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SPECIAL ISSUE
ALEUTIANS

Hunter-gatherers subsistence and impact on fauna in the Islands of Four Mountains, Eastern Aleutians, Alaska, over 3000 yr

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Abstract

This first zooarchaeological analysis for the Islands of Four Mountains (IFM), Aleutian Islands, Alaska, provides data about local hunter-gatherer resource exploitation over three thousand yr. The majority of zooarchaeological material represents faunal resources that were harvested within several kilometers of villages. Our analysis shows that IFM subsistence system was shaped by the small size of these islands, which is mostly true for all of the Aleutian Islands. The archaeological middens indicate that Aleuts readily exploited new resources when they became available, expanding their dietary niche. Despite human harvesting, most faunal populations remained stable; however, Aleuts overexploited the storm-petrel colony on Carlisle Island.

Keywords: Island zooarchaeology; Aleutian Islands; Islands of the Four Mountains; Niche breadth; Storm-petrel; Bird populations dynamics; Domestic dog; Red fox

INTRODUCTION

The question of human-environmental interactions in island ecosystems is important for understanding both cultural and ecological history. By virtue of their geography and history, the Aleutian Islands serve as model for observing human maritime adaptation to and interactions with the environment.

The Aleutian Islands are one of the most isolated geographic areas in the North Pacific, extending 1800 km between North America and Asia and separating the northern Pacific Ocean from the Bering Sea (Fig. 1). Volcanic in origin, the archipelago is comprised of more than 200 islands divided into six groups separated by ocean passages. The mixing Pacific and Bering Sea currents make highly productive ecosystems with decreasing productivity from east to west (Hunt and Stabeno, 2005; Mordy et al., 2005). Each island differs in size, shape, and extent of coastal habitats, and thus differs as to resource abundance available to indigenous people. This unique maritime environment was pivotal to the adaptations and survival of the Aleuts, the prehistoric peoples who settled the archipelago. Due to the lack of terrestrial fauna on islands west of Samalga Pass, coastal resources were critically important to prehistoric Aleuts. Local inhabitants intensively exploited shellfish, fish, birds, and mammals, especially in nearshore environments during the last 9000 yr (e.g., Knecht and Davis, 2001). Herein, we use economic systems analysis, which is an important method for studying subsistence system in hunter-gatherer societies. Aleutian maritime hunter-gatherers lived in permanent or semi-permanent settlements for thousands of years. Discarded bones, shellfish remains, other domestic waste, and cultural artifacts formed “kitchen middens” near Aleuts dwellings. Analysis of materials within these middens can provide a detailed proxy of the resource utilization by ancient hunters as well as dynamics of the faunal community over thousands of years.

For the Aleutians, McCartney (1977) suggested that the suitability for human occupation was based on each island’s relative productivity, and thus small islands with regular coastlines were less preferable for settlement than islands with protective bays. In the Aleutians, the ocean-land interface is the most productive environment: the longer and more complex the coastline, the richer the resource base. Corbett (1991) modeled Near Island Aleut catchments as half circles, oriented toward the sea, which we can apply to all Aleutian

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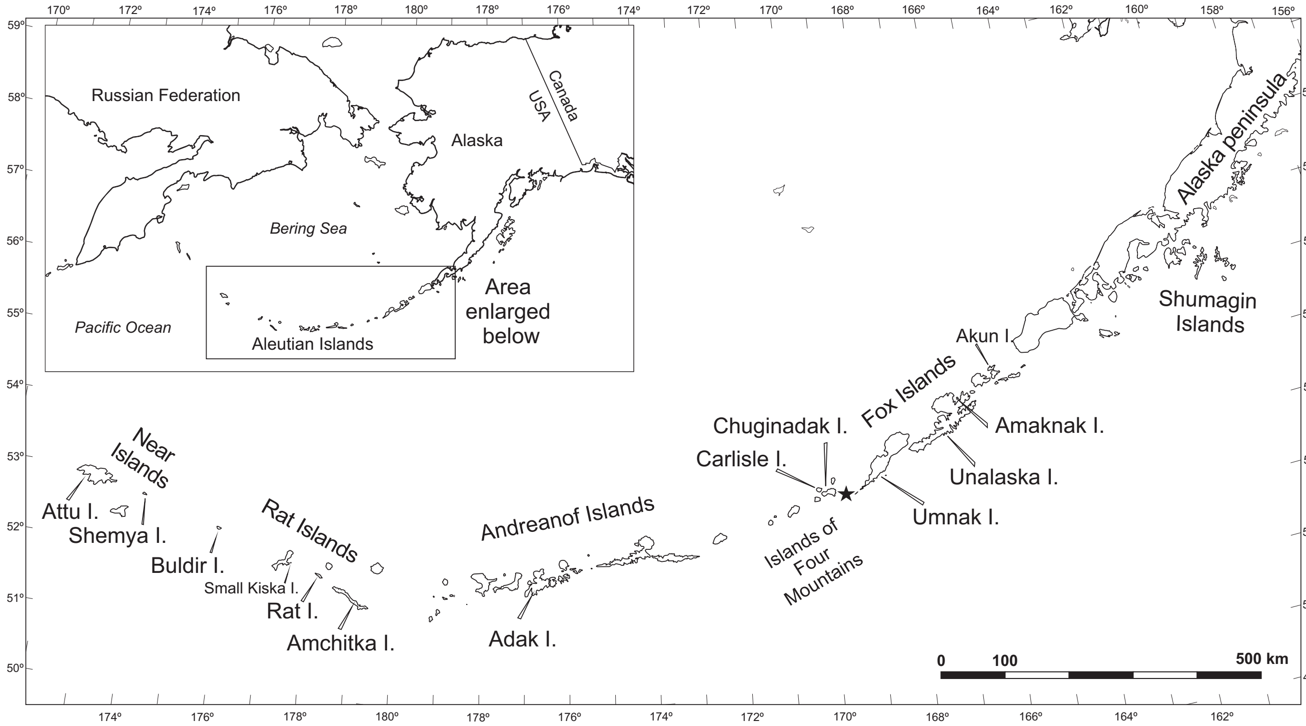

Figure 1. The Aleutian Islands map showing locations of major island groups and islands mentioned in the text. *, Samalga Pass.

hunter-gatherer subsistence systems. The smallest catchment circle extended out in a 1-km radius, which incorporates reefs, beaches, streams, inshore waters, and a variety of terrestrial habitats that provide shellfish, fish, shore and land birds, and plants. Presumably, this was the most intensively exploited zone (Corbett, 1991). The second catchment circle extends out in a 3 to 4-km radius, which, for the sample sites, added waterfowl, cliff and colony nesting birds, marine fish, seals, pelagic birds, and sea mammals to the site's resource inventory. Resources within this circle would have been accessible to people on foot traveling inland or along the beaches. The catchment also includes inshore kayaks or baidarkas (*iqyax*) fishing trips. Beyond these two catchments, resources were collected within 10 to 15 km of the sites. For these distances and resources, boats would have been necessary for efficient exploitation and transportation (Corbett, 1991). Resources in this circle included sea lions, pelagic fish, and birds such as albatrosses. The largest catchment circle encompasses long-range hunting expeditions using *iqyax*. Use of this zone might have been relatively rare.

Procurement system studies have a long history in Aleutian research, conducted on sites across the island chain (e.g., Yesner, 1977; Crockford et al., 2004; Corbett et al., 2010). However, resource utilization in the Islands of Four Mountains (IFM) are unknown. The IFM is a group of comparatively small islands separated from the larger Umnak Island by Samalga Pass (Fig. 1). Collectively, their small size should limit ecosystem diversity, because shorter shorelines, fewer reefs, and smaller inland areas limit foraging possibilities.

Subsistence strategies are the methods through which social groups procure food resources and are shaped by diverse cultural and ecological factors (Binford, 1980). Various models have been used to understand human subsistence strategies; these include niche breadth, optimal foraging theory, and prey choice (e.g., Jones, 2004; Loponte and Acosta, 2004). Changes in niche breadth might indicate either cultural or environmental change (e.g., Darwent, 2004) and, in different environments, the widening or narrowing of niche breadth can be interpreted in different ways (e.g., Jones, 2004). Niche breadth facilitates discussing food habits in terms of the variety of animals used in the site (diversity) and the evenness (equitability) with which those species were used. Zooarchaeologists have long used measures of evenness, which quantify the degree to which classes within an assemblage are equally represented by the individuals within that assemblage (Wing, 1963; Grayson, 1981). To measure niche breadth of IFM hunter-gatherers and to compare it with other Aleutian Islands, we use a measure of dominance to understand human subsistence in terms of generalist and specialist strategies. Decreasing dominance indicates either increasing niche/dietary breadth or decreasing availability of preferred prey types. On the other hand, increasing dominance indicates a narrowing of niche/dietary breadth due to resource constraints or an increase in the availability of preferred types of production. We suggest that, in the Aleutians, larger islands and islands with complex coastlines would have diverse environments providing more choices for foragers, allowing them to focus on the highly productive resources and ignoring less productive ones. In this case the width of the niche will be relatively narrow. In contrast,

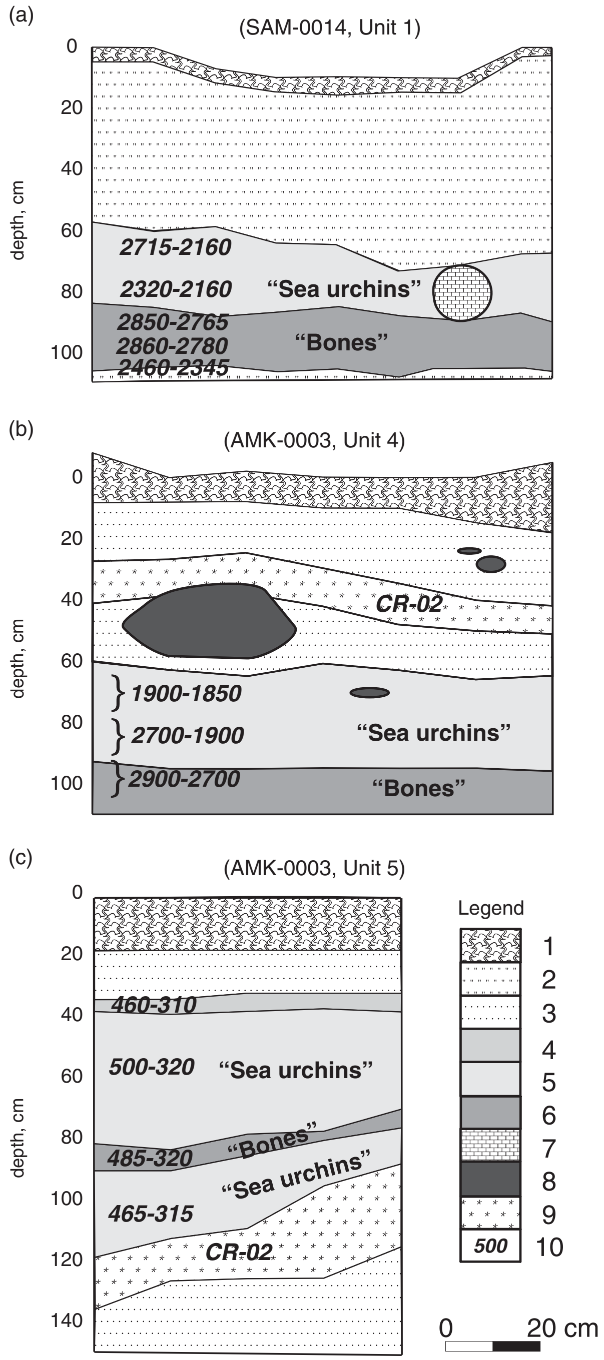

Figure 2. Schematic profiles of: (A) Tanax̂ Agunax̂ (SAM-0014) Unit 1; (B) Ulyagan site (AMK-0003) Unit 4; (C) Ulyagan (AMK-0003) Unit 5. Common legend for all units: 1, sod; 2, sterile layers; 3, cultural layer without faunal remains; 4, cultural layer with poorly preserved bones; 5, cultural layer with high sea urchin shell content, "Sea urchins"; 6, cultural layer with low sea urchins shell content, "Bones"; 7, bone; 8, stone; 9, tephra CR-02; 10, dates (cal yr BP).

smaller islands offered low resource diversity and limited foraging options; as a result, the width of the niche would be wide.

