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The carcass zone: salmon contribution to tree rings in old-growth Sitka Spruce (*Picea sitchensis*) throughout coastal British Columbia

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Abstract

The contribution of Pacific salmon to riparian forest biodiversity is widely recognized, yet the direct influence on conifer annual growth rings is less well-established. I examined broad spatial and temporal trends (1945–1999) in ring width, basal area increments (BAI), and nitrogen signatures in heartwood rings of 282 old-growth riparian Sitka Spruce (*Picea sitchensis*; average age ~300 years) from 79 watersheds in three regions of coastal British Columbia. Several large yearly fluctuations in salmon biomass entering streams were positively but weakly correlated with tree growth, lagged one to four years. General linear models indicate that tree age and salmon carcass proximity were the major growth predictors, while tree distance to stream and riparian slope were not significant. Average annual BAI (marginal means) in carcass zones were 80%, 150%, and 55% higher than adjacent control sites on the Mainland, Mid-coast Islands, and Haida Gwaii, respectively. Nitrogen isotope signatures ($\delta^{15}N$) in heartwood rings ranged from –8.6‰ to 8.0‰ and were about 3‰ higher in carcass trees than control trees. Total nitrogen (TN) ranged from 0.03% to 0.15% and was largely independent of salmon carcass occurrence. Bivariate plots ($\delta^{15}N$ against TN) indicate a geographical clustering of elevated TN in Haida Gwaii watersheds, lower $\delta^{15}N$ and TN in the Mid-coast Islands, and elevated $\delta^{15}N$ and TN in watersheds with exceptionally high salmon carcass transfer and bear activity. These cumulative data robustly quantify accentuated conifer growth from salmon-derived nutrients in riparian zones that are largely independent of climatic influences and tree age.

Key words: Basal area increment; old-growth; *Oncorhynchus*; ring width; riparian zone; salmon carcass; Sitka Spruce; stable isotopes; total nitrogen; *Ursus*

Introduction

The temperate rainforests of western North America are a globally unique ecosystem characterized by high biodiversity and high plant biomass and include some of the largest conifers on the planet (Orians and Schoen 2013). While precipitation and maritime climate contribute to the productivity of these ancient forests, marine-derived nutrients, including salmon (*Oncorhynchus* spp.), Pacific Herring (*Clupea pallasii*), and shellfish can be transferred by predators and scavengers into the riparian zone. This is known to increase productivity and biodiversity in select localities (Ben-David *et al.* 1998; Cederholm *et al.* 1999; Hilderbrand *et al.* 1999; Reimchen 2000; Helfield and Naiman 2001; Drake *et al.* 2002, 2011; Hocking and Reynolds 2012; Fox *et al.* 2014; Trant *et al.* 2016; Cox *et al.* 2020).

In coastal British Columbia, nutrient studies in riparian zones have focussed on sharp spatial gradients in salmon-derived nutrients such as below and above waterfalls that are impassable to salmon. These studies show differences in plant species assemblage above and below falls (Mathewson *et al.* 2003; Wilkinson *et al.* 2005) as well as corresponding differences in marine-derived nitrogen isotope signatures in diverse taxa of soil invertebrates (Hocking and Reimchen 2002; Hocking *et al.* 2009) and in songbirds (Christie and Reimchen 2008). Tree ring analyses also show salmon isotopic signatures (Reimchen *et al.* 2003), with a 19% to 30% greater annular growth in the presence of salmon nutrients (Reimchen and Fox 2013; Reimchen and Arbellay 2019). These results are relevant to understanding primary productivity in old-growth coastal forests but need to be given a broader geographical context.

In the current study, 79 watersheds from throughout coastal British Columbia (Mainland, Mid-coast Islands, Haida Gwaii) with old-growth Sitka Spruce (*Picea sitchensis* (Bongard) Carrière) were surveyed. In each watershed, tree cores were taken from the

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largest spruce trees adjacent to spawning gravels and from adjacent trees as control. I quantified annual ring width and basal area increment (BAI) over five decades (1945–1999) and isotopic nitrogen ($\delta^{15}N$) and total nitrogen (TN) during two time blocks (1950–1954, 1975–1979) on a subset of cores. The early time block comprises the first years when salmon counts were obtained for most streams (NuSEDS 2019), while the second time block corresponds to the outer edge of the heartwood and does not include the sapwood in which nitrogen levels greatly increase (Reimchen and Fox 2013; Reimchen and Arbellay 2019). These attributes are assessed in relation to tree size (diameter at breast height [DBH]), tree age, yearly salmon biomass entering the river, presence or absence of salmon carcasses, distance of the focal trees from the stream, and slope of the riparian zone. The results provide direct quantification of the contribution of salmon-derived nutrients to yearly growth rings of old-growth Sitka Spruce among and within watersheds throughout coastal British Columbia.

Methods

Study sites and sample collection

Surveys of 94 watersheds in coastal British Columbia were undertaken from 1999 to 2008 (Mainland, $n = 55$; Mid-coast Islands, $n = 23$; Haida Gwaii, $n = 16$) during the September and October salmon spawning season. Edaphic features for these sites are reported in Reimchen *et al.* (2003). I excluded 15 of these watersheds because there was evidence for historical logging in the vicinity of riparian old-growth Sitka Spruce (hereafter referred to as “spruce”). This left 79 watersheds for sampling (Figure 1, Table S1); three of these had no spawning salmon due to impassable waterfalls at the river mouth and the remaining had populations of spawning salmon. Depending on availability, up to six of the largest spruce were selected for coring; this included trees immediately adjacent to spawning gravels, usually within 50 m of the stream which characterizes the zone of carcasses. I also chose a control tree and for this, I typically walked about 50 m further into the forest beyond the

