Early human use of anadromous salmon in North America at 11,500 y ago

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Salmon represented a critical resource for prehistoric foragers along the North Pacific Rim, and continue to be economically and culturally important; however, the origins of salmon exploitation remain unresolved. Here we report 11,500-y-old salmon associated with a cooking hearth and human burials from the Upward Sun River Site, near the modern extreme edge of salmon habitat in central Alaska. This represents the earliest known human use of salmon in North America. Ancient DNA analyses establish the species as *Oncorhynchus keta* (chum salmon), and stable isotope analyses indicate anadromy, suggesting that salmon runs were established by at least the terminal Pleistocene. The early use of this resource has important implications for Paleoindian land use, economy, and expansions into northwest North America.

salmon | Paleoindians | Beringia | ancient DNA | stable isotopes

Each year along the Pacific coast of North America, millions of salmon migrate from the ocean to spawn and die in their natal rivers and lakes; however, during the last Ice Age, many of the rivers that today support salmon were blocked by glacial ice, severely restricting salmon ranges (1). A potential glacial refugium for salmon was Beringia, the mostly ice-free landmass that bridged northeast Asia and Alaska (1–3). Evidence for such a refugium comes from studies of present-day diversity and distributions of Pacific salmon (1, 2), but there is little direct evidence of the antiquity of salmon spawning runs in North America. Here we confirm the presence of an anadromous salmon species, *Oncorhynchus keta* (chum salmon) through ancient DNA (aDNA) and stable isotope analyses of fish remains at the Upward Sun River site located deep in the interior of Alaska, about 50 km downstream from the modern limit of major spawning areas (Fig. 1). These specimens, dating to the terminal Pleistocene, represent the oldest genetically confirmed Pacific salmon species in an archaeological context in North America. These data are important for testing competing models of subsistence strategies and diet breadths of Paleoindian populations in the New World (4, 5), as well as for understanding Beringian ecosystem biodiversity.

Oncorhynchus is a salmonid genus that includes several Pacific salmon and Pacific trout species; some species of this genus occur as both freshwater resident and anadromous forms, migrating from the sea to freshwater to spawn (6). The spawning behavior of anadromous Pacific salmon results in massive and predictable runs in freshwater streams over a short period, making these fish a potentially valuable human food resource (7). Salmon are also ecologically important because they transport rich marine-derived nutrients into relatively unproductive interior riparian areas (8). Five species of Pacific salmon and one species of Pacific trout presently occur in central Alaskan waters, including Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), chum (*O. keta*), sockeye (*Oncorhynchus nerka*), pink salmon (*Oncorhynchus gorbuscha*), and rainbow/steelhead trout (*Oncorhynchus mykiss*) (1).

Pleistocene-aged remains of Pacific salmon from North America are extremely rare in both paleontological and archaeological contexts. This scarcity is related in part to the spawning habitat of most salmon species, leading to death in river gravels where remains are unlikely to be preserved (9) and to the fragility of fish skeletal elements and their small size (inhibiting recovery), resulting in their underrepresentation in the archaeological record (10). Paleontological specimens of Pacific salmon have been recovered from middle Pleistocene sediments in the Skokomish Valley, Washington (United States) (9), and from late Pleistocene sediments at Kamloops Lake, British Columbia (Canada) (11). Although the remains from both of these locales were morphologically identified as *O. nerka*, carbon stable isotope analysis of specimens from Kamloops Lake suggests that the fish were likely the landlocked form of *O. nerka*, known as kokanee (11). Other late Pleistocene paleontological fish remains assigned to Pacific salmon derive from two additional sites in British Columbia, including Courtenay (Vancouver Island) and Gaadu Din 1 cave (Haida Gwaii) (12, 13). Specimens from the latter site were genetically identified as "salmon," but the details of the aDNA analysis were not reported (13).