We also want to understand the influence of human predation on local fauna in island contexts. The best-known example of the impact of human hunting on Aleutian fauna is the exploitation of sea otters in prehistoric and historic times (Konar, 2000; Corbett et al., 2008). Much less information exists regarding bird and fish populations. Some suggest that hunting practices of the early Aleuts had no demonstrable impact on the seabird community in the Aleutian Islands (Causey et al., 2005). While some changes have taken place, they are not consistent with long-term effects associated with local extirpation by overhunting, selective harvesting, or habitat perturbation. On Shemya Island, however, Savinetsky et al. (2014) suggest there was a dramatic impact on bird colonies following human colonization.

One of the goals of the interdisciplinary project "Geological Hazards, Climate Change, and Human/Ecosystems Resilience in the Islands of the Four Mountains" was to study the history of environment and human interactions in the eastern Aleutians. In this paper, we describe the zooarchaeological record from two sites on neighboring islands, located within a 10-km stretch of each other and spanning approximately 3000 yr. Fauna collected during archaeological excavations provide valuable information about ancient Aleut lifeways and adaptations in the IFM environment and Aleut impact on the local biota.

MATERIAL AND METHODS

Site descriptions

To understand the natural world within a cultural context, we studied zooarchaeological materials from four cultural deposits on Chuginadak and Carlisle Islands in the IFM (Fig. 1).

The first (SAM-0014, Unit 1) is located on the north coast of Chuginadak I and contained natural and cultural layers affiliated with the prehistoric Aleut village Tanax̂ Agunax̂. The Tanax̂ Agunax̂ village site is situated on a high cliff above a small cove (Hatfield et al., 2016). Unit 1 was excavated in a partially eroded house pit located on the edge of a steep bluff. The excavated area measured 0.5 × 1.5 m. At approximately 60–70 cm below ground surface, shell midden layers appeared (Fig. 2a). Using stratigraphy, we divided the excavated deposit into two parts: (1) midden containing numerous sea urchin, fish, and bird remains; and (2) midden composed of fish bones, a small amount of sea urchin, and silt.

Three other investigated midden deposits (AMK-0003, Units 2, 4, and 5) are associated with the Ulyagan site (AMK-0003), an ancient village located on the steep southeast coast of Carlisle Island. Units 1 and 3 from the Ulyagan site did not contain faunal remains and are described elsewhere (Hatfield et al., 2016).

The Ulyagan Unit 4 excavation area measured 1.5 × 0.5 m and was located on the western side of a steep ravine dividing the Ulyagan site. Evidence of cultural activity lay just below the sod, but a deposit containing midden and well-preserved organic material (sea urchins, shells, and bones of vertebrates) was located 60–90 cm below ground surface (Fig. 2b). Between 90 cm and 105 cm, a dark cultural layer contained few bones and invertebrate remains. Still deeper, at a depth of around 105 cm, faunal remains gradually disappeared.

The Ulyagan Unit 5 excavation was located on the east side of a ravine that divides the Ulyagan settlement area. We discovered a midden on a small terrace situated on the edge of a coastal cliff. The excavated area measured 1 × 0.5 m and 115 cm in depth. A cultural lens, dense with bones and sea urchin shells, lay below a thick sod layer (Fig. 2c). We divided the deposit into three parts: the upper layer was a dense faunal component; the middle layer was dark brown with low concentrations of faunal remains; and the lower layer contained numerous faunal remains. The CR-02 tephra complex dated 1050 cal BP (Okuno et al., 2017) lay beneath this cultural deposit.

Ulyagan site Unit 2 represented a thick midden deposit associated with a longhouse designated House Pit 36 (Hatfield et al., 2016). The midden contained dense accumulations of faunal remains including discrete lenses of sea urchins along with other cultural artifacts. The Unit 2 excavation measured 1 × 1 m and 105 cm deep. The shell midden itself was 50 cm thick.

Materials collected during excavations of the Tanax̂ Agunax̂ site (SAM-0014) Unit 1 and Ulyagan site (AMK-0003) Units 4 and 5 were water-screened through plastic 1.5-mm mesh. Matrix from the Ulyagan site Unit 2 was screened through 5-mm mesh in the field; for this unit, all vertebrate faunal remains retained in the screens or found directly in the pit were bagged for identification. One quarter of the Unit 2 matrix was water-screened through plastic mesh in order to recover smaller objects, including small fish bones. Then all Unit 2 material was combined.

Radiocarbon dating

In order to accurately radiocarbon date samples from these middens, special attention was paid to the material to be dated. The peculiar characteristic of the carbon cycle in ocean waters ultimately affects the radiocarbon ages of marine organisms (Stuiver and Braziunas, 1993). Thus, the most trusted dates originate from terrestrial plants and animals. In the treeless Aleutians, firewood was scarce and local people used driftwood for fire, tools, and construction. Radiocarbon dates obtained on driftwood might be subject to "old wood" problems in which dates may originate from (1) heartwood, which can be older than the archaeological layer in which the wood was found, or (2) wood that had a possible time-lag between the tree's death, use, reuse, and final deposition in an archaeological layer.

According to ethnographic accounts, eastern Aleutian Aleuts used locally growing crowberry (*Empetrum nigrum*) and other Ericaceous shrubs for fuel (Turner, 2008). In the IFM archaeological screened matrix, we recovered charred twigs of local shrubs (*Empetraceae/Ericaceae* species) and used them for dating. A second source for "terrestrial" dates included remains of animals that lived on land and consumed an exclusively terrestrial diet, which, in the IFM included only two bird species: rock ptarmigan (*Lagopus muta*) and cackling goose (*Branta hutchinsii*). The bones of small passerines are not useful for radiocarbon dating because these birds sometimes feed in the littoral zone. A littoral diet leads to the deposition of marine or "old" carbon into their tissues. For radiocarbon dating, we used cackling goose bones from two middens.

The W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory, University of California, Irvine radiocarbon dated all materials. Conventional ^{14}C ages were calibrated to "calendar" years in OxCal 4.3 program (https://c14.arch.ox.ac.uk/oxcal.html) using calibration curves IntCal13 (Reimer et al., 2013). To construct an age-depth model of cultural deposits that have complex stratigraphy and varying growth, we chose the Bchron 4.2.6 package in R v.3.4.1 (Parnell, 2016; R Core team, 2017). The program output includes assessments of probabilities of true date for each layer.

Faunal identification and quantification

Identification of faunal material from Tanax̂ Agunax̂ Unit 1 and from Ulyagan Units 4 and 5 were conducted using the osteological reference collection at the Laboratory of Historical Ecology, Institute of Ecology and Evolution, Russian Academy of Sciences. Crockford (2016) identified the faunal remains from Ulyagan Unit 2 using the comparative faunal collection at the Zooarchaeology Laboratory, Department of Anthropology, University of Victoria, Canada.

Preservation of faunal remains was good in all units. The vertebrate faunal data was primarily quantified using number of identified specimens (NISP; Lyman, 2008). We did not count unidentifiable fish and bird remains or vertebrae and ribs. Bivalves were quantified using the total number of umbos and barnacles (Cirripedia) using the number of plates (Savinetsky et al., 2012). Gastropods were quantified by counting shells when more than half was present (Bird et al., 2002); if fragments were small and broken, we only noted the presence. For sea urchin remains (*Strongilocentrotus* sp.), we calculated minimum number of individuals (MNI) by counting rotulas or hemipyramids, the most abundant elements of Aristotle's lanterns. To identify the age of northern fur seal juveniles, we used measurements and equations suggested by Etnier (2002) or reference collection (Crockford, 2016). We used the Pearson chi-square test (Lyman, 2008) with significance level 0.05 to compare the similarity of different taxa abundance in neighboring layers or periods.

Identifying bones of different species of geese recovered from an archaeological context can be very difficult. In the Aleutian Islands, cackling goose and emperor goose (*Anser canagicus*) are the most abundant goose species. However, these two species feed differently. Cackling goose exclusively feeds on terrestrial plants in tundra or grass communities (Mowbray et al., 2002). Emperor goose feeds on littoral vegetation or invertebrates as well as on grass and sedges in grassy tundra (Schmutz et al., 2011). Consequently, these two species possess distinctive collagen carbon and nitrogen stable isotope values. In order to reliably identify goose remains, we used stable carbon and nitrogen isotopes analysis because these isotopes reflect animal diet (Gorlova et al., 2015). Collagen extraction was conducted in the Laboratory of Historical Ecology, Institute of Ecology and Evolution, Russian Academy of Sciences, using a modified Longin (1971) method (Gorlova et al., 2015). Stable isotope composition of the bone collagen was determined using a Thermo-Finnigan Delta V Plus continuous flow IRMS coupled with an elemental analyzer (Thermo Flash 1112) in the Joint Usage Center at the Institute of Ecology and Evolution, Russian Academy of Sciences. The isotopic composition of N and C is expressed in the δ-notation relative to the international standard (atmospheric nitrogen or Vienna Pee Dee Belemnite, respectively). Samples were analyzed with reference gas calibrated against International Atomic Energy Agency reference materials USGS 40 and USGS 41 (glutamic acid). The drift was corrected using an internal laboratory standard (acetanilide and casein). The standard deviation of δ^{13}C and δ ^{15}N values in reference materials (n = 4–8) was <0.2‰. Nitrogen and carbon contents (as %) and C/N ratio were determined along with isotopic analyses.

Measure of dominance

To estimate the niche breadth of local hunter-gatherers, we used the dominance index which represents a D = 1 – Simpson index, where $D = \sum_i \left(\frac{ni}{n}\right)^2$, where n_i is number of individuals of taxon i (Hammer et al., 2001). The Simpson's Dominance Index is a reciprocal of the evenness index in that a high dominance index reflects "an unevenness" in distribution of the number of individuals among taxa. Ranges are from 0 (all taxa are equally present) to 1 (one taxon dominates the sample completely).

Because of different level of zoological material identification for different purposes, it is difficult to compare assemblages using species level identification. We did not use invertebrates for comparison because quantitative information is available for only a few assemblages. We combined vertebrates into several groups. Fish were combined into sculpins (Cottidae), greenlings (*Hexagrammos* sp.), Atka mackerel (*Pleurogrammos monopterygius*), flatfishes (all Pleuronectidae representatives), salmon (Salmonidae family), and others (mainly small-sized fishes, not main fishing objects). Birds were combined into alcids (Alcidae), migrating Procellariiformes (albatrosses and shearwaters), nesting Procellariiformes (fulmars and storm petrels), geese, ducks, cormorants, gulls, and others (eagles, passerines, etc.). Mammals were grouped into true seals (Phocidae), eared seals (Otariidae, sea lion, and fur seal), sea otter, whales, and terrestrial mammals. Data from archaeological sites with identified vertebrates are presented in Supplementary Table 1. For comparisons, we did not use assemblages with less than 50 bones. We divided the islands by size: small, total area is less than 100 km^2 (Shemya, Buldir, Rat, Little Kiska, Carlisle, and Chuginadak islands); medium, 100–1000 km^2 (Attu, Amchitka, Adak, and Akun islands); and large, more than 1000 km^2 (Umnak and Unalaska). For comparison of index values, we used nonparametric Kruskal-Wallis test following Dunn's multiple comparison test.

RESULTS

Radiocarbon dates and chronology

We calculated eight radiocarbon dates from terrestrial organic samples for Unit 1 of the Tanax̂ Agunax̂ site (Table 1). Although strata were distinct, dates appear somewhat inverted and the large range of dates suggests human disturbance and the introduction of younger materials into the deposit. In this particular case, we estimate deposit formation between 2800 and 2000 cal yr BP.

For the Ulyagan Unit 4, we calculated five radiocarbon dates for strata containing fauna (Table 1). We used terrestrial (local) wood for dating. For the most part, dates measure 2850 to 1850 cal yr BP. We divided the time of deposit formation into three periods by applying the age-depth model to date range probabilities (Fig. 3). These three periods are: 2900–2700 cal yr BP (low part of the midden); 2700–1900 cal yr BP (the lower part of the dense sea urchin layer); and 1900–1850 cal yr BP for the rapidly growing upper part of the dense sea urchin layer.

For Ulyagan Unit 5, we dated terrestrial sources to obtain four radiocarbon dates (Table 1). Radiocarbon dates indicated that this particular midden formed quickly at approximately 400 yr (Fig. 2c). Four radiocarbon dates of terrestrial material indicate that the Ulyagan Unit 2 midden formed approximately 150 cal yr BP (Table 1).

Relying on results of radiocarbon dating, we developed a chronological framework for the zoological material presented here: two middens, one on Chuginadak Island and one on Carlisle Island (Unit 4), accumulated almost simultaneously, although Unit 4 on Carlisle Island started slightly earlier (2900 cal yr BP) and stopped later (1850 cal yr BP); then there is a hiatus in the archaeozoological sequence until 400 cal yr BP, when Ulyagan Unit 5 was formed; finally, Ulyagan Unit 2 midden is deposited during the latest occupation, associated with the Russian era that potentially terminated during the historically documented Aleut Revolt in AD 1764 (Hatfield et al., 2016). Herein, we present our results by place and time of deposition from oldest to youngest, beginning with Chuginadak Island and then Carlisle Island.

