

Ecological, landscape, and climatic regulation of sediment geochemistry in North American sockeye salmon nursery lakes: Insights for paleoecological salmon investigations

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Abstract

We used multiple linear regressions across a Northeast Pacific region 56-lake set to examine the influence of sockeye salmon spawner densities and limnological, climatic, and watershed characteristics on sediment stable nitrogen isotope ($\delta^{15}\text{N}$) and C:N signatures, geochemical proxies used in paleolimnological reconstructions of prehistoric salmon abundances. Across all sites ($n = 56$), sedimentary C:N was primarily related to variables reflecting allochthonous organic matter and nutrient fluxes, with 67% of the variance explained by watershed vegetation type, watershed area, mean slope, and salmon spawner densities. In a subset of sites with nutrient data ($n = 41$), 63% of variance in C:N was explained by precipitation and watershed vegetation type. Sediment $\delta^{15}\text{N}$ was most strongly related to salmon spawner densities, but C:N and watershed area:lake area ratios explained significant residual variance (total 55%). In sites with nutrient data, salmon spawner densities, vegetation type, and spring nitrate explained 62% of the variance in $\delta^{15}\text{N}$. Sediment C:N and $\delta^{15}\text{N}$ values exhibited distinct interregional variation, typically varying inversely. Regional $\delta^{15}\text{N}$ -salmon density relationships (regression slopes) varied strongly with total annual precipitation ($r^2 = 0.89$, $p = 0.016$, $n = 5$), suggesting watershed organic matter and nutrient loading vary predictably in relation to regional biogeoclimatic conditions. Our findings demonstrate that paleolimnological analyses are useful for quantitative reconstruction of past salmon densities; however, inferences regarding past salmon populations must consider the factors regulating influxes of nitrogen from watershed sources.

Pacific salmon (*Oncorhynchus* spp.) production has been characterized by substantial variation over recorded history with many anthropogenic and natural drivers advanced as causal mechanisms (Mantua et al. 1997; Lichatowich 1999). Whether the fluctuations documented in relatively short and, in some cases, biased salmon fisheries harvest and escapement (fish returning to spawn) data are representative of natural production variation is debatable. This is a particularly critical issue at the southern extent of the Pacific salmon range, where parsing out the effects of human vs. natural influences on stock variability becomes increasingly important, given the depleted abundance of numerous stocks (Nehlsen 1997).

Extension of historic perspectives on salmon production in some areas is now possible using paleolimnological

approaches to infer past sockeye salmon (*Oncorhynchus nerka*) nutrients and population dynamics (Finney et al. 2002; Schindler et al. 2005; Selbie et al. 2007). These reconstructions represent an indirect measure of past fish abundance, since they track nutrient subsidies provided by anadromous and semelparous salmon to freshwater nursery lakes. Sockeye salmon carcasses are enriched in isotopically heavy nitrogen ($\delta^{15}\text{N}$, ~ 11 – 12‰) relative to terrestrial (~ -2 to $+2\text{‰}$) and atmospheric ($\sim 0\text{‰}$) nitrogen (N) sources (Satterfield and Finney 2002). As such, sedimentary stable nitrogen isotope ($\delta^{15}\text{N}$) signatures in nursery lake sediments, when corroborated by biological proxy data (e.g., algal microfossils and pigments), reflect salmon-derived nutrient (SDN) loading (nutrient influxes mainly from carcass decomposition), which is correlated with spawning densities (escapement km^{-2}) in numerous systems (Finney et al. 2000; Brock et al. 2007).

The relative contributions of SDNs to annual nursery lake nutrient budgets vary widely (0–95%; Naiman et al. 2002; Hyatt et al. 2004). It should therefore be expected that the sensitivity of lake sediments to record SDN signals should similarly vary across nursery ecosystems (Finney et al. 2000; Naiman et al. 2002). Challenges in detecting sedimentary salmon signals, recently highlighted in some

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systems, have been attributed to a number of factors, including limited SDN loading (e.g., small salmon runs; Holtham et al. 2004), nitrogen limitation (Brahney et al. 2006), dilution of sedimentary $\delta^{15}\text{N}$ through direct (deposition) or indirect (food web sequestration and sedimentation) loading of isotopically light inorganic nitrogen and nitrogenous dissolved organic matter (DOM) and particulate organic matter (POM; Holtham et al. 2004; Hobbs and Wolfe 2008), and mechanisms hindering the incorporation of SDN into the sediment record (e.g., fast flushing rates; Holtham et al. 2004; Hobbs and Wolfe 2007, 2008). While these previous studies have identified numerous factors that may influence sediment $\delta^{15}\text{N}$ in salmon nursery lakes, more rigorous quantitative analyses to define the relative importance and prevalence of such controls are generally lacking.

While the assessment of SDN loading and the influences of SDN incorporation in lake sediments can generally be made from fisheries' climatic, limnological, and physiographic data, the influence of terrestrial loading is more complicated, with multiple factors governing ultimate sedimentary organic matter (OM) source, condition, and fate (Tyson 1995). Bulk ratios of carbon to nitrogen (C:N) in lake sediments have long been used to delineate OM provenance in terms of terrestrial (values >20) vs. aquatic (values <10) sources (Meyers and Ishiwatari 1993; Tyson 1995; Meyers and Teranes 2001). Owing to their potential utility in broadly constraining landscape influences on sedimentary geochemical indicators (e.g., $\delta^{15}\text{N}$), sedimentary C:N ratios have frequently been used in paleolimnological studies to assess terrestrial influences on $\delta^{15}\text{N}$, and thus inferences of prehistoric salmon abundances (Finney et al. 2000; Holtham et al. 2004; Selbie et al. 2007). Despite the long use of C:N ratios in paleolimnology to infer OM provenance, however, limited empirical evidence exists to support source-based interpretations of C:N ratios, and alternate influences on sediment C:N have also recently been proposed for certain salmon nursery lakes (e.g., N limitation; Brahney et al. 2006).

Paleolimnological reconstructions are important for understanding natural variability and the mechanistic drivers of Pacific salmon production. Given the reliance of these techniques upon the geochemical proxies $\delta^{15}\text{N}$ and C:N, further clarification of their dominant controls is necessary. To address this shortcoming, we used a multiple regression approach to establish the limnological, ecological, physiographic, and climatic variables that best explain the variation in the $\delta^{15}\text{N}$ and C:N signatures of surface sediment samples collected across a spatially and limnologically diverse set of sockeye salmon nursery lakes in western North America.

Our findings quantitatively demonstrate that sedimentary $\delta^{15}\text{N}$ signatures vary in response to differences in salmon escapement to nursery lakes, but they further suggest that variability in the influx of terrestrial nutrients and organic matter is an important additional regulator of both sedimentary $\delta^{15}\text{N}$ and C:N. These insights can be used to optimize the selection of sites for the reconstruction of past salmon populations, as well as to avoid and interpret apparent discrepancies arising from climatic and anthropogenic changes in watershed nitrogen and OM fluxes to lakes.

Methods

Sockeye salmon make use of a diverse array of nursery lake habitats, spanning broad and varied limnological and biogeoclimatic gradients (Burgner 1991). To capture the wide range of conditions in spawner density, lake morphometry, landscape physiography, climate, water chemistry, and watershed vegetation, we analyzed new data and integrated previously published data from 56 salmon nursery lakes in the coastal and inland regions of British Columbia, Yukon Territory, and Alaska (Table 1; Fig. 1). Surface sediment samples (top 0.5–1 cm), representative of the past ~ 3 –5 yr of sedimentary deposition in salmon nursery lakes (Finney et al. 2000; Holtham et al. 2004; Selbie et al. 2007), were retrieved from the deep-water depositional zone of each system between 1993 and 2002 using gravity corers (Glew et al. 2001). For spatial comparison of sedimentary and environmental conditions, the nursery lakes were categorized into five regions (i.e., British Columbia–Yukon Territory Interior [BC-YT-INT]; British Columbia coast [BC-C]; southeast Alaska [SE-AK]; south-central Alaska [SC-AK]; southwest Alaska [SW-AK]) based upon similarities and differences in general biogeoclimatic settings (e.g., annual precipitation, vegetation cover and type), and spatial separation (Fig. 1).

