allows the user to adjust the relevant parameters: specifically, the

expected duration of the establishment phase, the degree of elevated mortality during the establishment phase, the probability of dispersal away from the release site, and how this dispersal probability varies as a function of sea otter age class and whether the release site is in an estuary. While the "true" values of these parameters are impossible to determine at present, given available data, we provide appropriate ranges based on the results of past translocations: varying the parameters to explore their effects on population viability is perhaps the most appropriate way to move forward at this stage. Conducting small scale experimental reintroductions may be the only means of improving the accuracy and precision of these parameters.

Using the ORSO model to simulate population dynamics after a reintroduction provides several key insights into the factors affecting viability of the reintroduced population. First and foremost, the results reveal a great deal of uncertainty associated with model projections, as indicated by the width of the 95% confidence interval band around plotted trends over time (e.g., Figure 3.2). Projection uncertainty associated with ORSO model results reflects a combination of many separate sources of variation and uncertainty about population dynamics during and after a reintroduction project (see Appendix A for details). This uncertainty is important to factor into the decision-making process because it highlights the level of risk associated with any proposed reintroduction scenarios. It is prudent to make decisions not only to maximize the average expected outcome for any single variable (e.g., future population size), but also to minimize the possibility of failure.

A second insight is that all reintroduction scenarios are likely to involve a period of "population establishment", during which population growth will be sluggish and very possibly negative (Figure 3.2a). This pattern is consistent with the post-release declines (and/or slow growth) observed after previous reintroductions, even when those reintroduced populations subsequently grew rapidly after the establishment phase (as with SE Alaska: see Chapter 2). To ensure a high probability that a reintroduced population does not go extinct, the results of the ORSO model suggest the following guidelines: 1) a sufficiently large number of individuals should be included in the initial reintroduction; 2) the release site should be carefully chosen (and post-release management conducted) to maximize the chance that animals remain near the release site; 3) supplementary introductions could be used (if possible) to enhance the probability of successful reintroduction (see Chapter 9 of this report). Supplementary introductions could consist of small numbers of rehabilitated juvenile animals added annually to the initial establishing population: this approach has been tested in Elkhorn Slough, CA (Mayer et al. 2019), and appears to be an effective means of improving population viability during the establishment phase (Figure 3.2b). In the absence of supplementary additions to enhance viability, the ORSO model results suggest that at least 120 animals would have to be included in an initial reintroduction to have a 90% probability of maintaining a population of at least 25 otters after 25 years (Figure 3.<mark>3</mark>).

A) Projected Sea Otter Population, 25 Years: mean = 73(95% CI 70 - 77)

Initial translocation of 100 located in section S6

B) Projected Sea Otter Population, 25 Years: mean = 176(95% CI 172 - 181)

Initial translocation of 100 located in section S6 supplemented by 3 subadults per year for 10yrs

400

300

100

2030

Year

Figure 3.2. Expected trends in sea otter abundance after a reintroduction to coastal Oregon, based on projections using the ORSO model assuming A) 100 otters introduced to section S6, or B) 100 otters plus supplementaty additions of 3 subadults per year for 10 years. In both plots the solid line shows the mean expected trend and grey bands indicate 95% confidence intervals.

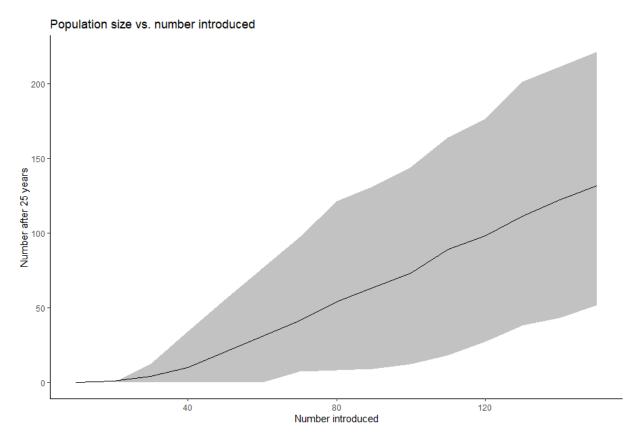


Figure 3.3. A plot of the relationship between the number of otters introducted to a release site in Oregon (coastal section S6 in this analysis) and the success of the reintriduction, as measured by the mean number of otters remaining after 25 years. The solid line indicates the mean expected value of all simulations, while the grey band represents the 80% confidence interval.