Invertebrates

We identified six taxa of invertebrates in the Tanax̂ Agunax̂ and Ulyagan deposits: sea urchins (*Strongilocentrotus* sp.), limpets (*Colisella* sp.), periwinkles (*Littorina* sp.), foolish mussels (*Mytilus trossulus*), and thatched barnacles

Table 1. Radiocarbon dates from the Islands of Four Mountains cultural layers with faunal material. Calibration curve – IntCal13.

Site	Unit no.	Level borders (cm)	Material	^{14}C age (yr BP)	δ^{13}C (‰)	Mean (cal yr BP)	Range (95.4%) (cal yr BP)	Lab no. (UCIAMS)
Tanax̂ Agunax̂ (SAM-0014)	1	60–75	Local wood	2485 ± 20		2590	2715–2490	167644
			Branta hutchinsii	2250 ± 20	−21.0	2250	2340–2160	183748
		75–90	Local wood	2230 ± 15		2225	2320–2160	175114
			Branta hutchinsii	2230 ± 15	−20.9	2225	2320–2160	183749
		90–95	Local wood	2710 ± 20		2810	2850–2765	167645
		95–100	Local wood	2730 ± 15		2820	2860–2780	175113
		100–105	Local wood	2375 ± 20		2390	2460–2345	167646
			Branta hutchinsii	2385 ± 15	−21.6	2390	2460–2345	183747
Ulyagan (AMK-0003)	4	65–72	Local wood	1905 ± 20		1850	1895–1820	167641
		84–89	Local wood	1925 ± 20		1870	1920–1825	167642
		89–93	Local wood	2165 ± 15		2215	2300–2120	175112
		93–99	Local wood	2620 ± 20		2750	2770–2740	175111
		99–101	Local wood	2760 ± 15		2845	2920–2790	175110
	5	35–40	Local wood	325 ± 20		385	460–310	167637
		55–60	Local wood	370 ± 20		420	500–320	167638
		80–85	Local wood	355 ± 15		405	485–320	167639
		105–120	Local wood	335 ± 15		385	465–315	167640
	2	0–50	Charcoal	130 ± 25		140	270–10	147363
			Branta hutchinsii	190 ± 15	−22.6	160	290–0	175344
			Branta hutchinsii	155 ± 15	−21.7	160	280–5	175345
			Branta hutchinsii	150 ± 15	−20.8	155	280–5	175346

(*Semibalanus cariosus*). The overwhelming majority of invertebrate remains in all deposits belong to sea urchins *Strongilocentrotus* sp. (52–98%; Tables 2–4). Identification of archaeological remains of *Strongilocentrotu*s genus is difficult and requires use of a scanning electron microscope or tomography for accurate species identification. Sea urchin remains from archaeological sites on Adak, Buldir, and Shemya islands were identified as *S. polyacanthus* (Antipushina and Pakhnevich, 2010). This species is common in the littoral zone of Amchitka Island (O'Clair, 1977), but is difficult to distinguish from *S. droebachiensis* (Ebert et al., 2018).

In the Tanax̂ Agunax̂ site deposit, limpet remains represented the second most abundant invertebrate (23.6%). In Ulyagan Unit 4, periwinkles represented up to 42.8% (MNI = 710) of invertebrates. In the layers formed between 1900–1850 cal yr BP of Unit 4, lenses of *Littorina* sp. shells represent a majority of specimens identified.

The excavation methodology used for Ulyagan Unit 2 did not allow comparable collection of invertebrate remains, we only noted the presence of urchins and limpet fragments. The concentration of urchins was lower in this unit compared to other deposits.

We observe invertebrate remains in all deposits, but taxa diversity is very low. The most diverse composition occurred in the older deposits noted at both Tanax̂ Agunax̂ and Ulyagan Unit 4.

Fish

The IFM assemblages had comparable number of fish taxa: nine from Tanax̂ Agunax̂; 10 from Ulyagan Unit 4; and 12 each from Ulyagan Units 5 and 2 (Tables 2–5; Fig. 4). Pacific cod (*Gadus macrocephalus*) dominated all assemblages (ranging from 42.1 to 74% of total fish NISP; Fig. 4). Irish lord (*Hemilepidotus* sp.) represents the second most abundant taxon in all units. Greenlings (*Hexagrammos* sp.) and Atka mackerel (*Pleurogrammus monopterigyus*) are a common hexagrammid species in Aleutian assemblages including in the IFM. Unidentifiable representatives of the Cottidae and Scorpaenidae families comprised small portion in all units, as did halibut (*Hippoglossus stenolepis*) and unidentifiable flatfish bones. Only a few bones of Alaska pollock (*Gadus chalcogrammus*) were identified. In all assemblages, evidence of fish butchering activity (cut marks) was noted, predominantly on Pacific cod bones (Supplementary Table 2).

Birds

In total, we found 39 bird taxa in all four units (Tables 2–5). Alcidae, in general, was the most commonly occurring family; whiskered auklet (*Aethia pygmaea*), ancient murrelet (*Synthliboramphus antiquus*), and puffins (*Fratercula/Lunda* sp.) were by far the most common species. At Tanax̂ Agunax̂ and Ulyagan Unit 2, alcid remains comprise more than 90% of identified bird bones. But in Ulyagan Units 4 and 5, a significant number of fulmar and storm-petrel bones were identified. In Unit 4, northern fulmar (*Fulmarus glacialis*, 21.7%) followed alcids in abundance. In Unit 5, storm petrels (*Hydrobates* sp.) were most abundant (41.2%) among avian bones. Bones of juveniles were very abundant, comprising 67% of fulmar (Unit 4) and 31.5% of storm-petrel (Unit 5) remains (Supplementary Table 3). Other bird groups like

Table 2. Faunal remains from Tanax̂ Agunax̂, (SAM-0014) Unit 1. *, difference with previous layer is significant (Pearson chi-square test, $P < 0.05$).

	Below shell midden		Shell midden		Total	
	MNI	%	MNI	%	MNI	%
Invertebrates						
Strongilocentrotus sp.	8	53	336	72.4	344	71.7
Colisella sp.	+	–	113	24.4	113	23.6
Littorina sp.	–	–	8	1.7	8	1.7
Nucella sp.	+	–	–	–	+	–
Mytilus trossulus	7	47	–	–	7	1.5
Semibalanus cariosus	0	–	7	1.5	7	1.5
Total invertebrates identified	15	100	464	100	479	100
	NISP	%	NISP	%	NISP	%
Fish						
Gadus macrocephalus	194	38.0	881	43.1	1075	42.1
Gadus chalcogrammus	–	–	1	0.05	1	<0.1
Scorpaenidae	10	2	1	0.05*	11	0.4
Hexagrammos sp.	168	32.9	256	12.5*	424	16.6
Pleurogrammus monopterigyus	25	4.9	2	0.1*	27	1.1
Cottidae	3	0.6	1	–	4	0.2
Hemilepidotus sp.	103	20.2	848	41.5*	948	37.1
Myoxocephalus sp.	1	0.2	–	–	1	0.04
Hippoglossus stenolepis	6	1.2	33	1.6	39	1.5
Total fish identified	510	100	2042	100	2552	100
Birds						
Branta hutchinsii	15	1.8	14	0.9	29	1.2
Anser canagicus	3	0.4	3	0.2	6	0.2
Somateria mollissima	9	1.1	11	0.7	20	0.8
Aythya marila	0	0	1	0.1	1	<0.1
Lagopus muta	1	0.1	1	0.1	2	0.1
Phoebastria albatrus	2	0.2	0	0	2	0.1
Hydrobates leucorhous	3	0.4	1	0.1	4	0.2
Hydrobates furcatus	12	1.5	20	1.3	32	1.3
Fulmarus glacialis	2	0.2	4	0.3	6	0.2
Phalacrocorax sp.	12	1.5	14	0.9	26	1.1
Lunda cirrhata	40	4.9	19	1.2*	59	2.4
Fratercula corniculata	8	1.0	9	0.6	17	0.7
Cyclorrhynchus psittacula	4	0.5	21	1.3	25	1
Aethia pusilla	2	0.2	0	0	2	0.1
Aethia pygmaea	416	50.5	874	55.1	1290	53.5
Aethia cristatella	3	0.4	3	0.2	6	0.2
Cepphus columba	4	0.5	16	0	20	0.8
Synthliboramphus antiquus	265	32.2	551	34.7	816	33.8
Uria sp.	12	1.5	14	0.9	26	1.1
Stercorarius parasiticus	1	0.1	0	0	1	<0.1
Haliaeetus leucocephalus	0	0	1	0.1	1	<0.1
Falco peregrinus	0	0	1	0.1	1	<0.1
Passeri	10	1.2	9	0.6	19	0.8
Total birds identified	824	100	1587	100	2411	100
Mammals						
Eumetopias jubatus	1		1		2	
Phoca sp.	1		1		2	
Enhydra lutris	2		–		2	
Total mammal identified	4		2		6	
Unidentified	89		154		243	84.4
Chips	17		22		39	13.5
Total mammals	110		178		288	100

Table 3. Faunal remains from Ulyagan (AMK-0003) Unit 4. *, difference with previous layer is significant (Pearson chi-square test, $P < 0.05$); +, fragments are present.

	2900–2700 cal yr BP		2700–1900 cal yr BP		1900–1850 cal yr BP		Total	
	MNI	%	MNI	%	MNI	%	MNI	%
Invertebrates								
Strongilocentrotus sp.	40	100	84	86.6	745	48.9	869	52.3
Colisella sp.	+	–	10	10.3	71	4.7	81	4.9
Littorina sp.	+	–	3	3.1	707	46.4	710	42.8
Nucella sp.	–	–	+	–	+	–	+	–
Mytilus trossulus.	–	–	–	–	+	–	+	–
Total invertebrates	40	100	97	100	1523	100	1660	100
	NISP	%	NISP	%	NISP	%	NISP	%
Fish								
Gadus macrocephalus	50	53.2	664	54.0	604	46.9*	1318	50.5
Gadus chalcogrammus	1	1.1	3	0.2	1	0.1	5	0.2
Scorpaenidae	6	6.4	51	4.1	112	8.7*	169	6.5
Hexagrammos sp.	10	10.6	71	5.8	87	6.8	168	6.4
Pleurigrammus monopterygius	7	7.4	86	7.0	33	2.6*	126	4.8
Cottidae	1	1.1	–	–	2	0.2	3	0.1
cf. *Gymnocanthus* sp.	–	–	1	0.	10	0.8	11	0.4
Hemilepidotus sp.	19	20.2	349	28.4	428	33.3	796	30.5
Myoxocephalus sp.	–	–	–	–	1	0.1	1	<0.1
Hippoglossus stenolepis	–	–	4	0.3	9	0.7	13	0.5
Total fish identified	94	100	1229	100	1287	100	2610	100
Birds								
Cygnus sp.	–	–	1	0.7	–	–	1	0.2
Branta/Anser	1	0.7	–	–	1	0.4	2	0.4
Somateria spectabilis	–	–	–	–	1	0.4	1	0.4
Somateria mollissima	–	–	–	–	1	0.4	1	0.4
Lagopus muta	–	–	2	1.3	2	0.8	4	0.7
Podiceps cristatus	–	–	–	–	1	0.4	1	0.2
Phoebastria nigripes	–	–	1	0.7	–	–	1	0.2
Phoebastria albatrus	1	0.7	2	1.3	1	0.4	4	0.7
Hydrobates furcatus	5	3.4	9	6.0	3	1.3*	17	3.2
Fulmarus glacialis	9	6.1	23	15.4*	84	35.1*	116	21.7
Phalacrocorax sp.	11	7.5	13	8.7	25	10.5	49	9.2
Charadrii	1	0.7	0	0	0	0	1	0.2
Lunda cirrhata	6	4.1	4	2.7	15	6.3	25	4.7
Fratercula corniculata	2	1.4	3	2.0	4	1.7	9	1.7
Ptychoramphus aleuticus	–	–	1	0.7	2	0.8	3	0.6
Cyclorrhynchus psittacula	1	0.7	3	2.0	–	–	4	0.7
Aethia pusilla	–	–	–	–	1	0.4	1	0.2
Aethia pygmaea	63	42.9	53	35.6	73	30.5	189	35.3
Aethia cristatella	1	0.7	0	0	1	0.4	2	0.4
Cepphus columba	0	0	0	0	1	0.4	1	0.2
Synthliboramphus antiquus	46	31.3	26	17.4*	13	5.4*	85	15.9
Uria sp.	–	–	6	4.0	7	2.9	13	2.4
Larus glaucescens	–	–	1	0.7	–	–	1	0.2
Falco peregrinus	–	–	1	0.7	–	–	1	0.2
Corvus corax	–	–	–	–	2	0.8	2	0.4
Passerine	–	–	–	–	1	0.4	1	0.2
Total birds identified	147	100	149	100	239	100	535	100
Mammals								
Vulpes vulpes	–	–	2	10.5	1	2.4	3	3.8
Eumetopias jubatus	8	47.1	7	36.8	10	23.8	25	32.1
Callorhinus ursinus	5	29.4	2	10.5	12	28.6	19	24.4
Phoca sp.	1	5.9	5	26.3	9	21.4	15	19.2
Enhydra lutris	3	17.6	3	15.8	10	23.8	16	20.5

Table 3. (*Continued*)

	2900–2700 cal yr BP		2700–1900 cal yr BP		1900–1850 cal yr BP		Total	
	MNI	%	MNI	%	MNI	%	MNI	%
Total mammals identified	17	100	19	100	42	100	78	100
Unidentified	80		87		301		468	
Chips	4		4		7		15	
Total mammals	101		110		350		561	

ducks and geese, cormorants, gulls, and passerines comprise very small percentages (Tables 2–5).

