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Assessing fluctuation in salmon abundance over the past 14,000 years in Larson Lake, Alaska

by

Zachery Richard Van Orsdel

A thesis

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To the Graduate Faculty:

The members of the committee appointed to examine the thesis of Zachery Richard Van Orsdel find it satisfactory and recommend that it be accepted.

____
Bruce Finney
Major Advisor

____
Glenn Thackray
Committee Member

____
Keith Reinhardt
Graduate Faculty Representative

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Assessing fluctuation in salmon abundance over the past 14,000 years in Larson Lake, Alaska

Thesis Abstract--Idaho State University (2019)

Larson Lake, Alaska provides a record of salmon abundance since the deglaciation of south-central Alaska following the Last Glacial Maximum. The length of this record allows for the study of long term changes in salmon abundance and how they relate to the changing climate of the last ~14,000 cal BP. The $\delta^{15}N$ record from Larson Lake shows salmon abundance increasing gradually as increasing temperature and precipitation drove increases in ocean and lake productivity. A pronounced increase in salmon abundance occurs from 9,300 to 8,300 cal BP after which salmon abundance reached levels similar to modern. Larson Lake's long record also allows for investigation to salmon availability into humans as they migrated to the region. Salmon were spawning in significant numbers by ~12,900 cal BP, 1,100 years before the earliest evidence for human habitation in the region around Larson Lake. However, current evidence suggests salmon were not intensely harvest until the last ~1,000 years despite their availability for thousands of years.

Keywords: *Oncorhynchus nerka*, Sockeye salmon, Stable isotope analysis, Paleoclimate, Pacific Decadal Oscillation, Prehistoric humans

1. Introduction

Salmon are vitally important to Alaskan's economic, cultural, and ecological health (Holtham et al., 2004; Clark et al., 2006; Guthrie, 2006; Romberg et al.; 2008, Halffman et al., 2015). In order to sustain salmon populations, effective management policies must be implemented. In order to create effective management practices the natural fluctuations of salmon abundance and their relationship with geologic, climatic, and anthropogenic influences must be well understood.

Sockeye salmon (*Oncorhynchus nerka*) spawn and die in freshwater lakes where nutrients regenerated from their carcasses are utilized by phytoplankton and subsequently deposited in the sedimentary record (Finney, 1998; Gregory-Eaves et al., 2009). Because salmon accumulate ~99% of their biomass in the ocean, their decomposing carcasses have the potential to be an important external nutrient source to lake ecosystems (Finney et al., 2000). Nitrogen derived from salmon carcasses can be used to track salmon abundance in lakes because salmon have a distinctly higher nitrogen isotope ratio ($\delta^{15}N$) compared to terrestrial nitrogen sources (Finney, 1998; Gregory-Eaves et al., 2009). The $\delta^{15}N$ in lake sediments from salmon nursery lakes can be used to estimate salmon abundance of those lakes with higher $\delta^{15}N$ values (Finney et al., 2000; Gregory-Eaves et al., 2009; Loso et al., 2017; Selbie et al., 2009).

When the organic matter in lake sediments is largely derived from aquatic sources, the $\delta^{15}N$ of that organic matter will reflect the influence of salmon N relative to other sources of N. However, terrestrial organic matter sources without strong linkages to contemporaneous salmon derived N, if important in lakes sediments, will complicate interpretations of $\delta^{15}N$. The weight percent ratio of carbon to nitrogen (C/N) is used to determine the relative proportion of organic matter in the lake sediments in terms of terrestrial or aquatic sources (Selbie et al., 2009). When used together, the C/N ratio and $\delta^{15}N$ can be used to determine the presence of salmon-derived nitrogen and reconstruct trends in salmon abundance from lake sedimentary records.

Salmon have complex life cycles which involve both freshwater and ocean habitats, meaning that factors in both habitats have the potential to affect their abundance. Historical data shows salmon abundance is strongly linked to changes in ocean and atmospheric circulations on decadal time scales (Hare et al., 1999; Mantua et al., 1997). Ocean and terrestrial conditions and climate controls were much different during the Last Glacial Maximum (LGM) (Anderson, Abbott, and Finney, 1999; Barber and Finney, 2000; Kaufman et al., 2004). Spawning and rearing habitat, and migration, was restricted by glaciation, and increased sea ice and reduced productivity affected ocean habitats (Addison et al., 2015; Praetorius et al., 2015). Because of this, it is unknown how salmon adjusted to these conditions and subsequent changes during the transition to modern climate regimes. In tandem with this climate transition, the first humans were migrating to North American through Alaska via the Bering Strait land bridge and/or coastal routes. New documentation of human use of salmon in Alaska goes back to 11,800 cal BP; however, little is known about the spatial extent of salmon availability and human utilization of salmon as a resource (Choy et al., 2016; Halffman et al., 2015).

This study focuses on Larson Lake, 200km north of Anchorage, Alaska (Fig.1) in the Susitna River basin. As our cores from Larson Lake cover the time since the lake formed as the region was experiencing deglaciation, they provide a unique opportunity to study long-term fluctuations in salmon abundance. With a record this long, the availability of salmon to prehistoric humans in Alaska can be explored in more detail by providing evidence of salmon abundance at times when prehistoric humans were in the Susitna River basin. Additionally, climatic patterns and oceanographic conditions affecting salmon abundances on longer timescales can be better assessed. This study has three goals. The first goal is to estimate fluctuations in salmon abundance over time in Larson Lake, utilizing $\delta^{15}N$, and other data, from lake sediment cores. The second goal is to determine how fluctuations in salmon abundance responded to changes in climate and environmental conditions. The third goal is to determine if salmon were present in Larson Lake, and by extension similar localities, at the time when prehistoric humans migrated to Alaska. This goal is of interest to a larger National Science Foundation (NSF) project as it can help determine the availability of salmon as a potential food source for prehistoric humans in central Alaska.

2. Study Site and Methods

2.1 Site location

Larson Lake is located at 62°20'15.39" N, 149°53'21.68" W, 135 river kilometers upstream from Cook Inlet, and is one of 13 sockeye lakes in the Susitna watershed. It lies 178m above sea level in the boreal forest vegetation zone. The lake is in the subarctic climate zone, and receives an average of 530mm/yr of precipitation with an average summer high of 19.4°C and average winter low of -15.6°C. It is about 5km long and 0.5km wide for a majority of its extent with a maximum water depth of 43m, a surface area of 1.77km^2, and a volume of 29,000,000 m^3 (Alaska Department of Fish and Game, 2017). The lake is an oligotrophic, clearwater lake, with an average total P of 7.2 (μg/L), an average total N of 565 (μg/L), an average pH of 6.8, an average conductivity of 70 (μS/cm), and an average temperature during spawning season of 14.5°C, ranging between 4-20°C (Table 1). During the winter temperatures are low enough that the lake freezes over.

Larson Lake was selected for this study because available data indicated a relatively high salmon abundance compared to the size of the lake, suggesting the potential for preservation of the distinct salmon $\delta^{15}N$ isotope signal in the lake's sedimentary record. Escapement numbers for Larson Lake are only available since 1984. During this period, the sockeye salmon escapement ranged between 15,000 and 50,000, however those numbers are considered lower than historical estimates before 1984 (M. Willette personal communication, 2019). In order to reach Larson Lake to spawn, sockeye salmon migrate from the Gulf of Alaska into northern Cook Inlet, where the Susitna River, a large, glacially fed system, discharges. One hundred fifteen kilometers upstream, they enter the large glacially fed Talkeetna River, 20 km above, they enter a small, short, clearwater stream which gives them access to Larson Lake.

2.2 Geologic history

A precursor to Larson Lake occupied a similar location during the Elmendorf advance (~16.4ka). This lake was bound on the south by a terminal moraine and the north by retreating glacial ice. During this time the lake would have drained south when the lake overtopped the terminal moraine; as the glacier to its north retreated further, that lake would have been able to drain north into what is now the Talkeetna River. Without the glacial ice damming water flow to the north, Larson Lake as it exists now would have been able to develop (D. Reger personal communication, 2019).

2.3 Coring

Sediment cores were collected from Larson Lake at two different locations (Fig. 2) in the summer of 2017 from a well anchored 5 meter inflatable "cataraft." A series of coring devices were used to develop a continuous sediment record at each site. Shorter hammer and gravity corers were used to collect overlapping cores, capturing the intact sediment-water interface; a percussion piston corer was used to obtain deeper sediment capturing glacial sediments corresponding to the lake's origin. After careful packaging in the field, the cores were returned to Idaho State University (ISU) for analysis.

In the laboratory, cores were split, described, and measured for magnetic susceptibility. Preliminary analysis of the two core locations indicated the deeper site better recorded salmon influence on Larson Lake. As such, a composite core of the deeper site was created from three individual cores spanning the sediment-water interface to the bottom of the longest core.

These cores were easily correlated using magnetic properties, several tephras, and prominent sediment packages (Fig. 3). This composite core had a total length of 321cm and represents the entirety of the sedimentary sequence from Larson Lake following glacial retreat. The composite core was sub-sampled continuously at 1 cm intervals using a volumetric sampler for physical properties and geochemical analyses. These samples were then analyzed for magnetic SI, water content, and wet and dry bulk density.

2.4 Stable isotope analysis

For isotopic analysis, the freeze-dried sub-samples were homogenized and then weighed into tin capsules. Bulk samples were analyzed, as carbonate was not detected, and the focus of this study is nitrogen isotopes. Isotope analysis was conducted at the Idaho State University Interdisciplinary Laboratory for Elemental and Isotopic Analysis (ILEIA) using a Costech ECS 4010 elemental analyzer interfaced to a Thermo Delta V Advantage continuous flow isotope ratio mass spectrometer. All stable isotopic data are reported in standard delta notation ($\delta^{13}C$, $\delta^{15}N$) relative to the Vienna PeeDee Belemnite (VPDB) and atmospheric N_2, reference standards. Analytical precision, calculated from analysis of standards distributed throughout each individual run, deviated less than ± 0.2‰ for both carbon and nitrogen stable isotopes, and less than ± 0.5% of the sample value for %N and %C.

2.5 Chronology

A chronology was developed utilizing accelerator mass spectrometry (AMS) radiocarbon analysis and by identifying the location of a well-known, dated, tephra. Radiocarbon samples were collected from 7 well-distributed localities by sieving subsamples through nested 125µm and 250µm sieves and picking terrestrial organic matter for dating (Stuiver et al., 2005). The

Watana tephra was used as an additional chronological marker (Riehle, Bowers, and Ager, 1990; Wallace et al., 2014). The radiocarbon ages were calibrated, and then used to create a Bayesian accumulation history for Larson Lake (Blaauw and Christen, 2011; Blaauw and Cristen, 2019).

