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Tracking Sockeye Salmon Population Dynamics from Lake Sediment Cores: A Review and Synthesis

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Abstract.—Pacific salmon *Oncorhynchus* spp. play a central role in coastal ecosystems that rim the North Pacific Ocean. Given the ecological, cultural, and economic importance of Pacific salmon, there is great interest in defining the magnitude and frequency of change in these fish stocks. Fisheries scientists, through analyzing harvest records, have demonstrated pronounced salmon production variability. The causes underlying such marked fluctuations are currently debated. Collating harvest records across a broad geographic range over the past ~80 years, fisheries scientists have advanced a plausible argument that climate-induced oceanographic changes explain a significant fraction of the variation in salmon catch records. However, without data that predate the introduction of large-scale human interventions (e.g., commercial harvesting, dams, hatchery releases), it is difficult to isolate the role of climate in shaping fish stock

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dynamics. Within the past decade, however, we have developed a paleolimnological approach for tracking past sockeye salmon *Oncorhynchus nerka* population abundances, and numerous papers have applied this approach to infer changes in these fish over the past hundreds to thousands of years. Here, we provide an overview of the approach and a synthesis of the work that has been conducted in this field to date. It is clear that numerous sockeye salmon populations have undergone pronounced changes, even prior to human interventions. Furthermore, tracking salmon populations over millennial timescales with paleolimnology has revealed modes of change that were previously never imagined possible. Such long-term perspectives indicate that sockeye salmon is a resilient fish species. We note, however, that when natural environmental changes are compounded by intense human impacts, populations have been particularly susceptible to extirpation.

Introduction

Pacific salmon *Oncorhynchus* spp. are an integral part of the ecology, economy, and culture of the North Pacific. Ecologically, Pacific salmon represent significant nutrient and food sources for biological communities. Despite the importance of this genus, we only have a limited understanding of the primary factors influencing their population dynamics. Analyses of harvest data have highlighted dramatic interannual and interdecadal variability in Pacific salmon abundances, and considerable controversy exists over the causes for such fluctuations (e.g., Mantua et al. 1997; Collie et al. 2000; Mann and Plummer 2000). This debate is heightened and perhaps more critical at the southern end of the range of Pacific salmon where numerous populations have been extirpated or are at risk (Nehlsen 1997).

A major stumbling block in determining the relative importance of the myriad of stressors acting on Pacific salmon populations, including commercial fishing, dam construction, habitat destruction, hatcheries, and climatic change, is that monitoring data do not predate the period of large-scale human interventions. Without knowledge of baseline conditions, it is difficult to assess the impact of individual stressors (Smol 2008). However, paleolimnological approaches have recently been developed to reconstruct past sockeye salmon *O. nerka* population dynamics using information preserved in nursery lake sediments (Finney et al. 2000). As sockeye salmon populations can markedly influence the limnological characteristics of their nursery lake systems (e.g., Naiman et al. 2009, this volume), changes in the numbers of sockeye salmon spawners are recorded as shifts in chemical and biological components of lake sediments. The objectives of this paper are to provide an overview of this paleolimnological approach, highlight some key findings from recent studies, and discuss the major challenges in the field.

We begin with a synopsis of the current state of knowledge regarding Pacific salmon population trends, based on historical monitoring records, as this forms the key impetus for this paleolimnological research. We then review the paleolimnological approach and highlight some of the key findings. Overall, we show that paleolimnological analyses of nursery lake sediments provide many important and otherwise missing data on the population dynamics of sockeye salmon, as well as crucial information on the changes in freshwater ecosystem where sockeye salmon rear as young.

Historical Trends in Pacific Salmon Abundances

Much of what we know about population trends for Pacific salmon comes from catch data. The commercial fishery, marked by the opening of the first cannery in California, began in 1864 (Lichatowich 1999), and not long after, commercial operations were opened up at more northern and remote locations (i.e., in 1878 in Alaska; Wertheimer 1997). Whereas one might think commercial catch records could be biased by socioeconomic factors (e.g., decreases in catches during times of war), fisheries scientists have argued that catch records since the 1920s are a reasonable proxy for total salmon production, as these fish have been targeted fairly consistently over this time (Beamish and Bouillon 1993; Hare et al. 1999).

At least on a localized scale, there is evidence that declines in numerous stocks of Pacific salmon have been linked to anthropogenic activities. One of the most striking examples of this is the dramatic loss of Fraser River (BC) pink salmon *O. gorbuscha* and sockeye salmon stocks originating from lakes and rivers upstream of Hell's Gate. A severe landslide in 1913, triggered by the construction of the Canadian National Railway, greatly restricted access to upstream spawning grounds. This event, combined with subsequent mismanagement of Pacific salmon fisheries until 1937, exterminated pink salmon stocks upriver of Hell's Gate (Northcote and Atagi 1997) and depressed sockeye salmon stocks to very low abundances for several decades (Mundy 1997).

Analyses of catch records on a broader geographical scale, however, demonstrate regionally synchronous patterns, providing evidence to suggest that Pacific salmon stocks are also influenced by changes in the basin-scale, coupled ocean-atmospheric system. Beamish and Bouillon (1993) were among the first fisheries scientists to analyze salmon catch records over the 20th century and demonstrate a broadly coherent, interregional pattern across Canada, the United States, and Russia.