A third important insight from the ORSO model results is that spatial considerations and selection of a release site can have substantial implications for the outcomes of a reintroduction project. Spatial differences in the likelihood of population establishment and future growth are partially a reflection of suitability of the release site, but also reflect the spatial granularity of sea otter populations and densitydependent population regulation. Sea otters have relatively small lifetime home ranges (Breed et al. 2013, Tarjan and Tinker 2016) and thus tend to be limited by habitat quality and resource abundance at local rather than regional scales (Bodkin 2015, Tinker 2015, Tinker et al. 2019). Population growth potential depends on carrying capacity, which can vary at local scales based on the recruitment dynamics and productivity of invertebrate prey (Tinker et al. 2021). Furthermore, the small home ranges and limited movements of adult sea otters means that spatial extent of the population distribution tends to change slowly (as compared to invasion potential for more mobile mammals): the long-term rate of range spread along linear coastlines has been documented at 2-5 km/year (Lubina and Levin 1988, Tinker et al. 2008). Together, these fundamental properties suggest that the population performance of a reintroduced population will depend on the quality of habitat and productivity of prey resources in the neighborhood around a reintroduction site, and the results of the ORSO model are consistent with this prediction. A previous application of a habitat-based model of sea otter carrying capacity to the Oregon coast (Kone et al. 2021) indicates substantial variation in habitat quality (as measured by the expected density of sea otters at K) along the coastline (Figure 3.4). Based on ORSO simulations, spatial differences in the expected success of reintroductions (the number of otters

remaining after 25 years) were consistent with these habitat differences: the highest growth potential occurred in coastal segments such as S6, SE2 or NE3 that encompass areas of high-quality habitat (Figure 3.5). In these high-quality habitat areas, a reintroduction of 70 sea otters (supplemented by 30 more over the next decade) would be expected to result in a successfully established population of >150 otters after 25 years, as compared to <50 otters for low quality areas.

A final key insight from the ORSO model results is that multiple release locations (resulting in multiple "seeds" of population growth) may be more effective than a single center, if logistically possible. There are two primary reasons why this is the case: first, from the perspective of risk management, two sites can add a degree of insurance against stochastic and un-predictable failure of a population to establish (if one re-introduced population fails, the other may persist). The second reason that two centers of growth can result in better performance is related to mathematical and demographic constraints of diffusion along a linear coastline. Because each population center is limited both by local density dependence and the rate of range spread to the north and south, the same number of animals divided between two centers will result in greater net growth than if they were combined into a single center (all else being equal and assuming that both populations are successfully established). A concrete example of this principle is provided by the SE Alaska translocation: one reason that sea otter numbers in SE Alaska are so high today is that the original 450 animals were divided among 6 release sites (see Chapter 2 of this report for details). Spatially distributed release sites in SE Alaska led to many separate population nodes, each growing exponentially and expanding outwards: the same number of animals introduced at a single release site would have resulted in a much smaller population with a more limited distribution (Tinker et al. 2019). Using the ORSO model to compare a reintroduction scenario of 100 animals introduced to a single site (S6) vs. a scenario of the same number of animals divided between two spatially distant sites (SE2 and CE4) resulted in almost 2x more animals after 25 years under the latter scenario (Figure 3.6). Comparing maps of the projected populations under the two scenarios reveals the reason for the difference: the two release sites resulted in two distinct population centers (Figure 3.7).

