Chemical profiling of ancient hearths reveals recurrent salmon use in Ice Age Beringia

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Current approaches to reconstruct subsistence and dietary trends in ancient hunter-gatherer societies include stable isotope analyses, but these have focused on human remains, cooking pottery, and food residues, which are relatively rare in the archaeological record. In contrast, short-term hearths are more ubiquitous worldwide, and these features can provide valuable evidence for ancient subsistence practices, particularly when faunal remains are not preserved. To test the suitability of hearths for this purpose, we conducted multiple chemical analyses: stable carbon and nitrogen isotope analyses of total organic matter (expressed as $\delta^{13}C$ and $\delta^{15}N$ values) and compound-specific carbon isotope analyses of individual fatty acids ($\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$) from 17 well-preserved hearths present in three occupations dating between ∼13,200–11,500 calibrated years B.P. at the Upward Sun River (USR) site in central Alaska. We combined $\delta^{15}N$ and $\delta^{13}C_{FA}$ data in a Bayesian mixing model (stable isotope analysis in R) with concentration dependency to each hearth. Our model values were tested against faunal indices, indicating a strong positive relationship between marine proportional contributions to each hearth and salmon abundance. Results of the models show substantial anadromous salmon use in multiple USR components, indicating recurrent use of the site for salmon processing during the terminal Pleistocene. Our results demonstrate that salmonid and freshwater resources were more important for late Pleistocene hunter-gatherers than previously thought and highlight the potential of chemical profiling of hearth organic residues for providing greater geographic and temporal insights into resource use by prepottery societies.

stable isotopes | hearths | organic residue analysis | GC-combustion-IRMS | Beringia

Inferences on ancient hunter-gatherer subsistence economies generally rely on zooarchaeologically derived abundance measures from sites with faunal preservation (1); however, these sites can be rare in late-Pleistocene deposits (2). Chemical profiling using compound-specific stable isotope analyses can provide another approach to reconstruct resource use and have been used to study food residues on pottery (3–8). These isotopic studies have provided insights into the proportional contributions of different food resources to human diets, particularly aquatic vs. terrestrial food sources. However, most hunter-gatherer societies did not use pottery, which is limited to <4,500 calibrated (cal) y B.P. in North America (9, 10). Thus, organic residue analysis has had limited application to the research of prepottery hunter-gatherer societies in North America.

Analyses of hearth sediments can inform us about mobility, subsistence behaviors, and activity areas of hunter-gatherer societies (11, 12). Recent analyses of burned residues in hearths have demonstrated their value for exploring associated food use; however, these investigations have focused on examining the use of animal bone and marine animal blubber for fuel and lighting at locations proximal to coastal environments (13–15). Most other dietary studies of resource use on hearths have involved zooarchaeological measures of abundance [i.e., number of identified specimens (NISP) and minimum number of individuals] (16). These measures likely underestimate certain taxa, particularly fish and small mammals, because of taphonomic issues (e.g., sediment pH, leaching, burning, compaction, and microbial action). For example, fish bones are more likely to be underrepresented compared with mammal bones because of differences in bone structure (17–20). Furthermore, many sites have variable faunal preservation, limiting these more traditional zooarchaeological approaches.

We addressed these limitations by using a combined approach of stable isotope and zooarchaeological analyses of hearth sediments at the Upward Sun River (USR) site. The USR site is located in loess deposits on a sand dune south of the Tanana River in central Alaska (Fig. 1), and details on its geology and chronology have been described (21–23). The site is well stratified with three major components: Component 1 (13,200 cal y B.P.) contains 2 hearth features and associated well-preserved fauna; component 2 (11,800 cal y B.P.) contains 4 hearths but few preserved fauna; and component 3 (11,500 cal y B.P.) contains 11 hearths, including 1 hearth within a residential feature associated with the burial of two infants (22) and a child cremation (21) (*SI Materials and Methods*). Faunal analyses indicated that the remains accumulated during processing/cooking/disposal events within the hearths (21, 22), and genetic analyses provided evidence for the presence of the salmonids that were marine (anadromous) chum salmon (*Oncorhynchus keta*) (23). Thus, USR offers important controls to evaluate proportional contributions of terrestrial, freshwater, and marine food resources reconstructed through chemical profiling of hearth sediments.