By examining the salmon catch records across a north–south gradient, fisheries scientists have recognized that interdecadal regime changes have both temporal and spatial components (Figure 1). Southern and northern populations of salmon from the North Pacific have shown synchronous but 180 degrees out-of-phase changes in 1947, 1977, and 1989 (Mantua et al. 1997; Hare et al. 1999; Hare and Mantua 2000). For example, Alaskan salmon stocks increased in abundance after 1977, while southern stocks showed lower than average returns (Figure 1; Mantua et al. 1997). Dramatic changes have also been identified around 1976–1977 in physical parameters of the North Pacific, primary and secondary productivity measures (e.g., Ebbesmeyer et al. 1991; Brodeur and Ware 1992), and abundances of other strictly marine fish (e.g., walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*, and Pacific halibut *Hippoglossus stenolepis*; e.g. Beamish

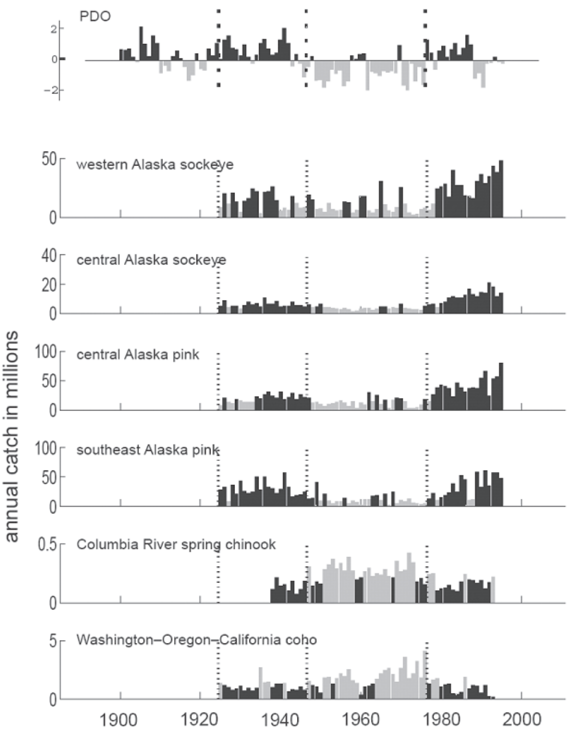

Figure 1.—Pacific salmon catch records from a north–south gradient along the coast of North America demonstrating changes that are synchronous with changes in the Pacific Decadal Oscillation (from Mantua et al. 1997).

1993; Clark and Hare 2002). These broad ecosystem-level changes have led numerous investigators to suggest that decadal-scale shifts in salmon abundances are likely driven by environmental changes in the North Pacific (e.g., Beamish and Bouillon 1993; Francis and Hare 1994; Mantua et al. 1997; Hare et al. 1999). The term "regime shift" was coined to describe the change in average characteristics of the North Pacific ecosystem that have persistent patterns at decadal scales, but then show abrupt transformations in states within a year or so (Hare and Mantua 2000). Further analyses of tree-ring data have revealed that the North Pacific climate has undergone repeated regime shifts with a periodicity of 50–70 years over the past few centuries (e.g., Minobe 1997; MacDonald and Case 2005).

The mechanism(s) through which physical changes in the North Pacific affect salmon (and other marine organisms) is still an area of active research, but several investigators have suggested that the mechanism(s) are not direct, as there are poor relationships between physical and biological variables on interannual time scales (Beamish and Bouillon 1993; Francis and Hare 1994). In an attempt to explain inverse salmon production regimes, Gargett (1997) proposed a comprehensive hypothesis that relates salmon abundances to environmental changes in the North Pacific. Her interpretation, which has since been widely cited by the scientific community, is centered on changes in the intensity of the Aleutian Low (a low pressure system that develops over the Aleutian Islands in winter). The Aleutian Low strongly couples the physical properties of the atmosphere with those of the North Pacific Ocean and is believed to be the key driving force in interdecadal patterns of variability in sea surface temperatures (i.e., the Pacific Decadal Oscillation; Mantua et al. 1997). In years when there is a strong Aleutian Low, temperatures along the coast of North America tend to be warmer and the coastal waters more strongly stratified. Coastal conditions are believed to be of prime importance to Pacific salmon because it is the early marine phase, when the smolts are in the coastal areas, that salmon are most sensitive to environmental changes (e.g., sea surface temperatures (SST); Pyper et al. 2005). Greater coastal stability has opposite effects on phytoplankton populations in the northern (Alaska) and southern (Pacific Northwest) regions of the northeast Pacific. These changes in phytoplankton production are significant to all marine organisms because they form the base of the food web (Miller et al. 2004). In the Gulf of Alaska, phytoplankton is believed to be light-limited, and thus greater water column stability allows for phytoplankton to remain in the photic zone longer and achieve higher production rates (Polovina et al. 1995). Meanwhile, further south, greater coastal stability is unfavorable for nutrient-limited phytoplankton because stronger water column stability deters the upwelling of deep, nutrient-rich waters with surface waters (McGowan et al. 2003). Gargett (1997) suggests that salmon abundances are largely affected by the availability of their forage, which in turn is driven by primary production, ultimately influenced by nutrient availability and water column stability.

While there is a reasonable case to be made that climatic shifts are driving marine production in the North Pacific, it is hard to isolate climate from other potentially important variables influencing Pacific salmon, given contemporary data sets. As stated above, numerous anthropogenic stressors have been introduced over the past century. In order to tease apart the impact of multiple stressors, it is necessary to extend records of Pacific salmon abundances back in time so that the predisturbance production variability (i.e., premid- to late 1800s) can be assessed. Hindcasts of past salmon abundances on these temporal scales will allow investigators to uncover natural salmon population dynamics and the role of climatic change, as well as constrain influences of anthropogenic impacts.

