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Moss, Madonna, Rodrigues, Antonia, Speller, Camilla Filomena orcid.org/0000-0001-7128-9903 et al. (1 more author) (2016) The historical ecology of Pacific herring: : Tracing Alaska Native use of a forage fish. *Journal of Archaeological Science Reports*. pp. 504-512. ISSN 2352-409X

<https://doi.org/10.1016/j.jasrep.2015.10.005>

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The Historical Ecology of Pacific Herring: Tracing Alaska Native Use of a Forage Fish

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Keywords: Ancient DNA, *Clupea pallasii*, fisheries, Northwest Coast

Abstract

Long-term use of herring by Alaska Natives is not well-documented over space or through time, yet this information can illuminate pre-industrial patterns of herring abundance and distribution. Such information is important to understand the sustained relationships Alaska Native fishers and egg collectors have had with herring. Understanding the genetics of pre-industrial herring may also inform management of the fish and fisheries to insure their survival into the future. In this paper, we attempt a contextualized account of the long-term history of Alaska Native herring fisheries, bringing together archaeological, ethnographic, and ethnohistorical data. We tie these together as background for presenting the preliminary results of the NSF-funded project, *The Archaeology of Herring: Reconstructing the Past to Redeem the Future* (No. 1203868). We have now tested 84 herring bone samples from 17 archaeological sites in Alaska expanding beyond Speller et al. (2012), having tripled the earlier archaeological dataset. The oldest herring bones identified archaeologically in Alaska are dated to more than 10,000 cal BP. Early Holocene and Middle Holocene sites have also yielded herring bones, although most of the record dates to the last 2400 years. Preservation of genetic information is effectively complete for the last 2400 years, but achievable back to the terminal Pleistocene (68% success rate for samples between 10,500 and 2400 cal BP). This gives considerable confidence to the potential to expand the analyses and develop a richer pattern of biological variability. The resulting data show genetic continuity between archaeological and modern herring populations. The main technical challenge for the future is to extract adequate amounts of nuclear DNA from the ancient samples for identifying more informative DNA markers that can be used to more effectively reveal any population diversity and/or population size changes over time when compared to modern herring.

1. Introduction

Pacific herring (*Clupea pallasii*) is a cultural keystone species for many Alaska Natives, and is a critical resource in the marine food web for much of coastal Alaska (Thornton 2015; Thornton and Hebert 2014; Thornton and Kitka 2015). The appearance of herring in the spring signals the start of the seasonal round after a long winter. Herring is a key dietary resource during this time, but to some, herring is an economic mainstay throughout the year. Alaska Natives, as well as a range of North Pacific species, depend on abundant and geographically widespread populations of herring. In 1989, the Exxon Valdez oil spill devastated Prince William Sound herring populations in the northern Gulf of Alaska (Thorne and Thomas 2008; Figure 1). The southern Gulf of Alaska has been impacted by commercial fishing, habitat

degradation, and environmental changes over the past century. Bering Sea communities also depend on herring; in the words of Nelson Islander Louise Kanrilak, “herring are very important to us. When we are out of herring, we are out of food”(Barker 1993:73). The scientific debate over the status of herring has been complicated by the lucrative commercial sac roe fishery that supplies herring eggs for Asian markets. Local and Traditional Knowledge bearers have witnessed the decline of herring (Thornton et al. 2010a) and many argue that herring are being managed in a depleted state. Alaska Native subsistence fishers and egg-collectors are sounding the alarm, while biologists debate whether herring populations are “endangered,” “threatened” or “struggling” (Carls et al. 2009). Herring have already abandoned some spawning locations (ADFG 2011), and several First Nations in British Columbia have been forced to stop harvesting herring and spawn altogether (Speller et al. 2012).

Archaeological assemblages from across coastal Alaska constitute an unmatched archive of environmental data. The NSF-funded project, *The Archaeology of Herring: Reconstructing the Past to Redeem the Future*, aims to develop a more complete understanding of the ancient Alaska Native use of herring to better assess the historical abundance, biogeography, and genetic diversity of herring in the past. We hope (ultimately) to contribute to improved herring fisheries management to benefit a wide range of stakeholders in the Arctic, subarctic, and beyond. In this paper, we present preliminary results of our ancient DNA analysis and describe obstacles we currently face. Herring bones are preserved in some of the oldest sites in the region, including one that dates to more than 10,000 cal BP at Upper Yatuk Creek (Carlson 2012). So far, 84 herring bone samples have been tested from 17 sites in southeast Alaska as part of this project. For samples less than 2400 years old, ancient mitochondrial DNA (mtDNA) is well-preserved as demonstrated by a 100% success rate for DNA recovery. The success rate for older samples is lower at 68%, but this is still promising. The next technical challenge will be to extract adequate amounts of nuclear DNA from ancient samples, targeting those more informative loci to more effectively monitor population diversity and size changes when compared to modern herring.

