ARTICLE

Influence of spawning salmon on tree-ring width, isotopic nitrogen, and total nitrogen in old-growth Sitka spruce from coastal British Columbia

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Abstract: Coastal watersheds of the North Pacific benefit immensely from bear-mediated uploading of salmon nutrients, which increases aquatic and terrestrial productivity. To quantify the influence of spawning salmon on tree-ring signatures, we analyzed 543 rings from the heartwood of 13 old-growth Sitka spruce (*Picea sitchensis* (Bong.) Carrière) trees from five geographically separated watersheds in coastal British Columbia. In comparison with adjacent control trees, those receiving salmon nutrients (salmon trees) have rings that are, on average, 1.5 mm wider, 4.5‰ more enriched in isotopic nitrogen, and 0.021% more elevated in total nitrogen ($P < 0.001$, Mann–Whitney–Wilcoxon test). In this study, salmon nutrients enhance average stem growth by 19%. Furthermore, salmon trees show that increases in tree-ring width and nitrogen values lag sporadic, high salmon runs by 0 to 5 years. Using differences between control and salmon trees from the same site, our results collectively indicate that tree-ring width, isotopic nitrogen, and total nitrogen are valid, complementary tools for investigating historic, annual fluctuations in salmon abundance in coastal watersheds. We recommend their use in future, tree ring based reconstructions of past nutrient cycling over decadal to centennial time scales.

Key words: salmon abundance, tree-ring width, nitrogen isotope, total nitrogen, Sitka spruce.

Résumé : Les bassins versants des côtes du Pacifique Nord bénéficient énormément de l'apport de nutriments provenant des saumons que transportent les ours, ce qui accroît la productivité des milieux aquatique et terrestre. Pour quantifier l'influence de la fraie du saumon sur la signature des cernes des arbres, nous avons analysé 543 cernes dans le bois de cœur de 13 vieilles tiges d'épicéa de Sitka (*Picea sitchensis* (Bong.) Carrière) situées dans cinq bassins versants géographiquement séparés sur les côtes de la Colombie-Britannique. Comparativement aux arbres témoins adjacents, les cernes des arbres qui reçoivent des nutriments provenant du saumon (arbres « saumon ») sont en moyenne 1,5 mm plus larges, 4,5 ‰ plus riches en azote isotopique et ont 0,021 % plus d'azote total ($P < 0,001$, test de Mann–Whitney–Wilcoxson). Dans cette étude, les nutriments provenant du saumon amélioraient la croissance moyenne de la tige de 19 %. De plus, les arbres « saumon » montrent que l'augmentation de la largeur des cernes et des quantités d'azote survient 0 à 5 ans après les apports sporadiquement élevés de saumon. En utilisant les différences entre les arbres témoins et les arbres « saumon » dans les mêmes sites, nos résultats indiquent collectivement que la largeur des cernes, l'azote isotopique et l'azote total sont des outils complémentaires valides pour étudier les fluctuations annuelles passées de l'abondance du saumon dans les bassins versants côtiers. Nous recommandons leur utilisation pour les reconstitutions futures à partir des cernes annuels du recyclage passé des nutriments à des échelles décennale et centennale. [Traduit par la Rédaction]

Mots-clés : abondance du saumon, largeur des cernes annuels, isotope de l'azote, azote total, épicéa de Sitka.

Introduction

Each year, Pacific salmon (*Oncorhynchus* spp.) supply nutrients to many coastal ecosystems when returning from the ocean during spawning season, greatly enhancing aquatic and terrestrial productivity (Willson and Halupka 1995; Cederholm et al. 1999). Marine nutrient transfer to riparian soils by foragers such as bears and their uptake by scavengers and riparian vegetation demonstrate ecosystem-level interactions in the marine–terrestrial interface (Hilderbrand et al. 1999; Reimchen 2000, 2017; Mathewson et al. 2003; Wilkinson et al. 2005). Drake and Naiman (2007) presented a repeated pattern of positive correlations between salmon abundance and nonclimatic riparian tree-ring growth of conifers, while noting that tree-ring width (RW) is a relatively conservative proxy to assess the fertilization effects of salmon nutrients on riparian trees. Moreover, the substantial variability in RW among trees

within the same locality subject to the same climatic conditions may not allow capturing of the salmon signal due to preferential investment of nutrients into defense and structure rather than growth. Reimchen et al. (2003) provided evidence that marine nutrient uptake by riparian vegetation produces enriched nitrogen isotope ($\delta^{15}N$) signatures in conifer tree rings, expanding possibilities to investigate historic, annual fluctuations in salmon abundance in coastal watersheds.

Yet, the salmon signal of trees receiving salmon nutrients (salmon trees) has not been systematically isolated from other environmental influences on tree growth such as climate and cambial injury. In a first answer to this limitation, Drake and Naiman (2007) applied the method of differencing to salmon trees and control trees, where the control tree series was rescaled and subtracted from the salmon tree series to extract the salmon signal contained in RW series. Removal of the climate

Table 1. Characteristics of the five salmon watersheds situated in coastal British Columbia.

Watershed	ID	Region	Latitude (N)	Longitude (W)	Escapement Mean	Escapement Range
Browns Cabin Creek	BR	Haida Gwaii	53°07′58″	132°20′53″	15457	108230
Clatse Creek	CL	Midcoast	52°20′08″	127°50′17″	37350	83075
Neekas Creek	NE	Midcoast	52°28′22″	128°09′43″	71748	270000
Salmon River	SA	Haida Gwaii	52°42′14″	131°48′58″	33769	112440
Sedmond Creek	SE	Haida Gwaii	52°12′10″	131°09′19″	10096	46580

Note: Escapement data for the period of 1945–1979 were obtained from Fisheries and Oceans Canada (2018).

signal strengthens the positive relationship between RW and salmon abundance. In another answer to this issue, Reimchen and Fox (2013) highlighted the importance of using appropriate control trees that are matched for size and microsite in comparing RW and δ^{15}N signatures between salmon trees and control trees. Both differencing and appropriate control trees could be useful in studying the salmon signal of salmon trees.

