Multi-centennial cyclicity in Canadian sockeye salmon (*Oncorhynchus nerka*) production: A window into large-scale environmental forcing mechanisms

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Pacific Salmon

Pacific salmon represent an ecological, economic and cultural resource of significant importance to western coastal North America. Within the 20th century, however, stocks have exhibited declines. Owing largely to a variety of human-induced stressors, including harvest pressures, hydroelectric development, hatchery mismanagement and habitat destruction, these declines have occurred in the context of significant climate variability, recognized as a large-scale regulatory mechanism of Pacific salmon production [1-3].

By virtue of their anadromous and semelparous life history traits, Pacific salmon act as natural "counter-current nutrient pumps", transporting nutrients of marine origin to typically oligotrophic inland rearing habitats, where they are deposited when fish die following spawning (Fig. 1). In many aquatic ecosystems, this can comprise a significant proportion of aquatic nutrient budgets. Sockeye salmon (*Oncorhynchus nerka*) are unique among Pacific salmon in that they utilize lake habitats (as opposed to streams and rivers) to spawn and rear juveniles [4]. Nutrients from these salmon carcasses can stimulate food web dynamics in these systems, and are eventually recorded in lake sediments [3,5].

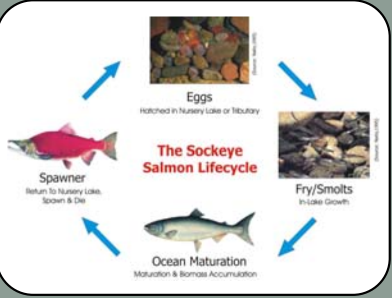

Figure 1: Life History of the Pacific sockeye salmon (*Oncorhynchus nerka*). Sockeye are hatched in freshwater nursery lakes or streams, where they rear for 1-3 yr. They then undergo smoltification and enter the open ocean where they accumulate the majority of their biomass and mature for 1-4 yr. They then return to their natal lakes and streams to spawn and die, releasing nutrients to these freshwater environments [4].

Sockeye Salmon Population Dynamics Over Six Millennia

Our sedimentary reconstruction of sockeye salmon production in Tahltan Lake, BC represents the longest and most comprehensive example of long-term salmon population variability in the NE Pacific to date, and indicates remarkable, natural productivity changes over the past ~6,000 yr. Both $\delta^{15}N$ and diatom proxies exhibit synchronous changes throughout the record, suggesting they are tracking salmon derived nutrient (SDN) influxes and ecological responses to them through time. Periods of high $\delta^{15}N$ correspond to increased occurrence of mesotrophic and eutrophic diatom taxa, and conversely, low $\delta^{15}N$ periods are marked by increases in oligotrophic taxa (Fig. 4). In addition, total diatom community shifts, as indicated by downcore Detrended Correspondence Analysis (DCA), track changes in $\delta^{15}N$ closely (Fig. 4).

The paleo-salmon record is characterized by multi-centennial to millennial shifts in salmon production. In the mid-Holocene (ca. 6150 – 3400 BP), productivity appears to have been the most variable over the course of the record, with extended periods of low abundance punctuated by shorter periods of very high abundance (Fig. 4). Conversely, following this, an extended period of sustained high salmon production is recorded ca. 3400-2700 BP. In the past ~3,000 yr, salmon production has been entrained to an apparently very ordered cyclicity, with a periodicity of ~740 yr (Fig. 4).

Currently, salmon production in this region appears to be at a low phase in natural cycling. Given that fishing pressures are a relatively novel stressor, perhaps caution is warranted in the continuation of substantial commercial exploitation of Pacific salmon in this region at this time.

Figure 2: Geographical location of Tahltan Lake, British Columbia, Canada. This system is the rearing habitat for the largest run of sockeye salmon on the Stikine River. Migration is transboundary through southeastern Alaska, USA and British Columbia, Canada.

Reconstructing Sockeye Salmon Populations

Novel application of established methods in paleolimnology have enabled reconstruction of salmon-derived nutrients (SDN) in nursery lakes, as a proxy of salmon productivity through time [3,5-7]. Stable nitrogen isotopes ($\delta^{15}N$) have proven useful as a temporal tracer of SDN in lake sediments [5]. Due to their relatively high position on the aquatic food web and the fact that salmon derive >99% of their biomass in the marine environment (an enriched pool of $\delta^{15}N$), their carcasses are enriched in the rarer, heavier isotope of nitrogen, $\delta^{15}N$. Upon dying, these enriched nutrients are released into freshwater lakes, typically depleted in $\delta^{15}N$ [2]. Remains from organisms responsive to nutrient loading in lakes such as siliceous algae (diatoms, chrysophytes) and cladoceran zooplankton, are also stratigraphically preserved in lake sediments and serve as proxies of lake nutrient dynamics and associated trophic changes [3,8]. Analysis of changes in these proxies in dated sediment cores (e.g. using ^{210}Pb, ^{137}Cs, ^{14}C, volcanic tephras) from sockeye salmon nursery systems, allows relative records of past salmon productivity to be inferred.