Sedimentary carbon and nitrogen elemental concentrations (%N and %C) and stable nitrogen isotope ratios ($\delta^{15}\text{N}$) were measured on homogenized, freeze-dried bulk sediment samples following standard methods (Meyers and Teranes 2001; Talbot 2001). All carbon values reflect organic components. Carbonates are rare in the study lakes; however, where present, samples were acid washed (dilute HCl) to remove the carbonate fraction. Bulk %N and %C were estimated using Carlo Erba or Costech elemental analyzers with analytical precision better than $\pm 5\%$ of the sample value. The ratio of carbon to nitrogen (C:N) in each sediment sample was presented relative to atomic masses. Nitrogen isotopes were estimated using a Finnigan Delta Plus mass spectrometer, with an analytical uncertainty better than $\pm 0.2\%$. Isotopic values are reported in the standard δ (delta) notation ($\delta = ([R \text{ sample}/R \text{ standard}] - 1)1000$, where $R = {}^{15}\text{N}/{}^{14}\text{N}$) relative to atmospheric N_2 ($\sim 0\%$), the international standard.

Salmon escapement estimates were acquired from published records and unpublished time series kept by Fisheries and Oceans Canada (DFO), the Alaska Department of Fish and Game (ADFG), and the University of Washington (see the Web Appendix; www.aslo.org/lo/toc/vol_54/issue_5/1733a.pdf). Escapement estimates were predominantly derived from weir enumeration. However, in the rare cases where these data were not available, sonar or tower counting estimates were used. To approximate time integration in sedimentary intervals, escapements were averaged over the 5-yr period prior to sediment sampling. Average escapements were expressed relative to lake area (number of fish km^{-2}) to standardize estimates of sockeye densities across nursery lakes of varying size. In the few instances where aggregate stock assessment techniques precluded escapement estimates to single lakes (e.g., Naknek-Brooks, Clark-Kijik, Nonvianuk-Kukaklek, and

Table 1. Least squares multiple linear regression (MLR) results with both forward and backward selection.

Treatment	Dependent variable*	Significant explanatory variables*	Collinear variables*	Standard coefficient	<i>p</i> value (two tail)	<i>n</i>	<i>r</i> ²
All sites	C:N	watershed % tree cover	√(precipitation)	0.499	<0.0001	56	0.67
			WS % herbaceous cover				
			WS % nonvegetated (log(<i>x</i> + 1))				
		watershed area (log)	√(precipitation)	-0.331	0.001		
		mean slope	maximum slope				
	$\delta^{15}\text{N}$	escapement km ⁻² (log(<i>x</i> + 1))	lake area (log)	WS % nonvegetated (log(<i>x</i> + 1))	-0.266	0.005	
			mean slope	WS % herbaceous cover	0.221	0.017	
			escapement km ⁻² (log(<i>x</i> + 1))	WS % herbaceous cover	0.498	<0.0001	
		C:N		√(precipitation)	-0.324	0.003	
			WSA:LA (log)	watershed area (log)	-0.207	0.034	
Sites with nutrient data	C:N	√(precipitation)	mean slope	0.545	<0.0001	41	0.63
			watershed area (log)				
			spring epilimnetic TP (log)				
	$\delta^{15}\text{N}$	√(WS % herbaceous cover)	escapement km ⁻² (log(<i>x</i> + 1))	√(WS % tree cover)	-0.443	<0.0001	
			√(WS % herbaceous cover)	√(WS % tree cover)	0.539	<0.0001	
	√(spring epilimnetic NO ₃ ⁻)	√(spring epilimnetic NO ₃ ⁻)	-0.226	0.035	40	0.62	

* Variables: $\delta^{15}\text{N}$, C:N, precipitation, maximum slope, mean slope, watershed area (WSA), escapement km⁻², lake area (LA), watershed % tree cover, watershed % herbaceous shrub cover, watershed % unvegetated, WSA:LA, spring total phosphorus (TP), spring nitrate (NO₃⁻).

Skilak drainages), densities were calculated from estimates of total drainage spawner returns averaged across the total surface area of known available lacustrine spawning habitat.

To assess broad variation in lake nutrient status and influences on sediment geochemistry, spring, ice-free, epilimnetic nitrate (NO₃⁻), and total phosphorus (TP) values were obtained from monitoring time series maintained by DFO and ADFG and from previously published studies (*see* the Web Appendix). Data over the 5 yr prior to sediment sampling were averaged; however, in the limited instances where continuous records did not exist, long-term averages were used. Measurements following spring lake mixing likely provide an approximation of general phosphorus and nitrogen availability for autotrophic production, which should vary among nursery lakes relative to allochthonous (e.g., watershed, salmon carcass) sources and processes modulating nutrient retention (e.g., lake flushing).

Total annual precipitation data were acquired from Canadian and U.S. networks of land-based weather stations to assess climatic effects on nursery lake geochemistry across lakes. Annual estimates for British Columbia and Yukon Territory watersheds were compiled from daily measurement data in the Canadian Daily Climate Data Database (CDCD; Environment Canada 2002). For sites in Alaska, U.S. National Climate Data Center (NCDC) monthly average values (NOAA 2006) were used to obtain annual estimates. Precipitation values (mm yr⁻¹) from the closest land-based station with representative climatic

conditions to each lake were averaged over the 10-yr period prior to sampling. Although most stations had excellent temporal coverage, in the rare instances where data were missing (mostly less than a few months), long-term averages were used. Precipitation values include all forms of annual precipitation. Nonliquid precipitation (e.g., snow) was uniformly converted to liquid equivalents at the data source.

Geographic information system (GIS) techniques were used to capture physiographic and land cover variables (e.g., watershed area, slope, glacier coverage, vegetation type and coverage, and lake area) of potential influence on sediment geochemistry. Watersheds were defined for each nursery lake as the upstream land surface from the outlet (not including the nursery lake surface) from digital elevation models (DEM) using ESRI ArcGIS version 9.1. For Canadian sites, DEM data from the Canadian Digital Elevation Data Level 1 (CDED1; www.geobase.ca) were used, with feature overlays from the Canadian National Topographic Database (NTDB; www.geogratis.ca). Alaskan DEM data were obtained from the U.S. Geological Survey (USGS) seamless data distribution system (<http://seamless.usgs.gov>), with hydrological and landscape features from the USGS national hydrographic dataset (<http://nhd.usgs.gov>). Maximum and mean slope statistics were calculated using watershed overlays on DEM data. Quantitative estimates of spatial coverage for landscape features (e.g., glaciers, vegetation) were obtained by subtracting respective feature areas from total watershed areas. Vegetation parameters (i.e., tree cover, herbaceous