Total nitrogen (TN) is recognized as a measure of primary productivity in trees (Yoder and Pettigrew-Crosby 1995). While foliar TN has been assessed across spatial gradients of salmon carcasses and bear activity (Mathewson et al. 2003; Reimchen 2017), tree-ring TN has rarely been investigated in the marine–terrestrial interface mainly due to the low nitrogen content of wood and its mobility in the stem. Reimchen and Arbellay (2018) have recently provided evidence for substantial intra-annual variability in TN and δ^{15}N values in the heartwood of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) despite past nitrogen translocation. Radial translocation of mobile nitrogen occurs in sapwood rings when parenchyma cells die and lose nitrogen to growing regions (Meerts 2002). Nitrogen translocation may therefore blur temporal δ^{15}N and TN trends associated with environmental factors (Doucet et al. 2011; Gerhart and McLauchlan 2014). Most attempts to resolve this issue have focused on chemical wood pretreatment to remove mobile nitrogen. This approach aims at only analyzing immobile nitrogen, rather than TN; however, wood pretreatment has yielded contrasting results between studies, with no consensus regarding its impact on tree-ring δ^{15}N and TN values (Doucet et al. 2011). Recent studies have concluded that solvent-based extraction is not effective in removing all mobile nitrogen (Bunn et al. 2017) or that wood pretreatment is completely unnecessary (Doucet et al. 2011).

In this study, we measured RW, δ^{15}N, and TN values in 543 rings from the heartwood of 13 old-growth Sitka spruce trees from five geographically separated watersheds in coastal British Columbia. We present annually resolved data for the period of 1945–1979, where salmon escapement is known. Supplementary data were also obtained for the periods of 1910–1926 and 1868–1877, where salmon escapement is unknown. We measured δ^{15}N and TN values in the heartwood of both salmon trees and control trees in an attempt to alleviate the implications of past nitrogen translocation. While we caution that the δ^{15}N and TN values attributed to specific years are not necessarily indicative of the nitrogen acquired during those years, the differences in δ^{15}N and TN values between salmon trees and control trees in those years are relevant. In studying the salmon signal of salmon trees, we used both differencing and control trees that were matched as close as possible for size and microsite. The aims of this research were to (*i*) examine multi-decadal, annual variations in RW, δ^{15}N, and TN values in relation to recorded salmon abundance and (*ii*) discuss the prospects of using these combined tree-ring proxies to extend our historical understanding of short-term and possibly long-term annual variability in nutrient cycling at the marine–terrestrial interface.

Materials and methods

Study sites and sample procurement

The five salmon watersheds of this study are situated in two different regions of coastal British Columbia separated by as much as 400 km. Browns Cabin Creek (Government Creek), Salmon River, and Sedmond Creek are located in Haida Gwaii, whereas Clatse Creek and Neekas Creek are located on the midcoast of mainland British Columbia (Table 1). The two latter systems are characterized by impassable falls at about 1.5 km upstream. Mean escapement between 1945 and 1979 varies from 10 000 salmon at Sedmond Creek to 72 000 salmon at Neekas Creek (Table 1). The range of escapement at a particular location varies from 47 000 salmon (Sedmond Creek) to 270 000 salmon (Neekas Creek). All watersheds are dominated by Chum salmon (*Oncorhynchus keta*) and Pink salmon (*Oncorhynchus gorbuscha*). In such ecosystems, TN input to soils from the combined effects of bear and scavenger activity, as well as carcass input, reaches 18 g·m^{-2} within 10 m of the stream channel (Reimchen 2017). All watersheds are composed of old-growth forest dominated by Sitka spruce, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and red cedar (*Thuja plicata* Donn ex D. Don). The community structure of these forest stands shows a higher incidence of nitrogen-rich soil indicator species within the spawning reaches as a direct result of the influx of salmon nutrients (Mathewson et al. 2003). These old-growth stands have not been affected by forest management practices such as logging or thinning.

The findings of this study are based on 13 Sitka spruce trees (Table 2), including eight salmon trees and five control trees (one at each watershed). Trees were cored with a 12 mm increment borer during a coast-wide field survey of British Columbian riparian vegetation in autumn 1998–2002 (Reimchen et al. 2003). They were categorized as either salmon or control trees based on the potential of bear-mediated transfer of salmon to the riparian zone, as evidenced by the presence or absence of salmon carcasses at the site. Salmon trees are located within the spawning reaches, up to 24 m into the forest (Table 2). By contrast, control trees are located beyond the spawning reaches, i.e., above the falls at Clatse Creek and Neekas Creek, or from 100 to 270 m into the forest at Browns Cabin Creek, Salmon River, and Sedmond Creek. Owing to their impassable falls, Clatse Creek and Neekas Creek are model systems in comparing salmon trees and control trees. In line with Mathewson et al. (2003) and Wilkinson et al. (2005), we aimed to reduce potentially confounding effects of precipitation, substrate, and other abiotic variables at each watershed by making comparisons across a sharp ecological gradient in salmon carcass availability. Moreover, the control tree sampled at each watershed is the closest tree that matched its respective salmon trees for size. At Clatse Creek and Neekas Creek, for instance, the control tree was sampled immediately above the falls, allowing comparisons across a sharp ecological boundary of salmon abundance due to the waterfall barrier to salmon migration.

Table 2. Characteristics of the 13 old growth Sitka spruce trees sampled at the five salmon watersheds.

