

Long-Term Variability of Alaskan Sockeye Salmon Abundance Determined by Analysis of Sediment Cores

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Records of prehistoric variations in salmon abundance are reconstructed from analysis of stable nitrogen isotopes in sediment cores. This new application of N isotopes is based on the observation that Pacific salmon supply nutrients into freshwater systems when they return to spawn. Nitrogen derived from adult salmon is enriched in ^{15}N relative to terrestrially-derived N. Thus input of salmon-derived N can be quantified by analysis of ^{15}N . Changes in the number of returning adult salmon will be reflected by downcore changes in sedimentary $\delta^{15}\text{N}$. Sedimentary $\delta^{15}\text{N}$ has been analyzed in two cores from Karluk Lake, Kodiak Island, Alaska. The record spans the past approximately 500 years and shows large changes in $\delta^{15}\text{N}$ and thus inferred escapement. Significant minima occurred during the mid to late 1900s, the early 1800s, the early 1700s and the mid 1500s. Relatively high values are observed from the mid 1800s to the early 1900s, the late 1700s, around 1700, the early to mid 1600s, the late 1500s, and the early 1500s. The record is not well correlated with estimates of Gulf of Alaska sea surface temperature (SST) determined from coastal tree ring records. Low salmon abundance during the early 1800s corresponds with a prolonged period of anomalously cold SST throughout a large region of the North Pacific. However, the period of high estimated abundance in the late 1800s and early 1900s was also a period of lower than average temperatures in the Gulf of Alaska. If variations in the abundance of Karluk Lake sockeye are influenced by ocean conditions, the differing responses during periods of cool temperature may indicate that different circulation patterns in the North Pacific may result in cool temperatures in the Gulf of Alaska, and impact biological systems differently. The decline in $\delta^{15}\text{N}$ that began in the mid 1900s is the most extreme in the record. However, tree ring based temperature trends suggest that conditions similar to the mid 1900s occurred several other times during the last few hundred years. Commercial harvest may have influenced the recent decline in $\delta^{15}\text{N}$ and salmon abundance at Karluk Lake, through impacts on freshwater nutrient input.



INTRODUCTION

Information on past changes in North Pacific salmon abundance prior to those reflected by catch data would provide valuable insight into the relationships between climate and salmon abundance. Such long-term data would provide a perspective on variability prior to anthropogenic influences, such as harvest, habitat alteration, hatchery production and greenhouse gas buildup, on biological and physical systems. In addition, longer time-series are required to detect responses to lower frequency changes, such as the 50 to 75 year period in temperature suggested by some records (Ware 1995). Finally, long-term data allow for testing of hypotheses regarding the response of salmon to changes in ocean/climate state.

This paper focuses on recent research aimed at

reconstructing past changes in the abundance of Pacific salmon. The first part of this paper will describe the methodology used to reconstruct past changes in salmon abundance from sediment core analysis. In the second part, this methodology will be used to estimate variations in sockeye salmon abundance in Karluk Lake on Kodiak Island, Alaska over the past 500 years. This record will be compared to paleoclimatic data to explore relationships between salmon abundance and climate change.

Physical and limnological characteristics of Karluk Lake, which has been studied for more than 70 years, are shown in Table 1. Relative to other sockeye nursery lakes, the lake is very productive in terms of adult fish production per lake size (Burgner 1991), though the lake has suffered a long-term decline in production (Barnaby 1944; Koenings and

Table 1. Physical and limnological characteristics of Karluk Lake, Alaska.

Surface Area	39.5 km ²
Volume	1,920 m ³ x 10 ⁶
Elevation	106 m
Mean depth	48.6 m
Annual precipitation	172 cm
Water residence time	4.8 yr
Light compensation point	23 m
Total phosphorus (May-October)	7.8 µg/L
Total nitrogen (May-October)	121.3 µg/L
Chlorophyll a (May-October)	2.5 µg/L
Sockeye escapement (mean 1922-1995)	646,000 fish

From Koenings and Burkett (1987 a,b).

