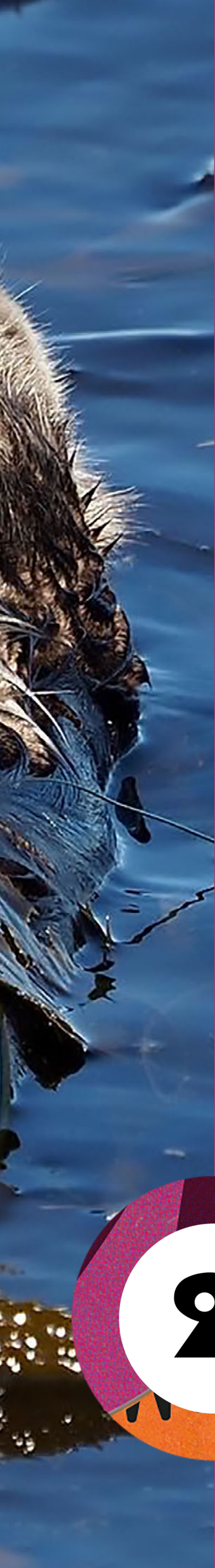
Photo by Ingrid V. Taylar on Flickr



Chapter 2

HISTORY OF PRIOR SEA OTTER TRANSLOCATIONS

James L. Bodkin, James A. Estes, and M. Tim Tinker

Editor's note: Hyperlinks for the cross-references to other chapters from *Reintroducing Oregon Sea Otters to Oregon: A Feasibility Study* are nonfunctional in this chapter-specific PDF.

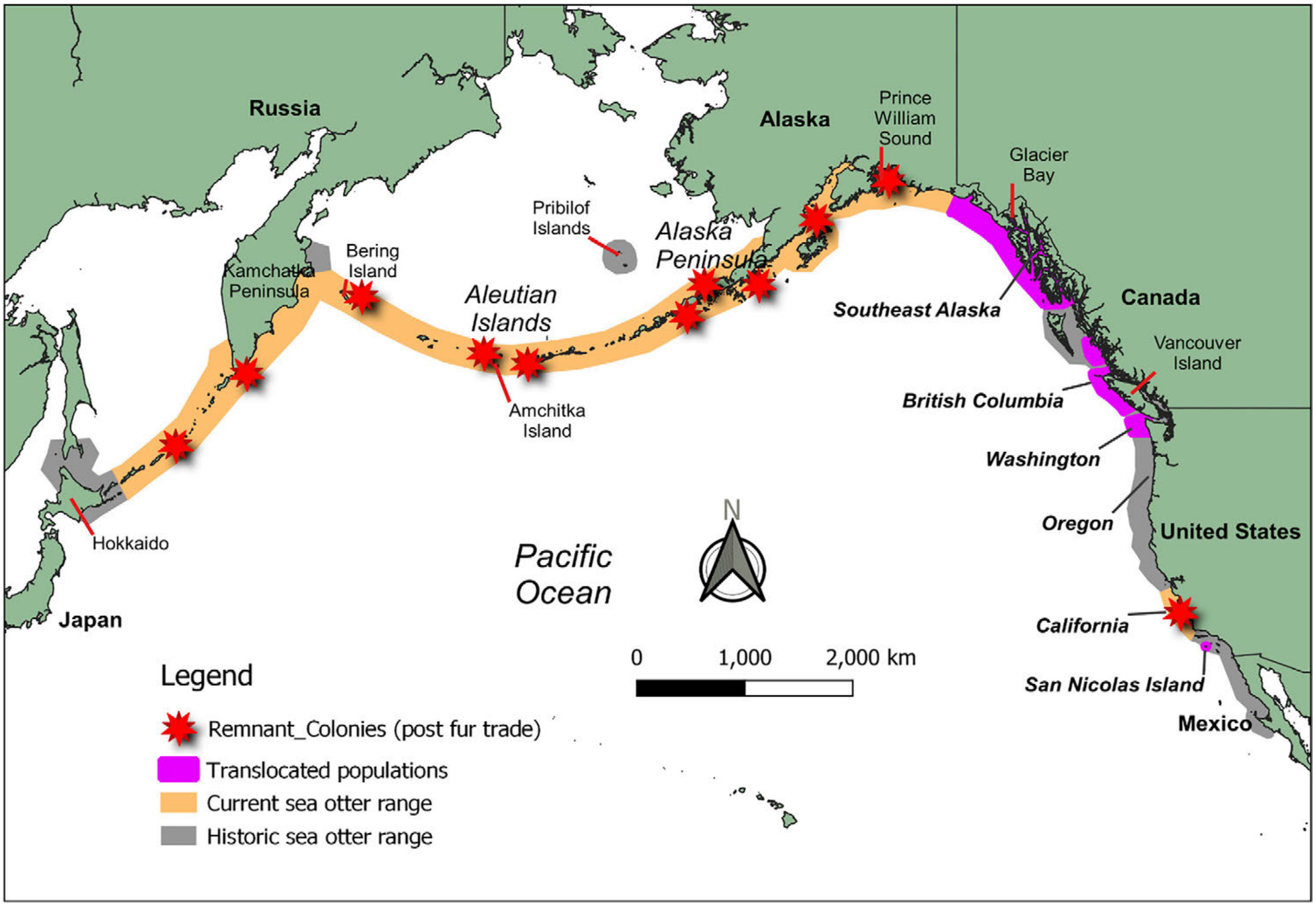
Translocations or reintroductions of wildlife are often employed as a tool to mitigate human activities' direct or indirect effects that result in the loss or reduction of species in all or parts of their historical habitat (Griffith et al. 1989, Seddon et al. 2014). Following a growing recognition of the important role that keystone species—often apex predators—can play in the structure and function of ecosystems (Paine 1966, Power et al. 1996), the goals of translocations and reintroductions have also come to include ecosystem restoration (Moritz 1999, Hale and Koprowski 2018). Most recently, establishing genetic connectivity and the recovery of genetic diversity within species and across habitats have become desired attributes and explicit objectives in the reintroduction of species, particularly those with a demonstrated loss of genetic diversity (Larson et al. 2015, Zimmerman et al. 2019). A rich history of sea otter (*Enhydra lutris*) recovery following the North Pacific maritime fur trade and translocations since the mid-19th century (Table 2.1 and Figure 2.1) provides a powerful demonstration of each of these complementary benefits (Estes and Duggins 1995, Bodkin et al. 1999, Bodkin 2015, Hughes et al. 2019).

