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# GENETIC AND HISTORICAL CONSIDERATIONS OF OREGON SEA OTTERS

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## HISTORICAL CONSIDERATIONS

Sea otters (*Enhydra lutris*) have an extensive history of population extirpations and reductions by humans spanning thousands of years (Bodkin 2015, Salomon et al. 2015). Historically, sea otter populations were distributed along the North Pacific Rim from northern Japan in the northwestern Pacific to Baja California, Mexico, in the eastern Pacific (Kenyon 1969). Their abundance across this range before 1750 has been estimated as 150,000 to 300,000 animals (Johnson 1982). The most well-known and widespread extirpation, as well as the most recent, was the commercial sea otter harvest conducted during the international maritime fur trade from the mid-1700s to 1910 (Kenyon 1969). During the height of the maritime fur trade in the 18th and 19th centuries, an estimated 99% of the sea otter population was extirpated from much of its original range, leaving only 13 small, isolated, and scattered populations, 11 of which survived as founders for the populations extant today (Lensink 1960, Kenyon 1969, Bodkin 2015). Refer to Figure 4.1 for a map of the historical and current sea otter range, including locations of remnant populations from the fur trade and those populations resulting from successful translocations.

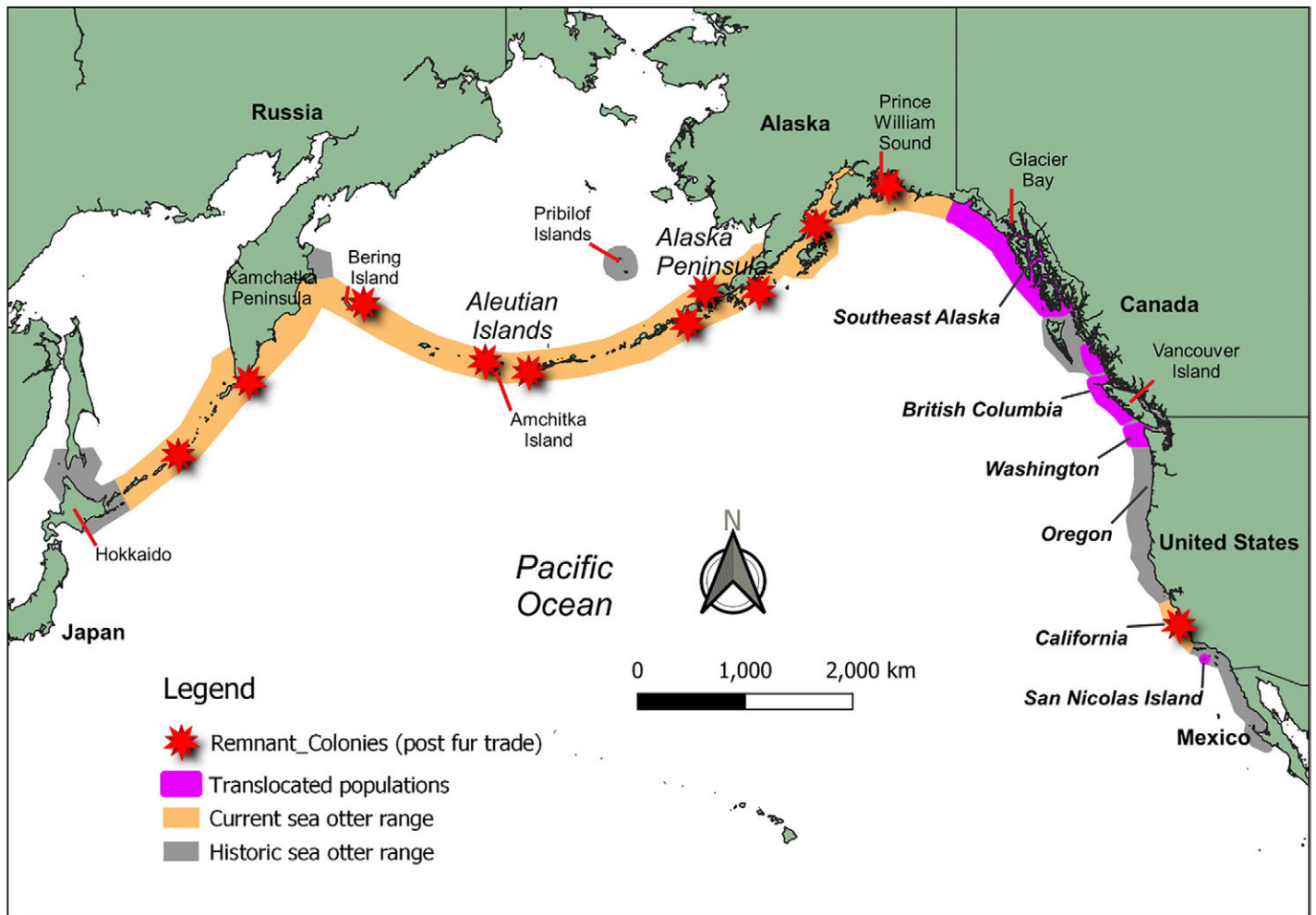
Before the commercial fur trade extirpations, sea otters were hunted by the Indigenous populations of North America for at least 10,000 years for food and ceremonial purposes, as well as for the management of shellfish stocks (Simenstad et al. 1978, Salomon et al. 2015). According to oral historical accounts, sea otter hunting was a respected skill and honored tradition among coastal Indigenous communities, and only certain people had the privilege to hunt, such as the chief or a hunter designated by the chief (Salomon et al. 2015). Like many coastal resources used by Indigenous Peoples, it is believed that sea otters were managed spatially, with male rafts targeted more often than female-dominated areas (i.e., areas used by reproductive females and territorial males and from which non-territorial males are mostly excluded). Spatial management practices likely reduced or excluded sea otters from some areas while leaving abundant populations in other areas, thus resulting in a patchwork of sea otter populations and sea otter exclusion areas, otherwise known as an ecological mosaic. Shellfish harvests could be optimized in areas from which sea otters were excluded, while the maintenance of healthy sea otter populations in other areas ensured their availability for ceremonial uses, as otter fur and teeth were highly valued and used to demonstrate high social status (Salomon et al. 2015).