Burkett 1987a; Schmidt et al. 1997). The timing of the sockeye spawning has been described as having a bimodal distribution; spawning by the early (spring) run generally peaks in early to mid-July, and spawning by the late (fall) run peaks in September (Koenings and Burkett 1987a). Numerous spawning streams are distributed around the lake (Juday et al. 1932, Baranaby 1944). In general, the early spawning fish favor streams, while the late run fish utilize lake beaches in addition to streams (Koenings and Burkett 1987a). The lake is estimated to have produced returns greater than 5 million fish before its decline (Koenings and Burkett 1987a). Weir-based escapement data has been collected since 1922 (Fig. 1). Escapements averaged more than 1 million fish from the beginning of the record until the late 1930s, declining to an average of 300,000 to 400,000 fish in the 1960s and 1970s. Escapements generally increased in the 1980s and 1990s, but the lake remains below historical high production levels (Koenings and Burkett 1987a; Schmidt et al. 1997).

METHODS

Sediment cores were obtained using a hand operated gravity core with a messenger activated valve. This type of corer has been designed to take samples without disturbing the sediment-water interface, and inspection of the cores after recovery indicated that the core tops were well preserved. Core 2, 17 cm long, was recovered in Oct. 1994, and Core 3, 43 cm long, was recovered in Aug. 1995. Both cores were taken in the main basin of the lake near Station 3 of Juday et al (1932) and the Alaska Department of Fish and Game (57°25' N, 154°5' W, 52 meters water depth). The cores were continuously sampled at 0.5 cm increments shortly after recovery using an extruding device. Each sample was measured for wet and dry (85°C) weight, and magnetic susceptibility. Nitrogen isotopes were

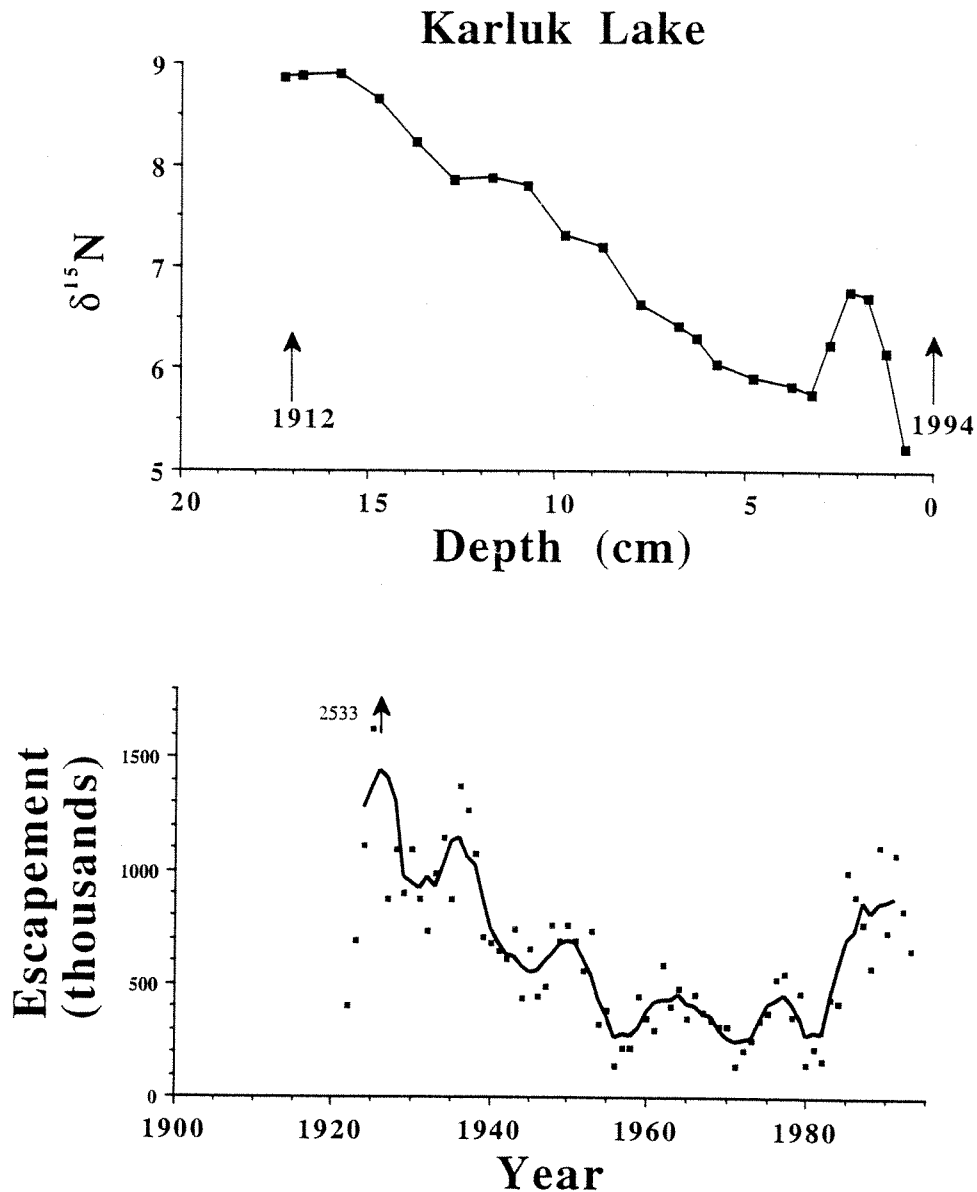
measured on bulk samples using a Europa Scientific 20/20 mass spectrometer equipped with a Roboprep combustion device. The isotopic analyses are reported in the standard δ notation relative to atmospheric N₂. Analytical precision is better than ± 0.2 ‰.