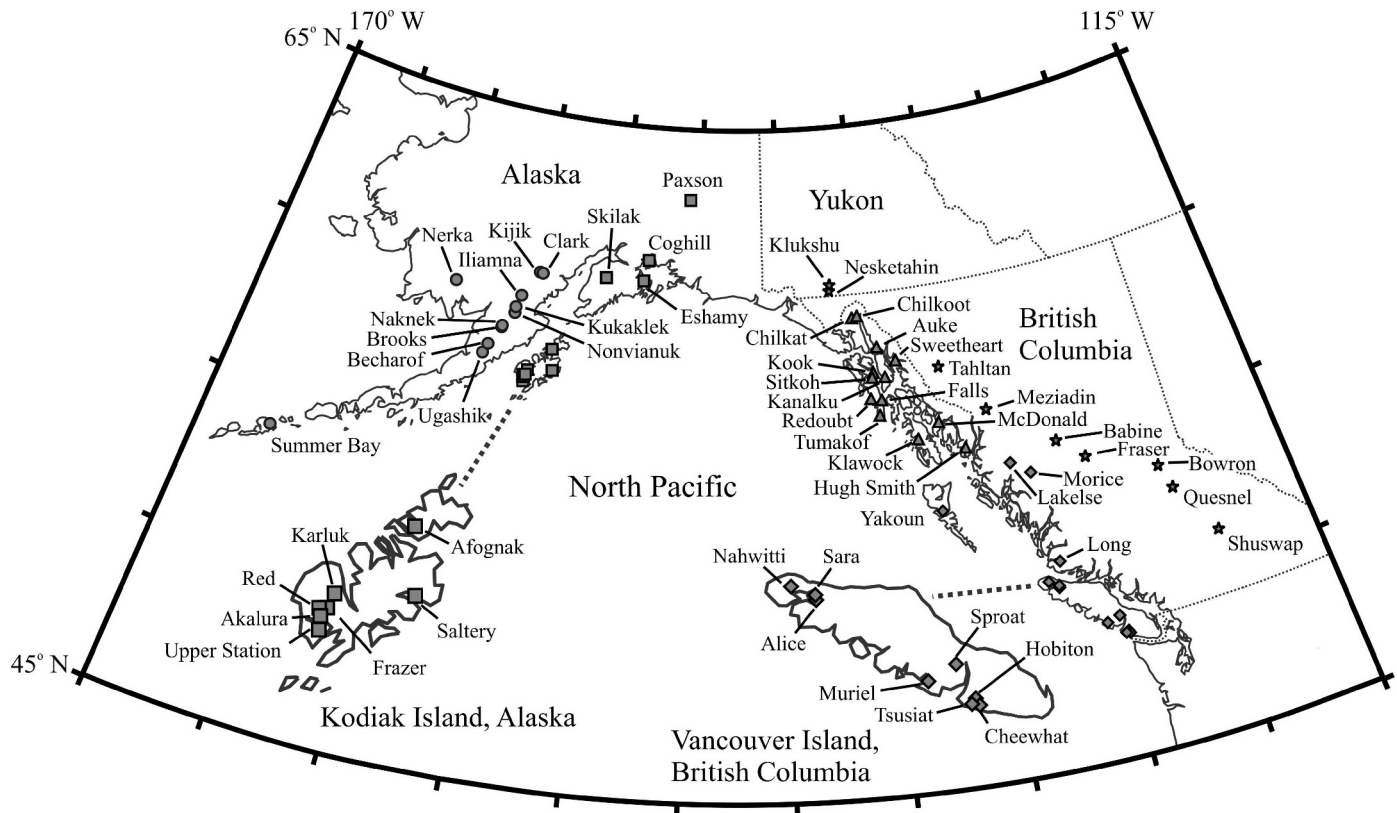


Fig. 1. Site map indicating the location of the 56 western North American study lakes. Symbols delineate different regions: southwest Alaska (circles); south-central Alaska (squares); southeast Alaska (triangles); coastal British Columbia (diamonds); interior British Columbia and Yukon Territory (stars). Expansions of areas with a high site density (Kodiak Island, Alaska, and Vancouver Island, British Columbia) are inset.

vegetation cover, areas of no vegetation) were extracted from watershed overlays of the moderate-resolution imaging spectroradiometer (MODIS) vegetation continuous fields (VCF) 2001 dataset (Hansen et al. 2003). To minimize distortion, all geospatial estimates were made from Albers equal-area projections using the British Columbia Environment Albers equal-area conic (Canada) and Alaskan Albers equal-area conic (U.S.) projections for Canadian and U.S. sites, respectively.

Intraregional and interregional variation in sedimentary, landscape, climatic, limnological, and ecological parameters were defined using box and whisker plots and analysis of variance (ANOVA), with Tukey post hoc tests used to assess significance in differences between regional mean values. Stepwise multiple linear least squares regression (MLR) analyses, with both forward and backward selection ($\alpha = 0.05$), were performed to determine empirical relationships between sedimentary $\delta^{15}\text{N}$ and C:N (dependent variables) and landscape, climatic, limnological, and ecological parameters (independent variables) using SYSTAT version 11 software. All variables were assessed for normal distributions and logarithmically, $\log(x + 1)$, or square-root transformed as appropriate. Prior testing for correlated predictor variables was conducted using Pearson correlation matrices with Bonferroni-adjusted probabilities. Where incidences of multicollinearity in predictor variables occurred ($p < 0.05$), only the parameter

explaining the most variance in the dependent variable was included in our MLR analyses.

Model selection was independently explored using an information theoretical approach employing Akaike's information criterion (AIC; Akaike 1974) to maximize parsimony in explanatory models. This was conducted using both stepwise (forward and backward selection) and all possible model combination selection procedures, implemented with the MASS version 7.2-39 and Leaps version 2.7 packages, respectively, in the open-sourced R statistical package version 2.6.1 (R Core Development Team 2007). These model selection procedures yielded similar results, suggesting that our MLR analyses are statistically robust.

Results

Interregional and intraregional variation in sedimentary $\delta^{15}\text{N}$ and C:N—Strong regional variation was evident in sedimentary $\delta^{15}\text{N}$ signatures (Figs. 2A, 3A). South-central Alaska (SC-AK) exhibited the highest and most variable $\delta^{15}\text{N}$ values, which were significantly greater than coastal sites in southeast Alaska (SE-AK) and coastal British Columbia (BC-C, Fig. 2A). Salmon lakes within interior British Columbia and Yukon (BC-YT-INT) and southwest Alaska (SW-AK) had similar mean $\delta^{15}\text{N}$ signatures but were not significantly different from any other regions

(Fig. 2A). In general, $\delta^{15}\text{N}$ values from southeast Alaska and British Columbia coastal sites (BC-C, SE-AK) were indistinguishable from the sedimentary $\delta^{15}\text{N}$ of 100 nonsalmon reference lakes in British Columbia and Alaska (e.g., within +1 SD of the mean, D. T. Selbie and B. P. Finney unpubl. data). In contrast, most sites in SC-AK, SW-AK, and BC-YT-INT were isotopically enriched relative to this range (Figs. 2A, 3A).

Distinct spatial variation was also observed in sedimentary C:N signatures (Figs. 2B, 3B). Sediment C:N values in southeastern Alaska and British Columbia coastal sites (BC-C, SE-AK) were similar and were significantly higher than any other region (Fig. 2B). C:N values from these regions were also within the range of lakes receiving organic matter (OM) of predominantly allochthonous origins (Figs. 2B, 3B; Meyers and Teranes 2001). In contrast, sites in the other regions were similar and lower (e.g., BC-YT-INT, SW-AK, SC-AK), with values indicative of sites receiving predominantly autochthonous OM (Figs. 2B, 3B).

Interregional and intraregional variation in ecological, climatic, physiographic, and limnological variables—The lakes examined in our study currently receive a broad range of sockeye salmon spawner densities (escapement km^{-2}). Lakes in SC-AK received the highest modern salmon densities and range of variability in any region, and were significantly higher than those in BC-YT-INT, BC-C, and SW-AK (Fig. 2C). Spawner density values were also generally lower in SE-AK and similar to BC-YT-INT, BC-C, and SW-AK, but did not vary significantly from SC-AK, since some lakes in the region receive very high spawner densities (i.e., McDonald and Tumakof lakes).

Lake nutrient chemistry varied broadly within most regions, and no significant differences in spring nitrate concentrations were detected (NO_3^- ; Fig. 2D). Of note, however, BC-C demonstrated a very narrow range of variation and generally lower spring NO_3^- concentrations (Fig. 2D). Similarly, the range of variation in spring total phosphorus (TP) was lowest in BC-C, with significantly lower mean values than in SC-AK (Fig. 2E). Other regions demonstrated broader spring TP ranges, and interregional differences were not significant (Fig. 2E).