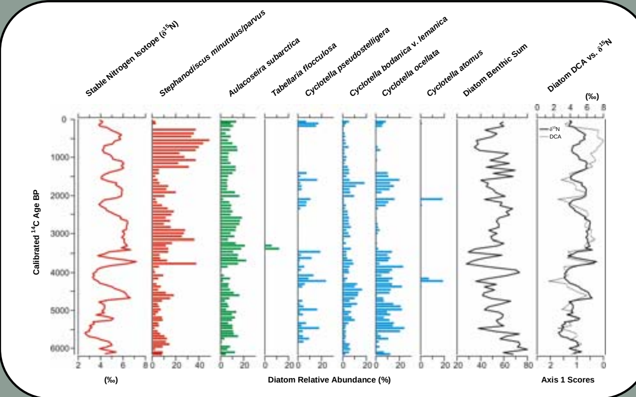

Figure 4: Stratigraphic representation of stable isotope $\delta^{15}N$ and dominant diatom assemblage (>5% in at least 2 intervals) changes from a Tahltan Lake, BC sediment core representing the past ~6,000 yr. Eutrophic diatom taxa are illustrated in red, mesotrophic species in green, and oligotrophic taxa in blue. Dates are reported in calibrated years before present (0 = 1950 AD), using the Calib v. 5.0 program [19, 20].

Study Site: Tahltan Lake, BC, Canada

Tahltan Lake is a dimictic, sub-arctic sockeye salmon nursery lake within the Stikine River drainage of northern British Columbia (131°37'1"W, 57°57'37"N)(Fig. 2). The catchment is forested and dominated by Engelmann spruce and fir [9]. Tahltan Lake is oligotrophic with relatively low algal and zooplankton productivity (Table 1), but currently supports a large proportion of the overall Stikine River sockeye production. Escapement in the past decade has averaged 34,665 fish•year^{-1}, although returns were considerably low for the 2000-02 year classes [10]. Annual and inter-decadal variation for this stock is considerable for the period of recorded escapement since 1959 (1,471-67,326 fish•year-1). In response to lower recent escapement, Tahltan Lake sockeye production has been augmented with hatchery produced fry since 1990 [10].

Table 1: Physical & limnological characteristics of Tahltan Lake, BC

Elevation (m)	812
Surface Area (km^2)	4.86
Maximum Depth (m)	48
Mean Depth (m)	23
Distance to Pacific Ocean (km)	250
Watershed Area (km^2)	56.8
Mean Secchi Depth (m)	11.7
Mean TP epilimnetic (μg•L^{-1})	7.9
Mean NO3 epilimnetic (μg•L^{-1})	1.2
Chlorophyll *a* epilimnetic (μg•L^{-1})	0.6
Zooplankton biomass ((μg•L^{-1})	100

Relationship of Salmon Escapement to Long-Term Potential Climatic Drivers

A recent ~2,200 yr salmon reconstruction from Alaska [3] hinted at the possibility of multi-centennial scale regimes in salmon production and similar but opposite trends in more southerly fish species. Our ~6000 yr record confirms this suspicion and illuminates the cyclical nature of this relationship, particularly over the past ~3,000 yr. Perhaps more importantly, it enables the comparison of salmon productivity to large-scale population forcing mechanisms such as NE Pacific climate variability. In particular, variability in Tahltan Lake sockeye production over the course of the sedimentary record exhibits similar variation patterns to those observed in alkenone-inferred NE Pacific coastal sea surface temperature (SST) [21] over the past ~6000 yr (Fig. 5). In fact, over the past ~3,000 yr, we record ~740 yr cyclic production in salmon, which is similar to the ~0.73 ka cycles observed in a past SST [21] (Fig. 5). In addition, many of the periods of strong salmon recruitment and higher SST coincide with St. Elias glacier advances, and reconstructed intensifications/easterly intrusions of the Aleutian Low (AL), a semi-permanent low pressure cell located over the Gulf of Alaska, which elicits cyclonic flow of warm moist Pacific air inland [22,23] (Fig. 5). North Pacific fish productivity is known to fluctuate in response to the strengthening of the AL on shorter time scales, which is correlated with positive phases of the PDO, favouring northern pelagic fish species[1,24]. The cyclical nature of the salmon production in the last ~3000 yr coincides with the end of a period of overall intensification of the AL and the BC Neoglacial [25], as well as the onset of increased AL variability [23]. Our data suggest that North Pacific salmon recruitment is positively related to NE Pacific SST and stronger periods of the AL over multi-centennial time scales not apparent from contemporary datasets.

