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Spawning sockeye salmon fossils in Pleistocene lake beds of Skokomish Valley, Washington

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Abstract

An assemblage of fossil sockeye salmon was discovered in Pleistocene lake sediments along the South Fork Skokomish River, Olympic Peninsula, Washington. The fossils were abundant near the head of a former glacial lake at 115 m elevation. Large adult salmon are concentrated in a sequence of death assemblages that include individuals with enlarged breeding teeth and worn caudal fins indicating migration, nest digging, and spawning prior to death. The specimens were 4 yr old and 45–70 cm in total length, similar in size to modern sockeye salmon, not landlocked kokanee. The fossils possess most of the characteristics of sockeye salmon, *Oncorhynchus nerka*, but with several minor traits suggestive of pink salmon, *O. gorbuscha*. This suggests the degree of divergence of these species at about 1 million yr ago, when geological evidence indicates the salmon were deposited at the head of a proglacial lake impounded by the Salmon Springs advance of the Puget lobe ice sheet. Surficial geology and topography record a complicated history of glacial damming and river diversion that implies incision of the modern gorge of the South Fork Skokomish River after deposition of the fossil-bearing sediments.

Keywords: Fossil salmon; Sockeye; Skokomish River; Washington

Introduction

Four species of salmon are known from Miocene deposits in northwestern United States. Two of the species belong to the extinct tusk-tooth salmon group related to sockeye salmon—*Oncorhynchus* (*Smilodonichthys*) *rastrosus*, from Oregon, California, and Washington (Cavender and Miller, 1972; Smith et al., 2000) and its dwarf, landlocked relative from Idaho (Smith et al., 1984). Two species with more modern traits, related to sockeye and chum salmon, are known from late Miocene sediments of the Chalk Hills Formation of Oregon and Idaho (Eiting and Smith, 2007). Salmon other than sockeyes are uncommon in the fossil record because of their anadromous spawning habitat, leading to death in gravels of degradational environments unlikely to be preserved in a sedimentary or fossil record. Non-migratory salmonids also occur in Cenozoic lacustrine deposits of western North America. Fossil chars occur in Miocene sediments of Nevada, Idaho, and Oregon (Smith et al., 1984, 2002; Smith and Miller, 1985). Trout occur in the Late Miocene to Pleistocene of Mexico, Idaho, Oregon, New Mexico, Colorado, and Utah (Cavender and Miller, 1982; Smith et al., 1984, 2002; Rogers et al., 1985). The oldest North American member of the salmon and trout clade is *Eosalmo driftwoodensis*, from the Eocene of British Columbia (Wilson, 1977; Wilson and Li, 1999).

Fossil salmon are unknown from the rich geological record of Washington, except for specimens of tusk-tooth salmon collected by Eric Gustaffson from the Late Miocene lower Ringold Formation east of the Columbia River at White Bluffs (Smith et al., 2000). Curiously, the abundant fossil fishes from the Late Pliocene upper Ringold Formation of Washington include sturgeon, catfish, minnows, suckers, muskellunge, and

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sunfish, but no salmonids (Smith et al., 2000), while the contemporaneous Miocene and Pliocene beds of the western Snake River Plain, Idaho and Oregon, above Hells Canyon, contain a diversity of salmon, trout, chars, and whitefish (Smith et al., 1984), probably in higher elevation, colder waters.

In August 2000, Jeff Heinis and Summer Burdick discovered fossil salmon along the banks of the Skokomish River in Mason County, Washington, in forested property of the Simpson Resource Company (now the Green Diamond Resource Company) of Shelton, Washington. The discovery was brought to the attention of paleontologists of the Burke Museum of the University of Washington, who collected and prepared numerous specimens. Additional collection and research was kindly encouraged and supported by the Green Diamond Resource Company. Here we describe and identify the fossil salmon, with geological interpretation of the age, habitat, environment of deposition, climate, and behavior of the fish at the time of death and preservation.

Methods

Slabs of sediment with compressed salmon and salmon bones were collected by Jeff Heinis, James Goedert, Keith Smith, Carol Serdar, and the authors. Geological and paleobotanical work, respectively, was conducted by David Montgomery and Estella Leopold of the University of Washington. Fish bones were compared and identified in the Museum of Zoology, University of Michigan. Eighteen 2-cm cubes of tephra-rich clay were carved out of layers about 1 m apart (with duplicates) from two outcrops and marked with vertical orientation and compass direction for paleomagnetic analysis. Josep Pares of the Paleomagnetics Laboratory of the University of Michigan conducted analysis of magnetic polarity of sediment samples including demagnetization to remove any magnetic overprint. Clean, unaltered vertebrae and teeth were selected for oxygen isotopic analysis, which was conducted by William Patterson, Antoine Zazzo, and Elise Dufour of the Isotope Laboratory, Department of Geological Sciences, University of Saskatchewan (Zazzo et al., 2006).

Geological setting

The Skokomish River flows from the Olympic Mountains southeast to Puget Sound (Fig. 1). Continental glacial deposits cover the grooved, glacially scoured upland surface into which the modern South Fork of the Skokomish River flows through a >100-m-deep gorge incised into the underlying basalt of the Eocene Crescent Formation. Evidence for older, pre-Fraser continental glacial deposits extends farther SW than does the limit of Fraser-age continental glacial deposits. The salmon fossils were discovered in isolated, previously unmapped, lake deposits outcropping along the South Fork of the Skokomish River, below Holocene alluvium inset about a hundred meters below a low-relief upland surface formerly and repeatedly occupied by the Puget lobe of the Cordilleran ice sheet. The fossil-bearing outcrop is located about 3 km WSW of similar lake sediments reported in Frigid Creek (Westgate et al., 1987), near the southwestern margin of the Fraser age advance of the Puget lobe ice sheet (Fig. 2). The fossil-bearing outcrop lies several hundred meters upstream of the head of the modern

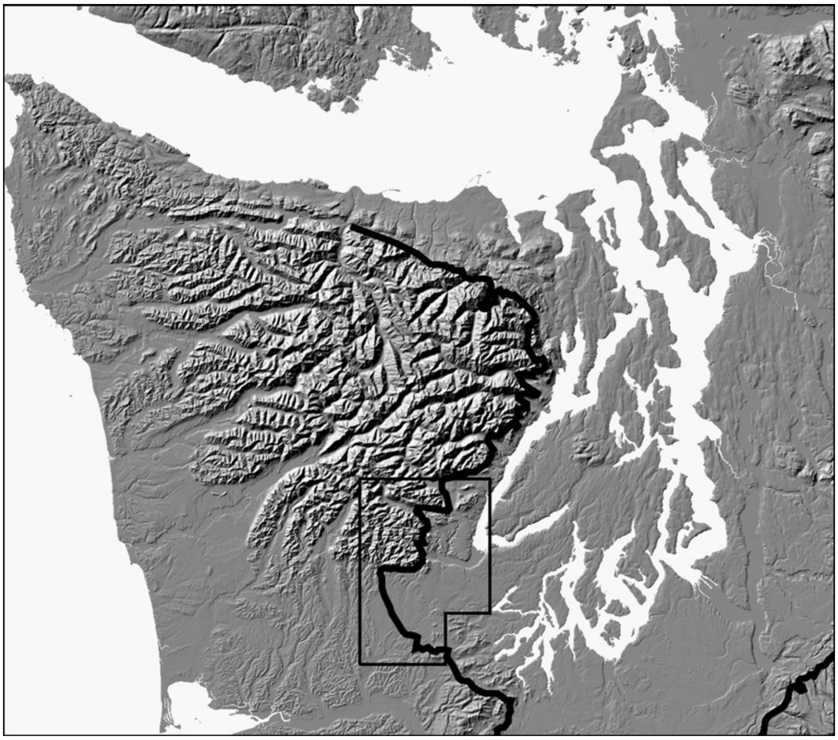

Figure 1. Location map of the study area in the Olympic Peninsula, Washington, showing extent of the Puget lobe during the Vashon stade of the continental Fraser glaciation, based in Thorson (1980). Inset box shows extent of Figure 2.