The Paleolimnological Approach for Reconstructing Sockeye Salmon Population Dynamics

Paleolimnology, the study of the biological, chemical, and physical indicators preserved in lake and river sediments, is now a well-established science (Smol 2008). Lake sediments represent natural environmental archives of local and regional conditions as autochthonous (i.e., derived from within the lake) and allochthonous (i.e., coming from outside the lake) materials are continuously deposited at the bottom of lakes. To date, a vast array of paleolimnological indicators have been studied to define changes in a wide range of environmental variables (e.g., nutrients, pH, temperature; Smol 2008). Unfortunately, reconstructing past fish abundances has always been a challenge for paleolimnologists because fish bones and scales are rarely preserved in sufficient numbers in deepwater lake sediments (Smol 2008). However, Pacific salmon, particularly sockeye salmon, have a somewhat unique life history that enables paleolimnologists to infer past population dynamics through changes in proxy indicators preserved in nursery lake sediments.

Pacific salmon have an anadromous life cycle (i.e., organisms that migrate from the ocean to freshwaters to spawn) and most are semelparous (spawn once and then die). Sockeye salmon differ from other Pacific salmon in that they make use of nursery lakes and their tributary streams to spawn (other species use streams and rivers exclusively). The annual return and subsequent death of thousands to millions of sockeye salmon spawners in nursery lake environments may represent a significant source of nutrient loading (Krohkin 1975; Koenings and Burkett 1987; Kline et al. 1997). As a result, changes in spawner abundances can greatly alter nursery lake nutrient conditions (Koenings and Burkett 1987; Gregory-Eaves et al. 2003). The technique described herein could be extended to other anadromous lake-rearing fish that have a similar influence on the water chemistry of their nursery environment (e.g., alewife *Alosa pseudoharengus*; Durbin et al. 1979). More often than not, however, other anadromous lake-rearing fishes contribute only a small fraction of the total nutrient pool (e.g., Swanson and Kidd 2009, this volume).

Finney (1998) demonstrated that alterations in salmon-derived nutrient loading (and thus sockeye salmon spawner abundances) could be inferred by analyzing the stable isotopic signature of lake sediments. Finney et al. (2000) were the first to use multiple paleolimnological indicators to track sockeye salmon population dynamics in Alaskan nursery lakes over the past ~300 years. Below, we summarize key aspects of the main indicators used in these reconstructions.

Stable Nitrogen Isotope Ratio $\delta^{15}N$

The stable isotope ratio $\delta^{15}N$ has repeatedly been shown to be a valuable tracer of anadromous salmon in both food web and paleolimnological research (e.g., Kline et al. 1993; Finney 1998). Salmon are enriched in ^{15}N (relative to the much more common isotope ^{14}N) in part because they feed relatively high on the food web and in part because they accumulate most of their biomass in the marine environment (i.e., >95%, Burgner 1991). Adult salmon feed on a diet of small pelagic fish, squid, and small crustaceans (Burgner 1991), which results in ^{15}N enrichment in sockeye salmon relative to lower trophic levels. As was first demonstrated by Minagawa and Wada (1984), $\delta^{15}N$ progressively increases in organisms of higher trophic levels because the lighter ^{14}N isotope is preferentially excreted. Feeding in the marine environment further contributes to the heavy $\delta^{15}N$ signature of adult salmon. The $\delta^{15}N$ signature of the marine environment (based on analyses of nitrate, particulate matter, and organisms) is relatively enriched because the primary source of nitrogen is upwelled nitrate, which has been enriched in ^{15}N via denitrification (a process that occurs in oxygen-depleted waters; reviewed in Michener and Schell 1994). Finney's (1998) paper demonstrated that the sedimentary $\delta^{15}N$ profile from Karluk Lake, Alaska, was significantly correlated to the historical time series of sockeye salmon spawners, which had been monitored since 1922. Finney et al. (2000) went on to demonstrate that sedimentary $\delta^{15}N$ was not only related to escapement through time, but that similar patterns were present from a wide spectrum of Alaskan lakes.

There are, however, numerous factors that can also influence $\delta^{15}N$ in lakes, including changes in organic matter source, nitrogen utilization, nitrogen fixation, denitrification, and ammonia volatilization (Finney et al. 2000). Careful consideration of these factors is necessary when interpreting $\delta^{15}N$ profiles. For example, a sudden input of terrestrial organic matter (e.g., as a result of a forest fire or earthquake) would dilute the salmon-derived nutrient signal and could lead an investigator to conclude that sockeye salmon populations decreased. Such an interpretation, however, can be constrained by plotting ratios of sedimentary carbon to nitrogen (C:N; e.g., Holtham et al. 2004), as terrestrial organic matter sources have higher C:N than those of aquatic organic matter due to higher cellulose concentrations in land-based plants (Meyers and Ishiwatari 1993). Sedimentary charcoal analysis could also be used to isolate forest fire events and evaluate whether deviations in $\delta^{15}N$ were influenced by fires (Whitlock and Larsen 2001). Depletion of a lake's nitrogen supply and the shift in the organic matter source of nitrogen to that fixed by cyanobacteria (i.e., atmospheric N with a $\delta^{15}N$ of 0 ‰) is less likely in most sockeye salmon nursery lakes, as these systems tend to be P-limited more than N-limited (Edmundson and Carlson 1998; Shortreed et al. 2001). However, data regarding the water chemistry (e.g., TN:TP, POC:PON), as well as analysis of algal pigments in the sediments, can help to confirm that changes in the N source in the lake are minimal. In contrast to the processes described above, which can depress the $\delta^{15}N$ signal, denitrification, and ammonia volatilization, are two pathways through which sedimentary $\delta^{15}N$ can be enriched without the influence of salmon-derived nutrients. These pathways are, however, not likely to be prevalent in sockeye salmon nursery lakes, as they only operate with any magnitude under rather severe environmental conditions (i.e., low oxygen for denitrification and high pH for ammonia volatilization). Along with evaluating the relative importance of such conflicting factors in a paleolimnological analysis, a robust approach includes the analysis of several, independent proxies. For example, biological microfossil indicators (as discussed below) are less susceptible to postdepositional alterations than geochemical tracers (e.g., $\delta^{15}N$) and have proven to be a valuable complement (Gregory-Eaves et al. 2003; Gregory-Eaves et al. 2004; Holtham et al. 2004).