Age control is based on identification of ash layers, and by ²¹⁰Pb dating. Ash layers were identified by the presence of peaks in magnetic susceptibility, and were confirmed by microscopic observation. The Katmai 1912 ash was identified by comparing the chemical composition of glass shards, determined by microprobe analysis, to that of glass of known Katmai 1912 origin (Beget et al. 1994). Both cores contain the Katmai 1912 ash, and the longer Core 3 has an older ash fall event that occurred c.a. 1720. The age of 1912 was assigned to the depth of the peak in magnetic susceptibility associated with the Katmai event for each core. Age estimates are determined by assuming a constant sediment accumulation rate on a dry mass basis, using the rate determined during the period from 1912 to the time of core collection (13.7 mg/cm²/yr). The rate based on the ²¹⁰Pb data (14.0 mg/cm²/yr) is in close agreement with this accumulation rate estimate. The error of age estimates, particularly in the older sections, is difficult to assess. The character of the sediments is uniform throughout, suggesting no major changes in depositional processes.

Reconstructing Salmon Escapement

The method I have employed to estimate past changes in salmon escapement is based on downcore measurements of $\delta^{15}\text{N}$ in sediments. This new application of N stable isotopes is based on several observations determined from previous research. Adult salmon transport significant quantities of marine-derived nutrients (MDN) into some

Fig. 1. Upper figure shows downcore plot of sedimentary $\delta^{15}\text{N}$ in Karluk Lake Core 2. The location of the Katmai 1912 ash is indicated. Lower figure shows the weir based sockeye salmon escapement history for Karluk Lake. The bold line is a 5 year running mean.