Variability in total annual precipitation across regions showed the same general pattern as that noted in sedimentary C:N. British Columbia and southeast Alaska coastal sites (BC-C and SE-AK) receive similar total annual precipitation, and mean values were significantly higher than in any other region (Fig. 2F). The range of variability in total annual precipitation at BC-YT-INT sites was notably much lower than in other regions (Fig. 2F).

Physiographic characteristics varied greatly across study regions. Mean watershed slopes were greatest in SE-AK and BC-C and were significantly higher than other regions (Fig. 2G). Maximum watershed slopes were lowest in SC-AK and differed significantly from those of BC-YT-INT and BC-C (Fig. 2H). However, maximum slopes in SE-AK and SW-AK were not significantly different from other regions (Fig. 2H). Nursery lakes in BC-YT-INT had significantly larger watershed areas (WSA) than BC-C,

SE-AK, and SC-AK (Fig. 2I). Watersheds in SW-AK spanned a broad range of sizes, which were not significantly different from other regions (Fig. 2I). Lake areas (LA) were largest and displayed the greatest range in SW-AK (Fig. 2J); this region possesses some of the largest sockeye salmon nursery lakes in the world (e.g., Iliamna and Becharof lakes). In SW-AK, LA were significantly greater than BC-C, SE-AK, and SC-AK, but not BC-YT-INT (Fig. 2J). Despite the pronounced and significant differences in LA and WSA across regions, watershed area to lake area ratios (WSA:LA) were similar across most regions (BC-C, SW-AK, SE-AK, SC-AK), except for BC-YT-INT, which displayed significantly higher values and a broader range (Fig. 2K).

With such a wide range in climatic and physiographic conditions, it is not surprising that landscape cover characteristics also varied strongly in extent and type among regions (Fig. 2L–O). Watershed (WS) tree coverage in BC-C was significantly greater than in SE-AK, and both were significantly greater than all other regions except BC-YT-INT (Fig. 2L). In contrast, watersheds in SC-AK and SW-AK tended to have significantly higher herbaceous shrub coverage than other regions (Fig. 2M). No significant differences existed among regions in the amount of nonvegetated landscape or watershed glacier coverage, although SC-AK had a notably broader range of glacial influence (Fig. 2N,O).

Variation in sedimentary C:N—Our MLR model significantly explained 67% of the total variation in sedimentary C:N across the full data set. Most of the variation was explained by WS vegetation type and physiographic and climatic variables (Table 1), with WS % tree cover the strongest positive predictor. However, given that WS % tree cover was strongly correlated with other watershed vegetation parameters ($\sqrt{(\text{WS \% herbaceous shrub cover})}$, $r = -0.89$, $p < 0.0001$, $n = 55$; WS % nonvegetated ($\log(x + 1)$), $r = -0.66$, $p < 0.0001$, $n = 55$) and with annual precipitation ($\sqrt{(\text{precipitation})}$, $r = 0.47$, $p = 0.01$, $n = 56$), it likely reflects general vegetation and climatic patterns among watersheds. Watershed area was selected by MLR as an additional variable of importance and was negatively correlated with sedimentary C:N values (Table 1) but was also strongly correlated with other variables (maximum slope, $r = 0.67$, $p < 0.0001$, $n = 56$; LA (log), $r = 0.94$, $p < 0.0001$, $n = 56$; $\sqrt{(\text{precipitation})}$, $r = -0.46$, $p = 0.02$, $n = 55$). Salmon loading (escapement km^{-2}) explained a small but significant amount of variation in C:N (Table 1) but was also correlated with $\sqrt{(\text{WS \% herbaceous shrub cover})}$ ($r = 0.48$, $p = 0.02$, $n = 56$).

Similar watershed vegetation, physiographic, and climatic variables were selected in our MLR analysis of the subset of sites where nutrient chemistry data were available ($n = 41$). In these sites, two predictors explained 63% of the variation in sedimentary C:N (Table 1). Precipitation was identified as the largest positive influence, although it was correlated with physiographic variables (mean slope, $r = 0.53$, $p = 0.037$, $n = 41$; WSA (log), $r = -0.53$, $p = 0.033$, $n = 41$) and spring TP (log, $r = -0.59$, $p = 0.005$, $n = 41$).

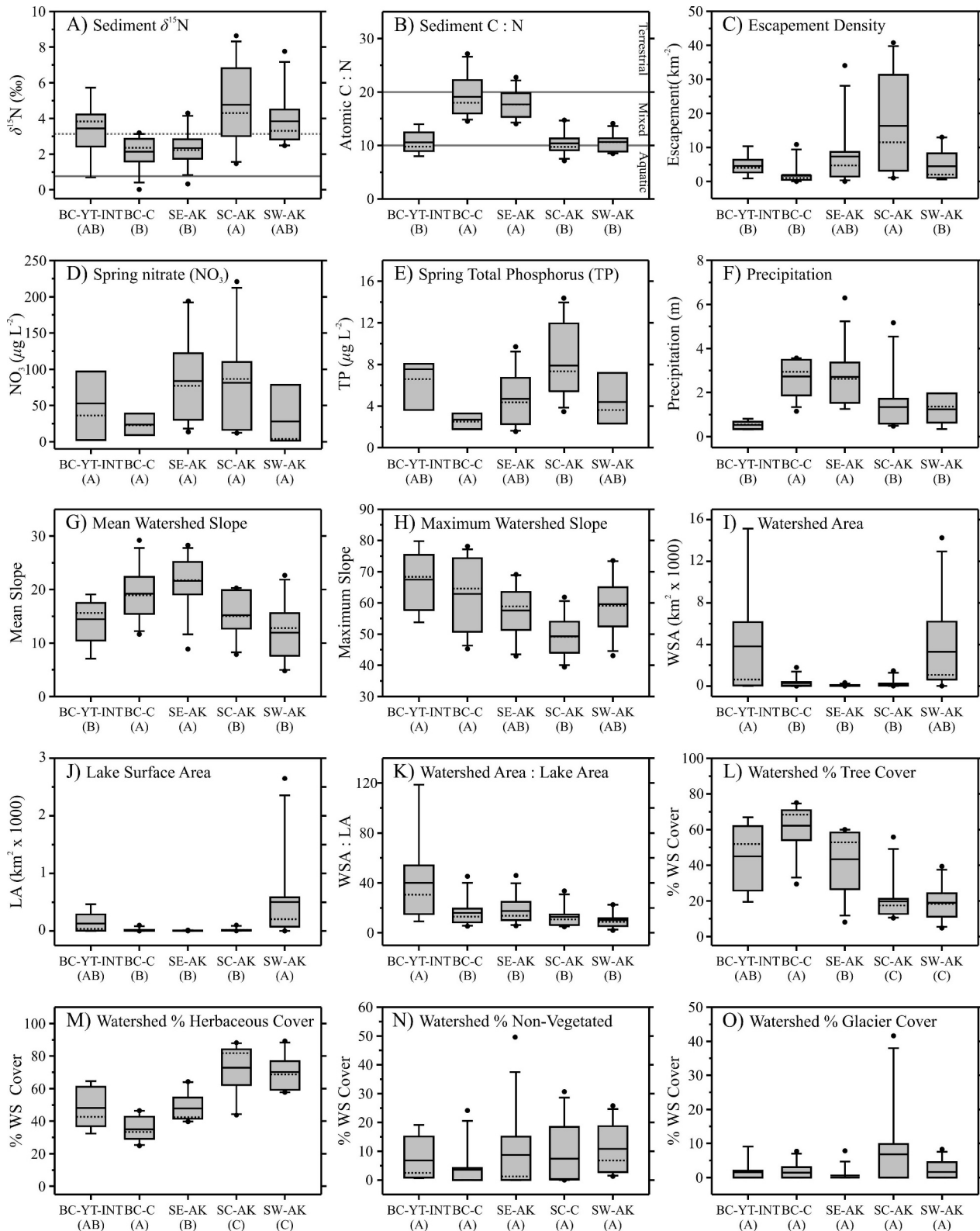


Fig. 2. Box and whisker diagrams illustrating interregional and intraregional variation in sedimentary, limnological, ecological, physiographic, and climatic variables included in our multiple linear regression (MLR) analyses. Horizontal lines within each box indicate regional mean (solid) and median (dashed) values. Box and whisker extents represent 25th and 75th and 10th and 90th percentiles. Dots indicate sites exhibiting values outside of the 10th and 90th percentiles. Significant differences between regional means were assessed using ANOVA with Tukey post hoc tests. Letters located below each region indicate significant differences (different letters) or interregional similarity (same letters) in mean values (BC-C, British Columbia coast; SE-AK, southeast Alaska; BC-YT-INT,