Translocation success often depends on a variety of recognized factors, including an appropriate number and the health of founding individuals, suitable habitat, adequate food resources, and realized reproductive potential and survival rates (Griffith et al. 1989). However, it is becoming evident that other, less well-recognized factors, such as movements and behaviors, can contribute to the success or failure of reintroductions (Batson et al. 2015, Berger-Tal et al. 2020). The history of sea otter translocations and the knowledge gained from research during the recovery process illustrate many biological, ecological, and behavioral aspects that will play a role in the success of future translocations. Assessing the feasibility of reintroducing sea otters to the Oregon coast will benefit from a comprehensive review of prior sea otter translocations and allow for the evaluation of achieving specific translocation goals.

HISTORY OF SEA OTTER TRANSLOCATIONS

The first documented sea otter translocation was in Russia in 1937, when nine sea otters were captured at Medny Island, in the Commander Islands, for transport to the Murman coast in the southern Barents Sea, more than 5000 km from their natural distribution in the North Pacific (Barabash-Nikiforov 1947/1962). The intent of the translocation was to establish an additional colony to supplement Russian fur production through captive and wild rearing. It included developing techniques to hold sea otters in captivity before translocation. Although the Russian translocation was outside the historical range of the sea otter, we describe the effort here because it was the first recorded translocation of the species. Several aspects of this initial effort are particularly relevant in considering future translocations. The first is recognizing the need for and documenting suitable environmental conditions and habitats with adequate and appropriate prey resources at the release site before translocation (Barabash-Nikiforov 1947/1962). The second is that animal husbandry practices appropriate to the species are criti-

Figure 2.1. Map of the North Pacific showing historical and current sea otter ranges.



Note. The current sea otter range includes translocated populations. The locations of the remnant colonies left at the end of the fur trade (from which present-day populations are descended) are also shown.

cal to translocation success, particularly while in transport. The third is that holding animals in captivity is feasible, and acclimating animals at release sites could contribute to translocation success. Unfortunately, only two males survived the long and complex journey, which occurred first by ship and then by train, but these two survivors lived in captivity and in the wild for more than four years, thus demonstrating the feasibility of translocating and long-term holding of this species in captivity (Barabash-Nikiforov 1947/1962).