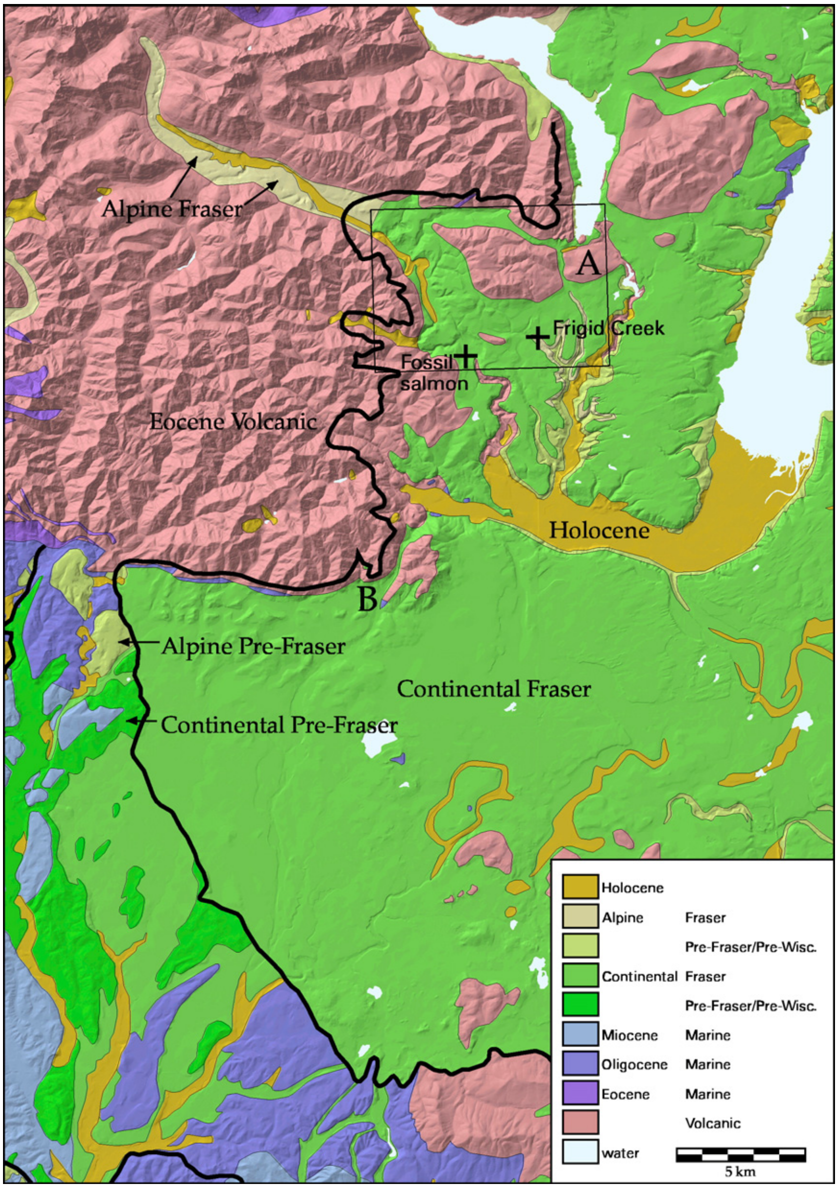

Figure 2. Geological map of the southeastern Olympic Peninsula draped on shaded relief portrayal of a 10-m grid digital elevation model showing location of the fossil locality in relation to extent of the Puget lobe glacier, rivers, and Pleistocene Frigid Creek lake beds. Geological map and margin of Fraser and pre-Fraser advances of the Puget lobe (thick black lines) based on Washington Department of Natural Resources, Division of Geology and Earth Resources, Digital Geologic Mapping Project by C.F.T. Harris (1998) and R.L. Logan (2003). Box shows location portrayed in Figure 8.

gorge. The fossil site is probably not far from the ancient ice front because downstream from the fossil fish locality a thin till (probably Vashon) lies on top of bedrock (Fig. 2).

Fossil site

At the fossil fish site, basal sediments begin at 115 m elevation. The section of lake sediment at this site extends at least several meters upward to an unconformity with overlying Holocene alluvium. Exposure of the lake sediment section increases downstream to >10 m immediately upstream of the entrance to the gorge on the South Fork Skokomish River. Fossil fish bones are restricted to the basal section of the laminated lake sediments. Near the base, varves (Fig. 3) vary in thickness between 2 and 20 mm, and average about 7 mm thick. The varves are tan near where the lake beds contact the underlying basaltic stream gravel, and consist of couplets of dark/light-gray silt-size grains where exposed farther downstream.

The fossil site is near the head of the lakebeds where they lap onto foreset stream gravels of a small delta deposit (Fig. 4). The elevation of the contact between the lakebeds and the foreset gravels fluctuates up- and down-stream several meters at the site (Fig. 4). The thickest concentration of fish carcasses is within about 2 m of the delta gravels, horizontally, at the base of the section of lake sediments. Downstream from this concentration, which includes nearly whole fish, only disarticulated vertebrae, skull bones, fins, and patches of scales are found in decreasing abundance for several tens of meters (Fig. 4). Articulated

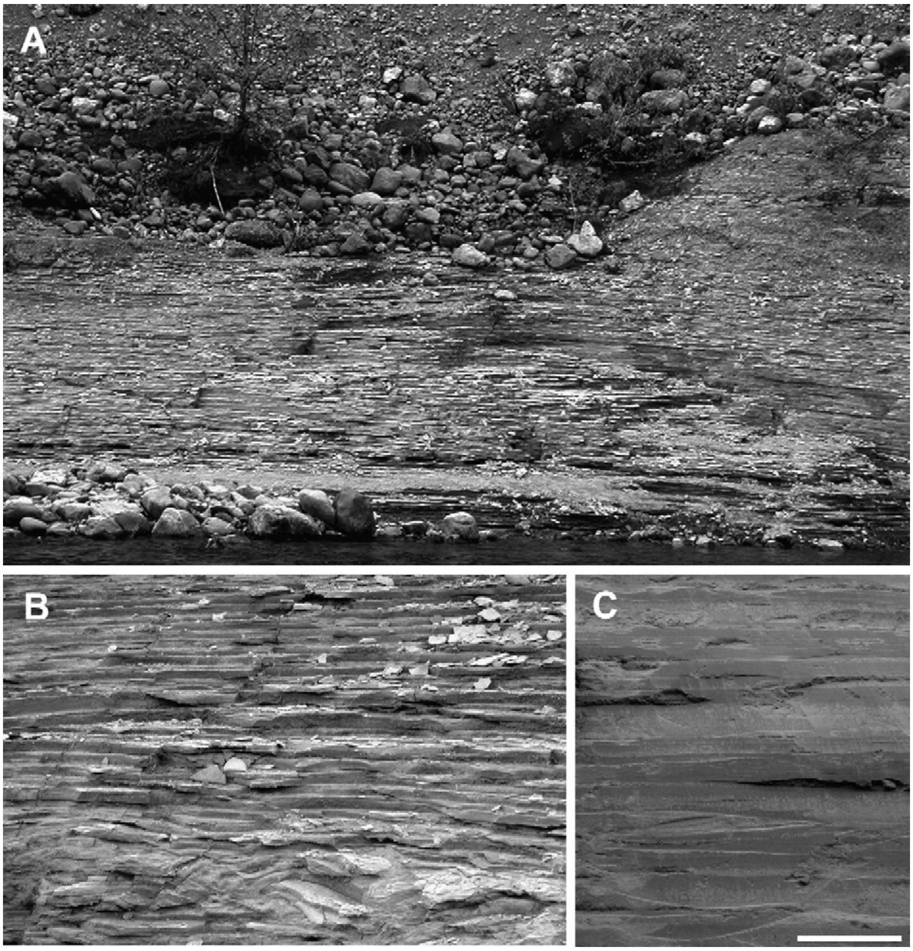

Figure 3. Varves exposed in the fossil-bearing outcrop. (A) Several meters of exposed varves. (B) Weathered varves; 1-m section. (C) Scraped and brushed varves showing fining upward texture within couplets; scale = 5 cm.

