

# Life history variation in upper Columbia River Chinook salmon (*Oncorhynchus tshawytscha*): a comparison using modern and ~500-year-old archaeological otoliths

Jessica A. Miller, Virginia L. Butler, Charles A. Simenstad, David H. Backus, and Adam J.R. Kent

**Abstract:** Conservation planning often occurs only after a species has been extirpated from portions of its historical range and limited information is available on life history diversity prior to development. To provide information on Chinook salmon (*Oncorhynchus tshawytscha*) life history before and after local extirpation, we examined the chemical ( $^{87}\text{Sr}:$  $^{86}\text{Sr}$ , Sr:Ca) and structural composition of modern and archaeological otoliths from the upper Columbia River. We compared otoliths from modern spring (yearling migrant,  $n = 15$ ) and summer–fall (yearling ( $n = 7$ ) and subyearling ( $n = 12$ ) migrants) runs with those from extirpated runs ( $n = 8$ ) to estimate the number of and similarity among natal environments and reconstruct aspects of the migratory history. Presumptive natal sources were most similar between the archaeological collections and the modern summer–fall run. Chinook salmon represented by the archaeological otoliths also displayed life history traits, including size at freshwater emigration and adult size at return to fresh water, most similar to the summer–fall subyearling run. These data indicate that there is the potential to maintain aspects of predevelopment Chinook salmon life histories in the Columbia River, and strategies that promote maintenance of that life history diversity may be warranted.

**Résumé :** La planification de la conservation se produit souvent seulement une fois qu'une espèce a été éliminée de plusieurs parties de son aire historique et qu'il n'existe plus que peu d'information sur la diversité des cycles biologiques d'avant le développement économique. Afin d'obtenir des informations sur le cycle biologique de saumons chinook (*Oncorhynchus tshawytscha*) avant et après leurs extirpations locales, nous avons analysé la composition chimique ( $^{87}\text{Sr}:$  $^{86}\text{Sr}$ , Sr:Ca) et structurale d'otolithes modernes et archéologiques provenant du cours supérieur du fleuve Columbia. Nous avons comparé les otolithes des montaisons modernes du printemps (migrateurs d'un an,  $n = 15$ ) et de l'été–automne (migrateurs d'un an,  $n = 7$  et de moins d'un an,  $n = 12$ ) à des otolithes provenant de montaisons éliminées ( $n = 8$ ) afin de déterminer le nombre de milieux d'origine et la similarité entre eux et de reconstituer certains aspects de l'histoire de la migration. Les milieux d'origine présumés sont plus semblables entre les collections archéologique et les montaisons modernes d'été–automne. Les saumons chinook représentés par les otolithes archéologiques présentent aussi des traits de cycle biologique, et en particulier la taille à l'émigration depuis l'eau douce et la taille adulte lors du retour en eau douce, plus semblables à ceux de la montaison d'été–automne des poissons de moins d'un an. Ces données indiquent qu'il existe une possibilité de maintenir certains aspects des cycles biologiques des saumons chinook du Columbia d'avant le développement économique et qu'il y aurait lieu de mettre en place des stratégies qui favorisent le maintien de la diversité des cycles biologiques.

[Traduit par la Rédaction]

## Introduction

Effective management and conservation of biological populations relies on accurate classification of existing genetic, ecological, and life history diversity. However, conservation planning often commences only after a species has been ex-

tirpated from portions of its historical range and limited information is available on life history variation prior to development. Although phenotypic variation can be challenging to quantify and conserve, it may be critical for the maintenance of certain populations (Conover et al. 2006). Furthermore, as local adaptation and selection can occur

Received 13 June 2010. Accepted 30 December 2010. Published at [www.nrcresearchpress.com/cjfas](http://www.nrcresearchpress.com/cjfas) on 12 April 2011. J21873

Paper handled by Associate Editor Bronwyn Gillanders.

**J.A. Miller.** Oregon State University, Coastal Oregon Marine Experiment Station, Department of Fisheries and Wildlife, 2030 SE Marine Science Drive, Newport, OR 97365, USA.

**V.L. Butler.** Portland State University, Department of Anthropology, P.O. Box 751, Portland, OR 97207, USA.

**C.A. Simenstad.** University of Washington, School of Aquatic and Fishery Sciences, Box 355020, Seattle, WA 98195-5020, USA.

**D.H. Backus.** Williams College, Department of Geosciences, 947 Main Street, Williamstown, MA 01267, USA.

**A.J.R. Kent.** Oregon State University, Department of Geosciences, 104 Wilkinson Hall, Corvallis, OR 97330, USA.

**Corresponding author:** Jessica A. Miller (e-mail: [Jessica.Miller@oregonstate.edu](mailto:Jessica.Miller@oregonstate.edu)).

over relatively short time scales (Hendry and Kinnison 1999; Unwin et al. 2000; Connor et al. 2005), determining whether substantial life history variation has been lost is highly relevant to conservation efforts. Therefore, we completed a preliminary analysis to determine the feasibility of reconstructing aspects of life history variation in an extirpated population of Chinook salmon based on archaeological otolith collections.

Chinook salmon (*Oncorhynchus tshawytscha*) is an anadromous species that has been extirpated from ~40% of its historical freshwater range in the contiguous USA (Gustafson et al. 2007). In the Columbia River Basin, which is the second largest watershed in the USA, extensive habitat and population loss has occurred because of hydropower development and landscape modifications. Chinook salmon currently spawn up to Chief Joseph Dam (47°59'N, 119°38'W), which is 877 km from the mouth and marks the upstream extent of contemporary salmon distribution. Historically, there were >500 km of potential salmon habitat accessible upstream of the dam (Fulton 1968).

Evolutionarily significant units (ESUs), which are based on genetic, ecological, and life history diversity, are used to classify diversity in biological populations in the USA (Waples et al. 2001; Gustafson et al. 2007). Currently, there are 17 ESUs established for Chinook salmon throughout the contiguous USA and two within the upper Columbia River (Myers et al. 1998): (i) the upper Columbia River spring run, which is listed as endangered under the Endangered Species Act (Good et al. 2005); and (ii) the upper Columbia River summer–fall run. The run time (spring vs. summer–fall) refers to the season during which adults return to their natal rivers for reproduction. In general, the spring run displays a yearling life history, where juveniles emigrate from fresh water after 1 year, whereas the summer–fall run displays a subyearling life history, where juveniles emigrate from fresh water during their first year and tend to reside longer in estuaries and coastal habitats (Healey 1991). However, both juvenile migratory behaviors can occur in either run (Myers et al. 1998). Additionally, runs with yearling life histories typically display smaller adult body size-at-age compared with runs with subyearling life histories (Healey 1991).

Large numbers of salmon are produced in hatcheries to compensate for loss of habitat within the Columbia River. For example, >100 million hatchery-produced spring and summer–fall run Chinook salmon from upper Columbia River stocks were released between 1999 and 2008 (Regional Mark Processing Center: <http://www.rmhc.org/>). Hatcheries release primarily larger, older individuals; such practices can promote the dominant tactic, or phenotype, and reduce life history variation within a population, which may in turn reduce population resiliency (Healey 2009). Currently, there is minimal information about whether substantial life history variation has been lost in these populations and whether contemporary life history traits are representative of predevelopment populations.

Our capacity to determine life history traits retrospectively has expanded with the development of biogeochemical markers. Elemental and isotopic analyses of biological structures have been used to reconstruct aspects of an individual's life history, including determination of provenance and migration patterns in humans (Hedman et al. 2009), birds (Hob-

son 1999), woolly mammoths (Arppe et al. 2009), and fishes (Koch et al. 1992; Campana 2004; Dufour et al. 2007). For fishes, otoliths provide an excellent forensics tool because they grow continuously, display no evidence of resorption, and record high frequency (daily) aspects of the environment in which a fish resided. Examination of otolith strontium ( $^{87}\text{Sr}:^{86}\text{Sr}$  and Sr:Ca) has been used to determine provenance (Kennedy et al. 1997; Ingram and Weber 1999) and reconstruct movement patterns and migration histories in both Pacific (Zimmerman et al. 2003; Miller et al. 2010a; Volk et al. 2010) and Atlantic (*Salmo salar*) salmon (Kennedy et al. 2002). These approaches are based on positive relationships between otolith and water strontium composition (Kennedy et al. 1997; Zimmerman 2005).

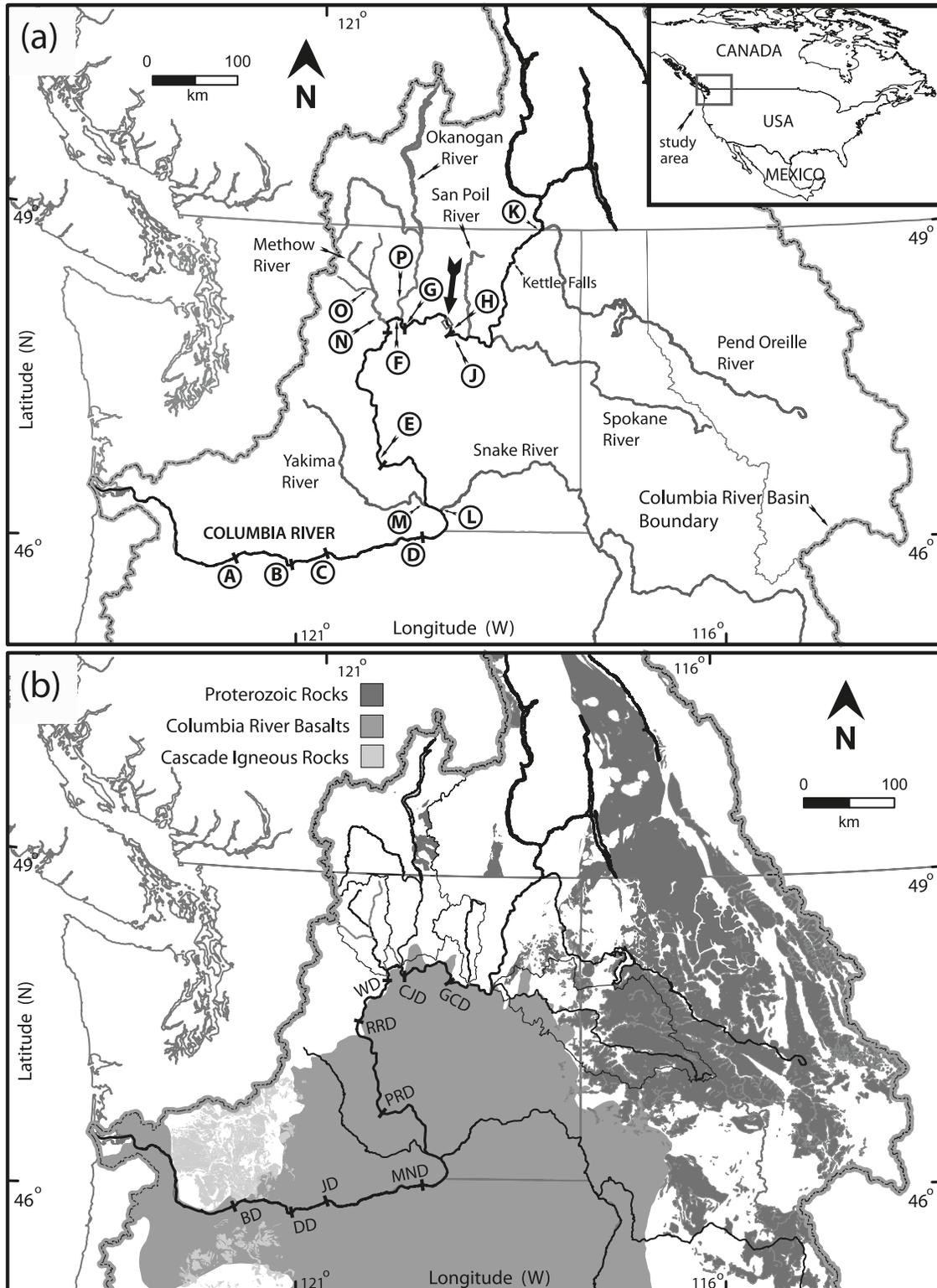
We obtained otoliths from modern and extirpated populations of Chinook salmon in the upper Columbia River Basin to determine if we can reconstruct aspects of this species' life history. The direct comparison of individuals from the same geographic region before and after non-indigenous human settlement and hydropower modification would provide empirical evidence on life histories prior to widespread human impacts. We based our approach on otolith chemical ( $^{87}\text{Sr}:^{86}\text{Sr}$ , Sr:Ca) and structural analyses because otoliths provide a chemical record adequate to differentiate between fresh and marine waters and among freshwater systems and growth structures amenable to robust back-calculation of individual size (Francis 1990). Our primary study objectives were to (i) estimate the number of and similarity among natal environments and (ii) reconstruct aspects of the life history, including determination of size at freshwater emigration, life history type (yearling vs. subyearling), and adult body size upon return to fresh water. Additionally, we assessed the archaeological otoliths for evidence of diagenesis, which refers to any chemical or physical change after initial deposition. There can be partial to complete exchange of the original elemental constituents with locally derived sources; extensive diagenesis could remove the original Sr record and lead to an uninterpretable pattern of Sr within the otolith.