Initial efforts to restore sea otter populations within their historical range along the coasts of North America began in 1951 (Kenyon and Spencer 1960, Kenyon 1969). Between 1951 and 1959, five attempts to translocate 86 sea otters failed. They were translocated in groups of five to 35 individuals from Amchitka Island in the central Aleutians (Figure 2.1) to the Pribilof Islands (total of 81) in the Bering Sea and Attu Island (total of five) in the western Aleutians. Fifty-three of the animals captured in these early translocations died in captivity before transport, and almost none of the animals released are known to have survived following their release. These early attempts at husbandry and translocation apparently failed due to several different factors (or combinations of factors), including inadequate holding facilities and husbandry practices before and during transport, long transport times by ship that resulted in high rates of mortality (in some cases up to 100%), and in two cases (five to Attu in 1956 and six to the Pribilof Islands in 1957), an inadequate number of individuals (Kenyon 1969). The 1959 relocation to the Pribilof Islands was novel in being comprised exclusively of tagged animals and being partially successful, as at least one of seven juveniles relocated in

Table 2.1. Summary statistics for 10 previous sea otter translocation and reintroduction efforts.

Release location	Year(s)	Source	Intended for release	Number released	Success	Approx. founding number	Recent estimate
Murman Peninsula	1937	Bering Island, Russia	9	2	no	1	0
Pribilof Islands	1951	Amchitka, Alaska	35	0	no	0	0
	1955	Amchitka, Alaska	31	19	no	0	0
	1957	Amchitka, Alaska	8	0	no	0	0
	1959	Amchitka, Alaska	10	7	unknown	3	0
	1968	Amchitka, Alaska	55	55	temporary	unknown	0
Attu	1956	Amchitka, Alaska	5	5	no	0	NA
California	1969	California	17	17	no	NA	NA
North SE Alaska	1965–1969	Amchitka & Prince William Sound, Alaska	297	297	yes	100–150	11,600
Central SE Alaska	1968		51	51	yes	30	13,200
South SE Alaska	1968		55	55	yes	21	
		SE Alaska — TOTAL	**403**	**403**	**yes**	**150**	**> 25,000**
British Columbia	1969–1972	Amchitka & Prince William Sound, Alaska	89	89	yes	28	7000
Washington	1969–1970	Amchitka, Alaska	59	59	yes	10	> 2000
Oregon	1970–1971	Amchitka, Alaska	93	93	no	0	0
San Nicolas Island, CA	1987–1990	California	142	139	yes	12	121
Elkhorn Slough, CA	2002–2016	California	37	37	yes	37 + ~25 wild	120

Note. NA means "not available," and SE means "southeast."

1959 was sighted two years after release. It is also possible that the Pribilof Islands, lying near the northern extent of the sea otters' range, provided a less-than-optimal habitat.

Concurrent with both the Russian and U.S. early translocation attempts, work was undertaken to develop animal husbandry methods that might increase the survival of sea otters in captivity (Barabash-Nikiforov 1947/1962, Kenyon and Spencer 1960, Kenyon 1969). High mortality during holding and transport in both the Russian and American initial attempts identified the critical need for sea otters to maintain their fur's integrity to achieve thermal neutrality. Early husbandry practices also included inadequate quantities of food (< 10% of their body weight/day) and provisioning of atypical foods (e.g., meat of waterfowl and seal). Access to clean water and appropriate food and space while in holding and transport proved to be instrumental in reducing mortality before introduction and improving future translocation success. While early translocations resulted in high mortality and largely failed efforts, insights gained eventually led to what became a highly successful marine conservation effort (Bodkin 2015).

The first successful North American translocation took place in 1965 when 41 sea otters were captured and moved by amphibious aircraft from Prince William Sound to Southeast (SE) Alaska. Twenty-three of these animals survived to be released to Chichagof Island in SE Alaska (Kenyon 1969). Although pre-release mortality was high (44% of the 41 otters) due to overheating in flight, possibly related to tranquilizing, at least some individuals were resighted in 1966.