Tree	Type	MA (years)	DBH (cm)	DF (m)	DM (m)	Slope (°)	Rings analyzed at annual resolution		
BR-1	Salmon	65	124	2	1450	0			1945–1979
BR-2	Salmon	111	198	2	1400	0			1945–1979
BR-0	Control	186	80	150	1500	30			1945–1979
CL-1	Salmon	178	150	22	1050	45	1868–1877	1910–1926	1945–1979
CL-0	Control	148	163	1	1250	45	1868–1877	1910–1926	1945–1979
NE-1	Salmon	238	159	5	2050	45			1945–1979
NE-2	Salmon	60	73	7	1000	10			1945–1979
NE-0	Control	93	100*	1	2200	15			1945–1979
SA-1	Salmon	68	140	11	500	0			1945–1979
SA-2	Salmon	82	121	24	200	0			1945–1979
SA-0	Control	116	78	270	720	45			1945–1979
SE-1	Salmon	105	137	10	650	0		1910–1926	1945–1979
SE-0	Control	98	88	100	250	0		1910–1926	1945–1979

Note: Tree codes contain the ID of the watersheds (see Table 1). Trees were categorized as either salmon or control based on the potential of bear-mediated transfer of salmon to the riparian zone. MA, minimum age; DBH, diameter at breast height (*, estimated); DF, distance into the forest; DM, distance from the mouth of the river.

Sample analysis

Cores were prepared using standard dendrochronological methods (Stokes and Smiley 1996; Supplementary Table S1[1]). We measured RW, δ^{15}N, and TN values in 543 rings in total and focused on the period of 1945–1979, where rings are all part of the heartwood and where salmon escapement is known. Visual inspection of the TN series for each tree showed that the heartwood–sapwood transition varied between 1985 and 1995. At Clatse Creek and Sedmond Creek, supplementary data were also obtained for the periods of 1910–1926 and 1868–1877, where salmon escapement is unknown.

Rings were measured and cross-dated using CooRecorder and CDendro 9.2 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). They were separated for nitrogen analyses using a scalpel blade under the microscope. Each ring was powdered; the powder was packaged in tin capsules (30 mg powder per capsule) and sent to the University of California Davis Stable Isotope Facility for analysis using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Owing to important fertilization of riparian vegetation by spawning salmon (Reimchen et al. 2003), rings (n = 543) were sufficiently wide (3.3 ± 1.7 mm on average) to provide enough material for analysis and maintain annual resolution. In the case of narrow rings (<0.5 mm), two or more sequential years were combined to obtain sufficient mass. TN values represent percentage of total nitrogen, whereas δ^{15}N values were calculated by

$$\delta^{15}\text{N (‰)} = (R_{\text{sample}}/R_{\text{standard}}) - 1$$

where R equals the ratio of ^{15}N/^{14}N stable isotopes. R_{standard} is the ratio of ^{15}N/^{14}N stable isotopes in atmospheric N_2. Repeatability of TN and δ^{15}N values on wood reference samples (n = 135) averaged ±0.012% for TN and ±1.0‰ for δ^{15}N (T.E. Reimchen, unpublished data).

Statistical analysis

A three-year moving average was applied on RW, δ^{15}N, and TN series of salmon trees and control trees. At each watershed, each individual salmon tree was compared with it respective control tree to extract the salmon signal contained in RW, δ^{15}N, and TN series. We used the method of differencing to isolate the salmon signal from other environmental influences on tree growth such as climate and cambial injury. A differential chronology (DF) was produced for each proxy by rescaling and subtracting the series of

the control tree from the series of the salmon tree using the following equation:

$$\text{DF} = S_{\text{salm; year } t} - ((\text{SD}_{\text{salm}}/\text{SD}_{\text{control}})(S_{\text{control; year } t} - M_{\text{control}}))$$

where $S_{\text{salm; year } t}$ is the series of the salmon tree in year t; SD_{salm} and $\text{SD}_{\text{control}}$ are the standard deviations of the salmon series and control series, respectively, for the common period shared by both series; $S_{\text{control; year } t}$ is the series of the control tree in year t; and M_{control} is the mean of the control series for the common period. The RW, δ^{15}N, and TN series that we used consisted of raw data, where no adjustments were employed to account for age trends inherent to time series. Nevertheless, we discuss the conundrum posed by age trends in reconstructing past salmon abundance from tree rings over long time scales.

The Mann–Whitney–Wilcoxon test was used at each watershed to determine whether RW, δ^{15}N, and TN series differed significantly ($P < 0.05$) between each individual salmon tree and its respective control tree for the period of 1945–1979 (Table 3). This nonparametric test is analogous to the t test but is distribution-free (Sprent and Smeeton 2007), providing more robust results when the number of samples is limited. Furthermore, we produced combined bar and line charts plotting spawning salmon numbers and RW, δ^{15}N, and TN values over time (Figs. 1–3). These charts are useful to identify local (timely confined) effects of salmon abundance on tree-ring signatures. Nevertheless, in an effort to also characterize global effects across the 1945–1979 period, we calculated cross-correlations between RW, δ^{15}N, and TN values and spawning salmon numbers for that period using the differential chronologies (Table 4; Supplementary Figs. S1 and S2[1]). We report the strongest significant ($P < 0.05$) correlation (if any) within the lag interval of 0 to 5 years. All data were processed with SPSS 24 (IBM, USA).

Results

Tree-ring signatures differ between salmon trees and control trees. We found that RW, δ^{15}N, and TN values are higher in most salmon trees in comparison with their respective control tree (Figs. 1–3; Table 3). Of the eight salmon trees investigated, five show higher RW values, while seven show higher δ^{15}N and TN values (Table 3). Salmon trees have rings that are, on average, 1.5 mm wider (range: −3.2 to +3.4), 4.5‰ more enriched in ^{15}N (range: −1.1 to +9.1), and 0.021% more elevated in TN (range: −0.001 to +0.060). As an illustration, the salmon tree BR-2 displays ele-

Table 3. Differences in tree-ring width (RW), isotopic nitrogen (δ^{15}N), and total nitrogen (TN) values between salmon trees and control trees.