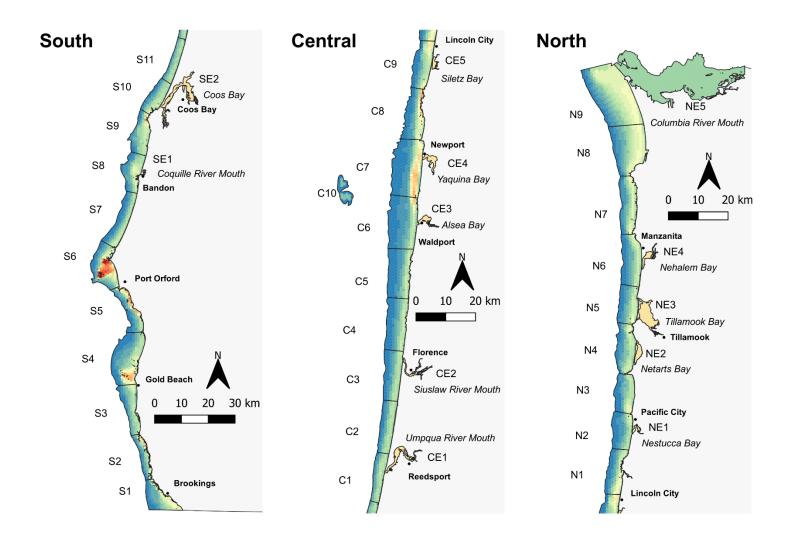


Figure 3.4 Results of a habitat-based model of sea otter carrying capacity to the Oregon coast (Kone et al. 2021), showing variation in the expected density of sea otters at K resulting from differences in habitat suitability.

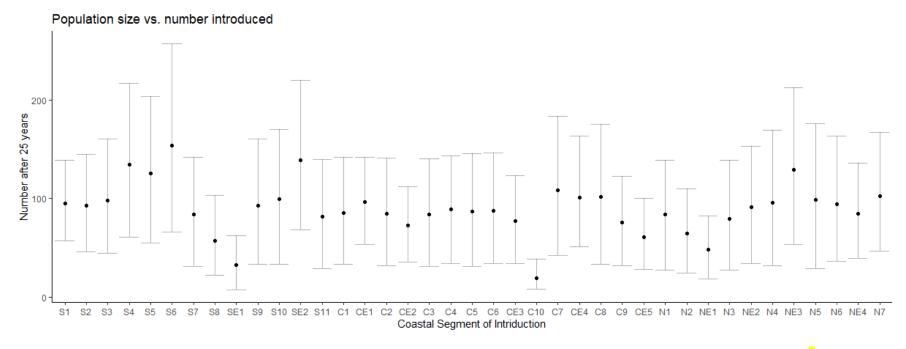


Figure 3.5. Comparison of expected number of sea otters after 25 years based on reintroductions of 100 sea otters to different coastal segments (see map, Figure 3.4). Each scenario consisted of an initial reintroduction of 70 animals, followed by supplementary additions of 3 otters per year for 10 years. The establishment phase was assumed to last for 10 years, with an elevated mortality rate of 0.14 during that period, and an average probability of post-introduction dispersal away from the translocation site of 75% for adults but only ½ that rate for sub-adults.

A) Projected Sea Otter Population, 25 Years: mean = 69(95% CI 66 - 72)

Initial translocation of 100 located in section S6

B) Projected Sea Otter Population, 25 Years: mean = 126(95% CI 123 - 130)

Initial translocation of 70 divided among sections, SE2, CE4 supplemented by 3 subadults per year for 10yrs

300

200

2030

Year

Figure 3.6 Comparison of projected sea otter trends after two reintrodiction scenarios: A) An initial translocation of 100 animals to a single coastal area (section S6 – see map in Figure 3.4); B) An initial translocation of 70 animals divided equally amongh two sections (SE2 and CE4), with supplemental additions of 3 subadults per year for 10 years (also divided equally between the two areas). Despite the fact that both scenarios involved reintroduciton of 100 animals, the second scenario resulted in an expected abundance after 25 years that was twice that of the first scenario. The difference reflects the benefits of multiple populaiton centers, as well as using supplementary additions of animals to improve viability of the population at a given release site.

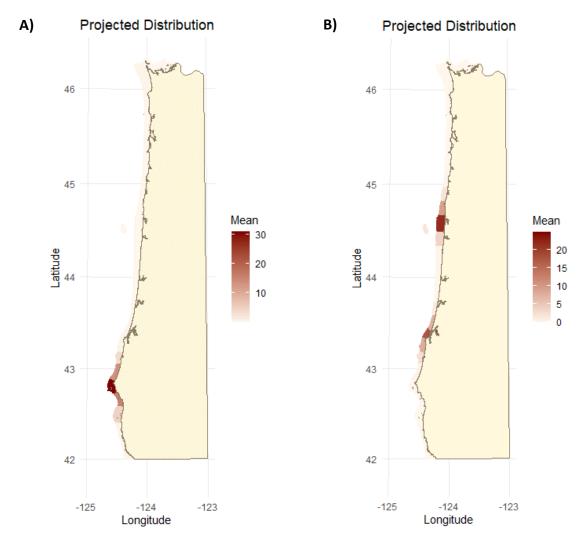


Figure 3.7. Comparison of projected sea otter distribution after 25 years for two reintrodiction scenarios (see Figure 3.6 for details): A) An initial translocation of 100 animals to a single coastal area (section S6 – see map in Figure 3.4); B) An initial translocation of 70 animals divided equally amongh two sections (SE2 and CE4), with supplemental additions of 3 subadults per year for 10 years (also divided equally between the two areas). The second scenario resulted in two spatially disjunct populaiton centers, and a net abundance that was approximately two times that of the first scenario.