This event was the beginning of 13 separate translocations of 708 individuals from Amchitka Island and Prince William Sound to various locations between 1965 and 1972 (Jameson et al. 1982). Fifty-five individuals were moved to the Pribilof Islands in 1968; 389 to six release sites in SE Alaska from 1965 to 1969; 89 to the west coast of Vancouver Island, British Columbia, from 1969 to 1972; 59 to the Olympic coast of Washington from 1969 to 1971; and 93 (63 females and 30 males; 44 adults and 39 juveniles, with 10 of unknown age) to two releases sites on the coast of Oregon in 1970 and 1971 (Jameson 1975, Jameson et al. 1982).

The series of translocations and reintroductions between 1965 and 1972 had mixed success. Sea otters persisted in the Pribilof Islands for at least 10 years, with sporadic observations of independent animals until at least 1976 (Schneider 1981). There was some suggestion that their continued presence may have reflected immigration from otters reoccupying historical habitat along the north Alaskan Peninsula. In addition to the eventual failure of the Pribilof translocation, the other translocation that ultimately failed was to Oregon: Surveys reported declining abundance from the initial 93 animals that were reintroduced until only a single animal could be found by 1981 (Jameson et al. 1982). However, the presence of pups provided clear evidence of successful reproduction in the Oregon population during the decade after 1971. It seems likely that post-release mortality contributed to the failure of the Oregon translocated population to become established, but it is also likely that at least some of the Oregon animals dispersed north to Washington, thus contributing to the eventual success of the translocated Washington population and possibly even the British Columbia population (Jameson et al. 1982). The eventual failures of the Pribilof Islands and Oregon efforts highlight two key points: (1) The success or failure of reintroductions may take a decade or more to manifest. (2) Frequent and systematic monitoring of post-release populations during the first decade could help inform management actions to influence successful establishment, perhaps through enhancing survival, reducing mortality, or augmenting abundance via supplementary introductions of additional animals.

The reintroductions to SE Alaska, British Columbia, and Washington clearly established the feasibility of reintroductions as a tool to enhance the recovery of sea otters across their range. In SE Alaska, the 412 animals translocated by 1969 resulted in more than 25,000 by 2011/2012 (Bodkin 2015, Tinker et al. 2019). By 2013, nearly 7000 individuals resided along British Columbia (Nichol et al. 2015), and more than 2000 along the Washington coast in 2017 (Jeffries et al. 2017). Today it is likely that sea otter abundance from translocations alone exceeds 50,000 animals (based on observed recent rates of increase of about 10% annually), a number that may represent more than a third of the current overall number of sea otters in the North Pacific Ocean.

Between 1987 and 1990, the U.S. Fish and Wildlife Service (USFWS) conducted the most recent translocation of 139 animals from the mainland central California coast to San Nicolas Island, 110 km off the coast of southern California (Rathbun et al. 2000). This effort was the first translocation to explicitly aid in the recovery of the southern subspecies of sea otter listed under the Endangered Species Act. It was also the first translocation to rigorously evaluate the health of individuals, define the specific age and sex of animals to be moved, and closely monitor the translocated animals post-release. While plans and pens were constructed to acclimate animals at the release site to encourage retention (Ames et al. 1986, USFWS 1987), sea conditions compromised the safety of the penned animals, and they were released within a few days of transport to the island. As with all previous translocations, the number of animals remaining at San Nicolas Island declined dramatically during the post-release population establishment phase—to just 16 animals by 1991 (Rathbun et al. 2000)—and reached a nadir in 1993 of 12 animals observed. However, counts of sea otters at San Nicolas Island began to increase in the late 1990s (10 years after the translocation), and a recent census reported a population of 121 animals in 2019, with a five-year average annual rate of increase of 10% (Hatfield et al. 2019). While not assured, the long-term viability of this latest translocation now seems likely.

The differences in outcomes of previous translocation events, as well as some of the similarities, suggest several key factors that may contribute to successful reintroductions. While adequate food resources are obviously essential to successful translocation, it is unclear whether prey abundance was a factor in the failure of the Oregon effort or any of the prior failures, or indeed to the delayed success of any of the successful translocations. Both the initial Russian and the San Nicolas translocations dedicated significant efforts to ensuring suitable and abundant prey was available at release sites (Barabash-Nikiforov 1947/1962, USFWS 1987). While abundant prey resources do not ensure the rapid and successful establishment of any introduced population, they are nonetheless essential to ensure that appropriate and adequate prey are available at and near the locations of any future sea otter reintroductions. Other considerations include a sufficient number of individuals of the appropriate age and sex classes; the existence of protected areas for resting and pup rearing (e.g., reliable kelp beds or protected bays/inlets); minimal levels of disturbance from human activities (e.g., commercial and recreational boat traffic or tourism activity); and low levels of threats such as toxins, fishing gear entanglement, or disease vectors that could lead to elevated mortality during the establishment phase (see Chapter 6 on habitat suitability and Chapter 10 on health and welfare considerations).