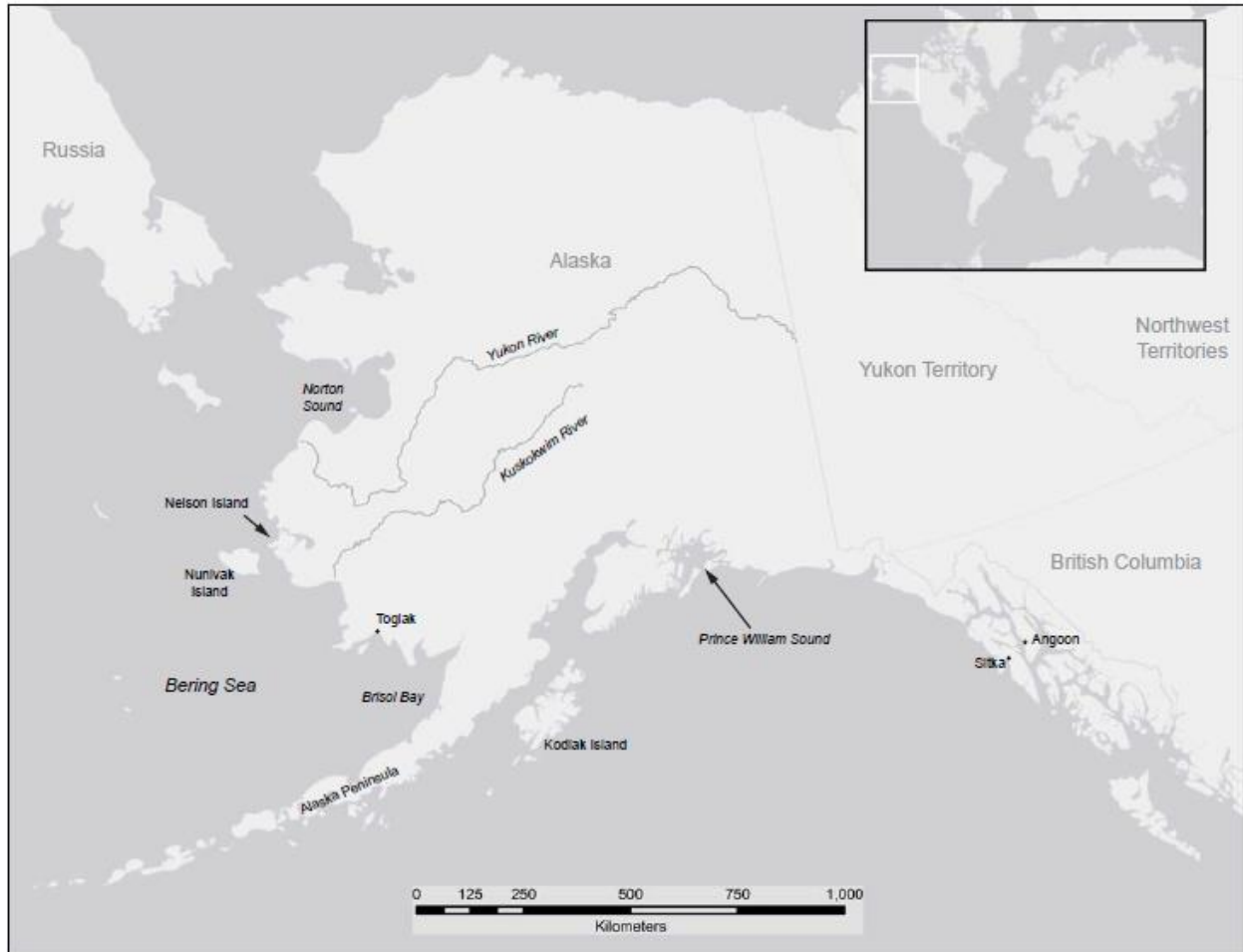


Figure 1: Map of Alaska showing places mentioned in the text.

2. Alaska Native Use of Herring

Forage fish compensate for their small size by forming schools that can become immense shoals moving along coastlines and migrating across open water. Herring and other forage fish play a crucial role in ocean food webs because they feed on phytoplankton and zooplankton near the bottom of the food chain. Forage fish convert this energy into their flesh that then feeds other fish, seabirds, and mammals, including people (e.g., Anderson et al. 2009). In southeast Alaska, herring (*yaaw* in Tlingit, *iinaang* in Haida) were (and are) eaten as fresh food, dried and smoked, rendered for their oil, and used as bait (see Moss et al. 2011:282-283 for more detail). The spring arrival of herring was/is especially important because this is when eggs are harvested (Thornton et al. 2010a, 2010b; Pete 1984, 1991). Besides eggs, schooling herring and a wide range of their predators (gulls, ducks, geese, eagles, chinook and coho salmon, lingcod, halibut, Pacific cod, hake, black cod, dogfish, harbor seals, Steller sea lions, porpoises, whales) were also taken (cf. Monks 1987). Besides the early spring fishery, Alaska Natives also took herring later in the spring, during summer, and into the fall seasons (Moss et al. 2011; Thornton 2010). Herring were dried and cured for storage and their oil was rendered and used to preserve other foods. Herring was an important resource used throughout much of the seasonal cycle, from March through the spring and summer and into late October for as many as eight months of the year although this varied across the coast (Emmons 1991; Pete 1984; Thornton 2010).

In Prince William Sound, herring is one of only two species determined “not recovering” by the Exxon Valdez Oil Spill Trustee Council (Bernton 2009). The fate of herring is not fully understood; some believe that the 16,000 gallons of oil still buried in the region is an on-going deterrent to herring spawning. The oil spill occurred when herring had just hatched, and both the young-of-the-year and adult herring were affected. The weakened stocks may have been particularly vulnerable to disease, over-fishing, predation, or climate change, but scientists have not agreed on the relative impacts of these factors, nor can they explain why herring have not recovered. Nonetheless, Alaska Natives did use herring (*jikatuy-paq* in Chugach) in Prince William Sound. Birket-Smith (1953:23, 39) reported that large numbers of herring were taken each year, and that the season extended from mid-June until November.