This scenario is supported by the fact that sea otter remains can still be found and investigated in curated Indigenous *middens* (layers of discarded animal bone, shells, and other artifacts from historical human occupation) throughout the west coast of North America that represent thousands of years of continuous occupation. Indigenous subsistence hunting was thus sustainable in the sense that sea otter populations persisted throughout their North American range before the arrival of Europeans, although genetic analyses have suggested one or more population



# 4

**Figure 4.1.** Map of the North Pacific showing historical and current sea otter ranges.



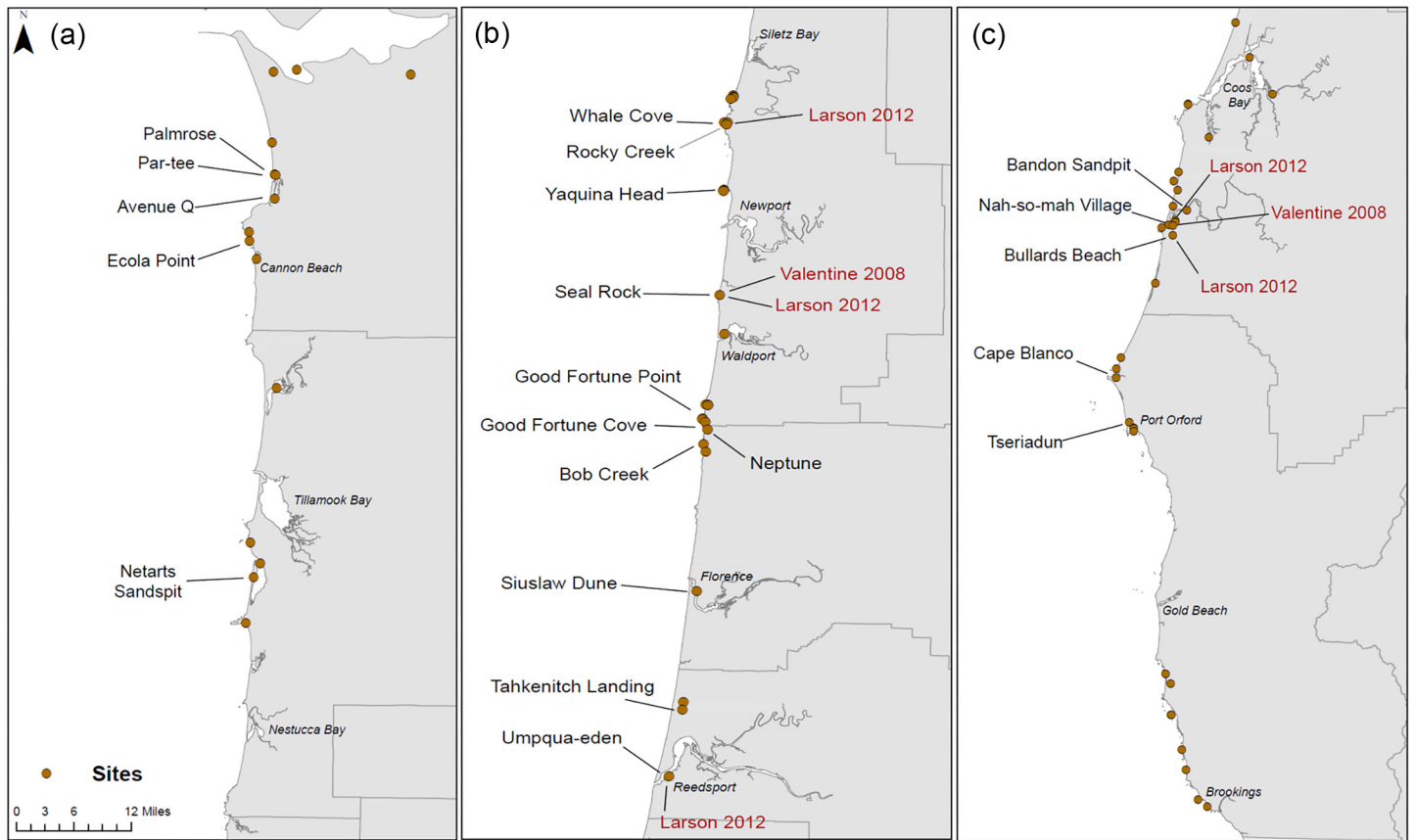
Note. This map includes the locations of remnant populations from the fur trade and those populations resulting from successful translocations.

bottlenecks (of unknown severity or duration) that potentially affected genetic diversity over this period (Aguilar et al. 2008, Beichman et al. 2019). Even though there were likely long-term and widespread harvests of sea otters by Indigenous Peoples, the maritime fur trade continues to be accepted as the primary mechanism of sea otter population extinctions and reductions throughout their former range (Lensink 1960, Kenyon 1969, Jameson et al. 1982, Bodkin 2015).

Range expansion following fur trade extirpations in portions of the Aleutian archipelago was relatively rapid due to the presence of several remnant populations and the relatively short distances between populations (10s of kilometers), which were well within the range of sea otters' movements in Alaska (Lensink 1960, Kenyon 1969, Garshelis and Garshelis 1984, Tinker and Estes 1996). However, even though some populations recovered relatively quickly, much of the