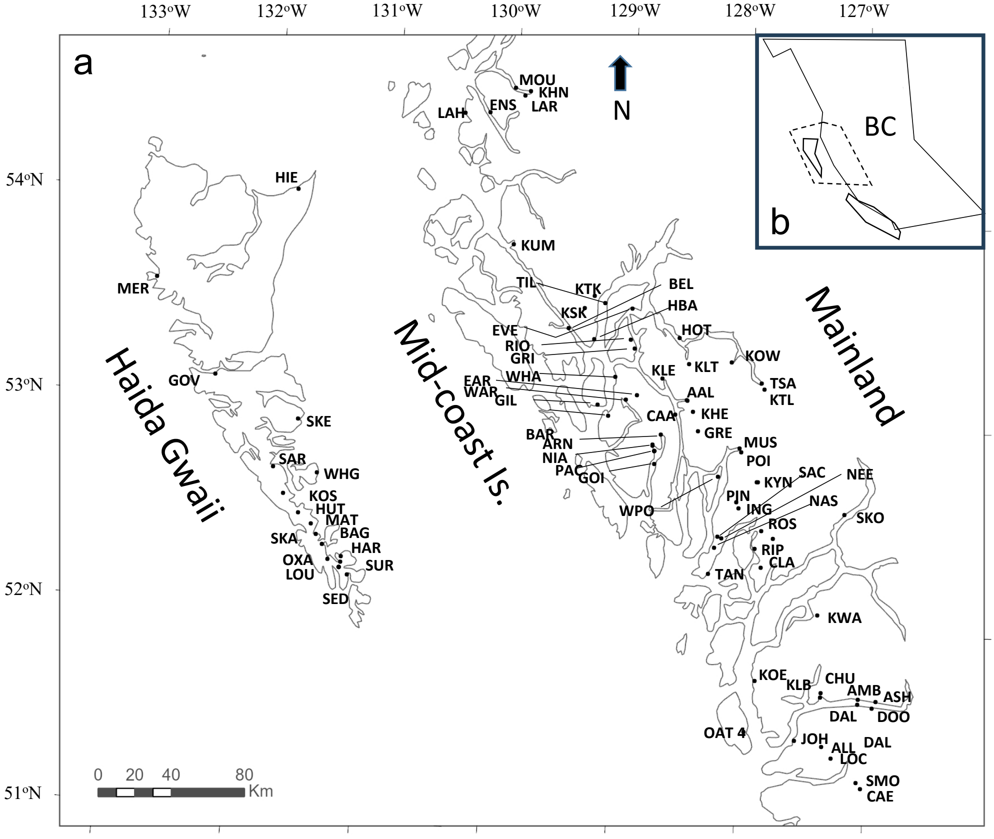

FIGURE 1. a. Watersheds surveyed in coastal British Columbia to examine the relationship between salmon carcasses and Sitka Spruce (*Picea sitchensis*) growth. Full locality names and number of Sitka Spruce trees used in tree ring analyses are listed in Table S1. b. Outline of British Columbia (BC) and study area (in dashed line).

last carcass and chose the largest spruce for coring. In the three watersheds with impassable waterfalls, the largest riparian trees immediately above the waterfalls and adjacent to the stream were cored. Obtaining cores from trees in close proximity to each other with and without exposure to salmon-derived nutrients largely removed the correlated influences of climatic factors such as rainfall and temperature.

For all trees, distance to the stream (± 1 m; DISTFOR), riparian slope (SLOPE), and presence/absence of salmon carcass remnants (CARCASS) in the vicinity of the tree were recorded. The carcasses largely originate from the foraging activities of bears (Reimchen 2000) although other taxa including marten (*Martes* spp.), river otter (*Lutra* spp.), and wolves (*Canis* spp.) can also be vectors (Ben-David *et al.* 1998; Darimont *et al.* 2003; Reimchen 2017). Most salmon carcasses occur within 20 m of the stream with occasional carcasses up to 50 m because bears prefer to maintain visual contact with stream activity, particularly that of other bears (Reimchen 2000, 2017; Reimchen and Fox 2012). I scored three categories of CARCASS for each target tree as (1) carcass-near: carcass remnants present within 10 m of the trunk; (2) carcass-far: no carcasses visible (visibility usually ~10 m) from the target tree but present at nearby trees; and (3) control: no evidence of carcass remnants. My replicated yearly surveys at Bag Harbour, Haida Gwaii, showed that fresh bony remnants are generally overgrown with mosses by the following year but occasionally I found old jaws with moss growth from previous years. Categories 1 and 2 are referred to as the "carcass zone". The method is described more fully in Reimchen (2000).

As a proxy for historical salmon abundance, I used databases of spawning salmon (NuSEDS 2019). For each stream, I used yearly adult salmon abundance and calculated total biomass (SALMBIO) using average biomass of each species (pink: *Oncorhynchus gorbuscha*, 2.2 kg; chum: *Oncorhynchus keta*, 3.0 kg; sockeye: *Oncorhynchus nerka,* 2.7 kg; coho: *Oncorhynchus kisutch*, 3.2 kg; chinook: *Oncorhynchus tshawytscha,* 13.6 kg; Groot and Margolis 1991). Average salmon biomass (kg ± SD) per stream (1950–1998) differed among regions (Mainland, 73 800 kg ± 75 000; Mid-coast Islands, 16 000 ± 16 000; Haida Gwaii, 37 800 ± 32 000, ANOVA on square root normalized SALMBIO, $F_{2,72} = 9.2$, $P < 0.001$).

Tree circumference was measured at breast height (150 cm) and converted to DBH. Using a 1.2 × 40 cm increment borer, one or two cores were extracted from each tree, excluding dead trees as well as those with a noticeable lean. I chose the cleanest core if two were taken. Average core length was 34 cm (range 7–40 cm). Four to six trees were cored in most watersheds.

Cores were prepared using standard dendrochronological methods (see Reimchen and Fox 2013). They were dried for a minimum of three weeks at 60°C, then transferred to a grooved board and smoothed using a progression from coarse to fine grit sandpaper, following which the cores were placed in individual PVC troughs and then scanned at 720 dpi. Cores that were broken, or had growth anomalies from branch whorls or decay, were excluded. Rings (1945–1999) on 502 trees were measured and cross-dated using CooRecorder and CDendro 9.2 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). I did not determine the repeatability of the ring width (RW) measurements because these were done directly from the CooRecorder software that defines the rings and the distances between them. I cross-referenced multiple ring measurements from the software directly under the microscope and the software measurements were either the same or more consistent than my own.

I determined BAI using:

$$\mathrm{BAI} = \pi\, r^2_{\mathrm{i}} - \pi\, r^2_{\mathrm{i}-1}$$

where r_{i} is the tree radius at the end of the annual increment and $r_{\mathrm{i}-1}$ the radius at the beginning of the annual increment which partially corrects for tree size effects (Dietrich and Anand 2019). To obtain nitrogen data, individual rings were removed (detailed method in Reimchen and Fox 2013). In the current study, for each of 234 trees, I processed 10 heartwood rings covering the years 1950–1954, the earliest period where salmon abundance is known for most watersheds, and 1975–1979, the latest period within the heartwood prior to the transition to sapwood where nitrogen levels greatly increase (Reimchen and Fox 2013). Each of the rings was powdered and 30 mg packaged in tin capsules. In trees with very small growth, occasionally two adjacent rings were combined to yield sufficient volume. Isotopic data were extracted at the University of California Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, United Kingdom). Total nitrogen (TN) values represent percentage of total nitrogen in the wood sample, whereas δ^{15}N‰ values were calculated by:

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

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 (average of the raw mean differences between the two replicates) on wood reference samples ($n = 135$) averaged ± 0.012% and ± 1.0‰, respectively (Reimchen *et al.* 2003).

