Chapter 4. Genetic and historical consideration of Oregon sea otters

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Historical Considerations

Sea otters 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). Prior to 1750, their abundance across this range 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 fur trade remnant populations and those populations resulting from successful translocations.

Prior to the commercial fur trade extirpations, sea otters were hunted by the indigenous populations of North America (henceforth First Nations) for at least 10,000 years for food and ceremonial purposes, as well as for 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 an honored tradition among coastal First Nations 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 First Nations, 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, or 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 First Nations middens (layers of discarded animal bone, shells, and other artifacts from historic human occupation) throughout the west coast of North America and that represent thousands of years of continuous occupation. First Nations subsistence hunting was thus sustainable in the sense that sea otter populations persisted throughout their North American range prior to the arrival of Europeans, although genetic analyses suggest one or more population 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 First Nations people, the maritime fur trade remains 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).

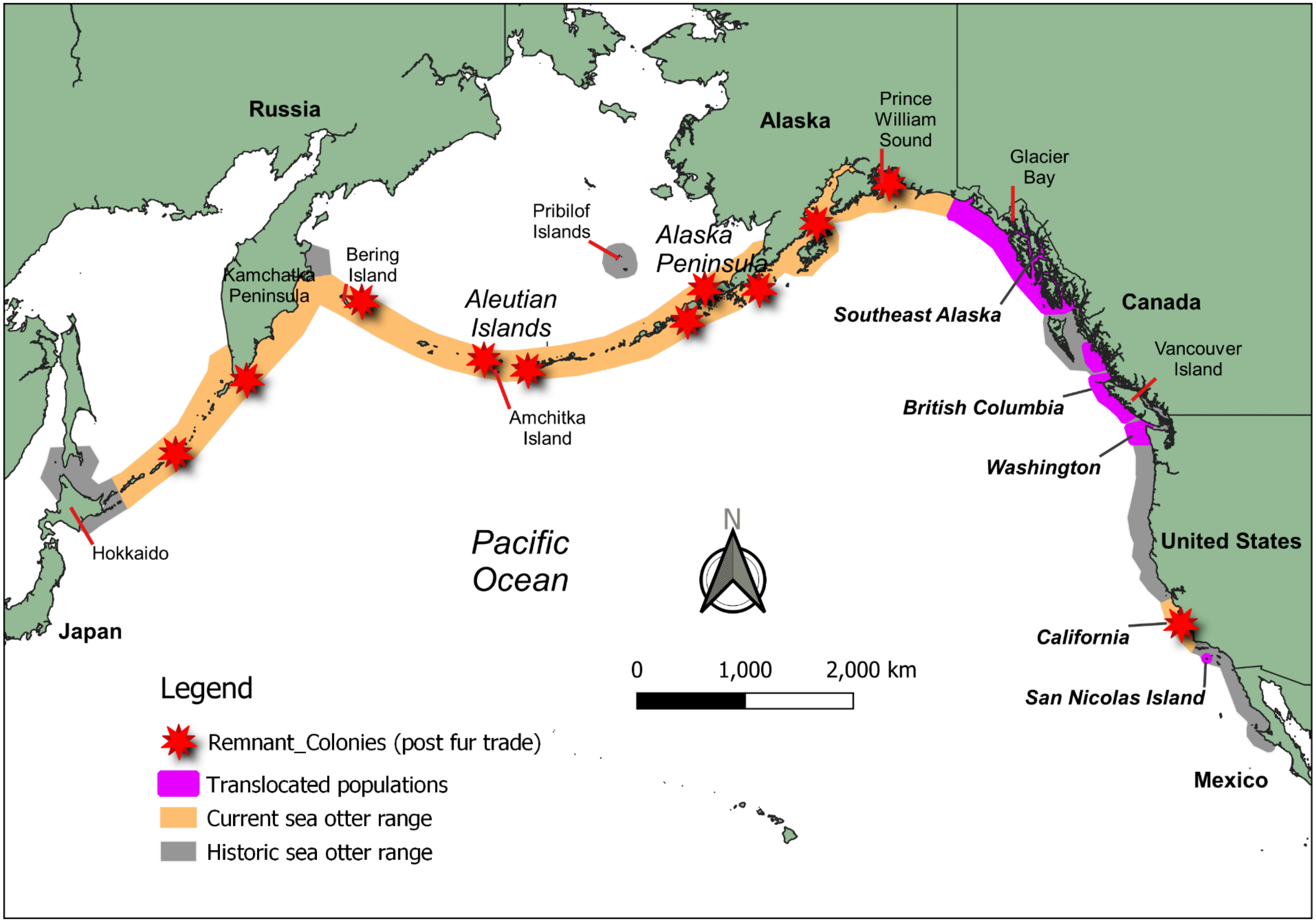

Figure 4.1 Map of the historical and current sea otter range, including locations of fur trade remnant populations and those populations resulting from successful translocations