In summary, the ORSO population model provides an easy-to-use tool for exploring the factors that may affect the future viability of re-introduced sea otter populations in Oregon. Broadly speaking, the takehome message is that a reintroduced population (or populations) of sea otters in Oregon could indeed be viable, but there is an unavoidable and high degree of uncertainty associated with the outcome of any one reintroduction scenario. A prudent approach would therefore be to use the model to consider a wide range of options with the goal of identifying an appropriate set of candidate scenarios for which the level of uncertainty (risk of failure) is "acceptable" to all stakeholders. Each of these candidate scenarios should also be evaluated through the lens of potential ecological effects on local ecosystems (see Chapter 5), local habitat suitability (see Chapter 6), possible socio-economic impacts (see Chapter 7), logistical constraints and considerations (see Chapter 9) and other potential risk factors (see Chapter 10). While this process may be time-consuming and labor intensive, it will almost certainly result in a greater chance of success and a lower likelihood of unintended and undesirable outcomes.

Implications of Reintroduction for the Species

One simple way to consider the net impacts of an Oregon sea otter reintroduction program for the species overall is to tabulate a ledger of negative consequences for the source population and positive consequences for the recipient location. Assuming that a reintroduction is successful, the analyses presented here suggest that it is highly likely that such a tabulation exercise will result in a net positive outcome: this is because the negative impacts to the viability of a source population are small (assuming that an appropriate source population is selected, following the above-described guidelines) relative to the positive impacts of growth in a new habitat. However, such a simple accounting exercise does not really capture the full species level implications of a reintroduction to Oregon. A more robust assessment needs to consider the historical biogeographic context of the current distribution of sea otters, and issues of demographic and genetic connectivity.

The north Pacific fur trade of the 18th and 19th centuries dealt a severe blow to sea otters, completely extirpating them from a vast stretch of their historical range in North America (Kenyon 1969). This event greatly increased susceptibility of the species to total extinction due to the demographic risks of small population size, as well as the genetic consequences of population reduction and fragmentation (see Chapter 4 of this report). Just as importantly, it eliminated their functional role as a keystone apex predator in nearshore ecosystems from Mexico to Alaska (Estes and Duggins 1995, Estes et al. 2004). One of the primary challenges faced by managers in facilitating the recovery of sea otters and restoration of their functional roles in coastal ecosystems is that natural range expansion is extremely slow in this species: as discussed above, this is due to inherent traits in sea otters of limited mobility and high site fidelity of reproductive adults. Because of these traits, natural recolonization of sea otters to all their former habitats in western North America from the remnant colonies in Alaska and California could have taken centuries. Instead, this process was greatly accelerated by translocations from SW Alaska to SE Alaska, British Columbia, and Washington (Jameson et al. 1982). However, there remains a sizable stretch of unoccupied coastline between the Washington population and California population, and given the relatively slow rate of range spread for both these populations, the point at which they converge naturally could be many decades away. From a species-level perspective, the significance of a managed reintroduction to Oregon would be acceleration of the return of the species to the entirety of its former range, restoration of its functional role in those habitats, and reestablishment of a nearcontinuous (albeit patchy) distribution along the west coast of North America. Restoring a nearcontinuous distribution is a necessary requirement for allowing pre-fur trade levels of gene flow (Larson

et al. 2002, Wellman et al. 2020) and would also greatly enhance the potential for demographic "rescue effects" (the process by which natural dispersal from one area can "rescue" a neighbouring subpopulation that has experienced decline from disease, predation or anthropogenic impacts like oil spills). When considering the species-level implications of an Oregon reintroduction, this biogeographic perspective is more relevant than is a simple tabulation of sea otter numbers.

