Title

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EVALUATING THE USE OF MARINE-DERIVED NITROGEN IN RIPARIAN TREE RINGS AS AN INDICATOR OF HISTORICAL NUTRIENT FLUX AND SALMON ABUNDANCE

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Abstract

We examined the potential for using riparian conifer trees (coast redwood and Douglas-fir) to assess historical nutrient flux and salmon escapement (fish that escape capture by commercial fisheries in the open ocean and are able to return to their natal stream to spawn) to a pair of coastal California watersheds (Mill Creek and Waddell Creek). In each basin, periods of known annual salmon escapement were compared with data on tree-ring growth, nitrogen content [N] and stable nitrogen isotope ratios ($\delta^{15}N$). All tree-ring variables (lagged by +1 year) were positively correlated with Mill Creek salmon escapement, but relationships were inconsistent at Waddell Creek and highly dependent on the time lag applied (0 to 7 years). Annual ring $\delta^{15}N$ was especially variable among individual trees growing at the same location with differences as high as 4.8‰ at spawning sites and 6.8‰ at salmon-free control sites. Linear regression-based models were used to reconstruct historical escapement for the periods 1946-2002 and 1904-2003 in the Mill Creek and Waddell Creek watersheds, respectively. Tree-ring based reconstructions indicated considerable variation in historical escapement to both basins, and contemporary population declines which began in the 1960s (Mill Creek) and 1970s (Waddell Creek) and appeared to level off in the 1990s. Although $\delta^{15}N$ was easily quantified in annual tree rings, stream, soil, and within-tree nitrogen dynamics greatly hinder the robust assessment of marine-derived versus autochthonous sources of nitrogen from riparian tree rings.

Introduction and Problem Statement

Over the past two decades, the ecological significance of anadromous Pacific salmon (*Oncorhynchus* spp.) has been well documented in aquatic ecosystems throughout the Pacific coastal ecoregion. The annual return of salmon to freshwaters and the associated decomposition of post-reproductive carcasses result in the transfer of marine-derived nutrients (MDN) and biomass to largely oligotrophic receiving ecosystems. Such inputs have been shown to increase primary production (Richey et al. 1975, Schuldt and Hershey 1995, Johnston et al. 2004), invertebrate diversity and biomass (Piorkowski 1995, Walter et al. 1998), and fish growth rates (Bilby et al. 1996, Wipfli et al. 1998). Since rates of primary production are typically low in many coastal salmon-bearing streams, even small nutrient inputs from anadromous salmon may stimulate autotrophic and heterotrophic production (Larkin and Slaney 1997) and produce cascading effects through the entire aquatic food web.

In addition to subsidizing riverine biota, salmon-borne MDN also benefit vegetation within the riparian corridor (Bilby et al. 1996, Ben-David et al. 1998, Hilderbrand et al. 1999, Helfield and Naiman 2001, Naiman et al. 2002). Marine nutrients are delivered to the terrestrial environment via deposition of carcasses during flood events, absorption and uptake of dissolved nutrients by riparian vegetation and removal of carcasses from the stream by piscivorous predators and scavengers (Cederholm et al. 1989, Ben-David et al. 1998, Reimchen 2000, O'Keefe and Edwards 2003). Empirical studies have shown that as much as 30% of the foliar nitrogen in terrestrial plants growing adjacent to salmon streams is of marine origin (Ben-David et al. 1998, Bilby et al. 2003, Bartz and Naiman 2005) and that growth rates of riparian trees may be significantly enhanced as a result of salmon-derived subsidies (Helfield and Naiman 2001, Drake et al. 2006, Drake and Naiman 2007). Nitrogen availability, in particular, is often a growth-limiting factor in many temperate forests (Hedin et al. 1995) and annual inputs of marine-derived nitrogen (MD-nitrogen) may be critical to the maintenance of riparian health and productivity in Pacific coastal watersheds.

Our understanding of the ecological importance of MDN subsidies has been greatly advanced by the application of natural abundance stable isotope analyses. A biogenic consequence of feeding in the marine environment is that adult anadromous salmon are uniquely enriched with the heavier isotopic forms of many elements (e.g., C, N and S) relative to terrestrial or freshwater sources of these same elements. When fish senesce and die after spawning, these isotopically heavy nutrients are liberated and ultimately incorporated into aquatic and terrestrial food webs. Our research has determined that the stable nitrogen isotope "fingerprint" (^{15}N:^{14}N or $\delta^{15}N$) of adult anadromous salmon returning to coastal California basins is 15.46 ± 0.27‰ (mean ± 1 SEM, $n = 35$; J. Kiernan unpublished data), a value markedly higher than most other natural N sources available to biota in coastal watersheds. This salient isotopic signal allows the application of stable isotope analyses to trace how salmon-borne nutrients are incorporated and cycled by organisms in the receiving watersheds.

Researchers interested in the utilization of MDN by riparian trees have generally inferred sequestration and incorporation from foliar $\delta^{15}N$ values. Nitrogen is a very minor constituent of wood cellulose (typically <0.05% by weight) and natural abundance levels of $\delta^{15}N$ in tree rings have rarely been determined. Poulson et al. (1995) were among the first to successfully analyzed $\delta^{15}N$ from trees (eastern hemlock; *Tsuga canadensis*), but analysis required combustion of prohibitively large quantities (>400 mg) of material per sample. Since that time, advancements in stable isotope analytical techniques have made it possible to detect $\delta^{15}N$ from small samples (~20-30 mg) of material (Hart and Classen 2003). This permits for non-destructive sampling of live trees via increment cores and provides a novel opportunity to assess the transfer of salmon-derived (SD) nitrogen into the riparian zones of salmon-bearing watersheds. Reimchen et al. (2003) recently reported that wood samples extracted from western hemlock (*Tsuga heterophylla*) trees in British Columbia yielded clear evidence of SD-nitrogen incorporation with reproducible $\delta^{15}N$ values. Intuitively, if spawning salmon represent a significant source of nitrogen to riparian trees in salmon-bearing watersheds, information on salmon abundance may be recorded in the growth and chemical composition (e.g., $\delta^{15}N$) of annual tree rings. By quantifying the nitrogen stable isotope composition of tree xylem it would be possible to explore changes in SD-nitrogen over decadal or sub-decadal time increments and determine whether the nutrient capital of riparian biota has been affected by diminished salmon returns. Moreover, if $\delta^{15}N$ can be quantified from annual growth rings, it may be possible to infer changes in salmon abundance over time and reconstruct historical salmon returns for periods and locations where no such information presently exists. Nearly all salmon recovery programs are built upon very uncertain estimates of population sizes prior to European settlement. The development of robust paleoecological methods to determine historical salmon abundance and variability would greatly assist resource managers in identifying and establishing appropriate restoration targets.

Objectives

The overall objective of this study was to determine whether the $\delta^{15}N$ values of riparian conifer tree rings could be used to assess historical marine-derived nutrient transfer and salmon abundance in two coastal California watersheds. We hypothesized that (*i*) a salmon vectored marine-derived nitrogen signal would be detectable in riparian wood samples, (*ii*) tree-ring $\delta^{15}N$

values would be higher in years of higher salmon abundance, and (*iii*) the dendrochemistry of riparian tree-ring variables could be used to reconstruct past salmon abundance.

Procedure

Site Descriptions

Our study was carried out in two geographically disparate coastal basins that are widely regarded as important salmonid spawning and rearing habitat in California. The initial method development phase of our research was conducted in the West Branch (WB) Mill Creek watershed, a fourth-order (Strahler 1957) tributary of the Smith River in northern California (Del Norte County; 41º44'N, 124º05'W). The WB Mill Creek drains an area of 23.6 km^2 and supports five species of anadromous salmonids: coho salmon (*Oncorhynchus kisutch*), fall chinook salmon (*O. tshawytscha*), chum salmon (*O. keta*), steelhead trout (*O. mykiss*), and coastal cutthroat trout (*O. clarki clarki*).

The WB Mill Creek watershed has an extensive history of timber harvest dating back to the mid 1800s, with concentrated commercial harvest of coast redwood (*Sequoia sempervirens* [D. Don] Endlicher) and Douglas-fir (*Pseudotsuga menziesii* [Mirabel] Franco) occurring between 1950 and 2000. In 2002, a major portion of the Mill Creek watershed was acquired by Save-the-Redwoods League and subsequently incorporated into the California State Parks system. Coast redwood trees presently dominate the upland forest while the riparian zone is comprised mainly of second-growth redwood and Douglas-fir, Bigleaf maple (*Acer macrophyllum* Pursh), willow (*Salix* spp.), red alder (*Alnus rubra* Bong.), and California-laurel (*Umbellularia californica* [Hook. & Arn.] Nutt.). The WB Mill Creek was selected for study because standardized annual salmon escapement surveys have been conducted since 1980 (Waldvogel 2006) providing 23 years of continuous abundance data. The stream at this location is low gradient (0.7 %) and the channel is largely unconfined with an extensive floodplain. Additional reach characteristics are described in Waldvogel (2006).

Our second study site was Waddell Creek, a small (67.3 km^2 drainage area) coastal watershed in Santa Cruz County, California (37˚08'N, 122˚15'W). The headwaters of Waddell Creek originate in the Santa Cruz Mountains at an elevation of approximately 600 m and the creek drains to the Pacific Ocean ~27 km north of Monterey Bay, California. Waddell Creek has two major forks, East and West Waddell, which join to form the main stem approximately 4.8 river km from the ocean. Approximately 84% of the Waddell Creek watershed is located within the boundaries of Big Basin Redwoods State Park. Waddell Creek supports steelhead trout and one of the southernmost extant populations of coho salmon (Moyle 2002). Both anadromous species have access to the main stem of Waddell Creek, the lowermost 2.4 m of the East Fork Waddell (to a 10 m waterfall) and up to 10 km of the West Fork Waddell. High stream gradient and natural barriers restrict coho distribution in the West Fork, however, and they are scarcely reported upstream of the confluence of Henry Creek (Rischbieter 2000).

Field methods

For our initial pilot study we collected increment cores from 10 extant riparian Douglas-fir trees growing adjacent to WB Mill Creek. All trees were located within 10.0 m of the active stream channel. Core samples were collected on 17 January 2004 from a 250 m section of riparian zone located immediately downstream of the 2.7 km index stream reach used by Waldvogel (2006) to derive minimum annual escapement estimates. Small diameter (5.15 mm) increment core samples were extracted from each tree and prepared for dendrological analysis using standard methods (Phipps 1985). We concurrently collected a second, large diameter (12.0 mm), increment core from four trees for determination of annual nitrogen content and natural abundance stable nitrogen isotope ratios ($\delta^{15}N$). Diameter at breast height (DBH; measured at 1.37 m above the ground on the upslope side of the tree), distance from the active stream channel, and general site characteristics were also recorded for each tree sampled.