We present chemical analyses of dietary biomarkers from 17 terminal Pleistocene-Age hearths from component 1 ($n = 2$), component 2 ($n = 4$), and component 3 ($n = 11$) at USR (Fig. 1 and

Significance

Reconstructing subsistence practices of ancient hunter-gatherers requires quantitative data on food resources, which rarely preserve. Here we use chemical profiling of hearth sediments from three Ice Age occupations in Alaska (13,200–11,500 years ago), including compound-specific stable isotope analyses and a Bayesian mixing model, to estimate proportional contributions of marine (salmon), freshwater, and terrestrial resources. The model is verified through zooarchaeological analyses and demonstrates the importance of salmonid and freshwater resources to these early Americans. Our study also provides evidence for the earliest use of salmon in the Americas.

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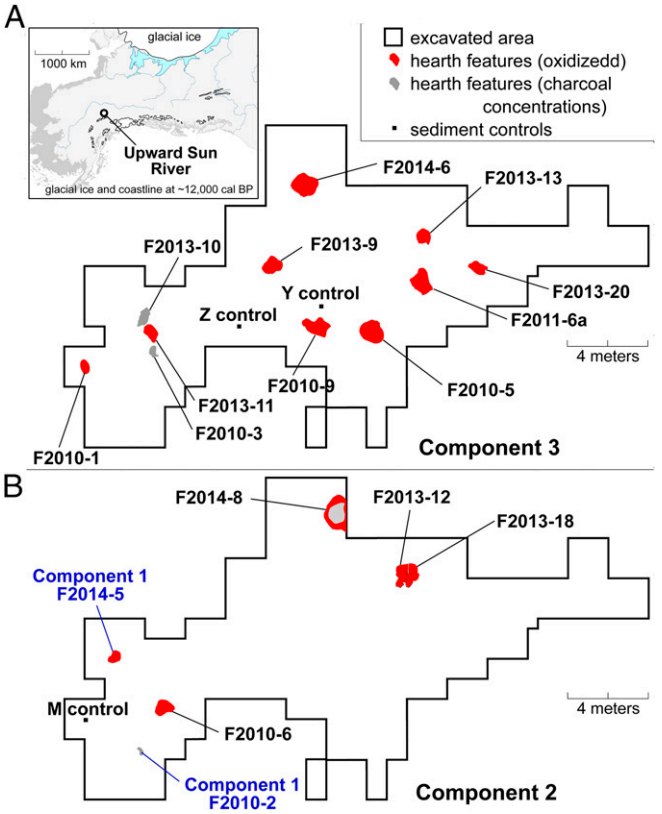

Fig. 1. Location map of the study site in central Alaska (inset) and the distribution of hearths in component 3 (*A*) and components 1 and 2 (*B*) in the USR site.

Table S1). Our aim was to determine the proportional contribution of terrestrial, freshwater, and marine (salmon) resources. Previous zooarchaeological studies have shown that early Eastern Beringians had a broad-spectrum economy, incorporating large and small mammals, birds, and fish (22, 24, 25), but proportional data are lacking. This study provides quantitative estimates of early Beringian resource use at a residential camp. We directly measured the $\delta^{13}C$ and $\delta^{15}N$ values of total organic matter in hearths to identify marine resource processing (26) and extracted lipids to measure the $\delta^{13}C$ values of individual fatty acids (FAs) present, which have been used to discriminate terrestrial vs. marine sources using organic residues from pottery (5, 7). We used an isotope mixing model [stable isotope analysis in R (SIAR); *SI Materials and Methods*] to estimate the proportional contribution of different food-resource categories to each hearth (27). We generated this model using data from modern animal species from central Alaska and zooarchaeological remains from USR to infer the potential food resources used by the terminal Pleistocene hunter-gatherers that were present at the USR site. We also tested our model using a zooarchaeologically derived salmon index for eight hearths from component 3.