3. Results

3.1 Site selection

Of the two sites cored (Fig. 2), site 2, which was taken at a deeper lake depth, was the core utilized for this study. Both of the sites cored showed similar overall stratigraphy and similar isotopic trends in the upper 30cm. Site 2 was chosen because its $\delta^{15}N$ showed less influence from terrestrial organic material based on its C/N. The core from site 2 is also longer with a faster sedimentation rate, resulting in a higher sampling resolution.

3.2 Chronology

The radiocarbon dates (Table 2), along with the age of the Watana tephra, were calibrated and used to create a Bayesian accumulation history (Fig. 4). A linear regression between the lowermost two calibrated dates was used to extrapolate ages to the bottom of the composite core which is estimated to be 15,200 cal BP. This estimate is provisional, as it does not account for changes in sedimentation rate that may have been occurring while Larson Lake was undergoing more rapid deglaciation. Larson Lake's average sedimentation rate is 50cm/yr with a period of slight deviation from this average 153 to 186cm in the composite core.

3.3 Stratigraphic units

The sediments of Larson Lake's composite core can be divided into three distinct intervals based on appearance, physical properties and composition (Fig. 5).

3.3.1 Unit 1: 0-211cm (Present-10,600 cal BP)

The upper 211cm are laminated silt with an overall color of brown (2.5Y 3/2) with occasional thin (~1cm or less) organic rich black (2.5Y 2.5/1) layers. There are isolated thin clayey layers (~2mm), as well as two thicker clayey layers (1 - 1.5cm) at 206cm and 209cm respectively. The thick Watana tephra (Begét et al., 1991; Riehle et al., 1990; Wallace et al., 204) occurs between 93-111cm. A thin (~2mm) layer of lake sediments occurs within the Watana tephra at 108.5cm. In addition, multiple thin tephras, ~2mm or less, are observed at 46, 64, 121, 124 and 129cm. The %C of this unit ranges from 0.1 to 9.2 with an average of 5.9. %C decreases from the top of this unit with deviation from this trend with maximum values near the top of the Watana tephra (93 cm). The C/N ratio averages 12.4 for this unit. Smear slide and other observations indicate that carbonates are not present. Diatoms are abundant throughout this unit and account for ~45% of the sediment. Magnetic susceptibility and dry bulk density (DBD) are low in this unit except where tephras are located.

3.3.2 Unit 2: 211-295cm (10,600-14,100 cal BP)

The second unit of the composite core, shows a downcore shift to increasing silt content, density and magnetic susceptibility as well as a color change from brown (2.5Y 3/2) to brown gray (5Y 4/2). From 211 to 232cm the core alternates between brown gray (5Y 4/2) and brown (5Y 3/2) on a cm-scale. At 232cm the color shifts to gray (5Y 4/1) with ~2mm layers of dark gray to black (5Y 3/2) occurring occasionally until 273cm, below which they occur in regular intervals of ~5cm until the end of this unit. Coarser units are limited to a tephra at 291cm, and a ~1cm thick anomalous layer of very fine sand at 293cm. There is black mottling seen throughout below 232cm, some of which appears to be planar. The %C of this unit generally decreases downcore, and ranges from 0.5 to 4.9 with an average of 1.8 while the C/N ratio is relatively uniform and averages 10.3. Smear slide and other observations indicate that carbonates are not present. Diatoms are abundant throughout the upper portion of this section and grade to common for the bottom 10cm accounting for ~40% and ~30% of the sediment respectively.

3.3.3 Unit 3: 295-321cm (14,100-15,200 cal BP)

The third unit transitions into a gray (5Y 5/1) clay while also showing a more significant increasing trend in magnetic susceptibility than the previous interval. There are no tephras and very little variation in color in this interval. The %C of this unit ranges from 0.5 to 0.9 with an average of 0.6 while the C/N ratio averages 13.4. Smear slide and other observations indicate that carbonates are not present. Diatoms are uncommon to rare (<10%) for the first 10cm of this unit and were not observed in the bottom 15cm. Coring could not proceed below 321cm due to encountering rocky substrate. Stable isotope data is only available for this unit through 304cm, below this point there is too little organic material for analysis.

3.4 Elemental and stable isotope analysis

Stable Isotope data is available to 301cm of the composite core (Figs. 5 and 6). The average $\delta^{15}N$ is 3.5‰. Values of $\delta^{15}N$ generally rise from the bottom of the core to 177cm (8,300 cal BP), after which they remain fairly stable until the present. Unit 3 has an average $\delta^{15}N$ of 2.7‰ for the 7cm with isotope data. Unit 2 sees a slight decline in $\delta^{15}N$ for the first 1/3 followed by a rise for the rest of the unit. Unit 2's average $\delta^{15}N$ is 2.9‰. Unit 1 has a period of highly variable $\delta^{15}N$ for the lowermost 18cm, followed by 17cm of mostly steadily increasing $\delta^{15}N$. Above this depth (177cm) $\delta^{15}N$ stabilizes around an average of 4.5‰.

The average $\delta^{13}C$ value is -29.4‰, with the general trend of rising $\delta^{13}C$ from ~-32‰ at the bottom of the core to 266cm (12,750 cal BP), after which it levels off at 29 +/- 1‰.

4. Discussion

4.1 Is Larson Lake $\delta^{15}N$ a proxy for relative changes in salmon abundance?

The potential impact of sockeye salmon on the N signature of Larson Lake can be assessed by several methods. There is only a short record of escapement data for Larson Lake; the average escapement between 1984 and 2010 was ~35,000 sockeye salmon (M. Willette personal communication 2019). Using this mean escapement, Larson Lake has an escapement to lake area ratio of 19.8 (1000s fish/km^2). Finney et al. 2000 found a strong positive relationship between this ratio and near surface sediment $\delta^{15}N$ for a suite of Alaskan sockeye salmon lakes. Based on this relationship, the expected sediment $\delta^{15}N$ corresponding to Larson Lakes' escapement to lake area ratio would be ~6‰. This is close to the $\delta^{15}N$ in Larson Lake's most recent sediments of ~5‰. In addition, this value is much higher than most non-salmon lakes in Alaska, which average $\delta^{15}N$ of 1.5 +/- 0.9‰ (Finney et al., 2002). This indicates that salmon-N loading to Larson Lake is substantial and should result in sediment $\delta^{15}N$ well above background. Additionally, Larson Lake's $\delta^{15}N$ is much higher than that of four nearby (~70km) non-salmon lakes (Bigelow et al, 2019).

Comparison of the escapement record to downcore changes of $\delta^{15}N$ in recent sediments is not possible due to the short available escapement record and the low temporal resolution of the sediments which average ~50 years/cm. Larson Lake does not show a decline in $\delta^{15}N$ after industrial fishing began in 1880 seen in most salmon nursery lakes of Alaska (Rogers et al., 2013). This period is only represented by the upper few cm, which show little change. The lack of decline has been observed in several other lake records and may be due to natural processes that increased salmon abundance during the last ~150 years which counteracted the effects of commercial fishing (McCarthy, Rinella, and Finney, 2018; Rogers et al., 2013). Alternatively, as Larson Lake is one system within the larger Susitna River basin which has 13 sockeye lakes, it is possible that commercial fishing, which mainly occurs in Cook Inlet, did not target Larson Lake sockeye.

Sources of organic matter to lake sediments may influence lake sediment records of $\delta^{15}N$. After spawning, salmon carcasses release their isotopically enriched N into the nursery lake. This N becomes part of the lakes dissolved inorganic N (DIN) pool which is subsequently utilized by phytoplankton that are deposited in the lake sediments. It is through this process that the isotopic signal of salmon is delivered to lake records. If terrestrially derived organic matter is a significant component in sediments, it will complicate interpretations as its low $\delta^{15}N$ would dilute the salmon influence on $\delta^{15}N$ of aquatic organic matter.

With a range between 17.3 and 8.2, and an average of 11.5, the C/N of the composite core (Fig. 7) is indicative of mainly aquatic sources of organic material (Meyers and Ishiwatari, 1993). The watershed size and topography, precipitation amount, and surrounding vegetation are likely factors contributing to minor terrestrial organic matter input to Larson Lake (Selbie et al. 2009). The moderate C/N may indicate some terrestrial influence, which likely accounted for the $\delta^{15}N$ differences between the 2 coring sites. However, there is not a negative relationship between $\delta^{15}N$ and C/N in the record, as would be expected if changes in terrestrial input were the main control on $\delta^{15}N$ variability (Fig. 8). Therefore, interpretations of salmon derived nutrient (SDN) over time are unlikely to be complicated by changes in source or dilution by terrestrial organic matter which can complicate isotope interpretations in some Alaskan lakes (Selbie et al., 2009).

4.2 First evidence for salmon

When did salmon become established in Larson Lake? As discussed in Loso et al. 2017, $\delta^{15}N$ is not a good indicator of lake colonization as salmon runs need to reach a critical size to affect lake nitrogen budgets and increase $\delta^{15}N$ above non-salmon background. Therefore, the exact timing of the first salmon runs in Larson Lake is difficult to ascertain using its $\delta^{15}N$ record (Fig. 6).

In order to determine background (non-salmon) $\delta^{15}N$ levels, three different methods will be used and their implications explored. The first method is to use $\delta^{15}N$ from four non-salmon lakes in the Susitna River basin that are within ~70km of Larson Lake (Bigelow et al., 2019) which average 1.9 +/- 0.5‰ with an instrumental error of less than +/- 0.2‰. Considering the uppermost standard deviation and instrumental error, any $\delta^{15}N$ above 2.6‰ would likely indicate salmon derived nitrogen. The second method uses data from Finney et al., 2000 which utilizes non-salmon nursery lakes (n=33) to calculate a background $\delta^{15}N$ of 1.5 +/- 0.9‰, which also estimates a non-salmon $\delta^{15}N$ upper background of 2.6‰ when considering the uppermost standard deviation and instrumental error. The third method to determine background $\delta^{15}N$ uses the lowermost 89cm (before $\delta^{15}N$ reached 4‰ for the first time) from Larson Lake with stable isotope data to create a background specific to Larson Lake. This method suggests a background $\delta^{15}N$ of 3.1‰ when including the upper end of instrumental error.

Starting with a background of 3.1‰, the most conservative estimate, Larson Lake's $\delta^{15}N$ record suggests salmon may have had intermittent success spawning in numbers large enough to be recorded by the lake's N record as early as 14,400 cal BP. The $\delta^{15}N$ then drops below 3.1‰ shortly thereafter, and not rising above this level until ~10,500 cal BP. Subsequently, after

~900 years $\delta^{15}N$ drops below 3.1‰ until ~9,200 cal BP; after this time salmon were spawning in significant numbers consistently.