Increment core samples from Waddell Creek were collected on 16-18 October 2005. Collections were made from two distinct areas within the watershed: (*i*) a ~750 m length of riparian zone adjacent to the creek where salmon spawning is known to occur (hereafter, salmon site), and (*ii*) a ~500 m section of riparian zone located above a natural barrier to salmon migration (hereafter, control site). We collected paired increment cores (i.e., 5.15 mm and 12.0 mm) from a total of 10 Douglas-fir and 16 coast redwood trees in the Waddell Creek watershed (Table 1). Distances from the stream channel, DBH, and site characteristics were also determined for each tree sampled. Two coast redwood cores from the upstream control site (sample IDs: WDRW03 and WDRW13) were later determined to be damaged or unreliable and excluded from our analyses.

Laboratory Procedures

Small-diameter increment core samples were air dried, mounted, and sanded for analysis of annual growth rings. Prepared cores were converted to digital images and ring widths were measured to the nearest 0.001 mm using an OPTIMAS (Media Cybernetics, Inc. Silver Spring, MD.) image analysis system. Each increment core was measured in triplicate and mean ring-widths values were used to generate a time series for each tree. Each time series was then detrended using the tree-ring program ARSTAN (Cook 1985, Cook and Holmes 1999) to remove trends in ring-width due to non-environmental factors such as increasing age and tree size. Detrending was accomplished using a cubic smoothing spline function that preserved ~50% of the variance contained in the measurement series at a wavelength of 32 years. Individual growth index values were derived by dividing the actual ring-width value by the value predicted from ARSTAN regression equations. Chronologies using the growth index values were subsequently combined into a robust (relative and dimensionless) growth index series for each sample site. Cross-dating of coast redwood trees from Waddell Creek was not successful due to the presence of anomalous rings, a high degree of ring complacency (i.e., a lack of ring variability) in some cores, and small sample sizes.

Pretreatment of increment cores

Previous dendrochemical research has found than nitrogen may be highly mobile in the xylem of some tree species (Cutter and Guyette 1993, Sheppard and Thompson 2000, Elhani et al. 2003). Although the degree to which coast redwood and Douglas-fir trees exhibit radial translocation of nitrogen is largely unknown, such mobility could potentially obscure interpretation of nitrogen availability at the time of ring formation (Drake et al. 2002, Hart and Classen 2003). To minimize potentially confounding effects associated with the translocation of nitrogenous products across ring boundaries, increment core samples from Waddell Creek were pretreated to remove soluble forms of nitrogen (primarily sap residues) following the "shortduration" protocol outlined in Sheppard and Thompson (2000). Briefly, tree-ring samples were sequentially Soxhlet extracted for 4 h in a mixture of ethyl alcohol and toluene (1:1 v/v), 4 h in 100% ethyl alcohol, and 1 h in distilled water (Sheppard and Thompson 2000). Increment cores collected from Mill Creek as part of our pilot study were not treated or extracted prior to stable isotope analysis.

Stable isotope analyses

Annual growth from large diameter cores was excised using a razor blade and dissecting microscope at 10-20× magnification. Individual wood samples were placed in glass scintillation vials and dried in a laboratory oven at 60˚C for ≥30 days. Dried samples were transferred to stainless steel grinding capsules and triturated for 90 sec. in a Capmaster (S.S. White Co., Philadelphia, Pennsylvania, USA) high-speed dental amalgamator. Powdered wood samples were dried for an additional 72 h at 60°C prior to stable isotope analysis. Samples of 15-40 mg of material were transferred into 9 x 5 mm tin capsules for continuous flow mass spectrometry analysis of nitrogen. All isotopic analyses were performed at the stable isotope facility at the University of California at Davis using a PDZ Europa Scientific 20/20 isotope ratio mass spectrometer with an analytical error (± 1 standard deviation) of ± 0.4‰ for nitrogen. We express nitrogen isotope ratios in standard delta (δ) value notation to reflect the per mil (‰) ratio of the heavier to lighter isotope according to the following equation:

$$\delta^{15}\mathrm{N}\ (‰) = \left(\frac{\mathrm{R}_{\mathrm{sample}} - \mathrm{R}_{\mathrm{standard}}}{\mathrm{R}_{\mathrm{standard}}} \right) 10^{3} \tag{1}$$

where R is the molar ratio of ^{15}N to ^{14}N and atmospheric N is used as the conventional isotopic standard. All tree-ring δ^{15}N samples containing < 10μg of N were deemed unreliable and excluded from our analyses (D. Harris, U.C. Davis Stable Isotope Laboratory, personal communication).

Results and Discussion

West Branch Mill Creek Reconstruction:

The strongest correlations between known salmon escapement and all tree variables examined at Mill Creek occurred when a lag time of one year was applied (i.e., salmon escapement in year$_n$ versus tree-ring variables in year$_{n+1}$). There was a significant positive linear relationship ($b_1 = 150.94$, $r^2 = 0.273$, $p = 0.011$) between salmon escapement and indexed Douglas-fir growth in the WB Mill Creek watershed (Fig. 1). Ring nitrogen content ([N], %) and δ^{15}N values were not correlated with each other ($b_1 = -0.001$, $r^2 = 0.004$, $p = 0.789$; Fig. 2). Further, tree-ring [N] was only weakly correlated with salmon escapement in the previous year ($b_1 = 1102.01$, $r^2 = 0.120$, $p = 0.11$; Fig. 3). One data point representing the outermost complete tree-ring (year 2002) was removed from this analysis as it contained extremely high [N] and was determined to be a statistical outlier (DFFITS >-1.037). Among the tree-ring variables examined at WB Mill Creek, annual δ^{15}N exhibited the most significant positive correlation with known salmon escapement ($b_1 = 18.02$, $r^2 = 0.465$, $p = <0.001$; Fig. 4).

We used the empirical relationship between escapement and tree-ring δ^{15}N in a linear regression model to reconstruct annual salmon escapement for the period 1946 to 2002 (Fig. 5). The relationship between δ^{15}N and salmon escapement (fish·km^{-1}) in the WB Mill Creek watershed was described by the following equation:

$$\text{Escapement for year}_i = 102.37 + 18.02 \times \delta^{15}\text{N}_{i+1} \tag{2}$$

When compared to years of known salmon escapement (1980-2002) our model failed to accurately predict extremes in escapement (i.e., high and low salmon returns) but properly tracked general population trends. The period of reconstruction (1946-1979) indicated a general decline in salmon abundance over time with years of high escapement occurring in 1947, 1951, 1953, and 1963 with estimates of 139, 125, 142, and 119 fish·km^{-1}, respectively (Fig. 5). Conversely, low escapement was predicted for the years 1968, 1973, and 1977 with returns of 53, 58 and 54 retuning salmon·km^{-1}of stream, respectively. The addition of indexed annual growth and [N] as additional explanatory variables did not statistically improve overall model performance (adj r^2 = 0468, p = 0.002; Fig. 6). The multiple linear regression-based reconstruction for WB Mill Creek was described by the following equation:

$$\begin{aligned}\text{Escapement for year}_i = {} & \text{-33.02} + 48.86\left(\text{ring index}_{i+1}\right) \\ & + 16.28\left(\delta^{15}\text{N}_{i+1}\right) + 1181.42\left([\text{N}]_{i+1}\right)\end{aligned} \tag{3}$$

This model suggested a less significant decline in salmon abundance over the period 1946-1979. Results indicated years of high salmon escapement in 1947, 1949 and 1953 with estimated returns of 126, 116 and 116 fish·km^{-1}, respectively (Fig. 6). Conversely, low escapement was predicted in 1977, 1979 and 1957 (45, 46 and 49 fish·km^{-1}, respectively). For both reconstructions, present day (known) escapement to WB Mill Creek (i.e., 2000-2002) is as strong as the historical maxima values predicted by the models.

Collectively, the initial results from WB Mill Creek suggest that salmon abundance may be reflected in riparian tree-ring variables such as indexed growth, [N], or δ^{15}N. However, interpretation of results in this watershed is hindered by two important issues: (*i*) the lack of comparative experimental controls, and (*ii*) the potentially confounding effects associated with the translocation of nitrogenous compounds across annual tree-ring boundaries. In order to infer the uptake of MD-nitrogen by riparian trees it is necessary to have ecologically analogous reference sites that are uninfluenced by anadromous salmonids. Robust experimental reference sites could potentially include proximate drainages (i.e., the use of paired watersheds) or stream reaches located above impoundments that block access to anadromous salmon. No such sites were available in the vicinity of WB Mill Creek, however, as all salmon-free locations had significantly different site characteristics, especially with respect to stream gradient, floodplain development and soil characteristics.

It is especially important to note that increment cores from WB Mill Creek demonstrated enriched δ^{15}N and elevated [N] in the last (most recent) 3-5 years of growth. Since we did not pre-treat our increment cores prior to analysis, it is unclear whether this enrichment is a true environmental signal resulting from increased salmon abundance and MD-nitrogen availability, or the product of internal translocation of nitrogen by the trees. Whatever the case, this late enrichment significantly influenced the results of our reconstructions since both high [N] and

$\delta^{15}N$ coincided with years of very high escapement to WB Mill Creek (see years 2000-2003 in Fig. 6).

Waddell Creek Reconstruction:

As an initial step to our Waddell Creek analysis, we attempted to generate a robust proxy for the very limited record of escapement to the watershed (i.e., 9 years [1933-1941]; Shapovalov and Taft 1954). However, attempts to correlate known escapement counts to longer time series such as regional commercial salmon catch data (i.e., Ports of Monterey and San Francisco) and climate indices (e.g., annual rainfall, sea surface temperature anomalies, and Pacific Decadal Oscillation) were each unsuccessful.

Increment core chronologies for coast redwood trees in the Waddell Creek watershed ranged from 61 to 213 years at the salmon site (mean = 112, *n* = 10) and from 100-162 years at the control site (mean = 121, *n* = 4; Table 1). Douglas-fir chronologies were shorter covering from 65 to 118 years at the salmon site (mean = 90, *n* = 5) and from 100-162 years at the control site (mean = 87, *n* = 5; Table 1). The structural nitrogen content (post-solvent extraction) of coast redwood tree rings from both control and salmon influenced sites exhibited very little temporal variability until approximately 1973 (Fig. 7). Prior to 1973, [N] time series averages (± 1 SEM) were 0.08 ± 0.002% (range = 0.06 to 0.15%, *n* = 87) at the control site and 0.09 ± 0.003% (range = 0.06 to 0.32%, *n* = 90) at the salmon site. In contrast, mean [N] of redwood trees for the period 1973-2005 was elevated to 0.18 ± 0.01% (range = 0.07 to 0.36%, *n* = 33) and 0.30 ± 0.01% (range = 0.17 to 0.36%, *n* = 33) for control and salmon trees, respectively (Fig. 7). Interestingly, no such temporal increase in [N] was observed for Douglas-fir trees growing at the same locations (Fig. 8). Riparian Douglas-firs consistently contained lower [N] than did coast redwoods averaging 0.05 ± 0.001% (range = 0.03 to 0.07%, *n* = 102) at the control site and 0.05 ± 0.001% (range = 0.03 to 0.09%, *n* = 117) at the salmon site.