freshwater systems when they return to spawn and subsequently die and decompose (Koenings and Burkett 1987a; Kline et al. 1993). In some systems, salmon may be the largest source of N and P annually (Koenings and Burkett 1987a; Stockner 1987). In Karluk Lake, for example, 1 million sockeye bring in more N (64,100 kg/yr) than that supplied by rivers (estimated to be 43,200 kg/yr when the effects of spawning salmon are excluded) and rain (800 kg/yr). N fixation is assumed to be low as blue green algae are a minor component of the phytoplankton assemblage (Juday et al. 1932). The $\delta^{15}\text{N}$ of adult sockeye averages about 11 to 12 (Kline

et al. 1993; Welch and Parsons 1993) as they feed at an elevated trophic level in the ocean. The other main source of N into freshwater systems is much lower in ^{15}N as it is derived from atmospheric N ($\delta^{15}\text{N} = 0$). This large difference in $\delta^{15}\text{N}$ of nitrogen sources allows salmon-derived N to be traced and quantified into freshwater environments.

I hypothesize that past changes in abundance of adult salmon returning to freshwater will be recorded by downcore changes in sedimentary $\delta^{15}\text{N}$. Periods of high abundance will result in high loadings of salmon-derived N into freshwater systems, and thus high sedimentary $\delta^{15}\text{N}$. Conversely, periods of low

abundance will result in deposition of sediments with low $\delta^{15}\text{N}$. Initial studies have focused on sockeye salmon because they generally require a lake for rearing. Many studies have shown that lake sediments are often well suited for high-resolution paleoenvironmental analysis due to relatively fast sedimentation, low bioturbation, and continuous deposition (e.g., Schelske 1991; Charles et al. 1991).

To test this hypothesis, I sampled a suite of 12 Alaskan sockeye lakes over a large region of the northern Gulf of Alaska. The average sedimentary $\delta^{15}\text{N}$ in these lakes is positively correlated ($R^2 = 0.88$) with the ratio of salmon escapement (in numbers) divided by the lake surface area, which is a measure of the relative input of salmon-derived N (Finney unpublished data). This indicates that the $\delta^{15}\text{N}$ recorded by sediments is reflecting input of MDN and hence escapement. The salmon/sediment $\delta^{15}\text{N}$ hypothesis can also be evaluated by comparing temporal trends in sedimentary $\delta^{15}\text{N}$ with historical counts of salmon escapement. In Frazer Lake, Kodiak Island, a sharp increase in sediment $\delta^{15}\text{N}$ closely matches the time when salmon were introduced into this system (McNeil 1997). For Karluk Lake the trend in sediment $\delta^{15}\text{N}$ closely follows the 75 year historical escapement record (Fig. 1). In fact, the strong positive relationship

between the decadal averages of $\delta^{15}\text{N}$ and escapement ($R^2 = 0.85$) establishes a calibration to hindcast past escapement in Karluk Lake (Fig. 2). These lines of evidence offer support for the use of sedimentary $\delta^{15}\text{N}$ to reconstruct possible changes in sockeye salmon abundance.

RESULTS

Sediment $\delta^{15}\text{N}$ profiles for the two cores from Karluk Lake show high overall values (averaging about 8‰) compared to many sockeye and non-sockeye lake sediments (Fig. 3). There is a large range in $\delta^{15}\text{N}$ of about 4‰, with values ranging from about 5.5‰ to 9.5‰. The $\delta^{15}\text{N}$ records in both cores are very similar in the overlapping portion indicating that the sedimentary $\delta^{15}\text{N}$ trends are reproducible. Prominent minima in $\delta^{15}\text{N}$ are observed in the mid to late 1900s, the early 1800s, the early 1700s, and the mid 1500s. Periods with relatively high values in $\delta^{15}\text{N}$ occurred in the mid 1800s to the early 1900s, the late 1700s, around 1700, the early to mid 1600s, the late 1500s and the early 1500s. The data suggest that major periods of escapement variation occurred over time scales of 50 to 100 years before the onset of commercial fishing (c.a., 1890; Koenings and Burkett 1987a).