Tree	Type	RW (mm)			δ^{15}N (‰)			TN (%)		
		Mean ± SD	Diff.	P value	Mean ± SD	Diff.	P value	Mean ± SD	Diff.	P value
BR-1	Salmon	5.9±1.4	+3.4	<0.001	−1.4±0.6	−1.1	<0.001	0.052±0.006	+0.002	0.001
BR-2	Salmon	3.5±0.6	+1.0	<0.001	1.8±0.7	+2.1	<0.001	0.066±0.009	+0.017	<0.001
BR-0	Control	2.5±0.7			−0.3±0.8			0.050±0.004		
CL-1	Salmon	1.4±0.3	−0.9	<0.001	5.1±0.8	+6.3	<0.001	0.056±0.009	+0.002	0.438
CL-0	Control	2.3±0.3			−1.3±0.9			0.054±0.007		
NE-1	Salmon	1.4±0.5	−3.2	<0.001	6.3±1.2	+9.1	<0.001	0.078±0.010	+0.034	<0.001
NE-2	Salmon	5.1±1.4	+0.5	0.061	3.3±1.0	+6.0	<0.001	0.043±0.002	−0.001	0.016
NE-0	Control	4.6±1.1			−2.7±0.7			0.044±0.001		
SA-1	Salmon	2.9±0.7	+0.8	0.001	7.0±0.5	+3.9	<0.001	0.074±0.007	+0.007	<0.001
SA-2	Salmon	3.8±0.8	+1.7	<0.001	5.0±1.0	+1.9	<0.001	0.092±0.004	+0.024	<0.001
SA-0	Control	2.1±1.1			3.1±1.0			0.068±0.003		
SE-1	Salmon	3.2±1.3	−2.3	<0.001	−4.2±0.9	+2.5	<0.001	0.119±0.034	+0.060	<0.001
SE-0	Control	5.5±0.7			−6.6±1.5			0.059±0.012		
Mean			+1.5			+4.5			+0.021	

Note: Tree codes contain the ID of the watersheds (see Table 1). The Mann–Whitney–Wilcoxon test was used at each watershed to compare RW, δ^{15}N, and TN series between each individual salmon tree and its respective control tree for the period of 1945–1979. SD, standard deviation; Diff., difference.

vated RW, δ^{15}N, and TN signatures in comparison with the control tree BR-0 (Fig. 2), where values are higher by 1.0 mm, 2.1‰, and 0.017%, on average, for the period of 1945–1979 (Table 3). Similarly, at a different watershed, the salmon tree SA-2 also displays elevated RW, δ^{15}N, and TN signatures in comparison with the control tree SA-0 (Fig. 2), where values are higher by 1.7 mm, 1.9‰, and 0.024%, on average (Table 3). Differences in tree-ring signatures between salmon trees and control trees are mostly highly significant ($P < 0.001$).

Salmon trees show that RW, δ^{15}N, and TN values can be moderately to strongly correlated with spawning salmon numbers, with a lag of 0 to 5 years (Table 4; Supplementary Figs. S1[1] and S2[1]). Of 13 significant ($P < 0.05$) correlations, eight are positive ($r = 0.39$ to 0.64) and five are negative ($r = −0.39$ to −0.78). Nevertheless, as previously noted, these results represent global trends across the 1945–1979 period and, as such, should be interpreted with caution. They facilitate the identification of local (timely confined) effects of salmon abundance on tree-ring signatures presented in the charts (Figs. 1–3).

Salmon abundance at Clatse Creek displays two salmon pulses (sporadic, high salmon runs), in the 1950s and in the mid-1960s (Fig. 1). Overall, the differential RW and TN chronologies follow spawning salmon numbers more adequately (significant correlations, no lags) than the differential δ^{15}N chronology (no significant correlation) (Fig. 1; Table 4). Hence, the late 1910s peak in the differential RW and TN chronologies may be indicative of high salmon runs around that period. The differential δ^{15}N chronology shows a lagged increase after the salmon pulse of the 1950s but not after that of the mid-1960s, which likely prevented any significant correlation between δ^{15}N values and spawning salmon numbers. It is thus possible that the mid-1920s peak in the differential δ^{15}N chronology corresponds to a lagged response to the high salmon runs of the late 1910s.

Similarly to Clatse Creek, salmon abundance at Browns Cabin Creek, Neekas Creek, and Salmon River also displays salmon pulses in the 1950s and in the mid-1960s (Figs. 1 and 2). The differential chronologies at these watersheds further illustrate that tree-ring signatures can relate to salmon abundance in several manners. They may show a lagged response after each salmon pulse, as in the RW increases of NE-1 and NE-2 (Fig. 1). They may show a lagged response after one salmon pulse but not after the other, as in the RW increases of SA-1 and SA-2 (Fig. 2). Notwithstanding inherent lags, they may follow the envelope of salmon abundance closely (each salmon pulse), as in the δ^{15}N values of NE-2 or the TN values of BR-1, or only partially (one salmon pulse but not the other), as in the TN values of NE-1 and NE-2 (Figs. 1 and

2). The representative power of each proxy therefore varies among trees and among years.

Salmon abundance at Sedmond Creek is markedly high in the mid-1960s, with as much as three times the average number of spawning salmon (Fig. 3). Overall, the differential RW, δ^{15}N, and TN chronologies follow spawning salmon numbers with little success (no significant correlations) (Fig. 3; Table 4). Nevertheless, the differential RW chronology matches the salmon pulse of the mid-1960s. It is thus difficult to determine whether the early 1920s peak in the differential RW and TN chronologies is indicative of high salmon runs around that period.