Annual δ^{15}N signatures of riparian coast redwood tree rings were highly variable over time (Fig. 9). Mean coast redwood δ^{15}N across the entire time series was -0.04 ± 0.08‰ (range = -4.28 to 1.19‰, *n* = 120) at the control site and -0.01 ± 0.05‰ (range = -2.02 to 2.25‰, *n* = 129) at the salmon site. For riparian Douglas-fir trees, series means were similar at both sites averaging 0.05 ± 0.08‰ (range = -1.52 to 3.07‰, *n* = 119) at the upstream control site and 0.07 ± 0.09‰ (range = -2.11 to 2.41‰, *n* = 103) at the salmon site (Fig. 10). However, it is especially important to note that annual δ^{15}N values among individual Douglas-fir trees growing at the same location were extremely variable. Among-tree differences in δ^{15}N ranged from 0.03 to 6.80‰ (mean = 0.84 ± 0.12‰, *n* = 69) at the control site and from 0.06 to 4.76‰ (mean =1.29 ± 0.10‰, *n* = 83) at the salmon site. Our inability to accurately cross-date coast redwood cores precluded an assessment of annual δ^{15}N variability among individual trees of this species. However, a comparison of mean annual δ^{15}N values for Douglas-fir trees at salmon and control sites revealed that salmon-influenced trees were not consistently ^{15}N-enriched. In fact, trees at the salmon site only exhibited elevated δ^{15}N values on 58 of the 103 (56%) years examined (Fig. 11).

To determine the relationship between known Waddell Creek total salmonid escapement (steelhead + coho) and riparian tree-ring variables (i.e., indexed growth, [N], δ^{15}N) we tested the relative performance of both linear and non-linear models. In all cases, linear relationships provided the best overall fit. Additionally, since forest fertilization studies conducted throughout the Pacific Northwest have reported lagged or "carry-over" growth responses following N addition (e.g., Miller and Tarrant 1983), we examined the change in fit (coefficient of determination) that resulted from lagging each tree-ring variable behind escapement from 0 through 7 years (Tables 2-4). Given our *a priori* expectation of a positive relationship between salmon escapement and tree-ring parameters, we disregarded all regressions that did not yield a positive slope ($b_1 \geq 0$). Of the regressions that met this criteria, the strongest correlation with Waddell Creek escapement occurred at a lag of +3 years for natural log-transformed (ln) indexed growth ($r^2 = 0.526$, $t = 0.027$; Table 2), no time lag (i.e., +0) for ln [N] ($r^2 = 0.156$, $t = 0.027$; Table 3), and +2 years for δ^{15}N ($r^2 = 0.019$, $t = 0.726$; Table 4). These relationships were subsequently used to parameterize a multiple linear regression (MLR) model and predict historical annual total escapement to WB Mill Creek. Escapement for year *i* was described by the following equation:

$$\text{Escapement for year}_i = 4250.82 + 129.02 \times \ln \text{indexed growth}_{i+3} + 1069.99 \times \ln\,[\text{N}]_i - 16.61 \times \delta^{15}\text{N}_{i+2} \qquad (4)$$

The final multivariate reconstruction for Waddell Creek covered the period 1904-2003 (99 years; Fig. 12). The goodness of fit of the Waddell Creek MLR model (adj $r^2 = 0.493$, $p = 0.101$) was less robust than results generated for WB Mill Creek (see Fig. 5). The reconstruction indicated years of especially high escapement to Waddell Creek in 1904, 1923, 1944 and 1963 with estimated total returns of 1230, 1313,1240 and 1200 fish (coho + steelhead), respectively. Conversely, low escapement was predicted in, 1917, 1922, 1952, 1981 and 2001 (444, 402, 528, 505 and 495 fish, respectively). Decadal-scale means illustrate broad population trends and highlight periods of high (years 1920-1929; interval mean = 928 ± 86 fish·yr^{-1}) and low escapement (years 1910 and 1919; interval mean = 682 ± 61 fish·yr^{-1}; Fig. 13). When the data are collapsed and examined at a decadal-scale, the reconstruction suggests that Waddell Creek has experienced a steady decline in total escapement from ~1970 to present (Fig. 13).

Unfortunately, there are little present day escapement data from which we may validate the results of our Waddell Creek watershed reconstruction. Smith (1999, 2001) reported that only a single year class of coho salmon (i.e., 1993, 1996, 1999) is still strong in Waddell Creek and that the other year classes are presently weak or largely absent. While this cyclical variability is not directly reflected in our reconstruction, our results estimate coho + steelhead returns to the watershed and we are unable to separate the relative contribution of each species to our total escapement estimates.

Reconstructing salmon populations:

Few paleoecological studies have successfully modeled changes in either marine-derived nutrient transfer or salmon abundance prior to European settlement. Finney et al. (2000, 2002) used stratigraphic variation in lake sediment δ^{15}N and fossilized cladocerans and diatoms to infer changes in sockeye salmon (*Oncorhynchus nerka*) abundance in Alaskan nursery lakes. Their ≈ 2200-year reconstruction revealed that large fluctuations in sockeye abundance were commonplace and that multi-decadal to century-long climatic regimes largely drove population cycles. Unfortunately, analogous stratigraphic methods are generally not applicable in low to mid-order rivers or floodplains due to scour, entrainment and redistribution of sediments (Constantine et al. 2005). Consequently, our understanding of historical population dynamics across much of the geographic range of Pacific salmon has been limited to written records which provide little basis for understanding trends, especially within the context of long-term climatic drivers.

Drake et al. (2002) used relationships between tree growth, climate (PDO index), and periods of known salmon escapement to model historical salmon returns to riverine sites in two regions of Alaska. The authors found that records of annual escapement (weir counts) were significantly and positively correlated with indexed annual tree growth in southeast Alaska (but not southwestern Alaska) and used this relationship to reconstruct historic salmon returns back to 1820 A.D. Drake and Naiman (2007) later expanded the scope of their initial work and examined tree-ring growth in nine geographically disparate Pacific Northwest drainages. Using dendrological techniques they were able to generate reconstructions for five rivers (i.e., found positive correlations between tree growth and escapement at 5 of 9 study sites) and each compared well to site-specific population benchmarks such as years of high escapement or the construction of barriers to migration such as dams. Collectively, the works of Drake et al (2002) and Drake and Naiman (2007) corroborated earlier reports that anadromous salmon positively affected the radial growth of riparian trees (e.g., Helfield and Naiman 2001, but see Kirchhoff 2003) and demonstrated that salmon abundance could be inferred from annual tree-ring growth in some watersheds.

What has remained unsubstantiated to date, however, is whether salmon abundance is accurately reflected in the chemical composition of annual tree rings. While using annual variations in tree-ring $\delta^{15}N$ to infer salmon abundance in Pacific Rim watersheds is academically alluring, no significant relationship between escapement and annual tree-ring chemistry has been established, despite repeated attempts to do so (Drake and Naiman 2007). In general, the use of $\delta^{15}N$ to infer the contribution of salmon-borne nitrogen to freshwater and riparian ecosystems is predicated on the ability to determine differences in $\delta^{15}N$ within and among species and habitats. Adult anadromous salmon are uniquely enriched in ^{15}N by +10 to +15‰ relative to most N sources in terrestrial ecosystems and numerous studies have used this salient signature to demonstrate that riparian plants adjacent to salmon-bearing streams incorporate MDN inputs (e.g., Bilby et al. 1996, Ben-David et al. 1998, Helfield and Naiman 2001, Bilby et al. 2003, Merz and Moyle 2006). However, reported differences in plant $\delta^{15}N$ between salmon and salmon-free sites are often small (generally < 3.0‰) and may be easily confounded by various biologically-mediated processes occurring in both the water and soil (e.g., assimilation, nitrification, and denitrification) that significantly alter (fractionate) the initial salmon $\delta^{15}N$ value prior to plant assimilation (Fig. 14).

Microbial denitrification, in particular has been shown to significantly affect the isotopic signature of soil N pools, especially in riparian areas that are frequently inundated (Sebilo et al. 2003). Clement et al. (2003) provided evidence that denitrifying bacteria preferentially select for the lighter isotope (^{14}N) resulting in enriched groundwater $\delta^{15}N\text{-}NO_3$ (from +5 to +28‰). Consequently, the $\delta^{15}N$ of overlying vegetation at their study sites was similarly enriched (from +1.7 to +14.2‰) when compared to the typical isotopic range for plants in the region. Scott et al. (2008) recently measured soil and Douglas-fir foliar $\delta^{15}N$ values along transects that originated stream-side and extended upslope in the Coast Range of Oregon. Contrary to the expectation of near-stream ^{15}N-enrichment due to MDN inputs and denitrification processes, Scott et al. (2008) found that soil $\delta^{15}N$ was progressively depleted nearer the stream channel with upslope (30 m) to stream bank differences approaching 2.0‰. This trend was in opposition to foliar $\delta^{15}N$ of trees at the site which were enriched nearer the stream.

Empirical studies have highlighted that marine-derived nutrients are delivered to riparian zones through the deposition of carcasses during high flows (Cederholm et al. 1989), transport and consumption by piscivorous predators and scavengers (Ben-David et al. 1998, Hilderbrand et al. 1999), and along hyporheic flowpaths (O'Keefe and Edwards 2003). While both the magnitude and spatial extent of hyporheic transfer is poorly understood, terrestrial carcass decay studies have shown that salmon typically only alter soil nutrient concentration over a relatively small (~2.5 m^2) area (Drake et al. 2005). Hence, carcass inputs are extremely patchy relative to other forms of N in riparian ecosystems such as litterfall. While riparian trees are uniquely able to capitalize on MDN inputs due to their extensive root systems and high capacity for nutrient storage (Drake et al. 2005), the true magnitude of the annual salmon input may not be reflected in all trees equally.

Högberg (1997) outlined that vascular plant $\delta^{15}N$ values are determined by (*i*) the source of N, (*ii*) the soil depth from which N is sequestered, (*iii*) the form of N utilized (e.g., organic N, NO_3^--N, or NH_4^+-N), (*iv*) mycorrhizal associations, (*v*) fractionations during and after N uptake by plants, and (*vi*) plant phenology. With respect to the interpretation of marine-derived $\delta^{15}N$ in riparian trees, particularly confounding isotopic fractionation may occur during N uptake and subsequent internal translocation. (Handley and Scrimgeour 1997). For example, Robinson (2001) grew plants hydroponically on a constant source of $\delta^{15}N$ (1.0 ‰) and found that individuals exhibited a 1.3‰ range in $\delta^{15}N$. Furthermore, $\delta^{15}N$ has been reported to differ within the tissues of individual plants (e.g., xylem, phloem, leaves, and roots) (Bergersen et al. 1988, Neilson et al. 1998). In our study, we found considerable variation in annual $\delta^{15}N$ among trees as has been reported elsewhere (e.g., Poulson et al. 1995, Saurer et al. 2004). For example, Poulson et al. (1995) quantified $\delta^{15}N$ from the xylem of two eastern hemlock trees growing within 5 m of each other and found that while the overall isotopic trends were similar, annual $\delta^{15}N$ values differed by 0.6 to 5.3‰ between trees. In our study, annual among tree differences in Douglas-fir $\delta^{15}N$ were as much as 4.6‰ at salmon sites and 6.8‰ at reference sites. Given this variability, the determination of statistically robust mean $\delta^{15}N$ values would require the analysis of many trees and be extremely costly.