historical sea otter habitat along the west coast of North America remained vacant, from the remnant population in Prince William Sound, Alaska, to the remnant California population centered around Big Sur (Kenyon 1969, Estes 1990). This situation changed rapidly in the 1960s and early 1970s when state and federal agencies made several translocations of sea otters from the Aleutian Islands and Prince William Sound populations to vacant habitat along North America's west coast (see [Chapter 2](#); Jameson et al. 1982).

Roughly 700 otters were captured at Amchitka Island in the Aleutian chain and in Prince William Sound, Alaska, and released into previously occupied habitats in Southeast (SE) Alaska, Vancouver Island in British Columbia, Washing-

**Figure 4.2.** Coastal Oregon archaeological sites with known vertebrate faunal remains, plotted by region.



Note. The regions plotted are (a) North, (b) Central, and (c) South Oregon. Labeled sites are known to have held sea otter remains, and sites that were previously sampled for genetic studies are labeled in red. From Curran et al. (2019).

ton, and Oregon. An important detail from a genetic standpoint is that the SE Alaska and Vancouver Island translocations were founded by animals from Amchitka and Prince William Sound, while the Washington and Oregon translocations were founded only by Amchitka animals (Jameson et al. 1982, Bacon 1994, Bodkin et al. 1999). All these translocations resulted in viable sea otter populations extant today except the one to Oregon, which failed for unknown reasons (Jameson et al. 1982). There is speculation that the surviving otters eventually swam north to join the population in Washington (see [Chapter 2](#) for details and Figure 4.1 for a map of successful translocations).