Fig. 2. Relationship between sedimentary $\delta^{15}\text{N}$ in Core 2 and sockeye escapement in Karluk Lake for the period since 1921 (decadal averages). An exponential curve fit ($R^2=0.85$) excludes the uppermost point (open square), which may be low due to recent additions of fertilizer with $\delta^{15}\text{N}=0$ into the lake. The nonlinear relationship is expected because as escapement increases, the relative contribution of salmon-derived N decreases (see Finney and McNeil, in review, for more details).

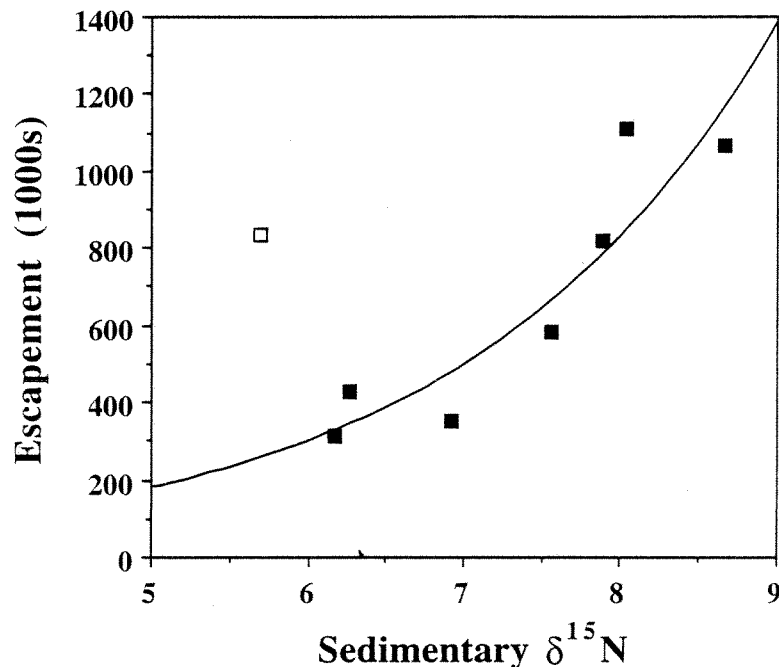
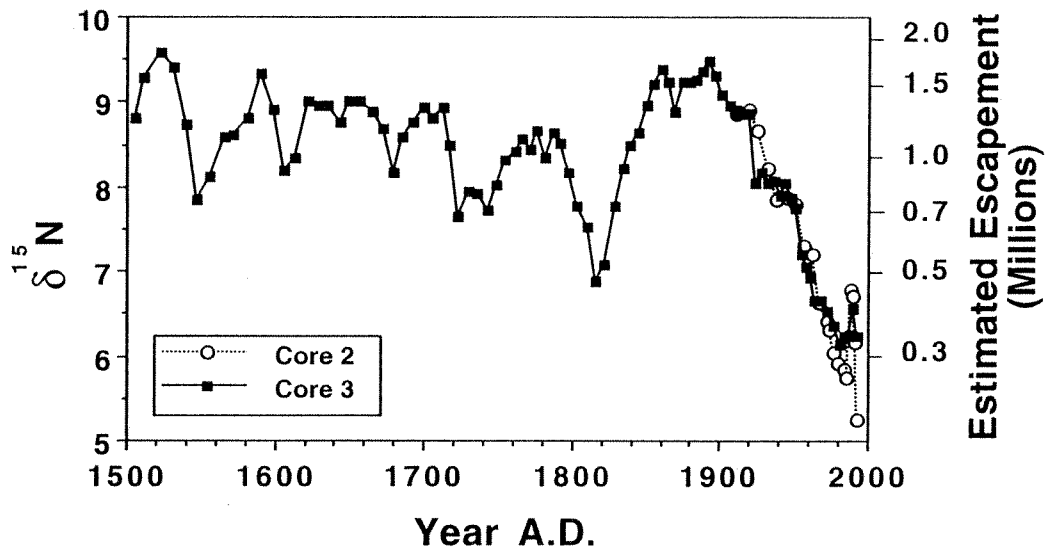


Fig. 3. Karluk Lake sediment $\delta^{15}\text{N}$ variations since about 1500. Note the similar trends in Cores 2 and 3 over the overlapping period. Estimated escapement is based on the equation from the exponential fit shown in Figure 2.