Because of the large size of most trees, few of the cores reached the pith and this limited direct aging. As a result, tree age (AGE) was extrapolated for these larger trees based on Altman *et al.* (2016):

$$AGE = N + (GR - PCL - MBW) / MRW$$

where N is the number of annular rings visible on the core, GR is the geometric radius of the tree (mm), PCL is partial core length (mm), MBW is the width of the bark (mm), and MRW is the mean ring widths (mm) for the five most inner rings on the core.

Statistical methods

For most analyses of RW and BAI growth parameters, I partitioned the dataset into the three geographical regions: Mainland, Mid-coast Islands, and Haida Gwaii. Because 1999 was the first year of obtaining tree cores, on cores obtained in subsequent years (2000–2008), I added the yearly growth ring increments on trees and subtracted this from the measured DBH to provide a corrected DBH value for 1999 for all trees.

Frequency distributions of DBH, AGE, RW, BAI, and SALMBIO for the entire dataset were all significantly right-skewed (Kolmogorov-Smirnov Z [K-S], all $P < 0.05$). For DBH, RW, and SALMBIO, this was normalized with two square root transformations (K-S, all $P < 0.03$). For BAI, a single square root transformation approached normality (K-S = 0.039, $P = 0.06$). Statistical trends were similar with and without transformations. When plotted against year (1950–1999), RW, BAI, and SALMBIO showed significant negative slopes. To examine any potential correlations between the yearly oscillations in these variables, I extracted residuals from linear regressions which removed the longer term trends. DISTFOR and SLOPE were also highly skewed and were categorized (DISTFOR; 0–20 m = 1, >20 m = 2; SLOPE: 0–20 degrees = 1; >20 degrees = 2). For $\delta^{15}N$ and TN, I computed means for annual rings of each tree separately for the combined time blocks (1950–1954, 1975–1979) and then compared these for the three geographical regions. Statistical tests (SPSS version 28) included Pearson r, Spearman rho, K-S Z, linear regression for slope and unstandardized residuals, ANOVA, and general linear model (GLM) with covariates.

I analyzed the data using two approaches. Initially, I used the entire dataset of 502 trees in the 79 watersheds. In 11 of the watersheds, additional trees (10–39) had been cored for more detailed studies (Reimchen and Fox 2013; Reimchen and Arbellay 2018, 2019). To reduce the disproportionate contributions from these 11 watersheds, I limited the data to a maximum of six trees per watershed, three of the largest trees in the carcass zone, and three (if available) of the largest controls. This reduction produced a partial dataset of 282 trees. The majority of trends were similar for the full and partial data sets, although the statistical support was variable. In the current paper, I use the partial dataset as it provides a more reliable comparison among regions. Yearly trends for BAI are highly correlated with RW for both the full and partial data sets (Mainland, $r = 0.88$, $P < 0.001$, $n = 157$; Mid-coast Islands, $r = 0.90$, $P < 0.001$, $n = 53$; Haida Gwaii, $r = 0.86$, $P < 0.001$, $n = 72$); as such, I present primarily BAI data. Supplementary Materials include companion results from the full dataset (Table S2) and comparison figures (Figures S1–S6).

Results

Tree size and age

Within each region, DBH of the focal spruce ranged from one to three metres and was positively correlated with salmon biomass entering the stream, those on Haida Gwaii having about 30% greater diameter than those on the Mainland and Mid-coast Islands (Figure 2). In each region, trees from carcass zones had about a 40% higher DBH relative to adjacent control trees, with the carcass-near category having larger trees than carcass-far trees for the Mainland and Haida Gwaii but not for the Mid-coast Islands (Figure 3). Average age of the trees was 300 years which differed among regions, being higher on Haida Gwaii (Mainland, $\bar{x}$ (mean) = 247 yr, $n = 157$; Mid-coast Islands, $\bar{x} = 315$ yr, $n = 53$; Haida Gwaii, $\bar{x} = 403$ yr, $n = 72$) and which differed among carcass categories, with those in the carcass-far zone being younger ($\bar{x} \pm$ SD; carcass-near 349 ± 183 yr, $n = 55$; carcass-far: 271 ± 174 yr, $n = 163$; control: 332 ± 190 yr, $n = 64$; REGION: $F_{2,273} = 14.9$, $P < 0.001$; CARCASS: $F_{2,273} = 4.5$, $P < 0.02$). Inclusion of AGE as a covariate in a GLM indicates that, relative to control trees, those in the carcass zones were 32% larger on the Mainland ($F_{1,155} = 20.1$, $P < 0.001$), 66% larger on the Mid-coast Islands ($F_{1,50} = 25.1$, $P < 0.001$), and 45% larger on Haida Gwaii ($F_{1,70} = 28.5$, $P < 0.001$).

Basal Area Increment (BAI)

Relative to control trees, average BAI yearly growth in the carcass zones was 108% higher on the Mainland ($\bar{x} = 7966$ mm^2 versus 3954 mm^{2,} with square root transformed BAI, $F_{1,155} = 20.5$, $P < 0.001$), 238% higher on the Mid-coast Islands ($\bar{x} = 5962$ mm^2 versus 1763 mm^2, $F_{1,51} = 19.5$, $P < 0.001$), and 68% higher on Haida Gwaii ($\bar{x} = 8551$ mm^2 versus 5087 mm^2, $F_{1,70} = 5.6$, $P < 0.03$; Figure 4). There were no differences between carcass-near trees and carcass-far trees ($F_{1,212} = 0.68$, $P = 0.41$). Ring width (RW) data (Figure S1) is broadly similar to the BAI data.

Yearly oscillations occurred in BAI. Growth differences between trees in the carcass zone and control trees persisted over five decades, apart from Haida Gwaii that showed greater growth in control trees over time leading to smaller differences with carcass zone trees in more recent years (Figure 5).