The first time $\delta^{15}N$ rises above a background level of 2.6‰ is ~14,300 cal BP. However, following this initial rise, values decrease and oscillate near 2.6‰ until ~12,900 cal BP after which they are consistently above this threshold.

Using only the highest background level, salmon were consistently established in Larson Lake ~9,200 cal BP. However, considering that two independent datasets suggest background $\delta^{15}N$ values above 2.6‰, we provisionally use this background level for the rest of this study. At this background level, salmon were established in Larson Lake by 12,900 cal BP or potentially 14,300 cal BP.

4.3 General trends in Larson Lake's salmon abundance as inferred from $\delta^{15}N$

Using 2.6‰ as background level, salmon were spawning in significant numbers by ~12,900 cal BP. After this time, there is a gradual increase in salmon abundance for ~2,000 years. $\delta^{15}N$ then goes through a period of high variation for ~1,500 years followed by a large increase of $\delta^{15}N$ seen from 9,300 to 8,300 cal BP. After ~8,000 cal BP, $\delta^{15}N$ values became more stable, fluctuating around 4.5 +/- 0.5‰ with no large changes. Notably, this is the time when the modern boreal forest was established in the region, and the climate reached more stable, modern conditions (Bigelow et al., 2019).

Salmon variability from 8,300 cal BP to the present, shows minor shorter term variation. The main time-scale of minor oscillations is ~100 - 200 years. The length of these potential cycles is similar to those found in Rogers et al., 2013 (~120 and ~200) across 20 sockeye salmon nursery lakes in southwestern Alaska over the past 500 years. However, as each sample represents ~50 years, it is difficult to explore variability on these shorter timescales with this record.

4.4 Influences on salmon abundance

4.4.1 Glaciation history

As the region warmed following the LGM, glaciers retreated inland from the Gulf of Alaska and by ~11,000 cal BP glaciers had retreated to near their modern positions, allowing for more stable conditions to prevail in river and lake systems in central Alaska (Calkin et al. 2001). Before ~16.5ka a precursor to Larson Lake existed as a moraine and ice dammed lake that drained south over the moraine dam. As glaciers retreated further, Larson Lake and its watershed were able to develop into what they are today with the lake draining to the north into the Talkeetna River (R. Reger personal communication, 2019). Once free of ice and with a path available for salmon through the Susitna and Talkeetna Rivers to Larson Lake, it could serve as a nursery lake for sockeye salmon.

Larson Lake's sedimentary record provides a chronology to estimate the time of glacial retreat. Sediments below 301cm were likely deposited in close proximity to glacial ice based on a significant increase in the magnetic susceptibility of the sediments, a disappearance of diatoms, extremely low organic content, and shift to dense gray clay. The closest radiocarbon date is from 293-296cm which calibrated to 14,000 cal BP; the age model extrapolation estimates an age of 14,400 cal BP for 301cm (Fig. 4). The sediments still appear to be influenced by glacial material until a depth of 211cm (~10,500 cal BP). This glacial material was likely not from watershed glaciers as Larson Lake's watershed is small and relatively low in elevation. We hypothesize that the glacial material seen from 301-211cm (14,400-10,500 cal BP) was material deposited by retreating glaciers and subsequently delivered into Larson Lake through runoff until a time when the watershed substrate was stabilized by vegetation. Above 211cm (10,500 cal BP), the magnetic susceptibility drops to almost zero, diatoms become abundant, and the sediments lose any trace of gray coloration related to glacial material. The timing of deglaciation closely matches the glacial history of the region from Bigelow et al., 2019; Calkin et al. 2001; Mann and Hamilton, 1995; Reger 2019.

Our data, as well as regional glacial evidence suggests that by ~14,000 cal BP Larson Lake was largely free of direct glacial influence and a more modern topography was developing. At this time, salmon migration from the Pacific was viable, allowing salmon consistent access to Larson Lake and its spawning habitat (Bigelow et al., 2019; Calkin et al. 2001; Mann and Hamilton, 1995; Reger 2019).

4.4.2 Ocean temperature and productivity

Sockeye salmon spend one to two years in their nursery lakes before migrating to the Pacific Ocean where they put on a ~99% of their biomass; after one to four years in the ocean sockeye salmon return to their nursery lakes to spawn (Quinn and Dittman, 1990, Hinch et al., 1995). Thus, both factors in their freshwater and ocean habitats can affect salmon survival and abundance. Because sockeye salmon put on nearly all of their biomass in the ocean, it is thought that ocean productivity is critical to salmon abundance, especially during the first few months after salmon reach the ocean as they need to grow quickly in order to survive (Beauchamp, 2009; Pauly, Risher, and Thomas, 1989; Mantua et al., 1997). Evidence supporting the role of ocean temperature and productivity on salmon abundance is derived by comparing the Pacific Decadal Oscillation (PDO) to historic salmon catch records. Salmon abundance positively correlates to changes of the PDO, which is driven the strengthening and weakening of the Aleutian Low. During the positive PDO phase, a strong Aleutian Low provides warmer temperatures and higher nutrient fluxes to the coastal northeast Pacific, and enhanced streamflow to southern Alaska, creating ocean conditions favorable for high biological productivity (Mantua et al., 1997; Polovina, Mitchum, and Evans, 1995). This mechanism by which increased ocean temperatures and productivity drive salmon abundance creates a template for understanding how salmon abundance fluctuates with climate on longer timescales (Hare et al., 1999; Mantua et al., 1997).

Unfortunately, there are few paleoceanographic records of ocean conditions in the Gulf of Alaska for which to compare our salmon record. Opal% and total marine organic carbon (TMOC) are proxies for ocean productivity, and are available for a coastal marine site in the northern Gulf of Alaska. The record of Opal% and TMOC show a period of low productivity from 17,000 – 15,000 cal BP. At 15,000 cal BP productivity quickly spikes and is followed by slow decline until 11,000 cal BP. From 11,000 cal BP to present these proxies indicate productivity remaining fairly stable above levels seen 17,000 – 15,000 cal BP with TMOC elevated from ~8,500 – 6,000 cal BP. Both records indicate an increase in productivity over the last ~2000 cal BP (Addison et al., 2012; Praetorius et al., 2015). The $\delta^{15}N$ from Larson Lake shows similarity to ocean productivity records at times in the past (Figs. 9 and 10). There are two peaks in $\delta^{15}N$ that are similar to peaks in TMOC and opal% seen at ~14,300, and ~11,000 cal BP. The significant rise in $\delta^{15}N$ from 9,300 to 8,300 cal BP coincides with an increase in TMOC, but little change is seen in the opal% during this time. This comparison seems to indicate that salmon abundance may be related to ocean productivity during the time of rapid change during deglaciation ~

14,500 cal BP. However, some care must be taken in these comparisons due to the location of the ocean sediment core utilized, as this core site is currently near the boundary where iron limitation is important in the Gulf of Alaska (Fietcher et al., 2009; Olgun et al., 2012). During deglaciation this site would have been more coastal, but as sea-level rose, its current location (Fig. 1) is beyond the typical reach of iron transported into the ocean. Thus the site is not optimal for understanding coastal ocean productivity during the Holocene.

Sea-surface temperature (SST) records allow for an additional examination of paleoproductivity. SSTs are low from 17,000 – 15,000 cal BP with a sharp increase at 15,000 cal BP. SSTs then decreases until the Holocene. At the beginning of the Holocene SSTs increase to temperatures seen in the modern over ~1,000 years and then remain fairly stable (Praetorius et al., 2015). Changes in SST inferred from this site are likely representative of the coastal region. When comparing salmon abundance and SST (Fig. 10) it is clear that salmon abundance didn't reach modern levels until SSTs stabilized near modern conditions. If relationships between SST and coastal productivity apply on longer time scales this may also suggests that the coastal ocean became consistently more productive with the warming in the early Holocene, potentially increasing the survivability of salmon when they first enter the ocean.

4.4.3 Lake productivity

While ocean productivity and temperature are currently considered the most important variables when studying changes in salmon abundance, lake productivity is important as well as it controls smolt production and survival, and likely changed dramatically over these long time-scales.

In general, regional climate was getting wetter from the time of the establishment of Larson Lake until at least the mid-Holocene (Anderson, Abbott, and Finney, 1999; Barber and Finney, 2000; Kaufman et al., 2004). It is possible that the small stream that flows from Larson Lake to the Talkeetna River may have restricted salmon migration during periods of more arid climate, however, there is no data to directly assess this possibility. Perhaps more importantly, the increasing precipitation would have transported more nutrients into the lake, increasing its productivity and thus carrying capacity for juvenile salmon (Hyatt et al., 2004). The increase in organic carbon in the record provides some measure of changes in lake productivity (Fig. 11) and generally tracks changes in $\delta^{15}N$.

Changes in climate also bring changes in vegetation that may influence productivity and nitrogen fluxes. Based on regional pollen records (Bigelow et al., 2019), during deglaciation, Larson Lake's watershed was populated by willow (Salix), sedges (Cyperaceae), and birches (*Betula papyrifera*). By 11,800 cal BP birches were abundant and the dominant vegetation with alders (Alnus crispa) and spruces (*Picea glauca* and *Picea mariana*) becoming established by ~9,000 cal BP and gradually becoming abundant by ~6,000 cal BP (Bigelow and Edwards, 2001; Bigelow et al., 2019). Alders are especially of note as they are nitrogen fixers. The increase in Alder may have increased N fluxes to Larson Lake and played a role in the observed increase in lake productivity (Hu, Finney, and Brubaker, 2001). As the $\delta^{15}N$ of N from N fixers is ~0‰, this may have affected the $\delta^{15}N$ of the lake. However, the $\delta^{15}N$ of lake sediments increases during this time, opposite expectations for decreasing $\delta^{15}N$ due to addition of fixed N. We conclude that any effects on the sediment $\delta^{15}N$ from alders did not counter our interpretation that salmon were also increasing in abundance during this time. Effectively, these N fixers could have increased the productivity of Larson Lake, allowing for more smolts to thrive, without obscuring the $\delta^{15}N$ signal of salmon.