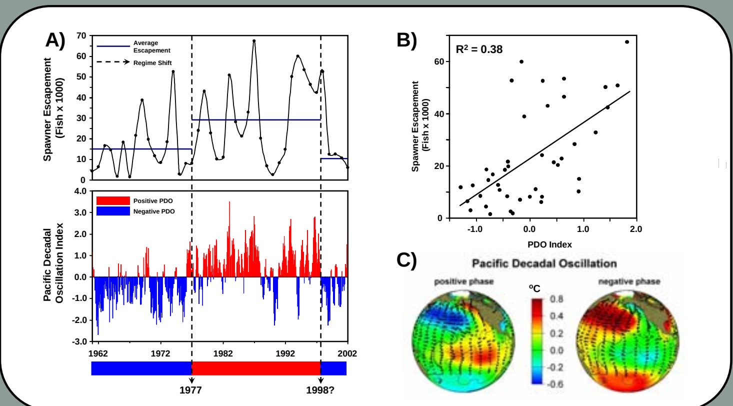

Figure 3: A comparison of annual Tahltan Lake sockeye escapement data (weir counted wild fish) and the Pacific Decadal Oscillation (PDO) Index. The PDO Index is defined as the leading principal component of an un-rotated Empirical Orthogonal Function (EOF) analysis of monthly, residual North Pacific sea surface temperature anomalies north of 20°N (residual = observed SST anomaly minus the monthly mean global average SST anomaly) [11]. A) Annual sockeye returns to Tahltan Lake and monthly PDO index values. A 2 yr lag is applied to the escapement data. B) Regression analysis of sockeye escapement (2 yr lag) and annual averaged PDO Index values (R^2 = 0.38, P<0.0001). C) Comparison of warm versus cool phase PDO sea surface temperature (SST), sea level pressure (SLP), and surface wind stress anomaly patterns. PDO data and graphic courtesy of N. Mantua [12].

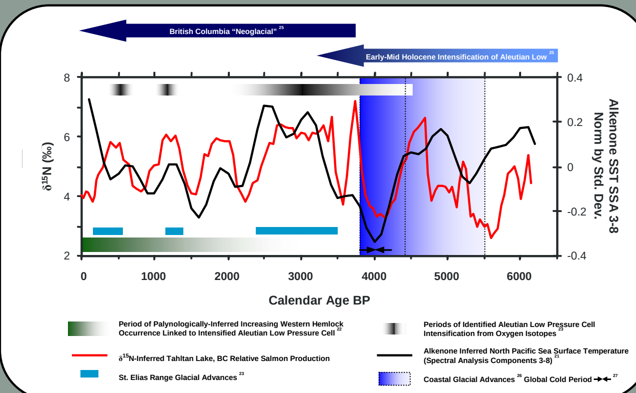

Figure 5: A comparison of the $\delta^{15}N$-inferred salmon production in Tahltan Lake and alkenone-inferred sea surface temperature (SST) in relation to Aleutian Low (AL) intensity and periods of coastal glacial advance for the period ~6,500 BP to present. Periods of high salmon productivity coincide with intense AL and glacial advances. A period of very low salmon abundance, SST and intense coastal glacier advance occurred ca. 4000 BP, which coincides with a period of cooling observed on a global scale [27].

Contemporary Climate-Salmon Relationship: The Pacific Decadal Oscillation (PDO)

Fisheries records are inherently noisy, however, relationships between pelagic fish productivity and underlying climatic influences have recently been established. The Pacific Decadal Oscillation (PDO), is a dominant mode of North Pacific climate variability, which oscillates on time scales of 15-25 yr and 50-70 yr [13]. The PDO has been shown to directly influence NE Pacific production dynamics for pelagic fish species, in particular, Pacific salmon [1]. Positive and negative phases of this climate oscillation create so-called "Inverse Production Regimes" [14], with opposite influences on northern vs. southern salmon production. NE Pacific pelagic fish production is largely driven by bottom-up trophic dynamics [15], and it has been shown that the PDO directly influences primary and secondary production in the Pacific Ocean [16]. During positive phases (Fig. 3) Central Pacific SST are cooler, coastal SST's are warmer, and winter SLP is low over the North Pacific, leading to predominantly clockwise surface winds, and enhanced production of salmon in northern British Columbia and Alaska. Conversely, during negative phases conditions are reversed, and southern British Columbia and Pacific Northwest US stock production is favoured. "Regime Shifts" associated with polarity shifts in the PDO (ca. 1947 and 1977) have occurred over the instrumental record [11], but this variability has been shown to be persistent back further in time through analysis of dendroclimatological records [17,18]. Our analysis of Tahltan lake sockeye salmon escapement in relation to annual PDO Index values for the period 1959-2002 (Fig. 3) suggests that these fish exhibit enhanced production during positive PDO regimes, and diminished production during negative phases. The last established regime shift occurred in 1977, towards a positive PDO state. In 1998, it is suspected that another shift in the PDO may have occurred (although it is too early to determine), which would disfavour northern stocks such as Tahltan. These relationships between climate and fish production suggest a sensitivity that may hold true over longer time scales. In order to assess long-term sensitivity of salmon production to climate, pre-historical records of salmon production and climate variability are necessary.

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