## Materials and methods

### Modern otolith collection

Sagittal otoliths from Chinook salmon spawners representative of current runs were obtained in 2007 by Washington Department of Fish and Wildlife (WDFW) personnel. Individuals from the spring ( $n = 15$ ) and summer–fall ( $n = 19$ ) runs were collected at the Wells Dam and Hatchery facilities (47°57'N, 119°52'W) (Fig. 1). Individuals were assigned to one of these two seasonal runs based on the time of collection and verified with genetic analysis (Seeb et al. 2007; C. Snow, WDFW, 20268 Highway 20, Suite 7, Twisp, Washington, unpublished data). Most hatchery fish could be visually identified because all yearling and many of the subyearling fish had their adipose fin clipped prior to release as juveniles. WDFW personnel also collected information on fork length (FL, cm) and classified fish as hatchery or naturally spawned based on scale analysis (e.g., Connor et al. 2005). We wanted to compare naturally occurring life history variation in modern runs with our archaeological collections; therefore, we only included fish that were classified as naturally spawned based on scale analysis. The naturally spawned

**Fig. 1.** Map of Columbia River and tributaries. (a) Majority of the Columbia River watershed, including the Snake, Yakima, Methow, Okanogan, San Poil, Pend Oreille, and Spokane rivers. Locations where riverine  $^{87}\text{Sr}:^{86}\text{Sr}$ , Sr (ppb), and Sr:Ca ( $\text{mmol}\cdot\text{mol}^{-1}$ ) data were collected are identified by letters (data are presented in Table 1). Approximate location of archaeological site is indicated by black arrow. (b) Distribution of major rock units in the Columbia River watershed, including Cascade Igneous rocks (mean  $^{87}\text{Sr}:^{86}\text{Sr} \pm 1$  standard deviation (SD) =  $0.7034 \pm 0.0004$ ,  $n = 99$ ); Columbia River Basalt Group ( $^{87}\text{Sr}:^{86}\text{Sr} = 0.7046 \pm 0.0010$ ,  $n = 224$ ); and Proterozoic rocks ( $^{87}\text{Sr}:^{86}\text{Sr} = 0.8847 \pm 0.1028$ ,  $n = 77$ ). Mainstem dams, including Bonneville (BD), The Dalles (DD), John Day (JD), McNary (MND), Priest Rapids (PRD), Rocky Reach (RRD), Wells (WD), Chief Joseph (CJD), and Grand Coulee (GCD), are identified.



Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by 131.252.193.101 on 04/12/11  
For personal use only.

individuals from the spring run likely originated within the Methow River Basin, whereas those from the summer–fall run likely originated within the Methow or Okanogan river basins (Fig. 1) (C. Snow, WDFW, 20268 Highway 20, Suite 7, Twisp, Washington, personal communication, 2009). Prior to the construction of Grand Coulee Dam in 1942, Chinook salmon were intercepted on their upstream migration, spawned, and their offspring released into tributaries below the future dam location as part of the Grand Coulee Fishery Maintenance Project (Myers et al. 1998). Therefore, modern runs in this region may have been influenced by introgression as a result of these introductions.

### Archaeological site and otolith collection

The archaeological site (site No. 45-DO-285) (Fig. 1a), which is located above Chief Joseph Dam, was excavated in 1978–1980 prior to expansion of the dam and subsequent pool rise. The site is located on the west bank of the Columbia River in Douglas County, downriver of Grand Coulee Dam. Specific site location information is withheld given tribal concerns. The site was occupied from 3000 to 250 years BP, and most of the site's fish remains were recovered from the most recent occupation zone, dating between 250 and 500 years BP (Miss et al. 1984). The fish assemblage is dominated by otoliths from Chinook salmon; bony specimens of the cranium and vertebral column are extremely uncommon. The scarcity of cranial bony specimens probably results from deterioration after deposition. Vertebrae are extremely robust, however, and their absence more likely is because carcasses were not deposited at the site (Butler 1990). Previous researchers suggest that the most recent occupation represents a seasonally occupied fishing camp rather than a village (Miss et al. 1984). Salmon were likely procured at a nearby rapid (now drowned by the reservoir) and then brought to the site where heads were cut off and deposited while the remainder of the carcass was taken elsewhere (Butler 1990). Such butchering–processing activities are known for numerous Native American groups throughout the Pacific Northwest (see references in Butler and Chatters 1994). The particular season of fishery activities is difficult to estimate from existing archaeological records (Miss et al. 1984). According to local ethnographic records obtained in the 1920s, “salmon is present in the middle Columbia from May until November” (Ray 1933, p. 57); salmon represented in the archaeological site could have been taken any time in that period.

We obtained permission to analyze ten sagittal otoliths from Chinook salmon (identified using Casteel 1974) collected from the site. To determine life history characteristics of fish closest in age but prior to the time of major hydro-power development and in-channel modifications, we selected otoliths from the most recent occupation zone (250–500 years old) (Miss et al. 1984).

### Otolith preparation and elemental analyses

Sagittal otolith thin sections were prepared using established protocols for element analysis (e.g., Miller 2009). Otolith elemental and isotopic data were collected along transects that intersected the otolith core (Figs. 2a, 2c). We collected  $^{87}\text{Sr}:^{86}\text{Sr}$  and Sr:Ca data from 21 modern ( $n = 10$  for spring yearling; 5 for summer–fall yearling; and 6 for summer–fall

subyearling migrants) and 8 of the 10 archaeological otoliths (two were damaged during preparation). We collected only  $^{87}\text{Sr}:^{86}\text{Sr}$  data from the remaining 13 modern otoliths ( $n = 5$  for spring yearling; 2 for summer–fall yearling; and 6 for summer–fall subyearling migrants).

To quantify otolith  $^{87}\text{Sr}:^{86}\text{Sr}$ , we used a NuPlasma multi-collector inductively coupled plasma mass spectrometer (MC-ICP-MS) and a New Wave DUV193 excimer laser. We followed the general method of Woodhead et al. (2005) as described in Miller and Kent (2009) to correct for potential Kr and Rb interferences and monitor for Ca argide–dimer formation. The laser was set at a pulse rate of 10 Hz with a 40  $\mu\text{m}$  ablation spot size and travelled at 2  $\mu\text{m}\cdot\text{s}^{-1}$ . Data were collected across the otolith growth axis to generate a life history profile; data were generated in blocks composed of two, 2 s cycles and represent the average value across 8  $\mu\text{m}$  of the otolith. To assess instrument accuracy, we determined the  $^{87}\text{Sr}:^{86}\text{Sr}$  of a marine gastropod ( $= 0.70918$ ) and consistently obtained a mean value ( $\pm 2$  standard errors, SE) of  $0.709291 \pm 0.000008$  ( $n = 18$ ); otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  values were corrected for this difference.

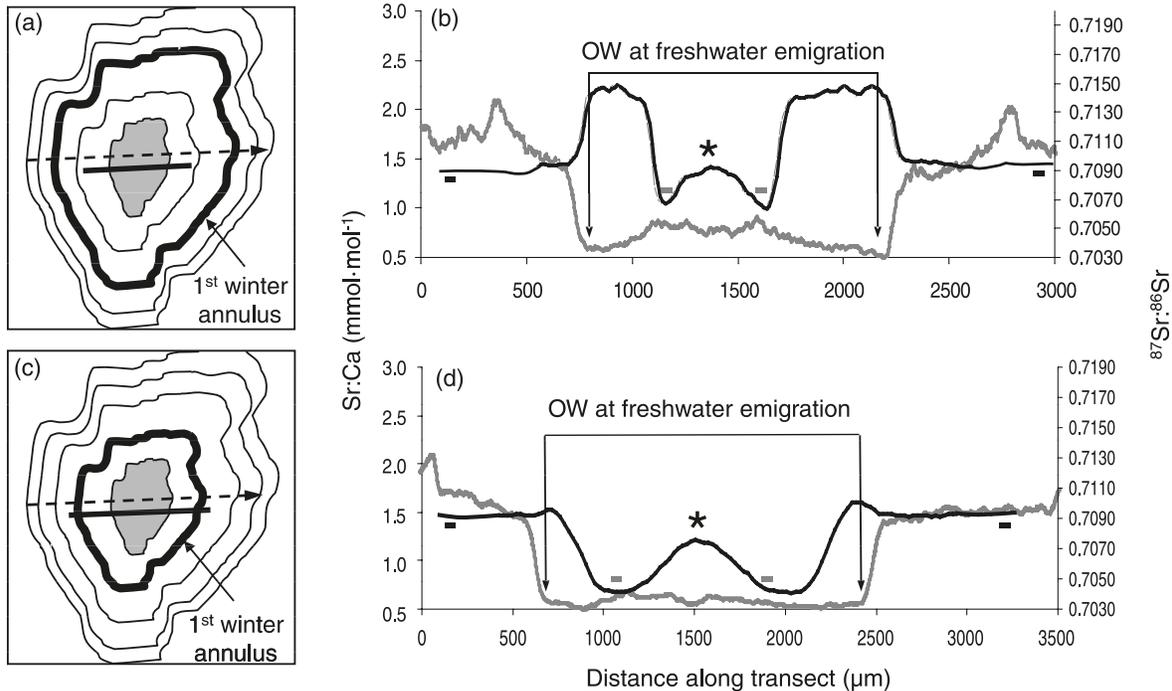
To quantify otolith Ca and Sr concentrations along the otolith growth axis, we used a VG PQ ExCell ICP-MS (Thermo Scientific) with a New Wave DUV193 excimer laser. The laser was set at a pulse rate of 15 Hz with a 40  $\mu\text{m}$  ablation spot size and travelled at 5  $\mu\text{m}\cdot\text{s}^{-1}$ . Normalized ion ratios were converted to molar ratios based on our measurements, known average elemental concentrations of National Institute of Standards and Technology (NIST) 612 glass standards, and molar mass of Ca and Sr. Limits of detection (ppm) were calculated as three standard deviations (SDs) of background measurements: Ca = 0.07, Sr = 0.09. The mean percent relative SDs for glass standards were  $^{43}\text{Ca} = 2.6\%$  and  $^{86}\text{Sr} = 5.6\%$ . A calcium carbonate standard prepared by the United States Geological Society (USGS MACS-1) provided an estimate of accuracy (99% for Sr:Ca).

### Natal sources

Spatial variation in riverine values of  $^{87}\text{Sr}:^{86}\text{Sr}$ , which reflect the age and mineralogy of the surrounding geology, can be used to differentiate among natal environments in anadromous fishes (Kennedy et al. 1997, 2002).  $^{87}\text{Sr}$  is produced by the radioactive decay of  $^{87}\text{Rb}$ ; rocks of the continental crust (e.g., granites) are relatively high in rubidium, whereas rocks typical of oceanic crust (e.g., basalts) have much lower concentrations (Faure 2001). Because the half-life of  $^{87}\text{Rb}$  is on the order of 49 billion years, very old continental rocks, sedimentary rocks eroded from very old continental crust, or younger igneous rocks contaminated when passing through very old continental crust will have accumulated more  $^{87}\text{Sr}$  and have higher  $^{87}\text{Sr}:^{86}\text{Sr}$  ratios than oceanic crust and some surface basalt flows.