Discussion

Tree-ring signatures

In comparison with adjacent control trees, salmon trees have higher RW, δ^{15}N, and TN signatures, which can be accounted for by their higher exposure to spawning salmon carcasses due to their closer proximity to spawning grounds. Salmon carcasses provide nutrient pulses of nitrogen and phosphorus to riparian vegetation through their decomposition (Naiman et al. 2002), thereby influencing the nitrogen cycle and increasing the annual growth of Sitka spruce and other coastal conifers (Drake et al. 2002, 2011; Drake and Naiman 2007; Reimchen and Fox 2013; Starheim et al. 2013).

Enhanced stem growth in salmon trees following nitrogen addition may relate to increased needle area and, thereby, increased canopy-level photosynthesis (Krause et al. 2012a). Although phosphorus is much less abundant in salmon carcasses compared with nitrogen (Naiman et al. 2002), it may co-influence stem growth by increasing nitrogen uptake and photosynthetic efficiency (Blevins et al. 2006). At the same time, elevated TN and δ^{15}N values in tree rings of salmon trees may increase demands for phosphorus due to the need of plants to rebalance stoichiometric relations (Ågren 2008) but lead to continuous nitrogen uptake due to their inability to only assimilate the most limiting nutrient (Mayor et al. 2015). In line with our findings, Gerhart and McLauchlan (2014) highlighted that experimental fertilization studies often report ^{15}N enrichment in stem wood following nitrogen addition but, unlike the present study, often do not report a similar increase in TN.

Some salmon trees presented lower RW, δ^{15}N, and TN signatures in comparison with their respective control tree. Equivalent or reduced stem growth in salmon trees despite nitrogen and phosphorus additions may reflect limited salmon nutrient fertilization or preferential investment of nutrients into defense and structure rather than growth (Mayor et al. 2015; Heuck and Spohn

Fig. 1. Relationships between tree-ring proxies and salmon abundance at Clatse Creek and Neekas Creek. Salmon series are given in red (thick, solid line) (CL-1, NE-1 and NE-2), control series are in blue (solid line) (CL-0 and NE-0), and differential chronologies are in black (dashed line). All are three-point moving average series. Escapement data were obtained from Fisheries and Oceans Canada (2018). Data are only available starting in 1950 at these two watersheds. [Colour online.]
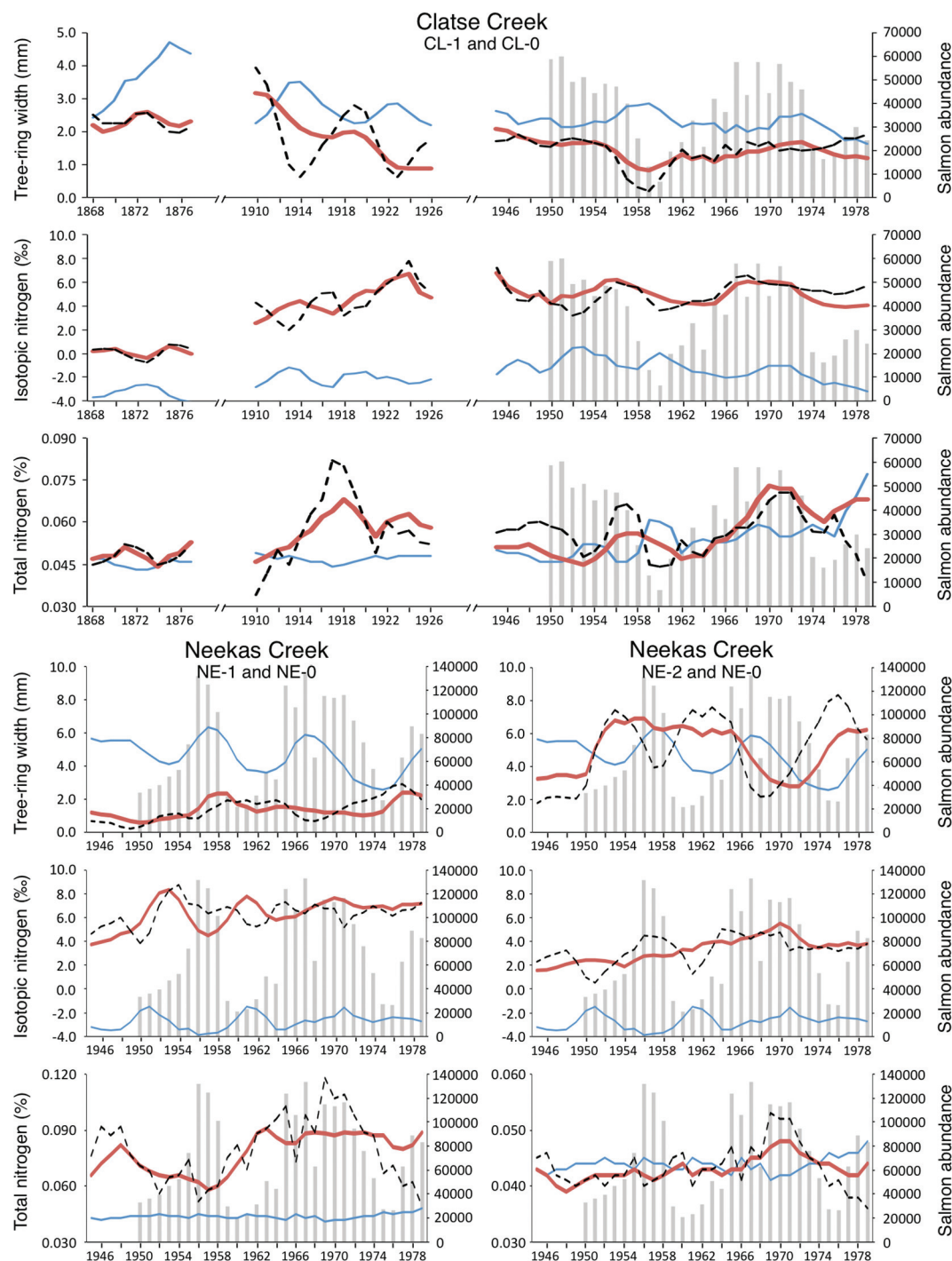
2016). Nitrogen fertilization may also increase mortality of primary roots, thereby decreasing nutrient uptake for growth (Gill and Lavender 1983). Low δ^{15}N or TN signatures in salmon trees may also be explained by limited salmon nutrient fertilization, notably due to their location on steeper terrains where nutrients were likely scoured by runoff. Moreover, low δ^{15}N values in tree rings of salmon trees may be symptomatic of a nitrogen-saturated soil, as suggested for low δ^{15}N values in foliar tissues of plants growing in salmon carcass zones (Reimchen 2017). Plants will dis-