Diatoms and Other Algal Indicators

A second proxy group demonstrated to indirectly track past sockeye salmon abundances through salmon-derived nutrient loading are algal indicators (e.g., Gregory-Eaves et al. 2003; Schindler et al. 2005). Numerous investigators have observed the presence of dense algal mats in areas near decomposing salmon carcasses (e.g., Mathisen 1972). Because algal growth is often limited by nutrients, salmon-derived nutrient loading can influence both algal production (e.g., Fisher-Wold and Hershey 1999) and species composition (e.g., Gregory-Eaves et al. 2003, 2004).

Diatoms (Bacillariophyceae) have been widely applied in paleolimnology because (1) they are a ubiquitous group, present in large abundances in many aquatic habitats; (2) they are responsive indicators with short generation times; (3) they are identifiable to the species level or lower; (4) they are a very diverse group, with different species having specific optima and tolerances to numerous environmental variables; and (5) their siliceous cell walls preserve well in most lake sediments (Smol 2008). A common application of diatoms has been to trace past lake trophic status, as nutrient concentrations have been shown to be a significant factor in influencing diatom species assemblages (reviewed by Hall and Smol 1999). Other variables, however, are also known to influence diatom community composition (e.g., pH and salinity), and therefore it is important to select lakes where salmon-nutrient loading is likely to be the strongest signal. In particular, this technique is only likely to be effective where salmon-derived nutrients (SDN) make up a significant fraction of the total nutrient budget (or at least did in the past). The diatom analysis should be done in conjunction with a marine tracer such as $\delta^{15}N$, as the investigator is unable to determine the nutrient source from the diatom community composition alone. Numerous lakes on the west coast of North America satisfy these conditions, as many salmon nursery systems are remote and thus are less influenced by large nutrient inputs from human activities or by other sources of anthropogenic impact. In such lakes, Finney et al. (2000) and Gregory-Eaves et al. (2003) have demonstrated that fossil diatom assemblages can be strongly correlated to historical numbers of returning adult spawners (i.e., escapement).

Sedimentary algal pigments have also been used for tracking past algal responses to salmon-derived nutrients (Schindler et al. 2005; Brock et al. 2006, 2007). The preservation of chlorophylls and carotenoids in the sediment record allows investigators to quantify the magnitude of change in algal production and to infer how different algal groups (e.g., siliceous algae, chlorophytes, and cyanobacteria) have varied over the course of the time (Leavitt and Hodgson 2001). Since the development of the use of algal pigments in paleolimnology, there have been some concerns about the preservation of pigments (e.g., poor preservation under alkaline conditions and changes in preservation with lake depth), but salmon lakes tend to be circumneutral in pH and deep, open drainage systems (and thus relatively insensitive to changes in atmospheric moisture balance; Shortreed et al. 2001).

Biogenic silica is another geochemical indicator of algal production and is easily measured from sediment samples. Biogenic silica is often used as a surrogate measure for diatom production as diatoms are commonly the most abundant siliceous algae (e.g., Conley and Schelske 2001). Total diatom production, in turn, has been shown to be a reasonable proxy for inferring changes in phosphorus loading in many lakes until silica becomes a limiting nutrient (Conley and Schelske 2001). Therefore, in lakes where the sockeye salmon returns are relatively high and silica is not a limiting nutrient, biogenic silica can track changes in SDN loading. This approach was used successfully in Packers Lake, Alaska, where Gregory-Eaves et al. (2004) demonstrated that biogenic silica was strongly correlated to $\delta^{15}N$ and the changes in diatom species assemblages.

Zooplankton

The study of zooplankton remains can provide insight into the extent to which salmon nutrients are incorporated into freshwater food webs as well as information on the predation pressure by juvenile sockeye salmon. Cladocerans, and to varying degrees copepods and aquatic insect larvae, are primary prey items of juvenile sockeye salmon, that will spend up to 3 years in the nursery lake (Burgner 1991). The chitinous exoskeletons of cladocerans, though disarticulated into several parts in the sediments, are well preserved and are used to reconstruct a key component of the zooplankton assemblage (Korhola and Rautio 2001). Both the species composition and the size structure of the cladocerans provide insightful metrics.