The estimated escapement values are based on the calibration shown in Figure 2. These estimates assume that there has been no significant change in sockeye size or their $\delta^{15}\text{N}$ values over this period. The rate of input and isotopic content of N from non-salmon sources is also assumed to remain constant. The estimates probably reflect averages for 5 to 10 year periods as the sampling increment averages several years of deposition. Bioturbation may also smooth the $\delta^{15}\text{N}$ profile. In addition, some dampening of changes in the lakes N budget due to escapement would be due to water residence time effects, which is 4.8 years in Karluk Lake (Koenings and Burkett 1987a). The average estimated escapement has ranged from about 300,000 to 2 million fish/year over the past 500 years. The average estimated escapement prior to commercial exploitation was on the order of 1 million fish/year.

DISCUSSION

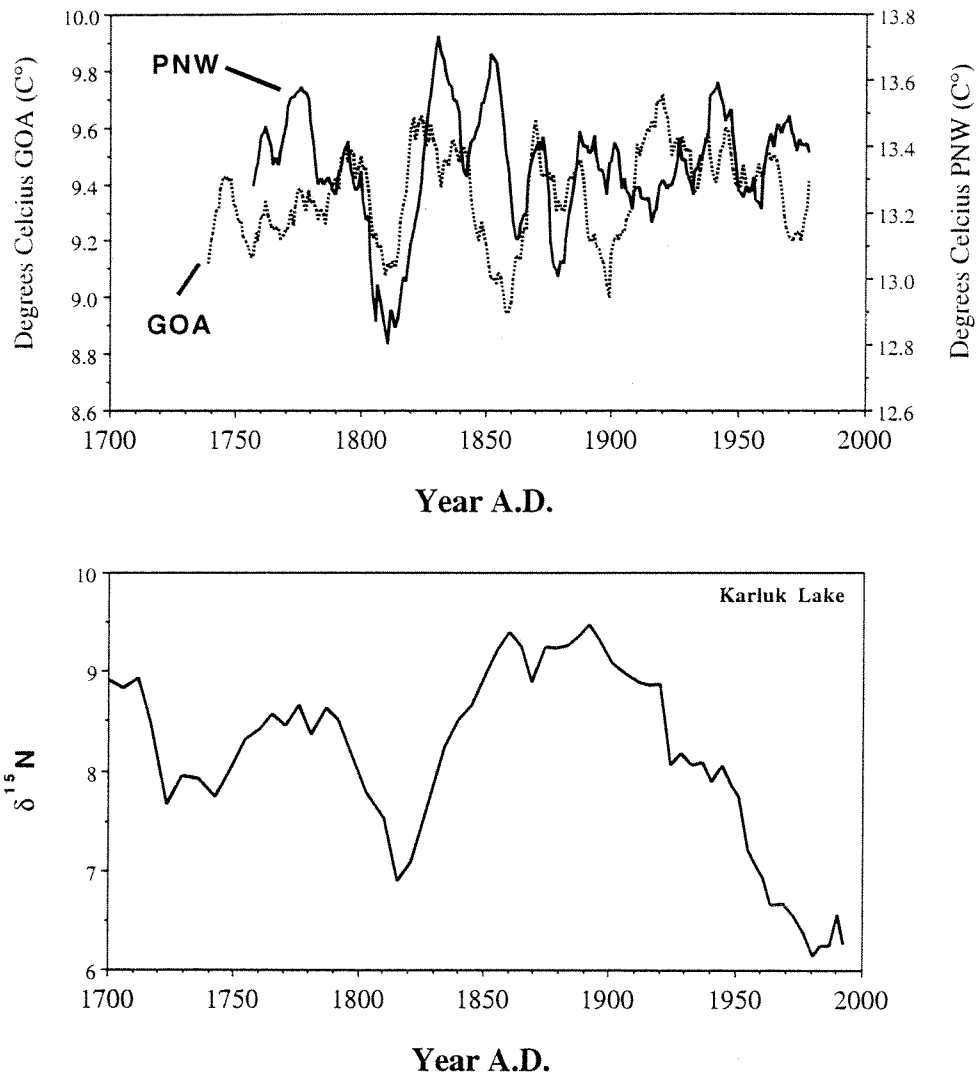
Evaluation of potential mechanisms to explain the long-term changes in Karluk Lake sockeye abundance is challenging because detailed information on concurrent climate, oceanic and lacustrine conditions is sparse. Sockeye production is influenced by conditions in both the oceanic and freshwater phases (e.g., Burgner 1991). In addition, both physical (e.g. water mass structure, temperature, nutrient flux) and biological (e.g. prey and predator abundance) factors are likely to be important in regulating salmon populations.