criminate against ^{15}N when nitrogen supply exceeds requirements, and as a result, their tissues will be depleted in the heavy isotope (Nadelhoffer and Fry 1994).

Tree-ring signatures and salmon abundance

Salmon abundance greatly differs among watersheds, within watersheds (e.g., above vs. below falls), and among years at each watershed. Sporadic, high salmon runs between 1945 and 1979 at our watersheds mostly relate to fishing closures and favorable

Fig. 2. Relationships between tree-ring proxies and salmon abundance at Browns Cabin Creek and Salmon River. Salmon series are given in red (thick, solid line) (BR-1, BR-2, SA-1 and SA-2), control series are in blue (solid line) (BR-0 and SA-0), and differential chronologies are in black (dashed line). All are three-point moving average series. Escapement data were obtained from Fisheries and Oceans Canada (2018). [Colour online.]
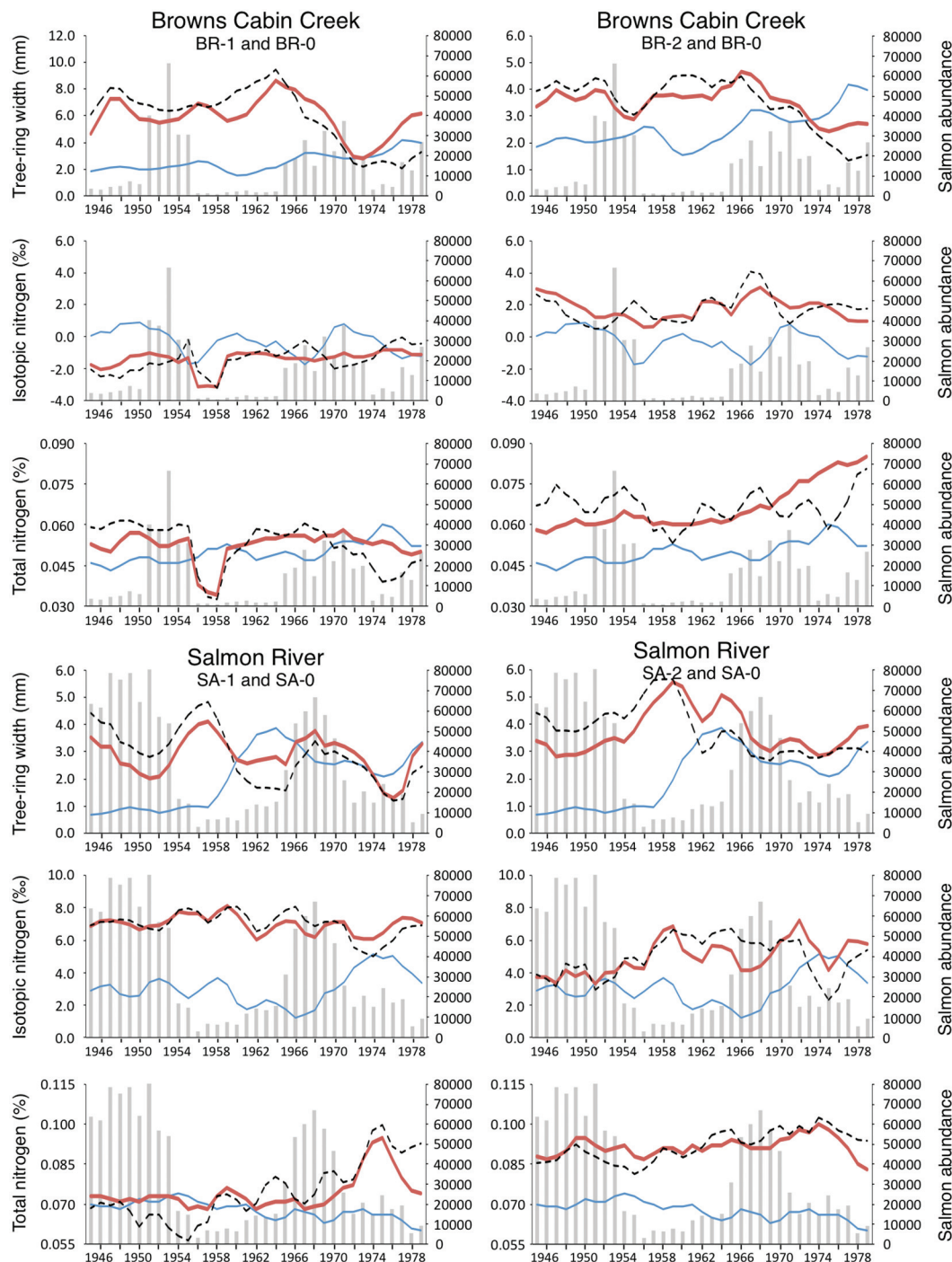

water conditions during spawning season (Marshall et al. 1978a, 1978b; Manzon and Marshall 1981). Inversely, low salmon runs could result from heavy fishing, reduced oceanic survival, or unusually low or high stream water levels.