The only report of *Oncorhynchus* remains from a Pleistocene-age archaeological site in North America comes from Upward Sun River, located adjacent to the Tanana River (a major tributary of the Yukon River) in central Alaska (14) (see also *SI Text*) (Fig. 1). Here, 308 *Oncorhynchus* specimens were recovered from the central hearth of a residential feature, also associated with a cremated 3-y-old child (15). A double infant burial with associated grave goods was located directly below (40 cm) this hearth. Radiocarbon and contextual data suggest near contemporaneity between the hearth

Significance

Fish bones from the 11,500-y-old Upward Sun River site in interior Alaska represent the oldest evidence for salmon fishing in North America. We used ancient DNA analysis to identify the fish specimens as chum salmon (*Oncorhynchus keta*), and stable isotope analysis to confirm that the salmon were anadromous (sea-run). The exploitation of salmon at this early date is noteworthy because Paleoindians are traditionally portrayed as big-game hunting specialists. Furthermore, the presence of salmon at Upward Sun River over 1,400 km upriver from the coast shows that spawning runs had been established by the end of the last Ice Age. The early availability and use of anadromous salmon has important implications for understanding Paleoindian economies and expansion into North America.

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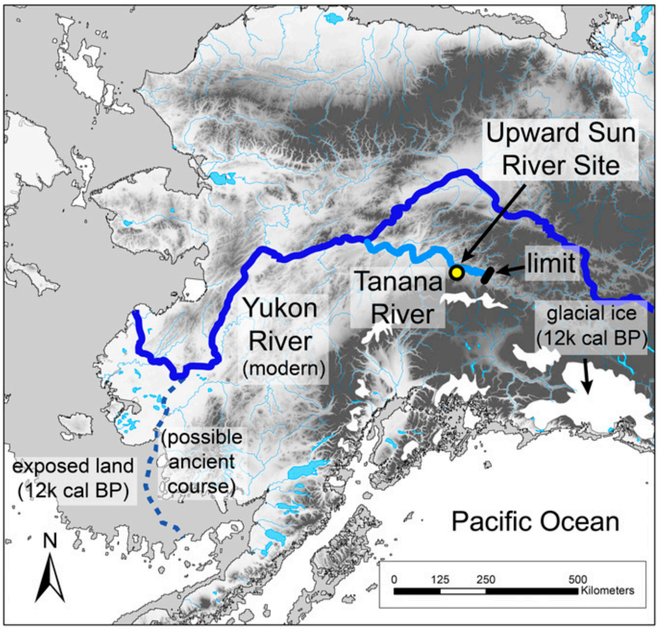

Fig. 1. Location of Upward Sun River Site, course of the Tanana-Yukon River and possible course across the Bering Shelf during lower sea level, and modern chum salmon fall spawning limit along the Tanana River. Details are provided in *SI Text*.

and the burial pit, with a mean pooled age of 9,970 ± 30 B.P. (11,600–11,270 cal B.P.); thus, these represent the oldest known human remains in the North American Arctic/Subarctic (Fig. 2 and *SI Text*). A total of 29 additional *Oncorhynchus* specimens were found within the pit fill. The fish remains were mostly fragmentary and over 90% were burned and calcined. The component and burials are culturally affiliated with the Denali Complex, which was widespread in Eastern Beringia from ∼12,700 cal B.P. to the early Holocene (3, 16).

The fish vertebrae were morphologically identified as *Oncorhynchus* using a modern comparative collection based on their large size, fenestration pattern, and characteristic shape (17) (Fig. 2). Based on overall size and occupation season, based on other fauna, the vertebrae resembled *O. keta* (Fig. S1 and Table S1); however, species-level identifications based on morphology remain ambiguous without genetic confirmation (18, 19). Species distinctions are critical to separate salmon from trout and other salmonids, because although some other members of this family are anadromous, they do not typically form the extensive and massive spawning runs that make salmon such an exceptional resource (6, 20). Additionally, salmon species differ in habitat requirements, run timing and abundance, and body size and fat content, all of which have implications for understanding past human land use and subsistence strategies (18, 19, 21, 22). aDNA analysis provides more accurate identifications of fish remains, and has recently been successfully applied to fish assemblages from Holocene archaeological sites in the Pacific Northwest of North America (18, 19, 23, 24).

Genetic identification cannot resolve questions about anadromy because salmon life history pattern is variable. Most Pacific salmon stocks are anadromous; however, natural or introduced freshwater stocks also occur for all species except chum, and captive chum have been reared to maturity in fresh water (25). Stable isotope analysis is an appropriate technique for distinguishing between anadromous and nonanadromous salmon because the isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are typically elevated in marine compared with freshwater food consumers (26). This technique has been successfully applied to identify life history patterns in modern salmonid stocks (27–30).