Results

Bulk stable isotope values of modern muscle tissues were significantly different in $\delta^{13}C$ values (Kruskal–Wallis ANOVA, $\chi^2 = 17.025$, df = 2, $P < 0.001$) and $\delta^{15}N$ values (Kruskal–Wallis ANOVA, $\chi^2 = 15.096$, df = 2, $P < 0.001$) among the terrestrial, freshwater, and marine food groups (Fig. 2 and Table S2). Marine (anadromous salmon) samples had higher $\delta^{15}N$ values (13.8 ± 0.7‰) compared with freshwater (9.7 ± 3.1‰) and terrestrial food groups (2.6 ± 0.8‰). The terrestrial food group had lower $\delta^{15}N$ values than the freshwater and marine (salmon) food groups ($P < 0.001$). $\delta^{15}N$ values clearly separated marine (salmon) from the terrestrial food groups. However, the range of $\delta^{15}N$ values of the freshwater food group (11.8 ± 3.0‰) overlapped with salmon (13.8 ± 0.7‰). To separate the salmon and freshwater food groups, we compared the $\delta^{13}C_{FA}$ values ($\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$) from all three food groups (Table S2). We found significant differences in $\delta^{13}C_{16:0}$ (Kruskal–Wallis ANOVA, $\chi^2 = 12.812$, df = 2, $P < 0.001$) and $\delta^{13}C_{18:0}$ (Kruskal–Wallis ANOVA, $\chi^2 = 13.791$, df = 2, $P < 0.001$) values among the three food groups. Marine (anadromous salmon) had higher $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values ($\delta^{13}C_{16:0}$: −27.4 ± 1.1‰, $\delta^{13}C_{18:0}$: −25.8 ± 1.1‰) compared with freshwater ($\delta^{13}C_{16:0}$: −34.4 ± 3.6‰, $\delta^{13}C_{18:0}$: −33.8 ± 3.2‰) and terrestrial food groups ($\delta^{13}C_{16:0}$: −31.1 ± 2.4‰, $\delta^{13}C_{18:0}$: −31.1 ± 2.1‰). The freshwater food group had lower $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values than the marine (salmon) and terrestrial food groups (multiple comparison post hoc test, $P < 0.001$). The $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values clearly separated freshwater resources from the salmon resources (Fig. 3), which were not feasible using $\delta^{15}N$ values alone. $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen from the faunal samples taken from the cremation hearth F2010-5 are shown in Fig. 2 and Table S3, and these faunal remains included terrestrial animals, aquatic birds, and salmon. Our isotopic data show that there is an isotopic fractionation (~3.5‰) between modern muscle and ancient bone collagen samples associated with $\delta^{13}C$ values, but $\delta^{15}N$ values of ancient species are similar to modern anadromous salmon, aquatic bird, and terrestrial food groups (Fig. S1).

The bulk $\delta^{13}C$ and $\delta^{15}N$ values for USR hearths are shown in Fig. 2 and Table S1. We compared bulk $\delta^{13}C$ and $\delta^{15}N$ values between USR hearths and the three different food groups and found significant differences in $\delta^{13}C$ (Kruskal–Wallis ANOVA, $\chi^2 = 39.660$, df = 3, $P < 0.001$) and $\delta^{15}N$ values (Kruskal–Wallis ANOVA, $\chi^2 = 31.231$, df = 3, $P < 0.001$). USR hearths had higher $\delta^{13}C$ values (−24.0 ± 0.9‰) than the freshwater (−28.4 ± 3.6‰) and terrestrial food groups (−23.8 ± 1.3‰), but lower values compared with the marine (anadromous salmon) food group (−20.1 ± 1.4‰). USR hearths had higher $\delta^{15}N$ values (6.5 ± 3.0‰) than the terrestrial food group (2.6 ± 0.8‰), but lower $\delta^{15}N$ values than freshwater (9.7 ± 3.1‰) and salmon (13.8 ± 0.7‰) food groups. We also compared bulk isotope values among 17 USR hearths and found significant differences in $\delta^{15}N$ ($P < 0.001$), but not in $\delta^{13}C$ ($P = 0.100$), values (Fig. S2). Most hearths had elevated $\delta^{15}N$ values relative to nonhearth control samples (mean $\delta^{15}N$ value = −0.8‰) in the same stratigraphic layers from three separate blocks (blocks M, Y, and Z). Most hearths had similar $\delta^{15}N$ values from the center to the edges of hearth with a mean range of ~2‰ (Fig. S3*A*). There was a clear difference in $\delta^{15}N$ values between top and bottom layers. $\delta^{15}N$ values in the bottom, oxidized layer of measured hearths were slightly higher (mean 2.3‰) than the top layer of hearths (Table S4). $\delta^{15}N$ values of samples extending beyond the hearth F2013-09 had very similar values in the edge of the hearth (Fig. S3*B*).