Salmon themselves also facilitate increased lake productivity as salmon-derived nutrients (SDN) can make a lake more productive, increasing smolt production and survival (Schindler et al., 2005). This creates a positive feedback wherein the more salmon that return to spawn, the more productive the lake, the more smolt survive, potentially increasing the number of salmon that will return in the future to further increase lake productivity. When comparing lake productivity to $\delta^{15}N$ it becomes apparent they are generally positively related (Fig. 11). Lake productivity trends upward from 14,400 to ~8,500 cal BP, then levels off until ~5,000 cal BP before entering a period of trending slightly downward. Importantly, lake productivity was increasing during the time period salmon abundance increased. While it is difficult to determine how much productivity increased due to SDN vs. watershed and climatic factors, the increase in lake productivity would likely have enhanced smolt production and survival.

It has been shown that volcanic ash can increase lake productivity through iron or other nutrient fertilization which would increase lake productivity, which could lead to a brief increase in smolt survival in nursery lakes (Gregory-Eaves et al., 2004; Kurenkov, 1966; Larson, 1993). However due to the short lived effects of such fertilization, it is unlikely that these events effected the long-term $\delta^{15}N$ record. There is no consistent short-term change in $\delta^{15}N$ or %C following tephra deposition, including the Watana tephra, a large 17 cm thick tephra, in the Larson Lake record, that supports the tephra fertilization hypothesis.

4.5 How did salmon abundance fluctuate with climate?

Looking at millennial scale fluctuations in salmon abundance in Larson Lake, there are three distinct time periods. The first is from 14,400 to 10,000 cal BP. During this time period there is a general upward trend in $\delta^{15}N$ with a few deviations on the centennial scale. Deglaciation allowed salmon to spawn in lakes they previously couldn't reach; once access and habitat were available. As climate and environmental change as Alaska moved towards more stable, modern conditions that Larson Lake's record indicates conditions were more favorable for salmon. The gradual increase in $\delta^{15}N$ coincides with an increase in ocean productivity and temperature as well as lake productivity, all of which would contribute to increasing salmon abundance during this period.

The second time period is from 10,000 to 8,300 cal BP; during this time $\delta^{15}N$ in the corresponding lake sediments crash after the steady increase in the previous period, followed by a 1,000 year long steady recovery and expansion to levels similar to present which are then sustained. There are no other long term, sustained changes of this magnitude in Larson Lake's sedimentary record. This time period represents a time when climate conditions were stabilizing near modern conditions, the result of thousands of years of warming and increased precipitation (Anderson, Abbott, and Finney, 1999; Barber and Finney, 2000; Kaufman et al., 2004). Alaska's climate and the northeastern Pacific Ocean were steadily warming after the LGM until ~8,000 cal BP (Kaufman et al., 2004; Marcott et al., 2013; Marret et al., 2001; Moore Jr., 1997) Based on the PDO's effects on productivity, these changes would have been creating conditions that would increase ocean productivity. Lake productivity during this period was also increasing due to more precipitation and more available N through fixation by alders. Through a combination of factors increasing both ocean and lake productivity, optimum conditions were reached for salmon that resulted in a large increase in their abundance. While the general increase in $\delta^{15}N$ is consistent with improving climate, we can not correlare the rapid decline in $\delta^{15}N$ with any published proxy record.

The third time period is from 8,300 cal BP until the present. This time period is characterized by fairly stable climate conditions that keep ocean and lake productivity stable (Anderson, Abbott, and Finney, 1999; Barber and Finney, 2000; Kaufman et al., 2004; Moore Jr., 1997). This stability is seen in Larson Lake's $\delta^{15}N$ record as during this time period it only varies slightly (4.5 +/-0.5‰).

4.6 Estimating escapement from $\delta^{15}N$

In order to quantify rough estimates of salmon escapement numbers, a simple mixing model was created and uses this equation

$$E = \frac{\delta^{15}N_{sed} \times N_{ws} - \delta^{15}N_{ws} \times N_{ws}}{\delta^{15}N_{sal} - \delta^{15}N_{sed}}$$

from Schindler et al., 2005 where E represents escapement. $\delta^{15}N_{sed}$ being the $\delta^{15}N$ measured from the lake sediments. $\delta^{15}N_{ws}$ represents the $\delta^{15}N$ of the watershed around the lake, this value was assumed to be the background levels previously mentioned and two iterations of this equation were completed in order to account for each background level. $\delta^{15}N_{sal}$ is the $\delta^{15}N$ of sockeye salmon which is 11.24+/- 0.56‰ (Satterfield IV and Finney, 2002). N_{ws} (the mass of N loaded from the watershed into the lake) was calculated by solving the above equation for N_{ws} and using an average escapement of 35,000 from the available 20 years of escapement counts from Larson Lake and the $\delta^{15}N$ of the upper 1cm of core (Fig. 12).

The equation from Schindler et al., 2005 does not consider changes in precipitation that could alter N_{ws}. Given the significant changes in climate that occurred over our record, the assumption of constant N_{ws} is unlikely. During periods of lower precipitation, and/or periods of reduced soil development, it is likely that N transport into a lake from its watershed would be lower. To assess how such changes may affect interpretation of the $\delta^{15}N$ record, the equation was modified to account for changes in N_{ws}:

$$E = \frac{\delta^{15}N_{sed} \times N_{ws} \times P - \delta^{15}N_{ws} \times N_{ws} \times P}{\delta^{15}N_{sal} - \delta^{15}N_{sed}}$$

P represents the fraction of precipitation of modern levels received during the time period of interest. Figure 13 shows the results of this equation applied to Larson Lake's $\delta^{15}N$ and using estimates for ranges in Alaska precipitation (Barber and Finney, 2000) as a fraction of modern. When applying this equation, escapements under ~10,000 were minimally effected, with those escapements only changing by a few hundred. When escapement was above ~10,000, the differences were larger, ranging up to almost 7,000 salmon different. During times when precipitation was lower, it took fewer salmon to get the same $\delta^{15}N$ values. If precipitation amounts have been generally rising during the last ~12,000 cal BP, then salmon abundance has been increasing more than indicated by $\delta^{15}N$ (Fig. 13).

4.7 What does salmon abundance in Larson Lake mean for prehistoric humans?

The best current documentation of when prehistoric humans began harvesting salmon in Alaska is currently 11,800 cal B.P. (Choy et al., 2016; Halffman et al., 2015; Guthrie, 2006). The data from Larson Lake suggests that salmon were consistently available for harvest by ~12,900 cal BP with the potential of being available as early as 14,400 cal BP. This timing would have allowed for prehistoric humans venturing near Larson Lake to use salmon as a food source. Humans arrived in the Susitna River basin by 10,520-11,200 cal BP as evident by sparse, short-term, task-specific archeological sites (Blong et al., 2018). From 8,000 to 4,000 cal BP there are denser artifact deposits and evidence of a shift towards camps being used full time (Blong et al., 2018). There is a shift in the tool used between 7,100 and 5,800 as well as a void in upland artifacts ~6,000 cal BP at a site ~30km east of Larson Lake both of which suggest a shift to near-river salmon harvesting; however, the void in artifacts could be a result of the Oshenta tephra causing humans to leave the area temporarily (Wygal and Gloebel, 2012; Blong et al., 2018). After ~4,000 cal BP, full time use camps shifted locations, likely related to changing land use patterns (Blong et al., 2018). There is evidence from the notching of stones that has been interpreted as netting fishing as early as ~5,000 cal BP (B. Potter 2019, personal communication). However, intense harvest of salmon did not begin until ~1,000 cal BP (B. Potter 2019, personal communication).

5. Conclusion

The sediment composition, %C, %N, $\delta^{13}C$, and $\delta^{15}N$ from Larson Lake were used to reconstruct trends in salmon abundance over the last 14,400 cal BP to better understand how salmon interacted with both climate and humans. Depending on background $\delta^{15}N$ interpretations, salmon were spawning in significant numbers in Larson Lake as early as 14,400 or as late as 9,000 cal BP. In general, on long time scales, as the climate warmed, precipitation increased, and ocean productivity increased, so did salmon abundance. During the cooler, dryer, and less productive period following the LGM, salmon abundance was low or potentially absent. Climatic changes that occurred during the transition into the early Holocene resulted in both increased ocean and lake productivity while salmon began to spawn in larger numbers. As climate has stayed relatively stable over the past ~8000 years, so has salmon abundance. Salmon were likely available to the first humans to reach interior Alaska, which current evidence for salmon harvesting by humans in interior Alaska dating to 11,800 cal BP. There is evidence for a shift towards increased salmon harvesting from 7,100 - 4000 cal BP, but current evidence suggests that humans did not start intensely harvesting salmon until ~1000 cal BP in the Susitna River region. However, salmon were spawning in the Susitna River basin before current evidence of prehistoric human arrival, suggesting that while the archeological evidence may not exist, salmon could have been a valuable resource for prehistoric humans as they first made their way through Alaska.