Reconstructions of variation in coastal temperatures derived from tree ring records along the northeast Pacific coast are the most suitable currently

available paleoclimatic data to compare with the $\delta^{15}\text{N}$ trends. Wiles et al. (1996) have recently published tree ring based reconstructions of spring and summer coastal land temperatures for sites along the northern Gulf of Alaska and the Pacific Northwest coast (Fig. 4). These coastal air temperature reconstructions are positively correlated with sea surface temperatures (SSTs) over a large region of the adjacent ocean during the period the records overlap (44 years, Wiles et al. 1996). Though the exact mechanism is unclear, changes in historical production of Alaskan salmon appear to have followed large scale changes in temperature during the 20th century. Periods of high salmon production, including those for Kodiak Island sockeye, tend to be associated with warm regimes in the Gulf of Alaska (Francis and Hare 1994). Changes in the strength of the Aleutian Low have been suggested as one possible mechanism. During periods of a more intense low, productivity and hence prey abundance is increased, and warmer SSTs are observed in the Gulf of Alaska (Beamish and Bouillon 1993).

A comparison of the Karluk Lake $\delta^{15}\text{N}$ record with the tree ring temperature reconstruction (Figs. 3 and 4) shows higher frequency variability in the temperature reconstruction. This would be expected due to the averaging effects in the sediment record discussed above. In using the $\delta^{15}\text{N}$ data to evaluate hypotheses regarding the influence of climate on salmon abundance, it is assumed that the interpretation of the sedimentary $\delta^{15}\text{N}$ data is correct, and that sockeye populations at Karluk Lake are representative of a larger region. Based on the discussion above, positive relationships between $\delta^{15}\text{N}$ and temperature might be expected. However, there

Fig. 4. Reconstructions of the northeast Pacific coastal temperatures since about 1750 from tree ring records (upper panel; from Wiles et al., 1996). The Gulf of Alaska (GOA) record is based on Alaskan trees from the northern GOA coast, and the Pacific Northwest (PNW) record is based on coastal trees in the Puget Sound region. The data represent warm season temperatures (May-October) and are plotted as 10 year running means. For comparison, the Karluk Lake sediment $\delta^{15}\text{N}$ record for this same period is shown in the lower panel.



are both similarities and differences in the temperature and $\delta^{15}\text{N}$ records. Intervals of low $\delta^{15}\text{N}$ appear to correspond with negative temperature anomalies during some periods, such as the mid 1900s and the early 1800s. In contrast, the period of high $\delta^{15}\text{N}$ during the late 1800s/early 1900s appears to coincide with relatively cool temperatures.