The organic residues from hearths at the USR site contained a significant amount of extractable lipids, consisting almost entirely of free and esterified FAs identified by their FA methyl ester mass spectra (Fig. S4). The most abundant constituents were even and odd carbon-number long-chain saturated FAs (C14:0 to C26:0) with hexadecanoic acid (C16:0) dominating over octadecanoic (C18:0) acids. Significant amount of unsaturated FAs (C16:1, C18:1, and C18:2) were also detected, with octadecenoic (C18:1) acids present in high abundance. Isoprenoid FAs (4,8,12-TMTD, pristanic acid, and phytanic acid) and other FAs [long-chain ω-(*o*-alkylphenyl) alkanoic acids, and dihydroxy FAs] used as marine biomarkers (3–8, 43) were absent from the USR hearths.

The $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values from the USR hearths were measured to discriminate between marine and freshwater food

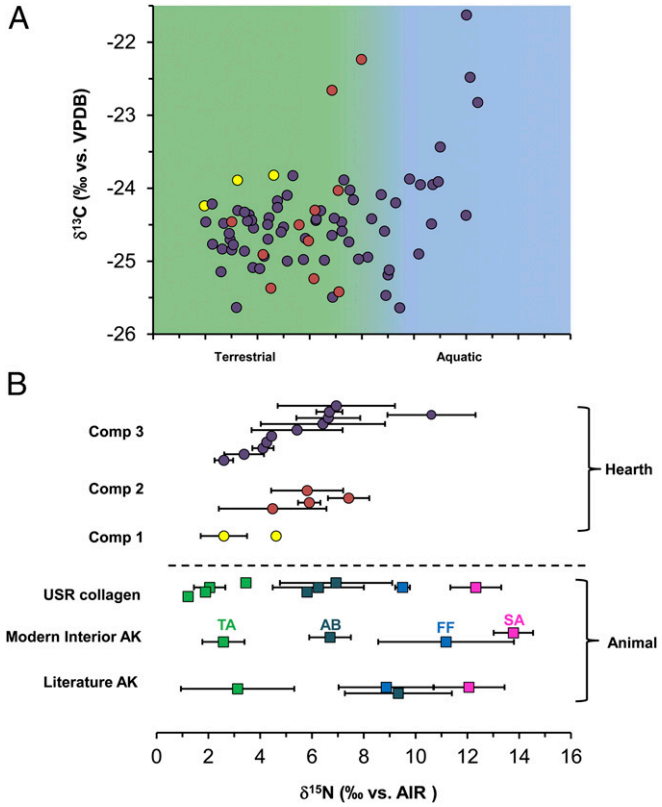

Fig. 2. Bulk $\delta^{13}C$ and $\delta^{15}N$ values from hearths in component 1 (yellow circle), component 2 (orange circle), and component 3 (dark circle) from USR site. (*A*) Distribution of $\delta^{15}N$ values of components 1, 2, and and 3 in USR hearths and reference samples. (*B*) Animal muscles from Alaska in literature (28–36), from modern interior Alaska (in this study), and bone collagen from USR fauna (in this study), and other ancient salmon in Alaska (23, 37–39). AB, aquatic bird (red square); FF, freshwater fish (blue square); SA, salmon (pink square); TA, terrestrial animals (green square).

groups, which could not be achieved using $\delta^{15}N$ values alone. We compared $\delta^{13}C$ values of two FAs ($\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$) between the USR hearths and the three different food groups. We found significant differences in $\delta^{13}C_{16:0}$ values (Kruskal–Wallis ANOVA, $\chi^2 = 21.208$, df = 3, $P < 0.001$) and $\delta^{13}C_{18:0}$ values (Kruskal–Wallis ANOVA, $\chi^2 = 27.627$, df = 3, $P < 0.001$) from the hearths and relative to the three food groups (Fig. 3 and Table S5). USR hearths had higher $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values ($\delta^{13}C_{16:0}$: −30.9 ± 0.6‰, $\delta^{13}C_{18:0}$: −29.1 ± 0.8‰) than the freshwater ($\delta^{13}C_{16:0}$: −34.4 ± 3.6‰, $\delta^{13}C_{18:0}$: −33.8 ± 3.2‰) and terrestrial food groups ($\delta^{13}C_{16:0}$: −31.1 ± 2.4‰, $\delta^{13}C_{18:0}$: −31.1 ± 2.1‰), but lower than anadromous salmon ($\delta^{13}C_{16:0}$: −27.4 ± 1.2‰, $\delta^{13}C_{18:0}$: −25.8 ± 1.1‰). Combined $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values from the USR hearths showed that the hearths distributed between salmon and terrestrial food groups (Fig. 3).