On Kodiak, herring (*iqalluarpak* in Alutiiq), spawn in more than 35 bays around the island, and have been historically abundant in Marmot Bay, Chiniak Bay, Sitkalidak Strait, and the fjords of Western Kodiak (Alutiiq Museum 2011). Alutiiq families still collect herring eggs where they adhere to eelgrass, rockweed, or kelp. Subsistence use of herring eggs begins during the peak of spawning in May, and continues through June, as the fish move offshore. The fish were used as well.

Large numbers of herring spawn along the Bering Sea coast from Togiak to Norton Sound, but herring are not so abundant in the Aleutian Islands (NPRB 2005:71). One of the most important Alaskan herring stocks is the Bristol Bay-Alaska Peninsula stock. The commercial fishery here occurs on the “largest discrete spawning biomass of Pacific herring in Alaskan waters” (Buck 2010:1). Herring spawning in the Togiak area begins in late April and continues through early June. Commercial sac roe harvest began here in 1968. Togiak Islanders have been very active in the commercial herring and herring roe-on-kelp fishery over the last decade (Krieg et al. 2007:24), but subsistence fishing and egg-collecting have also been practiced (Wright and Chythlook 1985). Historically, herring eggs were dried and stored in open-weave baskets. Like elsewhere in Alaska, herring eggs were often dipped in seal oil when consumed. Herring were available along the east coast of Nunivak Island (Lantis 1946:164), although Nunivak Islanders do not appear to have been as dependent on herring as were Nelson Islanders.

Nelson Island is located half way between the mouths of the Kuskokwim and Yukon rivers. Island streams are too small to support many salmon, but the rocky shoreline provides excellent spawning habitat for herring (Barker 1993; Pete 1991). Herring is the main fish upon which Nelson Islanders depend; seal is their other most important resource (Lantis 1946:178). As Fienup-Riordan (1983:94) explained, “[d]ried iqalluarpiit, or herring, are the staple food during the winter, and their preparation a matter of great concern as well as excitement. Of all the fish sought, herring are the most important in terms of quantity, ease of storage, and nutritional value. . . . The size of the herring run means the difference between feast and famine in the late winter and early spring.... it [herring] is the food that maintains the family when other stores are depleted.” The herring runs are relatively short, so the time spent processing the catch is intense (Fienup-Riordan 1983:100). On Nelson Island, herring arrive in three groups; the first fish are large, very oil-rich, and hard to dry, while the second group have less oil and are preferred for drying. The last fish are the youngest group and are too lean to be preferred (Barker 1993:71). Traditionally, a man’s mother, sisters, and wife were all required to process a fisherman’s herring (Fienup-Riordan 1983). The herring are left to soften, and then each herring is gutted by hand, and the eggs are removed and dried separately (Frink 2002; Frink and Knudson 2010). The fish are braided onto ryegrass garlands holding 70-100 fish (Knudson and Frink 2010). These are set to dry on racks. After a few weeks the fatter herring must be split for further drying. Herring can be stored in grass baskets, in seal pokes (i.e., bags full of oil), or in the freezer (Fienup-Riordan 1983:102-104). Based on their observations that herring populations had declined due to foreign offshore fisheries in the 1960s and 1970s, Nelson Islanders protested the introduction of domestic commercial herring

fishing in 1979 (Fienup-Riordan 1983:139). Nonetheless, this area was opened to commercial fishing in 1985.

3. The Decline of Herring Populations

Funk (2010) reconstructed the history of the commercial herring fishery in southeast Alaska using state and federal (pre-statehood) agency management reports, scientific publications, and the U.S. Census. The Northwest Trading Company began operations on Killisnoo Island, near Angoon, Alaska, in 1878. This was the first herring reduction plant anywhere in Alaska or British Columbia and was the only such plant for 40 years. In 1882, the oil works began processing herring, expanding to guano production in 1884. Later it also produced salt-cured herring. In the 1920s, other herring operations were established in the area. When the town of Killisnoo was largely destroyed by fire in 1928, the plant closed.

Between 1883 and 1910, between 2000 and 10,000 tons of herring were caught annually to supply the Killisnoo plant. Almost all the herring commercially caught in southeast Alaska during this period were processed into oil at the Killisnoo plant. Between 1910 and 1922, the catch increased, and dramatically large catches characterize the period between 1925 and 1940. Fishing herring for food became significant; in 1911, a fishery for salt-cured herring expanded, and between 1912 and 1922, food production averaged 35% of the overall herring harvest. Yet under this pressure, large herring became scarce in southeast Alaska, and salt-curing operations moved north to Prince William Sound and Kodiak. The herring reduction industry (to produce oil) expanded in the 1920s (after World War I), and production peaked in 1929, when over 80,000 tons of herring were harvested. Although the Killisnoo plant closed in 1928, production shifted to several other reduction operations in southeast Alaska, most located along Chatham Strait. In 1939, the yield dropped sharply, after which fishing effort shifted to Sitka. Commercial fishing for herring other than for bait was prohibited in August, 1939. All of southeast Alaska was closed to herring fishing in 1942, but not for long. During the rest of the reduction fishery period, from 1943 to 1967, especially large catches were made in 1947 (45,000 tons) and 1959 (50,000 tons). Yet declines in abundance and yearly fluctuations led to weakened demand for Alaska herring, when Peruvian anchovies and other products could be obtained more cheaply and reliably. The last herring reduction plant in Alaska, at Washington Bay, closed after the 1966 season. The Alaskan sac roe fishery started in 1971, after that industry collapsed in Japan (Hamada 2009). The harvest of herring caught for bait continued at low levels (averaging 2600 tons) between 1910 and 1970.