It is informative to compare the reconstructed temperature trends from the two widespread regions (Fig. 4). The Pacific Northwest sites are near the transition zone between the subarctic gyre and the California Current system, as opposed to the Gulf of Alaska sites which are solidly in the gyre system. Not all intervals with cool temperature anomalies in the Gulf of Alaska correspond with cool temperatures in the Pacific Northwest. For example, inferred temperatures during the early 1800s were cool in

both regions, but cool periods in the Gulf of Alaska around 1850 and 1890 coincided with relatively warm temperature anomalies in the Pacific Northwest. This indicates that different circulation patterns may result in cool temperatures in the Gulf of Alaska. If this is the case, then the different circulation patterns may also result in different oceanographic conditions such as nutrient flux, productivity and prey abundance. Thus depending on the resultant physical and biological conditions, salmon populations may respond differently to cooler conditions. Coupled physical/biological models for the North Pacific are needed to study these processes.

The Karluk Lake sediment record has the lowest $\delta^{15}\text{N}$ values during the mid to late 1900s (Figs. 1 and 3). The reconstructed temperatures during this

period, however, are moderate relative to other cool periods. Furthermore, according to the tree ring reconstructions, several periods with similar temperature patterns occurred during the last few hundred years without being accompanied by the low $\delta^{15}\text{N}$ values that are observed during this century. Thus the Karluk Lake sediment $\delta^{15}\text{N}$ data may show a significant impact on salmon production by commercial fishing, as has been suggested by other workers (see Koenings and Burkett 1987a).

The long-term data from Karluk Lake also provide a view on variations in the carrying capacity of the system prior to commercial harvest that is useful for management. The data indicate that escapement fluctuated around an average of about 1 million fish/year for about 400 years prior to commercial exploitation. Such levels are not predicted from analysis of recent zooplankton stocks (Schmidt et al. 1997). This discrepancy points to the possible role of escapement in influencing the carrying capacity of the lake through nutrient input. A positive feedback may result from higher escapements through increased nutrient input, and subsequently higher production of nursery lake prey. The significant role of sockeye carcasses in the budgets of phosphorus (Koenings and Burkett 1987a) and nitrogen (this work), and the correspondence between escapement and sedimentary $\delta^{15}\text{N}$, suggest this feedback process may be important.

CONCLUSIONS

1. Sediment $\delta^{15}\text{N}$ appears to be a useful tool for reconstructing past changes in salmon abundance. In Karluk Lake, Kodiak Island, Alaska, sedimentary $\delta^{15}\text{N}$ tracks the historical record of escapement over the past 75 years.
2. The pattern in $\delta^{15}\text{N}$ and thus inferred sockeye escapement in Karluk Lake shows significant variation over the past 500 years. Significant changes in $\delta^{15}\text{N}$ occur over periods of 50 to 100 years. Prominent minima in $\delta^{15}\text{N}$ are observed in the mid to late 1900s, the early 1800s, the early 1700s, and the mid 1500s. Periods with relatively high $\delta^{15}\text{N}$ values occurred during the mid 1800s to the early 1900s, the late 1700s, around 1700, the early to mid 1600s, the late 1500s and the early 1500s. Estimated escapement was larger on average prior to commercial exploitation of the system.
3. There is no simple relationship between Karluk Lake sediment $\delta^{15}\text{N}$ and coastal temperature records reconstructed from tree rings. Some, but not all, periods of lower $\delta^{15}\text{N}$ correspond with negative temperature anomalies. If variations in the abundance of Karluk Lake sockeye are influenced by ocean conditions, the

differing responses during cool periods may indicate that very different oceanic conditions can result when the Gulf of Alaska experiences cool temperatures. There may be more than one mode or pattern of circulation in the North Pacific that results in relatively cool temperatures in the Gulf of Alaska, and thus the impacts on biological processes and hence salmon may be different. Further work on validating salmon abundance and temperature trends is clearly needed to support the preliminary ideas presented here. However, long-term data on salmon abundance and concurrent climatic and oceanic conditions, may provide insight to better understand how salmon production may respond to future climatic changes.

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