In sum, it is clear that sea otters occupied Oregon before the fur trade, as evidenced by Indigenous Peoples' oral histories, sea otter remains in Oregon's Indigenous middens (Valentine et al. 2008, Hall 2009), and written accounts of sea otters by explorers such as Meriwether Lewis and William Clark and by fur traders (La Follette and Deur 2021). However, a clear account of the density and distribution of otters throughout Oregon before the fur trade extirpation is missing. Studies of Indigenous middens along Oregon's coast suggest that sea otters likely inhabited much of the coast (Figure 4.2), although actual numbers of individual otters in these middens have not been analyzed. The Lewis and Clark Expedition in the winter of 1805–1806 mentioned that sea otters were "plentiful" along the northern Oregon coast yet hard to kill (La Follette and Deur 2021). Some researchers have concluded that sea otters were less numerous in Oregon than they were to the north and south (Ogden 1941), as evidenced by the scarcity of sea otter harvest records during the fur trade, the dearth of international trading ships that could easily make port along Oregon's coast, and the observation that native Oregon sea otters had been hunted to extinction by the beginning of the 20th century despite the apparently limited harvest efforts (La Follette and Deur 2021).

## GENETIC CONSIDERATIONS

Over this extensive history—from Indigenous communities’ interactions for thousands of years to the massive and extensive fur trade extirpations to the translocations of small numbers of otters and subsequent population recovery—many extant sea otter populations are thought to have suffered from not just one but multiple reductions in population size over time (Larson et al. 2002a, Larson et al. 2002b, Aguilar et al. 2008, Beichman et al. 2019). Populations that suffer one or many severe reductions in population size and isolation due to reduced population connectivity are recognized to be at risk for a loss of genetic diversity (Frankham 2005, Lankau and Strauss 2007, Ralls et al. 2018). Genetic studies focused on sea otters have used a variety of variable nuclear genetic markers and have demonstrated relatively low genetic diversity (average of 50% diversity within the genome) within all extant sea otter populations. Compare the otters to mammals that have no known population bottlenecks and typically have diversity metrics between 70% and 80% diversity within the genome (Cronin et al. 1996, Scribner et al. 1997, Larson et al. 2002a, Larson et al. 2002b, Aguilar et al. 2008, Larson et al. 2012, Gagne et al. 2018).

To estimate pre-exploitation sea otter genetic diversity, Larson et al. (2002b, 2012) used nuclear microsatellite markers and 600-year-old to more than 10,000-year-old sea otter bones found in Indigenous midden collections. These ancient sea otter samples had levels of genetic *heterozygosity* (a measure of genetic diversity) ranging from 62% in ancient California to 86% in ancient Alaska, indicating a loss of about 30%–40% of pre-bottleneck heterozygosity (Larson et al. 2002b, Aguilar et al. 2008, Larson et al. 2012, Gagne et al. 2018).

The sea otter populations with the highest measured levels of genetic diversity to date are from the translocated groups founded by more than one source population: SE Alaska (60%) and Vancouver Island, British Columbia (54%), both founded by a combination of Amchitka Island and Prince William Sound otters. In addition, recent genetic evidence suggests that the Washington translocated population, which was originally founded by Amchitka animals, has been mixing genetically with the Vancouver, British Columbia, population, thereby increasing its genetic diversity to 56% and approaching 80% of estimated pre-fur-trade genetic diversity levels (Larson et al. 2012, Larson et al. 2021). The California sea otter population has the lowest genetic diversity, stabilizing over the past 40 years at 49% diversity, most likely because of past bottlenecks, relatively slow growth rates, and continued isolation from other sea otter populations (Gagne et al. 2018).