The decline of herring in southeast Alaska is documented through local and traditional knowledge (LTK). Thornton conducted interviews with 86 individuals as part of the *Herring Synthesis* project (Thornton et al. 2010a) and also reviewed records of 117 unpublished interviews. In exhaustive detail, these herring fishers and egg-collectors provided accounts of the significant declines in herring abundance and distribution that they witnessed in their lifetimes. For example, Harvey Kitka observed that declines in herring around Sitka have adversely affected the abundance of halibut, salmon, and fur seals that also feed on herring. The significance of such information for southeast Alaska is that starting in the 1980s and continuing today, the Alaska Department of Fish and Game (ADFG) established that a 20% maximum exploitation rate was appropriate for herring. Using an exploitation-rate-based harvest policy assumes that managers can accurately estimate herring biomass. Yet it is extremely difficult to estimate herring numbers, and historical baselines for herring have been receding. Present herring stocks, even in those areas that have remained highly productive (e. g., Sitka Sound), are being managed in a depleted status (Thornton 2015; Thornton et al. 2010a, 2010b; Thornton and Kitka 2015). Herring of today represent a fraction of their historical abundance and distribution. Significant long-term impacts to the distribution and abundance of southeast Alaska's herring have been a result of commercial exploitation.

Thornton et al. (2010b) argued that the maintenance of diverse spawning locations in southeast Alaska is critical to conserving intra-specific biodiversity and regional marine food webs.

Although the historical ecology of herring elsewhere in Alaska has not been reconstructed in the detail provided by Funk for southeast Alaska, the health of herring populations across the north Pacific is in jeopardy. There is no longer a commercial herring fishery in Port Clarence, Norton Sound, or along the coast of the Yukon or Kuskokwim rivers (ADFG 2011). In Prince William Sound, there is no subsistence or commercial fishing of herring due to the impacts of the 1989 Exxon Oil Spill, but locals retain knowledge of herring (Brown et al. 2002). The reason that Japanese consumers pay such a high price for herring eggs is that this ceremonial food is no longer available in Japanese waters because of over-fishing prior to 1970 (Hamada 2009). Nelson Islanders witnessed declines in herring in the 1960s due to foreign fleets, and they resisted commercialization of the herring fishery. Alaska Department of Fish and Game rejected the Sitka Tribe of Alaska's 2008 proposal to close off some areas from commercial sac roe fishing to protect areas of traditional egg harvest (Thornton and Kitka 2015). Across British Columbia, First Nations also have testified to the decline of herring on Haida Gwaii, along the Central Coast, and on the west coast of Vancouver Island (Atleo 2011; Newman 2011; Wilson 2011). Herring have completely disappeared from some areas along the Strait of Georgia where they were formerly abundant (Washington 2011). Declines have also occurred in Puget Sound, WA, and Yaquina Bay, OR. The Cherry Point stock in Washington has been almost completely wiped out (Stick 2011).

Although the various types of climate variability in the North Pacific (Pacific Decadal Oscillation, North Pacific Gyre Oscillation, Arctic Oscillation, Pacific-North American Pattern, North Pacific Index, and El Niño Southern Oscillation) have probably affected herring populations, Litzow et al. (2014) found that these cannot explain herring declines over the last 44 years. As these authors write, "...the view of decadal-scale ecological variability in this study region as being dominated by internal climate variability should be expanded to include the effects, at least, of commercial fishing and climate change unrelated to internal variability" (Litzow et al. 2014:45). Although climate variability is worth consideration, it is beyond the scope of this paper because the chronological resolution of such climate data cannot be matched by the temporal resolution of our archaeological data (see also McKechnie et al. 2014). The effects of climate change over century to millennial scales might be detectable archaeologically. We argue that the archaeology of herring is important for the future: archaeological evidence has the potential to reveal information about the past abundance and distribution of herring prior to commercial over-fishing. If we find herring populations to be robust and consistently diverse over long periods of time, it becomes possible to assess anthropogenic effects more effectively. When we better understand pre-industrial fishing, we will have a better idea as to the goals of management efforts to allow for the recovery of herring.

4.1 The Archaeology of Herring

For southeast Alaska, Moss et al. (2010) created a database summarizing current knowledge of zooarchaeological records. Taxonomic information for herring and other vertebrate and invertebrate fauna were compiled from all archaeological site reports. The database listed published and unpublished site reports, excavation methods, including screen size, volume excavated, condition, age estimates, and site location. The screen size used during excavations clearly affected measures of taxonomic abundance. Given their small size, herring bones are especially prone to loss and are numerically under-represented unless fine mesh sieving and laboratory analysis of bulk samples are undertaken (see Moss et al. 2011 for more detail). Screens with mesh sizes of 1/8 inch or smaller are needed to ensure

recovery of herring bones (Cannon 2000; Moss 2007). Of sites in southeast Alaska where adequate recovery methods were used, herring bones were found in 75% of the excavated or tested sites.

In a much larger but similarly structured review that included sites in British Columbia and Alaska, McKechnie et al. (2014) built a database of 435,777 NISP from 171 assemblages that used methods capable of recovering herring bones. Of these, herring was the most abundant taxon in 95 assemblages and the second-most abundant taxon in another 41 assemblages. This is a striking result in a culture area where salmon have been considered the most important fish. This database has been expanded to include more recently reported assemblages as well as sites in Washington and Oregon (McKechnie and Moss, this volume). In this database of 513,605 NISP from 222 archaeological sites, herring were found in 98% of the assemblages. Where sampling methods are adequate for the recovery of its small bones, herring is the most ubiquitous fish in Northwest Coast archaeological assemblages.

