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On the validity of the radiographic method for determining age of ancient salmon

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ABSTRACT

White rings visible on the centrum face of salmon vertebrae with X-rays have been used since the 1980s to age Pacific salmon (*Oncorhynchus* spp.), which in turn have been used to determine salmon species, season of capture and season of site occupation. This approach relies on a variety of assumptions, the most fundamental of which is that rings represent true years. Recent aDNA analysis has shown that the X-ray approach has flaws but the source of the error has been unknown. Given the value of reconstructing salmon population demographics and life history from ancient remains, establishing a valid and reliable method of ageing salmon vertebrae is extremely worthwhile. The main goal of our study was to evaluate if X-ray images of ring patterns on vertebrae provide a valid method of estimating fish age. Vertebrae from 66 adult Chinook salmon (*O. tshawytscha*) of known age were studied with X-rays, thin sections or low-powered (10–30×) magnification. We found that the white bands observed in X-rays are structural walls that do not grow annually. While X-rays are not a valid method for ageing salmonids, incremental growth seen on the surface of fish centra shows great promise for reconstructing ancient fish life history.

1. Introduction

For decades incremental growth patterns on fish "hard parts" such as otoliths, vertebrae, and spines, and shells from invertebrates, have been used to address a range of questions. Archaeologists have determined the season in which prey were harvested and in turn, timing of site occupation, contributing to our understanding of prehistoric mobility, development of sedentism, and overall land use (Andrus, 2011; Brewer, 1987; Burchell et al., 2013; Cannon and Burchell, 2009; Casteel, 1972; Claasen, 1986; Colley, 1990; Disspain et al., 2016; Higham and Horn, 2000; Monks, 1981; Morey, 1983; Quitmyer et al., 1997; Stutz, 2002; Van Neer et al., 1999; Waselkov, 1987; Wheeler and Jones, 1989). The use of incremental growth structures for age determination is an integral area of fisheries biology because it contributes to our understanding of fish population dynamics. This method is used to calculate growth and mortality rate and productivity, which inform fisheries management (Campana, 2001; Disspain et al., 2016). Likewise, archaeozoology has studied incremental growth to reconstruct demographics of ancient prey populations, and track population dynamics in the face of changing human predation intensity and environmental change, long before development, habitat loss and overfishing of the industrial age (Andrus, 2011; Cannon and Burchell, 2009; Miller et al., 2011; Turrero et al., 2013, 2012).

Incremental growth studies are developed most fully for aquatic organisms like fish and shellfish which, are poikilotherms or "cold-blooded": body temperature is not internally regulated, but rather varies with external water temperature. In temperate waters with seasonal changes in temperature, organisms typically experience slow winter growth (seen as dark narrow bands under reflected light) associated with low water temperature and reduced food supply and more rapid summer growth (seen as broad white bands) associated with an increase in water temperature and a more abundant food supply (Beckman and Wilson, 1995; Kusakari, 1969; Rojo, 1987). A pair of wide and narrow bands would reflect a full year of growth. However, other factors, including reproductive cycles, population density, local water conditions, and non-temperature controls on food availability also affect ring formation (Beckman and Wilson, 1995; Irie, 1960; Morey, 1983). Incremental growth rings *may* represent one year of growth but these other factors influencing ring formation may cause false annuli or growth checks which do not represent a year of growth. Given these confounding variables, and likely because the stakes are so high, fisheries biologists have protocols for assessing the validity of growth rings, determining if incremental bands represent true years or not. In simple terms, this usually involves comparing patterns in growth increments on

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structures (scales, otoliths) from modern fish of known age (established through tagging or aquaria experiments) with expectations given the true age (Beamish and McFarlane, 1987, 1983; Baker and Timmons, 1991; Campana and Thorrold, 2001; Campana, 2001).

In the Pacific Northwest of North America, Aubrey Cannon (1988, 1991) pioneered the use of radiography to document incremental growth rapidly on vertebrae from archaeological sites, to estimate fish age and season of capture of Pacific salmon (*Oncorhynchus* spp.). He suggested that growth increments were often not visible on the centrum surface and thus looked to X-rays to provide a rapid way to establish the growth characteristics of a large number of vertebrae. He X-rayed ~1875 salmon vertebrae (Cannon, 1988: 107) from the ~6500 year old deposits from Namu, coastal British Columbia (Canada); and concluded that two, three and four year old fish were captured in early-mid October. While subsequent research, including that by Cannon himself (Cannon and Yang, 2006; Speller et al., 2005; Yang et al., 2004) has challenged aspects of the findings using aDNA, the radiographic method for ageing fish is still suggested to be valid (Orchard and Szpak, 2011; Turrero et al., 2013, 2012).

What are radiographic images documenting and do they reflect annual growth? Cannon (1988) mentions validating his method with a modern collection of individuals of known age, but the particulars of the study were not presented. Given the great potential for using incremental growth on fish vertebrae to study past dynamics in fish populations (Hofkamp, 2015; Robinson et al., 2009; Turrero et al., 2013, 2012), we need to develop valid and reliable methods for ageing fish using vertebrae. If radiographic methods of age assessment are indeed valid we need to be using them; if they are invalid, we need to focus on other methods.