The Columbia River Basin drains a large (~660 500  $\text{km}^2$ ) and geologically complex area that provides an opportunity to examine natal sources using  $^{87}\text{Sr}:^{86}\text{Sr}$  (Fig. 1b). We separated the region into dominant rock assemblages and associated chemical signatures. Rocks with the highest  $^{87}\text{Sr}:^{86}\text{Sr}$  values (typically  $>0.7199$ ) are found in the northern and eastern ends of the basin and are derived from Proterozoic basement rock (Obradovitch and Peterman 1968; Criss and Fleck

**Fig. 2.** (a) Schematic (sagittal section) of a sagittal otolith of an adult summer–fall run subyearling Chinook salmon. Dashed line indicates laser path for elemental analysis and solid line represents otolith width (OW) at freshwater emigration. The maternally influenced region of the otolith, which represents the egg and very early juvenile life history, is shaded and the first winter annulus is labelled. (b) Sr:Ca ( $\text{mmol}\cdot\text{mol}^{-1}$ ) (gray line) and  $^{87}\text{Sr}:^{86}\text{Sr}$  (black line) across an otolith from an adult summer–fall run, subyearling Chinook salmon. Measurement of OW ( $\mu\text{m}$ ) at freshwater emigration is identified. The asterisk identifies the maternally influenced region of the otolith; the gray dashes identify the region across which  $^{87}\text{Sr}:^{86}\text{Sr}$  was averaged to characterize natal source; and the black dashes identify the region across which  $^{87}\text{Sr}:^{86}\text{Sr}$  was averaged to characterize marine residence. (c) Schematic of sagittal otolith from an adult spring run yearling Chinook salmon. Annotations are the same as in (a). (d) Sr:Ca ( $\text{mmol}\cdot\text{mol}^{-1}$ ) (gray line) and  $^{87}\text{Sr}:^{86}\text{Sr}$  (black line) across an otolith from an adult spring run yearling Chinook salmon. Annotations are the same as in (b).



1987). Rocks that underlie the central and western portions of the Basin are parts of terranes accreted to the western edge of North America during the Mesozoic Era. Each terrane has a geologic history that is distinct from its neighbor until they are amalgamated and (or) pushed up against the North American (NA) craton (i.e., a stable portion of a continent that forms the central mass of the continent).

As groups of terranes were accreted to the NA craton, they were commonly stitched together by plutons (i.e., intrusive igneous rocks associated with a subduction zone). Studies of these Mesozoic- and Cenozoic-age plutons and their eruptive equivalents report  $^{87}\text{Sr}:^{86}\text{Sr}$  values  $<0.7210$ , and the ratio generally decreases from east to west with distance away from the edge of the NA craton (Armstrong et al. 1977; Carlson et al. 1981; Armstrong 1988). The boundary between Proterozoic basement and accreted basement rocks in north-central Washington State is approximated by the Okanogan River, the likely source of the modern summer–fall run samples included in this study. Much of the central and western portions of the basin were subsequently covered by the Columbia River Basalts (Fig. 1b), which erupted between 17 and 6 million years ago and have average  $^{87}\text{Sr}:^{86}\text{Sr}$  values of 0.7046 in central Washington (Ramos et al. 2005) but higher values ( $\sim 0.7060$ – $0.7145$ ) for the youngest flows erupted near the tri-state corner of Oregon, Washington, and Idaho (McDougall 1976; Hooper and Hawksworth 1993; Brandon and Goles 1995). To the west of the Columbia River Plateau

basalts, the river passes through the High Cascades region where rocks associated with Eocene to Pleistocene age volcanoes (Cascade Igneous Rocks in Fig. 1b) have average  $^{87}\text{Sr}:^{86}\text{Sr}$  values around 0.7039 (Hedge et al. 1970; Church and Tilton 1973; Schmidt et al. 2008).

Overall, the geologic data indicate that the waters of the upper reaches where the modern and extirpated Chinook salmon in our study originated span a broad range of  $^{87}\text{Sr}:^{86}\text{Sr}$  values (Wadleigh et al. 1985; Goldstein and Jacobsen 1987; Singleton et al. 2006). As noted above, the modern spring and summer–fall run fish likely originated from the Methow and the Okanogan river basins (Fig. 1). Based on the available  $^{87}\text{Sr}:^{86}\text{Sr}$  data, the bedrock geology of these basins may be further divided into three regions: the Methow; the Western Okanogan, including the Similkameen River; and the Eastern Okanogan. The Methow Basin includes igneous rock units of Jurassic–Cretaceous age, which typically have  $^{87}\text{Sr}:^{86}\text{Sr} = 0.7029$  to  $0.7052$  (Greig et al. 1992; Smith and Thorkelson 2002). The Western Okanogan region has igneous rocks similar to those found in the Methow Basin but also has rocks with  $^{87}\text{Sr}:^{86}\text{Sr}$  values from 0.7046 to 0.7093 and minor rock units with values as high as 0.7355 (Menzer 1970; Petó and Armstrong 1976). The Eastern Okanogan Basin includes rocks with relatively high  $^{87}\text{Sr}:^{86}\text{Sr}$  values ( $\sim 0.7199$  to  $0.7270$ ) (Kyser et al. 1994; Hinchey and Carr 2006). In the southern part of the Okanogan Basin,  $^{87}\text{Sr}:^{86}\text{Sr}$

river values would also be influenced by rocks on the west side of the river with lower average values ( $\sim 0.7065$ ) (Dostal et al. 2003). The archaeological otoliths would have come from fish migrating up the Columbia River mainstem to the headwaters or possibly tributaries such as the San Poil, Spokane, or Pend Oreille rivers (Fig. 1).

To supplement the information on bedrock geology, we collected water samples from various river locations (Fig. 1a) for determination of  $^{87}\text{Sr}:^{86}\text{Sr}$ , Sr, and Ca. Samples were collected in acid-washed plastic bottles, chilled, filtered ( $0.25\ \mu\text{m}$ ) within 24 h, and acidified with high purity  $\text{HNO}_3$ . Riverine  $^{87}\text{Sr}:^{86}\text{Sr}$  was determined using MC-ICP-MS at the University of Washington (Seattle, Washington); data were normalized relative to standard reference material NBS 987 ( $\pm 25$  ppm; 2 SE). Sr and Ca data were collected using a Teledyne Leeman Prodigy ICP-optical emission spectrometer. Standard calibrations were generated with standard reference material of known concentration (SPEX Certiprep Group). Samples of standard reference material NIST1643e were introduced throughout the run to estimate accuracy ( $\pm 2\%$ ) and precision ( $\pm 2\%$ ).

In anadromous salmonids, the region of the otolith that is formed prior to yolk-sac absorption can be enriched in marine Sr because vitellogenesis begins during maternal ocean residence (Kalish 1990; Miller and Kent 2009). To characterize only the natal source, otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  data must be collected outside of the maternally influenced region. Therefore, to generate an estimate of  $^{87}\text{Sr}:^{86}\text{Sr}$  during initial river residence, we averaged  $^{87}\text{Sr}:^{86}\text{Sr}$  data across a  $40\ \mu\text{m}$  portion of the otolith immediately outside of the maternally influenced region (Fig. 2). Freshwater otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  values were then grouped by similarity and compared using analysis of variance (ANOVA) on rank-transformed data to meet assumptions of normality and homogeneity of variance (Zar 1996). Statistically homogeneous groups were determined using the Tukey honestly significant difference (HSD) test. Statistica (version 9.1, StatSoft Inc., Tulsa, Oklahoma) was used for all analyses.

Natal otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  values will differ among and within sample groups if individuals originated in rivers with distinct  $^{87}\text{Sr}:^{86}\text{Sr}$  values. However, given that all individuals inhabited marine waters with  $^{87}\text{Sr}:^{86}\text{Sr} = 0.70918$  during the later portion of their life history, this portion of the otolith should display consistent and similar values. Therefore, we averaged  $^{87}\text{Sr}:^{86}\text{Sr}$  data across a  $40\ \mu\text{m}$  portion near the outer edge of each otolith to generate a mean marine otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  (Figs. 2b, 2d). Differences in otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  during marine residence were compared among sample groups (i.e., modern spring run, modern summer–fall run, and archaeological) using ANOVA on rank-transformed data. This provided a quantitative assessment of marine otolith  $^{87}\text{Sr}:^{86}\text{Sr}$ ; significant differences between modern and archaeological marine  $^{87}\text{Sr}:^{86}\text{Sr}$  values would indicate postdepositional alteration.

### Reconstruction of juvenile migratory history

Habitat transitions of individual fish, such as movement from riverine to brackish–oceanic waters, can be identified by variation in otolith composition when there is adequate chemical variation among the habitats of interest. For anadromous species, increases in otolith Sr:Ca can be used to iden-

tify individual movement into brackish–oceanic waters if freshwater Sr:Ca is lower than marine Sr:Ca (Secor et al. 1995; Kraus and Secor 2004; Miller et al. 2010a). Additionally, freshwater  $^{87}\text{Sr}:^{86}\text{Sr}$  is often distinct from the global marine value ( $= 0.70918$ ) (Palmer and Edmond 1989; Bacon et al. 2004). Therefore, variation in  $^{87}\text{Sr}:^{86}\text{Sr}$  between freshwater and marine systems can also be used to identify diadromous movements (Kennedy et al. 2002; Bacon et al. 2004).

We used Sr:Ca and  $^{87}\text{Sr}:^{86}\text{Sr}$  values obtained along transects of the modern and archaeological otoliths to estimate when juveniles emigrated from fresh water. We identified the time of freshwater emigration (i.e., initial entrance into brackish waters) by the inflection points on the life history profiles of Sr:Ca and (or)  $^{87}\text{Sr}:^{86}\text{Sr}$  prior to stabilizing at marine values (Figs. 2a–2d). We then measured otolith width (OW,  $\mu\text{m}$ ) at this transition and used a previously developed relationship between OW and fork length (FL, mm) to estimate juvenile size at freshwater emigration (Miller et al. 2010a). All OWs were measured with Image Pro Plus (Media Cybernetics, Bethesda, Maryland). Fish were classified as yearling or sub-yearling based on size at freshwater emigration and the location of the first winter annulus (i.e., before or after freshwater emigration, respectively). Differences in size at freshwater emigration among the four groups of Chinook salmon were compared with ANOVA on rank-transformed data.

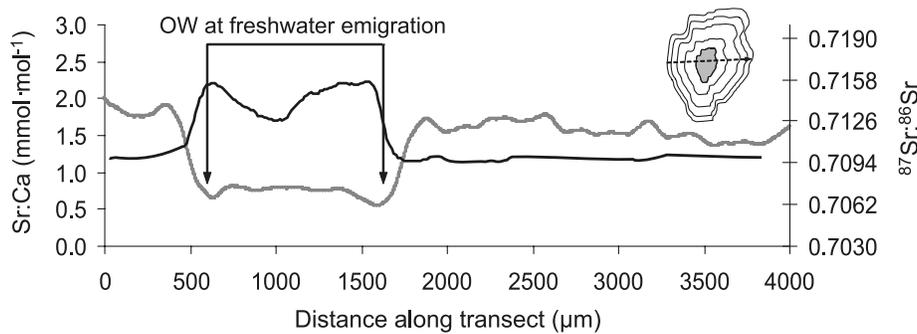
### Estimation of adult body size upon return to the Columbia River

We completed a linear regression analysis of adult FL (cm) and otolith length (OL, mm) along the anterior–posterior growth axis for the modern adult otolith samples and used the relationship to estimate adult size (FL) upon return to the Columbia River for the archaeological samples. For the adult stage, OL is a better predictor of FL than OW. All OLs were measured with Image Pro Plus (Media Cybernetics). Differences in observed FL of the modern runs and estimated FL of the archaeological samples were compared with ANOVA on rank-transformed data.