Although not a reintroduction in the traditional sense of moving sea otters into unoccupied historical habitat, the most recent managed introduction of sea otters involved the release of captive-raised juvenile sea otters into a coastal estuary in central California. Between 2001 and 2017, a total of 37 stranded pups were raised in captivity at the Monterey Bay Aquarium, with older female sea otters acting as surrogate mothers (henceforth "surrogates"). Once these pups reached the typical weaning age (six to eight months), they were transported and released into Elkhorn Slough, an estuary at the head of Monterey Bay, California (Mayer et al. 2019). Originally, the selection of Elkhorn Slough was made based on logistical considerations, as it was easier to monitor the rehabilitated juveniles within the enclosed estuary and recapture them if they required supplementary care. A secondary objective of this reintroduction was to enhance the local sea otter population (Mayer et al. 2019). This effort is notable for several reasons. First, it engaged captive adult female surrogates in the rehabilitation and raising of stranded juvenile sea otters explicitly for release over time. Second, animals were held and raised in captivity for extended periods of time during their development, a step that may have facilitated socializing and bonding among the animals eventually released. Third, in contrast to all prior translocation release sites, which were in or near outer coastal rocky reef habitats, these animals were released into a sheltered, soft-sediment estuarine environment. Also relevant is the fact that the juvenile sea otters were added to an area already occupied by otters for at least two decades, although in limited numbers and primarily by males. (No reproduction had occurred in the slough before the reintroductions, and the first females observed with pups within the slough were, in fact, rehabilitated females.) Perhaps most importantly, this reintroduction process, although often requiring the recapture of juveniles and further rehabilitation in captivity before subsequent re-release, did not incur the large-scale losses of individuals due to emigration or mortality that were ubiquitous in earlier translocations.

METHODS OF SEA OTTER TRANSLOCATION

In general, methods employed in all sea otter translocations consist of individuals' capture, holding, transport, and release, either as a single group in early translocations or, more recently, in a series of individuals or groups over time. Various methods are employed to capture free-ranging sea otters, including *tangle nets* set in the water near where animals reside and long-handled *dip nets* on haul outs or in open water when they are at rest. Most recently, specially designed diver-operated traps, called *Wilson traps*, have been used to capture otters from under the water (Ames et al. 1986, Monson et al. 2001). Federal and state/provincial governments highly regulate the capture of sea otters and require adherence to stringent permitting conditions. In the United States, sea otter permits fall under the purview of the USFWS Division of Management Authority. Permit acquisition is predicated on demonstrating expertise in the safe and humane capture and handling of sea otters, meeting animal health and welfare requirements, and describing how proposed activities benefit species conservation and management. Obtaining the necessary permits for translocation depends on the source population(s) status and the proposed release sites and may take several years.

Once captured by tangle net, dip net, or scuba-operated Wilson traps, otters are transferred to specially designed boxes or kennels for transport to holding facilities where the animals are accumulated in pools and prepared for transport to the release site. Transport is usually accomplished by van or truck to either ship (in the earlier translocations) or aircraft (in translocations since 1965). Over time, methods of capture, handling, holding, transport, and release have been refined to the point where serious injury or death has become an exceedingly rare event, but even with the greatest care, some low rate of morbidity should be expected when handling large numbers of sea otters. Additional details on current capture, holding, transport, and release procedures can be found in Chapter 9 and in Ames et al. (1986).