The main goal of our study was to evaluate if X-ray images of ring patterns on vertebrae provide a valid method of estimating fish age. Vertebrae from 66 modern adult Chinook salmon (*O. tshawytscha*) of known age were studied with X-rays, thin sections or low-powered (10-30×) magnification. We focused our study on Chinook salmon for several reasons. The species is the longest-lived of the seven eastern Pacific salmonid species, allowing us to evaluate age and growth from a broad range of age categories (Table 1). Chinook are also the focus of considerable research which has resulted in substantial knowledge of its life history; and finally, we were able to obtain a relatively large number of modern fish of known age, essential to our test for validity.

2. Archaeological background

Using incremental growth to establish when an organism died or was captured is typically achieved by estimating the amount of growth within one year of the increment and measuring the proportion of a year's growth past the last increment (e.g. Brewer, 1987; Carpenter, 2002; Morey, 1983). Microanalytic study of growth lines provide estimates of capture to a fortnight or even a particular day (Hallmann et al., 2009; Andrus, 2011). Cannon's approach to seasonality of salmon capture did not rely on incremental growth in a given year, but rather on a chain of reasoning that began with variation in life history and adult age across salmon species. Salmon begin life in freshwater where they reside for a few weeks to a few years. Following this freshwater residency, they migrate to sea, where they spend a varying length of time before migrating back to their natal stream to spawn and die. Cannon considered the potential that five species of Pacific salmon were present at Namu and each had a specific life history, spawning at a unique age and predictable time of year. Cannon presumed that Pacific salmon were mostly available to native fishers at the time of their return to spawning streams and therefore, when procured, salmon would be of spawning age. Cannon first estimated fish age at death by counting white rings visible in the radiographic images (Fig. 1) and then matched the estimated age to the species which best fit the life history profile based on historic and modern records on the typical spawning season for each species. For example, according to Cannon, because chum (*O. keta*) mainly spawn in late summer or fall, and fishers would most likely catch fish as they moved into spawning streams, the vertebrae assigned to chum based on ring count would represent fish caught in late summer or fall.

Table 1
Life history of Pacific salmon (*Oncorhynchus* spp.).
(From Groot and Margolis, 1991 unless otherwise noted).

Species	Freshwater residency	Age at spawning	Spawning season
Sockeye (*O. nerka*)[b]	1 month–3 years	2–7 years	Late summer–fall
Pink (*O. gorbuscha*)[b]	1 month	2 years	August–November
Chum (*O. keta*)[b]	1 month	2–7 years	May–January
Chinook (*O. tshawytscha*)[b]	3 months–2 years	3–8 years	Generally May to October
Coho (*O. kisutch*)[b]	1 year or more	1–3 years of age[a]	March to August
Rainbow/steelhead (*O. mykiss*)	1–3 years[a]	1–5 years[a]	Highly variable[a]
Cutthroat (*O. clarkii*)	1–6 years[a]	Highly variable[a]	Feburary–March[a]

[a] Wydoski and Whitney, 2003

[b] Species considered in Cannon's seasonality study.

Further, Cannon suggested that chum salmon mainly spawn in their third or fourth year of life, thus a vertebra with three or four rings would be assigned to chum.

Other researchers have utilized Cannon's method since his original study. Trost (2005) employed Cannon's method to attempt species identification of a small sample of salmon vertebrae from the Cove Cliff site in British Columbia and Berry (2000) applied the X-ray approach to an archaeological salmonid assemblage from the Keatley Creek site, on the Fraser River of eastern British Columbia. Recently, Orchard and Szpak (2011) have taken the use of radiographic techniques a step further by employing digital imaging technology to obtain X-rays and assign specimens from coastal British Columbia to a year class. They used X-rays and vertebra size, which they link to species groups, to determine species.

Cannon's method relies on many assumptions. First, it relies on the notion that species reach spawning age and end of life in a narrow window of time, within one or two years, when many species reach a wide range of ages (Table 1). Moreover, there is considerable overlap in the maximum age across salmon species. For instance, a fish three years of age could possibly be four of the five species discussed in Cannon's original study (Table 1). This logic also relies on an assumption that the spawning season has remained consistent over thousands of years, which may be problematic in light of the variation observed in modern salmon life histories which have likely evolved as adaptations for survival (Groot and Margolis, 1991). The most fundamental assumption is that one ring observed in an X-ray is equivalent to one year of life.

aDNA analysis of vertebrae highlights problems with Cannon's approach. Yang et al. (2004) tested Cannon's species identifications from Namu and found, among other discrepancies, sockeye salmon (*O. nerka*) was identified in the assemblage from aDNA, but not from the X-ray approach. In the archaeological salmonid assemblage from the Keatley Creek site, Speller et al. (2005) did not find evidence of pink salmon (*O. gorbuscha*) from aDNA, which Berry (2000) had identified as present using the radiographic method.

Because of the chain of reasoning, the source of the discrepancy is unclear—is It because of overlap across species in adult spawning age, or because the rings visible in X-rays are not annular rings? Additionally, rings visible in X-rays can appear ambiguous, and thus difficult to reliably count. For example, we see the same number of white rings, two, in examples "B" and "C" from Cannon's research (Fig. 1), which are supposed to be from fish of different ages. Despite these problems, others have followed Cannon's approach (Berry, 2000; Orchard and Szpak, 2011; Trost, 2005) for ageing salmonids and species identification. Recent studies of ancient Atlantic salmonid life history cite Cannon's radiographic method as potentially useful (Turrero et al., 2013, 2012).