The successful reintroductions of sea otters to Washington, Vancouver Island in British Columbia, and SE Alaska were responsible for a combined abundance of approximately 50,000 animals as of 2012 (Nichol et al. 2015, Jeffries et al. 2017, Tinker et al. 2019), representing approximately one-third of the estimated 125,000 sea otters existing at that time (Bodkin 2015). In addition, as evidenced by new genetic migrant analyses, these reintroductions have been instrumental in increasing population connectivity, with evidence of migrants and thus gene flow between neighboring sea otter populations spanning from the Alaska Peninsula to Prince William Sound to SE Alaska and down into British Columbia and Washington (Larson et al. 2021). These successful translocations have arguably been the most successful management tool employed to recover extirpated sea otter populations and their genetic diversity. However, because of the failure of the Oregon translocation, there remains a large stretch (approximately 1200 km) of unoccupied habitat from northern California to southern Washington. Recolonization of this unoccupied stretch, either naturally or via managed reintroduction, would effectively complete the genetic connectivity of sea otters throughout their historical range. Current rates of natural range expansion in Washington and California have slowed or stalled in recent years (Jeffries et al. 2017, Tinker et al. 2017, Hatfield et al. 2019, Tinker et al. 2021), so managed reintroduction would clearly accelerate this goal’s achievement. If such a management action were to be undertaken, a key question would be which sea otter population should be used as a source population.

The selection of a source population for a new reintroduction to Oregon should take into consideration two factors from a genetic perspective: (1) maximization of genetic diversity and (2) genetic consistency with the original pre-fur-trade population in Oregon. The sea otters native to Oregon have been analyzed genetically by three different researchers to determine whether they more closely resembled southern sea otters, northern sea otters, or a mixture of both. Remains from pre-fur-trade Oregon sea otters were sampled from Indigenous midden sites. The actual number of

individual sea otters in Oregon Indigenous middens remains unknown, but they were one of the most common marine mammals found along with Steller sea lions and harbor seals (Hall 2009). Valentine et al. (2008) sequenced a portion of the mitochondrial DNA (mtDNA) from ancient Oregon otter teeth at two separate locations, the Seal Rock location in north-central Oregon and the Nah-So-Mah Village location in southern Oregon near Bandon. They sequenced 16 mtDNA signatures, or *haplotypes*, matching both modern northern and southern sea otters, as well as two new haplotypes not yet recorded. Valentine et al. (2008) found the dominant haplotype matching southern sea otters and suggested that one reason the translocation in the mid-20th century to Oregon failed was because the founders from Amchitka were not genetically suited to colonize the Oregon coast.

Larson et al. (2012) looked at nuclear genetics from ancient/historical sea otters sampled throughout the range. They sampled ancient/historical pre-fur-trade Oregon sea otters from midden remains (bones) from five archaeological sites: (1) Little Whale Cove (site number: 35-LNC-43) on the northern Oregon coast; (2) near the mouth of the Umpqua River and (3) near Seal Rock State Park, both on the central Oregon coast; and (4 and 5) two sites near the mouth of the Coquille River near Bandon on the southern Oregon coast. They found that the Oregon samples were genetically similar to both ancient/historical California (southern sea otters) and Washington samples (northern sea otters). However, the majority of the ancient/historical Oregon samples were assigned to the group containing ancient/historical Washington samples, suggesting more gene flow moving northwards than in a southerly direction. This finding using nuclear markers contrasted with the earlier finding based on mtDNA (Valentine et al. 2008). Together, these findings suggest a possible hybrid zone between southern and northern sea otters in Oregon, although the location and extent of such a hybrid zone are unclear.

Finally, new research by Wellman et al. (2020) presented the results of a sequence of the complete mtDNA genome (the mitogenome) from 20 archaeological sea otter teeth: 10 from the Par-Tee site and 10 from the Palmrose site in northern Oregon. The researchers also sequenced two teeth from historical otters collected near Port Orford in southern Oregon during the height of the fur trade in the mid-1800s. Wellman et al. (2020) found 10 archaeological Oregon haplotypes, six unique to single individuals and similar to other northern sea otters (specifically historical Washington and British Columbia haplotypes) that were substantially different from California haplotypes. The two fur-trade-era haplotypes from southern Oregon also clustered close to northern haplotypes (Wellman et al. 2020). These results are perhaps unsurprising in light of the previous analyses, given that their archeological samples were exclusively from northern Oregon.