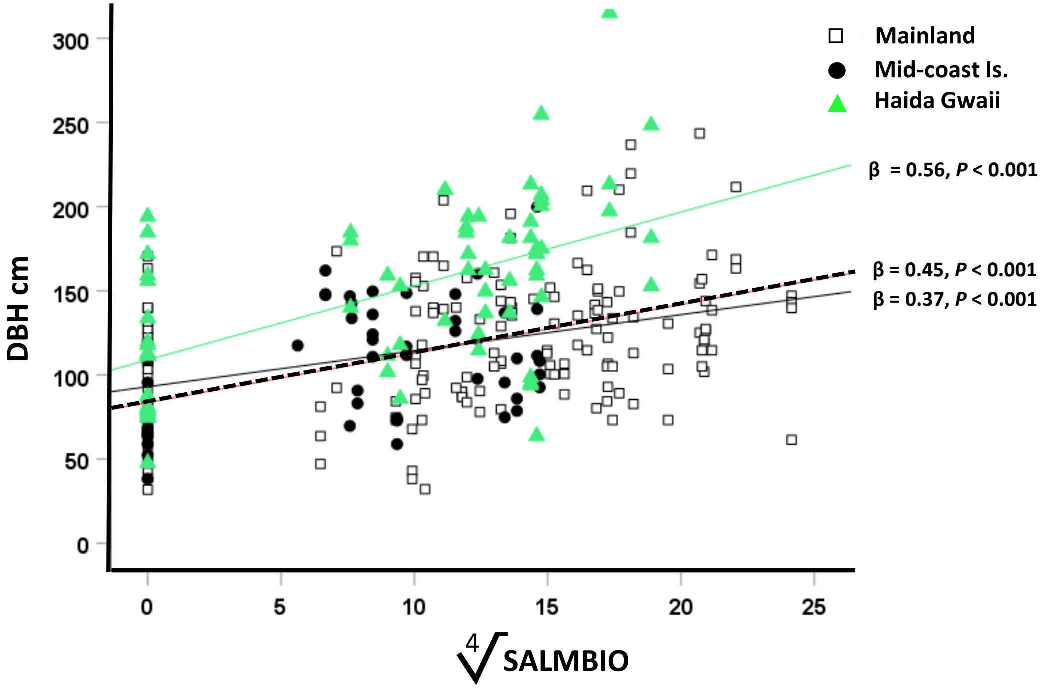

FIGURE 2. Regional trends in diameter at breast height (DBH) of 282 Sitka Spruce (*Picea sitchensis*) trees and salmon biomass (SALMBIO) in each of the 79 British Columbia watersheds. Salmon biomass normalized with the fourth root.

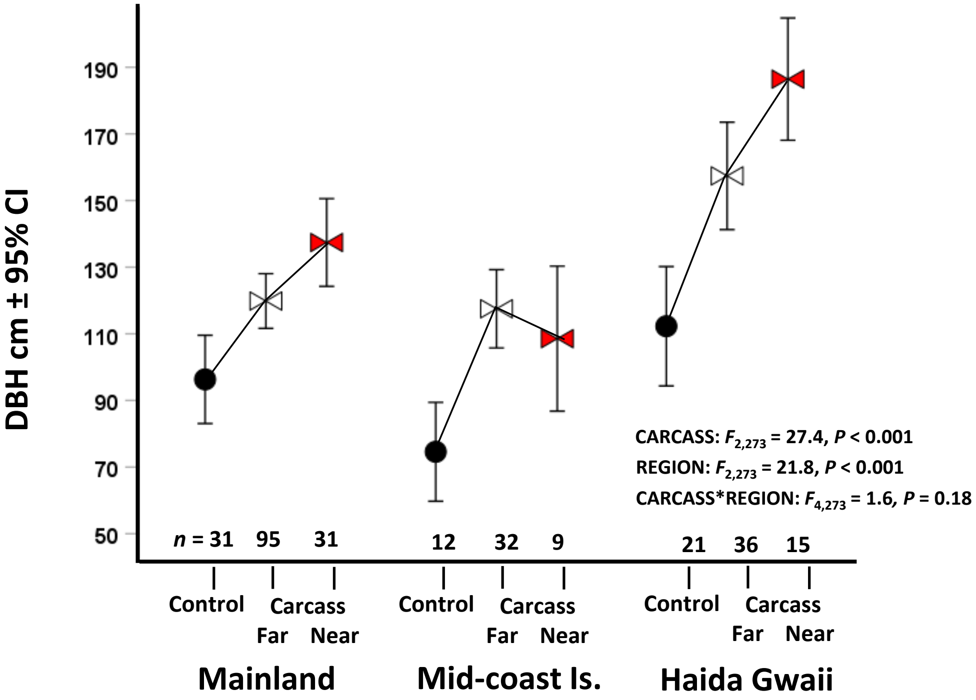

FIGURE 3. Regional trends in average diameter at breast height (DBH) of 282 riparian Sitka Spruce (*Picea sitchensis*) in relation to salmon carcass occurrence in coastal British Columbia.

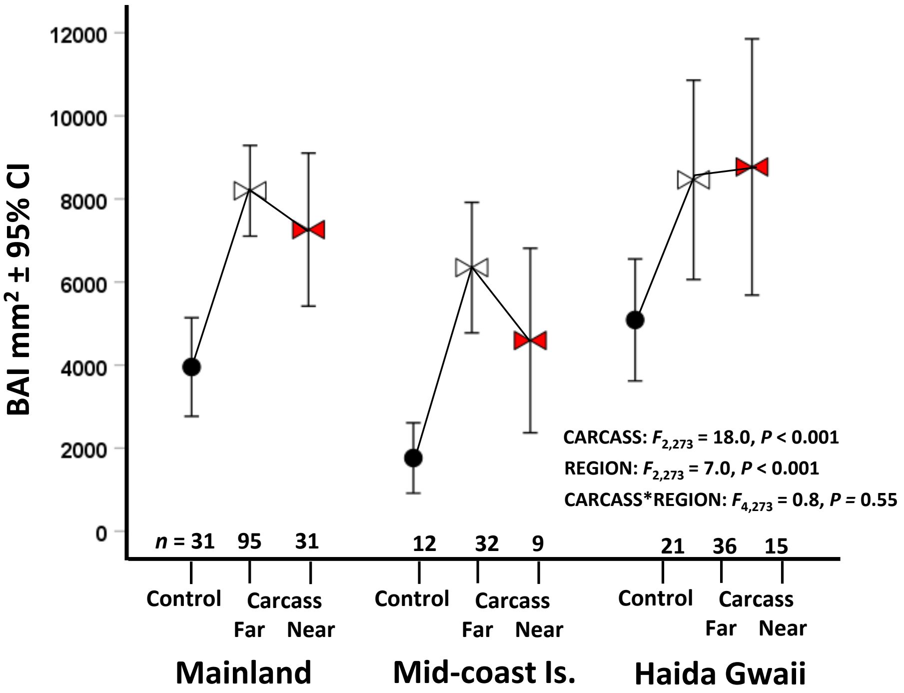

FIGURE 4. Regional trends in average basal area increment (BAI) of 282 riparian Sitka Spruce (*Picea sitchensis*) in relation to salmon carcass occurrence in coastal British Columbia.