Perhaps the greatest single obstacle to the use of tree-ring $\delta^{15}N$ to infer salmon abundance is the extensive internal cycling of N by trees. Merrill and Cowling (1966) reported that trees frequently recover N from dying cells during the process of converting sapwood to heartwood. The mobilization and transport of N across annual ring boundaries has subsequently been documented for both conifer and hardwood species and greatly hinders accurate interpretation of past N availability (Poulson et al. 1995). In fact, ^{15}N tracer studies have provided unambiguous evidence that N inputs can move bi-directionally in the bole and significantly affect the $\delta^{15}N$ signature of annual rings both before and after the tracer was applied (Elhani et al. 2003, Hart and Classen 2003). In a study designed to emulate salmon decay, Drake et al. (2006) reported that ~96% of the ^{15}N tracer taken up by trees existed as mobile xylem and phloem sap, whereas only ~4% was actually incorporated into structural tissues. While the use of solvents to remove mobile forms of N likely improves the veracity of tree-ring $\delta^{15}N$ data (Sheppard and Thompson 2000) it renders the residual wood extremely N poor and greatly increases the amount of sample material required for isotopic analysis (combustion). Although the effect of extraction on wood $\delta^{15}N$ values was not the focus of our study, our results from Mill Creek support previous findings that untreated cores produced inflated [N] values, especially at the late end (see Cowling and Merrill 1966, Poulson et al. 1995). Curiously, our redwood cores from the Waddell Creek watershed exhibited highly elevated [N] over the last ~30 years despite having undergone pre-treatment procedures (Fig. 7). We believe that the solvent extraction method applied to these samples was inadequate to remove all the soluble forms of exchangeable N between annual rings in coast redwoods. Clearly, even if inputs from anadromous salmon contributed a major proportion of the N utilized by riparian trees, internal cycling and isotopic fractionation would make quantifying annual (or even decadal) contributions extremely difficult.

Conclusions and future direction

Currently, it is unclear if the data are consistent with our hypotheses. While $\delta^{15}N$ was measurable in annual tree rings, stream, soil and within-tree nitrogen dynamics potentially obscure the robust determination of marine-derived versus autochthonous sources of N. With respect to the hypothesis that salmon abundance is directly reflected in the $\delta^{15}N$ value of annual tree rings, results were conflicting at our two study locations. There was a statistically significant positive relationship between annual tree-ring $\delta^{15}N$ and salmon escapement in the WB Mill Creek watershed, but this result is tempered by the fact that increment cores were not extracted prior to chemical analysis. Consequently, the goodness of fit of the WB Mill Creek reconstruction may have been unduly influenced by inflated [N] and $\delta^{15}N$ during late years (due to radial translocation) which correlated by chance with years of high escapement. By comparison, we found no statistically significant relationship between tree-ring $\delta^{15}N$ and escapement to Waddell Creek. However, a sample size of nine years provides very little power for detecting any significance in analyses with lagged relationships.

On balance, our data do not lend strong support to the idea that $\delta^{15}N$ in tree rings can be used to generate numerical targets for salmonid restoration. Nevertheless, tree-ring based analyses may help identify and understand trends in salmon increase or decline across broad geographic areas. For example, our reconstructions indicate general population declines which began between the 1960s (WB Mill Creek; Fig. 5) and 1970s (Waddell Creek; Figs. 12 and 13) and appeared to taper off in the 1990s. If such trends are indeed genuine, and could be demonstrated across a wide geographic area, they would indicate the importance of broad-scale drivers of salmonids abundance such as climate and ocean condition. Conversely, a lack of commonality across watersheds or regions would implicate more localized factors of decline such as habitat loss or degradation.

Fundamentally, dendroecological studies seek to isolate and quantify a specific environmental signal of interest from considerable background noise. It is unclear whether the nutrients delivered by anadromous salmon are of a significant magnitude to alter terrestrial N cycles and produce a distinguishable signal in riparian trees. Under nutrient limited conditions, it is reasonable to assume that tree-ring parameters would not exhibit a response to salmon-derived nutrient inputs until some minimum contribution threshold was exceeded (see Drake and Naiman 2007). The level of escapement necessary to generate such a response remains speculative and would depend on a myriad of site-specific physical and biological characteristics. We conducted our studies in watersheds that largely contain low-density spawning salmonids and only examined two riparian conifer tree species. Admittedly, many other tree taxa and geographic locations may be more amenable to dendroecological investigation than those encompassed by our study. The basic appeal of coast redwood and Douglas-fir trees is that they are extremely long-lived and commonly occur in California's coastal salmon-bearing watersheds. Nevertheless, accurate cross-dating among increment cores is a fundamental step in all dendrological analyses (Stokes and Smiley 1977) and especially imperative when attempting to derive robust relationships between time-series variables such as annual escapement and tree-ring $\delta^{15}N$. While coast redwood trees potentially provide an opportunity to examine changes in environmental conditions over many centuries (Stephens and Fry 2005), exact calendar years frequently cannot be assigned to specific growth increments with confidence (Fritz and Averill 1924, Fritz 1940, Waring and O'Hara 2006, 2008). Conversely, Douglas-fir trees are readily cross-dated and hold more promise as a candidate for future dendrochemical studies. A number of additional tree species common to salmon-bearing watersheds have been identified as suitable for dendrochemical investigations (Cutter and Guyette 1993) and warrant an objective assessment.

Especially informative would be the analysis of tree rings from locations where once prodigious populations of anadromous salmon have been extirpated due the construction of dams. This would permit a coarse comparison of pre- and post-dam δ^{15}N values and provide information regarding the magnitude of ^{15}N-enrichment in wood due to SD-nitrogen inputs. Moreover, it would be instructive to examine the annual chemistry of tree rings in watersheds that contain a single dominant odd or even year population of pink salmon (*O. gorbuscha*) and few fish in the alternate years. Such conditions, if recorded with fidelity, would be expected to produce an unambiguous saw-toothed pattern of alternating high and low δ^{15}N and [N]. However, all tree-ring based reconstructions will be essentially limited by the availability of robust escapement data for watersheds where old-growth riparian trees still exist.

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Table 1. Riparian coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) trees sampled from the Waddell Creek watershed. Trees from the salmon site category were growing adjacent to areas of known salmon spawning while control trees were located upstream of a barrier to salmon passage. Distance represents the linear distance from the active stream channel. Diameter at breast height (DBH) was measured at 1.37 m above the ground.

Increment Core ID	Site Category	Distance (m)	DBH (cm)	Chronology[‡]	Years
coast redwood					
WDRW04	Control	4.9	294.6	1905-2005	100
WDRW12	Control	2.5	335.3	1843-2005	162
WDRW15	Control	5.2	218.4	1886-2005	119
WDRW16	Control	83.0	205.7	1899-2005	106
WDRW01	Salmon	20.0	228.6	1897-2005	108
WDRW02	Salmon	23.5	213.4	1898-2005	107
WDRW05	Salmon	8.5	215.9	1792-2005	213
WDRW06	Salmon	33.0	251.5	1893-2005	112
WDRW07	Salmon	25.0	302.3	1944-2005	61
WDRW08	Salmon	7.0	213.4	1900-2005	105
WDRW09	Salmon	22.0	271.8	1906-2005	99
WDRW10	Salmon	4.0	297.2	1939-2005	66
WDRW11	Salmon	10.0	284.5	1878-2005	127
WDRW14	Salmon	4.5	200.7	1874-2005	131
Douglas-fir					
WDDF01	Control	4.0	264.2	1887-2005	118
WDDF05	Control	14.1	287.2	1936-2005	69
WDDF06	Control	28.0	320.0	1925-2005	80
WDDF07	Control	17.5	160.1	1940-2005	65
WDDF09	Control	9.3	240.7	1899-2005	106
WDDF02	Salmon	15.0	210.8	1891-2005	114
WDDF03	Salmon	5.0	269.2	1900-2005	105
WDDF04	Salmon	6.7	309.9	1922-2005	83
WDDF08	Salmon	28.0	180.3	1922-2005	83
WDDF10	Salmon	19.4	229.7	1938-2005	67

[‡] Coast redwood trees could not be cross-dated so the chronology is estimated.

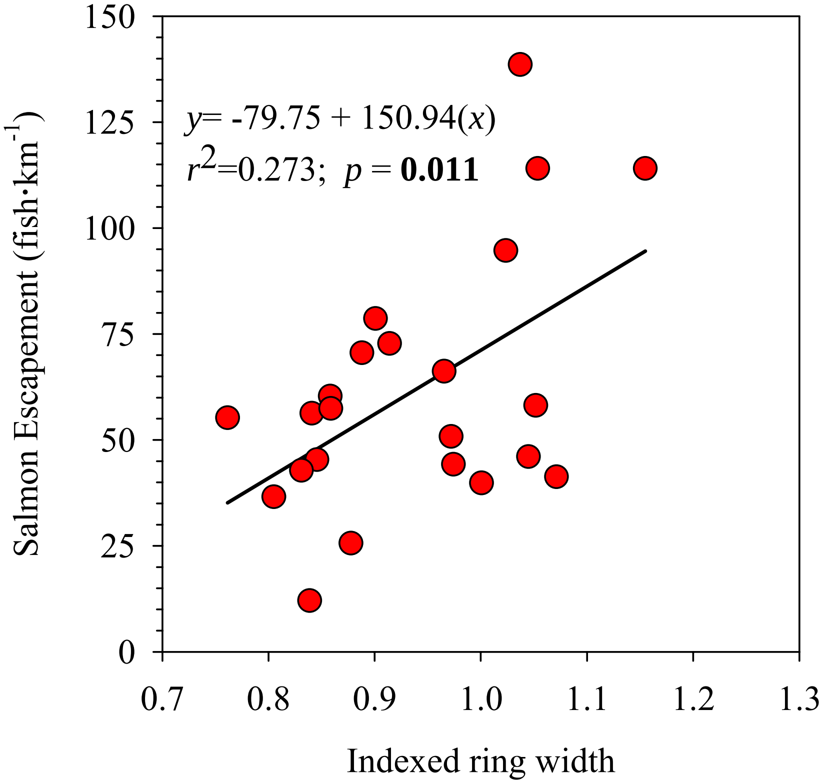

Figure 1. West Branch Mill Creek salmon escapement versus indexed ring width (mean annual growth) for riparian Douglas-fir trees. Tree growth is lagged by +1 year. Escapement data are from Waldvogel (2006).