specimens also grade upward into disarticulated parts, presumably as the contact between lake and stream migrated upstream during filling of the lake. The gradient from abundant articulated specimens to sparse disarticulated specimens, away from the lacustrine-fluvial contact, suggests that the fish were dying and accumulating in the reduced-energy zone at the head of the lake below the stream delta. An estimate of the number of fish-rich varves suggests that this particular site was visited by fish for no more than 70 yr, assuming the varves represent annual deposits.

Figure 4. Lake beds (left, downstream), lapping onto deltaic sediments at the upper end of the lake, several meters upstream from the site of Figure 3.

Higher on the west wall of the valley, at an elevation of about 160 m, there is a small outcrop of similar tan lacustrine clays, although with no observable laminae or fish. The relationship between the two outcrops is obscured by younger inset alluvial terraces and floodplain deposits. However, any intervening lake sediments are either absent or covered by younger Holocene alluvial terrace deposits.

Reconnaissance mapping of surficial deposits indicates that continental glacial deposits, which are readily distinguishable from local alpine glacial deposits by the presence of exotic granitic clasts, blanket the upland surface up to at least 300 m elevation. In our reconnaissance mapping we were unable to locate exposures of the contact between the lake sediments and the continental glacial deposits, but the lake sediments consistently occur at lower elevations, and R. L. Logan (2006, personal communication) reports that there is a contact between overlying granitic clast-bearing till and varved lake sediment at NE1/4 SE1/4 Sec 9 22N/5W. Radiocarbon dates obtained on wood recovered from the lower, middle, and upper portions of the fossil-bearing outcrop were all older than the limit of radiocarbon dating (i.e., >40 ka), indicating that the lake sediments predate the most recent advance of the Puget lobe. It remains uncertain as to whether the upper exposure of lake sediments is younger than, and inset into, or correlative with the fossil-bearing outcrop exposed along the Skokomish River.

The thickness of the lake sediments and the average varve thickness can be used to estimate the longevity of the lake by adopting the common assumption that each varve couplet represents an annual cycle. Using an average varve thickness of 7 mm conservatively estimates the >10 m of exposed lake section in the bottom of the valley to represent >1400 yr of sedimentation. Assuming that the lake sediments exposed at 160 m elevation on the valley walls are correlative with the fossil-bearing lake sediments implies an approximately 45-m-thick section, which would correspond to a lake duration >6400 yr, a surprisingly long duration for a glacial impoundment near the southern terminus of the Puget lobe. We favor the interpretation that the lake sediments represent two distinct glacial advances, with the higher elevation, several-meter-thick exposure corresponding to a relatively brief impoundment, because Porter and Swanson's (1998) chronology for the most recent (Fraser) advance of the Puget lobe indicates that ice would have dammed the Skokomish River for several centuries at most.

The fish-bearing lake beds along the South Fork of the Skokomish River are approximately correlative with the Frigid Creek lake beds in a sister tributary, 3–5 km to the east at about the same elevation, and which contained 1-Ma-old Lake Tapps tephra. Previous work by Westgate et al. (1987) suggested that the tephra was deposited "into a deep glacial lake that may have formed behind a moraine related to the underlying Olympic till, a possibility suggested by basalt dropstones, which point to a provenance in the Olympic Mountains. Alternatively, the moraine may have been built by the Puget lobe, or the lake simply may have formed in front of the western margin of the Puget lobe due to blocking by that glacier of eastward-flowing drainage from the Olympic Mountains" (Westgate et al., 1987, p. 352). Field evidence for the latter interpretation is apparent in a streambank exposure in the NE1/4 SE1/4 Sec 9 22N/5W, where a granitic clast bearing till rests directly on and locally deforms laminated silt lakebeds (R. L. Logan, 2006, personal communication). As the fossil-bearing lake sediments are older than the resolution of radiocarbon dating, and thus pre-date the most recent advance of the Puget lobe, we correlate the fossil-bearing outcrop with the Frigid Creek lake sediments. Paleobotanical evidence confirms that the salmon fossil-bearing sediments accumulated during a cold, glacial climate. Most diagnostic were several cones and numerous needles from Lodgepole pine (*Pinus contorta*) recovered from lake sediments several tens of meters downstream from the fossil salmon. The fossil site is currently occupied by a Western hemlock (*Tsuga heterophylla*) forest zone and upstream at higher elevations Silver fir (*Abies amabilis*) and Mountain hemlock (*Tsuga mertensiana*) (Henderson et al., 1989). Lodgepole pine is virtually unrepresented in all of these present day forest series. Although pollen preservation was poor in the lake sediments, what little was obtained from samples was consistent with a Lodgepole pine dominated community (E. Leopold, personal communication, 2005). Previous palynological work in the Olympic Peninsula (Whitlock, 1992) found Lodgepole pine to be associated with cold, pro-glacial conditions, confirming a glacial or near-glacial climate at the time when the lake existed.

Paleomagnetic analysis

Easterbrook et al. (1981, 1988) and Westgate et al. (1987) obtained fission-track dates of the Lake Tapps Tephra and paleomagnetic polarity in Frigid Creek lake beds to estimate an early Pleistocene ("Salmon Springs" of Crandell, 1963) age for the lake sediments there. The correlative exposures of Lake Tapps tephra-bearing sediments at Sumner and Auburn have reversed magnetic polarity except for two samples at the top of the Auburn section, which show fluctuations. The Lake Tapps tephra is interbedded between two drift deposits of the Salmon Springs glaciation at Lake Tapps and at Frigid Creek; fission-track dates on the tephra range from 0.65 to 1.06 Ma, with most of the estimates between 0.84 and 0.90 Ma (Westgate et al., 1987), supporting an age interpretation within the Matuyama epoch. A series of preliminary samples of lacustrine clays bearing the fossil fish have normal magnetic polarity at the fish level (suggesting the Jaramillo normal event, 1.04–0.98 Ma), possibly transitional higher in the section, and normal at the top. These results are more or less consistent with those obtained in the Frigid Creek section.