We used the $\delta^{15}N$, $\delta^{13}C_{16:0}$, and $\delta^{13}C_{18:0}$ values from hearths and food groups in a SIAR mixing model to estimate the proportional contribution of terrestrial, freshwater, and marine food groups (Fig. 4). The model outputs and ranges of contributions of each food group to the USR hearths revealed that hearth residues represented a wide range of contributions from the terrestrial (10–75%) and marine (anadromous salmon) food groups (4–64%) (Fig. 4 and Table S6). Estimates of the proportional contributions of anadromous salmon to hearths based on the model were positively correlated with contribution of the freshwater food group ($r = 0.665$, $P < 0.001$), but negatively correlated with the contribution of the terrestrial food group ($r = -0.978$, $P < 0.001$). Three hearths (F2014-06, F2013-20, and F2013-09) in component 3 had the highest contribution of salmon (≥45%), and one hearth (F2010-06) in component 2 had the highest contribution of salmon (31%) compared with other hearths from that component.

We identified 14,481 faunal NISP and 759 human NISP within the hearths, the latter from the cremation hearth (F2010-05), and all were generally small, highly fragmented calcined bone fragments (Table S7). Most of these fragments could not be recovered by using 1/8" (3.2-mm) mesh typically used in archaeological excavations. No fish were recovered from components 1 and 2, yielding Salmonidae indices of 0. Component 3 hearths contained variable presence of Salmonidae, yielding Salmonidae indices between 0 and 19.5 (Table S7). There was a strong positive correlation between Salmonidae abundance derived from the faunal remains and the marine proportional abundance derived from the SIAR mixing model ($r = 0.880$, $P < 0.001$) (Fig. 5). This relationship demonstrates the utility of the hearth sediments for chemical profiling to track salmon abundance.

Discussion

Our stable isotope data ($\delta^{15}N$, $\delta^{13}C_{16:0}$, and $\delta^{13}C_{18:0}$ values) indicate that aquatic animals (salmon and freshwater) were important food resources at the USR site at the Pleistocene/Holocene transition (Fig. 4). These results are significant in terms of

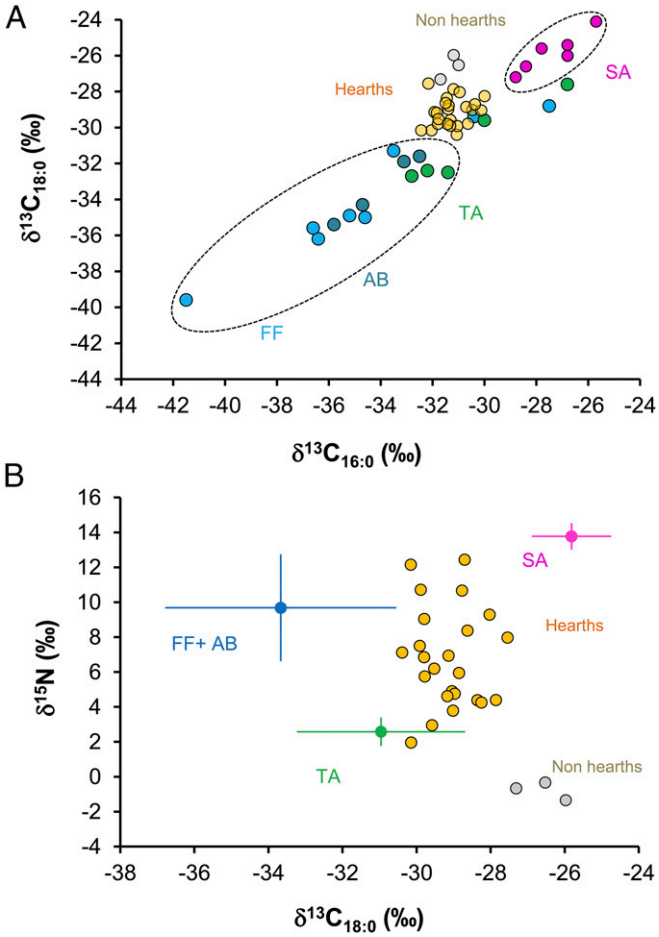

Fig. 3. $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values of lipids from USR hearth residues and modern reference animals (*A*) and $\delta^{15}N$ vs. $\delta^{13}C_{18:0}$ values from USR hearths and modern animals in Alaska (*B*). AB, aquatic bird; FF, freshwater fish; SA, salmon; TA, terrestrial animals. To allow comparisons between modern and archaeological data, $\delta^{13}C$ values of all modern samples were adjusted for the addition of the effects of postindustrial carbon (Table S2 and refs. 40–42).