To differentiate bones of the two most common geese species, we conducted stable carbon and nitrogen isotope analyses of geese bones from Tanax̂ Agunax̂ and Ulyagan Unit 2. In both units, we found two distinct groups of geese (Fig. 5). At Tanax̂ Agunax̂, we identified six bones of adult emperor goose (mean ± SD, $\delta^{13}C = -13.2 \pm 0.4‰$, $\delta^{15}N = +13.4 \pm 1.6‰$) and 29 bones of cackling goose ($\delta^{13}C = -21.4 \pm 0.3‰$, $\delta^{15}N = +1.1 \pm 1.2‰$). From Ulyagan Unit 2, three bones of cackling goose ($\delta^{13}C = -22.1 \pm 1‰$, $\delta^{15}N = +2.1 \pm 2.4‰$) and two bones of emperor goose ($\delta^{13}C = -13.5 \pm 0.2‰$, $\delta^{15}N = +16.4 \pm 4.8‰$) were analyzed. C/N ratio for all analyzed bones was within the range of well-preserved collagen (DeNiro, 1985)

In addition to juvenile fulmar and storm-petrel bones, juvenile bones of whiskered auklet, ancient murrelet, and other species were recovered (Supplementary Table 3). At Ulyagan Unit 5, we found medullary bones of whiskered auklet (N = 2) and parakeet auklet (*Cyclorrhynchus psittacula*, N = 1).

In all assemblages, we found bird-butchering and skinning activity. In the Tanax̂ Agunax̂ site deposit, tibiotarsus bones of both whiskered auklets and ancient murrelet have cut marks (Supplementary Table 5). A total of 85.4% of the ancient murrelet tibiotarsi (41 of 48) and 14.8% of whiskered auklet tibiotarsi (13 of 88) exhibited cut marks near the distal ends. We also identified stages of tool manufacture on some bones from different units (Supplementary Table 6).

Mammals

Mammals comprise the smallest percentage of zooarchaeological material from all studied units (Tables 2–4), with only Ulyagan Unit 2 mammal bones representing a significant proportion (Table 5). We identified all major sea mammals typical of Aleutian archaeological sites except whales; one whale bone was found during excavation in Unit 1 of Tanax̂ Agunax̂ (Fig. 2a).

Sea lion (*Eumetopias jubatus*) remains were most numerous in Units 4 and 2 of Ulyagan, especially in Unit 2 (52%). We found bones of all age classes, including juveniles less than one yr old (Supplementary Table 4). Northern fur seal (*Callorhinus ursinus*) was represented in all units of Ulyagan, where there are bones of adults, subadults, and juveniles, but not juveniles younger than four months (Supplementary Table 4). We found one very small and porous scapula fragment from Ulyagan Unit 4 that probably represented a fur seal fetus. True seal (*Phoca* sp.) are represented by adults and subadults remains, as well as sea otter (*Enhydra lutris*).

We found the bones of Canidae family in two units, which is unusual for the Aleutian zooarchaeological record. From Ulyagan Unit 4, we identified three bones of red fox (*Vulpes vulpes*) in the assemblage (Table 3) and, based on epiphyseal fusion (Harris, 1978), a left distal tibia and a left astragalus represented a six-month-old individual and one unfused ulna fragment with cut marks on the distal end represented a four-month-old fox (Vasyukov et al., 2018). From Ulyagan Unit 5, we identified two Canidae teeth, which compared favorably with domestic dog (*Canis familiaris*). We also collected the humerus of a subadult dog from midden layers exposed in the bluff near Unit 5 (for detailed description, see Vasyukov et al., 2018).

Cut marks, indicating butchering and skin processing, occurred on bones of all sea mammal species in all IFM assemblages (Supplementary Table 5). We recovered a large quantity of large and small unidentifiable pieces of chopped and shaved sea mammal bone, representing manufacturing waste (Supplementary Table 6).

IFM intersite comparison

The number of identified faunal taxa from excavated units is almost equal in all units. The most diverse groups are birds and fish (Fig. 4). Mammals and invertebrates are represented by only a few species. In spite of comparable taxa numbers, the proportion of different groups in the studied units is different.

In the Tanax̂ Agunax̂ midden, percentages of fish and bird bones are similar, 51.4 and 48.5%, respectively (Table 6). This situation is uncommon for the Aleutian Islands, where fish remains are frequently the most abundant in middens and comprise from 60 to 90% of vertebrates remains (Lefèvre et al., 2010, 2011; Crockford, 2012). In the Ulyagan middens, fish bones were always more abundant (from 80.3 to 89.5% of identified vertebrate bones) and bird bones are much less frequent (from 7.3 to 19.5%). Mammal bones are always rare, especially in the Tanax̂ Agunax̂ midden; however, in the

Table 4. Faunal remains from Ulyagan (AMK-0003) Unit 5. *, difference with previous layer is significant (Pearson chi-square test, $P < 0.05$); +, fragments are present.

	Below dark layer		Dark layer		Above dark layer		Total	
	MNI	%	MNI	%	MNI	%	MNI	%
Invertebrates								
Strongilocentrotus sp.	269	100	57	98.3	545	96.8	871	97.9
Colisella sp.	+	–	1	0.7	18	3.2	19	2.1
Mytilus trossulus	+	–	–	–	–	–	+	–
Total identified invertebrates	269	100	58	100	563	100	890	100
	NISP	%	NISP	%	NISP	%	NISP	%
Fish								
Gadus macrocephalus	1104	65.8	302	54.8*	2757	56.6	4163	58.7
Gadus chalcogrammus	–	–	–	–	4	0.1	4	0.1
Scorpaenidae	33	2	21	3.8*	174	3.6	228	3.2
Hexagrammos sp.	88	5.2	54	9.8*	163	3.3*	305	4.3
Pleurogrammus monopterygius	5	1.5	48	8.7*	863	17.7*	936	13.2
Cottidae	4	0.2	3	0.5	2	0.04	9	0.1
cf. *Gymnocanthus* sp.	2	0.1	–	–	3	0.1	5	0.1
Hemilepidotus sp.	417	24.9	121	22.0	847	17.4*	1385	19.5
Myoxocephalus sp.	1	0.1	–	–	6	0.1	7	0.1
cf. *Malacocottus* sp.	0	0	1	0.2	3	0.1	4	0.1
Pleuronectidae	0	0	1	0.2	9	0.2	10	0.1
Hippoglossus stenolepis	4	0.2	–	–	38	0.8	42	0.6
Total fish identified	1678	100	551	100	4869	100	7098	100
Birds								
Branta/Anser	8	1.7	6	3.1	30	2.8	44	2.6
Clangula hyemalis	–	–	–	–	4	0.4	4	0.2
Somateria spectabilis	–	–	–	–	1	0.1	1	0.1
Bucephala clangula	–	–	–	–	1	0.1	1	0.1
Histrionicus histrionicus	–	–	1	0.5	–	–	1	0.1
Aythya fuligula	–	–	–	–	2	0.2	2	0.1
Anas sp.	–	–	–	–	1	0.1	1	0.1
Lagopus muta	1	0.2	–	–	4	0.4	5	0.3
Phoebastria albatrus	0	0	–	–	1	0.1	1	0.1
Hydrobates sp.	184	39.2	84	43.1	443	41.8	711	41.2
Fulmarus glacialis	5	1.1	5	2.6	35	3.3	45	2.6
Ardenna tenuirostris	0	0	0	0	1	0.1	1	0.1
Ardenna grisea	1	0.2	0	0	0	0	1	0.1
Phalacrocorax sp.	23	4.9	6	3.1	34	3.2	63	3.7
Lunda cirrhata	7	1.5	4	2.1	14	1.3	25	1.4
Fratercula corniculata	2	0.4	1	0.5	9	0.8	12	0.7
Ptychoramphus aleuticus	11	2.3	2	1.0	8	0.8	21	1.2
Cyclorrhynchus psittacula	23	4.9	9	4.6	19	1.8*	51	3.0
Aethia pusilla	1	0.2	0	0	2	0.2	3	0.2
Aethia pygmaea	138	29.4	39	20.0	245	23.1	422	24.5
Aethia cristatella	3	0.6	2	1.0	6	0.6	11	0.6
Cepphus columba	1	0.2	0	0	3	0.3	4	0.2
Synthliboramphus antiquus	50	10.7	33	16.9	160	15.1	243	14.1
Uria sp.	6	1.3	–	–	1	0.1	7	0.4
Larus glaucescens	–	–	–	–	4	0.4	4	0.2
Passeri	5	1.1	3	1.5	33	3.1	41	2.4
Total birds identified	469	100	195	100	1061	100	1725	100
Mammals								
Canis familiaris	–		–		2		2	
Eumetopias jubatus	1		1		1		3	
Callorhinus ursinus	4		–		2		6	
Phoca sp.	1		–		–		1	

Table 4. (*Continued*)

	Below dark layer		Dark layer		Above dark layer		Total	
	MNI	%	MNI	%	MNI	%	MNI	%
Total mammals identified	6		1		5		12	
Unidentified	133		75		238		446	
Chips	26		4		62		92	
Total mammals	165		80		305		550	

youngest deposit, Ulyagan Unit 2, mammal bone percentages are higher compared to the other IFM middens (Table 6).

The proportion of fish and bird taxa also differs. Tanax̂ Agunax̂ midden Pacific cod bones are nearly equal to numbers of medium- and small-sized fish like Irish lord and greenling (Fig. 4). At synchronous Ulyagan Unit 4, small-sized fish are abundant as well, with fewer greenling and the addition of rockfish and Atka mackerel. In the younger Ulyagan Unit 5, there is a high proportion of cod, as well as Atka mackerel and a higher percentage of butchered cod bones compared to other units. The proportion of cod bones is the highest in the youngest midden, Ulyagan Unit 2, whereas this unit contains the fewest small fish. We identified significant numbers of greenling bones from the Tanax̂ Agunax̂ midden, but in the Ulyagan middens, greenling bones comprise only 10% of the assemblage. Most species of *Hexagrammos* are associated with kelp beds in nearshore sublittoral or littoral zones (Mecklenburg et al., 2002). Shallow coves near Tanax̂ Agunax̂ were probably better for greenling fishing than the sublittoral zone near Ulyagan. In our analyses, Irish lord remains were significantly more abundant in the oldest excavated layers on both islands and less abundant in the younger units at Ulyagan.

Interestingly, the bird composition (Fig. 4) in both the Tanax̂ Agunax̂ and Ulyagan Unit 4 deposits, which formed almost at the same time, are different. Ulyagan settlers procured many northern fulmars, including juveniles, whereas at Tanax̂ Agunax̂, situated 10 km from Ulyagan, settlers procure ancient murrelets and whiskered auklets in mass, but not fulmars. The younger Ulyagan Unit 5 Aleuts obtained large quantities of storm petrels, both adults and juveniles, and the youngest Ulyagan Unit 2 midden is comprised predominantly of small alcids and puffins. The small colonial birds, such as whiskered auklet, ancient murrelet, and storm petrels, were the most abundant bird species in all IFM middens.

For mammals, we note that mammal bones are most frequent at Ulyagan Unit 2 and are comprised mostly of sea lion remains.

Dominance indexes

To estimate niche breadth of IFM hunter-gatherers and to compare it within Aleutian Islands, we use a measure of dominance indexes.