Considering all the ancient Oregon archaeological studies to date, the results strongly point to genetic variation along a latitudinal cline and suggest that, before sea otter extirpation in the fur trade, the Oregon coast served as a transitional zone between southern and northern sea otters and could serve a similar function in the future. Further investigation is required to increase the archaeological, historical, and modern nuclear and mitogenome data sample size from locations throughout the sea otters' former range.

## CONCLUSION

The history of sea otters in western North America—including information from Indigenous oral histories, archaeological remains, and genetic studies—suggests that sea otters in Oregon represented a hybrid zone between southern and northern sea otter populations. Based on this evidence, an argument could be made that any future reintroduction effort would benefit from a design that keeps this history in mind and, thus, aims to recreate such a hybrid zone. This could be achieved in several ways: (1) using both southern and northern source populations for an Oregon reintroduction, (2) using northern sea otters as a source population for a northern Oregon release site and southern sea otters as a source population for a southern Oregon release site, or (3) pairing an Oregon reintroduction that uses a northern sea otter source population with a northern California reintroduction that uses southern sea otters as a source population. In the last scenario, the hybridization of northern and southern sea otters would reoccur naturally. Any one of these strategies would further the recovery of genetic diversity by restoring the mixing of northern and southern sea otters and restoring the potential for gene flow to the largest remaining gap in sea otter distribution within their current range.

## LITERATURE CITED

- Aguilar, A., D. A. Jessup, J. Estes, and J. C. Garza. 2008. The distribution of nuclear genetic variation and historical demography of sea otters. *Animal Conservation* **11**:35–45.
- Bacon, C. E. 1994. *An ecotoxicological comparison of organic contaminants in sea otters (Enhydra lutris) among populations in California and Alaska* [Master's thesis, University of California, Santa Cruz].
- Beichman, A. C., K.-P. Koepfli, G. Li, W. Murphy, P. Dobrynin, S. Kliver, M. T. Tinker, M. J. Murray, J. Johnson, and K. Lindblad-Toh. 2019. Aquatic adaptation and depleted diversity: a deep dive into the genomes of the sea otter and giant otter. *Molecular Biology and Evolution* **36**:2631–2655.
- 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.
- Cronin, M. A., J. Bodkin, B. Ballachey, J. Estes, and J. C. Patton. 1996. Mitochondrial-DNA variation among subspecies and populations of sea otters (*Enhydra lutris*). *Journal of Mammalogy* **77**:546–557.
- Curran, L. S., D. V. Kone, and B. J. Wickizer. 2019. *Assessing the feasibility of a sea otter reintroduction to Oregon through a coupled natural-human lens*. Corvallis: Oregon State University. [https://ir.library.oregonstate.edu/concern/technical\\_reports/c821gs71d](https://ir.library.oregonstate.edu/concern/technical_reports/c821gs71d).
- Estes, J. A. 1990. Growth and equilibrium in sea otter populations. *Journal of Animal Ecology* **59**:385–402.
- Frankham, R. 2005. Stress and adaptation in conservation genetics. *Journal of Evolutionary Biology* **18**:750–755.
- Gagne, R. B., M. T. Tinker, K. D. Gustafson, K. Ralls, S. Larson, L. M. Tarjan, M. A. Miller, and H. B. Ernest. 2018. Measures of effective population size in sea otters reveal special considerations for wide-ranging species. *Evolutionary Applications* **11**:1779–1790.
- Garshelis, D. L., and J. A. Garshelis. 1984. Movements and management of sea otters [*Enhydra lutris*] in Alaska [USA]. *Journal of Wildlife Management* **48**:665–678.
- Hall, R. L. 2009, November 2. *Background resources and references for “The Oregon coast before the arrival of Europeans”* [Conference symposium]. Conference of Coastal and Estuarine Research Foundation (CERF), Portland, OR.
- 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.
- 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.
- Johnson, A. M. 1982. The sea otter, *Enhydra lutris*. Pages 525–531 in S. J. Holt, editor. *Mammals in the seas*. Rome, Italy: Food and Agriculture Organization of the United Nations.
- 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>.
- La Follette, C., and D. Deur. 2021. “The sea otter is plenty”: sea otters, empire, and the struggle for the northwest coast. Pages 6–13 in C. S. Jenkinson and C. Jenkinson, editors. *We proceeded on*. Bismark, ND: Lewis and Clark Heritage Foundation.
- Lankau, R. A., and S. Y. Strauss. 2007. Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science* **317**:1561–1563.