Figures

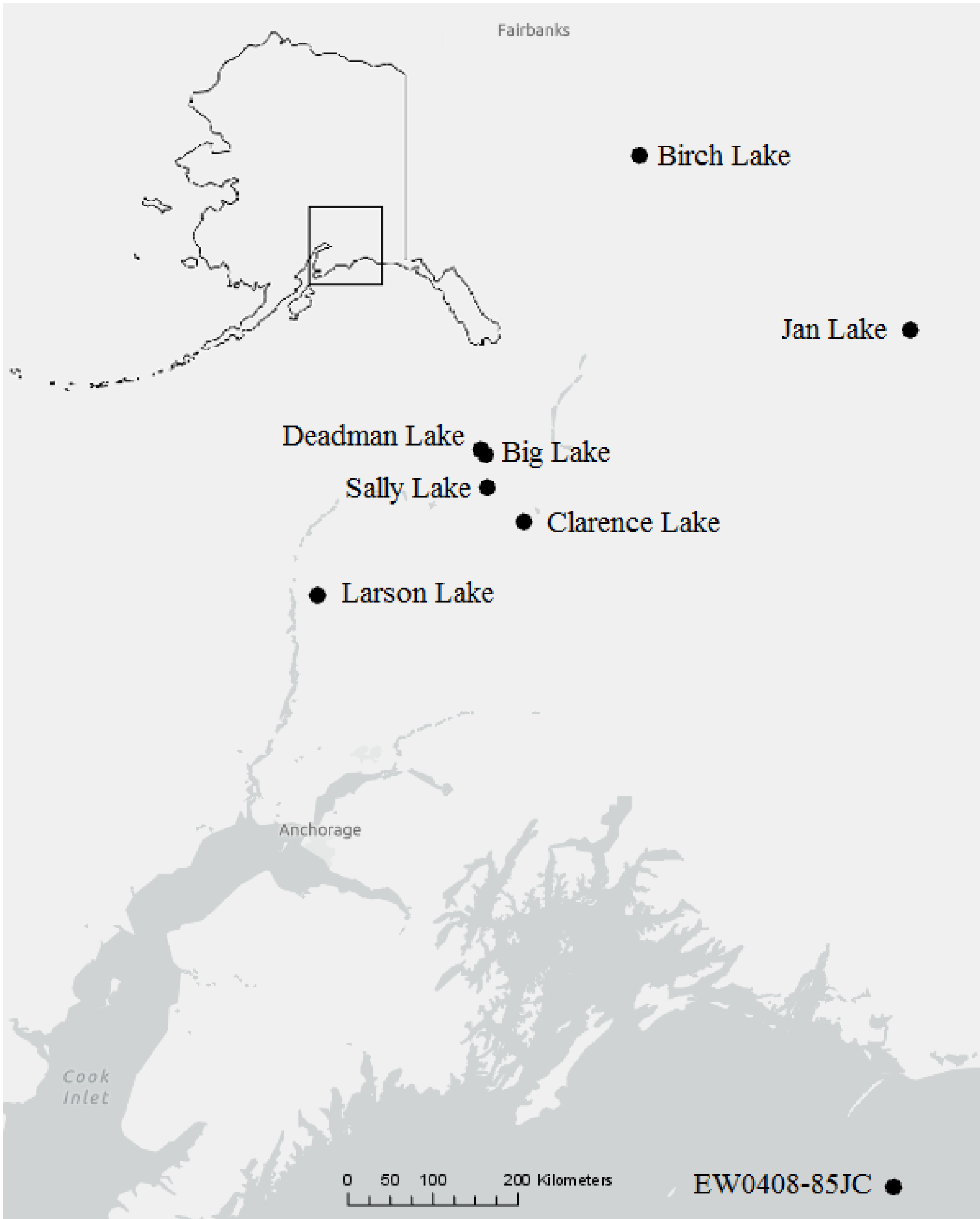

Figure 1. Map showing the location of Larson Lake, nearby non-salmon lakes (Deadman, Big, Sally, and Clarence Lake) lakes referenced for paleoclimate data (Birch and Jan Lake), and ocean sediment core EW0408-85JC.

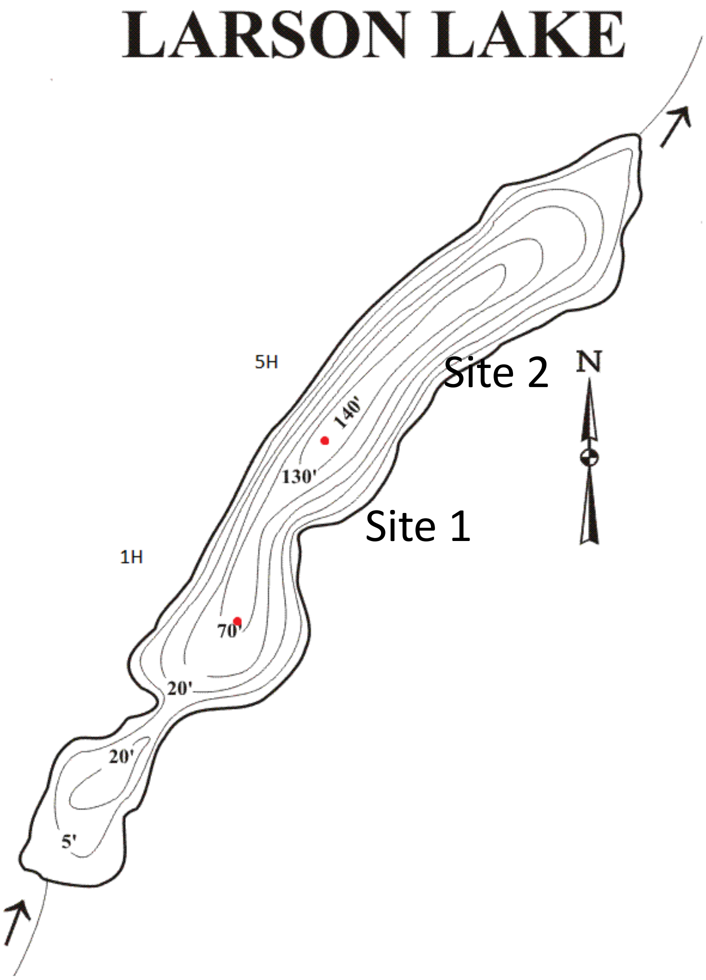

Figure 2. Bathymetric map (in ft) of Larson Lake showing the two core collection sites. Site 2 was chosen to be the focus of this study due to its better preservation of salmon presence and less terrestrial influence on its sedimentary record.

Figure 3. The three cores from Site 2 utilized to make the composite core with their correlation locations. The red arrows indicate the locations where sampling switched from one core to the other. The leftmost arrow indicates a transition between cores that took places directly below the 17cm thick Watana Tephra. The second arrow indicated a transition between cores that took place below a distinct sedimentary package present in both cores.

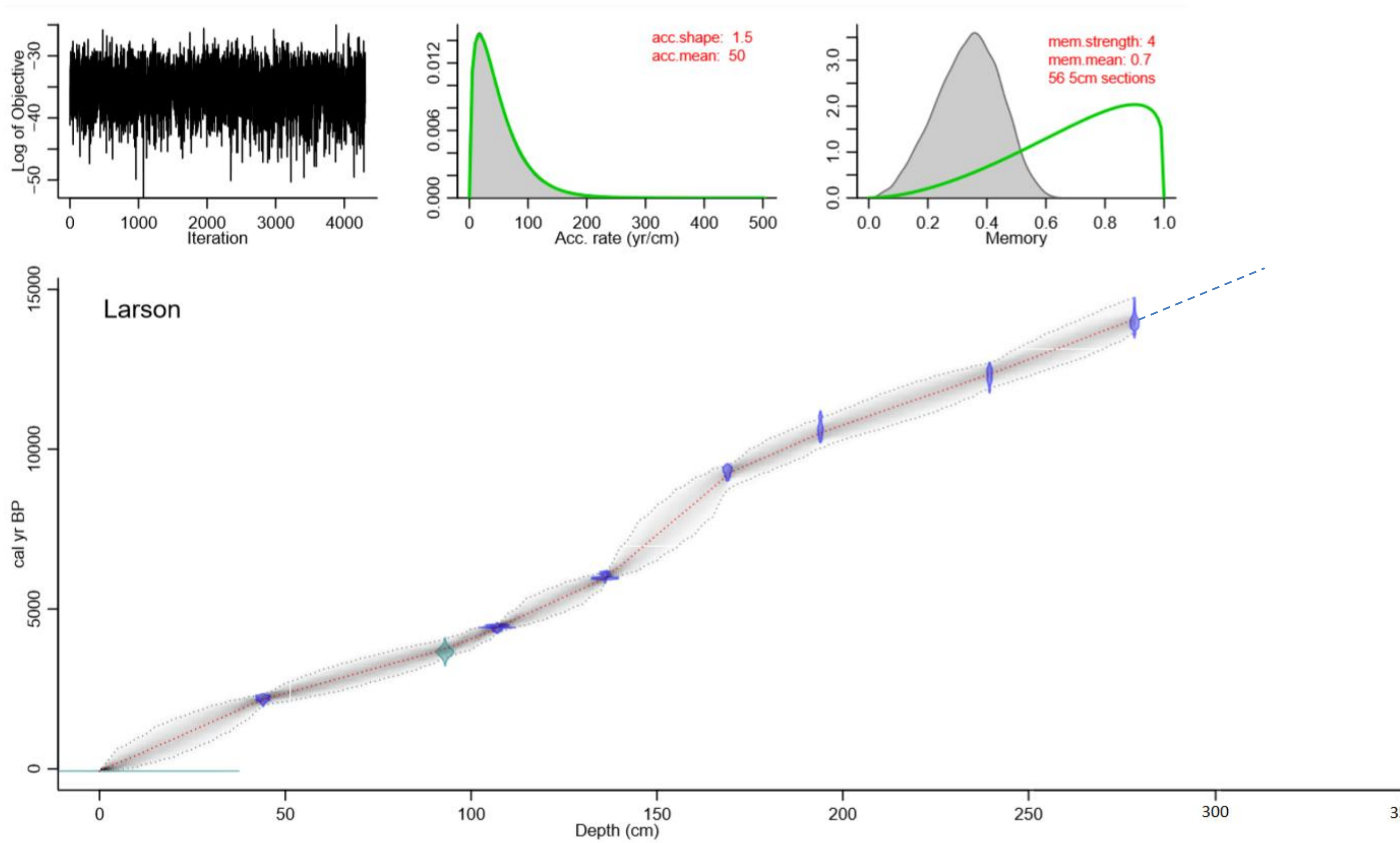

Figure 4. Bayesian accumulation history for Larson Lake based on 7 radiocarbon dates and the Watana Tephra. The 17cm thick Watana Tephra is represented by a gray box, and its thickness was removed from the age modeling. The resulting average accumulation rate is 50cm/year. The sedimentation rate remained constant throughout with slight deviation from the general trend seen only between depths of 153 and 186cm. The dashed blue line represents the linear regression from the lowermost two radiocarbon dates .extended to the core bottom.

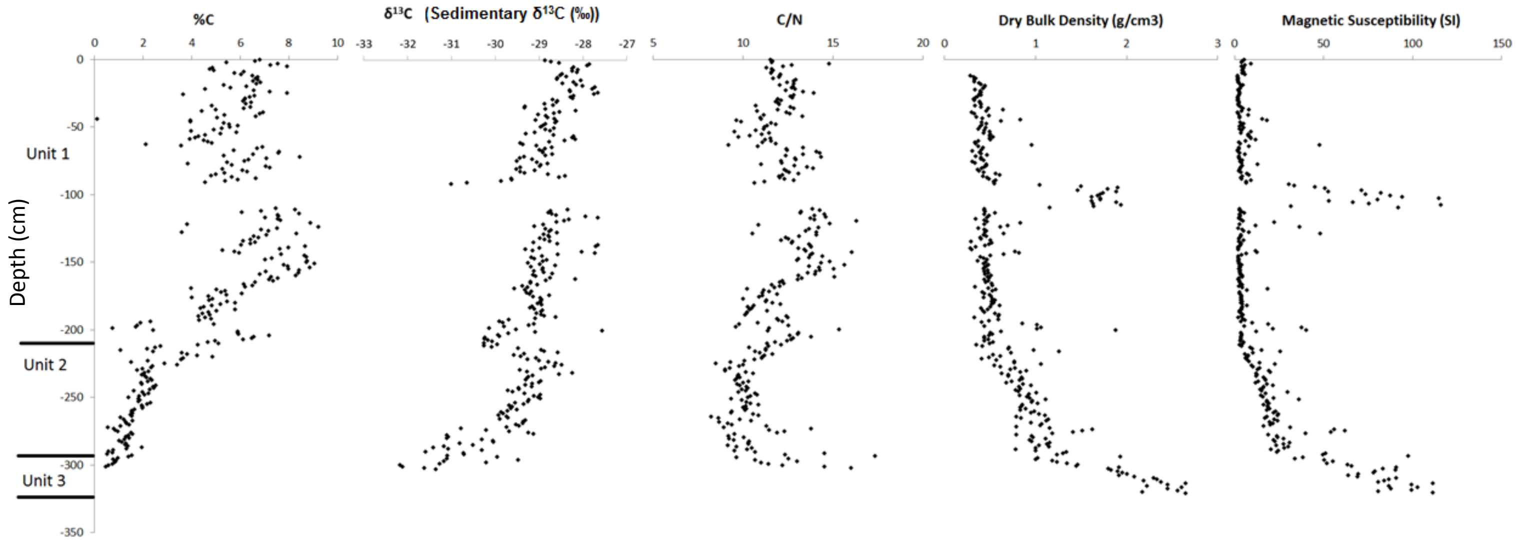

Figure 5. A comparison of stable isotope and sedimentary characteristics with depth, subdivided into three units. Note the transition from low %C and high bulk density and magnetic susceptibility following deglaciation.