Indexes of fish are very similar among small and medium islands but differ for large islands (Fig. 6). For three sites located on large islands, all from the Fox Islands, dominance indexes are higher because Pacific cod remains dominate and differ significantly from small island indexes (Kruskal-Wallis test, $P = 0.0184$). The index shows that the width of the niche on the large islands is narrower than that of small and medium islands. Inhabitants of large islands were focused on Pacific cod fishing; on medium and small islands, Aleuts obtained a variety of fish. Average dominance indexes for small island bird groups are significantly higher than for medium and large islands (Kruskal-Wallis test, $P = 0.0006$). At the same time, indexes for five small island sites (Shemya, Buldir, Chuginadak, and Carlisle Island-Unit 2) are the most variable, with values more than 0.5. The most homogeneous values are within groups of medium and large islands. Within medium islands, two sites from Adak Island show high values. For the rest, medium and large islands are very similar. In all cases with high dominance index, alcids dominate the bird remains and we can interpret high indexes as narrow niche breadth and focused usage of specific bird resources. There are few sites with sufficient mammal bones for comparisons. Mammal indexes are the highest for two sites: Shemya Island, where eared seals dominate, and from Ulyagan Unit 2, where sea lions dominate. There is no clear association with island size (Kruskal-Wallis test, $P = 0.625$).

DISCUSSION

Resource use

Combined, the four IFM faunal assemblages characterize the IFM Aleut interaction with local fauna during the last 3000 yr. The remains of resources from the two smaller catchment circles dominate these assemblages. Our data suggests that IFM sites were occupied year-round. In the spring and early summer, IFM occupants harvested nesting birds and their chicks, fished for Pacific cod, and hunted juvenile sea lions. During the late summer and fall, they harvested Atka mackerel and young fur seal. Winter occupation is more difficult to determine because resource availability was sparse. Famine was common at the end of the winter and beginning of the spring (Veniaminov, 1984; Unger, 2014). In at least two middens, we recovered the remains of emperor goose, a species that only winters in the Aleutian Islands, appearing between October and April (Gibson and Byrd, 2007). King eider, long-tailed duck, and common goldeneye also winter in the Aleutians from autumn

Table 5. Faunal remains from Ulyagan (AMK-0003) Unit 2 (from Crockford, 2016).

	NISP	%
Fish		
Gadus marocephalus	7155	73.8
Gadus chalcogrammus	2	0.0
Sebastes sp.	87	0.9
Anoplopoma fimbria	1	<0.1
Hexagrammos sp.	398	4.1
Pleurogrammus monopterygius	822	8.5
Hexagrammos / Pleurogrammus	124	1.3
Hemilepidotus sp.	894	9.2
Myoxocephalus sp.	1	0.0
Aptocyclus ventricosus	2	0.0
Liparidae	19	0.2
Batymaster signatus	1	<0.1
Hippoglossus stenolepis	191	2.0
Total fish identified	9697	100.0
Birds		
Branta hutchinsii	3	0.4
Anser canagicus	2	0.3
Somateria mollissima	6	0.8
Polysticta/Somateria sp.	2	0.3
Phoebastria albatrus	4	0.5
Hydrobates sp.	4	0.5
Fulmarus glacialis	1	0.1
Ardenna bulleri	1	0.1
Ardenna sp.	4	0.5
Phalacrocorax sp.	18	2.3
Charadrii	7	0.9
Cerorhinca monocerata	4	0.5
Fratercula corniculata	2	0.3
Fratercula/Lunda sp.	168	21.3
cf Aethia cristatella	14	1.8
Aethia pusilla/pygmea	49	6.2
Cyclorrhynchus psittacula	16	2.0
Cepphus columba	2	0.3
Synthliboramphus antiquus	311	39.4
Uria sp.	21	2.7
Alcidae very small	1	0.1
Alcidae small	128	16.2
Alcidae medium	4	0.5
Alcidae large	10	1.3
Stercorarius sp.	2	0.3
Larus sp.	1	0.1
Haliaeetus leucocephalus	1	0.1
Passeri	3	0.4
Total birds identified	789	100
Mammals		
Callorhinus ursinus	50	14.3
Eumetopias jubatus	209	59.7
Phoca largha	1	0.3
Phoca vitulina	20	5.7
Enhydra lutris	2	0.6
Pinnipedia	68	19.4
Total mammals identified	350	100

to the end of spring (Gibson and Byrd, 2007). According to Veltre and Veltre (1983), Atka Aleuts obtained ducks and geese from October to April. Finally, according to ethnographic data from Veniaminov (1984), there were several permanent settlements on Chuganadak and Carlisle islands at the time of contact with Russian explorers and fur hunters although, subsequently, these people were exterminated by Glotov at the request of the Umnak Aleuts (Veniaminov, 1984).

We found few remains of animals, like sea lions or halibut, from the largest catchment circle, like sea lions or halibut. In the youngest IFM deposit (Ulyagan Unit 2), which formed during Russian contact, we found comparatively large quantities of sea lion bones. Overall, mammal samples were small, however, and it is interesting to note that all the major mammalian species (Steller sea lion, fur seal, harbor seal, and sea otter) were represented in the limited numbers at all sites. Only whales and dolphin remains, common in sites in the eastern and western Aleutians (Davis, 2001; Knecht and Davis, 2003; Crockford et al., 2004; Lefèvre et al., 2010), were not found. Only one unidentified whale bone was found in the pit wall of Tanax̂ Agunax̂. The remains of albatross are scarce, as well.

There are two possibilities for the scarcity (especially mammal scarcity) of resources from the largest catchment circle. This scarcity may be sampling error due to small excavation areas. In many cases, Aleutian sites with small excavation volumes reveal small amounts of mammal bones (for example, on Shemya, Rat, and Adak islands; Supplementary Table 1). In contrast, large excavation volumes, like on Unalaska Island, yield thousands of mammalian bones (Davis, 2001; Knecht and Davis, 2003; Crockford et al., 2004). The second possible reason is that butchering patterns occur away from settlement sites, which is common for large animals, often butchered in special places with only select skeletal elements transported to the settlement (e.g., Grayson, 1984). This also would explain the scarcity of halibut in IFM deposits. The large quantity of mammal bone chunks and pieces, the byproduct of toolmaking, indicate mammal bones were actively used in tool manufacture.

The remains of prey harvested in the smallest catchment circle are much more abundant than resources from the largest catchment circle. In the IFM middens, these include the remains of invertebrates and some fish. In all IFM middens, invertebrate diversity is very low and dominated by sea urchins. We observed that the modern littoral zone around Chuginadak and Carlisle islands exhibits poor invertebrate diversity. During the 2014 and 2015 field seasons, we paid special attention to the current littoral zone invertebrates and found only sea urchins, several species of limpets, and periwinkles. We suggest that the current topography, narrow shelves possessing precipitous coastlines and high-energy habitats, must resemble the IFM topography of past littoral zones that supported these same invertebrate types. The

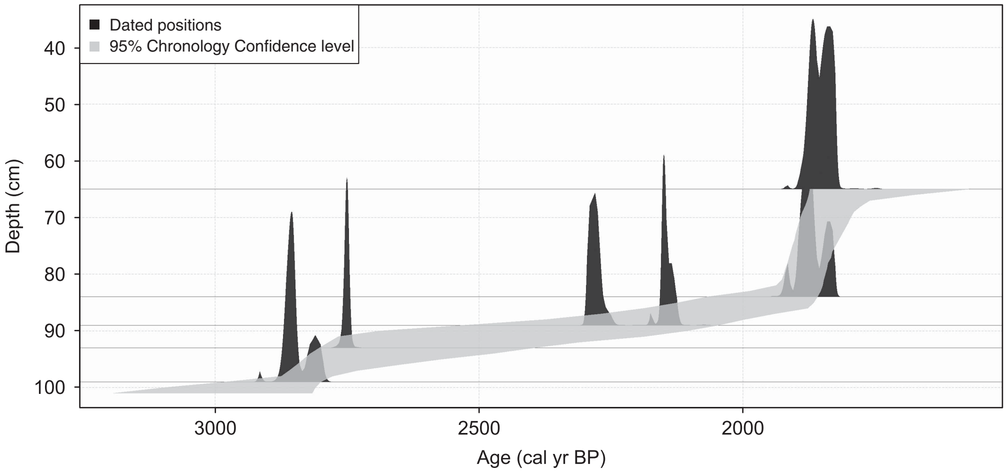

Figure 3. Age-depth model of Ulyagan (AMK-0003) Unit 4.

absence of sandy bottoms near the studied sites today explains the total absence in the archaeological record of infaunal shellfish species like burrowing bivalves. Although the IFM littoral zone lacks species diversity, sea urchin and limpet are frequent. During low tide, we observed large numbers of sea urchins. A comparable invertebrate composition is represented on Buldir Island, where invertebrate remains were sparse and included sea urchins, foolish mussel, and periwinkle (West et al., 2012). Much of the Buldir Island coastline is precipitous and the littoral zone near the excavated Aleut settlement represents a high-energy environment lacking rocks that serve as holdfasts. The same observation was made for Kuril Island middens on more oceanic, small islands where poor littoral zones included large proportions of sea urchins and periwinkle (Fitzhugh et al., 2004). In middens from islands with rich littoral zones (Amaknak, Adak, Amchitka, Shemya, and Agattu), invertebrate diversity was much higher (Spaulding, 1962; Desautels et al., 1971; Knecht and Davis, 2003; Lefèvre et al., 2010; Savinetsky et al., 2012; West et al., 2012).

The archaeological and ethnographic records reveal that Aleuts used all available shellfish resources. In the past, Aleut women and children harvested sea urchins during low tide, but also used long shafts with prongs to harvest at high tide (Quimby, 1944; Laughlin, 1980; Jochelson, 2002). Aleuts consumed all sizes of shellfish, even small periwinkles (*Littorina* sp.). For example, twentieth-century Commander Islands Aleuts consumed periwinkles, “*chimigix*” in Unangum Tunuu (Bergsland, 1994), which translates as “Aleut seeds.” These small gastropods can be found from mean low water up to the littoral fringe (Raid, 1996). A lens of *Littorina* shells in the upper layer of the Ulyagan Unit 4 midden suggests that Aleuts collected these for food.

Greenling and Irish lords are also resources from the smallest catchment circle. Both kinds of fish are abundant in ancient Aleutian middens. Greenlings are especially abundant in middens in the central Aleutian Islands, including Adak and Rat islands (Funk, 2011; Lefèvre et al., 2011; Crockford, 2012; Savinetsky et al., 2012).

In IFM middens, the resources from the second catchment circle dominate, including Pacific cod, Atka mackerel, and many birds. Aleuts of the IFM caught at least 40 different bird species, although only a few comprise the largest percentages of bird bones from the faunal assemblages. The main targeted bird groups were species occurring in high abundance and concentrated in colonies within the second catchment circle. In the IFM, these include storm petrels, fulmars, ancient murrelets, and whiskered auklets. Collecting these birds from nesting colonies was likely easier than catching spatially dispersed species.

Pacific cod represented the most numerous identifiable remains in IFM middens and comprised the largest percentage of fish bones from eastern and western Aleutian archaeological sites at different times (Denniston, 1972; Aigner, 1976; Knecht and Davis, 2003; Orchard, 2003; Crockford et al., 2004; Lefèvre et al., 2010; Crockford, 2012). Exceptions are archaeological sites on Adak, Rat, and Buldir islands where greenlings or Atka mackerel were more abundant (Lefèvre et al., 1997, 2010; Funk, 2011; Crockford, 2012; Savinetsky et al., 2012). The ethnographic record reveals the importance of cod fishing. In the Aleutian Islands, humans fished for cod during different seasons of the year, but mainly from early spring to midsummer (Veniaminov, 1984; Turner, 2008). Prehistorically, Aleuts fished for cod using bone hooks tied to lines made of seaweed (Jochelson, 2002; Veniaminov, 1984; Turner, 2008).