These trends were also present in the full dataset (Figure S2). In analyzing the tree ring data, it appeared that there might be more yearly variability in BAI in the carcass zone relative to adjacent control sites. This was present in larger trees for the Mainland and Mid-coast Islands but not for Haida Gwaii and did not occur in smaller trees (Figure 6).

Are there other biophysical factors that might inflate the apparent importance of carcasses to annular spruce growth? BAI was inversely correlated with tree AGE (r_s = −0.40, P < 0.01), with DISTFOR (r_s = −0.12, P < 0.05), and with riparian SLOPE (r_s = −0.34, P < 0.01). The GLM with square-root transformed BAI as dependent, CARCASS, SLOPE, and DISTFOR as independents, square root transformed AGE as a covariate and all two-way interactions produced a significant model ($F_{8,275}$ = 13.3, P < 0.001). All two-way interactions as well as DISTFOR were statistically insignificant in each region and removed from the model. The reduced model was significant (P < 0.001), accounting for 30%, 60%, and 30% of the variance in BAI for the Mainland, Mid-coast Islands, and Haida Gwaii, respectively (Table 1). Although SLOPE and AGE were significant predictors of BAI in each region, when controlling for these independents, CARCASS remained a significant contribution to BAI on the Mainland and the Mid-coast Islands but had only a marginal contribution on Haida Gwaii. Relative to control trees, estimated marginal means of BAI for carcass trees were 78% larger on the Mainland, 148% larger on the Mid-coast Islands, and 55% larger on Haida Gwaii. Bivariate plots of BAI and AGE indicate that carcass trees had on average, elevated BAI across a broad range of tree ages for the Mainland and the Mid-coast Islands but had limited effects for Haida Gwaii (Figure 7). The full dataset (Figure S3) showed similar trends.

Salmon biomass (SALMBIO)

I examined whether the extent of yearly (1950–1998) fluctuations of SALMBIO were associated with yearly fluctuations on BAI. Average SALMBIO oscillated over the five decades with general concordance of oscillations among regions (Mainland versus Mid-coast Islands, r = 0.59, P < 0.001; Mainland versus Haida Gwaii, r = 0.52, P < 0.001; Mid-coast Islands versus Haida Gwaii, r = 0.36, P < 0.02). Apart from an increase in the late 1990s, there was a marginal reduction in SALMBIO over this interval, the effects being larger on the Mainland and Haida Gwaii (Mainland: β = −0.07, t = 3.1, P < 0.003; Mid-coast Islands, β = −0.05, t = 1.1, P = 0.29; Haida Gwaii, β = −0.25, t = 6.9, P < 0.001). Bivariate plots indicate that the major peaks and lows of SALMBIO corresponded

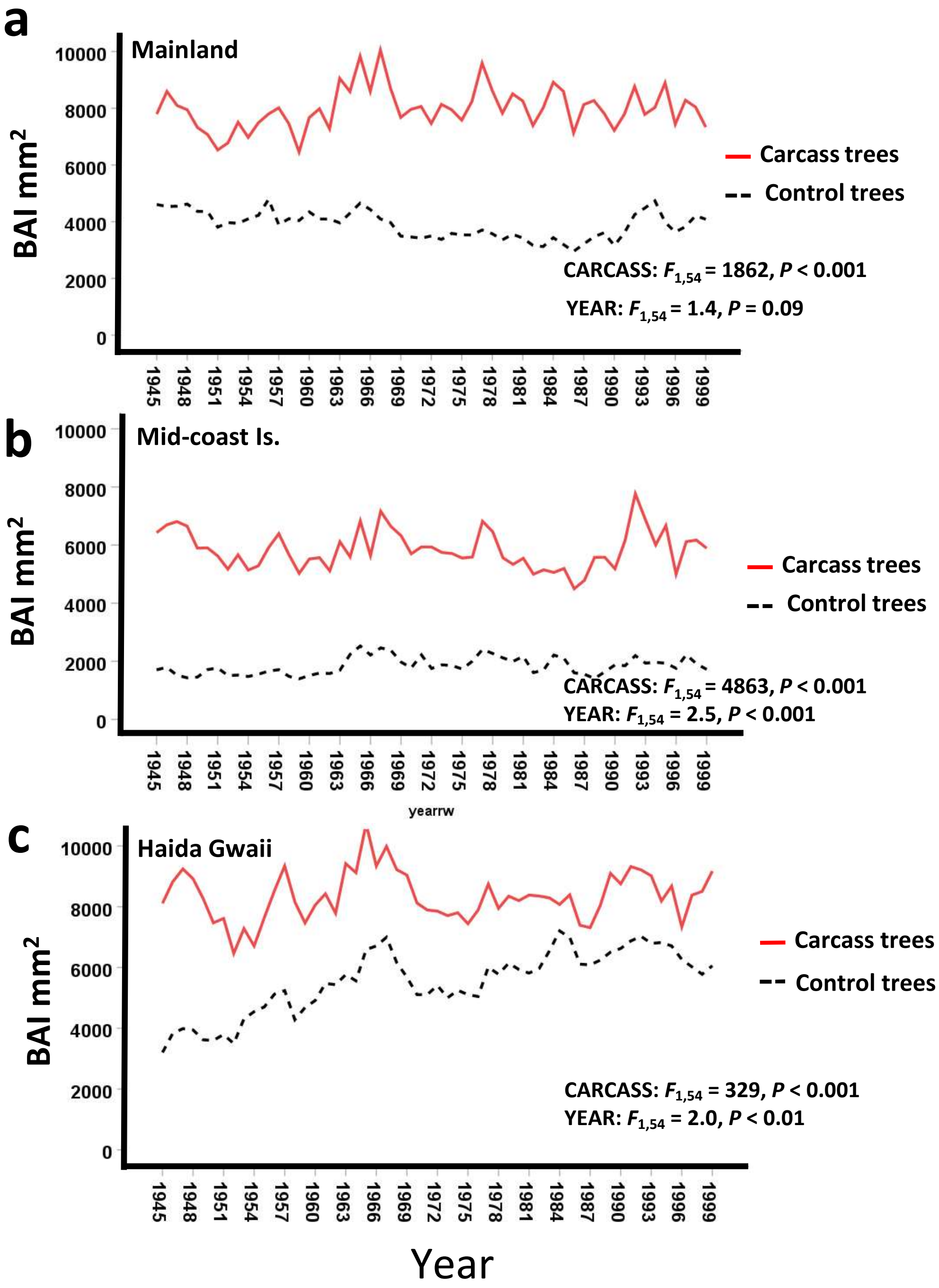

FIGURE 5. Regional and temporal (1945–1999) comparisons of 282 Sitka Spruce (*Picea sitchensis*) basal area increment (BAI) in relation to salmon carcass occurrence against adjacent control sites.

to the major peaks and lows for BAI with a lag time of one to four years (derived from computation [*r*]) and not from visual assessment); these effects were most pronounced during the first two decades (Figure 8a). Shorter lags were more prevalent on the Mainland than on Haida Gwaii (Figure 8b).