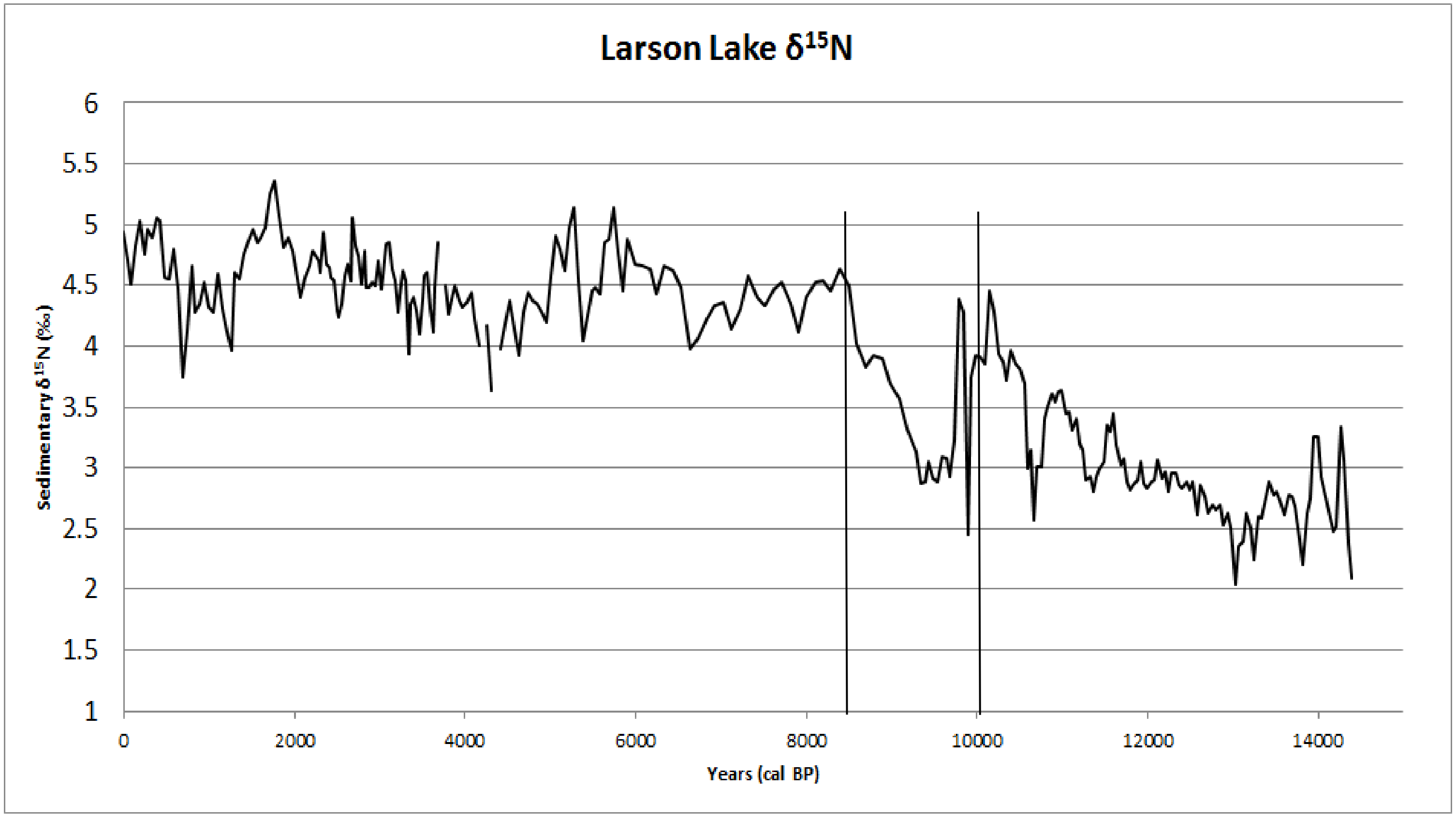

Figure 6. $\delta^{15}N$ results for Larson Lake. Gaps in the data represent significant tephra deposits. The blue and red horizontal lines represent a background $\delta^{15}N$ for non-salmon lakes of 2.6‰ and 3.1‰ respectively. The two thin vertical lines separate the record into three time periods discussed in the text.

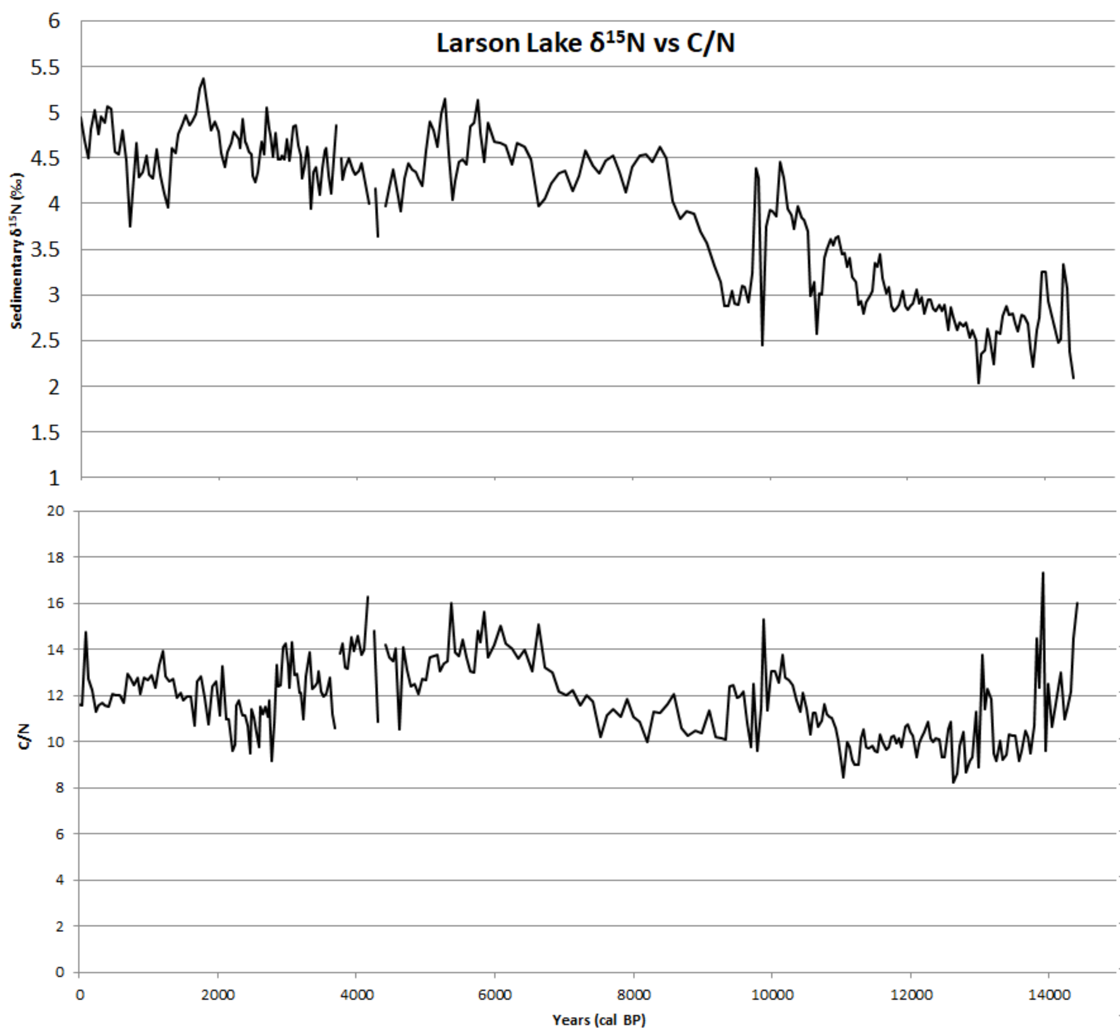

Figure 7. Comparison of Larson Lake $\delta^{15}N$ and C/N showing they are not related. C/N ratio results for Larson Lake showing that the vast majority of the organic matter analyzed is marine derived as it is below ~15, indicated by the thing horizontal line (Meyers and Ishiwatari, 1993).

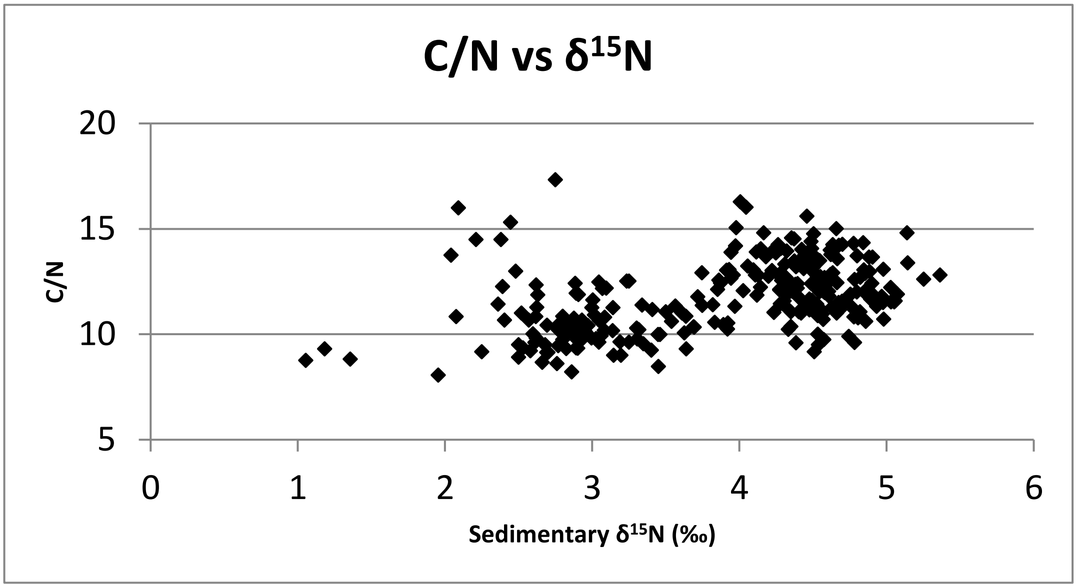

Figure 8. C/N plotted against $\delta^{15}N$ showing a slight positive correlation indicating that terrestrially sourced organic material is not being measured. If terrestrial organic matter were being measured, this relationship would show a negative correlation.