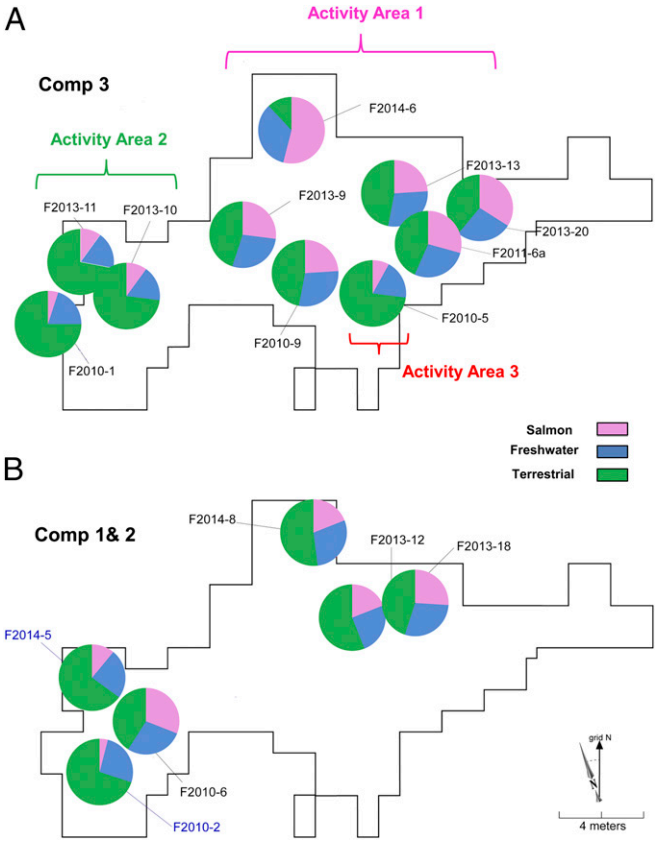

Fig. 4. The proportional contribution of three different food groups (terrestrial, freshwater, and salmon) to hearths in component 3 (*A*) and components 1 and 2 (*B*) in USR site. The pie chart represents mean values of the proportional contribution in case of multiple measured hearths and the contribution of hearth F2010-09 is estimated mean value based on only bulk $\delta^{15}N$ values. Three hearths (F2014-06, F2013-20, and F2013-09) in component 3 (≥45%) and one hearth (F2010-06) in component 2 (31%) have the highest contribution of salmon. There are three distinct activity areas in component 3: (*i*) salmon processing/disposal in hearths, (*ii*), terrestrial mammal processing/disposal, and (*iii*) both mammal and salmon processing at the indoor hearth F2010-05.

understanding the nature of salmon exploitation at USR component 3, as well as broader subsistence and seasonal patterns of early Beringians. Within component 3, six of the nine analyzed hearths (67%) contained Salmonidae at varying proportions. The hearths with the highest relative number of salmonids have the highest marine contribution estimated by using the stable isotope mixing model, further indicating that these were anadromous salmon (Figs. 4 and 5). This finding suggests more extensive use of salmon at multiple hearths in component 3. The variation in salmon processing based on chemical profiling and zooarchaeological analyses across the occupation suggests three distinct activity areas: (*i*) salmon processing/disposal in hearths surrounding the central residential feature (24–68% marine); (*ii*) terrestrial mammal processing/disposal in the hearth cluster to the west (5–10% marine); and (*iii*) both mammal and salmon processing within the central hearth (F2010-05) of the residential feature (9% marine) (Fig. 4). This central hearth yielded relatively low $\delta^{15}N$ values compared with neighboring hearths, despite salmon remains (22); however, this result is likely due to the larger relative contribution of terrestrial animals, including the human cremation (Figs. 4 and 5). Our chemical evidence for salmon/freshwater resource exploitation at the USR site is supported by the zooarchaeological data (this study) and genetic data from the fish bones, indicating large salmonids such as anadromous chum salmon (*Oncorhynchus keta*) (23). Because we observed multiple cranial and vertebrate parts within USR hearths, we suggest that the salmon were captured in low quantities and were consumed on site rather than dried/cached for later consumption. Thus, detritus from cooking and consumption activities adjacent to the hearths were incorporated into hearth sediments.