- Larson, S., R. B. Gagne, J. Bodkin, M. J. Murray, K. Ralls, L. Bowen, R. Leblois, S. Piry, M. C. Penedo, and M. T. Tinker. 2021. Translocations maintain genetic diversity and increase connectivity in sea otters, *Enhydra lutris*. *Marine Mammal Science* **37**:1475–1497.
- Larson, S., R. Jameson, J. Bodkin, M. Staedler, and P. Bentzen. 2002a. Microsatellite DNA and mitochondrial DNA variation in remnant and translocated sea otter (*Enhydra lutris*) populations. *Journal of Mammalogy* **83**:893–906.
- Larson, S., R. Jameson, M. Etnier, M. Fleming, and P. Bentzen. 2002b. 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.
- Larson, S., R. Jameson, M. Etnier, T. Jones, and R. Hall. 2012. Genetic diversity and population parameters of sea otters, *Enhydra lutris*, before fur trade extirpation from 1741–1911. *PLOS ONE* **7**:e32205.
- Lensink, C. J. 1960. Status and distribution of sea otters in Alaska. *Transactions of the North American Wildlife and Natural Resource Conference* **41**:172–183.
- Nichol, L. M., J. 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. Nanaimo, British Columbia: Fisheries and Oceans Canada.
- Ogden, A. 1941. *The California sea otter trade: 1784–1848*. Berkeley: University of California Press.
- Ralls, K., J. D. Ballou, M. R. Dudash, M. D. Eldridge, C. B. Fenster, R. C. Lacy, P. Sunnucks, and R. Frankham. 2018. Call for a paradigm shift in the genetic management of fragmented populations. *Conservation Letters* **11**:e12412.
- Salomon, A. K., B. J. W. Kii'iljuus, X. E. White, N. Tanape, and T. M. Happynook. 2015. First Nations perspectives on sea otter conservation in British Columbia and Alaska: insights into coupled human–ocean systems. Pages 301–331 in S. E. Larson, J. L. Bodkin, and G. R. VanBlaricom, editors. *Sea otter conservation*. New York: Elsevier.
- Scribner, K. T., J. L. Bodkin, B. E. Ballachey, S. R. Fain, M. A. Cronin, and M. D. Sanchez. 1997. Population genetic studies of the sea otter (*Enhydra lutris*): a review and interpretation of available data. Pages 197–208 in A. E. Dizon, S. J. Chivers, and W. F. Perrin. *Molecular genetics of marine mammals: incorporating the proceedings of a Workshop on the Analysis of Genetic Data to Address Problems of Stock Identity as Related to Management of Marine Mammals*. Lawrence, KS: Society for Marine Mammalogy.
- Simenstad, C. A., J. A. Estes, and K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. *Science* **200**:403–411.
- 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. 2021. *An integrated population model for southern sea otters* (Open-File Report No. 2021–1076). Reston, VA: U.S. Department of the Interior, Geological Survey.
- Tinker, M. T., and J. A. Estes. 1996. *The population ecology of sea otters at Adak Island, Alaska* (Final Report to the Navy, Contract # N68711-94-LT-4026). Santa Cruz, CA.
- 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. Tomoleoni, N. LaRoche, L. Bowen, A. K. Miles, M. Murray, M. Staedler, and Z. Randell. 2017. *Southern sea otter range expansion and habitat use in the Santa Barbara Channel, California* (OCS Study BOEM 2017-002, Open-File Report No. 2017-1001). Reston, VA: U.S. Department of the Interior, Geological Survey.
- Valentine, K., D. A. Duffield, L. E. Patrick, D. R. Hatch, V. L. Butler, R. L. Hall, and N. Lehman. 2008. Ancient DNA reveals genotypic relationships among Oregon populations of the sea otter (*Enhydra lutris*). *Conservation Genetics* **9**:933–938.
- 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.