Ancient murrelets are nocturnal, pigeon-sized birds that are widespread in the Aleutian Islands and the Gulf of Alaska (Gaston, 1992). In the Aleutians, ancient murrelets normally nest in burrows dug in soft soil rather than in rock crevices. In historic times, introduced Arctic foxes (*Vulpes lagopus*) probably destroyed many colonies in the Aleutian Islands. Following the removal of foxes, these birds have recolonized some islands and ancient murrelet numbers have generally increased in the Aleutians since the 1990s (Gaston and Shoji, 2010). Ancient murrelet bones are commonly identified in Aleutian archaeological sites and they were the dominant avian type in sites on Adak and Buldir islands (Lefèvre et al.,

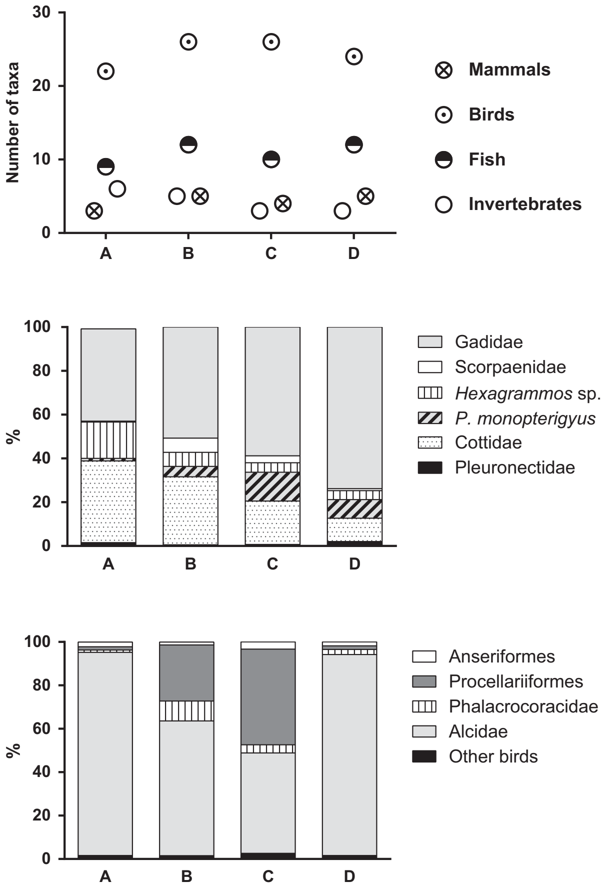

Figure 4. Number of identified taxa (top), composition of fish (middle), and birds (bottom) in studied units from Islands of Four Mountains region: (A) Tanax̂ Agunax̂ (SAM-0014) Unit 1; (B) Ulyagan (AMK-0003) Unit 4; (C) Ulyagan (AMK-0003) Unit 5; and (D) Ulyagan (AMK-0003) Unit 2.

1997; Crockford, 2012). Ethnographic records mention nothing about the pre-contact importance of murrelets. The lack of historic records complicates our understanding of how ancient Aleuts caught these birds. Today, there is no known nesting colony of ancient murrelets in the IFM region (Gibson and Byrd, 2007; Rojek and Williams, 2018).

Whiskered auklets are small alcids that are common throughout the Aleutian Islands. Whiskered auklets generally breed in low densities over a wide range of habitat types (Williams et al., 2003). In other Aleutian archaeological sites on Buldir and Adak islands, whiskered auklets were commonly identified, but they did not dominate avian assemblages (Lefèvre et al., 1997; Lefèvre et al., 2011; Crockford, 2012).

Pacific, or northern, fulmars are familiar birds at sea in the Pacific areas of their range (Mallory et al., 2012). Bones of juvenile fulmars in Ulyagan Unit 4 indicate that Aleuts captured these birds from nesting colonies. We found few fulmar bones at Tanax̂ Agunax̂ Unit 1, however. The people who deposited this particular midden lived at approximately the same time as those who created the midden at the Ulyagan Unit 4 on Carlisle Island. It seems likely that fulmars did not nest near the Tanax̂ Agunax̂ settlement on Chuginadak. Aleuts harvested fulmars on Carlisle for a millennium from 2850 to 1850 cal yr BP but fulmars were far less common on Carlisle by approximately 400 cal yr BP. Fulmars were found only in significant numbers in prehistoric sites on Shemya Island in the western Aleutians (Lefèvre et al., 2010). Northern fulmars are known to nest only on eight islands in the Aleutians today (Gibson and Byrd, 2007; Rojek and Williams, 2018). Large passes play an important role in the distribution of fulmars in the Aleutians today and the largest breeding colonies are situated near big passes (Byrd et al., 2005). The Carlisle colony probably arose due to the productivity of nearby Samalga Pass.

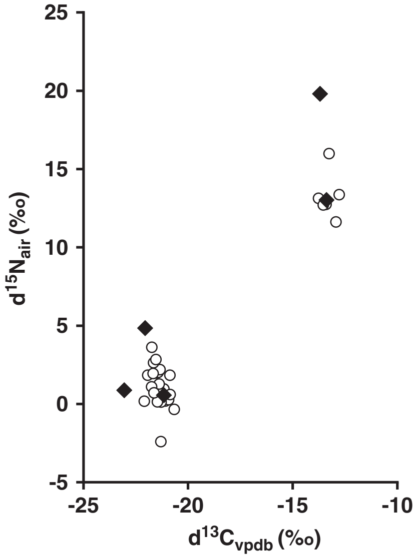

Figure 5. Nitrogen stable isotope composition (δ15N) of geese remains from two Islands of Four Mountains excavated units. Open circles, Tanax̂ Agunax̂ (SAM-0014) Unit 1; black diamonds, Ulyagan (AMK-0003) Unit 2.

The large number of storm-petrel bones identified in Ulyagan Unit 5 indicates that these sea birds nested in a large colony on Carlisle during the formation of this deposit. Two species of storm petrels are common for the Aleutian Islands, fork-tailed storm petrel (*Hydrobates furcata*) and Leach's storm petrel (*Hydrobates leucorhoa*). Various skeletal elements have different identification values, especially if the bones belong to juveniles. Because of this we, combined all bones of storm petrels in one group, *Hydrobates* sp.

Niche breadth

Along the Aleutian chain, we observe similar subsistence strategies and combinations of resources, albeit in different proportions on each island. We analyzed different groups of vertebrates separately because all of them had different importance and different catchment methods. Fish is one of the most important resources for ancient Aleuts. On small and medium islands, there is no dominant fish group and Pacific cod input in catches is moderate. Aleuts did not concentrate on one species; the use of different groups of fish was relatively even. On Umnak and Unalaska (big islands), Pacific cod dominates in assemblages: therefore, consumption of cod

Table 6. Relative abundance of vertebrate groups from Islands of Four Mountains sites.

	Tanax̂ Agunax̂ site (SAM-0014)		Ulyagan Site (AMK-0003)					
	Unit 1 (2800–2000 cal yr BP)		Unit 4 (2900–1850 cal yr BP)		Unit 5 (400 cal yr BP)		Unit 2 (150 cal yr BP)	
	NISP	%	NISP	%	NISP	%	NISP	%
Fish	2552	51.4	2610	85.8	7098	80.3	9697	89.5
Birds	2411	48.5	535	11.6	1725	19.5	789	7.3
Mammals	6	0.1	78	2.6	12	0.2	350	3.2
Total identified vertebrates	4969	100	3041	100	8835	100	10,836	100

was much higher, probably due to the higher abundance of cod on the wide shelf of the Fox Islands (Logerwell et al., 2005). In contrast, bird consumption along the chain appears restricted in diversity, especially on small islands, focusing on colonial nesting birds. On medium and large islands, bird hunting reflected more diversity with the presence of waterfowl and, in some places, albatrosses and shearwaters. On small islands, we observe both wide and narrow niche breadth. For example, on Carlisle Island, when additional resources such as colonies of nesting fulmars and storm petrels appeared, local inhabitants exploited these as well as other resources. At the same time on Chuginadak, humans concentrated on small alcids. On small Buldir Island, catchment was also concentrated on alcids. On small Shemya Island, which has a more complex coastline, birds were more diverse and included migrating albatross. On large islands, niche breadth is wider due to more diversity of waterfowl, albatross, and shearwaters. At the same time, concentrated breeding colonies of alcids are less likely to be found and exploited on large islands. In contrast to our expectations, we do not see intensive consumption of more profitable bird species (i.e., geese) on large islands. Perhaps in the case of large islands this is directly related to the dispersed location of colonies or aggregations of such profitable taxa.

Focused consumption of sea mammal rookeries on small islands is more prominent than on large islands where seal and sea otters are more common in catchment circles. Our analyses indicate that focused consumption on birds and mammals occurs mainly on small islands, probably forced by resource restriction. When resource availability increased, people widen their dietary niche; with fish, however, the opposite is true. Where Pacific cod is more available (around the Fox Islands), small and less-profitable fish decline in importance.

Human influence on island fauna

Human impact on animal populations arises from intensive exploitation of some resources on small islands. Because we recovered very few remains of sea mammals, especially sea otters, we can say nothing about hunting impact on their populations. In addition, we have a significant lack of information about the impact of Aleut harvesting of fish. Our zooarchaeological analysis, however, suggests the humans did sometimes impact bird populations in the IFM. The Aleutian Islands are often referred to as a bird paradise because of the abundance of nesting sea birds. Bird abundance in the Aleutians is associated with the absence of terrestrial carnivores on the islands west of the Umnak Island. The long history of human occupation in the Aleutians, however, is often not taken into account. Marine hunter-gatherers occupied the eastern Aleutians for 9000 yr and the western Aleutians for 3500 yr (Hatfield, 2010). Throughout this time, Aleuts hunted a variety of sea birds. Contradictory information is reported in previous research. Causey et al. (2005) found no evidence of long-term effects associated with local extirpation by overhunting, selective harvesting, or habitat perturbation. In contrast, on Shemya Island, the composition of nitrogen stable isotopes in local peat deposit suggest human predation negatively impacted local nesting sea bird colonies soon after occupation (Savinetsky et al., 2014), after which human occupants shifted toward hunting alcids to albatrosses (Lefèvre et al., 2010).

Although Aleuts harvested a variety of sea birds nesting in different habitats for millennia, humans probably impacted some bird species much more dramatically than others. Storm-petrels, for instance, are burrow-nesting seabirds that breed on islands in colonies ranging from fewer than 100 to more than 1,000,000 birds (Boersma et al., 1980; Boersma and Silva, 2001; Byrd et al., 2005). Two species of storm petrels today are the most abundant burrow-nesting planktivores in the Aleutians and occur on 51 islands (Byrd et al., 2005). During nesting, they typically dig earthen burrows in densely vegetated slopes and also nest in rock crevices or under debris. These habitats are very common and widespread in the Aleutians, including the IFM. The impact of environmental conditions (climate and food availability) on Aleutian Island storm-petrel populations is unclear but there is no evidence of substantial change in population size on Buldir Island since data collection began in the mid-1970s (Byrd et al., 2005). Predation on breeding colonies is probably the main cause of mortality. Historically, in the Aleutian Islands, introduced predators, including red fox, Arctic fox, and Norway rat (*Rattus norvegicus*), had devastating effects on storm-petrel populations (Denlinger, 2006). But we cannot exclude the decrease of storm-petrel's population only due to fox and rat predation. There are examples of colonies of fork-tailed storm petrels in the Commander Islands, where Arctic foxes lived long before the first people appeared there in AD 1741.

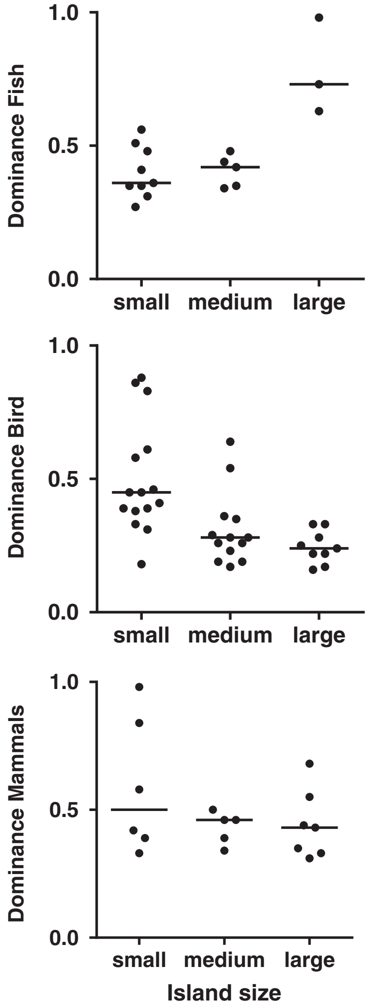

Figure 6. Dominance indexes of fish (top), bird (middle), and mammal (bottom) groups from archaeological middens for small, medium, and large Aleutian Islands. Horizontal line, median.