### Related assessment of otoliths

Initial inspection of archaeological otoliths indicated varying levels of breakage, surface erosion, and surface accretion (i.e., irregular growth on surface). Given that fracturing can accelerate chemical alteration (Banner 1995), breakage and (or) visual expression of surface alteration may be an indicator of postdepositional alteration. Therefore, we developed a ranking criteria (Behrensmeier 1978) to quantify visual damage based on digital images of the distal surface of whole otoliths: 0–1: no visual damage, similar to modern otolith; 1–2: one break or light surface erosion or accretion; 2–3: two breaks or heavy surface erosion or accretion; 3–4: more than two breaks or heavy erosion and (or) accretion; 4–5: more than two breaks and heavy erosion and accretion. Otoliths were ranked independently by two of the authors and a mean rank was calculated. We determined if mean rank was correlated with observed marine otolith  $^{87}\text{Sr}:^{86}\text{Sr}$ . We used the marine  $^{87}\text{Sr}:^{86}\text{Sr}$  because unlike the natal otolith  $^{87}\text{Sr}:^{86}\text{Sr}$ , the values are expected to be similar among all samples. One specimen (Archaeo 3) was excluded from the ranking because we did not have a whole otolith image. We also used scanning electron microscopy (Tescan Vega-II

**Fig. 3.** Sr:Ca ( $\text{mmol}\cdot\text{mol}^{-1}$ ) (gray line) and  $^{87}\text{Sr}:^{86}\text{Sr}$  (black line) across the ventral–dorsal growth axis of an archaeological Chinook salmon otolith. Measurements of otolith width (OW,  $\mu\text{m}$ ) at freshwater emigration are identified.



SBH) to acquire images of the daily increments in a modern and archaeological otolith for visual comparison.

## Results

### Otolith Sr:Ca and $^{87}\text{Sr}:^{86}\text{Sr}$

Sr:Ca across the growth axis of modern otoliths demonstrated the expected pattern of low Sr:Ca ( $<1.2 \text{ mmol}\cdot\text{mol}^{-1}$ ) during presumed freshwater residence and higher values during marine residence ( $1.4$  to  $2.5 \text{ mmol}\cdot\text{mol}^{-1}$ ) (Figs. 2b, 2d). Sr:Ca across the growth axis in the archaeological otoliths also met general expectations: Sr:Ca ratios were  $<0.9 \text{ mmol}\cdot\text{mol}^{-1}$  during presumed freshwater residence, and marine values ranged from  $1.5$  to  $2.2 \text{ mmol}\cdot\text{mol}^{-1}$  (e.g., Fig. 3).

$^{87}\text{Sr}:^{86}\text{Sr}$  across the growth axis of modern otoliths also demonstrated the expected pattern of variable freshwater and consistent marine values of  $0.70918$  (Fig. 2). Although transects of all archaeological otoliths displayed the expected general patterns of initial freshwater and then ocean residence (Fig. 3), the  $^{87}\text{Sr}:^{86}\text{Sr}$  data indicated that the archaeological otoliths were affected by some diagenesis. In particular,  $^{87}\text{Sr}:^{86}\text{Sr}$  values at the edges of the archaeological otoliths, which represent oceanic residence, were higher than the modern spring and summer–fall otoliths ( $F_{[2,24]} = 22.8$ ,  $p < 0.001$ , Tukey's HSD  $p < 0.05$ ). Seven of the modern fish were not included in this statistical analysis because  $^{87}\text{Sr}:^{86}\text{Sr}$  data were not collected at the outermost edge of their otoliths. The range in otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  during presumed ocean residence for the archaeological samples was  $0.70927$ – $0.70960$  (Fig. 4a), which represents a shift to more radiogenic values of  $90$ – $420 \text{ ppm}$ .

### Natal sources

The riverine  $^{87}\text{Sr}:^{86}\text{Sr}$  values confirmed our expectations based on bedrock geology and provided additional spatial resolution (Table 1, see Fig. 1a for locations). For example, the Okanogan River Basin displays a range of bedrock  $^{87}\text{Sr}:^{86}\text{Sr}$  values ( $0.7046$ – $0.7270$ ), yet the mainstem Okanogan River above the influence of the mainstem reservoir below Chief Joseph Dam (i.e., Lake Pateros) displays a moderate to low  $^{87}\text{Sr}:^{86}\text{Sr}$  value of  $0.70584$ . Within the reservoir, the water values ( $0.71528$ ) are clearly influenced by the mid-Columbia mainstem waters ( $0.714$ – $0.715$ ). Similarly, as expected, the highest water  $^{87}\text{Sr}:^{86}\text{Sr}$  values were observed within the most eastern portion of the basin, above Grand Coulee Dam ( $0.71727$ ).

Otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  values during initial freshwater residence indicate that there were four distinct natal sources for the modern Chinook salmon and at least four sources for the archaeological specimens (Fig. 4c). For the modern spring run, all but one individual displayed a consistent pattern of low freshwater  $^{87}\text{Sr}:^{86}\text{Sr}$ , indicative of residence in similar, if not the same, river systems (mean  $\pm 2 \text{ SE} = 0.70438 \pm 0.00096$ ,  $n = 14$ ) (Fig. 4c). One spring run individual was distinct (mean otolith  $^{87}\text{Sr}:^{86}\text{Sr} = 0.70683$ ). All the values except one are similar to the riverine  $^{87}\text{Sr}:^{86}\text{Sr}$  values for the Methow Basin ( $\sim 0.7043$ ). The summer–fall run samples displayed two dominant provenance patterns: mean otolith  $^{87}\text{Sr}:^{86}\text{Sr} \pm 2 \text{ SE} = 0.70651 \pm 0.00021$  ( $n = 8$ ) and  $0.71140 \pm 0.00020$  ( $n = 10$ ) (Fig. 4c). One individual had a mean otolith  $^{87}\text{Sr}:^{86}\text{Sr} = 0.71451$ . Based on bedrock and riverine  $^{87}\text{Sr}:^{86}\text{Sr}$  values, it is plausible that the summer–fall run individuals with  $^{87}\text{Sr}:^{86}\text{Sr} = 0.70651$  originated in the Okanogan River. Given  $^{87}\text{Sr}:^{86}\text{Sr}$  values in the mid-Columbia River region ( $0.714$ – $0.715$ ) (Table 1), the distinctive summer–fall individual may be the progeny of a mainstem spawner. However, it is unlikely that the individuals with  $^{87}\text{Sr}:^{86}\text{Sr} = 0.71140$  originated within the Okanogan River. Therefore, with the exception of the one summer–fall individual ( $^{87}\text{Sr}:^{86}\text{Sr} = 0.71451$ ), the remaining modern samples were visually grouped by natal otolith  $^{87}\text{Sr}:^{86}\text{Sr}$ , and mean differences among those three groups were statistically significant ( $F_{[2,30]} = 121.6$ ,  $p < 0.001$ , Tukey's HSD  $p < 0.05$ ) (Fig. 4b).

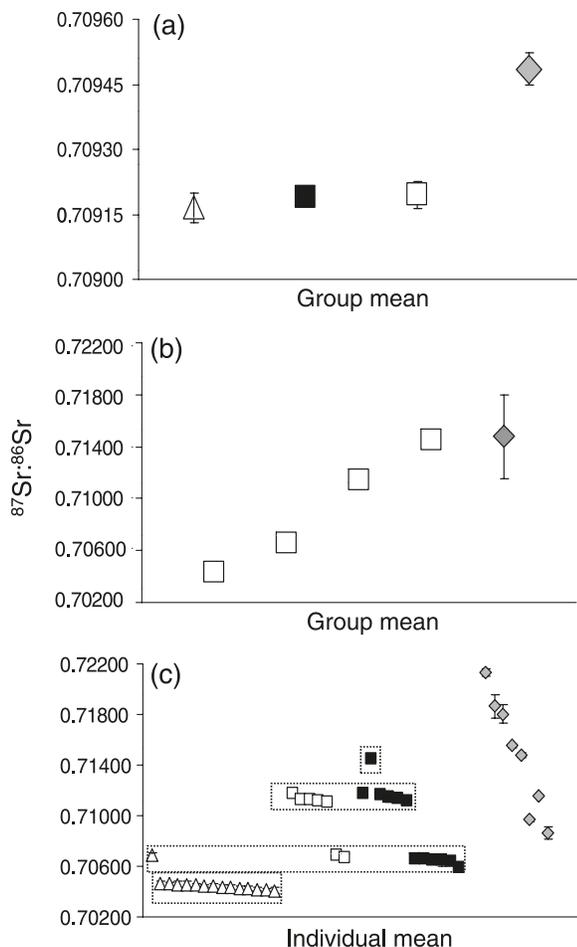
Natal  $^{87}\text{Sr}:^{86}\text{Sr}$  values of the archaeological otoliths ranged from  $0.70966$  to  $0.72134$  (Fig. 4c). Given the observed shift ( $90$ – $420 \text{ ppm}$ ) in the marine  $^{87}\text{Sr}:^{86}\text{Sr}$  values of the archaeological otoliths, it is likely that the natal  $^{87}\text{Sr}:^{86}\text{Sr}$  values also shifted since deposition. Therefore, natal  $^{87}\text{Sr}:^{86}\text{Sr}$  values of archaeological and modern otoliths were not compared in a quantitative manner. Despite the observed diagenesis, it appears that none of the archaeological samples originated in low  $^{87}\text{Sr}:^{86}\text{Sr}$  watersheds similar to the modern spring run Chinook salmon (Fig. 4c). Additionally, three of the archaeological otoliths displayed substantially more radiogenic  $^{87}\text{Sr}:^{86}\text{Sr}$  values ( $>0.7180$ ) than observed in any of the modern otoliths.

### Reconstruction of juvenile migratory history

We used eq. 1 to estimate juvenile size at freshwater emigration (Miller et al. 2010a).

$$(1) \quad \text{FL} = 0.060 (\pm 0.002 \text{ SE}) \times \text{OW} + 6.91 (\pm 2.19 \text{ SE})$$

**Fig. 4.** Otolith  $^{87}\text{Sr}:$  $^{86}\text{Sr}$  for modern and archaeological Chinook salmon. (a) Otolith  $^{87}\text{Sr}:$  $^{86}\text{Sr}$  (mean  $\pm$  2 standard errors, SE) during residence in oceanic waters for modern spring run Chinook salmon (triangles:  $n = 9$ ), modern summer–fall run yearlings (filled squares:  $n = 2$ ), modern summer–fall subyearlings (open squares:  $n = 8$ ), and archaeological otoliths (filled diamonds:  $n = 8$ ). (b) Mean ( $\pm$  2 SE) otolith  $^{87}\text{Sr}:$  $^{86}\text{Sr}$  during initial freshwater residence for statistically homogeneous groups for modern samples (open squares) along with the mean ( $\pm$  2 SE) for the archaeological collections (filled diamond). (c) Otolith  $^{87}\text{Sr}:$  $^{86}\text{Sr}$  during initial freshwater residence for Chinook salmon for modern and archaeological collections (individual mean  $\pm$  2 SE). Open triangles indicate modern spring run Chinook salmon; open squares indicate modern summer–fall run, yearlings; filled squares indicate modern summer–fall subyearlings; and gray diamonds indicate archaeological otoliths. Boxes denote individuals within each of the statistically distinct groups presented in (b).



For juveniles  $>175$  mm FL, eq. 1 underestimates FL. As the majority of Columbia River Chinook salmon ( $>90\%$ ) enter brackish waters at sizes  $<175$  mm FL (Rich 1920; Giorgi et al. 1994; Tiffan et al. 2000), we used this relationship to estimate juvenile size at the time of freshwater emigration to brackish–ocean waters.