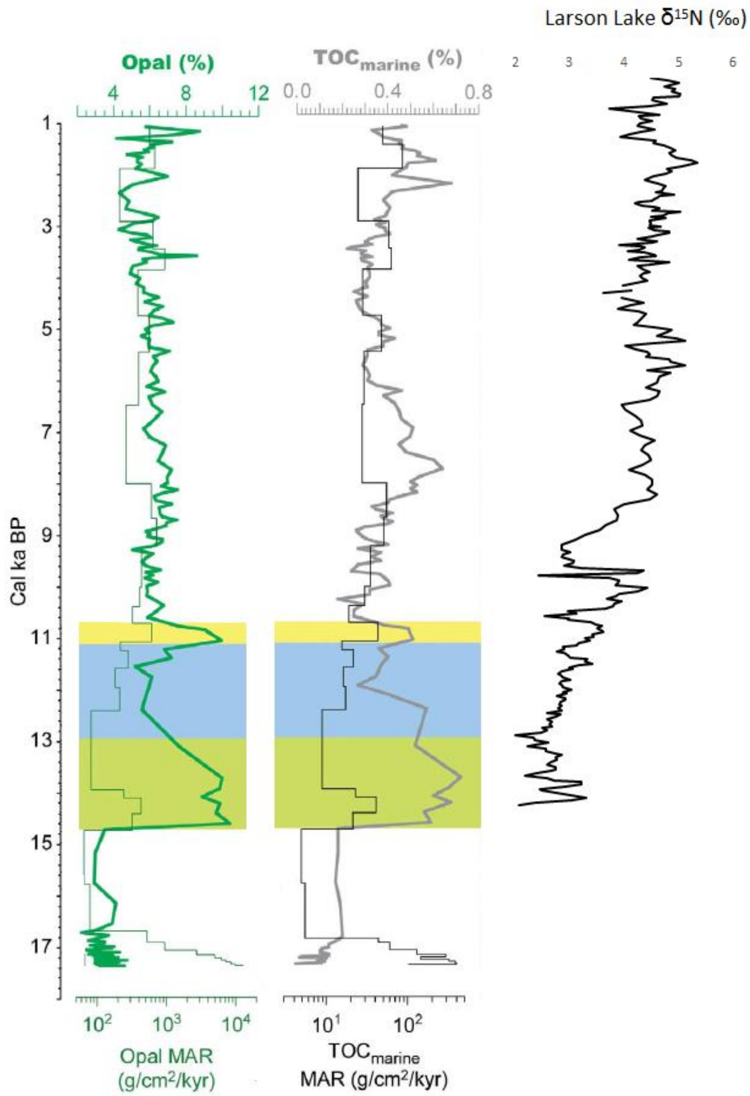

Figure 9. Ocean productivity proxies from Addison et al., 2012 compared to Larson Lake $\delta^{15}N$ showing their similar peaks ~14,300 and 11,000 cal BP. The productivity proxies also show the important trend of increased productivity after the LGM.

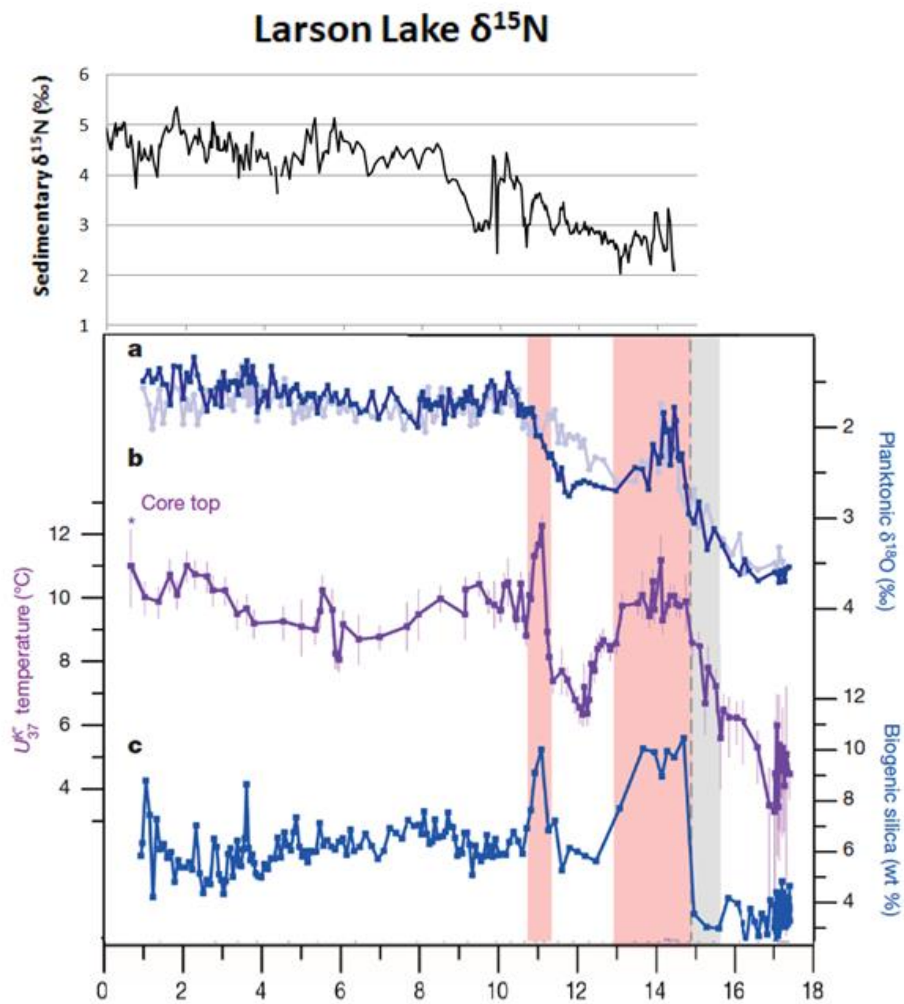

Figure 10. Larson Lake's salmon abundance record compared with two records of sea surface temperatures and one productivity record (Praetorius et al., 2015). All four records see a spike ~14,000 cal BP. The salmon abundance record does not reach modern levels until after sea surface temperatures have been at or near modern levels for ~1,000 years. The records of sea surface temperature may have more bearing on the salmon abundance due to the productivity record potentially

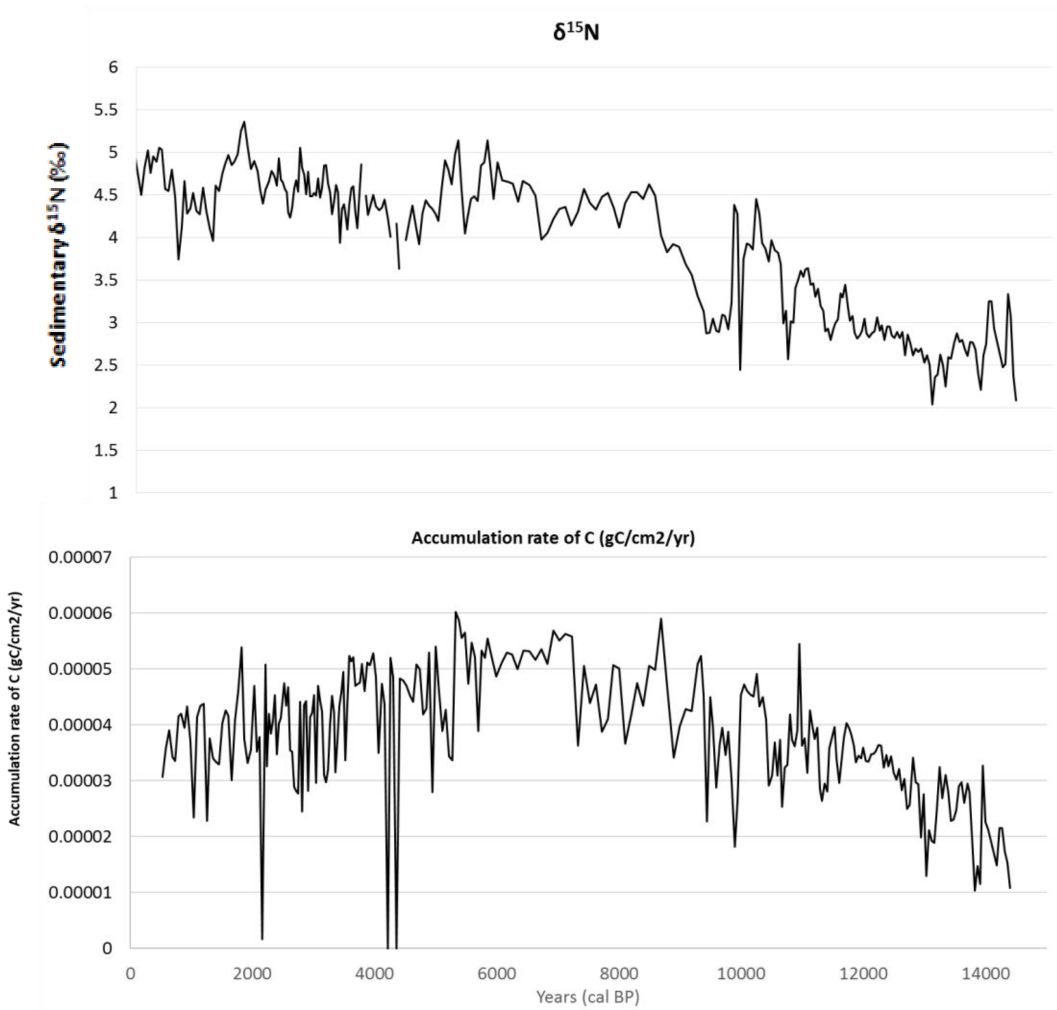

Figure 11. $\delta^{15}N$ compared to the accumulation rate of C in Larson Lake showing both records increasing from ~14,400 – 8,000 cal BP