Salmon identification

Specimens were diagnosed as Pacific salmon, *Oncorhynchus*, by the large body sizes, up to 70 cm in total length (Fig. 5C), small scales compared to salmonids in general (Figs. 7C, D), small dorsal fin usually with 12–13 rays (Figs. 5A, C), large anal and caudal fins (Fig. 5A), anal fin with 14 or more rays (Fig. 7D), large adipose fin (Figs. 5C, 7B), elongate postorbitals reaching posteriorly to near the preopercle (Figs. 5B,

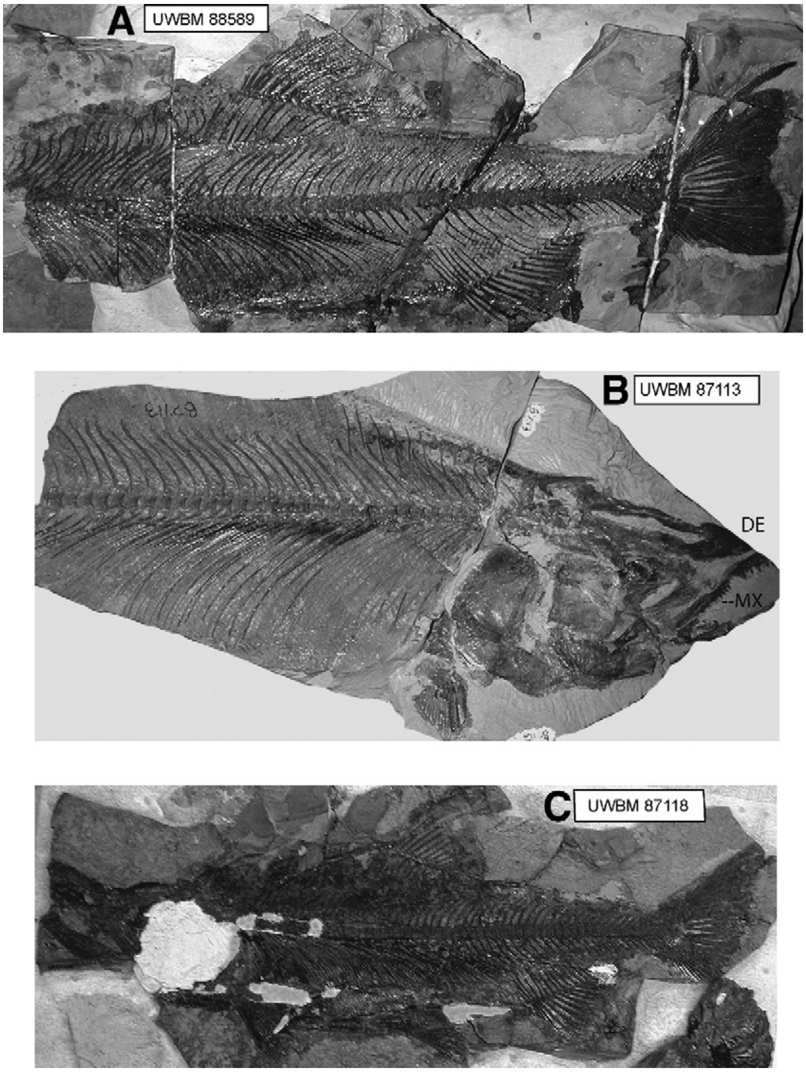

Figure 5. Three well-preserved Skokomish fossils showing the intermediate elevated back; in this trait, the fossils are more like Sockeye Salmon than Pink Salmon, in which present-day males have a more extremely elevated back. (A) UWBM 88589, showing 12 dorsal rays, 15 anal rays, and ca. 61 or 62 vertebrae, counts typical for most Pacific salmon except pink and Chinook salmon which usually have more vertebrae. (B) UWBM 87113, showing ca. 25 abdominal vertebrae (See also Fig. 6B). (C) UWBM 87118, male, showing ca. 12 dorsal rays, ca. 14 or 15 anal rays (see Fig. 7), standard length 62 cm, total length ca. 71 cm.

6E), and elongate jaws with mostly single rows of rather small teeth except for the enlarged breeding teeth on the premaxilla and anterior part of the dentary (sometimes with a secondary tooth row) (Figs. 6A, C, D). Pacific trout, including steelhead, *Oncohrynchus mykiss*, and chars have smaller anal fins, with fewer than 13 principle rays. All other salmonids have smaller post-orbitals, not reaching near the preopercles (Stearley and Smith, 1993). The enlarged teeth on the hooked premaxillae and anterior ends of the dentaries are characteristics of Pacific salmon (Figs. 6A, D). The observed traits firmly establish the fossils as salmon in the genus *Oncorhynchus*.

Among Pacific salmon, two groups are recognized. Chinook, Coho, and Masou Salmon have curved maxillae, which are concave ventrally. Chum, Pink, and Sockeye Salmon, have rather straight maxillae (Hikita, 1962). The Skokomish salmon have unambiguously straight maxillae like the latter group (Figs. 5B, 6A, C, D). The most salient osteological feature that diagnoses pink and sockeye from chum salmon is the presence of small teeth on the maxilla of pink and sockeye salmon, a feature also of the fossils (Figs. 6A, C, D); chum salmon have larger teeth.

The shapes of the dentary teeth, preopercle, dermethmoid, and frontals (Figs. 5, 6; Table 1) and the absence of an elevated back behind the skull, distinguish sockeye from pink salmon. Sockeye salmon possess a long lower limb of the preopercle and an expanded shoulder halfway up on the posterior edge of the upper limb of the preopercle (Fig. 6E); pink salmon possess a shorter lower limb and a slender, tapered dorsal limb of the preopercle. In this feature, the Skokomish fossils are clearly similar to sockeye salmon. The dermethmoid bone of pink salmon is usually slender, approximating an acute triangle with a long anterior process; in sockeye salmon the dermethmoid is abruptly widened posterior to the anterior process, the anterior process is less elongate, and the posterior notch is often wider and deeper. The fossils are variable, but Figure 6C shows that the dermethmoid is wide and expanded behind the anterior