Salmon trees show that increases in RW, δ15N, and TN values lag sporadic, high salmon runs by 0 to 5 years. In particular, the fact that elevated δ15N values in tree rings of salmon trees are concomitant with salmon pulses at Clatse Creek and Neekas Creek, our two model systems, greatly supports 15N enrichment of trees

through salmon nutrient fertilization rather than by denitrification (Pinay et al. 2003). In agreement with our results, previous studies have reported that salmon abundance and associated salmon nutrient fertilization enhance stem growth of Sitka spruce in the year of escapement (no lag) and (or) in the year following escapement (1-year lag), while longer lags of 2 to 6 years were also observed (Drake et al. 2002; Drake and Naiman 2007; Starheim et al. 2013). Because salmon spawning predominantly occurs in late summer and early fall in coastal British Columbia (Marshall et al.

Fig. 3. Relationships between tree-ring proxies and salmon abundance at Sedmond Creek. Salmon series are given in red (thick, solid line) (SE-1), control series are in blue (solid line) (SE-0), and differential chronologies are in black (dashed line). All are three-point moving average series. Escapement data were obtained from Fisheries and Oceans Canada (2018). [Colour online.]
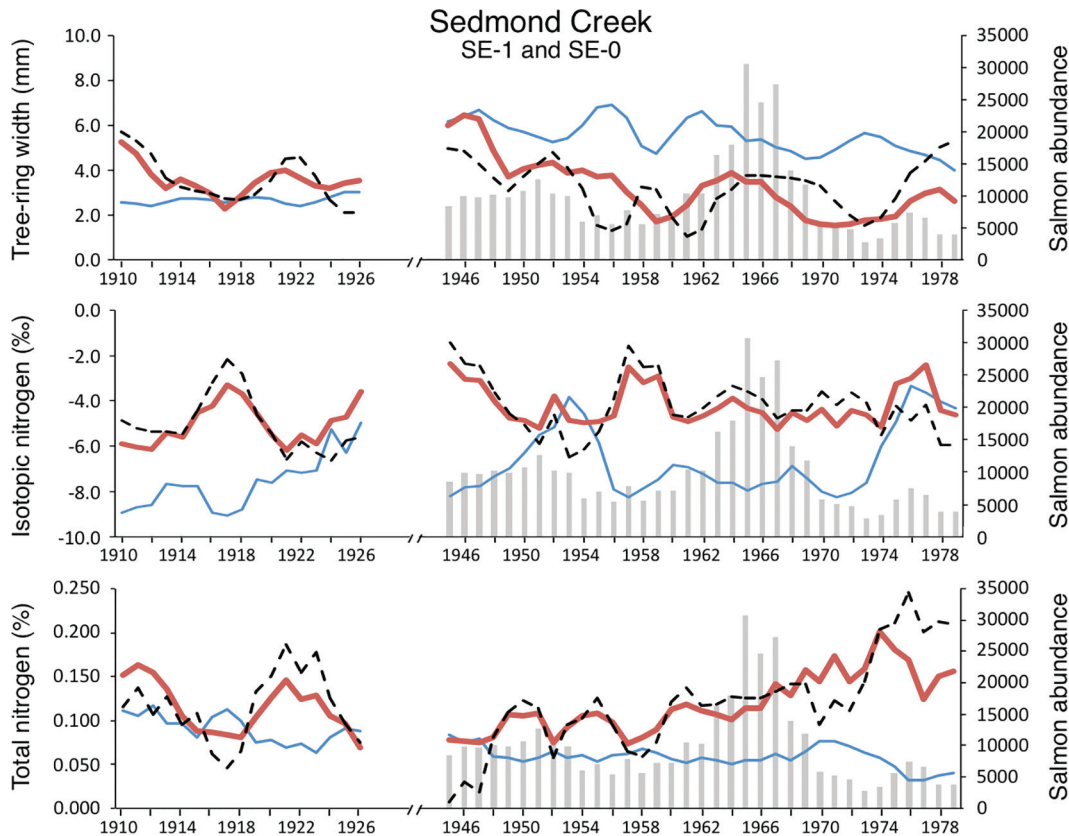
Table 4. Cross-correlations between tree-ring proxies and salmon abundance.

		RW–SA		δ^{15}N–SA		N–SA	
Tree	Type	Corr. (r)	Lag (years)	Corr. (r)	Lag (years)	Corr. (r)	Lag (years)
BR-1	Salmon	−0.30	2	**−0.42**	**5**	**−0.78**	**5**
BR-2	Salmon	−0.29	2	−0.29	5	**0.43**	**1**
CL-1	Salmon	**0.41**	**0**	0.28	1	**0.51**	**0**
NE-1	Salmon	**0.41**	**5**	−0.32	5	**0.39**	**2**
NE-2	Salmon	**−0.76**	**1**	**0.64**	**0**	**0.55**	**2**
SA-1	Salmon	**0.48**	**5**	−0.22	5	**−0.39**	**3**
SA-2	Salmon	0.31	5	**−0.49**	**5**	−0.36	5
SE-1	Salmon	0.25	1	0.14	5	−0.22	5

Note: Tree codes contain the ID of the watersheds (see Table 1). Cross-correlations (Corr.) were calculated between tree-ring width (RW), isotopic nitrogen (δ^{15}N), and total nitrogen (TN) values and spawning salmon numbers (SA) for the period of 1945–1979 using the differential chronologies. We report the strongest correlation within the lag interval of 0 to 5 years. Significant ($P < 0.05$) correlations are given in bold type.