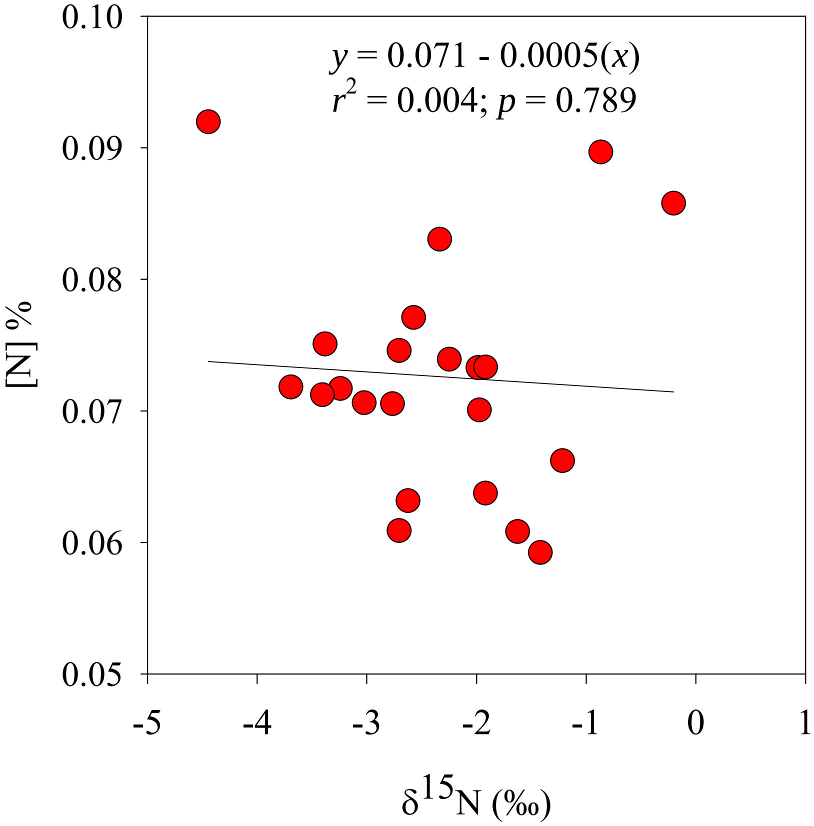

Figure 2. Relationship between annual tree ring structural nitrogen content ([N];%) and stable nitrogen isotope ratio ($\delta^{15}N$; ‰) for riparian Douglas-fir trees in the West Branch Mill Creek watershed.

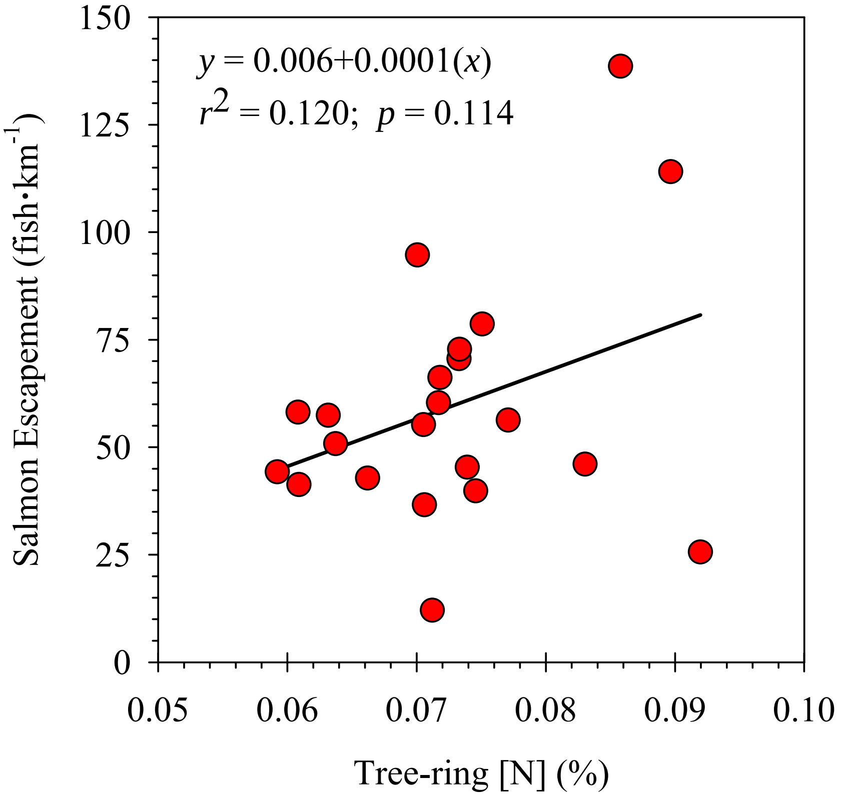

Figure 3. West Branch Mill Creek salmon escapement versus tree-ring percent nitrogen content ([N]) lagged by +1 year (i.e., escapement in 2001 is plotted against [N] in 2002). Escapement data are from Waldvogel (2006).

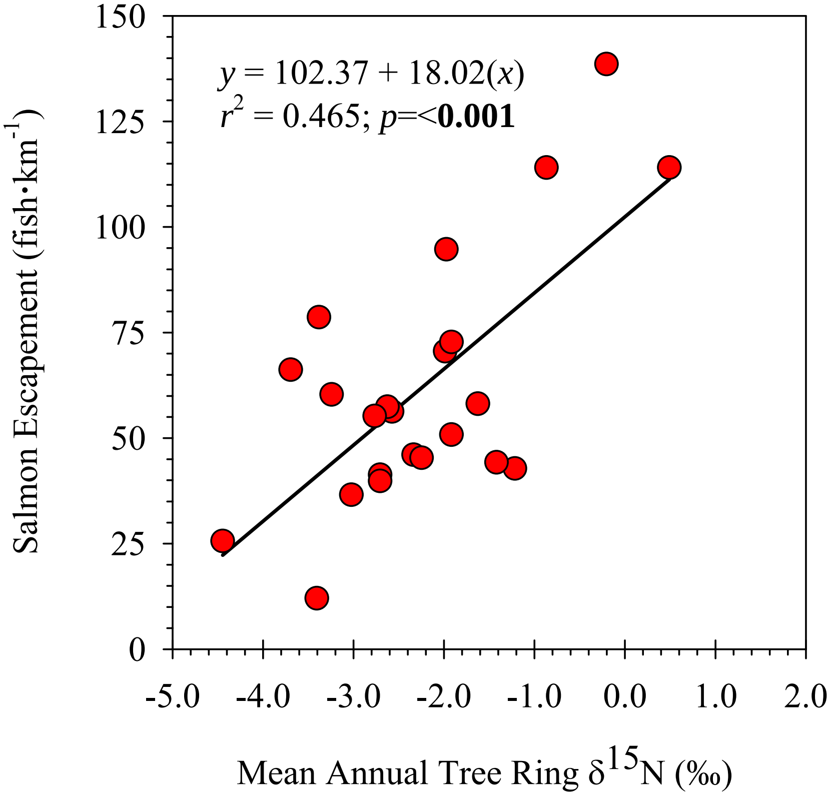

Figure 4. West Branch Mill Creek salmon escapement versus annual tree-ring δ^{15}N (‰) lagged by +1 year. Stable nitrogen isotope ratios represent the mean value of four riparian Douglas-fir trees. Escapement data are from Waldvogel (2006).

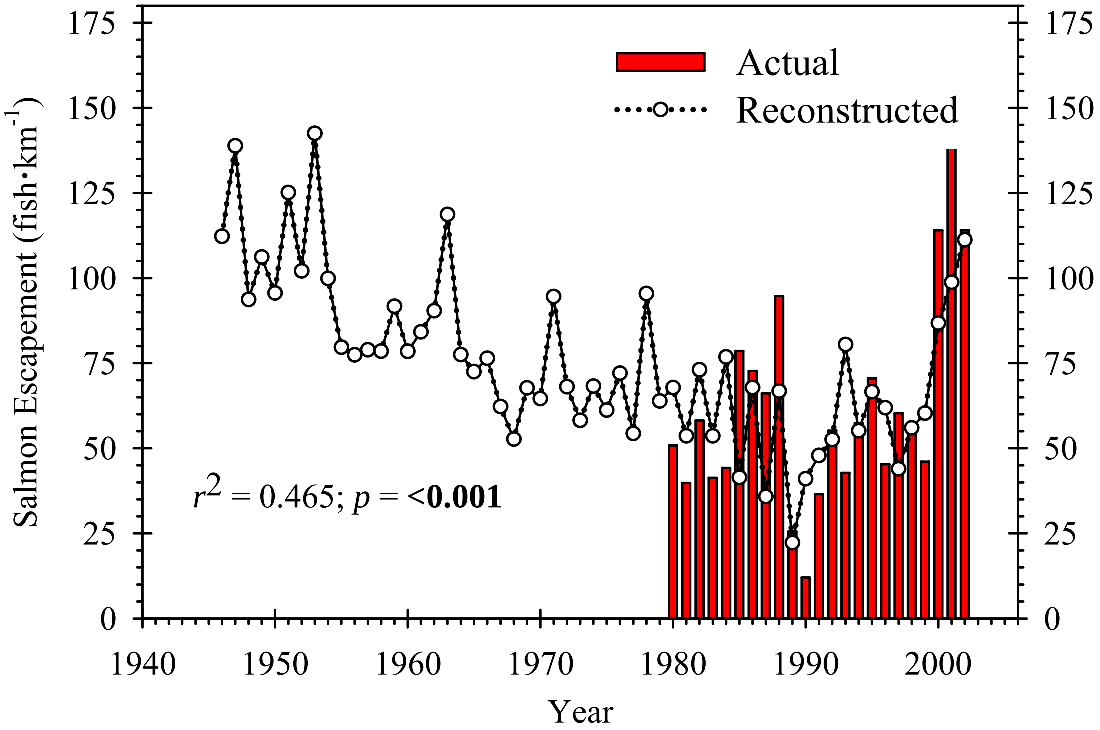

Figure 5. Reconstructed West Branch Mill Creek salmon escapement using annual tree ring $\delta^{15}N$ (‰). Bars represent actual escapement counts (fish·km^{-1} stream) and open circles represent predicted values. Escapement counts are from Waldvogel (2006).