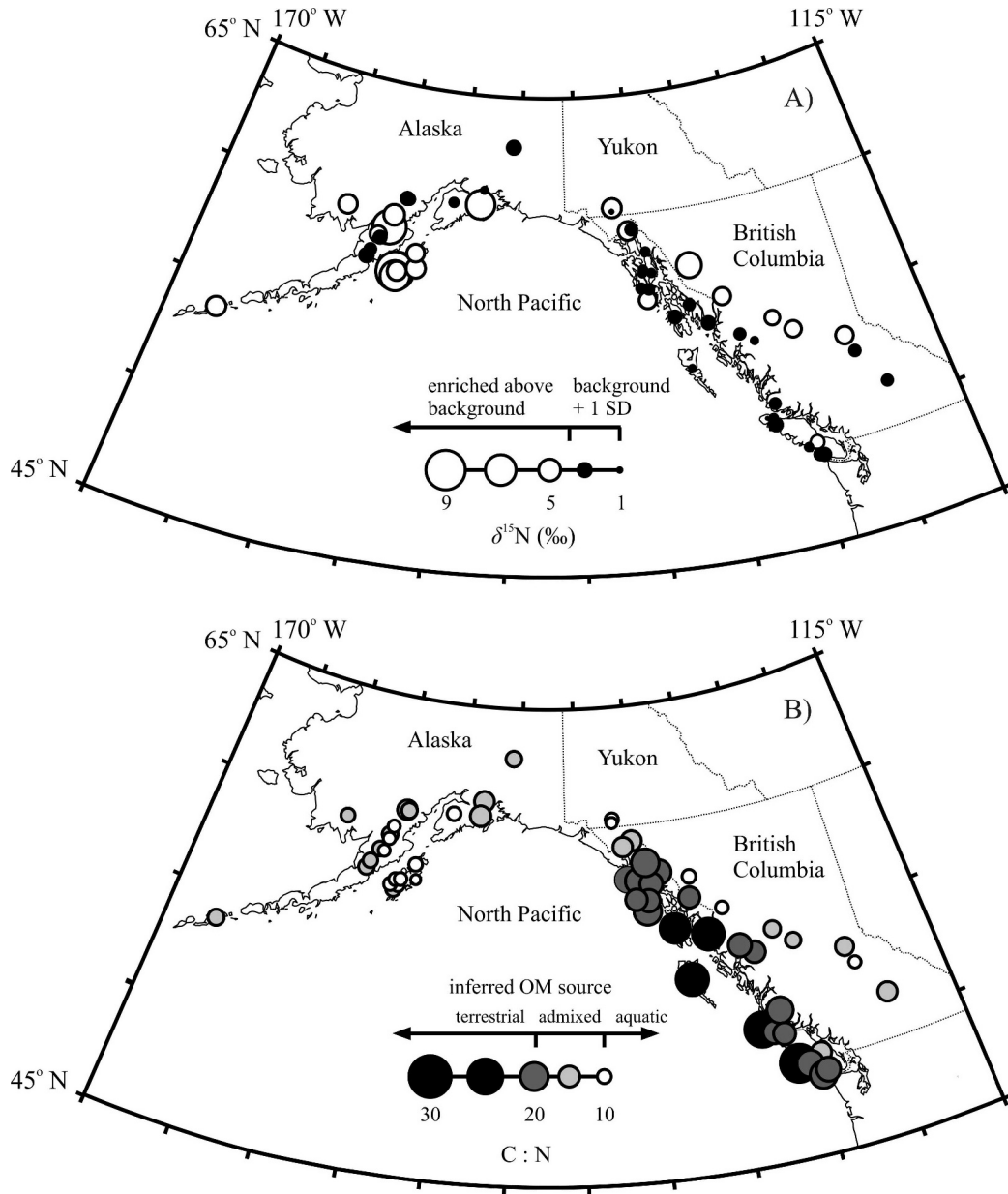


Fig. 3. Spatial distribution of surface sediment (A) $\delta^{15}\text{N}$ and (B) C:N across the 56 study lakes. Circle diameters scale with value magnitudes. (A) Open circles indicate $\delta^{15}\text{N}$ signatures enriched above the mean background value +1 SD from 100 nonsalmon lakes in British Columbia and Alaska (D. T. Selbie and B. P. Finney unpubl.). Solid circles indicate values indistinguishable from background signatures. (B) Grayscale shading indicates organic matter (OM) provenance interpretations based upon Meyers and Teranes (2001). Open circles (C:N < 10) are indicative of OM of primarily aquatic origin, light gray circles indicate admixture with terrestrial OM (C:N = 10–15), dark gray circles (C:N = 15–20) illustrate strong terrestrial OM admixture, and black circles (C:N > 20) indicate OM of primarily terrestrial origin.

←

British Columbia and Yukon interior; SC-AK, south-central Alaska; SW-AK, southwest Alaska). Horizontal lines in (A) represent the mean background sedimentary $\delta^{15}\text{N}$ value for 100 nonsalmon lakes in British Columbia and Alaska (solid) and +1 SD of the background mean (dashed; D. T. Selbie and B. P. Finney unpubl. data). Horizontal lines in (B) represent divisions in sediment organic matter provenance (aquatic vs. terrestrial) based upon the delineations made by Meyers and Teranes (2001).

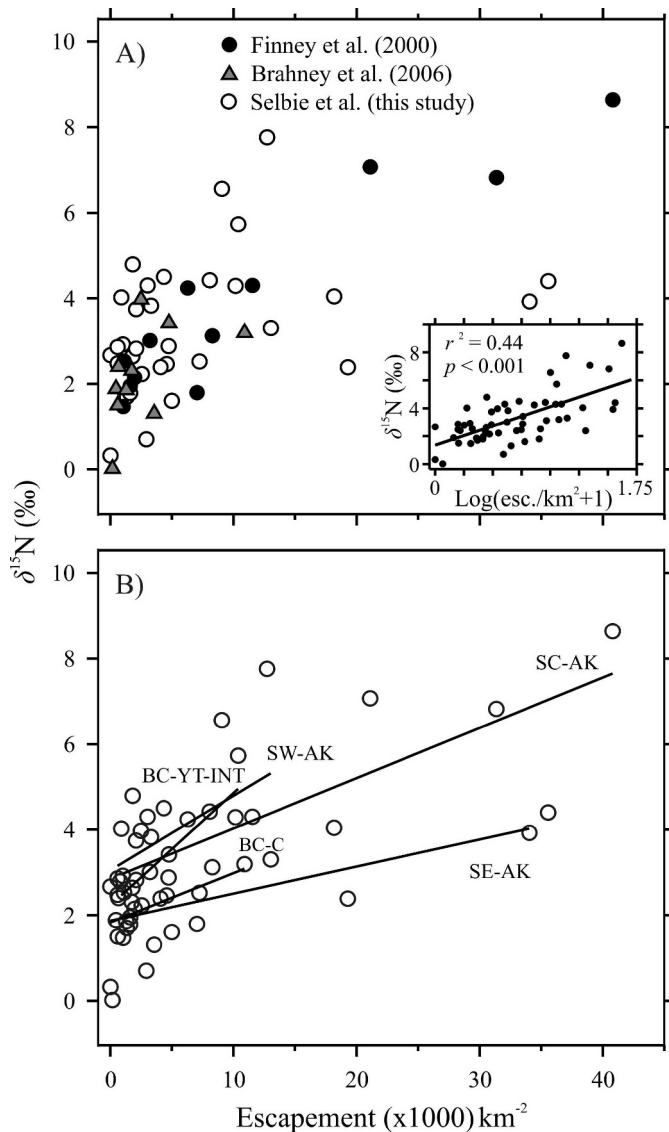


Fig. 4. Relationship between salmon spawner density (escapement km^{-2}) and sedimentary $\delta^{15}\text{N}$. (A) Sites symbols are coded by publication. Inset is the transformed relationship as presented in our MLR analyses. (B) Interregional decomposition of the spawner density- $\delta^{15}\text{N}$ relationship (BC-C, British Columbia coast; SE-AK, southeast Alaska; BC-YT-INT, British Columbia and Yukon Territory interior; SC-AK, south-central Alaska; SW-AK, southwest Alaska).