Based on archaeological data, Aleuts occupied the IFM by at least 4000 cal yr BP (Hatfield et al., 2019). We identified few storm-petrel bones in IFM sites with the exception of Ulyagan Unit 5, where storm-petrel bones, including those of many juveniles, were abundant between ca. 500–300 cal yr BP. This suggests a large storm-petrel nesting colony existed somewhere on the island at that time. Storm-petrel bones are not numerous in other Aleutian sites, even in middens contemporary to Unit 5 (e.g., from Buldir and Adak islands), but they are regularly identified in small numbers (Lefèvre et al., 1997, 2010, 2011; Crockford, 2012). Currently, very large nesting colonies of both storm-petrel species exist on Buldir Island (Byrd and Day, 1986), but their bones are rare in prehistoric Buldir middens (Lefèvre et al., 1997). This evidence suggests that, on Carlisle, a local event unconnected with environmental changes occurred throughout the Aleutian Islands. Changing nitrogen stable isotopes ratios of the 7000-yr-old peat deposit on Carlisle Island suggests that a large sea bird nesting colony arose on Carlisle Island after 2000 cal yr BP (Kuzmicheva et al., 2019). According to δ^{15}N dynamics, the bird colony reached its peak of development at 750–500 cal yr BP (Kuzmicheva et al., 2019), following a large eruption of Cleveland volcano on neighboring Chuginadak Island (CR-02 tephra fall, 1050 cal BP; Okuno et al., 2017). The sea bird colony then decreased very rapidly after 500 cal yr BP. This period coincides with the Ulyagan Unit 5 midden formation (500–300 cal yr BP). In a later deposit (Ulyagan Unit 2), which formed circa 150 cal yr BP, only four storm-petrel bones were identified. We believe that the most likely explanation for such a drastic storm-petrel depopulation is human harvesting. For some reason, humans left Carlisle Island circa 1800 cal yr BP. Based on a hiatus in the archaeological sequence between 1700 to ca.1100 cal yr BP, indications are that the island was abandoned (Hatfield et al., 2019). During this period, the storm-petrel breeding colony, as well as that of other sea birds, was established. When humans settled on the island again by 500 cal yr BP, they reduced the colony of storm petrels very rapidly. Thus, in the Aleutians, it appears humans had the ability to significantly impact some bird populations, especially those of storm petrels, immediately after colonization, as on Shemya Island (Savinetsky et al., 2014). Following colonization, more sustainable bird-harvesting subsistence strategies could have been established and no one bird species was exterminated to the same extent like that experienced by storm petrels. Intensively harvested species like ancient murrelet or whiskered auklet did not undergo the devastation of the storm petrel.

The coexistence of humans and birds in the Aleutians for millennia is obviously not comparable with the introduction of Arctic foxes. The introduction of Arctic foxes on many Aleutian Islands, first by Russian traders in eighteenth to nineteenth centuries and then by American fox farmers, dramatically impacted local bird populations, especially burrow-nesting species (Bailey, 1993; Byrd et al., 2005). Following fox eradication on some islands, populations of most bird species immediately began to recover (Byrd et al., 2005; Mini et al., 2011). The effect of fox predation on seabirds almost certainly depended on how many foxes were present on each island. Hundreds of thousands of foxes were harvested during the Russian era (1750–1867) and later (Carnarhan, 1979). Approximately 27,000 foxes were harvested in the Aleutians from 1913 to 1936 (Jones and Byrd, 1979). We know little about human population size in Aleutians prior to Russian contact, with estimations ranging from 8000 to 20,000 (Zlojutro, 2008). Consequently, we cannot estimate the connection between bird and human population sizes.

Our discovery of red fox remains in layers dating to 1900–1850 cal yr BP and domestic dog remains in layers dating around 400 cal yr BP is curious, given that several predators coexisted on these small IFM islands. We cannot confirm that significant fox populations lived on Carlisle Island nor that domestic dogs were permanent parts of prehistoric Aleut villages, and this question needs more detailed analysis and discussion (Vasyukov et al., 2018).

CONCLUSIONS

This first zooarchaeological analysis for the IFM provides data about resource exploitation by local inhabitants over 3000 yr. These small volcanic islands, geographically characterized by narrow shelves, precipitous coasts, narrow littoral zones, and small land areas, provided local hunter-gatherers with comparatively few resources. Prehistoric and post-contact human groups harvested IFM fauna for food, clothing, and tools. In faunal material from IFM excavations, we can observe the remains of resources that were harvested within several kilometers of villages.

Our analysis shows that subsistence system on IFM were shaped by the small size of these islands, which is true for most Aleutian Islands. Hunters on small (area <100 km^2) and medium (100–1000 km^2) Aleutian Islands used diverse fish species evenly; whereas, on large islands (>1000 km^2), Aleuts mostly relied on Pacific cod. On the other hand, bird exploitation on small islands illustrates a focus on few, often small, colonial species. On medium and large islands, harvested birds reflect more diversity; this includes waterfowl from larger catchment circles. The changes in resource use reflected in the middens from the Ulyagan site on Carlisle Island indicate that if a new type of resource, such as a breeding bird colony, appeared, humans exploited it, readily widening their dietary niche. The utilization of mammal resources depended on the location of breeding rookeries rather than on island size. This is reflected in IFM middens by the presence of juvenile sea lion and the absence of newborn fur seal remains. Invertebrate resource diversity, as reflected in IFM middens, is dependent on island size as well as coastline and shelf characteristics.

The high frequency of storm-petrel remains in deposits formed circa 400 cal yr BP is a unique situation for the Aleutian Islands. Humans apparently abandoned Carlisle Island after one or more volcanic eruptions; the resultant absence of human predation allowed a storm-petrel colony to establish or, at least, recover after a very long absence. Because storm petrels are especially vulnerable to human predation because they nest in burrows and establish dense colonies, the human recolonization of Carlisle Island had a severe impact on the bird colony. Our assumption of island abandonment before 500 cal yr BP is supported by: (1) the lack of sites identified in the IFM archaeological sequence (Hatfield et al., 2019) and (2) the evidence that both the birds' colony development and the human occupation history are supported by isotopic data from Carlisle peat deposits (Kuzmicheva et al., 2019).

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SUPPLEMENTARY MATERIAL

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REFERENCES

Aigner, J.S., 1976. Early Holocene evidence for the Aleut maritime adaptation. *Arctic Anthropology* 13, 32–45.

Antipushina, Zh.A., Pakhnevich, A.V., 2010. On species affiliation of sea urchin genus Strongylocentrotus at the archeological sites of Bering Sea region. In: Rozhnov, S.V. (Ed.), *VII All-Russian Scientific School for Young Scientists in Paleontology, Moscow, Russia. Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow*, pp. 7–8.

Bailey, E.P., 1993. Introduction of Foxes to Alaskan Islands - History, Effects on Avifauna, and Eradication. *United States Fish and Wildlife Service Resource Publication 193*. United States Department of Interior, Homer.

Bergsland, K., 1994. *Aleut Dictionary*. Alaska Native Language Center and University of Alaska, Fairbanks.

Binford, L., 1980. Willow smoke and dogs' tails: hunter-gatherer settlement systems and archaeological site formations. *American Antiquity* 45, 28–44.

Bird, D.W., Richardson, J.L., Veth, P.M., Barham, A.J., 2002. Explaining shellfish variability in middens on the Meriam Islands, Torres Strait, Australia. *Journal of Archaeological Science* 29, 457–469.

Boersma, P.D., Silva, M.C., 2001. Fork-tailed storm-petrel (*Oceanodroma furcata*). Cornell Lab of Ornithology, The Birds of North America Online (accessed January 1, 2001). http:// birdsna.org/Species-Account/bna/species/ftspet

Boersma, P.D., Wheelwright, N.T., Nerini, M.K., Stevens Wheelwright, E., 1980. The breeding biology of the fork-tailed storm-petrel (*Oceanodroma furcata*). *The Auk* 97, 268–282.

Byrd, G.V., Day, R.H., 1986. The avifauna of Buldir Island, Aleutian Islands, Alaska. *Arctic* 39, 109–118.

Byrd, G.V., Renner, H.M., Renner, M., 2005. Distribution patterns and population trends of breeding seabirds in the Aleutian Islands. *Fisheries Oceanography* 14, 139–159.

Carnarhan, J., 1979. Fox farming in the Aleutians. In: Spencer, D. (Ed.), *Aleutian Islands National Wildlife Refuge*. United States Fish and Wildlife Service, Anchorage, pp. 76–96.

Causey, D., Corbett, D.G., Lefèvre, C., West, D.L., Savinetsky, A.B., Kiseleva, N.K., Khassanov, B.F., 2005. The palaeoenvironment of humans and marine birds of the Aleutian Islands: three millennia of change. *Fisheries Oceanography* 14, 259–276.

Corbett, D., West, D., Lefèvre, C., 2010. History of the Western Aleutians Archaeological and Paleobiological Project. In:

Corbett, D., West, D., Lefèvre, C. (Eds.), *The People at the End of the World: The Western Aleutians Project and Archaeology of Shemya Island*. Alaska Anthropological Association Monograph Series, Anchorage, pp. 1–16.

Corbett, D.G., 1991. *Aleut Settlement Patterns in the Western Aleutian Islands, Alaska. Fairbanks, Alaska*. Masters' thesis, University of Alaska, Fairbanks.

Corbett, D.G., Causey, D., Clementz, M., Koch, P.L., Doroff, A., Lefèvre, C., West, D., 2008. Aleut Hunters, Sea Otters, and Sea Cows: Three Thousand Years of Interactions in the Western Aleutian Islands, Alaska. In: Rick T.C., Erlandson, J.M. (Eds.), *Human Impacts on Ancient Marine Ecosystems: A Global Perspective*. University of California Press, Berkeley, pp. 43–76.

Crockford, S., Frederick, G., Wigen, R., McKechnie, I., 2004. Final Report on the Analysis of the Vertebrate Fauna from Amaknak Bridge, Unalaska, AK, UNL050. Supplement to R. Knecht, R., Davis, The Amaknak Bridge Site Data Recovery Project Final Report, Project # MGS-STP-BR-0310(S)/52930. Unpublished report on file, Alaska Department of Transportation, Anchorage.

Crockford, S.J., 2012. Archaeozoology of Adak Island: 6000 years of subsistence history in the central Aleutians. In: West, D., Hatfield, V., Wilmerding, E., Lefèvre, C., Gualtieri, L., (Eds.), *The People Before: The Geology, Paleoecology and Archaeology of Adak Island, Alaska*. British Archaeological Reports International Series 2322. Archaeopress, Oxford, pp. 109–145.

Crockford, S.J., 2016. Islands of the Four Mountains: Vertebrate Fauna from Carlisle Island site AMK-003 (CR-02). Report submitted to D. West and V. Hatfield for the NSF funded project "Geological Hazards, Climate Change and Human/Ecosystems Resilience in the Four Mountains." Unpublished report on file, Museum of the Aleutians, Unalaska.

Darwent, C M., 2004. The highs and lows of high Arctic mammals: Temporal change and regional variability in Paleoeskimo subsistence. In: Mondini, M., Muñoz, S., Wickler, S. (Eds.), *Colonisation, Migration and Marginal areas: A Zooarchaeological Approach*. Oxbow Books, Oxford, pp. 62–73.

Davis, L.B., 2001. Sea Mammal Hunting and the Neoglacial: An Archaeofaunal Study of Environmental Change And Subsistence Technology At Margaret Bay, Unalaska. In: Dumond, D. (Ed.), *Archaeology in the Aleut Zone of Alaska, Some Recent Research*. University of Oregon Anthropological Papers, No. 58. University of Oregon Press, Eugene, pp. 71–85.

DeNiro, M.J., 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. *Nature* 317, 806–809.

Denlinger, L.M., 2006. *Alaska Seabird Information Series*. US Fish and Wildlife Service, Migratory Bird Management Nongame Program, Anchorage.

Denniston, G.B., 1972. *Ashishik Point: an Economic Analysis of a Prehistoric Aleutian Community*. PhD dissertation, University of Wisconsin, Madison.

Desautels, R.J., McCurdy, A.J., Flynn, J.D., Ellis, R.R., 1971. *Amchitka Island, Alaska, 1969–1970, Archaeological Report*. United States Atomic Energy Commission Report TID-25481. Archaeological Research, Los Angeles.

Ebert, T.A., Barr, L.M., Bodkin, J.L., Burcham, D., Bureau, D., Carson, H.S., Caruso, N., *et al.*, 2018. Size, growth, and density data for shallow-water sea urchins from Mexico to the Aleutian Islands, Alaska, 1956–2016. *Ecology* 99, 761.

Etnier, M.A., 2002. *The effects of human hunting on northern fur seal (Callorhinus ursinus) migration and breeding distributions in the late Holocene*. Ph.D. dissertation, University of Washington, Seattle.

Fitzhugh, B., Moore, S., Lockwood, C., Boone, C., 2004. Archaeological paleobiogeography in the Russian far east: The Kuril Islands and Sakhalin in comparative perspective. *Asian Perspectives* 43, 92–122.