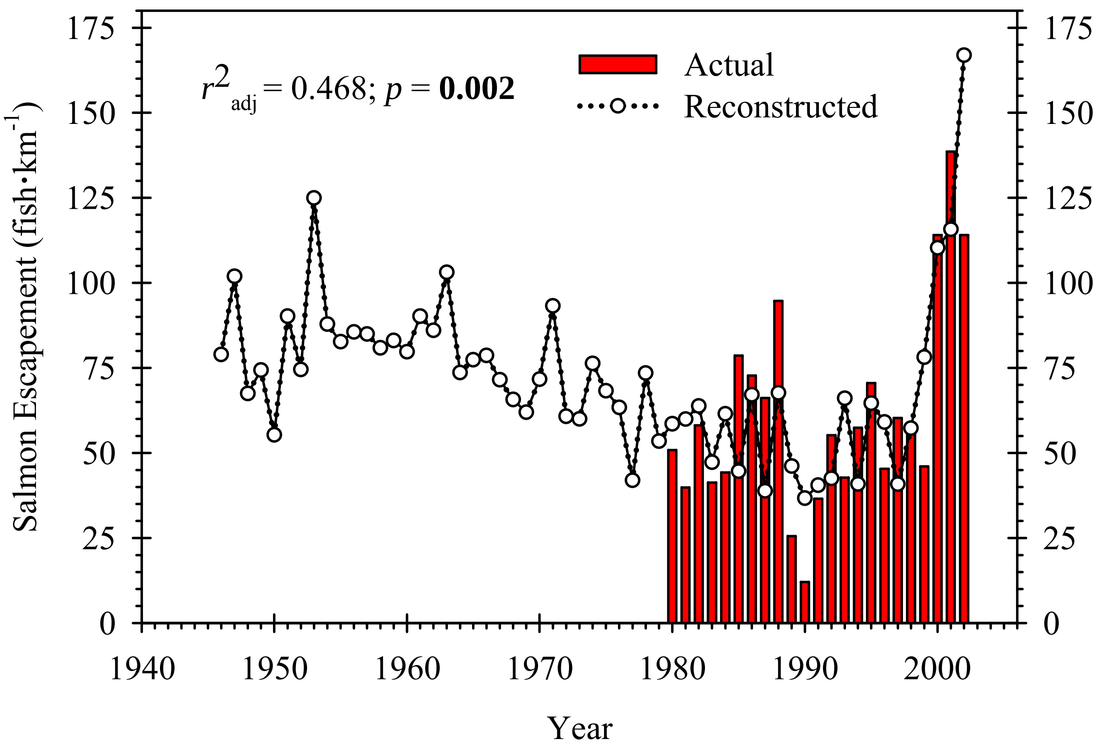

Figure 6. Reconstructed West Branch Mill Creek salmon escapement using annual tree-ring growth, % N content, and δ^{15}N (‰) as explanatory variables. Bars represent actual escapement counts (fish·km^{-1} stream; Waldvogel 2006) and open circles represent predicted values.

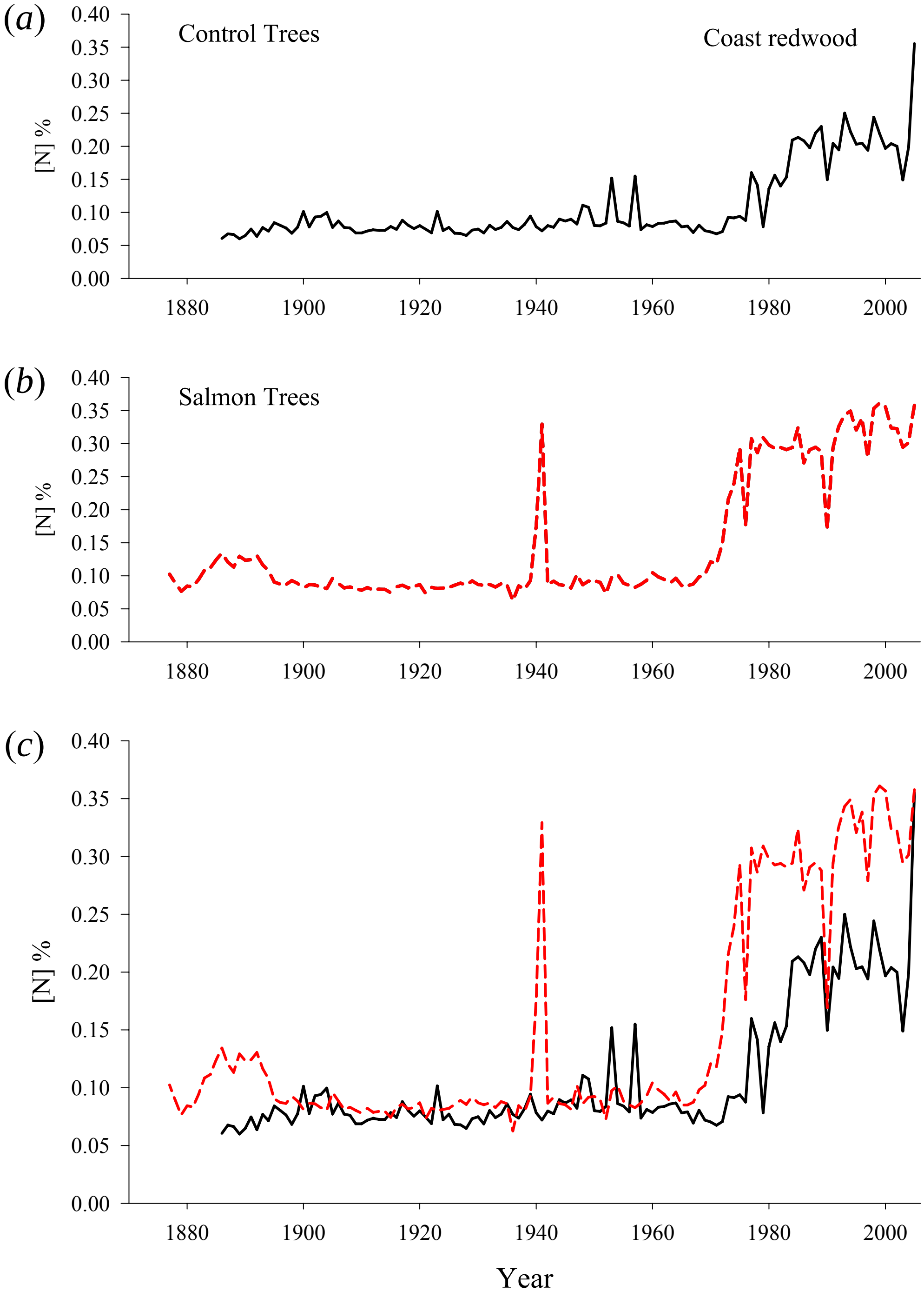

Figure 7. Time series of nitrogen concentration ([N], %) in coast redwood tree rings from control (a) and salmon influenced (b) sites in the Waddell Creek watershed. The bottom graph (c) contrasts the two time-series. Cross-dating was unsuccessful so years are estimated.

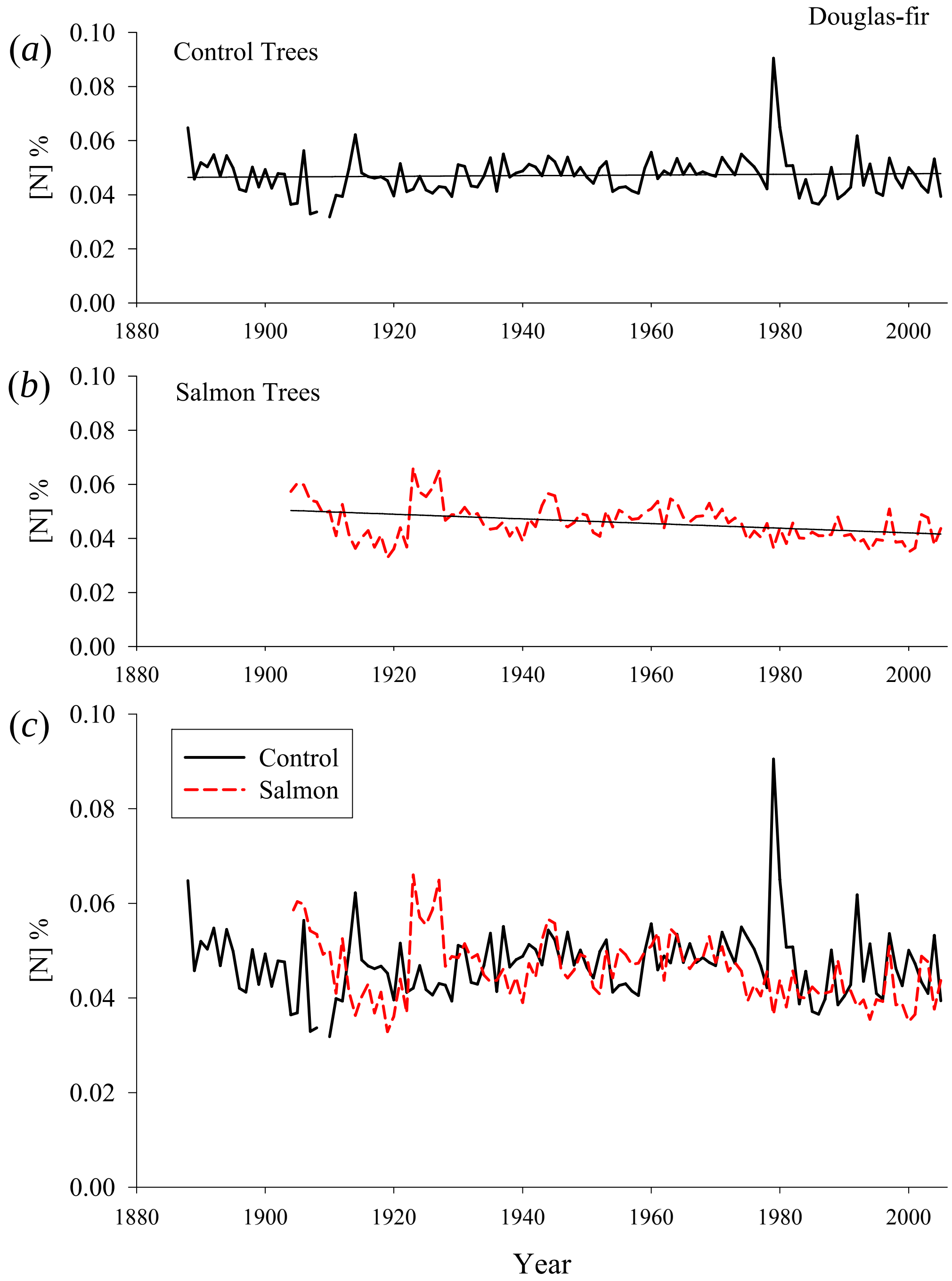

Figure 8. Time series of nitrogen concentration (%) in riparian Douglas-fir tree rings from control (a) and salmon influenced (b) sites in the Waddell Creek watershed. The bottom graph (c) contrasts the two time-series.