Conclusions

An assessment of the population impacts of a species reintroduction must form a core part of any feasibility study because the restoration of a viable population within the former range is a fundamental objective of conservation-based reintroductions (Seddon et al. 2007, IUCN 2013). Population viability should be considered from the perspective of the source population (i.e., the population from which individuals will be taken for the reintroduction), the proposed recipient location, and the species overall. Here we have used quantitative approaches to assess the population-level impacts of removing animals from putative source populations, and to assess the likely viability of an established Oregon population under various reintroduction scenarios. The model framework we have developed for this assessment (the ORSO web app) can be easily used by managers and a wide range of stakeholders to explore potential outcomes of alternative reintroduction scenarios, assess the relative risks and implications for coastal ecosystems and socioeconomic activities, and evaluate the factors likely to determine success or failure of a reintroduction. We emphasize that biological considerations (i.e., population viability and ecological impacts) represent just one set of variables to be factored into decisions about reintroduction, and must be placed in a broader context of social and economic considerations, legal and administrative considerations, and logistical considerations (Reading et al. 2002). We believe the OSRO model can help in evaluating all these subject areas, as it provides a spatially and temporally explicit tool for visualizing the outcomes of sea otter reintroduction under different scenarios and assumptions. Finally, in thinking about the species-level implications of reintroduction, we encourage a broad perspective that considers the history and biogeography of past and current sea otter populations.

Literature Cited

- Becker, S. L., T. E. Nicholson, K. A. Mayer, M. J. Murray, and K. S. Van Houtan. 2020. Environmental factors may drive the post-release movements of surrogate-reared sea otters. Frontiers in Marine Science **7**.
- Bodkin, J. L. 2015. Historic and Contemporary Status of Sea Otters in the North Pacific. Pages 43-61 *in* S. Larson, J. L. Bodkin, and G. R. Vanblaricom, editors. Sea Otter Conservation. Academic Press, Boston.
- Bodkin, J. L., B. E. Ballachey, M. A. Cronin, and K. T. Scribner. 1999. Population demographics and genetic diversity in remnant and translocated populations of sea otters. Conservation Biology **13**:1378-1385.
- Breed, G. A., M. T. Tinker, and E. A. Golson. 2013. Fitting California sea otter resight data to an Ornstein-Uhlenbeck biased correlated random walk with switching between multiple home-range centers. *in* Biennial Conference of the Society of Marine Mammalogy, Dunedin, New Zealand.
- Carswell, L. P. 2008. How Do Behavior and Demography Determine the Success of Carnivore Reintroductions? A Case Study of Southern Sea Otters, Enhydra Lutris Nereis, Translocated to San Nicholas Island. University of California, Santa Cruz.
- Esslinger, G. G., and J. L. Bodkin. 2009. Status and trends of sea otter populations in Southeast Alaska,1969–2003. U.S. Geological Survey Scientific Investigations Report 2009-5045., Reston, VA.
- Estes, J. A., E. M. Danner, D. F. Doak, B. Konar, A. M. Springer, P. D. Steinberg, M. T. Tinker, and T. M. Williams. 2004. Complex trophic interactions in kelp forest ecosystems. Bulletin of Marine Science **74**:621--638.
- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. Ecological Monographs **65**:75-100.
- Estes, J. A., and M. T. Tinker. 2017. Rehabilitating sea otters: Feeling good versus being effective. Pages 128-134 *in* P. Kareiva, M. Marvier, and B. Silliman, editors. Effective Conservation Science. Oxford University Press, Oxford.
- Hale, J., K. L. Laidre, S. Jeffreis, J. Scordino, D. Lynch, R. Jameson, and M. T. Tinker. in review. Status, Trends, and Equilibrium Abundance Estimates of the Translocated Sea Otter Population in Washington State. Journal of Wildlife Management.
- IUCN. 2013. Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. 57pp., IUCN (World Conservaiton Union) Species Survival Commission, Gland, Switzerland.
- Jameson, R. J., K. W. Kenyon, A. M. Johnson, and H. M. Wight. 1982. History and status of translocated sea otter populations in North America. Wildl. Soc. Bull. **10**:100-107.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. North American Fauna 68:1-352.
- Kone, D., M. T. Tinker, and L. Torres. 2021. Informing sea otter reintroduction through habitat and human interaction assessment. Endangered Species Research 44:159-176.
- Larson, S., R. Jameson, M. Etnier, M. Fleming, and P. Bentzen. 2002. Loss of genetic diversity in sea otters (Enhydra lutris) associated with the fur trade of the 18th and 19th centuries. Molecular Ecology **11**:1899-1903.
- Lubina, J. A., and S. A. Levin. 1988. The spread of a reinvading species: Range expansion in the California sea otter. American Naturalist **131**:526-543.
- Mayer, K. A., M. T. Tinker, T. E. Nicholson, M. J. Murray, A. B. Johnson, M. M. Staedler, J. A. Fujii, and K. S. Van Houtan. 2019. Surrogate rearing a keystone species to enhance population and ecosystem restoration. Oryx:1-11.
- Miller, M. A., M. E. Moriarty, L. Henkel, M. T. Tinker, T. L. Burgess, F. I. Batac, E. Dodd, C. Young, M. D. Harris, D. A. Jessup, J. Ames, and C. Johnson. 2020. Predators, Disease, and Environmental