Sedimentary C:N was also significantly influenced by vegetation parameters, particularly $\sqrt{(\text{WS \% herbaceous shrub cover})}$, which was strongly related to $\sqrt{(\text{WS \% tree cover})}$ ($r = -0.86$, $p < 0.0001$, $n = 41$). Sedimentary C:N values were not directly correlated with either spring TP or spring NO_3^- (Table 1).

Variation in sedimentary $\delta^{15}\text{N}$ —Salmon spawner densities, sedimentary C:N, and WSA:LA significantly explained 55% of the variation in sedimentary $\delta^{15}\text{N}$ in our MLR model across 55 salmon nursery lakes (Table 1). Despite broad biogeoclimatic gradients, sockeye salmon spawner densities ($\log(x + 1)$ transformed) were identified

as the predominant positive predictor of sedimentary $\delta^{15}\text{N}$ (Table 1; Fig. 4A). Sedimentary C:N was the primary negative predictor of $\delta^{15}\text{N}$ (Table 1), and, as noted in our previous analysis, C:N can be considered a synthetic variable, representing the effects of climatic, physiographic, and vegetation conditions. WSA:LA was also found to be negatively related to sedimentary $\delta^{15}\text{N}$ (Table 1).

In the subset of sites with lake nutrient chemistry data ($n = 41$), our MLR model extracted a similar set of significant predictors (e.g., salmon spawner density, vegetation type) and explained 62% of the variation in sedimentary $\delta^{15}\text{N}$ (Table 1). In addition, spring NO_3^- was significantly but weakly negatively related to sedimentary $\delta^{15}\text{N}$ (Table 1). Comparison of these results with a MLR model excluding lake nutrient chemistry variables (not shown) demonstrated spring NO_3^- significantly explained 6% of the variance in sedimentary $\delta^{15}\text{N}$ values.

Discussion

Defining the primary controls on sediment $\delta^{15}\text{N}$ and C:N is central to their application and interpretation in paleolimnological studies. Our analysis of surface sediments across 56 sockeye salmon nursery lakes in Alaska, Yukon, and British Columbia demonstrated that sedimentary $\delta^{15}\text{N}$ is most strongly governed by salmon spawner densities, consistent with the findings of previous spatially restricted studies (Finney et al. 2000; Brock et al. 2007). Our analyses, however, revealed that this relationship can be substantially modified by allochthonous nutrient and organic matter (OM) fluxes related to climatic and watershed vegetation and physiographic conditions. Our empirical analysis of sedimentary C:N across lakes suggested that C:N values primarily reflect factors governing OM provenance and delivery (e.g., watershed vegetation, physiographic and climatic conditions), consistent with previous qualitative results (Meyers and Teranes 2001).

Sediment $\delta^{15}\text{N}$ is a primary proxy indicator for inferring past sockeye salmon population dynamics. Our analyses indicate that $\delta^{15}\text{N}$ must be considered in a mass-balance context, since sedimentary values cannot be interpreted independently of watershed nitrogen fluxes. As such, this discussion first explores the primary influences on sedimentary C:N, then considers the controls on $\delta^{15}\text{N}$, and finally discusses the significance of these findings to paleolimnological site selection and interpretations.

Controls on sedimentary C:N variation in sockeye salmon nursery lakes—Bulk ratios of carbon to nitrogen (C:N) in lake sediments have routinely been used as a qualitative assessment of aquatic vs. terrestrial sedimentary OM provenance (Meyers and Ishiwatari 1993; Kaushal and Binford 1999; Meyers and Teranes 2001). As such, C:N has been used in paleolimnological salmon investigations to control for temporal variation in watershed-lake dynamics when interpreting isotopic (e.g., $\delta^{15}\text{N}$) and biological (e.g., diatom algae) indicators (Holtham et al. 2004; Selbie et al. 2007; Hobbs and Wolfe 2008).

Our MLR analyses provide empirical evidence in support of previous qualitative interpretations. Watershed

% tree cover was the strongest predictor of sedimentary C:N across all salmon lakes. Sediment C:N values are likely related to landscape vegetation through variation in both the amount and type of terrestrial biomass (Allan and Johnson 1997; Meyers and Teranes 2001), erosion processes, and landscape and in-lake residence and recycling differentials between vegetation types and geographic areas. The latter are functions of source OM recalcitrance, mobility, and burial (Post et al. 1985; Prescott et al. 2000); watershed soil and geological characteristics (Perakis and Hedin 2007); and temperature, moisture, decomposer communities (Elliot et al. 1993; Liski et al. 2003), as well as aquatic food web use (Webster and Benfield 1986).

Temperate rainforest sites in our lake set (coastal British Columbia and Southeast Alaska) exhibited significantly higher sedimentary C:N than other regions (Figs. 2B, 3B). Within this region, watersheds are characterized by high-biomass, coniferous vegetation (Pojar and MacKinnon 1994) and slow decomposition rates of terrestrial organic matter (e.g., cool temperatures, recalcitrant litter, partially water-saturated soils; Post et al. 1985; Webster and Benfield 1986; Hedin 1990), conditions that increase landscape OM loads. The strong influence of watershed vegetation on sediment C:N values is generally consistent with the role of terrestrial vegetation in regulating particulate (POM) and dissolved organic matter (DOM) in streams, the primary allochthonous OM pathway to lakes (Polis et al. 1997), particularly in forested watersheds (Dodds 1997; Golladay 1997; Lyons et al. 2000). The strong negative correlation between C:N and $\sqrt{(\text{WS \% herbaceous shrub cover})}$ ($r = -0.64$, $p < 0.0001$, $n = 56$) is also coherent with an importance of allochthonous OM loading and likely reflects lower OM production and export in these landscapes (Lyons et al. 2000). Previous research has demonstrated that autochthonous lotic OM fluxes dominate in nonarctic landscapes (Minshall 1978; Lyons et al. 2000), where internal decomposition and cycling are typically higher (Minshall 1978; Hedin 1990; Golladay 1997).

Precipitation, watershed morphometry, and topography have also been cited as dominant controls on allochthonous OM inputs to lake sediments (France 1995; Meyers and Lallier-Vergès 1999). Precipitation exerts strong and interactive controls on allochthonous OM contributions to streams and lakes through both direct (e.g., erosion, hydrological delivery; France 1995; Allan and Johnson 1997) and indirect effects (e.g., controls on landscape vegetation biomass and type; Golladay 1997; Webster and Meyer 1997). Consistent with these mechanisms, $\sqrt{(\text{annual precipitation})}$ was a strong positive correlate of C:N in our full lake dataset ($r = 0.65$, $p < 0.0001$, $n = 56$) and the primary positive correlate of sediment C:N in the smaller subset of lakes ($n = 41$) with water chemistry data (Table 1). Sustained precipitation enhances stream discharge and the hydrological connectivity of hill slopes and streams, increasing soil throughflow and landscape sheet flow (Sidle et al. 2000; Gomi et al. 2002; Lin et al. 2006). Consequently, watershed export of DOM and POM is often elevated during periods of high precipitation (e.g., wet periods, storm events; Golladay et al. 1987; Wallace et

al. 1995), which is consistent with higher C:N values in regions with elevated annual precipitation (e.g., coastal rainforests; Figs. 2B,F, 3B). It should be noted that the seasonality of precipitation trends may also be an important influence on nutrient fluxes and retention in sockeye salmon nursery lakes (Stockner 1987) and thus on sediment elemental and isotopic signatures.