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 kms) which are well within the range of the 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 historic 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 Americas west coast (Chapter 2 of this report, and 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 Alaska, Vancouver Island in British Columbia, Washington, and Oregon. An important detail from a genetic standpoint is that the Southeast 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), although 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 prior to the fur trade, as evidence by First Nations oral histories, sea otter remains in Oregon's First Nations middens (Valentine et al. 2008, Hall 2009), and written accounts of sea otters by explorers such as Lewis and Clark and fur traders (La Follette and Deur 2021). However, a clear account of the density and distribution of otters throughout Oregon prior to the fur trade extirpation is missing. Studies of First Nations 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" in the Northern Oregon Coast, yet also 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 fact that there were few international trading ships that could easily make port along Oregon's coast, and finally 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).

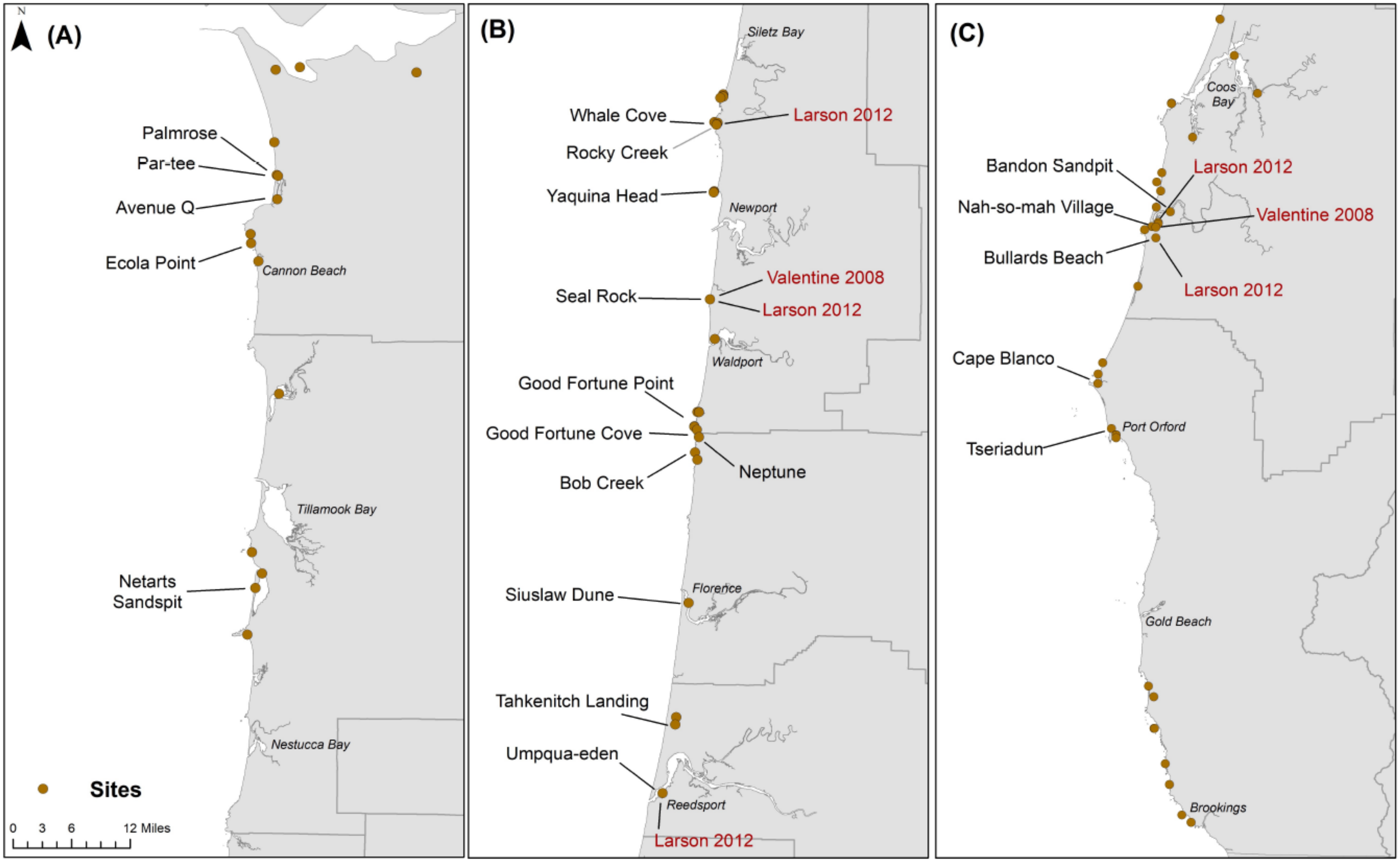

Figure 4.2. Coastal Oregon archaeological sites with known vertebrate faunal remains, plotted by region (A=North, B = Central and C = South). Labelled sites are known to have held sea otter remains, and sites that were previously sampled for genetic studies are labelled in red. (Source of Figure: Curran et al. 2019)

Genetic Considerations

Over this extensive history – from First Nations management 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 loss of genetic diversity (Frankham 2005, Lankau and Strauss 2007, Ralls et al. 2018). Genetic studies focused on sea otters using a variety of variable nuclear genetic markers have demonstrated relatively low genetic diversity (average of 50% diversity within the genome) within all extant sea otter populations, as compared to mammals that have no known population bottlenecks that typically have diversity metrics between 70-80% 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. (2002*b*, 2012) used nuclear microsatellite markers and 600 to >10,000-year-old sea otter bones found in First Nations 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, indicting 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: Southeast Alaska (60%) and Vancouver Island, BC (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 BC 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 B.C., and Southeast 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 geneflow between neighboring sea otter populations spanning from the Alaska Peninsula, to Prince William Sound to Southeast 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 1,200 km) of unoccupied habitat from northern California to southern Washington. Re-colonization 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 the achievement of this goal. If such a management action were to be undertaken, a key question is which sea otter population should be used as a source population.