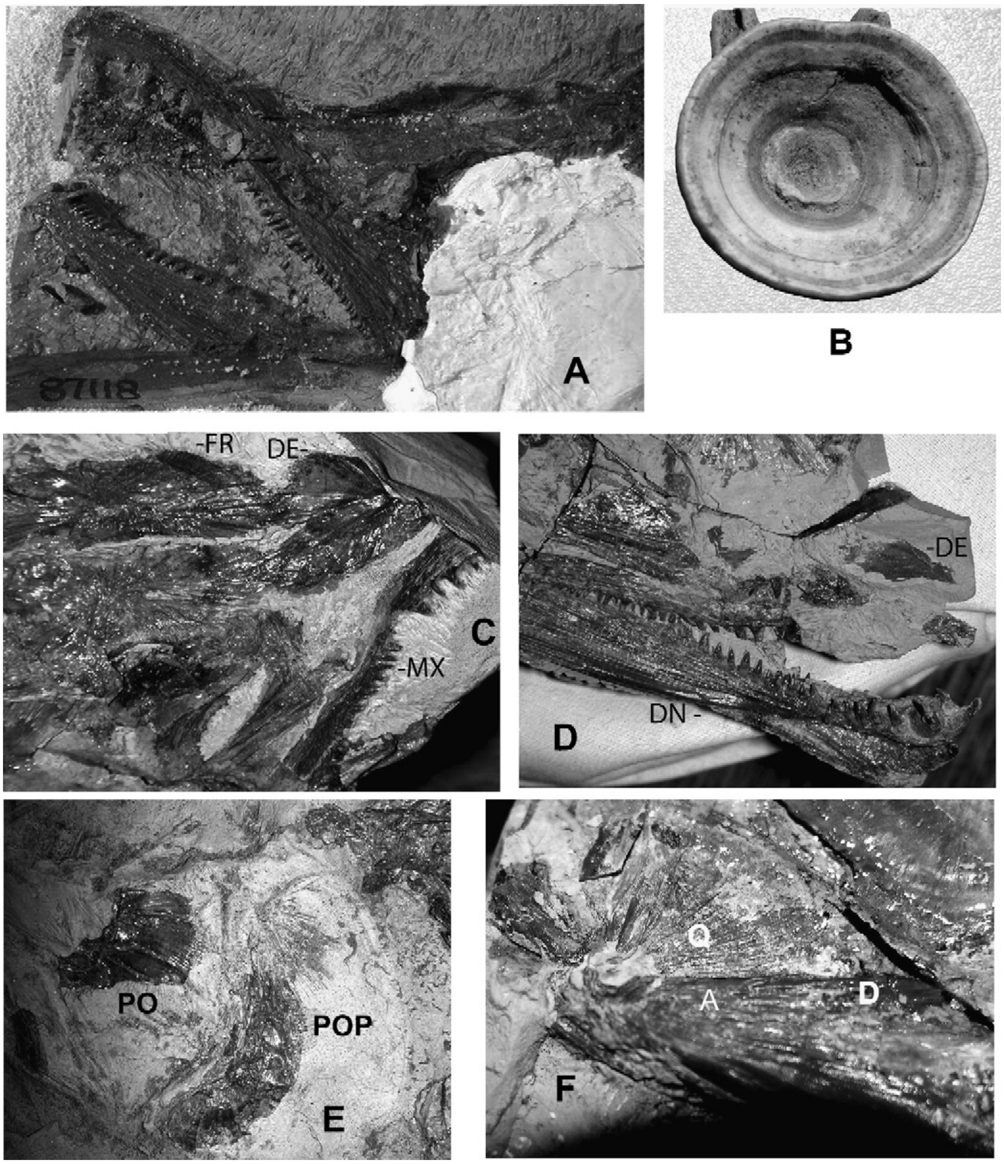

Figure 6. (A) UWBM 87118, male, showing straight maxilla with small teeth, enlarged premaxillary with enlarged teeth, and small dentary teeth, except anteriorly. (B) Skokomish fossil vertebra, UMMP 115081, showing four growth rings. (C) UWBM 87113, showing anterior expansion of lateral wings of the dermethmoid, DE; straight maxilla, MX, with small teeth, and shape of frontal bones, FR. (D) UWBM 87112, showing right dentary, DN, with small, somewhat compressed teeth, and fragment of dermethmoid, DE. (E) UWBM 87116, right side of face showing size and shape of post-orbitals, PO, and preopercle, POP. The post-orbitals are displaced from their normal position nearer the preopercle. (F) UWBM 87112, showing right quadrate, Q, and articular, A, with the low angle of the coronoid process leading to the dentary, D.

process as seen in sockeye salmon. The dentary teeth are often compressed in pink salmon and rounder in cross section in sockeye. The fossils are variable and intermediate (Fig. 6D). Pink salmon characteristically have a 2-yr life cycle while sockeye salmon usually have a 4-yr life cycle. The fossil vertebrae have four annual growth rings like sockeye (Fig. 6B). They tend to be 4–7 mm in maximum diameter. Fossil scales are abundant. They are ovate and about 2 mm long (Fig. 7C). Pink Salmon scales are smaller. The clear posterior field is often missing. Scales show a salient transition mark from narrow freshwater circuli to wide marine circuli near the end of their first year of growth, and distinct winter annuli in the ocean zone.

Isotopic analysis of salmon life history

Isotopic studies of salmon bones from the site were conducted by Antoine Zazzo et al. (2006) to test the hypothesis that the salmon had migrated to and from the sea against the possibility that the population was landlocked behind ice blocking the Pleistocene lake. Zazzo et al. (2006) found that the teeth of the fossil salmon do not show a marine oxygen isotopic signature, apparently owing to tooth replacement in fresh water in the mouth of the stream as the fish prepared to enter fresh water. But informatively higher $^{18}O(PO_4)$ values were found in fossil vertebrae compared to teeth. Assuming a similar rate of diagenetic isotope exchange of vertebrae and dentine with fresh

Table 1
Comparison of Skokomish fossils with *O. nerka* and *O. gorbuscha*

Trait	*O. nerka*	*O. gorbuscha*	Fossil
Breeding teeth on dentary (variable)	3 or 4, slightly compressed, slightly hooked	5 or 6, much compressed, strongly hooked	*nerka*
Articular-angular, post-dorsal process	No skirt lateral to condyle	Skirt extends lateral to condyle, extreme in advanced males	*nerka*
Articular-angular, lateral texture	Rows of homogeneous pits	Pits aligned between long, sharp ridges	*nerka*
Breeding teeth on premaxilla	Slightly compressed laterally, with distinct anterior addition to bone	Compressed antero-posteriorly, less developed anterior addition to bone	*nerka*?
Maxilla, anterior process (variable)	Often elongate	Moderately elongate	*nerka*
Maxillary teeth	Average relatively small	Small	*nerka*?
Preopercle shape	Dorsal limb posteriorly broad, irregularly rounded, un-serrated	Dorsal limb evenly contoured and usually serrated	*nerka*
Preopercle surface texture	Lateral striations and sensory canals coarse and irregular	Lateral striations and sensory canals fine and evenly spaced	*nerka*
Dermethmoid (variable)	Abruptly broadened behind anterior process	Slender, tapered behind long anterior process	*nerka*
Frontal, anterior	Pointed, tapered	Truncated	*nerka*
Dentary texture	Small pits	Rugose	*nerka*
Maxillary texture	Fine, elongate pits	Rugose	*nerka*
Glossohyal	Rounded anteriorly	Pointed anteriorly	?
Prevomer	Broad under tooth 1	Broad ahead of tooth 1	?
Hyomandibular	Anterodorsal angle 95°	Anterodorsal angle 90°	?
Life cycle	4 years	2 years	*nerka*

water, these results were interpreted to indicate formation of vertebrae in oceanic water. After correction for diagenetic alteration, the majority of the vertebral samples were within the range found in sea-run salmon, suggesting that the fossil fish formed their vertebral skeleton in the Pacific Ocean, and hence that there was an open water connection from the fossil lake to the sea. It is possible that the apparent limitation of salmon fossils to the lowest 70 yr of outcrop may record the time over which the lake maintained a salmon-navigable connection to the ocean.

Lidar analysis

A topographic profile generated from LIDAR data along the margin of the mapped extent of Fraser Continental glacial deposits reveals that when glacial ice dammed the North Fork Skokomish it diverted the river to the west (at point A in Fig. 2) where it flowed down the valley presently occupied by Brown Creek (Figs. 8 and 9). The longitudinal profile of the valley indicates that a diverted North Fork Skokomish River built a sediment ramp with a typical gravel-bed river slope of about 0.01 (I–K in Fig. 9), that decreases to <0.005 (F–I in Fig. 9) as would be expected for a river draining into a lake along the valley of the South Fork Skokomish River. Based on the projected profile running into higher elevations on the far valley wall (P–Q on Figs. 8 and 9) at an elevation of about 270 m, we consider the elevation of this ancient lake impounded by an advance of the Puget lobe to have been between 270 m and 280 m, somewhat higher than the elevation of potential topographically defined spillways to the southwest ranging in elevation from about 180 m to 250 m, implying an ice dam. Potential spillways for older, pre-Fraser outwash gravels mapped beyond the limit of Fraser deposits suggest a similar outlet for a pre-Fraser age lake. The extent of striated topography revealed by the LIDAR data (defined by thick white lines in Fig. 8) traces to roughly the lowest elevation of the Brown Creek terrace. Hence, we interpret an ice–lake contact to have occupied the area between the white lines in Fig. 8. The elevation difference between the glacially scoured topography (roughly 210 m at point B in Fig. 8) and the estimated lake surface elevation of 270–280 m implies an ice thickness of 60–70 m in the vicinity of the spillway draining the most recent lake at the fossil salmon site during the last advance of the Puget lobe.