Based on these estimates, modern yearling individuals were the largest upon freshwater emigration ( $F_{[3,38]} = 23.7$ ,  $n = 42$ ,  $p < 0.001$ , Tukey's HSD  $p < 0.05$ ). However, there was no difference between yearlings from the spring and

summer–fall runs (Tukey's HSD  $p > 0.10$ ). The mean calculated size at freshwater emigration for the archaeological samples was statistically similar, although slightly smaller, than the modern subyearlings (Fig. 5a). Our otolith-derived estimates for size at freshwater emigration for modern spring and summer–fall run individuals fall within the observed size range for middle and upper Columbia spring and summer–fall run juveniles collected in recent (2002–2007) beach and purse seines in the estuary (Fig. 6; D. Bottom, National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center (NOAA NWFSC), Newport, Oregon, and D. Teel, NOAA NWFSC, Manchester, Washington, unpublished data).

#### Estimation of adult size body upon return to the Columbia River

For modern adults, FL (cm) was linearly and positively related with OL for fish that were  $<95$  cm FL with OL  $<14$  mm ( $r^2 = 0.85$ ,  $n = 22$ ,  $p < 0.001$ ):

$$(2) \quad \text{FL} = 9.2 (\pm 0.9 \text{ SE}) \times \text{OL} - 24.3 (\pm 10.2 \text{ SE})$$

For otoliths  $\geq 14$  mm, OL underestimated adult FL. Eight modern individuals were excluded from this analysis because they had broken otoliths ( $n = 6$ ) or were classified as immature ( $n = 2$ ) based on their reproductive state. Because all archaeological otoliths were  $<14$  mm, we used eq. 2 to estimate adult body size of these samples (Appendix A, Table A1).

For modern runs, observed adult size (FL) ranged from 64 to 112 cm. Adult size ranged from 73 to 95 cm FL for spring run yearlings; 81 to 112 cm FL for summer–fall run yearlings; and 64 to 101 cm FL for summer–fall run subyearlings. Based on eq. 2, the estimated adult body size of the archaeological samples ranged from 67 to 94 cm FL. Mean adult body size was significantly different among the four groups ( $F_{[3,36]} = 3.7$ ,  $n = 40$ ,  $p = 0.02$ ). The estimated mean adult size of the archaeological samples was significantly smaller than the summer–fall run yearlings but similar to both the modern summer–fall run subyearlings and spring run yearlings (Fig. 5b).

#### Related assessments of otoliths

The mean rank of visual damage was positively and significantly correlated with observed marine  $^{87}\text{Sr}:$  $^{86}\text{Sr}$  otolith values (Pearson's  $r = 0.77$ ,  $n = 7$ ,  $p < 0.05$ ; Figs. 7a–7d). All of the archaeological otoliths were collected from the same layer and date to the same period (250–500 years ago); thus, we have no independent basis for determining whether the observed variation in marine  $^{87}\text{Sr}:$  $^{86}\text{Sr}$  among samples is related to length of time since deposition. However, we note that the variation in marine  $^{87}\text{Sr}:$  $^{86}\text{Sr}$  among archaeological otoliths was not correlated with otolith size (i.e., length, width, or total area) (Pearson's  $r < 0.30$ ,  $n = 7$ ,  $p > 0.50$ ). Fine-scale increment structure was visible in an archaeological otolith and appeared similar to a modern specimen (Figs. 7e–7f).

#### Discussion

The information extracted from the admittedly small sample size of archaeological Chinook salmon otoliths collected

**Table 1.** Riverine  $^{87}\text{Sr}:^{86}\text{Sr}$ , Sr (ppb), and Sr:Ca (mmol·mol<sup>-1</sup>) data for various locations in the Columbia River Basin.

ID	Location	Riverine $^{87}\text{Sr}:^{86}\text{Sr}$	Sr (ppb)	Sr:Ca (mmol·mol <sup>-1</sup> )	Source
A	Columbia River mainstem, below Bonneville Dam	0.713278	66.0	2.35	This study
B	Columbia River mainstem, below Dalles Dam	0.713042	62.6	2.32	This study
C	Columbia River mainstem, below John Day Dam	0.713906	73.0	2.36	This study
D	Columbia River mainstem, below McNary Dam	0.713570	66.9	2.30	This study
E	Columbia River mainstem, above Priest Rapids Dam	0.71400	81.5	—	Singleton et al. 2006
F	Columbia River mainstem, ~12 RK downstream of Chief Joseph Dam	0.715283	76.6	2.07	This study
G	Columbia River mainstem, below Chief Joseph Dam	0.716671	72.4	1.94	This study
H	Columbia River mainstem, below Grand Coulee Dam	0.716661	73.0	1.95	This study
J	Columbia River mainstem, above Grand Coulee Dam	0.717270	67.3	1.93	This study
K	Columbia River mainstem, below Pend Oreille River	0.71563	74.0	1.78	Wadleigh et al. 1985
L	Snake River, above confluence with Columbia River	0.710339	53.3	3.06	This study
M	Yakima River	0.70731	136.0	—	Singleton et al. 2006
N	Methow River, approximately RK 35	0.704275	83.7	3.23	This study
O	Twisp River, tributary to the Methow River	0.704374	55.7	2.58	This study
P	Okanogan River, at approximately RK 25	0.705838	128.4	3.26	This study

**Note:** Samples below mainstem dams were collected within 5 km of the dam unless otherwise noted. Sample sites are identified by letters; see Fig. 1 for approximate locations. RK, river kilometre; —, no data.

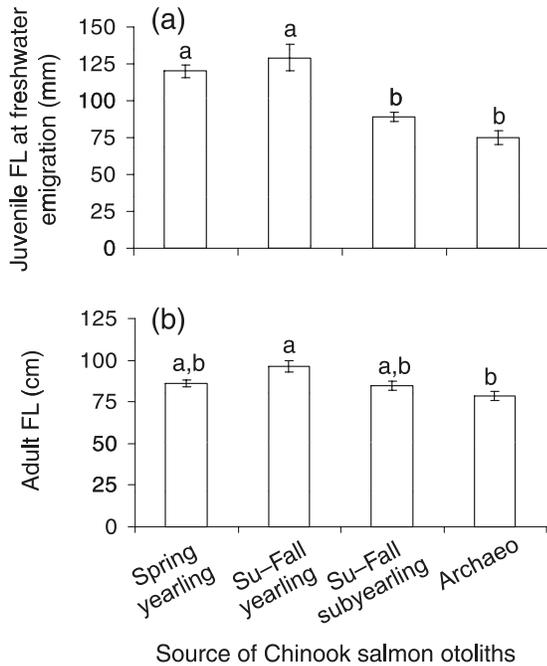
in the upper Columbia River Basin provides novel insights on the life history of extirpated salmon populations that is germane to contemporary salmon conservation and recovery. The combined evidence indicates that the life history of the fish represented by these archaeological specimens was most similar to the modern summer–fall subyearling run. We tentatively suggest that these individuals would be included in the modern definition of the upper Columbia summer–fall run ESU. As currently defined, the upper Columbia summer–fall run ESU is composed of fish that spawn in areas between McNary Dam (45°55'N, 119°17'W), which is located 470 km from the mouth of the Columbia River, and Chief Joseph Dam (Myers et al. 1998). Fish from this ESU primarily display a subyearling life history, and substantial differences in life history and genetics distinguish fish in this ESU from the middle and upper Columbia River spring run ESUs.

Prior to major hydropower development, Chinook salmon migrated some distance upstream of the current location of Grand Coulee Dam to spawn. According to Fulton (1968), individuals from the summer run migrated further upriver than those from the fall run, and there are reports of large, summer run Chinook salmon passing the natural obstruction at Kettle Falls and arriving at Windermere Lake, British Columbia, at the headwaters of the Columbia River (Bryant and Parkhurst 1950). Our data provide further evidence for a pre-development subyearling life history above Chief Joseph Dam, the current upstream extent of salmon distribution. The individuals we examined could have originated within the mainstem Columbia River anywhere above Chief Joseph Dam or within the Spokane or Pend Oreille rivers. However, origination in the San Poil Basin is unlikely for all except two of the archaeological samples because of low values of bedrock and riverine  $^{87}\text{Sr}:^{86}\text{Sr}$  (<0.7096) (Morris et al. 2000). The high  $^{87}\text{Sr}:^{86}\text{Sr}$  values (>0.718) observed in three of the archaeological otoliths indicate that these fish originated relatively high in the basin where more radiogenic waters may occur. Potential sources include the mainstem of the Columbia River upstream of the Pend Oreille River or within the Pend Oreille or Spokane rivers. However, there

was a major waterfall on the Spokane River, ~80 km upriver of its confluence with the Columbia River, which was a likely barrier (Fulton 1968).

We were interested in determining if the level of diagenesis would limit our ability to examine other samples from different locations or time periods. Chinook salmon otoliths are composed of aragonite, which is considered more prone to diagenesis than other polymorphs of calcium, such as calcite (Marshall 1992). Diagenesis can occur because of cementation, recrystallization, or replacement, and the rate of alteration depends on the local burial conditions and sample porosity, among other factors (Banner 1995; Cuif et al. 2008). Although fracturing alone does not usually lead to chemical alteration, it may aid the passage of fluids and allow, or accelerate, subsequent alteration (Banner 1995). Depending on the method of chemical alteration and the element or isotope under consideration, the pattern of diagenesis can result in a linear covariance between the original and local source, which would allow for correction via “backstripping” (i.e., extrapolation) if original values are known (Marshall 1992). In this study, all archaeological otoliths displayed similar directionality in their shift to more radiogenic  $^{87}\text{Sr}:^{86}\text{Sr}$  marine values. Given that marine  $^{87}\text{Sr}:^{86}\text{Sr}$  is increasing at a very slow rate (Hess et al. 1986), the increase in otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  values cannot be due to changes in the ocean values. Water  $^{87}\text{Sr}:^{86}\text{Sr}$  values in the mainstem Columbia River in the vicinity of the archaeological site were ~0.7167; therefore, local substitution should result in more radiogenic values as was observed. Furthermore, if substitution was occurring in a linear manner and the diagenetic Sr is similar to surface waters at the archaeological site, the overall substitution ranged from 3% to 16% within 250–500 years. If Sr diagenesis occurs at a constant rate, we would expect 32%–65% Sr substitution in 1000-year-old samples. One option for future analyses is to use the observed shift from expected marine  $^{87}\text{Sr}:^{86}\text{Sr}$  values during ocean residence, in conjunction with data on  $^{87}\text{Sr}:^{86}\text{Sr}$  values at the burial environment, to estimate the extent of local substitution and correct (or backstrip) the observed natal otolith

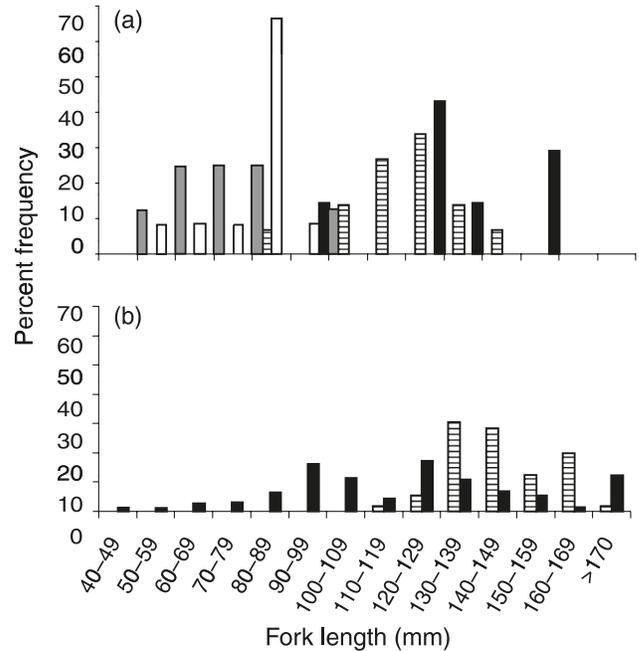
**Fig. 5.** Mean ( $\pm 2$  standard errors, SE) size of modern and archaeological Chinook salmon. (a) Estimated juvenile fork length (FL, mm) at freshwater emigration. Data are included for modern spring run yearlings, modern summer–fall (Su–Fall) run yearlings and sub-yearlings, and for archaeological samples. Statistically similar groups are denoted by the same letter. (b) Adult body size (FL, cm) for modern and archaeological specimens. For modern runs, body size was measured in the field, and for archaeological samples, body size was estimated using the observed relationship between body size and otolith length for modern runs.