Sweetman and Finney (2003) demonstrated the influence of both nutrient-stimulated production and predation pressure on zooplankton populations from two lakes (Karluk and Frazer) in Alaska. The two study lakes were selected because they both had long-term monitoring records of escapement and were similar in morphometries and geographic location but differed substantially in their histories. Due to a steep waterfall at the outlet of Frazer Lake, this system had no resident sockeye salmon population until two fish passes were constructed in the 1960s and 1970s. In contrast, Karluk Lake is a naturally producing sockeye salmon lake.

Interestingly, the sediment record from both lakes showed a positive relationship between the flux of the dominant zooplankton species *Bosmina longirostris* and historical sockeye salmon escapement, highlighting the significance of changes in salmon-derived nutrients in the production of zooplankton over broad temporal scales. Morphometric data for *B. longirostris*, however, showed different responses in each of the lakes to variation in sockeye salmon escapement, which could be explained in terms of the importance of different predators. In Frazer Lake, the size of *B. longirostris* was inversely related to the abundance of sockeye salmon, whereby strong predation pressure by introduced juvenile sockeye elicited an adaptive response in the zooplankton to become smaller and more evasive. Karluk Lake provides a contrasting picture, however, as a positive relationship was documented between the size of *B. longirostris* and the abundance of sockeye salmon. Given that Karluk Lake is more productive (which is likely related to its long history of strong sockeye salmon returns) and has a much more abundant zooplankton community than Frazer Lake, it is perhaps not surprising that the juvenile sockeye salmon are a less effective selection pressure than the impact of enhanced nutrient loading from salmon-derived nutrients. The relatively strong presence of the zooplanktivorous zooplankton *Cyclops* sp. in Karluk Lake may also have played a role in size increases of *B. longirostris*, as *Cyclops* sp. are unable to consume the larger sized zooplankton. Ultimately, the Sweetman and Finney (2003) study was instrumental in demonstrating the influence of salmon-derived nutrients on the density and size of sockeye salmon forage.

What Have We Learned so Far?

The use of paleolimnological approaches to track past salmon abundances is a relatively new area of research. However, several important questions have already been answered using information preserved in nursery lake sediment profiles. For example, the ability of paleolimnology to extend these historical records beyond the period of pronounced anthropogenic impact has allowed us to reconstruct natural population dynamics and bring forth understanding on the effects of anthropogenic stressors. The major findings in the area of sockeye salmon reconstructions can be summarized into the following categories: (1) broad-scale synchrony in northern salmon production over the past ~300 years, (2) pronounced and sustained variation in some populations over the past ~2,200 years, (3) sustained low population sizes in other systems for the past ~1,500 years, and (4) the importance of site characteristics in selecting a suitable lake for salmon reconstruction.

In the first paper to use a multiproxy approach to reconstruct past sockeye salmon abundances, Finney et al. (2000) showed evidence of broad regional synchrony in $\delta^{15}N$, a proxy for changes in sockeye salmon populations, over the past ~300 years (Figure 2). By

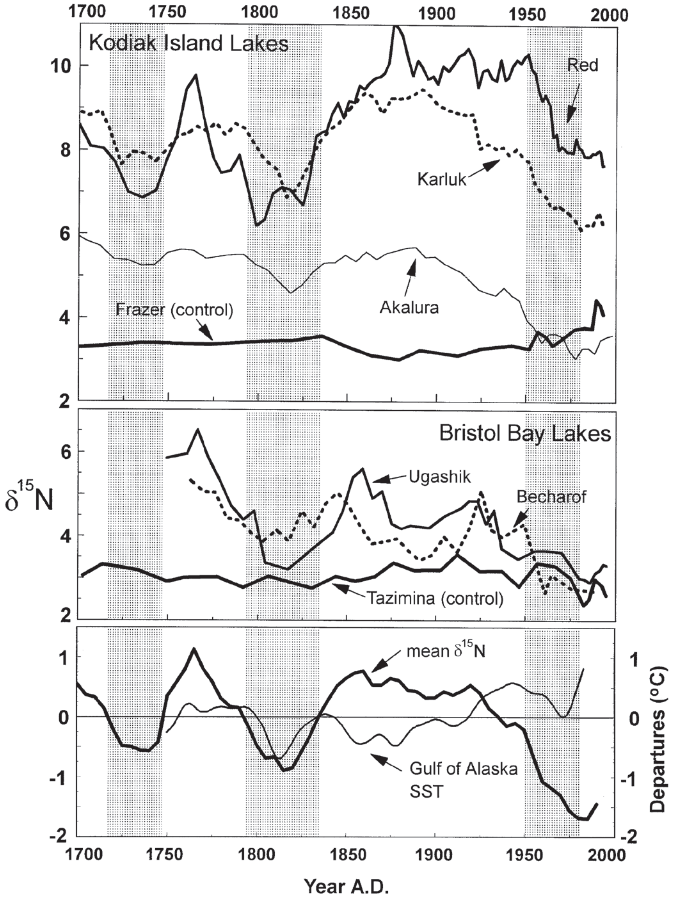

Figure 2.—Reconstructions of sockeye salmon population dynamics, as inferred from δ^{15}N profiles, from three nursery lakes on Kodiak Island and two nursery lakes in the Bristol Bay region (from Finney et al. 2000). Plotting the 250-years reconstruction of sea surface temperatures from the Gulf of Alaska (based on dendrochronological analysis; D'Arrigo et al. 1999) alongside our composite salmon index (bottom panel) illustrates that the early 1800 deviation in the salmon records corresponds to the coldest period on record.