Ethnographically, herring were taken in mass capture devices, and some archaeological weirs and traps are thought to have been used to take herring (Caldwell 2011; Greene 2010; Mobley and McCallum 2001; Monks 1987). Herring reportedly occurred in such concentrations that they could be raked into canoes; herring rakes were extensively used across the Northwest Coast (e.g., Drucker 1951:23; Emmons 1991:120). Small bone prongs are commonly found archaeologically, although they are hard to definitively identify as herring rake teeth. Ethnographically, herring were also caught in baskets or dip nets or by jigging (Hewes 1947; Schroeder and Kookesh 1990; Thornton 2010), but the remains of such equipment are unlikely to survive in the region's archaeological sites. Nelson Islanders set gill nets to take herring, situating nets perpendicular to the shoreline (Pete 1984). Unfortunately, the remains of such nets have not been identified archaeologically.

To harvest herring eggs from the intertidal or subtidal zones, Native peoples suspended hemlock or cedar branches or kelp fronds underwater. Herring deposit their eggs on these surfaces after which they are retrieved. Harvest of herring eggs is almost impossible to detect archaeologically, unless site seasonality studies point to the specific time of herring spawning, which occurs in different localities at different times. For example, herring spawn in Sitka in late March or early April, whereas they arrive in Togiak in mid- to late May.

4.2. Ancient DNA Analysis and Fish Conservation

Some types of overfishing remove large mature fish from the ecosystem and increase selection pressure on spawning of smaller animals, resulting in earlier maturation and reductions in age and size at maturation. Although decreasing maximum length of adult fish has been observed in several commercially important stocks over the last century (e.g., Atlantic cod, Northern pike, Atlantic salmon) (Allendorf et al. 2008), it does not reveal the underlying (and often cryptic) genetic changes that may also take place. In order to develop effective management practices for sustainable exploitation of marine resources, it is essential to understand the long-term genetic changes and evolutionary responses experienced by the exploited populations. For example, overharvesting can disrupt genetic subdivisions within a species and reduce overall productivity (Kenchington 2003). If the density of local subpopulations is reduced, immigration from other regions can promote gene flow and hybridization between subpopulations, potentially swamping local adaptations (Allendorf et al. 2010). Long-term loss of genetic variation (measured by rates of heterozygosity and allelic diversity in our study) can reduce productivity through the reduction of both individual fitness and the long-term potential for evolutionary adaptation (Allendorf et al. 2008).

In our ancient DNA study, we targeted mitochondrial DNA to examine the genetic diversity and population substructure of ancient herring from Alaska. We examined measures of allelic diversity (i.e.

mtDNA haplotype diversity, h) and heterozygosity (nucleotide diversity, π). We also phylogenetically compared the ancient mtDNA haplotypes to modern Northeast and Northwest Pacific herring to look for evidence of population substructure in the ancient remains.

4.3 Preliminary Results of Ancient DNA Analysis

The working hypothesis of our ancient DNA study is that ancient herring were more genetically diverse than those of today and may also differ from contemporary populations. To test this, we collected samples of ancient herring bones and modern herring from across coastal Alaska to analyze their mitochondrial and nuclear DNA. Including the herring bones tested in a previous study (Speller et al. 2012), we have now analyzed 84 ancient herring bones from 17 archaeological sites in Alaska. Samples from additional sites elsewhere in Alaska have been collected, but have not yet been tested, as we await more technological developments that will allow more effective comparisons to the DNA of modern herring.

Sites from which we have successfully recovered ancient DNA are Hidden Falls, two Angoon sites (Killisnoo Picnicground, Garnes Point), North Point, two sites at Coffman Cove (49-PET-067, 49-PET-556), Chuck Lake (Localities #1 and #3), Rosie's Rockshelter, Craig Administrative Site, Cape Addington Rockshelter, Kit'n'Kaboodle, four sites near Sitka (Jamestown Bay, Krestof, Starrigavan, and White Rock) and Upper Yatuk Creek (Table 1 and Figure 2). The oldest site of this group is Upper Yatuk Creek; to confirm the site's age Moss submitted a charcoal sample directly associated with herring bones that returned an age of 10,710-10,490 cal BP (Beta-370536).

The ancient samples were analyzed in the dedicated Ancient DNA Laboratory at Simon Fraser University using protocols and primers described in Speller et al. (2012), targeting the same 350bp fragment of mtDNA D-loop. The overall success rate of ancient DNA amplification was 82% (69 of 84 samples), a result consistent with the high likelihood of recovering long (i. e. >150bp) fragments of DNA from this geographic area (Hofreiter et al. 2015). The success rate for DNA amplification was influenced by the age of the sample, with a 100% success rate for samples dating <2400 cal BP, and increasing numbers of amplification failures from more ancient sites (Table 1), including Upper Yatuk Creek, Chuck Lake Locality #1 (9240-8490 cal BP), Chuck Lake Locality #3 (5450-5180 cal BP, and Hidden Falls (3500-880 cal BP).