To address the questions of taxonomic identification and life history of the Upward Sun River *Oncorhynchus* specimens, we subjected two unburned vertebral specimens (58-18 and 58-30) to aDNA analysis, one of which (58-18) was also subjected to carbon and nitrogen stable isotope analysis (*SI Text* and Table S1). An unsuccessful attempt was also made to analyze DNA from a third specimen (H-5446), a nearly complete but calcined vertebra. The three specimens shared the distinctive morphological and overall size characteristics of the larger number of burned and fragmented *Oncorhynchus* specimens.

Results and Discussion

DNA was extracted from the specimens following established methods (*SI Text*). The extracts for the unburned specimens were successfully PCR-amplified and sequenced for a region of the mitochondrial 12S gene that is useful for discriminating among Pacific salmonids and other fishes (31) (*SI Text*). Repeated sequence analysis demonstrated the samples to be *Oncorhynchus keta* (chum salmon) (Table S2). Additionally, one sample (58-18) was analyzed at an independent aDNA laboratory using discriminating fragments of the d-loop and cytochrome *b* regions of the salmonid mitochondrial genome (22), confirming the identification made with 12S (*SI Text*, Figs. S2–S4, and Table S3). Thus, repeatable and independent analyses of mitochondrial DNA (mtDNA) demonstrate that both samples are chum salmon.

Stable isotope analysis of bone collagen extracted from one of the confirmed *O. keta* vertebra produced $\delta^{13}C$ and $\delta^{15}N$ values of −15.1‰ and 12.6‰, respectively (*SI Text*). These values are consistent with previously reported isotope values for ancient and modern salmon from Alaska, and are elevated over those for ancient and modern freshwater fishes (Fig. 3 and Tables S4 and S5). These data indicate that the Upward Sun River chum salmon specimen was anadromous.

The confirmed presence of an anadromous Pacific salmon species, *O. keta*, at the terminal Pleistocene Upward Sun River site provides the earliest evidence for human use of salmon in North America, and adds to our understanding of Paleoindian adaptations. Previous reports of genetically identified Pacific salmon

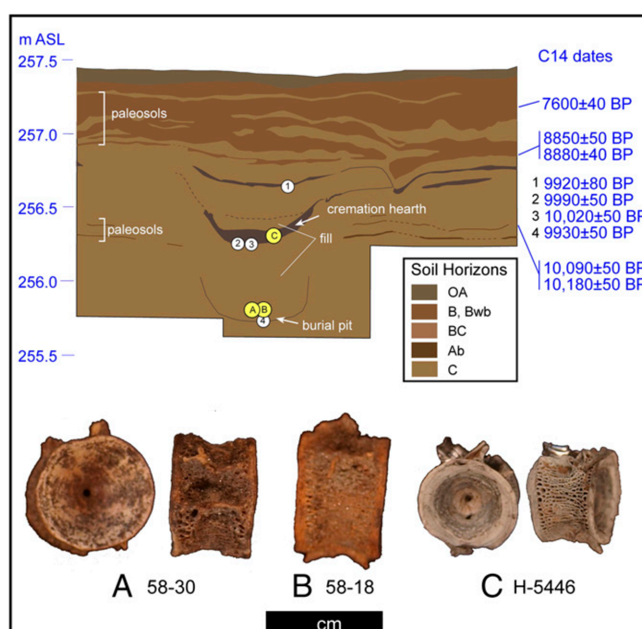

Fig. 2. Upward Sun River stratigraphy, chronology, and aDNA and stable isotope bone samples. Details provided in *SI Text* and Table S1.

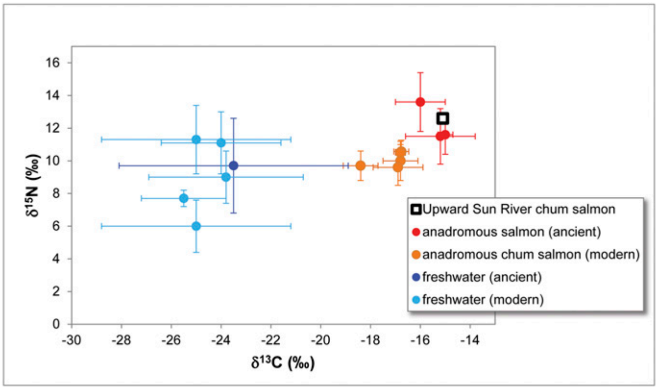

Fig. 3. Stable isotope values for the Upward Sun River sample compared with published values for ancient and modern anadromous and freshwater fishes in Alaska. Modern values have been adjusted for tissue offsets (muscle to bone collagen) and for the Suess effect (reduction of $\delta^{13}C$ in carbon reservoirs from industrial carbon emissions). Details provided in *SI Text* and Tables S4 and S5.