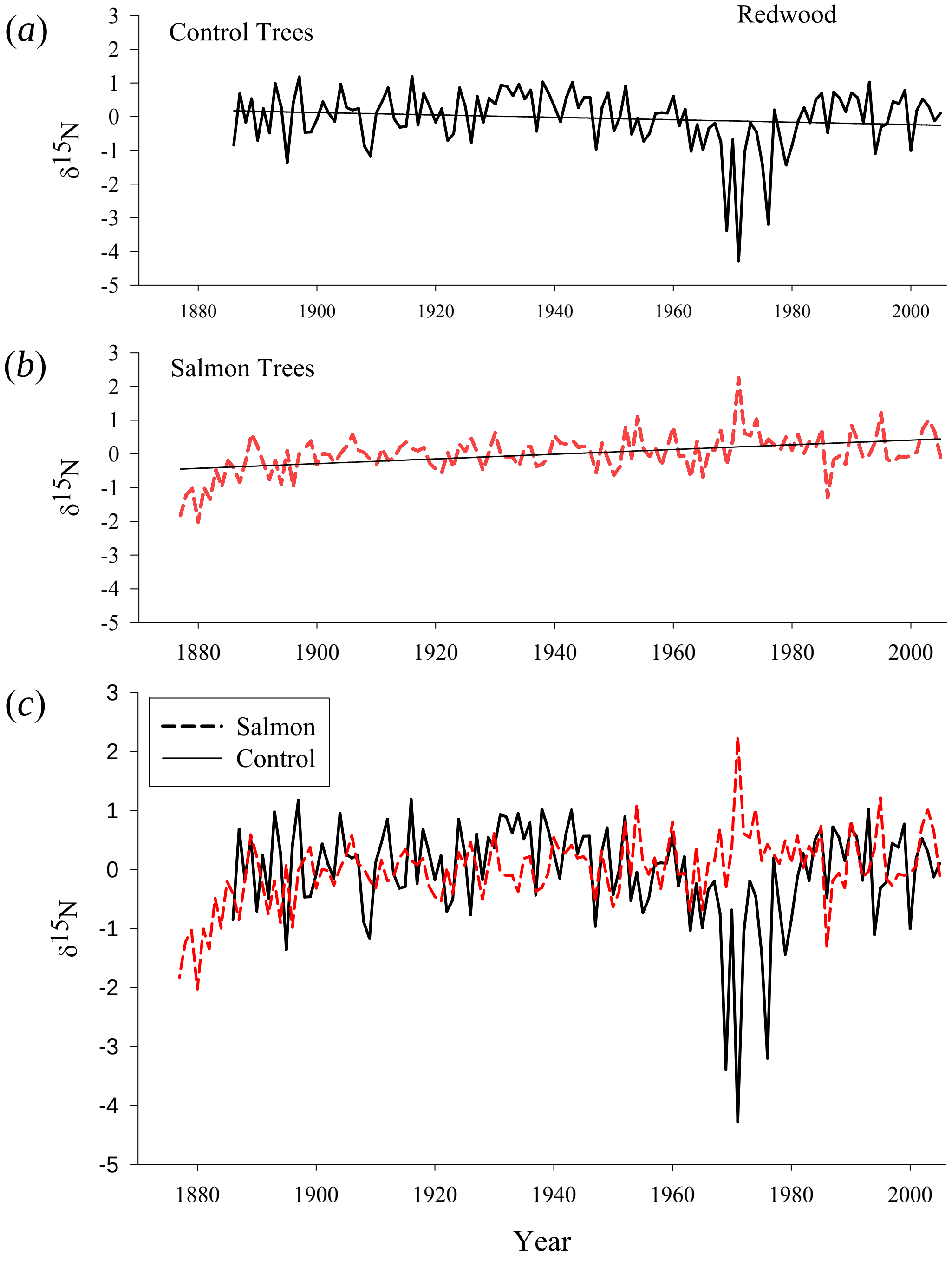

Figure 9. Time series of δ^{15}N (‰) in coast redwood tree rings from control (*a*) and salmon influenced (*b*) sites in the Waddell Creek watershed. The bottom graph (*c*) contrasts the two time-series. Cross-dating was unsuccessful so years are estimated.

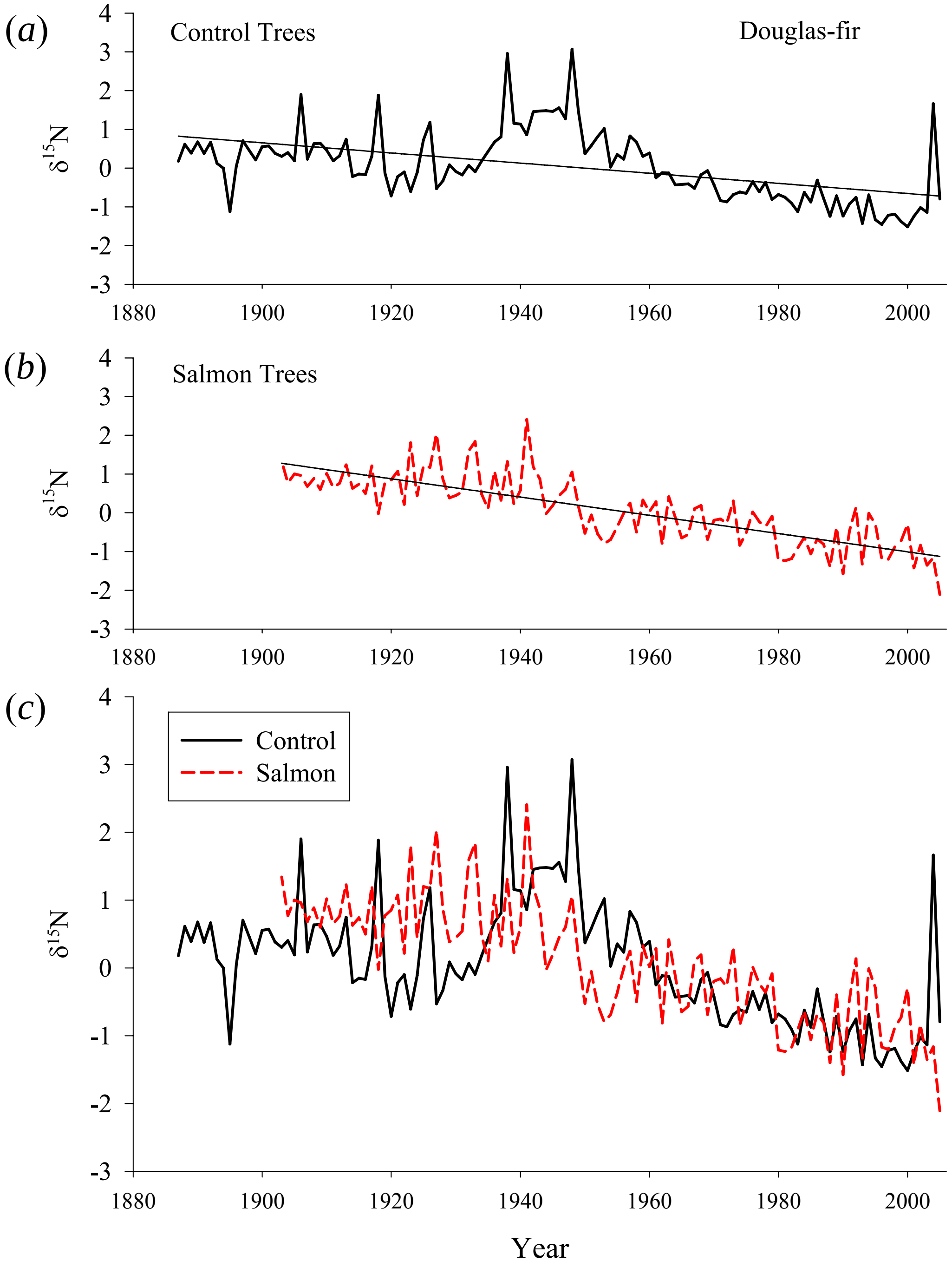

Figure 10. Time series of tree-ring $\delta^{15}N$ for riparian Douglas-fir trees from control (*a*) and salmon influenced (*b*) sites in the Waddell Creek watershed. The bottom graph (*c*) contrasts the two time-series.

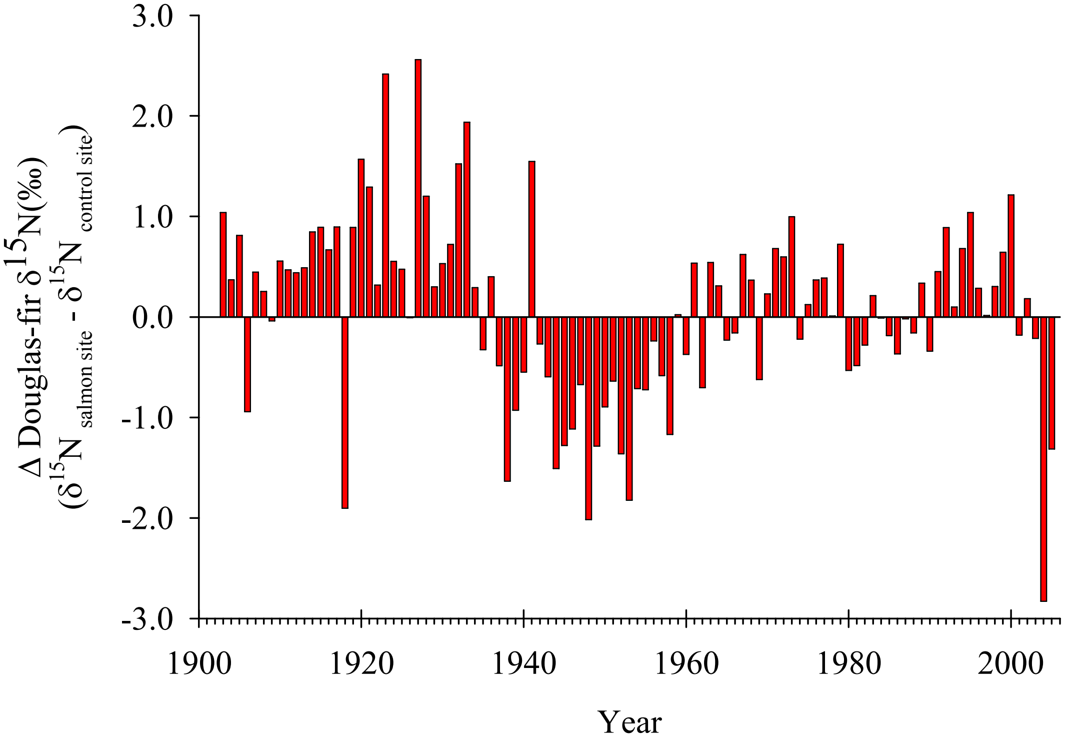

Figure 11. Annual tree-ring δ^{15}N enrichment (+) or depletion (-) for riparian Douglas-fir (*Pseudotsuga menziesii*) trees in the Waddell Creek watershed. Bars represent the mean isotopic difference (‰) between trees growing at salmon influenced and salmon-free (control) sites.

Table 2. Slope (b_1) estimates and 95% confidence intervals (CI) for the linear relationship between riparian Douglas-fir indexed ring width and annual total escapement (coho + steelhead) to Waddell Creek. Analogous estimates were derived for indexed ring-width lagged behind escapement by 0 to 7 years.

Lag (years)	b_1	95% CI	r^2	t
0	0.33	-162.95 to 163.61	0.000	0.996
1	-42.88	-199.55 to 113.80	0.056	0.538
2	31.52	-123.06 to 186.09	0.032	0.644
3	125.00	18.84 to 231.16	0.526	0.027
4	-0.17	-168.54 to 168.19	0.000	0.998
5	-110.74	-250.05 to 28.58	0.335	0.102
6	-71.17	-219.98 to 77.64	0.155	0.295
7	-28.79	-182.82 to 125.13	0.027	0.672

Table 3. Slope (b_1) estimates and 95% confidence intervals (CI) for the linear relationship between riparian Douglas-fir nitrogen concentration ([N]; %) and annual total escapement (coho salmon + steelhead trout) to Waddell Creek. Estimates were derived for [N] lagged behind escapement by 0 to 7 years.