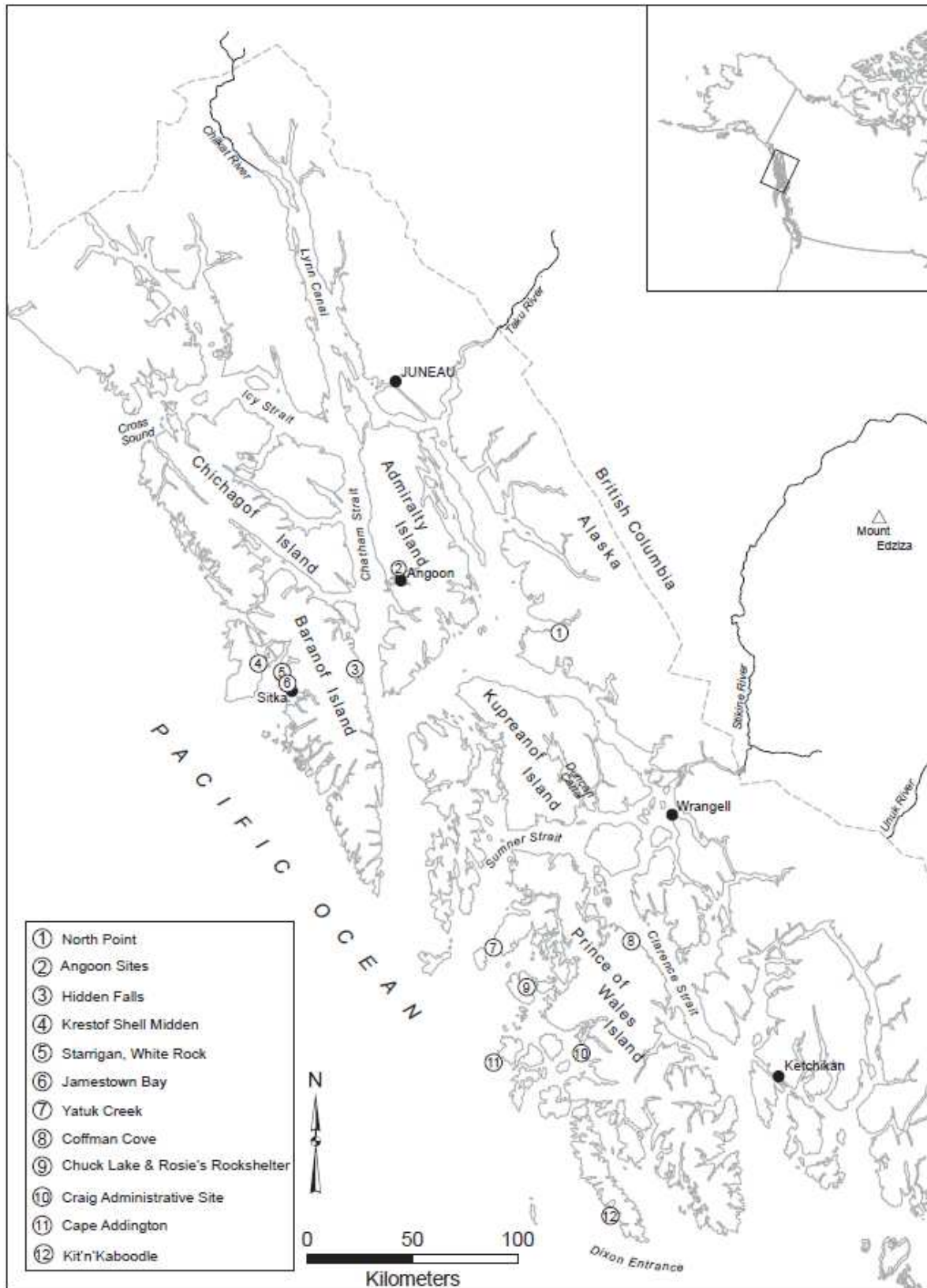


Figure 2: Archaeological sites in southeast Alaska tested for ancient DNA of Pacific herring.

Table 1: Sites from Alaska Yielding Ancient DNA from Herring Bones (ordered from oldest to most recent).

Site Number	Site Name	Radiocarbon Age	Reference	Success Rate for D-Loop Amplification
N/A	Upper Yatuk Creek	10,710-10,490 cal BP	Carlson 2012	1/4
49-CRG-237-1	Chuck Lake Locality 1	9240-8490 cal BP	Ackerman et al. 1985	1/3
49-PET-067	Coffman Cove Site	5500-400 cal BP	Moss et al. 2012	6/7
49-CRG-237-3	Chuck Lake Locality 3	5450-5180 cal BP	Ackerman et al. 1985	4/5
49-DIX-046	Kit'n'Kaboodle	5000-2000 cal BP	Moss & Erlandson 2010	5/5
49-CRG-236	Rosie's Rockshelter	3830-3600 cal BP	Ackerman et al. 1985	4/5
49-SIT-119	Hidden Falls	3500-880 cal BP	Davis 1989	6/8
49-SUM-025	North Point	2800-2500 cal BP	Bowers & Moss 2001	1/4
49-CRG-443	Craig Administrative Site	2360-2120 cal BP	Pierce 2008	4/5
49-PET-556	Coffman Ferry Terminal	2330-2130 cal BP	Moss 2008	4/5
49-CRG-188	Cape Addington Rockshelter	2000-400 cal BP	Moss 2004	5/5
49-SIT-124	Killisnoo Picnicground	1300-1000 cal BP	Moss 1989, 2007	5/5
49-SIT-304	Garnes Point	1280-1140 cal BP	Moss 1989	5/5
49-SIT-228	Jamestown Bay	780-560 cal BP	Moss 2011	5/5
49-SIT-229-1	Starrigavan	650-550 cal BP	Davis 1985; Moss 2011	5/5
49-SIT-246-1	White Rock Shell Midden	650-550 cal BP	Moss 2011	5/5
49-SIT-917-1	Krestof Shell Midden	630-540 cal BP	Moss 2011	3/3
Total				69/84