correlating the δ^{15}N profiles from sediment cores from five nursery lakes, many of the series have strong relationships (i.e., $r > 0.50$; Table 1). In contrast, the relationship between the composite δ^{15}N index from the pre-fishing era (Figure 2), based on the five salmon lakes and the reconstruction of SST from the Gulf of Alaska (based on tree ring data; D'Arrigo et al. 1999), is weak and nonsignificant ($r = 0.23$, $p = 0.37$, $n = 19$). The coldest period on record, however, corresponds to a marked deviation in the mean δ^{15}N. This finding is similar to analyses of historical time series where correlations between catch records and climate variables are weak at an interannual time scale. Climate regime changes in these historical records, however, have corresponded to marked deviations in catch (Francis and Hare 1994; Mantua et al. 1997). The direction of change, where colder conditions correspond to lower than average sockeye salmon abundances in northern populations, is also the same between the catch and paleolimnological time series. Thus, the paleolimnological time series confirmed that regime changes had occurred before the advent of intensive anthropogenic disturbances, supporting the notion that the 20th century regime changes were also likely climate-driven.

Table 1.—A spearkman rank correlation matrix of the $\delta^{15}N$ values from the pre-fishing era (pre-1880 AD) presented in Figure 2. The data were first interpolated such that they would be on the same time scale and resolution (n = 19) and then transformed into Z-scores. * indicates $p < 0.05$; ** indicates $p < 0.01$.

	Red	Karluk	Akalura	Becharof	Ugashik
Red	1.00				
Karluk	0.84**	1.00			
Akalura	0.72**	0.64**	1.00		
Becharof	0.05	-0.13	0.26	1.00	
Ugashik	0.52*	0.50*	0.72**	0.49*	1.00

Note: As there was significant first-order autocorrelation in all data series, the p-values are likely underestimated.

The Finney et al. (2000) study also presented striking declines in $\delta^{15}N$ (reflecting declines in the number of spawners) in all five sockeye salmon populations over the past century, which was inferred to be, at least in part, a product of the commercial fishery. The impact of the declines in the number of spawners, however, appears to have different consequences in different lakes (Finney et al. 2000). To address this issue more closely, Schindler et al. (2005) developed a mixing model formula to quantitatively infer past sockeye salmon escapement. When the historical catch record was added to the inferred escapement profile from Lake Nerka, Alaska, they showed that despite at least 50 years of commercial fishing and declines in the inferred escapement record, the total production of the system over the past few decades has been at a record high (Figure 3A). An ecological argument supporting this finding is that there was increased freshwater production of juvenile sockeye salmon as a result of less density dependence for spawning habitat and freshwater forage. In contrast, when we apply the same mixing model to Karluk Lake and add the historical catch record to the inferred sockeye salmon escapement profile, we can see that the current total production is at least three times lower than what is was at the turn of the 20th century (Figure 3B). This result from Karluk Lake, however, is not surprising, as increasing the returns of

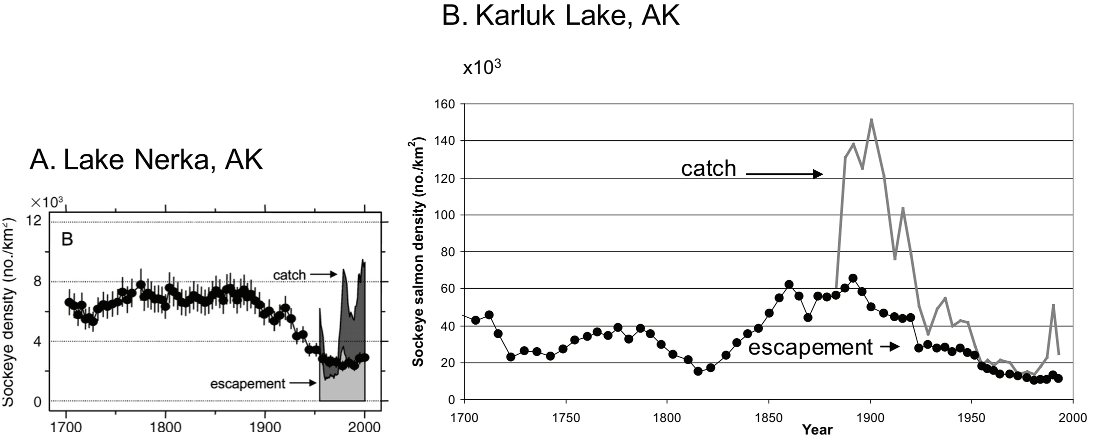

Figure 3.—The history of sockeye salmon total production (i.e., sum of escapement and catch) from two Alaskan systems that have responded very differently to the commercial harvest. (A) Lake Nerka has experienced the greatest total production in the past few decades (modified from Schindler et al. 2005). (B) The Karluk Lake time series shows that total production was greatest around the time that commercial harvesting began. Note: in both profiles, the catch series has been added to the escapement and thus reflects the best estimate of total production trends.

sockeye salmon spawners to the system have resulted in substantial increases in surface water total phosphorus concentrations (Koenings and Burkett 1987; Gregory-Eaves et al. 2003). Given that sockeye salmon nursery lakes represent a diversity of habitats (including glacial, meromictic, and clearwater systems; Edmundson and Carlson 1998), we reiterate that the importance of sockeye salmon in fertilizing these systems will vary greatly (e.g., Finney et al. 2000; Hyatt et al. 2004).