$^{87}\text{Sr}:^{86}\text{Sr}$  values (Marshall 1992). Alternatively, samples older than ~500 years could receive additional sample treatment, such as acid leaches, to remove diagenetic strontium (Dufour et al. 2007). In situations where adequate numbers of samples are available, those with the least extent of visible surface alteration could be included preferentially. Other analysis, such as X-ray diffraction, could also provide information on whether observed shifts in marine  $^{87}\text{Sr}:^{86}\text{Sr}$  of archaeological samples are correlated with replacement of aragonite by another mineral form (e.g., apatite or calcite; Stathopoulou et al. 2008; Kasiopas et al. 2010).

A related point on the ability to determine provenance in extant populations is highlighted by the lack of correspondence between regional and otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  in eight of the modern samples. Based on natal otolith  $^{87}\text{Sr}:^{86}\text{Sr}$ , it is highly unlikely that eight of the modern summer–fall run fish originated within the Okanogan River or the Columbia River mainstem upstream of Wells Dam. The Eastbank Hatchery, located on the Columbia River adjacent to Rocky Reach Dam, produces summer run Chinook salmon that are transferred to the Similkameen Acclimation Pond on the Okanogan River for 2 weeks prior to release. Because otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  can be influenced by food, otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  in hatchery fish is often shifted toward marine  $^{87}\text{Sr}:^{86}\text{Sr}$  values because of the use of feed dominated by marine protein ( $^{87}\text{Sr}:^{86}\text{Sr} = 0.70918$ ) (22%–42% food contribution; Miller et al. 2010b). Therefore, given mainstem river  $^{87}\text{Sr}:^{86}\text{Sr}$  (0.714–

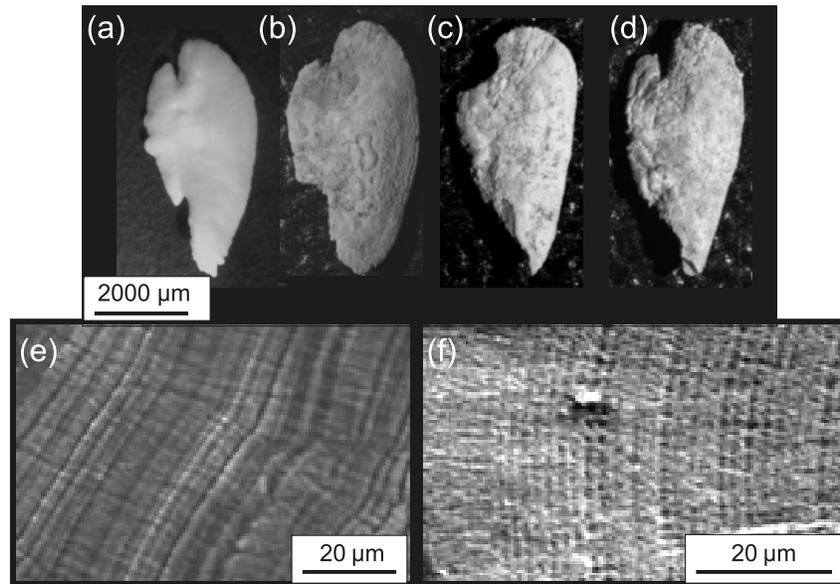
**Fig. 6.** Size frequency of juvenile Chinook salmon from the mid- and upper Columbia River. (a) Back-calculated size at freshwater emigration (fork length (FL), mm) for modern and archaeological Chinook salmon based on adult otolith analysis. Open bars indicate modern spring run Chinook salmon ( $n = 15$ ); hatched bars indicate modern summer–fall run yearlings ( $n = 7$ ); filled bars indicate modern summer–fall subyearlings ( $n = 12$ ); and gray bars indicate archaeological otoliths ( $n = 12$ ). (b) Size (FL, mm) of modern middle and upper Columbia River spring and summer–fall run Chinook salmon from estuarine beach and purse seines collections (2002–2007). Hatched bars represent modern spring run ( $n = 56$ ), and filled bars represent modern summer–fall run ( $n = 76$ ). Unpublished data for (b) provided by D. Bottom, NOAA NWFSC, Newport, Oregon, and D. Teel, NOAA NWFSC, Manchester, Washington.



0.715), it is most likely that the fish with natal  $^{87}\text{Sr}:^{86}\text{Sr} = 0.71140$  originated from the Eastbank Hatchery and were transferred to the Okanogan River as juveniles. This conclusion is supported by a recent study characterizing natal otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  values in several Columbia River hatcheries; Barnett-Johnson et al. (2010) reported natal otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  of  $0.71113 \pm 0.00023$  (mean  $\pm 1$  SD;  $n = 10$ ) for Eastbank Hatchery summer Chinook salmon, values very similar to the eight otoliths in this study. The accuracy of scale analysis to differentiate hatchery and naturally produced fish could be further evaluated through examination of natal otolith  $^{87}\text{Sr}:^{86}\text{Sr}$  in additional samples.

Waples et al. (2008) note the potential for evolutionary change in salmonid life history traits as a result of the Columbia River hydropower system, which has reduced average and peak stream flows, increased residence times of water, and altered water temperatures. Given that at least a component of juvenile migratory timing is heritable (Taylor 1991), alteration of the selective environment can lead to changes in migration timing (Waples et al. 2009); this is exemplified by the recent development of a reservoir-type life history within the predominantly subyearling Snake River fall run Chinook salmon population (Connor et al. 2005; Williams et al.

**Fig. 7.** Images of modern and archaeological otoliths. Distal surface of whole (a) modern and archaeological otoliths (b–d). Archaeological samples are arranged along a gradient of  $^{87}\text{Sr}:^{86}\text{Sr}$  ratios observed at the otolith edge (i.e., during presumed ocean residence). Marine  $^{87}\text{Sr}:^{86}\text{Sr}$  values are as follows: (a) 0.70919; (b) 0.709267; (c) 0.709495; (d) 0.70953. Note that the visible extent of surface erosion increases from (b) to (d). Scanning electron micrographs of daily increments in (e) modern and (f) archaeological otolith are also shown.



2008). Currently, the peak arrival time of upriver juveniles in the estuary occurs approximately 2 weeks later than historical accounts (Park 1969; Bottom et al. 2005). Although we cannot independently determine arrival time of the fish represented by our archaeological samples, we note that their comparatively small sizes (59–101 mm FL) point to a relatively early arrival.

Rich (1920) observed juvenile Chinook salmon 40–100 mm FL in the Columbia River estuary during June and July, which is similar to the estimated size at freshwater emigration for the archaeological samples (59–101 mm FL). Park (1969) noted that prior to the impoundments on the upper Columbia River, most juveniles from the summer runs emigrated in their first year of life. He further commented that “there was no significant downstream migration of juvenile Chinooks after June” at Bonneville Dam from 1946 to 1953 (Park 1969). Recent work indicates that upper Columbia summer–fall run Chinook salmon juveniles 40–173 mm FL comprised approximately 6% of the beach seine collections in the Columbia River estuary (D. Bottom, NOAA NWFSC, Newport, Oregon, and D. Teel, NOAA NWFSC, Manchester, Washington, unpublished data). In that study, 61% of the upper Columbia River summer–fall juveniles fell within the size range of our archaeological samples (59–101 mm FL) and were mostly captured in June and July sampling (D. Teel, NOAA NWFSC, Manchester, Washington, personal communication, 2009). Thus, it appears that the size at and approximate timing of juvenile migration observed in the archaeological samples is similar to a component of the extant upper Columbia summer–fall run.

We found no evidence of yearling emigrants in our archaeological samples. Although some information indicates that prior to the impoundments on the upper Columbia River, most juveniles from summer runs emigrated in their first year of life (Park 1969), Myers et al.’s (1998) synthesis indicates that 12%–42% of the summer run populations in the upper

Columbia River emigrated as yearlings. More archaeological samples are needed to draw any conclusions regarding the extent of variation in predevelopment life histories. Furthermore, if the indigenous fishery occurred mainly during late summer during low flow periods, the archaeological otoliths would represent a biased sample of the predevelopment Chinook salmon life histories. Although it is not clear how important yearling emigrants were to upper Columbia River Chinook salmon populations, there has been an increase in the number and proportion of summer–fall Chinook salmon released from upper Columbia River hatcheries as yearlings. In the early 1970s, less than 2 million summer–fall run Chinook salmon were released from hatcheries and none of these were yearlings. In the last 5 years, approximately 2–5 million fish were released annually and 26–56% of those were released as yearlings (Regional Mark Processing Center: <http://www.rmpc.org/>).

We have demonstrated the feasibility of reconstructing aspects of the life history of an anadromous species based on 250- to 500-year-old otoliths. With adequate background information, similar approaches would be applicable to other anadromous species. Information on life history variation prior to development provides a baseline with which to assess the status of extant populations. The combined evidence indicates that the extirpated population reflected in the archaeological otoliths represents a summer–fall run with a subyearling life history. The presence of similar life history traits in some of the extant samples suggests that this Chinook salmon life history pattern persists in the Columbia River system. As Healey (2009) notes, management strategies may promote the dominant tactic, or phenotype, thereby reducing life history variation, which may in turn reduce population resiliency. Alternatively, as exemplified by the recent development of the reservoir-rearing life history (Connor et al. 2005; Williams et al. 2008), changes in the selection environment can also promote novel phenotypes. The

relative importance of genetic vs. environmental factors in the development and maintenance of juvenile migratory history remains uncertain. However, a reduction in life history diversity in Chinook salmon has occurred since the development of the Columbia River Basin, at least partially because of the great reduction in historic spawning habitat, changes in hydrology, and the establishment of an extensive hatchery program (Bottom et al. 2005). It appears that the potential to maintain aspects of the predevelopment life history variation within the modified landscape of the Columbia River still exists, and further action to implement management strategies that promote maintenance of that life history diversity is warranted.

## Acknowledgements

J. Cook (Confederated Tribes of the Colville) facilitated the loan from the Nespelem Repository; the Confederated Tribes of the Colville Reservation kindly permitted this study of their archaeological remains; C. Snow (WDFW) collected modern otoliths and answered numerous questions about the samples; J. Sneva and L. Campbell (WDFW) provided information regarding the scale analysis; and D. Teel, L. Weitkamp, and C. Roegner provided seine data. We appreciate the assistance of B. Nelson (University of Washington) for water  $^{87}\text{Sr}$ : $^{86}\text{Sr}$  analyses and C. Young (University of Oregon) for SEM. Helpful comments on earlier versions of this manuscript were provided by D. Bottom, D. Teel, R. Waples, L. Weitkamp, K. Limburg, S. Turner, and an anonymous reviewer. Financial support came from Oregon State University Coastal Oregon Marine Experimental Station (J.A.M.) and the Bonneville Power Administration (C.A.S. and J.A.M.).