1978a, 1978b; Manzon and Marshall 1981), salmon nutrients most likely influence tree-ring signatures in the following year owing to the inherent seasonality of nitrogen cycling (Millard and Grelet 2010). In Sitka spruce, little nitrogen is stored in wood late in the growing season (Reimchen and Arbellay 2018) due to overwinter storage of nitrogen in foliage (Millard and Proe 1992). In the following year, added nitrogen to coniferous species primarily serves needle growth and photosynthesis, while stem growth is enhanced only in subsequent years (Drake et al. 2006). This may account for the lagged increases in RW and δ^{15}N values that we often observed after salmon pulses, as trees continue to accumu-

late added nitrogen from a given year for at least a decade thereafter (Nadelhoffer et al. 2004; Krause et al. 2012b). Moreover, we cannot exclude past nitrogen translocation as a potential cause of the lags observed.

Prospective modeling of past salmon abundance

In the light of our findings for the period of 1945–1979, we discuss the prospects of modeling past salmon abundance by means of annual variations in RW, δ^{15}N, and TN values to extend escapement records back in time. Tree ring based reconstructions of past salmon abundance (Drake et al. 2002; Drake and Naiman 2007; Starheim et al. 2013) are scarce despite the potential of tree rings to provide insights into salmon population dynamics over centennial time scales. In an attempt to model past salmon abundance, we produced specific indices that we refer to as differential chronologies, which were calculated at each watershed and for each proxy through comparison of each individual salmon tree with its respective control tree. Differential chronologies indicate RW, δ^{15}N, and TN values associated with salmon nutrient fertilization alone, which can lie above or below the original values attributable to all environmental factors together (salmon nutrient fertilization, as well as climate and cambial injury). Differencing was first used to assess changes in RW imputable to air pollution (Nash et al. 1975). The method was then applied to changes in RW related to insect defoliation (Swetnam et al. 1985). Drake and Naiman (2007) were first to use differencing to isolate the salmon signal in RW series, showing that removal of the climate signal strengthens the positive relationship between RW and salmon abundance. Capitalizing on this finding, we introduce differencing as a generalized method also applicable to nitrogen values. Because salmon trees are theoretically subject to the same climate forcing as control trees, the fertilization effects of salmon nutri-

ents can be weakened or muted in the RW, δ¹⁵N, and TN series of salmon trees by climate variations of the opposite sign (Figs. 1–3). We therefore recommend the differencing method in modeling past salmon abundance using these tree-ring proxies.

The RW, δ¹⁵N, and TN series that we used consisted of raw data, where no adjustments were employed to account for age trends inherent to time series. The standardization procedure for detrending tree-ring data, i.e., removing age trends through the fitting of a line of best fit (Cook and Kairiukstis 1990), may obscure temporal trends by removing low-frequency variations and reducing data variability (Esper et al. 2003; McCarroll and Loader 2004). Age detrending may remove the low-frequency signal related to historic salmon decline and have reconstructions underestimate salmon abundance in early years (Drake and Naiman 2007). Given the high spatiotemporal variability in salmon escapement at our watersheds, we chose to analyze raw (nondetrended) data to capture high-frequency and low-frequency variations in RW, δ¹⁵N, and TN values associated with salmon nutrient fertilization. Age-related variations translate into low-frequency variations because they are systematic and persistent over time (Esper et al. 2003). Age detrending corrects the systematically lower RW values and systematically higher δ¹⁵N values of biologically younger rings but, at the same time, eliminates any low-frequency variations attributable to salmon nutrient fertilization. Unless future tree ring based models aim at only capturing high-frequency variations caused by overspawning, we advise preserving as much low-frequency variability as possible. In that regard, the regional curve standardization method used in climate reconstructions may be worth exploring (Esper et al. 2003).

In addition to age trends, size trends have been shown to influence tree-ring δ¹⁵N signatures in trees fertilized by salmon nutrients (Reimchen and Fox 2013) and avian nutrients (Reimchen et al. 2013), with δ¹⁵N values being often higher in large-diameter trees. These two studies corrected δ¹⁵N values either through linear regression of tree size and δ¹⁵N values of all trees (Reimchen and Fox 2013) or standardization of δ¹⁵N values to the smallest tree (a sapling) (Reimchen et al. 2013). It was not possible to use either method of size detrending in this study due to the limited number of trees at each site and the unavailability of sapling data; however, we stress that future models need to account for the covariance of δ¹⁵N values with tree size, unless they are based on trees of similar size. The underlying reason may be that large-diameter trees with their more developed root system have access to increased nitrogen sources in the deeper soil (Koopmans et al. 1997) and, as a result, display higher δ¹⁵N signatures than small-diameter trees.

Conclusions

In comparison with adjacent control trees, salmon trees have rings that are, on average, 1.5 mm wider, 4.5‰ more enriched in ¹⁵N, and 0.021% more elevated in TN. In this study, salmon nutrients enhance average stem growth by 19%. Furthermore, salmon trees show that increases in RW, δ¹⁵N, and TN values lag sporadic, high salmon runs by 0 to 5 years. Using the differences between control and salmon trees from the same site, our results collectively indicate that RW, δ¹⁵N, and TN are valid, complementary tools for investigating historic, annual fluctuations in salmon abundance in coastal watersheds; however, because the representative power of each proxy varies among trees and among years, they are complementary tools. We recommend their use in future tree ring based reconstructions of past salmon abundance over decadal to centennial time scales. In that regard, isolating the salmon signals from other environmental trends, as well as from biological trends related to tree age and size, remains a key issue to address to increase confidence in the models.

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