While the ~300 year records have demonstrated that decadal-scale variability existed in salmon populations long before the commercial harvest, Finney et al. (2002) extended these time series over the past ~2,200 years and showed much more prolonged and pronounced changes. The ~2,200-year $\delta^{15}N$ records illustrated that sockeye salmon production could be depressed for hundreds of years and then return to peak abundances without large-scale interventions by humans. We never suspected, nor did many colleagues in the fisheries community, that relatively unperturbed sockeye salmon populations would be this variable. By comparing the Karluk Lake $\delta^{15}N$ profile to reconstructions of other marine fish to the south (i.e., southern British Columbia and California), Finney et al. (2002) suggested that northern and southern fish populations within the North Pacific region are broadly synchronous, but that southern fish are 180 degrees out of phase with northern populations. As previously discussed, similar patterns in north–south sockeye salmon populations have been observed historically (e.g., Mantua et al. 1997; Hare et al. 1999) but have been complicated by the presence of multiple stressors. These results show that we are just beginning to unravel the true range of spatiotemporal variability in the magnitude and persistence of sockeye salmon population dynamics.

Although the Alaskan paleolimnological work has revealed that some populations have undergone large changes in size (i.e., changes on the order of greater than 10,000 spawners/km^2), there have been a few studies where the $\delta^{15}N$ profiles show subtle to no variations over the time frames under study (Holtham et al. 2004; Selbie et al. 2007; Hobbs and Wolfe 2007, 2008). There are two possible reasons for this: (1) the sockeye salmon population has been naturally low and invariable over the course of history, and/or (2) the conditions of the lake and watershed are such that other factors swamp any signal that might have been recorded by salmon in the nursery lake sediments. An example of the former is highlighted in a recent paper by Selbie et al. (2007), who developed paleolimnological records from current (Redfish Lake) and past spawning habitat (Pettit Lake) of the federally endangered Snake River sockeye salmon in the Sawtooth Valley of Idaho. The key questions addressed in this study were (1) How abundant and variable were sockeye salmon populations in these systems prehistorically? (2) How important were salmon-derived nutrients to the rearing system ecology? (3) When did the population declines occur and what historical influences were most likely responsible? (4) What are and have been the potential impediments to stock recovery efforts? The $\delta^{15}N$ profiles from the two sockeye salmon nursery systems showed that although they are higher than the control lake profile in the pre-1950 sediments, the values were not as high or variable as in Alaskan nursery systems (mostly less than 4 ‰). Using the predictive equation from Finney et al. (2000) that would allow the approximate conversion of $\delta^{15}N$ values into spawner density numbers, we estimate that sockeye salmon spawner densities in Redfish Lake were generally less than 6,500/km^2. A pattern that was coherent across the Idaho salmon systems was a unidirectional decline in $\delta^{15}N$ beginning ~1860, which corresponds to the onset of commercial fishing on the Columbia River. A further negative inflection in the $\delta^{15}N$ profile was evident and coincident with completion of the Sunbeam Dam, a small hydroelectric project that represented a significant barrier to the passage of sockeye salmon from 1910 to 1934 (Selbie et al. 2007). Thus, although the Idaho study lakes have experienced substantial declines coincident with fishing and dam construction, mitigation targets of escapement of more than 6,500/km^2 in Redfish Lake would likely be unrealistic because the system likely has not supported larger densities over the past ~1,400 years.

By adopting a multiproxy approach in the Idaho study, Selbie et al. (2007) also demonstrated that there was a pronounced reorganization of the nursery lake food web following the decline in sockeye salmon and subsequent fisheries management interventions. Historical fisheries "enhancement" practices, consisting of the introduction of hundreds of thousands to millions of nonnative sockeye salmon and kokanee (lacustrine sockeye salmon) juveniles and eggs to Sawtooth Valley rearing systems, potentially augmented by changes in nutrient loading (i.e., atmospheric nitrogen deposition and climatically altered biogeochemical cycling), shifted the zooplankton community to a smaller, less energetically beneficial forage (from *Daphnia* to *Bosmina*) for juvenile Snake River sockeye salmon. Selbie et al. (2007) identified this as a likely factor impeding the success of restoration efforts in rebuilding the sockeye salmon run.

Paleolimnological analyses of sockeye salmon nursery lake sediments have also shown that the salmon signal preserved in sediments may be harder to detect in systems with high flushing rates (i.e., low water residence times), with relatively high loads of terrestrial organic matter, and/or where the nutrient loading from sockeye salmon is low. Holtham et al. (2004) addressed these issues with their paleolimnological investigations of coastal nursery lakes. Although two of their study lakes currently have high densities of sockeye salmon spawners (i.e., greater than 10,000 spawers/km^2), the sedimentary $\delta^{15}N$ profiles from two of the lakes were relatively low and invariant. Through a close examination of the limnology of their study systems, Holtham et al. (2004) identified that both lakes had very low water residence times (i.e., <0.5 years). Given that such low water residence times result in the swift flow through of nutrients and plankton (Stockner et al. 2005), the limnic conditions prevent planktonic communities from fully exploiting salmon-derived nutrients. The fast movement of plankton through the system also prevents this material from being deposited at the lake bottom in the form of sediments. Terrestrial organic matter can also be more important in such systems as watersheds receiving relatively high amounts of precipitation also receive greater loads of nutrients from the watershed through precipitation-fed streams and surface runoff (Gross et al. 1998). When terrestrial organic matter loading is very high, the sediment may be dominated by cellulose-rich matter, which has a high C:N ratio (as discussed above). This was particularly evident in Hobiton Lake, BC, where a prominent peak in the C:N profile was detected around the time of a major earthquake in the region (Holtham et al. 2004). Even when the C:N peaks were excluded, the $\delta^{15}N$ profile was consistently low, suggesting that sockeye salmon loading to the system was never substantial. Given that Hobiton Lake's water residence time is not extremely low (i.e., ~1 year), the most parsimonious hypothesis is that this site did not experience high sockeye salmon spawner densities over the past ~200 years. Overall, the Holtham et al. (2004) study emphasized the importance of site selection in developing a reconstruction of past sockeye salmon dynamics from lake sediments. To summarize the key factors that must be considered in selecting a suitable nursery lake for paleolimnological analysis, we have developed a conceptual model (Figure 4). This flow diagram not only highlights the factors that influence the strength of the salmon signal, but also suggests how these factors may be evaluated a priori.