Genetic diversity indices are high in the ancient Alaskan herring, comparable with modern populations from the same region (Table 2). Mitochondrial haplotype diversity and nucleotide diversity in the ancient Alaskan samples are almost identical to modern populations, and do not reveal a significant decline in mitochondrial DNA diversity over the last century, a result consistent with the previous study of ancient herring mitochondrial DNA. Likewise, phylogenetic analysis of the mtDNA D-loop haplotypes (following methods and reference dataset analyzed in Speller et al. 2012) indicates that the ancient Alaskan herring cluster with three haplogroups identified in modern Pacific herring: A, B, and C (Figure 2). Haplotype A occurs across the Northwest Pacific (Asia and Bering Sea) and Haplotypes B and C are distributed across the Northeast Pacific. The Alaskan samples tested in this project plot among the modern samples in the Northeast Pacific (Haplotypes B and C), with four Alaskan samples clustering among the Northwest Pacific (Haplotype A). The ancient Alaskan mitochondrial haplotypes do not display distinct subpopulations compared to other ancient or modern Northeast Pacific herring. Due to the generally high mtDNA diversity observed in modern herring populations, this analysis confirms the limited power of mtDNA for discriminating between sub-regional populations in high gene flow species such as herring (Speller et al. 2012); nuclear DNA is required for this level of resolution. The DNA results obtained in the study, however, demonstrate the viability of DNA in ancient Alaskan samples as old as 10,000 cal BP, and the potential for more refined analyses to detect more subtle changes in population dynamics associated with human exploitation.

Table 2: Haplotype (h) and Nucleotide Diversity (π) for Modern (from Liu et al. 2011) and ancient Alaskan herring populations.

Herring populations	n	Haplotypes	h	(SD)	π	(SD)
Ancient						
Craig	22	16	0.961	0.0278	0.024136	0.012951
Angoon	16	9	0.858	0.0772	0.022119	0.012184
Sitka	18	16	0.980	0.0284	0.029020	0.015553
Inner Coast	10	10	1.0	0.0447	0.028047	0.015876
Modern						
Simpson Sound	48	34	0.977	0.011	0.0268	0.00128
Yakutat Bay	48	37	0.987	0.008	0.02711	0.00128
North Sitka	42	29	0.98	0.01	0.02459	0.0015
South Sitka	47	38	0.989	0.007	0.02748	0.0011

Diversity indices calculated through Arlequin 3.5 (Excoffier and Lischer 2010); Craig (samples from Cape Addington Rockshelter, Craig Administrative Site, Kit'n'Kaboodle, Rosie's Rockshelter, Chuck Lake, and Upper Yatuk Creek); Angoon (Hidden Falls, Killisnoo Picnicground, Garnes Point); Sitka (Jamestown Bay, Starrigavan, White Rock Shell Midden, Krestof Shell Midden); Inner Coast (Coffman Cove Site, Coffman Cove Ferry Terminal, North Point).

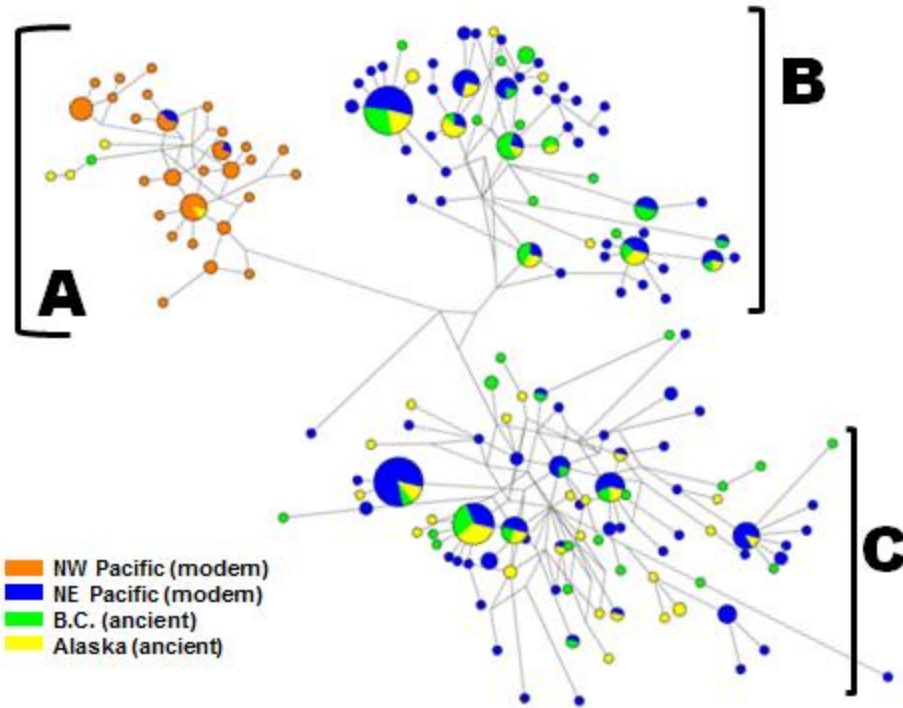


Figure 3: Network diagram showing three main haplogroups of Pacific Herring, with the ancient Alaskan samples in yellow, the ancient British Columbia samples in green (Northern Georgia Strait, Burrard Inlet, and West Coast of Vancouver Island, from Speller et al. 2012), modern Northeast Pacific in blue (Yakutat Bay, AK; Knight Inlet, Nootka Sound, Portage Inlet, BC from Liu et al. 2011) modern Northwest Pacific in orange (Aleksandrovsk from Liu et al. 2011).

In a study of modern herring, Wildes et al. (2011) recently analyzed 15 microsatellite loci (nuclear DNA) to find that “inner coast” herring (Berners Bay and Lynn Canal) were genetically distinct from “outer coast” herring (Sitka Sound and Prince of Wales Island). This is important because the Lynn Canal herring have been in decline since the 1970s. These researchers described the level of differentiation as “surprising” (Wildes et al. 2011:386), given the small geographical separation (235 km) and the high genetic connectivity among marine pelagic species such as herring. This shows that population structure among sub-regional groups of herring in southeast Alaska is detectable, and of course, ultimately, we want to see whether this is true for other areas in Alaska too.