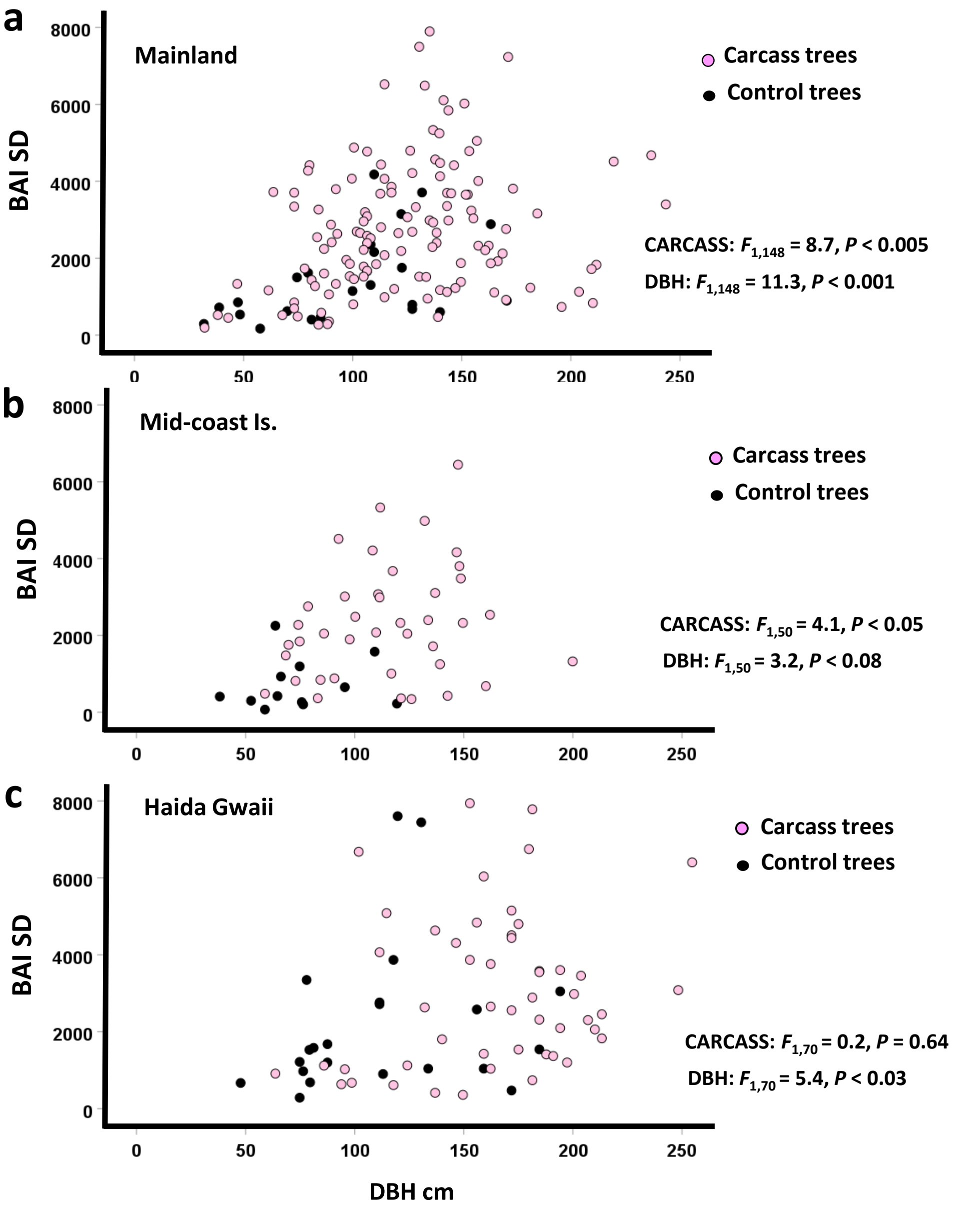

FIGURE 6. Yearly variability (SD) in basal area increment (BAI) of rings (1945–1999) in relation to size of 282 spruce (*Picea sitchensis*) diameter at breast height (DBH) separated for region and salmon carcass occurrence.

Nitrogen isotopes and total nitrogen

The coast-wide average δ^{15}N signature in tree rings was −0.87‰ and was highly variable over the study area (range −8.6‰ to 7.3‰, n = 147 trees). These isotopic signatures were positively correlated with SALMBIO on the Mainland (r = 0.30, P < 0.003, n = 89), on the Mid-coast Islands (r = 0.54, P < 0.004, n = 29), but not on Haida Gwaii (r = 0.17, P = 0.39, n = 29). I found no significant differences between time periods (1950–1954 versus 1975–1979; Mainland, Z = 0.01, P = 0.99; Mid-coast Islands, Z = 1.22, P = 0.22; Haida Gwaii, Z = 0.36, P = 0.77). In the Mainland and Mid-coast Islands watersheds, δ^{15}N was about 3‰ higher in carcass-near trees than adjacent control trees but there was minimal difference on Haida Gwaiii (Figure 9). The full dataset (Figure S4) shows in each region highest δ^{15}N signatures in carcass-near trees and lowest values in adjacent control

TABLE 1. General linear model analyses (partial dataset) of basal area increment (BAI; 1945–1999) of old-growth Sitka Spruce (*Picea sitchensis*) against tree age (AGE), riparian slope (SLOPE), and salmon carcass condition (CARCASS) for three geographical regions (Mainland, Mid-coast Islands, Haida Gwaii), British Columbia. Distance to the stream (DISTFOR and all two-way interactions were non-significant and removed from the model. Degrees of freedom (df), *F*-ratio (*F*), probability (*P*), partial eta squared (η), BAI normalized with a single square root.