Emerging Areas of Study and Conclusions

After approximately a decade of research, the field has made significant advances—perhaps most notable has been identifying the widespread role of natural factors in regulating population dynamics. When embarking on this kind of research, however, it is crucial that scientists evaluate the potential of a site to produce a high-quality salmon reconstruction. Our work to date provides a number of guiding principles that should be addressed before investing large amounts of resources into developing paleolimnological analyses.

Promising topics for future applications of the approach described herein include tracking sockeye salmon population dynamics in (1) the Pacific Northwest and California, (2) Russia, and (3) over longer term time scales such as over the course of the entire Holocene and into the full glacial period. There have also been some interesting developments that have shown that Pacific salmon are important vectors of contaminants (e.g., Ewald et al. 1998; Krümmel et al. 2003; Gregory-Eaves et al. 2007).

Paleolimnological research has and will continue to play a central role in defining sockeye salmon population variability. Given that monitoring data are lacking in many areas and, where they exist, are often of insufficient length or quality to determine how large-scale human interventions have impacted Pacific salmon, paleolimnological research is clearly a critical tool in developing sustainable fisheries management plans. This

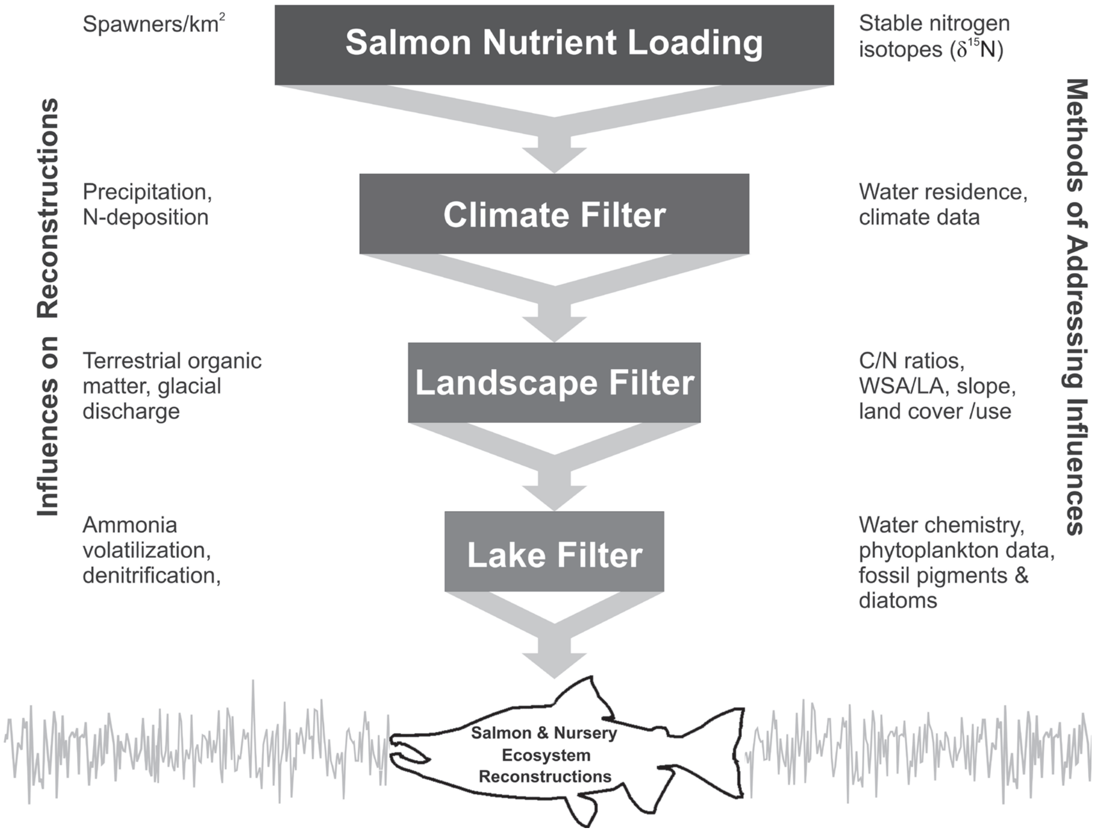

Figure 4.—A conceptual model that illustrates the hierarchy of decision making an investigator should consider when selecting a site for paleolimnological salmon reconstruction. Along the right of the diagram are methods that can be used to guide each level of decision making. (Modified from Selbie 2008)

need is further heightened by the importance of Pacific salmon in the ecology, economy, and culture of North Pacific communities and the threatened status of many stocks.

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