LESSONS LEARNED FROM PAST TRANSLOCATIONS

Over the past 80 years, nearly 1000 sea otters have been captured, held, transported, and released into unoccupied habitats to restore populations. It is evident that the earliest translocations gave inadequate attention to the physiological needs required for the sea otters to maintain the integrity of their pelage and that high mortality resulted from poor animal husbandry practices during holding and transport (Barabash-Nikiforov 1947/1962, Kirkpatrick et al. 1955, Kenyon 1969). Since these early efforts, improvements in capture, husbandry, and transport have nearly eliminated pre-release mortality (Ames et al. 1986, Rathbun et al. 2000, Mayer et al. 2019). In all translocations for which there are data, the numbers of sea otters reintroduced appeared to have declined rapidly following their release and, in most cases, appeared to stabilize at 10%-50% of the original number released. Researchers have a limited understanding of the causes behind this rapid diminishment following introductions due to the limited follow-up surveys after most translocations. Post-translocation surveys and the marking of individuals moved to San Nicolas Island provided new insights into this phenomenon. Intensive post-release surveys at San Nicolas and throughout California documented that at least 26% (36 of 139) of the translocated animals returned to their original capture locations (Rathbun et al. 2000, Carswell 2008). An additional but unknown number of animals may have perished during an attempt to return to their original home range (Carswell 2008), a phenomenon that may explain post-release movements and declines after other translocations (Jameson et al. 1982). This finding demonstrates the strong individual affinity in this species for their established home range and the associated likelihood of post-release dispersal that occurred at San Nicolas despite its selection as an appropriate release site based on habitat suitability and prey abundance (Rathbun et al. 2000).

Further, the decision to translocate predominantly subadult sea otters did not appear to prevent an initial loss of animals at San Nicolas (Rathbun and Benz 1991), although there is some indication that the youngest animals were less likely to disperse (Carswell 2008). This finding further indicates that factors other than prey can be important in determining the behavior of species being translocated and suggests that social, behavioral, and cultural attributes should be considered carefully. These considerations may be particularly relevant for sea otters, as they occupy small home ranges (Tarjan and Tinker 2016), exhibit specialized prey preferences that may be learned or culturally transmitted from other sea otters (Estes et al. 2003, Tinker et al. 2008), and demonstrate long-term relations among individuals within shared ranges (U.S. Geological Survey, unpublished data). Sea otters translocated into vacant habitats appear unlikely to remain where released, despite the general habitat suitability and prey abundance, because of their affinities for specific habitat features, prey preferences, and social interactions associated with their original home ranges.

Systematic surveys of early translocated populations were rare, usually only occurring after populations became established, and this dearth resulted in uncertainty about founding population sizes and early population growth rates (Bodkin et al. 1999). However, once fully established, translocated populations generally demonstrated growth rates at or near the maximum rates feasible for sea otters (Estes 1990), averaging approximately 20% per annum, and significantly greater than growth rates observed in remnant populations (≈ 10%; Bodkin et al. 1999). One recent exception to these results was the 1987 translocation to San Nicolas Island (Rathbun et al. 2000, Carswell 2008), where, following three years of consecutive translocations, the founding population of 139 quickly declined to 16 individuals and then remained essentially unchanged for almost a decade (Hatfield et al. 2019). The pattern of post-release decline at San Nicolas Island was similar to other successful translocations to SE Alaska, British Columbia, and Washington, but while these earlier translocations soon achieved annual growth rates of 20% or more, the annual growth rate at San Nicolas from 1999 to 2009 was only 6%. Rates of reproduction appeared adequate to sustain growth (pup:adult ratios were as high or higher than the mainland California population), and adult survival rates of tagged animals were very high (Bentall 2005), suggesting that subadults were being lost from the population, either through emigration or, more likely, fishery-related mortality (Hatfield et al. 2011). Interestingly, after 2009, the annual rate of population growth at San Nicolas increased to approximately 12%.

The history of the San Nicolas translocation provided new and vital information regarding factors important to translocation success. First, abundant habitat and prey resources are not by themselves sufficient to ensure high retention rates of introduced animals. Second, behavioral and cultural factors, likely related to familiarity with established home ranges and social relations, contribute to initial losses. Third, unanticipated sources of mortality (such as fishing gear entanglement) can adversely affect growth rates, particularly when the population size is small. And lastly, one of the legal conditions imposed on the San Nicolas translocation was that an "otter-free" zone would be maintained by capturing and removing sea otters outside San Nicolas between Point Conception and the Mexican border on the California mainland. After many years of trying to comply, in 2012, the USFWS abolished this requirement by declaring the translocation a failure (USFWS 2012), thus demonstrating the difficulty in spatially managing the distribution of sea otters by nonlethal means.