The negative influence of WSA and positive effect of mean slope on sedimentary C:N values are generally consistent with variation in the relative deliverability (retention vs. export) of allochthonous OM to lakes (France 1995; Polis et al. 1997). Streams in smaller, steeper catchments (typical of headwater systems) may receive higher amounts of allochthonous OM due to proximity to sources and reduced lotic processing and retention (Golladay 1997; Polis et al. 1997). Moreover, higher peak flows per unit area (Golladay 1997) and the dominance of debris flow events under higher precipitation in steep catchments (Gomi et al. 2002) enhance scouring and the downstream export of both DOM and POM to receiving waters (Gregory and Walling 1973; Golladay et al. 1987). In contrast, larger, more reticulate watersheds often act as OM sinks, with greater storage potentials and use (Gregory and Walling, 1973; Gomi et al. 2002).

As sediment geochemistry integrates the contributions of various OM sources, C:N signatures may also vary with autochthonous OM fluxes associated with lake production (Meyers and Teranes 2001). Consistent with such a mass balance, our MLR analyses identified salmon spawner densities (escapement km^{-2}) as a negative predictor of C:N (Table 1). This relationship likely reflects the stimulatory effect of salmon-derived nutrients (SDN) on autotrophic production in many salmon nursery lakes (Stockner and MacIsaac 1996; Hyatt et al. 2004), which probably increases the relative contributions of autochthonous OM to lake sediments.

Differences in sedimentary C:N ratios were not obviously related to the nutrient status of our nursery lakes. Brahney et al. (2006) described the potential for an additional effect of N limitation on sediment geochemistry ($\delta^{15}\text{N}$, C:N) in coastal sockeye salmon nursery lakes. While our MLR analyses detected no significant relationship between spring nutrient availability and sediment C:N ($\sqrt{(\text{NO}_3^-)}$, $r = -0.16$, $p = 1.00$, $n = 41$; TP (log), $r = -0.36$, $p = 1.00$, $n = 41$), this may reflect the nature of available water chemistry data, which precluded the comparison of N:P ratios (a useful metric of nutrient limitation in lakes; Davies et al. 2004). A reanalysis of the C:N data presented in Brahney et al. (2006), however, revealed that their C:N values were strongly related to watershed and lake morphometry (WSA (log), $r^2 = 0.75$, $p = 0.001$, $n = 10$; LA (log), $r^2 = 0.69$, $p = 0.003$, $n = 10$), a result consistent with our MLR analyses. Brahney et al. (2006) presented the negative correlation between C:N and total escapement ($r^2 = 0.62$, $p = 0.006$, $n = 10$) as evidence of N-limitation effects on sedimentary C:N. However, Finney et al. (2000) demonstrated that salmon spawner density (escapement km^{-2}) is a more appropriate measure of SDN loading and availability, since it is comparable across systems of differing size. Sediment C:N was not significantly corre-

lated to salmon spawner densities in the Brahney et al. (2006) lake set ($r^2 = 0.22$, $p = 0.168$, $n = 10$), and further comparison of total escapement to WSA and LA (WSA (log), $r^2 = 0.65$, $p = 0.005$, $n = 10$; LA (log), $r^2 = 0.80$, $p < 0.001$, $n = 10$) revealed Brahney et al. (2006) were potentially tracking a collinear relationship reflective of watershed parameters, consistent with the results of our MLR analyses on our broader lake set. In light of a general lack of field evidence for enrichment of C:N in lake sediments under N-deficient conditions, further study is required to determine whether N availability is indeed an important control on sediment C:N in salmon nursery lakes.

Overall, our empirical analyses support the interpretation that C:N values in lake sediments most strongly reflect OM source (Meyers and Ishiwatari 1993; Meyers and Teranes 2001). Consistent with previous paleoenvironmental research (see review by Meyers and Lallier-Vergès 1999), the variables selected by our multiple regression models substantiate the use of sedimentary C:N as a valuable proxy for constraining temporal variation in climatic and watershed processes influencing allochthonous contributions to lake sediments.

Controls on sedimentary $\delta^{15}\text{N}$ in sockeye salmon nursery lakes—Sedimentary $\delta^{15}\text{N}$ is currently the primary paleolimnological proxy used to trace salmon-derived nutrients (SDN) to inland lakes (Finney et al. 2000). Our MLR analyses confirmed that across a broad range of salmon nursery systems, salmon spawner density is the strongest predictor of sedimentary $\delta^{15}\text{N}$ values (Table 1). By capturing the broad spatial and biogeoclimatic gradients reflective of sockeye salmon nursery ecosystems, however, we have demonstrated greater variability in this relationship relative to that previously reported in multi-lake analyses (Finney et al. 2000; Brahney et al. 2006; Fig. 4A).

The integrative nature of lake sediments necessitates the consideration of sedimentary $\delta^{15}\text{N}$ signatures as a mass balance of autochthonous (e.g., salmon) and allochthonous (e.g., watershed vegetation, soil, nutrient) N sources. Because sockeye salmon appear to have a relatively constant, elevated isotopic signature ($\delta^{15}\text{N} \sim 11.1 \pm 0.57\%$; Satterfield and Finney 2002), the interregional variation observed in the $\delta^{15}\text{N}$ -escapement km^{-2} relationship (Fig. 4B) is unlikely to be explained by changes in salmon isotopic composition or spawner density. Instead, our models suggest that exogenous environmental factors regulating watershed N fluxes to lakes account for intraregional and interregional variation, and must be considered in future analyses.

The importance of landscape and climatic influences in shaping nursery lake sediment $\delta^{15}\text{N}$ is supported by our finding that sediment C:N was the strongest negative predictor of $\delta^{15}\text{N}$ (Table 1). In light of our previous C:N MLR analysis, this relationship suggests that local climate, watershed vegetation, and physiography can be important modulators of $\delta^{15}\text{N}$ in nursery lake sediments (Table 1). Given terrestrial N sources have much lower isotopic signatures than salmon tissues (Talbot and Johannessen

1992; Holtham et al. 2004; Brock et al. 2007), we would expect elevated terrestrial N loading to result in lower sedimentary $\delta^{15}\text{N}$ values. Consistent with this interpretation, we detected a strong negative correlation between interregional regression slopes from the $\delta^{15}\text{N}$ -escapement km^{-2} relationship and precipitation ($r^2 = 0.89$, $p = 0.016$, $n = 5$). This relationship likely reflects both terrestrial nitrogen source and delivery effects, since interregional variability in Pacific North American vegetation (primary watershed N source; Meyers and Teranes 2001; Talbot 2001) is strongly controlled by moisture gradients (Lenihan 1993; Brown et al. 2006), as are watershed hydrodynamics.

Allochthonous and autochthonous controls on sedimentary $\delta^{15}\text{N}$ are likely further modified by local physiographic conditions, as evidenced by the significant negative influence of watershed area to lake area (WSA:LA) in our MLR model (Table 1). Elevated ratios of WSA:LA are commonly associated with increased catchment nutrient loading to lakes (Kalff 2002) and may influence sedimentary $\delta^{15}\text{N}$ in salmon nursery systems through delivery of isotopically light watershed N nutrients (Holtham et al. 2004; Hobbs and Wolfe 2007, 2008). However, WSA:LA is also a common surrogate for lake water residence times (WRT), with a larger WSA:LA associated with a lower WRT (Kalff 2002; Hobbs and Wolfe 2007). Lake WRT is considered a control on the retention and use of SDN in sockeye salmon nursery lakes (Stockner 1987; Stockner and MacIsaac 1996), and thus a likely influence on the preservation of SDN (and thus enriched $\delta^{15}\text{N}$ signals) in nursery lake sediments (Holtham et al. 2004; Hobbs and Wolfe 2007).