Lag (years)	b_1	95% CI	r^2	t
0	1120.68	-1211.48 to 3452.80	0.156	0.293
1	380.19	-2696.49 to 3456.86	0.012	0.779
2	-44.74	-2189.16 to 2099.68	0.000	0.962
3	2.80	-1551.60 to 1557.24	0.000	0.997
4	-541.02	-1831.00 to 748.98	0.123	0.354
5	-417.15	-1743.39 to 909.08	0.073	0.481
6	-1191.60	-2208.60 to -174.50	0.523	0.027
7	-899.17	-2165.00 to 366.90	0.287	0.137

Table 4. Slope (b_1) estimates and 95% confidence intervals (CI) for the linear relationship between riparian Douglas-fir tree ring $\delta^{15}N$ (‰) and annual total escapement (coho salmon + steelhead trout) to Waddell Creek. Slope estimates were derived for $\delta^{15}N$ lagged behind escapement by 0 to 7 years.

Lag (years)	b_1	95% CI	r^2	t
0	11.38	-214.89 to 237.65	0.002	0.909
1	-124.04	-344.89 to 96.81	0.201	0.226
2	38.47	-211.04 to 287.98	0.019	0.726
3	-92.64	-323.51 to 138.22	0.114	0.374
4	-42.92	-275.27 to 189.42	0.027	0.675
5	-19.50	-256.90 to 217.90	0.005	0.852
6	-37.88	-281.34 to 205.60	0.019	0.742
7	207.79	37.63 to 377.95	0.544	0.023

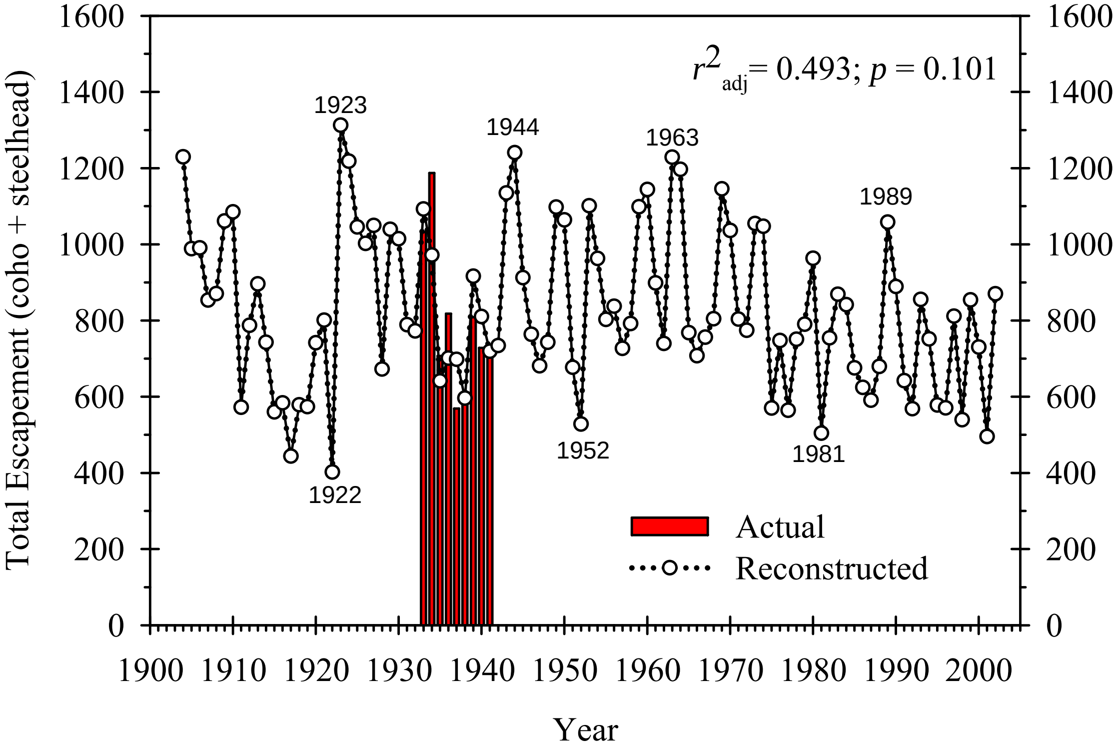

Figure 12. Reconstructed Waddell Creek salmon escapement using annual tree-ring indexed growth, N content (%), and δ^{15}N (‰) as explanatory variables. Bars represent actual escapement counts (coho + steelhead; Shapovalov and Taft 1954) and open circles represent predicted values.

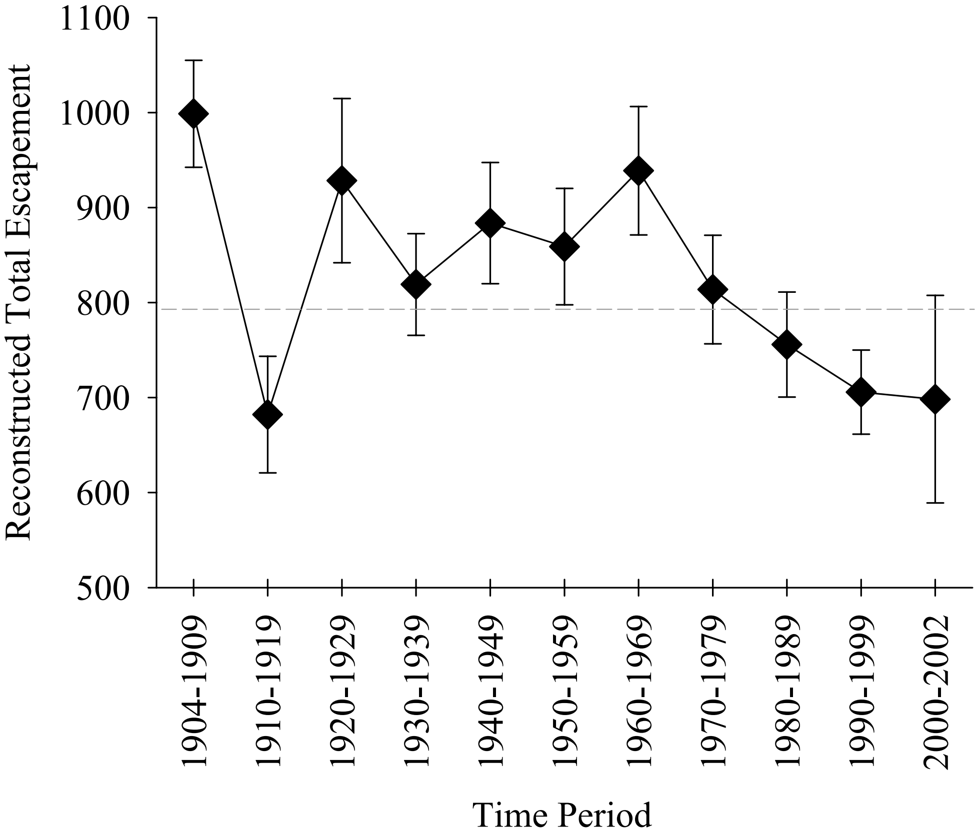

Figure 13. Decadal-scale mean total escapement to Waddell Creek (# coho salmon + steelhead trout) as predicted by the multivariate tree-ring reconstruction. Error bars represent ± 1SEM. The dashed line indicates mean total escapement for the period 1933-1941 as reported by Shapovalov and Taft (1954). Note the first and last data points represent intervals of less than 10 years.

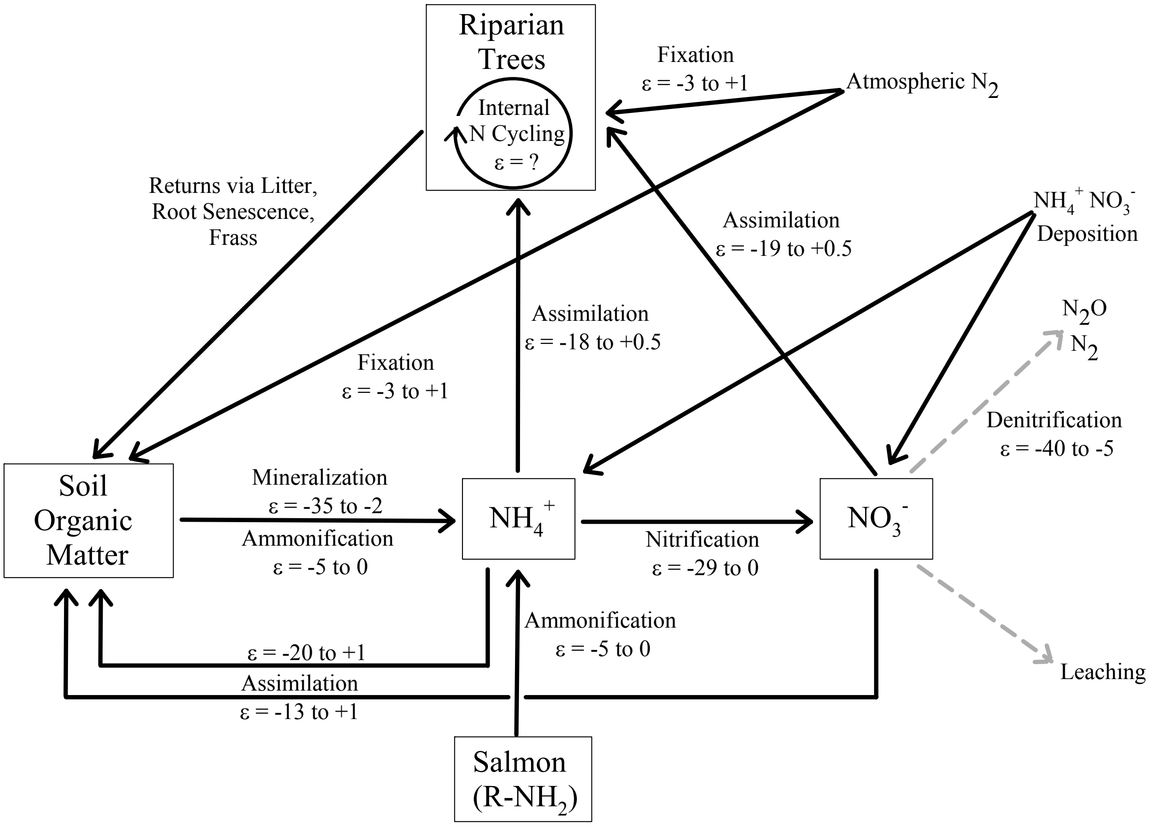

Figure 14. Nitrogen transformations and processes affecting $\delta^{15}N$ values in salmon influenced riparian ecosystems. Fractionation values (ε; $\delta^{15}N_{product} - \delta^{15}N_{source}$) next to each arrow represent the potential range of change in $\delta^{15}N$ (‰) of the product based on published literature. No data are available for fractionation estimates associated with internal translocation and cycling of N by trees. Schematic is modified from Nadelhoffer and Fry (1994).