CONCLUSIONS

Several lessons can be gained from past experiences with translocating sea otters to aid their conservation. First, the basic biology of the species must be accounted for: Early translocations were largely unsuccessful due to the lack of understanding of the basic physiology of sea otters and their dependence on maintaining a thermal balance through their pelage and on an unusually high metabolic requirement.

Second, given suitable habitat, prey resources, and protection from human or other mortality sources, translocations have proved an important tool in sea otter conservation. Assuming consistent rates of change over the past decade, about 30% of the global sea otter abundance today can be attributed to translocations to SE Alaska, British Columbia, and Washington (Bodkin 2015).

Third, even successful reintroductions often undergo an establishment phase during which their ultimate success can be questionable (see Chapter 3). During this phase, a variety of factors tend to reduce the founding population to a small fraction of the initial number translocated. It appears that with sea otters, behavior may be more important than food in determining the retention rates at release sites. Careful consideration of the behavior and social structure within parent populations that may affect the probability of retaining individuals at a translocation site may aid in forecasting the success of future translocations. The success of recent reintroductions in Elkhorn Slough using stranded juveniles—raised with the aid of surrogate mothers (adult female otters) in captivity and released into protected estuarine habitats where recapture was practical—should encourage consideration of alternative approaches in future translocation proposals.

Finally, translocations can play roles in restoring coastal marine ecosystem structure and function, from coastal rocky reefs to estuaries (Estes and Palmisano 1974, Hughes et al. 2019; see Chapter 5), and in recovering genetic diversity and facilitating genetic connectivity among sea otter populations (Larson et al. 2015; see Chapter 4). The roles provide ample justification for considering future efforts to continue restoring sea otters and coastal ecosystems.

LITERATURE CITED

Ames, J. A., R. A. Hardy, and F. E. Wendell. 1986. *A simulated translocation of sea otters,* Enhydra lutris*, with a review of capture, transport, and holding techniques* (Marine Resources Technical Report No. 52). Long Beach: California Fish and Game.

Barabash-Nikiforov, L. L. 1962. *The sea otter*. Translated from Russian by A. Birron and Z. S. Cole. Jerusalem, Israel: National Science Foundation, Israel Program for Scientific Translations. (Original work published 1947.)

Batson, W. G., I. J. Gordon, D. B. Fletcher, and A. D. Manning. 2015. Translocation tactics: a framework to support the IUCN guidelines for wildlife translocations and improve the quality of applied methods. *Journal of Applied Ecology* **52**:1598–1607.

Bentall, G. B. 2005. *Morphological and behavioral correlates of population status in the southern sea otter: a comparative study between central California and San Nicolas Island* [Master's thesis, University of California, Santa Cruz]. University of California, Santa Cruz and the U.S. Geological Survey, Estes & Tinker Lab and Santa Cruz Field Station. https://werc.ucsc.edu/Bio%20and%20tech/Bentall/Bentall_thesis.pdf.

Berger-Tal, O., D. Blumstein, and R. R. Swaisgood. 2020. Conservation translocations: a review of common difficulties and promising directions. *Animal Conservation* **23**:121–131.

Bodkin, J. L. 2015. Historic and contemporary status of sea otters in the North Pacific. Pages 43–61 *in* S. E. Larson, J. L. Bodkin, and G. R. VanBlaricom, editors. *Sea otter conservation.* Boston: Academic Press.

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.

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* [Master's thesis, University of California, Santa Cruz].

Estes, J. A. 1990. Growth and equilibrium in sea otter populations. *Journal of Animal Ecology* **59**:385–402.

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 J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* **185**:1058–1060.

Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. Individual variation in prey selection by sea otters: patterns, causes, and implications. *Journal of Animal Ecology* **72**:144–155.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* **245**:477–480.

Hale, S. L., and J. L. Koprowski. 2018. Ecosystem-level effects of keystone species reintroduction: a literature review. *Restoration Ecology* **26**:439–445.

Hatfield, B. B., J. A. Ames, J. A. Estes, M. T. Tinker, A. B. Johnson, M. M. Staedler, and M. D. Harris. 2011. Sea otter mortality in fish and shellfish traps: estimating potential impacts and exploring possible solutions. *Endangered Species Research* **13**:219.