- Change in the Nearshore Ecosystem: Mortality in southern sea otters (Enhydra lutris nereis) from 1998-2012. Frontiers in Marine Science **7**:582.
- Monson, D. H., D. F. Doak, B. E. Ballachey, A. Johnson, and J. L. Bodkin. 2000. Long-term impacts of the Exxon Valdez oil spill on sea otters, assessed through age-dependent mortality patterns.

 Proceedings of the National Academy of Sciences of the United States of America **97**:6562-6567.
- Nicholson, T. E., K. A. Mayer, M. M. Staedler, and A. B. Johnson. 2007. Effects of rearing methods on survival of released free-ranging juvenile southern sea otters. Biological Conservation **138**:313-320.
- Raymond, W. W., M. T. Tinker, M. L. Kissling, B. Benter, V. A. Gill, and G. L. Eckert. 2019. Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska. Ecosphere **10**:e02874.
- Reading, R. P., T. W. Clark, and S. R. Kellert. 2002. Towards an endangered species reintroduction paradigm. Endangered Species Update **19**:142-146.
- Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. Conservation Biology **21**:303-312.
- Tarjan, L. M., and M. T. Tinker. 2016. Permissible Home Range Estimation (PHRE) in Restricted Habitats: A New Algorithm and an Evaluation for Sea Otters. PLoS One **11**:e0150547.
- Tinker, M. T. 2015. The Use of Quantitative Models in Sea Otter Conservation. Pages 257-300 *in* S. Larson, J. L. Bodkin, and G. R. Vanblaricom, editors. Sea Otter Conservation. Academic Press, Boston, MA.
- Tinker, M. T., L. P. Carswell, J. A. Tomoleoni, B. B. Hatfield, M. D. Harris, M. A. Miller, M. E. Moriarty, C. K. Johnson, C. Young, L. Henkel, M. M. Staedler, A. K. Miles, and J. L. Yee. in press. An Integrated Population Model for Southern Sea Otters. US Geological Survey Open-File Report No. 2021-xxxx. Reston, VA.
- Tinker, M. T., D. F. Doak, and J. A. Estes. 2008. Using demography and movement behavior to predict range expansion of the southern sea otter. Ecological Applications **18**:1781-1794.
- Tinker, M. T., V. A. Gill, G. G. Esslinger, J. L. Bodkin, M. Monk, M. Mangel, D. H. Monson, W. E. Raymond, and M. Kissling. 2019. Trends and Carrying Capacity of Sea Otters in Southeast Alaska. Journal of Wildlife Management **83**:1073-1089.
- Tinker, M. T., J. L. Yee, K. L. Laidre, B. B. Hatfield, M. D. Harris, J. A. Tomoleoni, T. W. Bell, E. Saarman, L. P. Carswell, and A. K. Miles. 2021. Habitat features predict carrying capacity of a recovering marine carnivore. Journal of Wildlife Management **85**:303-323.
- Udevitz, M. S., B. E. Ballachey, and D. L. Bruden. 1996. A population model for sea otters in Western Prince William Sound. Exxon Valdez Oil Spill Restoration Project Final Report: Sea otter demographics. 93043-3, U.S. National Biological Service, Alaska Science Center, Anchorage, Alaska.
- USFWS. 2013. Southwest Alaska Distinct Population Segment of the Northern sea otter (*Enhydra lutris kenyoni*) Recovery Plan., U.S. Fish and Wildlife Service, Region 7, Alaska, Anchorage, AK.
- Wellman, H. P., R. M. Austin, N. D. Dagtas, M. L. Moss, T. C. Rick, and C. A. Hofman. 2020. Archaeological mitogenomes illuminate the historical ecology of sea otters (Enhydra lutris) and the viability of reintroduction. Proceedings of the Royal Society B **287**:20202343.