Funk, C., 2011. Rat Islands Archaeological research 2003 and 2009: Working toward an understanding of regional cultural, and environmental histories. *Arctic Anthropology* 48, 25–51.

Gaston, A.J., 1992. *The Ancient Murrelet*. T. and A.D. Poyser, London.

Gaston, A.J., Shoji, A.S., 2010. Ancient Murrelet (*Synthliboramphus antiquus*). Cornell Lab of Ornithology, The Birds of North America Online (accessed November 12, 2010). http://birdsna.org/Species-Account/bna/species/ancmur/

Gibson, D.D., Byrd, G.V., 2007. *Birds of the Aleutian Islands, Alaska*. Nuttal Ornithological Club and American Ornithologists' Union, Cambridge and Washington.

Gorlova, E.N., Krylovich, O.A., Tiunov, A.V., Khasanov, B.F., Vasyukov, D.D., Savinetsky, A.B., 2015. Stable-isotope analysis as a method of taxonomical identification of archaeozoological material. *Archaeology, Ethnology & Anthropology of Eurasia* 43, 110–121.

Grayson, D.K., 1981. The effects of sample size on some derived measures in vertebrate faunal analysis. *Journal of Archaeological Science* 8, 77–88.

Grayson, D.K., 1984. *Quantitative Zooarchaeology*. Academic Press, New York.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4, 9.

Harris, S., 1978. Age determination in the Red fox (*Vulpes vulpes*) - an evaluation of technique efficiency as applied to a sample of suburban foxes. *Journal of Zoology London* 184, 91–117.

Hatfield, V., Bruner, K., West, D., Savinetsky, A., Krylovich, O., Khasanov, B., Vasyukov, D., *et al.*, 2016. At the foot of the Smoking Mountains: The 2014 scientific investigations in the Islands of the Four Mountains. *Arctic Anthropology* 53, 141–159.

Hatfield, V., West, D., Bruner, K., Savinetsky, A., Krylovich, O., Vasyukov, D., Khasonov, B., Nicolaysen, K., Okuno, M., 2019. Human resilience and resettlement among the Islands of Four Mountains, Aleutians, Alaska. *Quaternary Research* (this volume). https://doi.org/10.1017/qua.2018.149.

Hatfield, V.L., 2010. Material Culture Across the Aleutian Archipelago. *Human Biology* 82, 525–556.

Hunt, G.L., Stabeno, P.J., 2005. Oceanography and ecology of the Aleutian Archipelago: spatial and temporal variation. *Fisheries Oceanography* 14, 292–306.

Jochelson, W., 2002. *History, Ethnology and Anthropology of the Aleut*. University of Utah Press, Salt Lake City.

Jones, E.L., 2004. Dietary evenness, prey choice, and human-environmental interactions. *Journal of Archaeological Science* 31, 307–317.

Jones, R.D. Jr., Byrd, G.V., 1979. Interrelations between seabirds and introduced animals. In: Bartonek, J.C., Nettleship, D.N. (Eds.), *Conservation of Marine Birds of Northern North America*. Wildlife Research Report 11. U.S. Fish and Wildlife Service, Washington, DC, pp. 221–226.

Knecht, R., Davis, R., 2003. *Archaeological Evaluation of Tanaxtaxak, The Amaknak Spit Site (UNL-00055): Final Report*. Museum of the Aleutians, Unalaska.

Knecht, R.A., Davis, R.S., 2001. A prehistoric sequence for the Eastern Aleutians. In: Dumond, D. (Ed.), *Archaeology in the Aleut Zone of Alaska, Some Recent Research*. University of Oregon Anthropological Papers 58. Eugene, pp. 269–288.

Konar, B., 2000. Limited effects of a keystone species: trends of sea otters and kelp forests at the Semichi Islands, Alaska. *Marine Ecology Progress Series* 199, 271–280.

Kuzmicheva, E.A., Smyshlyaeva, O.I., Khasanov, B.F., Krylovich, O.A., Vasyukov, D.D., Okuno, M., West, D.L., Hatfield, V., Savinetsky, A.B., 2019. A 7300-yr-old environmental history of seabird, human, and volcano impacts on Carlisle Island (the Islands of Four Mountains, eastern Aleutians, Alaska). *Quaternary Research*. https://doi.org/10.1017/qua.2018.114.

Laughlin, W., 1980. *Aleuts: Survivors of the Bering Land Bridge*. Holt, Rinehart and Winston, New York.

Lefèvre, C., Corbett, D., Crockford, S., Czederpiltz, J., Partlow, M., West, D., 2010. Faunal remains and intersite comparisons. In: Corbett, D., West, D., Lefèvre, C. (Eds.), *The People at the End of the World: The Western Aleutians Project and Archaeology of Shemya Island*. Alaska Anthropological Association Monograph Series, Anchorage, pp. 133–157.

Lefèvre, C., Corbett, D.G., West, D., Siegel-Causey, D., 1997. A Zooarchaeological Study at Buldir Island, Western Aleutians, Alaska. *Arctic Anthropology* 34, 118–131.

Lefèvre, C., West, D., Corbett, D.G., 2011. Zooarchaeological Analysis at ADK-011, Adak Island, Central Aleutian Islands, Alaska. *Arctic Anthropology* 48, 69–82.

Logerwell, E.A., Aydin, K., Barbeaux, S., Brown, E., Conners, M. E., Lowe, S., Orr, J.W., Ortis, I., Reuter, R., Spenser, P., 2005. Geographic patterns in the demersal ichthyofauna of the Aleutian Islands. *Fisheries Oceanography* 14, 93–112.

Longin, R., 1971. New method of collagen extraction for radiocarbon dating. *Nature* 230, 241–242.

Loponte, D. M., Acosta, A., 2004. Late Holocene hunter-gatherers from the Pampean *Wetlands, Argentina*. In: Mengoni Goñalons, (Ed.), *Zooarchaeology of South America*. British Archaeological Reports International Series 1298. Archaeopress, Oxford, pp. 39–57.

Lyman, L.R., 2008. *Quantitative Paleozoology*. Cambridge University Press.

Mallory, M.L., Hatch, S.A., Nettleship, D.N., 2012. Northern Fulmar (*Fulmarus glacialis*). Cornell Lab of Ornithology, The Birds of North America Online (accessed November 27, 2012). http://birdsna.org/Species-Account/bna/species/norful

McCartney, A.P., 1977. Prehistoric human occupation of the Rat Islands. In: Merritt, M.L., Fuller, R.G. (Ed.), *The Environment of Amchitka Island, Alaska*. National Technical Information Service, United States Department of Commerce, Springfield, pp. 59–113.

Mecklenburg, C.W., Mecklenburg, T.A., Thorsteinson, L.K., 2002. *Fishes of Alaska*. American Fisheries Society, Bethesda.

Mini, A.E., Bachman, D.C., Cocke, J., Griggs, K.M., Spragens, K. A., Black, J.M., 2011. Recovery of the Aleutian cackling goose *Branta hutchinsii leucopareia*: 10-year review and future prospects. *Wildfowl* 61, 3–29.

Mordy, C.W., Stabeno, P.J., Ladd, C., Zeeman, S., Wisegarver, D. P., Salo, S.A., Hunt, G.L. Jr., 2005. Nutrients and primary production along the eastern Aleutian Island Archipelago. *Fisheries Oceanography* 14, 55–76.

Mowbray, T.B., Ely, C.R., Sedinger, J.S., Trost, R.E., 2002. Cackling Goose (*Branta hutchinsii*). Cornell Lab of Ornithology, The Birds of North America Online (accessed January 1, 2002). http://birdsna.org/Species-Account/bna/species/cacgoo1

O'Clair, C.E., 1977. Marine invertebrates in rocky intertidal communities. In: Merritt, M.L., Fuller, R.G. (Eds.), *The Environment of Amchitka Island, Alaska*. National Technical Information Service, United States Department of Commerce, Springfield, pp. 395–449.

Okuno, M., Izbekov, P., Nicolaysen, K.P., Nakamura, T., Savinetsky, A.B., Vasyukov, D.D., Krylovich, O.A., *et al.*, 2017. AMS radiocarbon dates on peat section related with tephra and archaeological sites in Carlisle Island, the Islands of Four Mountains, Alaska. *Radiocarbon* 59, 1771–1778.

Orchard, T.J., 2003. An Application of the Linear Regression Technique for Determining Length and Weight of Six Fish Taxa: The Role of Selected Fish Species in Aleut Paleo Diet. *British Archaeological Reports International Series 1172*. Archaeopress, Oxford.

Parnell, A., 2016. Bchron: radiocarbon dating, age-depth modelling, relative sea level rate estimation, and non-parametric phase modelling. R package version 4.2.6. https://CRAN.R-project.org/package=Bchron

Quimby, G.I., 1944. *Aleutian Islanders: Eskimos of the North Pacific*. Chicago Natural History Museum, Chicago.

R Core Team, 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raid, D.G., 1996. *Systematics and Evolution of Littorina*. The Ray Society, London.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., *et al.*, 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887.

Rojek, N., Williams, J., 2019. Present day assemblage of birds and mammals in the Islands of the Four Mountains, Alaska. *Quaternary Research* (this volume).

Savinetsky, A.B., Khassanov, B.F., West, D.L., Kiseleva, N.K., Krylovich, O.A., 2014. Nitrogen isotope composition of peat samples as a proxy for determining human colonization of islands. *Arctic Anthropology* 51, 78–85.

Savinetsky, A.B., West, D.L., Antipushina, Zh.A., Khassanov, B.F., Kiseleva, N.K., Krylovich, O.A., Pereladov, A.M., 2012. The reconstruction of ecosystem history of Adak Island (Aleutian Islands) during the Holocene. In: West, D., Hatfield, V., Wilmerding, E., Lefèvre, C., Gualtieri, L., (Eds.), *The People Before: The Geology, Paleoecology and Archaeology of Adak Island, Alaska*. British Archaeological Reports International Series 2322. Archaeopress, Oxford, pp. 77–106.

Schmutz, J., Petersen, M.R., Rockwell, R.F., 2011. Emperor Goose (*Chen canagica*). Cornell Lab of Ornithology, The Birds of North America Online (accessed September 23, 2011). https://birdsna.org/Species-Account/bna/species/empgoo/introduction

Spaulding, A.C., 1962. Archaeological investigations on Agattu, Aleutian Islands. *University of Michigan, Museum of Anthropology, Anthropological Papers* 18, 3–74.

Stuiver, M., Braziunas, T.F., 1993. Modeling atmospheric 14C influences and 14C ages of marine samples to 10,000 BC. *Radiocarbon* 35, 137–189.

Turner, L.M., 2008. *An Aleutian Ethnography*. University of Alaska Press, Fairbanks.

Unger, S., 2014. *Qaqamiiĝux̂: Traditional Foods and Recipes from the Aleutian and Pribilof Islands*. Aleutian Probilof Islands Association, Anchorage.

Vasyukov, D.D., Krylovich, O.A., West, D.L., Hatfield, V., Savinetsky, A.B., 2019. Ancient canids of Aleutian Islands (new archaeological findings from the Islands of Four Mountains). *Quaternary Research* (this volume).

Veltre, D.W., Veltre, M.J., 1983. *Resource Utilization in Atka, Aleutian Islands, Alaska*. Technical Paper No. 88. Alaska Department of Fish and Game, Division of Subsistence, Anchorage.

Veniaminov, I., 1984. *Notes on the Islands of the Unalaska District*. Limestone Press, Fairbanks and Kingston.

West, D., Antipushina, Zh., Savinetsky, A., Krylovich, O., 2012. Invertebrate remains: a pan Aleutian comparison. In: West, D., Hatfield, V., Wilmerding, E., Lefèvre, C., Gualtieri, L., (Eds.), *The People Before: The Geology, Paleoecology and Archaeology of Adak Island, Alaska*. British Archaeological Reports International Series 2322. Archaeopress, Oxford, pp. 177–193.

Williams, J.C., Byrd, V.G., Konyukhov, N.B., 2003. Whiskered Auklets *Aethia pygmaea*, foxes, humans and how to right a wrong. *Marine Ornithology* 31, 175–180.

Wing, E.S., 1963. Vertebrate remains from the Wash Island Site. *Florida Anthropologist* 16, 93–96.

Yesner, D.R., 1977. *Prehistoric Subsistence and Settlement in the Aleutian Islands*. PhD dissertation, University of Connecticut, Storrs.

Zlojutro, M., 2008. *Mitochondrial DNA and Y-Chromosome Variation of Eastern Aleut Populations: Implications for the Genetic Structure and Peopling of the Aleutian Archipelago*. PhD dissertation, University of Kansas, Lawrence.