remains from archaeological sites date to as old as ∼6610–5940 cal B.P. from Namu on the central coast of British Columbia (23), and to as old as 9300–8200 cal B.P. for morphologically identified salmon from the Dalles Roadcut site on the Columbia River (32). Pacific salmon remains have not been previously reported for a late Pleistocene-age site, and, indeed, fish remains of any kind are rare in sites for this period in the Americas. In a broad review of taxa exploited by early Paleoindians (33), only two sites (Aubrey and Shawnee-Minisink) had evidence of fish (with no further taxonomic identification) in strong association with human occupation, though abundance values were low. Recently, Erlandson et al. (34) reported 78 specimens (1.4% of total) of various fish taxa (none are salmon) at three Paleoindian sites on the Channel Islands, California.

In Beringia, there is additional evidence for fish exploitation, particularly during the Younger Dryas (16). In central Alaska, Broken Mammoth Cultural Zone 3 (∼12,080 cal B.P.) contained 28 salmonid specimens (possibly grayling) (35), and Mead Cultural Zone 3 (∼11,990 cal B.P.) contained unidentified fish remains (16). In Kamchatka (Russia), Ushki 1 Level 6 (∼12,160 cal BP) contained an unspecified number of burned fish bones (possibly salmon) within houses (36). The salmon data from Upward Sun River reported here add an important component to Paleoindian diet breadth, with implications for seasonal exploitation and possibly storage that is markedly different from multiseasonal exploitation of freshwater fish.

Although Paleoindians are traditionally portrayed as specialist big-game hunters, evidence from Upward Sun River and other early sites in Beringia increasingly suggests a diversity of subsistence strategies, which included hunting, gathering, and fishing. Although the degree of reliance on salmon by early Beringians is currently unresolved, historically in subarctic Alaska, salmon were taken in great numbers in summer to early fall for drying and storing through the winter (37). The extent of salmon storage among early Beringians is also unknown, but chum are well suited for preservation because of their low oil content relative to other salmon species (23).

Our findings have important implications for the paleoecology and human colonization of Beringia and the Americas. Of the 40 earliest known components in northwest North America (dating between 14,000 and 11,500 cal B.P.) (16), 36 (90%) are located in the interior and the majority (60%) are associated with large interior river bottomlands, suggesting the importance of riverine resources to early foragers. Our data show that at least by 11,500 cal B.P., salmon had established spawning runs in the deep interior of eastern Beringia near their current limit of migration, an upriver distance of over 1,400 km from the current mouth of the Yukon, plus an additional ∼300 km of river on the exposed gradually sloping Bering Sea shelf (38) (Fig. 1). The addition of salmon to the early subsistence record further indicates that interior eastern Beringia was a productive landscape in the terminal Pleistocene, supporting a variety of large and small terrestrial mammals, waterfowl, and other fish. This resource diversity contrasts with the assumptions of very low resource availability in inland ecosystems in debates about New World migration corridors (39, 40).

Modern ocean foraging areas for chum salmon include the Bering Sea and the subarctic North Pacific Ocean. Although suitable salmon habitat was likely available in this region throughout the Late Pleistocene, during intervals within glacial periods habitat was probably suboptimal, and especially so near coastal areas surrounding the Bering Sea and the northern Gulf of Alaska (41, 42). Recent paleoceanographic data show that conditions improved dramatically between ∼17,000 and 13,000 cal B.P., depending on indicator and location, in terms of warming sea-surface temperatures, reduced cover of seasonal sea ice, and increased primary productivity (41, 42). River migration access and spawning habitat in the lower Yukon River basin during the Late Pleistocene was probably not an impediment to salmon, as it was not glaciated, even at maximum glacial extent (38, 43). These observations suggest that ocean habitat and migration barriers to Yukon-Tanana salmon were not substantial during the period of early human colonization. Given this, salmon may have been an important resource to earlier Paleoindian subsistence economies and may have played a role in the biogeographic expansions of humans into northwest North America.

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ANTHROPOLOGY