The results from the SIAR mixing model for component 2 hearths (Figs. 4 and 5) suggest that anadromous salmon were present at similarly high marine proportional values for all four hearths (19–31%) as Component 3 hearths containing salmonids. The faunal record of component 2 is markedly different from Component 3; there are few identifiable fauna present in the hearths (95 total NISP within two hearths, whereas the other hearths yielded no identifiable fauna) (Table S7). The similarities in high marine chemical signatures between components 2 and 3 are supported in part by similar hearth morphologies and content. In the Component 2 hearths, fauna is limited to burned remains disposed directly within hearths, which contrast with more typical hunting camp hearths in the region that did not contain bone-rich mealy concentrations within hearth matrices but did contain numerous low-yield large mammal elements scattered within and between hearths (24). Component 1 fauna are well-preserved, but no fish have been identified. The fauna are dominated by waterfowl and mammals (44). The very low SIAR mixing model estimates of the proportional contribution of salmon to these hearths (4–11%, with 95% CI overlapping with 0%) are consistent with the faunal data suggesting little or no salmon presence in this earliest occupation.

Intrahearth horizontal distributions of $\delta^{15}N$ values were consistent across each hearth (±1.8‰) (Fig. S3*A*). This pattern suggests that most USR hearths were used for specific activities. However, one hearth (F2013-20) had a wide range of $\delta^{15}N$ values (4.8–10.7‰), indicating that it was associated with a wide range of different food resources. Intrahearth vertical variation in $\delta^{15}N$ values may reflect some thermal variation of organic residues within each hearth. Bottom oxidized sediments had higher $\delta^{15}N$ values (mean 2.3‰) than the upper bone-rich layers. This finding may be associated with the concentration of organic molecules in bottom-oxidized layers by leaching or taphonomic process after cooking events. In addition, $\delta^{15}N$ values of extended occupation surfaces beyond hearths F2013-09 are similar to the hearth values (Fig. S3), indicating similar food-processing activities.

Interpreting chemical analysis of organic residues in hearths can be problematic because of the potential influences of diagenic

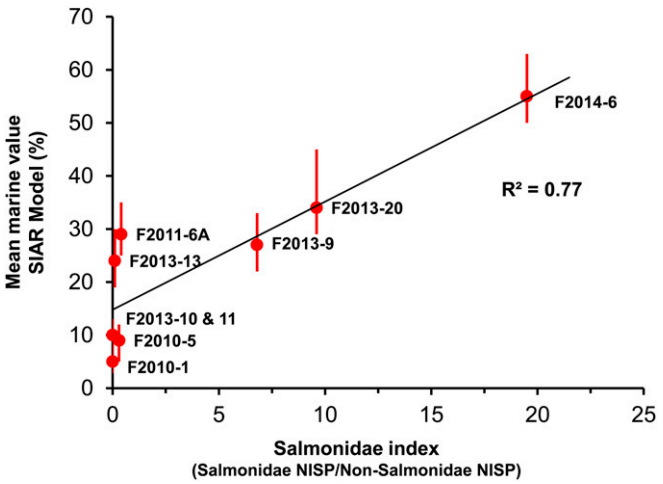

Fig. 5. Relationship between Salmonidae index values and the marine percent contribution (mean and 1 SD) in the SIAR model for each component 3 hearth.

agents, including thermal and microbial degradation (45). Food resources in hearths can also be difficult to discriminate because of the potential for admixture of fuel charcoal. Most previous studies have focused on the FA profiles, lipid biomarkers (13, 14), and $\delta^{13}C$ values of FAs from hearth residues (15, 46). Our bulk $\delta^{13}C$ values from all USR hearths were similar among all USR hearths (Fig. S1), and this result likely reflects the mixture of other carbon inputs into hearths, including fuel wood and the proportion of bone. However, our $\delta^{15}N$ data can separate animal-derived resources from the influence of wood charcoals and plant seeds. Fuel charcoals in hearths are unlikely to be a substantial contribution to the total nitrogen in the hearths because wood contains a negligible amount of nitrogen relative to animal resources. Our findings are consistent with analyses of modern archaeological sediments from a site on an Alaska island, where relatively high $\delta^{15}N$ values discriminated fish-processing areas from other activity areas at the site (26). Our research shows that by coupling $\delta^{15}N$ data with $\delta^{13}C$ values of two individual FAs ($\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$) from hearths, we could provide estimates of the proportional contribution of marine (anadromous salmonid), freshwater, and terrestrial resources to these hearths at an inland site (>1,000 km from coastal environments), where fish remains are not well preserved.