Region	Parameters	BAI			
		df	*F*	*P*	η
Mainland, 157 trees, 47 rivers	Model	3	21.0	<0.001	0.29
	AGE	1	15.1	<0.001	0.09
	SLOPE	1	15.0	<0.001	0.09
	CARCASS	1	12.6	<0.001	0.08
	Error	153			
Mid-coast, 53 trees, 16 rivers	Model	3	24.8	<0.001	0.60
	AGE	1	23.8	<0.001	0.33
	SLOPE	1	4.1	<0.050	0.08
	CARCASS	1	17.5	<0.001	0.26
	Error	49			
Haida Gwaii, 72 trees, 16 rivers	Model	3	9.8	<0.001	0.30
	AGE	1	22.1	<0.001	0.25
	SLOPE	1	0.1	0.890	0.00
	CARCASS	1	6.9	<0.020	0.09
	Error	68			

sites. The GLM with δ^{15}N as the dependent variable and REGION, CARCASS, DISTFOR, and SLOPE as independents, and AGE as a covariate accounts for 18% of the variance ($F_{11,135} = 2.6$, $P < 0.006$) with the highest positive effects for CARCASS ($F_{2,135} = 6.6$, P < 0.003) and inverse associations for SLOPE ($F_{1,135} = 5.5$, $P < 0.03$) and no effects for DISTFOR ($P = 0.66$) or for REGION ($P = 0.22$). The GLM with BAI as dependent and REGION as independent and δ^{15}N and AGE as covariates showed a significant effect for AGE ($F_{1,142} = 18.8$, $P < 0.001$) and no effect for REGION ($F_{2,142} = 1.9$, $P = 0.16$) or δ^{15}N ($F_{1,142} = 0.07$, $P = 0.79$).

Coast-wide TN of tree rings averaged 0.07% (range 0.03% to 0.14%) and was highest on Haida Gwaii ($\bar{x}$ ± SE 0.091 ± 0.03%, $n = 29$), lower on the Mainland (0.067 ± 0.03%, $n = 89$), and lowest on the Mid-coast Islands (0.055 ± 0.02%, $n = 29$). There were inconsistent associations with carcass categories, TN being higher in control trees on the Mainland but higher in carcass-near trees on Haida Gwaii (Figure 10). There was a significant excess of TN in the more recent period (1975–1979) compared to the older period (1950–1954) for the Mainland (Z = 3.1, $P < 0.001$) and for the Mid-coast Islands (Z = 3.8, $P < 0.001$) but not for Haida Gwaii (Z = 1.12, $P = 0.26$). Total nitrogen was not related to SALMBIO (Mainland, $r_s = -0.15$, $P = 0.18$, $n = 89$; Mid-coast Islands, $r_s = -0.17$, $P = 0.38$, $n = 29$; Haida Gwaii, $r_s = 0.24$, $P = 0.20$, $n = 29$). The full dataset (Figure S5) differed from the partial dataset in that each of the regions exhibited marginally greater TN values in control trees relative to trees in carcass zones.

There were no overall correlations between δ^{15}N and TN within carcass zone forests for each region (Mainland, $r = 0.07$, $P = 0.58$, $n = 76$; Mid-coast Islands, $r = 0.22$, $P = 0.28$, $n = 26$; Haida Gwaii, $r = -0.13$, $P = 0.63$, $n = 17$). However, regional differences as well as watershed specific trends were evident (Figure 11). For Haida Gwaii, 15/17 carcass trees had greater TN values than the coastal averages while for the Mid-coast Islands, 22/26 carcass trees had lower TN values than the coastal average ($\chi^2_1 = 11.6$, $P < 0.001$). Log-linear analysis (three regions × four quadrats) yielded a significant difference in the frequency distribution of trees among the four quadrats (two-way interaction $\chi^2_{11} = 83.8$, $P < 0.001$), the largest contribution being the excess of Mid-coast Islands trees in the low δ^{15}N and low TN quadrat (Z = 2.6, $P < 0.01$). Similar results were evident in the full dataset (Figure S6) including comparable statistical trends (two-way interaction $\chi^2_{11} = 104.2$, $P < 0.001$). While δ^{15}N and TN were not correlated overall within and among regions, the three watersheds with the highest combined δ^{15}N and TN were Neekas River on the Mainland and Salmon River and Bag Harbour on Haida Gwaii (Figure S6).