Given that the Frigid Creek sediments are likely from the same lake as the South Fork Skokomish fossil salmon, we suspect that Frigid Creek was the original course of the South Fork Skokomish, and that the modern reach of the South Fork immediately upstream of its gorge, where it abruptly enters a steep, narrow canyon incised >100 m into the basaltic bedrock, was formerly a tributary flowing back into the main South Fork Skokomish River routed down Frigid Creek. Although both the Frigid Creek and fossil salmon exposures were likely part of the 1 Ma lake, the geological evidence remains ambiguous as to whether diversion of the South Fork to its present location occurred in response to the Salmon Springs (1 Ma) or the Fraser (15,000 yr) advance of the Puget lobe.

We nonetheless favor the earlier episode for formation of the gorge as more reasonable because it does not require anomalously fast river incision into basalt strong enough to sustain steep gorge walls. If the modern South Fork of the Skokomish River dates from Fraser glaciation it implies an incision rate of about 7 mm yr^{-1} (100 m/15,000 yr), a rate comparable to the most rapidly incising topography in the world (e.g., Burbank, 2002; Montgomery and Brandon, 2002). If instead, the modern course of the Skokomish River was

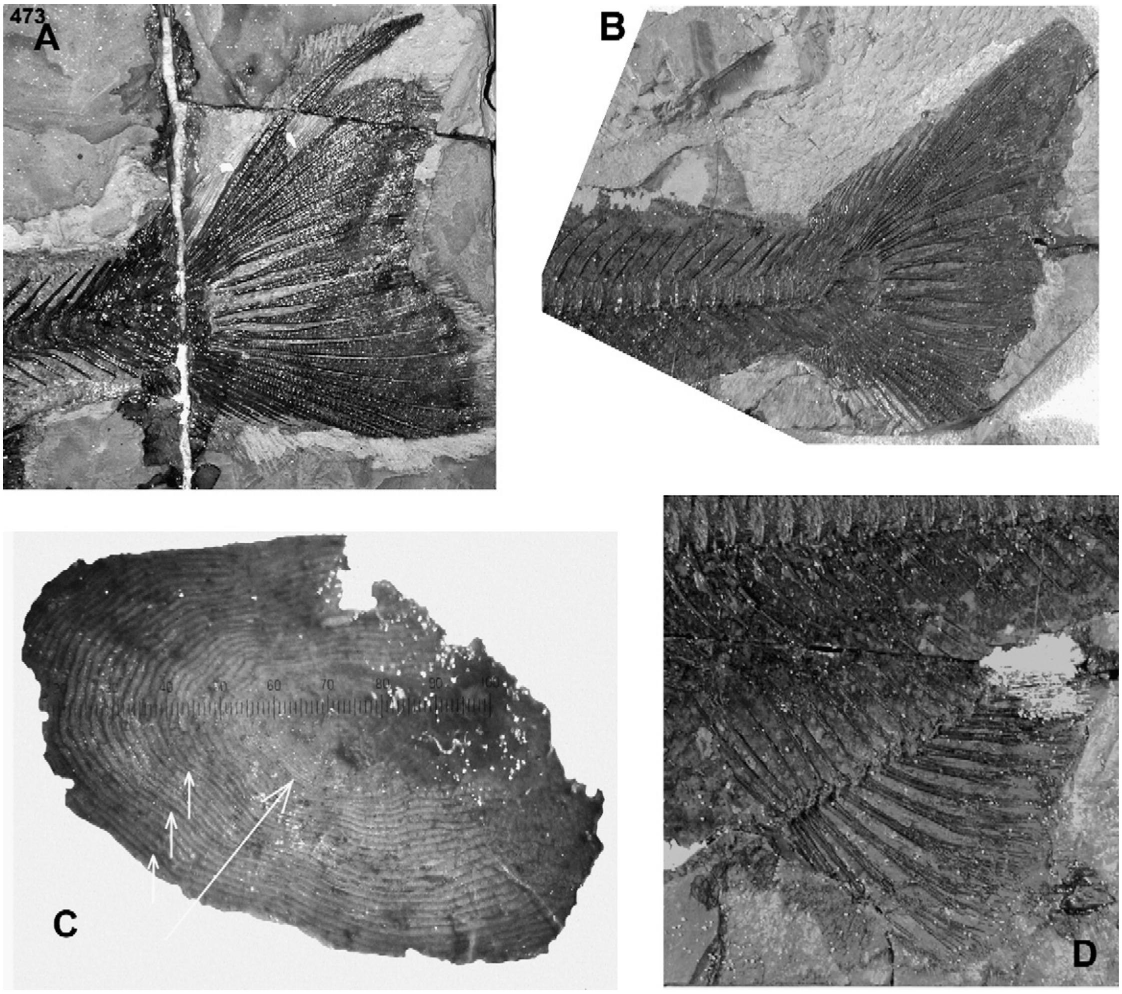

Figure 7. (A, B) Caudal fins of Skokomish fossil salmon showing worn tails, A (UWBM 88589), B (UWBM 87118). (C) Skokomish fossil scale, about 2.2 mm long in life, showing transition from freshwater (narrow circuli) to marine growth (wide circuli) and three marine winter marks; (D) Anal fin of UW BM 87118, showing 14 or 15 anal rays.

established closer to the age of the fossil-bearing beds (i.e., during the Salmon Springs advance of the Puget lobe), then the long-term incision rate of the Skokomish River gorge would be a more reasonable 0.1 mm yr^{-1} (100 m/Ma), much closer to the long-term rock uplift rate for the southern Olympic Mountains (Brandon et al., 1998). We further conclude that both the older (Salmon Springs) and younger (Fraser) lakes drained through spillways on the margin of the contact between sediments deposited by the Puget lobe and the Eocene volcanic rock of the Olympic Mountains. In this area, several large valleys with underfit streams indicate potential outlets through topography incised into mapped deposits of Fraser and pre-Fraser glacial outwash south of the modern Skokomish River valley (immediately to the right of location B in Fig. 2).

Discussion

The Skokomish salmon are in the Salmon Springs Formation, interpreted to be early Pleistocene, about 0.9 Ma (Matuyama epoch), based on fission track dates and reversed paleomagnetic polarity as determined in correlative beds in Frigid Creek by Easterbrook et al. (1981) and Westgate et al. (1987). However, preliminary paleomagnetic analysis of the lacustrine clays in which the fish occur reveals normal paleomagnetic polarity (possibly Jaramillo event, 0.93–0.87 Ma).

The fossils are determined to be sockeye salmon based on their skull bones, with some tooth variation shared with modern pink salmon. There are no features to suggest that the fossils represent a lineage close to chum salmon, before or during the splits among these three species. These observations are consistent with the hypothesis based on mtDNA that these lineages diverged in the Pliocene (Thomas et al., 1986), and fossil evidence that they diverged in the Late Miocene or earlier (Smith, 1992). Moreover, fossils related to ancestral *Oncorhynchus nerka* are found in the Chalk Hills Formation of the Snake River Plain in Idaho and Oregon; these date back to the Late Miocene, probably 6–7 Ma (Eiting and Smith, 2007).