In the subset of lakes with water chemistry data ($n = 41$), spring NO_3^- was identified by our MLR as a weak negative predictor of sedimentary $\delta^{15}\text{N}$ values (Table 1), an inverse relationship that could be related to two potential mechanisms. First, as the N budgets of salmon lakes are subsidized by watershed N sources (Schmidt et al. 1998), it would be expected that across a gradient of watershed N loading, but with comparable or low salmon densities, sedimentary $\delta^{15}\text{N}$ would be inversely related to spring NO_3^- derived from low $\delta^{15}\text{N}$ watershed N sources (Holtham et al. 2004; Hobbs and Wolfe 2008). Spring NO_3^- , however, was highly variable within most regions (except BC-C; Fig. 2D), and not significantly related to any other limnological, ecological, landscape, or climatic variables included in our analyses.

Alternatively, the negative relationship between spring NO_3^- and sediment $\delta^{15}\text{N}$ may reflect availability-induced variation in autotrophic N fractionation. Brahney et al. (2006) recently proposed that N limitation occurs in coastal British Columbia salmon nursery lakes, resulting in $\delta^{15}\text{N}$ enrichment of lake dissolved inorganic nitrogen pools and thus lake sediments, as a result of reduced algal discrimination against ^{15}N . The prevalence of N limitation in North American sockeye salmon nursery lakes, however, and the extent to which such a mechanism influences autotrophic production and sedimentary $\delta^{15}\text{N}$ signatures, remains largely uncertain. We highlight that these areas require significant further research, since many factors may influence the extent to which nutrient deficiencies exist and

affect sedimentary records. For instance, Davies et al. (2004) underscored the importance of plankton size in determining nutrient deficiencies in both interior and coastal British Columbia lakes, with autotrophs of $<3 \mu\text{m}$ (bacteria, picoplankton, and some nanoplankton) more commonly being P deficient and those $>3 \mu\text{m}$ (some nanoplankton and microplankton) more frequently N deficient. This finding has relevance to sockeye salmon nursery systems, since autotrophic picoplankton ($<2 \mu\text{m}$) often comprise a large component of overall algal biomass (up to 50–70% of total autochthonous production; Stockner and Shortreed 1989, 1994; Weisse and MacIsaac 2000). Thus autotroph type and size may play a role in sedimentary geochemistry in these systems. Additionally, the extremely low productivity of many oligotrophic nursery lakes (Stockner and MacIsaac 1996; Weisse and MacIsaac 2000), may influence the transmission of autochthonous $\delta^{15}\text{N}$ signatures (N limited or otherwise) from the water column to the sediments, since autochthonous OM sedimentation may be dominated by allochthonous OM fluxes, particularly in low escapement coastal systems. Moreover, at higher salmon densities N deficiencies may be induced due to the N:P stoichiometry of salmon carcasses (e.g., below the Redfield ratio; Moore and Schindler 2004).

Ultimately, salmon spawner densities appear to be the main factor regulating sedimentary $\delta^{15}\text{N}$ across a diverse array of sockeye salmon nursery lake ecosystems. Our results, however, indicate that climatic, landscape, and possibly in-lake factors can modulate the nitrogen budgets of these lakes and can have significant influences on $\delta^{15}\text{N}$ signatures in certain systems, which must be considered in paleolimnological studies.

Insights for paleolimnological reconstruction of Pacific salmon—Paleolimnological investigations have been used to gain essential insight into prehistoric Pacific salmon population dynamics and the ecology of salmon nursery ecosystems (Finney et al. 2002; Schindler et al. 2005; Selbie et al. 2007). However, as these techniques have been more broadly applied it has become apparent that regional discrepancies may exist in their applicability (Holtham et al. 2004; Brahney et al. 2006; Hobbs and Wolfe 2007). In light of our results, this should not be surprising, given the broad biogeoclimatic and physiographic gradients indicative of North American sockeye salmon nursery watersheds. Moreover, the substantial variation noted in salmon densities and sediment $\delta^{15}\text{N}$ signatures is generally consistent with a broad range in the importance of SDN to nursery lake nutrient budgets (i.e., 0–95%; Naiman et al. 2002; Hyatt et al. 2004).

Our study highlights the critical importance of appropriate site selection in attaining a sufficiently strong signal to infer past sockeye salmon population dynamics from lake sediments. Consistent with the findings of previous studies (Finney et al. 2000; Holtham et al. 2004; Hobbs and Wolfe 2007), relatively high spawner densities are a prime requisite for unambiguous paleolimnological inferences. Regional decomposition of the $\delta^{15}\text{N}$ -escapement km^{-2} relationship, however, reveals distinct spatial patterns (Fig. 4B), which we have identified to be largely modulated

by interregional differences in climate, vegetation, and watershed geomorphology (Table 1). In general, broad-scale coherence is evident in interregional $\delta^{15}\text{N}$ and C:N variation (Figs. 2, 3), which does not appear to vary in relation to known spatial patterns in exogenous controls on salmon production (e.g., harvest pressures, ocean-atmospheric climate variability). This suggests certain geographic areas may have a limited potential to yield interpretable paleolimnological salmon reconstructions. For instance, coastal sites in British Columbia and southeast Alaska generally had sedimentary $\delta^{15}\text{N}$ values indistinguishable from background levels (Figs. 2A, 3A) despite a range of spawner densities (Fig. 2C). Similarly, these sites exhibited sedimentary C:N values indicative of substantial terrestrial OM loading (Figs. 2B, 3B), which was consistent with higher regional precipitation, watershed tree cover, and mean slopes (Fig. 2F,L,G). In such lakes, the overall watershed N load must be high, thereby diluting the salmon-derived nitrogen contributions. Intraregional variation in influential factors, however, may also be large between proximally located but discrete watersheds. For instance, Holtham et al. (2004) demonstrated that despite very high sockeye salmon spawner densities, unambiguous salmon reconstructions were not possible in the eastern Kodiak Archipelago (Saltery and Afognak lakes) as a result of the high local precipitation and hydrological dilution of salmon-derived nitrogen. In contrast, this paleolimnological approach was first demonstrated less than 100 km away on western Kodiak Island (e.g., Karluk Lake; Finney et al. 2000), suggesting steep orographic, climatic, and aspect gradients can be important influences on the success of these techniques.

Given this variability, we suggest that an approach to site selection based upon the explicit consideration of nursery lake watershed characteristics (e.g., watershed vegetation type and extent, WSA, WS slope, WSA:LA, or WRT), climatic conditions (e.g., precipitation), and nutrient mass balances, will increase the probability of selecting sites capable of tracking sockeye salmon production using paleolimnological methods. However, influential environmental factors may vary throughout paleolimnological time series, particularly on Holocene timescales. Thus, as has proved critical in previous studies, we advocate a multiple-proxy approach to paleolimnological salmon reconstruction, employing indicators of autotrophic production (e.g., diatoms; Finney et al. 2000, 2002; algal pigments; Schindler et al. 2005), which are not subject to similar geochemical alterations as those possible for $\delta^{15}\text{N}$. Sedimentological assessment (e.g., sediment structure, grain size, visual and microscopic descriptions), as well as stratigraphic constraint of regional variability through the use of control (nonsalmon) lakes (Finney et al. 2002; Schindler et al. 2005; Selbie et al. 2007) are also important components of this approach. Moreover, as we have empirically demonstrated in this study, C:N ratios are a powerful control for the influences of biogeoclimatic variability on sedimentary $\delta^{15}\text{N}$.

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