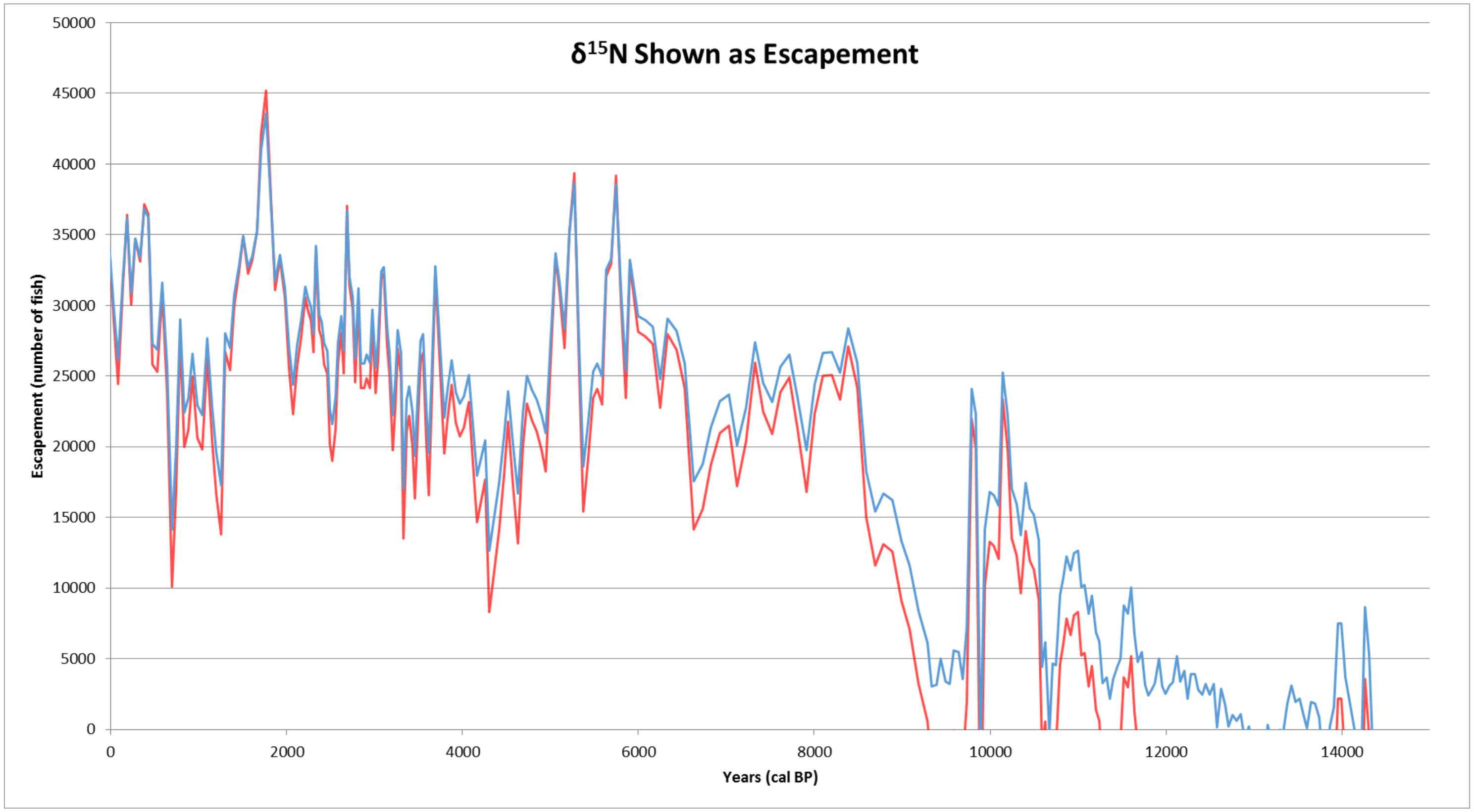

Figure 12. $\delta^{15}N$ converted to escapement numbers through the equation from Schindler et al., 2005 showing that salmon were spawning in Larson Lake in the tens of thousands by ~8,600 cal BP regardless of which background level is used in the calculation. The red and blue lines represent background levels of 3.1 and 2.6‰ respectively.

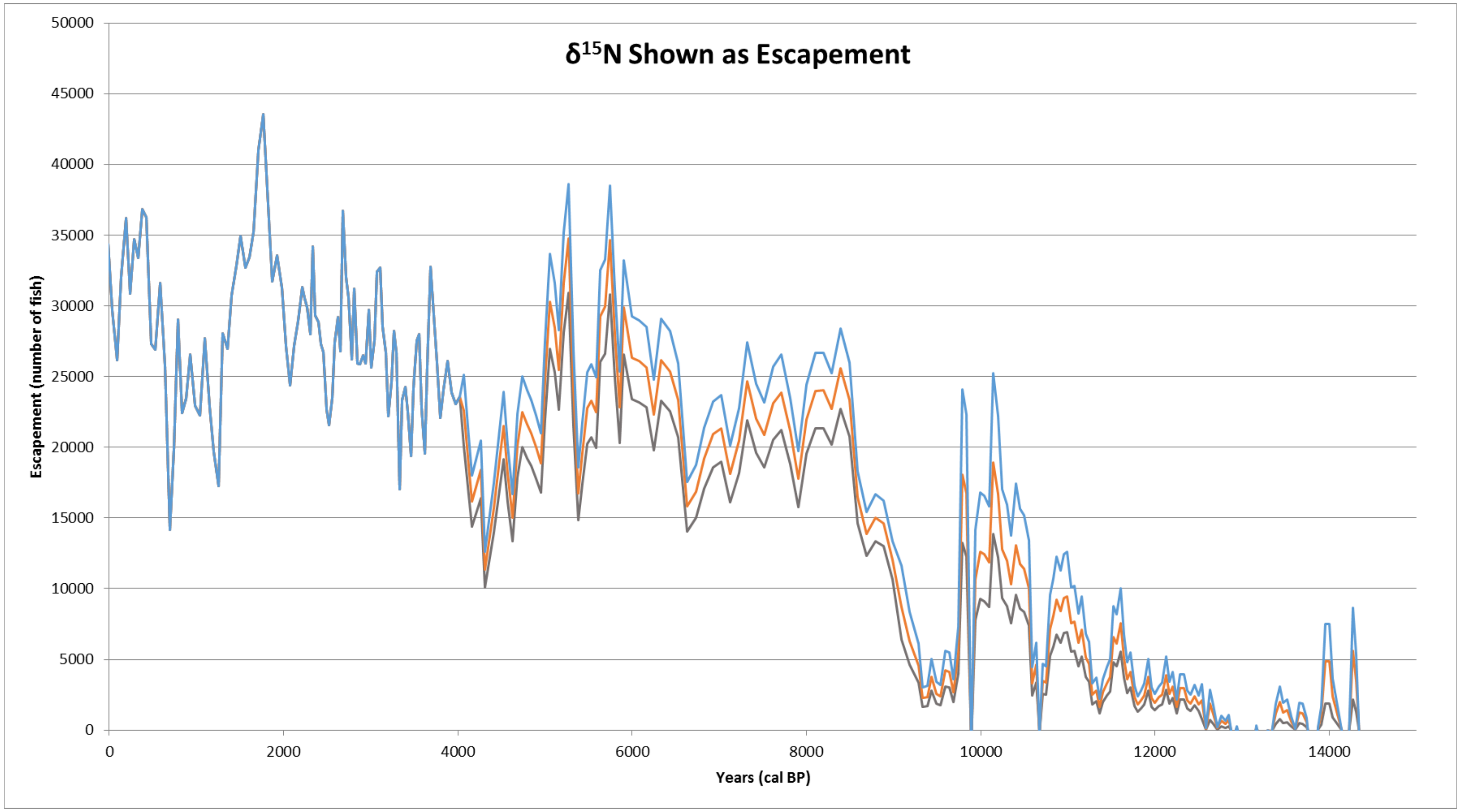

Figure 13. δ^{15}N converted to escapement numbers. The blue line represents salmon escapement using the 2.6 background with no adjustment for changing precipitation (Schindler et al., 2005). The orange and gray lines represent salmon escapement using the upper and lower estimates of precipitation as percent of modern (Barber and Finney, 2000) utilizing our newly proposed addition to Schindler et al., 2005's equation.

Tables

Year	TP (µg/L)	TN (µg/L)	Chlorophyll a (µg/L)	pH	Average Water Temperature (°C)	Water Temperature Range (°C)	Conductivity (µS/cm)
1981	8.1	713	0.3	6.6			51
1984	7.8	795	0.9	6.7			68
1985	5.1	767	0.7	6.7			68
1986	7.4	652	1.1	7			70
1987	14.7	321	1.7	7			66
1988	7.4	676					79
1993	3.2	697	0.7				69
2010	7.2	296.2	2.11	6.7	16	12-20	80
2011	4.2	168.8	0.87	7.2	13	4-20	78

Table 1. Available limnologic data for Larson Lake.

Original Core and Depth (cm)	Composite Depth (cm)	Material Dated	Lab Code	Radiocarbon Age (± 1 Sigma)	Calibrated age -2-sigma (median) +2-sigma
5H.1 33	45	Leaves, woody material, and seeds	CAMAS-180425 ISU_14C 2018 Larson 11	2185 ±50	2057 (2210) 2331
4H.2 21	124	Leaves and seeds	CAMAS-180413 ISU_14C 2018 Larson 04	3960 ±30	4378 (4431) 4452
4H.2 50	153	Leaves, seeds, and woody material	CAMAS-180414 ISU_14C 2018 Larson 05	5230 ±35	5914 (5975) 6025
4H.2 83	186	Leaves and woody material	CAMAS-180423 ISU_14C 2018 Larson 03	8340 ±100	9088 (9331) 9525
2P.2 41	211	Leaves and woody material	CAMAS-180424 ISU_14C 2018 Larson 07	9380 ±150	10249 (10629) 11094
2P.2 85-88	255-258	Leaves and woody material	CAMAS-180963 ISU_14C 2019 Larson01	10450±130	12321 (11950) 12686
2P.2 123-126	293-296	Leaves and woody material	CAMAS-180964 ISU_14C 2019 Larson02	12090±130	13957 (13573) 14374

Table 2: Accelerator Mass Spectrometry (AMS) radiocarbon dates and calibrated ages.

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