Selection of a source population for a new re-introduction 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 original 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 First Nations midden sites. The actual number of individual sea otters in Oregon first nations 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 (SR) location in north-central Oregon and the Nah-So-Mah Village (NV) 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 haplotyes not yet recorded. Valentine et al. (2008) found the dominant haplotype matching southern sea otters and suggested that one reason the translocation in mid-20th century to Oregon failed was because the founders from Amchitka weren't 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: Little Whale Cove (35-LNC-43) on the northern Oregon coast; near the mouth of the Umpqua River and near Seal Rock State Park on the central Oregon Coast, and two sites near the mouth of the Coquille River near Bandon on the southern Oregon Coast. They found that the ancient/historical 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 rather than in a southerly direction. This finding using nuclear markers contrasted with the earlier finding based on mitochondrial DNA (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 is not clear. Finally, new research by Wellman et al. (2020) presents 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. They 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 BC haplotypes) that were substantially different from California haplotypes. The two fur-trade era haplotypes from southern Oregon also clustered closely to northern haplotypes (Wellman et al. 2020). These results are perhaps not surprising (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, prior to sea otter extirpation in the fur trade, the Oregon coast apparently 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 their former range.

Conclusion

The history of sea otters in western North America, including information from First Nations oral histories, archaeological remains and genetic studies, suggest 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 might be designed with this history in mind, and thus aimed at recreating 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) by pairing an Oregon reintroduction using a northern sea otter source population, with a northern California reintroduction using southern sea otters as a source population. In the latter scenario, hybridization of northern and southern sea otters would re-occur naturally. Any one of these strategies would further the recovery of genetic diversity by restoring 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.

Summary

Oregon's sea otter population was hunted to extinction during the international maritime fur trade with the last native sea otter thought to have been killed in the early 20th century. Sea otters are thought to have occupied most or all of the Oregon Coast, as evidence by sea otter remains in archaeological sites within First Nations middens. However, the historical population size remains unknown, and it is thought that the numbers may have been relatively low due to the scarcity of information documenting Oregon otters hunted during the fur trade. Three studies have been done using genetics to determine the most closely related sub-species, northern or southern sea otters, of Oregon's extinct sea otter population (Valentine et al. 2008; Larson et al. 2012 and Wellman et al., 2020). Valentine et al. (2008) looked at a portion of the mitochondrial DNA and found most of the ancient Oregon otters had genetic signatures similar to the southern sea otter subspecies. Larson et al. (2012) looked at 5 variable nuclear microsatellites and found evidence of both southern and northern sea otter subspecies in the ancient Oregon otters. Finally, Wellman et al. (2020) looked at the entire genetic sequence of the mitochondrial DNA and found most of the ancient Oregon otters belonged to the northern sea otter subspecies. Thus, we conclude that the original Oregon sea otters likely represented a hybrid zone, with ancestors that genetically resembled both southern and northern sea otters.

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