Single nucleotide polymorphisms seem to hold the most promise for distinguishing herring (Speller et al. 2012). The challenge here is that it is difficult to identify which DNA markers are more informative and effective. To isolate and optimize such a set of genetic markers from modern herring is beyond the financial scope of the current project, although Lorenz Hauser, Molecular Ecologist in the School of Aquatic and Fisheries Sciences at the University of Washington, is currently pursuing this objective. Once these DNA markers have been identified, the excellent DNA preservation observed in the ancient herring suggests it will be feasible to target these regions through hybridization capture, followed by high-throughput sequencing (Carpenter et al. 2013), although this is beyond our current project.

Another finding (that was entirely unanticipated) is that some of the bones reported as herring in archaeological monographs are not herring. In other words, small fish bones have been mis-identified as

herring. So far, Moss has found that small fish bones reported as herring from four Alaskan sites (Nash Harbor, Rice Ridge, Karluk, and Mink Island) are not herring bones. Most of these mis-identified bones are small gadids (cod family). This may be because the overall size and shape of small gadid vertebrae resembles that of herring, and without magnification, the distinctive structure of vertebral centra is hard to observe. This reinforces the necessity of using magnification to identify small fish bones morphologically.

5. Summary and Implications

In this paper, we present a contextualized historical account of what has happened to Pacific herring over the past millennia. We bring together ethnographic, historical, archaeological, and genetic data to reconstruct the historical ecology of herring in Alaska. Since the 19th century, industrial herring catches have fluctuated in different places at different times, but we suspect that impacts from the commercial fishing industry have reduced the genetic diversity of Pacific herring. We have not yet proven this, however. Instead, we maintain that archaeological data are essential to extending the chronology of herring population changes and can potentially help us understand current declines. We have found that genetic information is well-preserved for the last 2400 years, and that ancient DNA can be extracted from samples dating back to the Late Pleistocene. This suggests great potential to expand the analyses and develop a richer pattern of biological variability of ancient herring. We have substantially enlarged the earlier dataset reported by Speller et al. (2012), and confirmed the overall genetic patterns. At this point in time, we observe genetic continuity between archaeological and modern herring populations, but technical advances in molecular analyses should make it possible to isolate more informative DNA markers that can be used to reveal any population diversity and/or population size changes over time.

It must be emphasized that the fate of the world's fishes is interconnected globally (e.g., Pauly 2010; Pikitch et al. 2012) and has been for a long time. For example, when another clupeid, Atlantic menhaden, declined on the east coast of North America in the 1870s, it prompted herring production at the Killisnoo plant in the 1880s (Funk 2010:260). In the 1970s, the over-exploitation of herring in Japan led to the explosion of the herring sac roe fisheries in Alaska and British Columbia (Hamada 2009). The mid-20th century decline in abundance of North America's west coast fisheries helped fuel the exploitation of Peruvian anchovies later in the 20th century. All of these fish are nutritionally rich taxa that play key roles in the health of complex ocean food webs (Essington et al. 2015). The health of forage fish throughout the ocean waters is important to the health of other marine organisms. Such forage fish are low tropic level species that tend to reproduce fast. If the forage fish are over-exploited by the fishing industry, seabirds and marine mammals that feed on them are vulnerable to nutritional stress, disease, etc. (Alder et al. 2008). Today, the fishing industry catches many forage fish to process into fish meal or fish oil to be used in industrialized agriculture or aquaculture. Fish meal and oil are feed for farmed fish (salmon, carp, catfish), chickens, cats, dogs, and horses. As zooarchaeologists studying fish, we have an important role to play in raising awareness of how industrial fishing differs in scale and impacts from pre-Columbian fishing practices by the indigenous peoples of the Americas.

Acknowledgements – This research was supported by National Science Foundation–Arctic Social Sciences Award No. 1203868 to Moss. For support of fieldwork in Sitka, Moss is grateful to the University of Oregon and the Sitka Tribe of Alaska, Jeff and Jonathan Feldpausch, Aaron Bean, Heather Woody, Brenda and Ben Campen, Karen Iwamoto, Nancy Yaw Davis, Jessica Gill, and Heather Riggs. Colleagues who have contributed to this research include Virginia Butler, Tait Elder, Lorenz Hauser, Anna Kerttula de Echave, Fritz Funk, Harvey Kitka, Dana Lepofsky, Iain McKechnie, Chuck Smythe, Tom Thornton, Sharon Wildes, and Rosita Worl. We are grateful to colleagues who provided or facilitated

samples: Robert Ackerman, Jim Baichtal, Aletheia Bouknight, Cynthia Berns-Lopez, Pete Bowers, Virginia Butler, Sarah Campbell, Mike Etnier, Dennis Griffin, Mark Hovezak, Karen Iwamoto, Bob Kopperl, Tim Marshall, Katie Myers, Megan Partlow, Laura Phillips, Josh Reuther, Patrick Saltonstall, Jeanne Schaaf, Scott Shirar, Amy Steffian, Steve Street, and Catherine West. We are grateful to Francisco Zangrando and Philippe Béarez for organizing *Ichthyoarchaeology in the Americas* at the 12th International Conference on Archaeozoology in San Rafael, Argentina, where a version of this paper was presented. Two anonymous reviewers invested substantial effort in helping us improve this paper, for which we are grateful.

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