Hatfield, B. B., J. L. Yee, M. C. Kenner, and J. A. Tomoleoni. 2019. *California sea otter (*Enhydra lutris nereis*) census results, spring 2019* (Data Series 1118). Reston, VA: U.S. Department of the Interior, Geological Survey.

Hughes, B. B., K. Wasson, M. T. Tinker, S. L. Williams, L. P. Carswell, K. E. Boyer, M. W. Beck, R. Eby, R. Scoles, M. Staedler, S. Espinosa, M. Hessing-Lewis, E. U. Foster, K. M. Beheshti, T. M. Grimes, B. H. Becker, L. Needles, J. A. Tomoleoni, J. Rudebusch, E. Hines, and B. R. Silliman. 2019. Species recovery and recolonization of past habitats: lessons for science and conservation from sea otters in estuaries. *PeerJ* **7**:e8100.

Jameson, R. J. 1975. *An evaluation of attempts to reestablish the sea otter in Oregon* [Master's thesis, Oregon State University]. Corvallis, OR.

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. *Wildlife Society Bulletin* **10**:100–107.

Jeffries, S., D. Lynch, S. Thomas, and S. Ament. 2017. *Results of the 2017 survey of the reintroduced sea otter population in Washington state*. Lakewood, WA: Washington Department of Fish and Wildlife, Wildlife Science Program, Marine Mammal Investigations.

Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. *North American Fauna* **68**:1–352. https://doi.org/10.3996/nafa.68.0001.

Kenyon, K. W., and D. L. Spencer. 1960. *Sea otter population and transplant studies in Alaska, 1959*. Washington, DC: U.S. Department of Interior, Fish and Wildlife Service.

Kirkpatrick, C. M., D. E. Stullken, and R. D. Jones. 1955. Notes on captive sea otters. *Arctic* **8**:46–59.

Larson, S. E., K. Ralls, and H. Ernest. 2015. Sea otter conservation genetics. Pages 97–120 *in* S. E. Larson, J. L. Bodkin, and G. R. VanBlaricom, editors. *Sea otter conservation*. Boston: Academic Press.

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* **55**:535–545.

Monson, D. H., C. McCormick, and B. E. Ballachey. 2001. Chemical anesthesia of northern sea otters (*Enhydra lutris*): results of past field studies. *Journal of Zoo & Wildlife Medicine* **32**:181–189.

Moritz, C. 1999. Conservation units and translocations: strategies for conserving evolutionary processes. *Hereditas* **130**:217–228.

Nichol, L. M., J. C. Watson, R. Abernethy, E. Rechsteiner, and J. Towers. 2015. *Trends in the abundance and distribution of sea otters (*Enhydra lutris*) in British Columbia updated with 2013 survey results* [Canadian Science Advisory Secretariat Research Document 2015/039]. Nanaimo, British Columbia: Fisheries and Oceans Canada.

Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones: identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *Bioscience* **46**:609–620.

Rathbun, G. B., and C. T. Benz. 1991. Third year of sea otter translocation completed in California. *Endangered Species Technical Bulletin* **14**:1–6.

Rathbun, G. B., B. B. Hatfield, and T. G. Murphey. 2000. Status of translocated sea otters at San Nicolas Island, California. *Southwestern Naturalist* **45**:322–328.

Schneider, K. B. 1981. Distribution and abundance of sea otters in the eastern Bering Sea. Pages 837–846 *in* D. W. Hood and J. A. Calder, editors. *The eastern Bering Sea shelf: oceanography and resources*, Vol. II. Juneau, AK: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of Marine Pollution Assessment.

Seddon, P. J., C. J. Griffiths, P. S. Soorae, and D. P. Armstrong. 2014. Reversing defaunation: restoring species in a changing world. *Science* **345**:406–412.

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., G. Bentall, and J. A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proceedings of the National Academy of Sciences of the United States of America* **105**:560–565.

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.

USFWS [U.S. Fish and Wildlife Service]. 1987. *Final environmental impact statement for translocation of southern sea otters*. Sacramento, CA.

USFWS. 2012. *Final supplemental environmental impact statement on the translocation of southern sea otters*. Ventura, CA.

Zimmerman, S. J., C. L. Aldridge, A. D. Apa, and S. J. Oyler-McCance. 2019. Evaluation of genetic change from translocation among Gunnison Sage-Grouse (*Centrocercus minimus*) populations. *The Condor: Ornithological Applications* **121**:duy006.