The accumulation of several dozen partially articulated specimens at the head of a lake within meters of the tributary inlet suggests a spawning assemblage (Fig. 10). Hooked jaws with anteriorly enlarged breeding teeth and abraded caudal fins

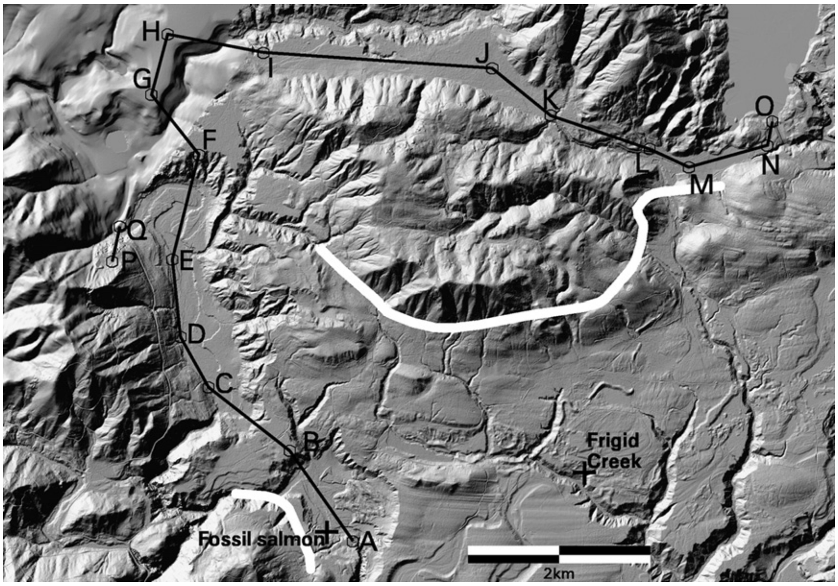

Figure 8. Shaded relief image created from LIDAR digital elevation data (data obtainable at http://pugetsoundlidar.ess.washington.edu/index.html) showing location of topographic profile shown in Figure 9, the fossil salmon and Frigid Creek sites (crosses) and inferred ice margin of latest Puget lobe advance (white line) based on reconnaissance field mapping and the extent of glacially grooved terrain discernable on the LIDAR image (note that this differs from that based on previous mapping shown in Fig. 2). Letters identify points also labeled in Figure 9.

in some (apparently female) individuals support the hypothesis that these fish migrated to the tributary at the head of the lake, built nests in fine gravel, spawned, and died, precisely as sockeye salmon do today (Quinn, 2005). Most commonly, fossils are concentrated in layers in the coarse silt fraction of varves, at the cleavage plain under the coarse fraction. Less commonly, fossil layers occur in the fine silt fraction. Although there is no reason to expect that climate near the glacial lobe at 1 Ma was like today's climate, if salmon migrated in September and October (as they tend to do now) then the observed presence of the fossils near the base of the coarse silt fraction of each varve couplet implies that flood conditions were most common in fall and winter months, as under the current climate.

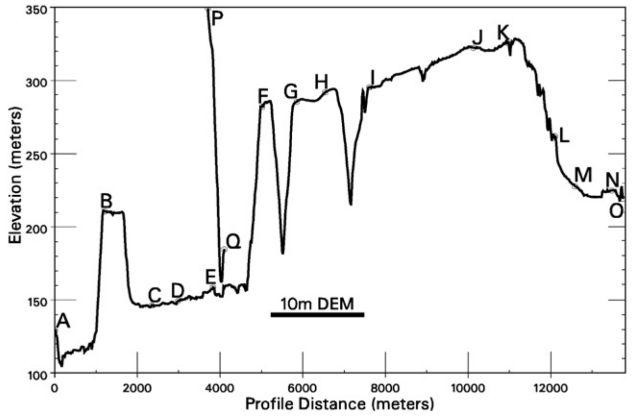

Figure 9. Topographic profile created from LIDAR digital elevation data (source: http://pugetsoundlidar.ess.washington.edu/) along river terrace (F–K) draining to lake, blocked by ice (at M). P–Q shows elevation of far valley wall projected along trend of HG. Black bar across base of figure shows extent of transect derived from 10-m-grid DEM where LIDAR data are unavailable.

The fossils occur in several vertical meters of lake sediments adjacent to the inlet gravels of the South Fork of the Skokomish River. The absence of fossils above this point suggests that spawning at the site ceased, either because preferred spawning habitat transgressed upstream or because access to migrating salmon was occluded by events downstream. The pronounced reduction in abundance of fossils and the extreme disarticulation of specimens below the concentrated aggregation supports the hypothesis that the salmon were a death assemblage that died after spawning at the head of the lake, year after year for about 70 yr.

Because evidence is lacking for alluvial fan dams, moraines, or other obstructions that might have dammed the Skokomish River, we conclude that lake sediments were deposited in water impounded by the Puget lobe. Indeed, there is strong evidence for several generations of glacier-dammed lakes along the South Fork of the Skokomish River. Evidence for a Fraser age lake comes from the longitudinal profile of an apparently west-diverted North Fork Skokomish River, whereas evidence for a much older (i.e., radiocarbon dead) lake comes from dating the fossil bearing sediments. The inferred history of glacial damming and river capture implies that the modern gorge of the South Fork Skokomish River likely began incising upon recession of the ice dam that formed the ca. 1 Ma lake.

Fish evidently migrated around the edge of the moraine or around the ice lobe advancing from east to west in front of the foothills and swam through the South Fork/Frigid Creek lake to spawn near the head of the growing lake. The evidence for upstream migration of the contact between the stream delta and lake beds and the extent and orientation of glacially striated

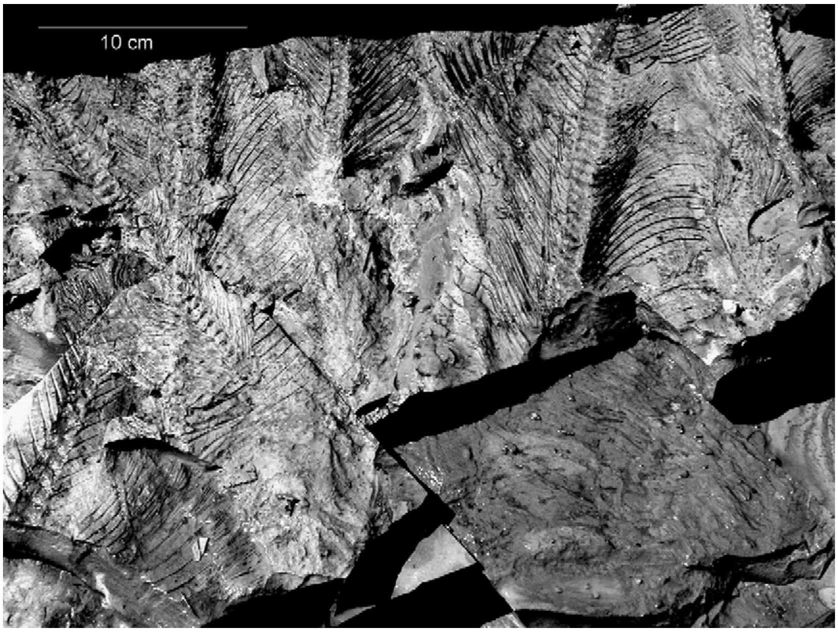

Figure 10. Death assemblage of Skokomish fossil salmon. Parts of eight skeletons are shown; others were in the same layers. Heads are oriented down dip (approximately SE 135°) into the paleo-lake, at a 90° angle to the present downstream direction (about S 225°). This orientation is opposite to that expected in response to current, suggesting that the fish were out of the inlet's current and possibly responding to wind-driven wave energy in the lake.

topography support the glacial dam hypothesis, with open access to the sea for at least several decades, judging from the occurrence of fish fossils vertically for several meters. The large size of the fossil salmon suggests suitable temperatures and nutrients for growth in the sea, but the predominance of Lodgepole pine needles and cones at the site and the cold climate (tundra) indicators in the Lake Tapps pollen suggest local temperatures significantly colder than the present (Heusser, 1977; Stuiver et al., 1978). We infer from these two lines of evidence that the salmon were spawning in temperatures similar to those of western Alaska, today (see Augerot and Foley, 2005, p. 76–77). Based on our analyses, sockeye salmon life-history attributes—including anadromy, spawning in tributaries to lakes, 4-yr lifecycle, growth to medium large size, and death after spawning—date back to at least 1 million yr ago in the early Pleistocene of the Pacific Northwest.