## References

- Armstrong, R.L. 1988. Mesozoic and early Cenozoic magmatic evolution of the Canadian Cordillera. *Geol. Soc. Am. Spec. Pap.* **218**: 55–91.
- Armstrong, R.L., Taubeneck, W.H., and Hales, P.O. 1977. Rb–Sr and K–Ar geochronometry of Mesozoic granitic rocks and their Sr isotopic composition, Oregon, Washington, and Idaho. *Geol. Soc. Am. Bull.* **88**(3): 397–411. doi:10.1130/0016-7606(1977)88<397:RAKGM>2.0.CO;2.
- Arppe, L., Karhu, J.A., and Vartanyan, S.L. 2009. Bioapatite  $^{87}\text{Sr}/^{86}\text{Sr}$  of the last woolly mammoths: implications for the isolation of Wrangel Island. *Geology*, **37**(4): 347–350. doi:10.1130/G25467A.1.
- Bacon, C.R., Weber, P.K., Larsen, K.A., Reisenbichler, R., Fitzpatrick, J.A., and Wooden, J.L. 2004. Migration and rearing histories of Chinook salmon (*Oncorhynchus tshawytscha*) determined by ion microprobe Sr isotope and Sr/Ca transects of otoliths. *Can. J. Fish. Aquat. Sci.* **61**(12): 2425–2439. doi:10.1139/f04-167.
- Banner, J.L. 1995. Application of the trace element and isotope geochemistry of strontium to studies of carbonate diagenesis. *Sedimentology*, **42**(5): 805–824. doi:10.1111/j.1365-3091.1995.tb00410.x.
- Barnett-Johnson, R., Teel, D.J., and Casillas, E. 2010. Genetic and otolith isotopic markers identify salmon populations in the Columbia River at broad and fine geographic scales. *Environ. Biol. Fishes*, **89**(3–4): 533–546. doi:10.1007/s10641-010-9662-5.
- Behrensmeier, A.K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology*, **4**(2): 150–162.
- Bottom, D.L., Simenstad, C.A., Burke, J., Baptista, A.M., Jay, D.A., Jones, K.K., Casillas, E., and Schiewe, M.H. 2005. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. US Dept. Comm. NOAA Tech. Memo. NMFS-NWFSC-68.
- Brandon, A.D., and Goles, G.G. 1995. Assessing subcontinental lithospheric mantle sources for basalts: neogene volcanism in the Pacific Northwest, USA, as a test case. *Contrib. Mineral. Petrol.* **121**(4): 364–379. doi:10.1007/s004100050102.
- Bryant, F.G., and Parkhurst, Z.E. 1950. Survey of the Columbia River and its tributaries. Part 4, Area III. Washington streams from the Klickitat and Snake Rivers to Grand Coulee Dam, with notes on the Columbia and its tributaries above Grand Coulee Dam. US Fish Wildl. Serv. Spec. Sci. Rep. Fish. **37**: 1–108.
- Butler, V.L. 1990. Distinguishing natural from cultural salmonid deposits in Pacific Northwest North America. Ph.D. dissertation, University of Washington, Seattle, Washington.
- Butler, V.L., and Chatters, J.C. 1994. The role of bone density in structuring prehistoric salmon bone assemblages. *J. Archaeol. Sci.* **21**(3): 413–424. doi:10.1006/jasc.1994.1039.
- Campana, S.E. 2004. Otolith elemental composition as a natural marker of fish stocks. In *Stock identification methods*. Edited by S. X. Cadrin, K.D. Friedland, and J.R. Waldman. Academic Press, New York. pp. 227–245.
- Carlson, R.W., Lugmair, G.W., and Macdougall, J.D. 1981. Columbia River volcanism: the question of mantle heterogeneity or crustal contamination. *Geochim. Cosmochim. Acta*, **45**(12): 2483–2499. doi:10.1016/0016-7037(81)90100-9.
- Casteel, R.W. 1974. Identification of the species of Pacific salmon (genus *Oncorhynchus*) native to North America based upon otoliths. *Copeia*, **1974**(2): 305–311. doi:10.2307/1442524.
- Church, S.E., and Tilton, G.R. 1973. Lead and strontium studies in the Cascade Mountains: bearing on andesite genesis. *Geol. Soc. Am. Bull.* **84**(2): 431–454. doi:10.1130/0016-7606(1973)84<431:LASISI>2.0.CO;2.
- Connor, W.P., Sneva, J.G., Tiffan, K.F., Steinhorst, R.K., and Ross, D. 2005. Two alternative juvenile life history types for fall Chinook salmon in the Snake River basin. *Trans. Am. Fish. Soc.* **134**(2): 291–304. doi:10.1577/T03-131.1.
- Conover, D.O., Clarke, L.M., Munch, S.B., and Wagner, G.N. 2006. Spatial and temporal scales of adaptive divergence in marine fishes and the implications for conservation. *J. Fish Biol.* **69**(Suppl. sc): 21–47. doi:10.1111/j.1095-8649.2006.01274.x.
- Criss, R.E., and Fleck, R.J. 1987. Petrogenesis, geochronology, and hydrothermal systems of the northern Idaho Batholith and adjacent areas based on  $^{18}\text{O}/^{16}\text{O}$ , D/H,  $^{87}\text{Sr}/^{86}\text{Sr}$ , K–Ar, and  $^{40}\text{Ar}/^{39}\text{Ar}$  studies. United States Geological Survey Professional Paper, **1436**: 95–137.
- Cuif, J.P., Dauphin, Y., Meibom, A., Rollion-Bard, C., Salome, M., Susini, J., and Williams, C.T. 2008. Fine-scale growth patterns in coral skeletons: biochemical control over crystallization of aragonite fibres and assessment of early diagenesis. *Geol. Soc. London Spec. Pub.* **303**(1): 87–96. doi:10.1144/SP303.7.
- Dostal, J., Breitsprecher, K., Church, B.N., Thorkelson, D., and Hamilton, T.S. 2003. Eocene melting of Precambrian lithospheric mantle: analcime-bearing volcanic rocks from the Challis–Kamloops belt of south central British Columbia. *J. Volcanol. Geotherm. Res.* **126**(3–4): 303–326. doi:10.1016/S0377-0273(03)00153-7.
- Dufour, E., Holmden, C., Van Neer, W., Zazzo, A., Patterson, W.P., Degryse, P., and Keppens, E. 2007. Oxygen and strontium isotopes as provenance indicators of fish at archaeological sites: the case study of Sagalassos, SW Turkey. *J. Archaeol. Sci.* **34**(8): 1226–1239. doi:10.1016/j.jas.2006.10.014.

- Faure, G. 2001. Origin of igneous rocks: the isotopic evidence. Springer, New York.
- Francis, R.I.C.C. 1990. Back-calculation of fish length: a critical review. *J. Fish Biol.* **36**(6): 883–902. doi:10.1111/j.1095-8649.1990.tb05636.x.
- Fulton, L.A. 1968. Spawning areas and abundance of Chinook salmon, *Oncorhynchus tshawytscha*, in the Columbia River Basin — past and present. US Fish Wildl. Serv. Spec. Sci. Rep. Fish. 571.
- Giorgi, A.E., Miller, D.R., and Sandford, B.P. 1994. Migratory characteristics of juvenile ocean-type chinook salmon, *Oncorhynchus tshawytscha*, in John Day Reservoir on the Columbia River. *Fish Bull.* **92**: 872–879.
- Goldstein, S.J., and Jacobsen, S.B. 1987. The Nd and Sr isotopic systematics of river-water dissolved material: implications for the sources of Nd and Sr in seawater. *Chem. Geol.* **66**: 245–272.
- Good, T.P., Waples, R.S., and Adams, P. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. US Dept. Comm. NOAA Tech. Memo. NMFS-NWFSC-66.
- Greig, C.J., Armstrong, R.L., Harakal, J.E., Runkle, D., and van der Heyden, P. 1992. Geochronometry of the Eagle Plutonic Complex and the Cohuilla area, southwestern British Columbia. *Can. J. Earth Sci.* **29**: 812–829.
- Gustafson, R.G., Waples, R.S., Myers, J.M., Weitkamp, L.A., Bryant, G.J., Johnson, O.W., and Hard, J.J. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. *Conserv. Biol.* **21**(4): 1009–1020. doi:10.1111/j.1523-1739.2007.00693.x. PMID:17650251.
- Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In Pacific salmon life histories. Edited by C. Groot and L. Margolis. UBC Press, Vancouver, British Columbia. pp. 313–393.
- Healey, M.C. 2009. Resilient salmon, resilient fisheries for British Columbia, Canada. *Ecology and Society*, **14**(1): 2. Available from <http://www.ecologyandsociety.org/vol14/iss1/art2/>.
- Hedge, C.E., Hildreth, R.A., and Henderson, W.T. 1970. Strontium isotopes from Cenozoic lavas from Oregon and Washington. *Earth Planet. Sci. Lett.* **8**(6): 434–438. doi:10.1016/0012-821X(70)90147-0.
- Hedman, K.M., Curry, B.B., Johnson, T.M., Fullagar, P.D., and Emerson, T.E. 2009. Variation in strontium isotope ratios of archaeological fauna in the Midwestern United States: a preliminary study. *J. Archaeol. Sci.* **36**(1): 64–73. doi:10.1016/j.jas.2008.07.009.
- Hendry, A.P., and Kinnison, M.T. 1999. Perspective: The pace of modern life: measuring rates of contemporary microevolution. *Evolution*, **53**(6): 1637–1653. doi:10.2307/2640428.
- Hess, J., Bender, M.L., and Schilling, J.-G. 1986. Evolution of the ratio of strontium-87 to strontium-86 in seawater from Cretaceous to present. *Science (Washington, D.C.)*, **231**(4741): 979–984. doi:10.1126/science.231.4741.979. PMID:17740296.
- Hinchey, A.M., and Carr, S.D. 2006. The S-type Ladybird leucogranite suite of southeastern British Columbia: geochemical and isotopic evidence for a genetic link with migmatite formation in the North American basement gneisses of the Monashee complex. *Lithos*, **90**(3–4): 223–248. doi:10.1016/j.lithos.2006.03.003.
- Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, **120**(3): 314–326. doi:10.1007/s004420050865.
- Hooper, P.R., and Hawksworth, C.J. 1993. Isotopic and geochemical constraints on the origin and evolution of the Columbia River. *J. Petrol.* **34**: 1203–1246.
- Ingram, B.L., and Weber, P.K. 1999. Salmon origin in California's Sacramento–San Joaquin river system as determined by otolith strontium isotopic composition. *Geology*, **27**(9): 851–854. doi:10.1130/0091-7613(1999)027<0851:SOICSS>2.3.CO;2.
- Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. *Fish Bull.* **88**(4): 657–666.
- Kasioptas, A., Geisler, T., Putnis, C.V., Perdikouri, C., and Putnis, A. 2010. Crystal growth of apatite by replacement of an aragonite precursor. *J. Cryst. Growth*, **312**(16–17): 2431–2440. doi:10.1016/j.jcrysgro.2010.05.014.
- Kennedy, B.P., Folt, C.L., Blum, J.D., and Chamberlain, C.P. 1997. Natural isotope markers in salmon. *Nature (London)*, **387**(6635): 766–767. doi:10.1038/42835.
- Kennedy, B.P., Klaue, A., Blum, J.D., Folt, C.L., and Nislow, K.H. 2002. Reconstructing the lives of fish using Sr isotopes in otoliths. *Can. J. Fish. Aquat. Sci.* **59**(6): 925–929. doi:10.1139/f02-070.
- Koch, P.L., Halliday, A.N., Walter, L.M., Stearley, R.F., Huston, T.J., and Smith, G.R. 1992. Sr isotopic composition of hydroxyapatite from recent and fossil salmon: the record of lifetime migration and diagenesis. *Earth Planet. Sci. Lett.* **108**(4): 277–287. doi:10.1016/0012-821X(92)90028-T.
- Kraus, R.T., and Secor, D.H. 2004. Incorporation of strontium into otoliths of an estuarine fish. *J. Exp. Mar. Biol. Ecol.* **302**(1): 85–106. doi:10.1016/j.jembe.2003.10.004.
- Kyser, T.K., Ghent, E.D., and Sevigny, J.H. 1994. Petrogenesis of two-mica granites, northern Monashee Mountains, British Columbia: evidence from oxygen, hydrogen, and strontium isotopic compositions. *Geol. Soc. Am. Bull.* **106**(12): 1531–1537. doi:10.1130/0016-7606(1994)106<1531:POTMGN>2.3.CO;2.
- Marshall, J.D. 1992. Climatic and oceanographic isotopic signals from the carbonate rock record and their preservation. *Geol. Mag.* **129**(2): 143–160. doi:10.1017/S0016756800008244.
- McDougall, I. 1976. Geochemistry and origin of basalt of the Columbia River group, Oregon and Washington. *Geol. Soc. Am. Bull.* **87**(5): 777–792. doi:10.1130/0016-7606(1976)87<777:GAOBO>2.0.CO;2.
- Menzer, F.J. 1970. Geochronologic study of granitic rocks from the Okanogan Range, north-central Washington. *Geol. Soc. Am. Bull.* **81**(2): 573–578. doi:10.1130/0016-7606(1970)81[573:GSOGRF]2.0.CO;2.
- Miller, J.A. 2009. The effects of temperature and water concentration on the otolith incorporation of barium and manganese in black rockfish (*Sebastes melanops* Girard). *J. Fish Biol.* **75**(1): 39–60. doi:10.1111/j.1095-8649.2009.02262.x. PMID:20738481.
- Miller, J.A., and Kent, A.J.R. 2009. The determination of maternal run time in Chinook salmon (*Oncorhynchus tshawytscha*) based on Sr/Ca and <sup>87</sup>Sr/<sup>86</sup>Sr within otolith cores. *Fish. Res.* **95**(2–3): 373–378. doi:10.1016/j.fishres.2008.09.030.
- Miller, J.A., Gray, A., and Merz, J. 2010a. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon (*Oncorhynchus tshawytscha*). *Mar. Ecol. Prog. Ser.* **408**: 227–240. doi:10.3354/meps08613.
- Miller, J.A., Bellinger, M.R., Golden, J.T., Gibson, L., Fujushin, L., and Banks, M.A. 2010b. Integration of natural and artificial markers in a mixed stock analysis of Chinook salmon (*Oncorhynchus tshawytscha*). *Fish. Res.* **102**(1–2): 152–159. doi:10.1016/j.fishres.2009.11.005.
- Miss, C.J., Campbell, S.K., and Livingston, S. 1984. Archaeological investigations at site 45-DO-285 Chief Joseph Dam Project, Washington. US Army Corps of Engineers, Seattle, Wash.
- Morris, G.A., Larson, P.B., and Hooper, P.R. 2000. 'Subduction style' magmatism in a non-subduction setting: the Colville Igneous Complex, NE Washington State, U.S.A. *J. Petrol.* **41**(1): 43–67. doi:10.1093/petrology/41.1.43.

- Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Lierheimer, L.J., Wainwright, T.C., Grant, W.S., Waknitz, F.W., Neely, K., Lindley, S.T., and Waples, R.S. 1998. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. US Dept. Comm. NOAA Tech. Memo. NMFS-NWFSC-35.
- Obradovitch, J.D., and Peterman, Z.E. 1968. Geochronology of the Belt Series, Montana. *Can. J. Earth Sci.* **5**: 737–747.
- Palmer, M.R., and Edmond, J.M. 1989. The strontium isotope budget of the modern ocean. *Earth Planet. Sci. Lett.* **92**(1): 11–26. doi:10.1016/0012-821X(89)90017-4.
- Park, D.L. 1969. Seasonal changes in downstream migration of age-group 0 Chinook salmon in the Upper Columbia River. *Trans. Am. Fish. Soc.* **98**(2): 315–317. doi:10.1577/1548-8659(1969)98[315:SCIDMO]2.0.CO;2.
- Petö, P., and Armstrong, R.L. 1976. Strontium isotope study of the composite batholiths between Princeton and Okanogan Lake. *Can. J. Earth Sci.* **13**: 1577–1583. doi:10.1139/e76-164.
- Ramos, F.C., Wolff, J.A., and Tollstrup, D.L. 2005. Sr isotope disequilibrium in Columbia River flood basalts: evidence for rapid shallow-level open-system processes. *Geology*, **33**(6): 457–460. doi:10.1130/G21512.1.
- Ray, V.F. 1933. The Sanpoil and Nespelem: Salishan peoples of northeastern Washington. University of Washington Publications in Anthropology No. 5. Seattle, Wash.
- Rich, W.H. 1920. Early life history and seaward migration of Chinook salmon in the Columbia and Sacramento rivers. *Fish Bull.* **37**: 1–73.
- Schmidt, M.E., Grunder, A.L., and Rowe, M.C. 2008. Segmentation of the Cascade Arc as indicated by Sr and Nd isotopic variation among diverse primitive basalts. *Earth Planet. Sci. Lett.* **266**(1–2): 166–181. doi:10.1016/j.epsl.2007.11.013.
- Secor, D.H., Henderson-Arzapalo, A., and Piccoli, P.M. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? *J. Exp. Mar. Biol. Ecol.* **192**(1): 15–33. doi:10.1016/0022-0981(95)00054-U.
- Seeb, L.W., Antonovich, A., Banks, M.A., Beacham, T.D., Bellinger, M.R., Blankenship, S.M., Campbell, M.R., Decovich, N.A., Garza, J.C., Guthrie, C.M., Lundrigan, T.A., Moran, P., Narum, S.R., Stephenson, J.J., Supernault, K.J., Teel, D.J., Templin, W.D., Wenburg, J.K., Young, S.E., and Smith, C.T. 2007. Development of a standardized DNA database for Chinook salmon. *Fisheries*, **32**: 540–552.
- Singleton, M.J., Maher, K., DePaolo, D.J., Conrad, M.E., and Dresel, P.E. 2006. Dissolution rates and vadose zone drainage from strontium isotope measurements of groundwater in the Pasco Basin WA unconfined aquifer. *J. Hydrol.* **321**(1–4): 39–58. doi:10.1016/j.jhydrol.2005.07.044.
- Smith, A.D., and Thorkelson, D. 2002. Geochemical and Nd–Sr–Pb isotopic evidence on the origin and geodynamic evolution of mid-Cretaceous continental arc volcanic rocks of the Spences Bridge Group, south-central British Columbia. *Geol. J.* **37**(2): 167–186. doi:10.1002/gj.907.
- Stathopoulou, E.T., Psycharis, V., Chryssikos, G.D., Gionis, V., and Theodorou, G. 2008. Bone diagenesis: new data from infrared spectroscopy and X-ray diffraction. *Palaeogeogr. Palaeoclim. Paleocol.* **266**(3–4): 168–174. doi:10.1016/j.palaeo.2008.03.022.
- Taylor, E.B. 1991. A review of local adaptation in salmonidae with particular reference to Pacific and Atlantic salmon. *Aquaculture*, **98**(1–3): 185–207. doi:10.1016/0044-8486(91)90383-I.
- Tiffan, K.F., Rondorf, D.W., and Wagner, P.G. 2000. Physiological development and migratory behavior of subyearling fall Chinook salmon in the Columbia River. *N. Am. J. Fish. Manage.* **20**(1): 28–40. doi:10.1577/1548-8675(2000)020<0028:PDAMBO>2.0.CO;2.
- Unwin, M.J., Quinn, T.P., Kinnison, M.T., and Boustead, N.C. 2000. Divergence in juvenile growth and life history in two recently colonized and partially isolated chinook salmon populations. *J. Fish Biol.* **57**(4): 943–960. doi:10.1111/j.1095-8649.2000.tb02203.x.
- Volk, E.C., Bottom, D.L., Jones, K.K., and Simenstad, C.A. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary, Oregon, using otolith microchemistry and microstructure. *Trans. Am. Fish. Soc.* **139**(2): 535–549. doi:10.1577/T08-163.1.
- Wadleigh, M.A., Veizer, J., and Brooks, C. 1985. Strontium and its isotopes in Canadian rivers: fluxes and global implications. *Geochim. Cosmochim. Acta*, **47**: 2311–2323.
- Waples, R.S., Gustafson, R.G., Weitkamp, L.A., Myers, J.M., Johnson, O.W., Busby, P.J., Hard, J.J., Bryant, G.J., Waknitz, F.W., Neely, K., Teel, D., Grant, W.S., Winans, G.A., Phelps, S., Marshall, A., and Baker, B.M. 2001. Characterizing diversity in salmon from the Pacific Northwest. *J. Fish Biol.* **59**: 1–41.
- Waples, R.S., Zabel, R.W., Scheuerell, M.D., and Sanderson, B.L. 2008. Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. *Mol. Ecol.* **17**(1): 84–96. doi:10.1111/j.1365-294X.2007.03510.x. PMID:18268786.
- Waples, R.S., Beechie, T., and Pess, G.R. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific salmon populations? *Ecol. Soc.* **14**: 3. Available from <http://www.ecologyandsociety.org/vol14/iss11/art13/>.
- Williams, J.G., Zabel, R.W., Waples, R.S., Hutchings, J.A., and Connor, W.P. 2008. Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. *Evol. Appl.* **1**(2): 271–285. doi:10.1111/j.1752-4571.2008.00027.x.
- Woodhead, J., Swearer, S., Hergt, J., and Maas, R. 2005. *In situ* Sr-isotope analysis of carbonates by LA-MC-ICP-MS: interference corrections, high spatial resolution and an example from otolith studies. *J. Anal. At. Spectrom.* **20**(1): 22–27. doi:10.1039/b412730g.
- Zar, J.H. 1996. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, N.J.
- Zimmerman, C.E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. *Can. J. Fish. Aquat. Sci.* **62**(1): 88–97. doi:10.1139/f04-182.
- Zimmerman, C.E., Stonecypher, R.W., Jr., and Hayes, M.C. 2003. Migration of precocious male hatchery Chinook salmon in the Umatilla River, Oregon. *N. Am. J. Fish. Manage.* **23**(3): 1006–1014. doi:10.1577/M02-015.

## Appendix A

Table A1 follows on next page.

**Table A1.** Life history characteristics of individual Chinook salmon based on archaeological (estimated) and modern (observed) otolith collections.

ID	OL (cm)	Adult FL (cm)	OW at freshwater emigration ( $\mu\text{m}$ )	Size at freshwater emigration (FL, mm)
<b>Archaeological</b>				
Archaeo 1	11.2	79	890	60.3
Archaeo 2	10.0	68	861	58.6
Archaeo 3	11.5	82	965	64.8
Archaeo 4	11.3	79	1128	74.6
Archaeo 5	11.1	78	1128	74.6
Archaeo 6	11.5	82	1217	79.9
Archaeo 7	12.9	94	1252	82.0
Archaeo 8	9.9	67	1571	101.2
<b>Modern</b>				
Sp yearling 1	NA	94	1272	83.2
Sp yearling 2	13.6	90	1548	99.8
Sp yearling 3	NA	92	1750	111.9
Sp yearling 4	13.6	95	1657	106.3
Sp yearling 5	NA	73	1800	114.9
Sp yearling 6	12.7	87	1800	114.9
Sp yearling 7	14.0	89	1865	118.8
Sp yearling 8	13.0	90	1968	125.0
Sp yearling 9	14.0	90	1886	120.1
Sp yearling 10	NA	93	2016	127.9
Sp yearling 11	NA	76	2016	127.9
Sp yearling 12	8.2	48*	2001	127.0
Sp yearling 13	NA	74	2112	133.6
Sp yearling 14	11.5	75	2184	138.0
Sp yearling 15	14.0	88	2307	145.3
Su–Fa subyearling 1	11	94	953	64.1
Su–Fa subyearling 2	13.5	77	1152	76.0
Su–Fa subyearling 3	11.5	80	1410	91.5
Su–Fa subyearling 4	9.1	55*	1425	92.4
Su–Fa subyearling 5	9.6	64	1410	91.5
Su–Fa subyearling 6	12.1	97	1460	94.5
Su–Fa subyearling 7	10	65	1499	96.9
Su–Fa subyearling 8	12.2	101	1440	93.3
Su–Fa subyearling 9	12.2	94	1547	99.7
Su–Fa subyearling 10	NA	96	1368	89.0
Su–Fa subyearling 11	10.4	68	1392	90.4
Su–Fa subyearling 12	10.5	94	1416	91.9
Su–Fa yearling 1	11.5	81	1380	89.7
Su–Fa yearling 2	13.3	100	1894	120.6
Su–Fa yearling 3	13.0	97	1896	120.7
Su–Fa yearling 4	NA	112	1944	123.6
Su–Fa yearling 5	13.3	99	2058	130.4
Su–Fa yearling 6	13.1	91	2480	155.7
Su–Fa yearling 7	12.9	94	2530	158.7

**Note:** Adult fork length (FL, cm), otolith width (OW,  $\mu\text{m}$ ) and length (OL, cm), and estimated size at freshwater emigration (FL, mm) are included. Sp = spring run, Su–Fa = summer–fall run. NA indicates otolith length could not be accurately measured because of breakage.

\*Immature.