The inference of anadromous salmon use at component 2 represents the earliest evidence of salmon exploitation in the Americas, at ~11,800 cal y B.P., during the Younger Dryas. Collectively, components 2 and 3 data indicate patterned, recurrent use of the area for seasonal anadromous salmon fishing and processing and that aquatic resources were more important than previously thought during the Late Pleistocene-Early Holocene transition. Our findings reveal that analysis of organic residues from hearth sediments can have great utility for reconstructing dietary trends and subsistence practices among mobile hunter-gatherers, particularly in contexts where faunal remains are poorly preserved.

Materials and Methods

We collected hearth samples (~1g) from 17 archaeological hearths from three components at the USR site (Table S1). We also sampled from horizontal locations in a subset of hearths and in adjacent activity areas to investigate horizontal variation, and we sampled stratigraphic layers to investigate vertical variation within hearths (top, bone-rich, 10YR 3/6, layer; middle, charcoal-rich, 10YR 3/1, layer; bottom, oxidized, 5YR 2.5/2 layer) (Fig. S3*B*). For control samples, we included nonhearth sediments from the same stratigraphic layers as the hearths, but distant from any cultural material (Table S1 and Fig. S2). Comparative data for potential food resources were derived from: (*i*) 23 muscle samples from 16 modern species of fauna from central Alaska (Table S2), and (*ii*) 21 bone collagen samples representing 10 faunal species from USR components 1 and 3 (Table S3).

Bulk $\delta^{13}C$ and $\delta^{15}N$ values from analyses of hearth sediment, bone collagen, and muscle tissue samples were measured at the Alaska Stable Isotope Facility (ASIF), University of Alaska Fairbanks, following established protocols (ref. 37 and *SI Materials and Methods*). Lipids in hearth and muscle samples were extracted by using standard protocols (refs. 43, 47, and 48 and *SI Materials and Methods*). The lipid profile of each FAME product was identified by gas chromatography-mass spectrometry (GC-MS), and $\delta^{13}C$ values of two individual FAs (C16:0 and C18:0) from hearth and muscle samples were analyzed by GC-combustion-isotope ratio spectrometer (GC-C-IRMS) at ASIF (*SI Materials and Methods*).

We categorized food resources into three food groups: marine (anadromous salmon), freshwater (i.e., freshwater fish and aquatic birds, e.g., mallard, teal, wigeon, and goose), and terrestrial (i.e., terrestrial mammals and terrestrial birds, e.g., spruce grouse and ruffed grouse). A nonparametric Kruskal–Wallis ANOVA followed by Bonferroni adjustment for multiple comparisons was used to test for differences between each food group and between hearths. Spearman's correlation was used to examine the relationship between each food group and between hearths. We incorporated the $\delta^{15}N$, $\delta^{13}C_{16:0}$, and $\delta^{13}C_{18:0}$ values of the hearths and food groups as well as burning enrichment factors ($\delta^{13}C$ ±0.1‰ and $\delta^{15}N$ ±0.3‰) (49) and concentration dependencies (50) in a SIAR mixing model to estimate the proportional contribution of the three food groups (marine, freshwater, and terrestrial) to each hearth (*SI Materials and Methods*).

All hearth matrices were collected by strata and 50 × 50-cm^2 horizontal quadrants and screened in the laboratory through an ASTM no. 16 sieve (1.18-mm mesh). The resulting faunal assemblage comprised small, calcined, and highly fragmented specimens. Fish remains were differentiated from birds and mammals based on skeletal morphology and vertebral fenestration patterns, which could be identified to the level of Salmonidae. The teeth and better-preserved vertebrae fragments of the large salmonids were consistent in size and morphology with the *Oncorhynchus* sp. described in the cremation feature (F2010-05) (21, 22). The NISP was calculated by using the method in Lyman (51) and is based on identifiability at the class level. Terrestrial fauna and Salmonidae NISP were used to generate a Salmonidae index for each hearth (Salmonidae NISP/non-Salmonidae NISP).

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