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References

Augerot, X., Foley, D.N., 2005. Atlas of Pacific Salmon. University of California Press, Berkeley.

Brandon, M.T., Roden-Tice, M.K., Garver, J.I., 1998. Late Cenozoic exhumation of the Cascadia accretionary wedge in the Olympic Mountains, northwest Washington State. Geological Society of America Bulletin 110, 985–1009.

Burbank, D.W., 2002. Rates of erosion and their implications for exhumation. Mineralogical Magazine 66, 25–52.

Cavender, T.M., Miller, R.R., 1972. *Smilodonichthys rastrosus*—A new Pliocene salmonid fish from western united States. University of Oregon Museum of Natural History Bulletin, vol. 18. Eugene.

Cavender, T.M., Miller, R.R., 1982. *Salmo australis*, a new species of fossil salmonid from south-western Mexico. University of Michigan Museum of Paleontology Contribution 26, 1–17.

Crandell, D.R., 1963. Surficial geology and geomorphology of the Lake Tapps quadrangle, Washington, US. Geological Survey Professional Paper 388A (84 p.)

Easterbrook, D.J., Briggs, N.D., Westgate, J.A., Gorton, M.P., 1981. Age of the Salmon Springs Glaciation in Washington. Geology 9, 87–93.

Easterbrook, D.J., Roland, J.L., Carson, R.J., Naeser, N.D., 1988. Application of paleomagnetism, fission-track dating, and tephra correlation to Lower Pleistocene sediments in the Puget Lowland, Washington. In: Easterbrook, D.J. (Ed.), Dating Quaternary Sediments. Geological Society of America Special Paper, vol. 227, pp. 139–165.

Eiting, T.P., Smith, G.R., 2007. Miocene salmon (*Oncorhynchus*) from Western North America: Gill Raker evolution correlated with plankton productivity in the Eastern Pacific. Palaeogeography, Palaeoclimatology, Palaeoecology 249, 412–424.

Henderson, J.A., Peter, D.H., Lesher, R.D., Shaw, D.S., 1989. Forested Plant

Associations of the Olympic National Forest. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, R6-ECOL-TP-001-88, 502 p.

Heusser, C.J., 1977. Quaternary palynology of the Pacific slope of Washington. Quaternary Research 8, 282–306.

Hikita, T., 1962. Ecological and morphological studies of the genus Oncorhynchus (Salmonidae) with particular consideration on phylogeny. Scientific Reports of the Hokkaido Salmon Hatchery 17, 1–97.

Logan, R.L., 2003. Geologic map of the Shelton 1:100,000 quadrangle, Washington, State of Washington, Department of Natural Resources, Division of Geology and Earth Resources, Open File Report 2003–15.

Montgomery, D.R., Brandon, M.T., 2002. Non-linear controls on erosion rates in tectonically active mountain ranges. Earth and Planetary Science Letters 201, 481–489.

Porter, S.C., Swanson, T.W., 1998. Radiocarbon age constraints on rates of advance and retreat of the Puget lobe of the Cordilleran Ice Sheet during the last glaciation. Quaternary Research 50, 205–213.

Quinn, T.P., 2005. The Behavior and Ecology of Pacific Salmon and Trout. University of Washington Press, Seattle.

Rogers, K.L., Repenning, C.A., Forester, R.M., Larson, E.E., Hall, S.A., Smith, G.R., Anderson, E., Brown, T.J., 1985. Middle Pleistocene (Late Irvingtonian: Nebraskan) climatic changes in south-central Colorado. National Geographic Research 1, 535–563.

Smith, G.R., 1992. Introgression in fishes: significance for paleontology, cladistics, and evolutionary rates. Systematic Biology 41 (1), 41–57.

Smith, G.R., Miller, R.R., 1985. Taxonomy of fishes from the Miocene Clarkia lake beds. In: Smiley, C.J. (Ed.), Late Cenozoic History of the Pacific Northwest. American Association for the Advancement of Science. Pacific Division, San Francisco, pp. 75–83.

Smith, G.R., Swirydczuk, K., Kimmel, P.G., Wilkinson, B.H., 1984. Fish biostratigraphy of late Miocene to Pleistocene sediments of the western Snake River Plain, Idaho. In: Bonnichsen, B., Breckenridge, R.M. (Eds.), Cenozoic Geology of Idaho, Idaho Bureau Mines and Geology Bulletin, vol. 26, pp. 519–542.

Smith, G.R., Morgan, N., Gustafson, E., 2000. Fishes of the Mio-Pliocene Ringold Formation, Washington: Pliocene Capture of the Snake River by the Columbia River. University of Michigan Museum of Paleontology Paper 32, 1–47.

Smith, G.R., Dowling, T., Gobalet, K.W., Lugaski, T., Shiazawa, D., Evans, R.P., 2002. Biogeography and timing of evolutionary events among Great Basin fishes. In: Hershler, R., Madsen, D.B., Currey, D.R. (Eds.), Great Basin Aquatic Systems History. Smithsonian Contributions to Earth Sciences, 33, pp. 175–234.

Stearley, R.F., Smith, G.R., 1993. Phylogeny of the Pacific trouts and salmons (Oncorhynchus) and genera of the family Salmonidae. Transactions of the American Fisheries Society 122, 1–33.

Stuiver, M., Heusser, C.J., Yang, I.C., 1978. North American glacial history back to 75,000 years B.P. Science 200, 16–21.

Thomas, W.K., Withler, R.E., Beckenbach, A.T., 1986. Mitochondrial DNA analysis of Pacific salmonid evolution. Canadian Journal of Zoology 64, 1058–1064.

Thorson, R.M., 1980. Ice-sheet glaciation of the Puget lowland, Washington, during the Vashon Stade (late Pleistocene). Quaternary Research 13, 303–321.

Westgate, J.A., Easterbrook, D.J., Naeser, N.D., Carson, R.J., 1987. Lake Tapps Tephra: an early pleistocene stratigraphic marker in the Puget Lowland, Washington. Quaternary Research 28, 340–355.

Whitlock, C., 1992. Vegetational and climatic history of the Pacific Northwest during the last 20,000 years: implications for understanding present-day biodiversity. The Northwest Environmental Journal 8, 5–28.

Wilson, M.V.H., 1977. Middle Eocene freshwater fishes from British Columbia. Royal Ontario Museum. Life Sciences Contributions 113, 1–61.

Wilson, M.V.H., Li, G.-Q., 1999. Osteology and systematic position of the Eocene salmonid †Eosalmo driftwoodensis Wilson from western North America. Zoological Journal Linnean Society 125, 279–311.

Zazzo, A., Smith, G.R., Patterson, W.P., Dufour, E., 2006. Life history reconstruction of modern and fossil sockeye salmon (*Oncorhynchus nerka*) by oxygen isotopic analysis of otoliths, vertebrae, and teeth: Implication for paleoenvironmental reconstructions. Earth and Planetary Science Letters 249, 200–215.