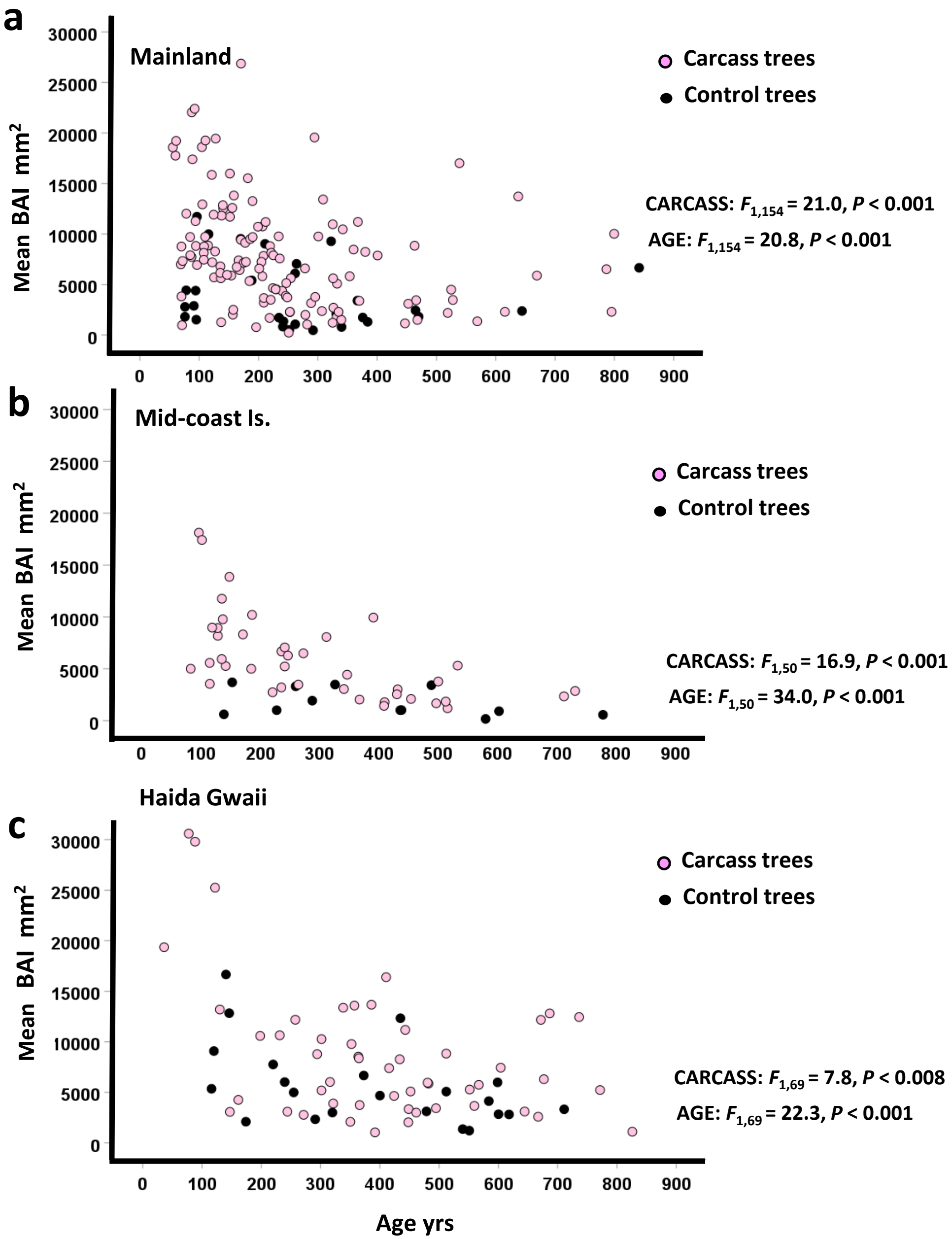

FIGURE 7. Relationship between mean basal area increment (BAI; 1945–1999) for each of 282 cores in relation to tree age of Sitka Spruce (*Picea sitchensis*) separated for region and carcass occurrence.

Discussion

I undertook a coastal survey in British Columbia to evaluate radial growth (RW and BAI) of the largest Sitka Spruce from riparian zones with and without access to salmon-derived nutrients. My results are broad at both regional (Mainland, Mid-coast Islands, Haida Gwaii) and local scales and suggest a much greater contribution to primary production in conifers than estimated in previous tree-ring studies (Drake *et al.* 2002; Reimchen *et al.* 2003; Reimchen and Fox 2013; Reimchen and Arbellay 2018, 2019).

Deficiency of soil nitrogen constrains productivity in many plant communities (LeBauer and Treseder 2008) and as such, it is not unexpected that the

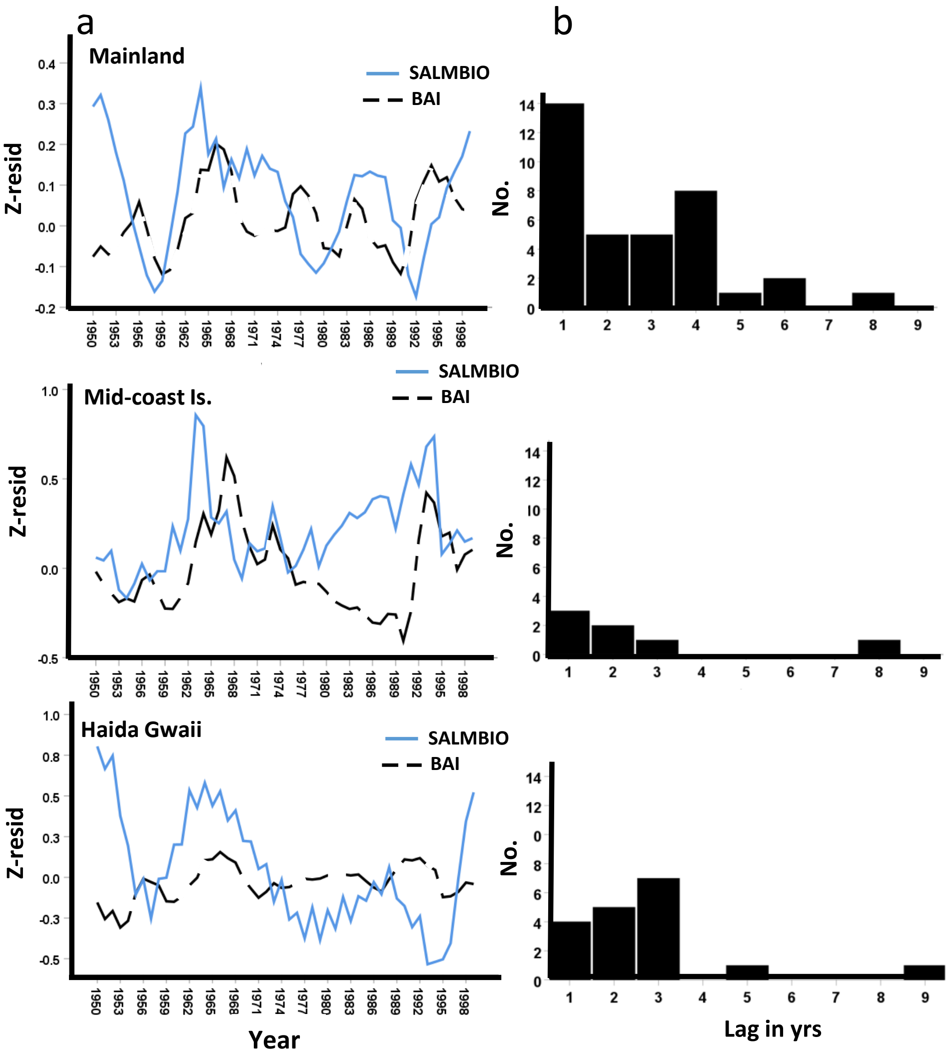

FIGURE 8. a. Relationship between yearly oscillations of average salmon biomass and average growth (basal area increment [BAI]) of 282 Sitka Spruce (*Picea sitchensis*) for 1945 to 1998. Salmon biomass and BAI each scaled to a mean of zero based on residuals from linear regression. b. Frequency of the yearly lags (LAG) for the major oscillation on salmon biomass and BAI based on each core.

salmon spawning migrations in the north Pacific and their predator-mediated transfer into riparian zones positively influences conifer size and growth (Ben-David *et al.* 1998; Cederholm *et al.* 1999; Hilderbrand *et al.* 1999; Reimchen and Fox 2013). Alder (*Alnus* spp.), a recognized nitrogen-fixer that is often common in riparian zones, was rare or absent in the areas with old growth spruce that I sampled. The spruce trees I surveyed adjacent to salmon-spawning gravels averaged 1.2 m DBH and 300 years in age (range 60–842 yr), those on Haida Gwaii being marginally larger and older than those on the Mainland and the Mid-coast Islands. Within each region, DBH increased in watersheds with more salmon entering the streams. Larger watersheds, usually with more salmon, often have wide non-sloping riparian zones, deeper soils, and potentially greater retention of nutrients from reduced hyporheic flow (O'Keefe and Edward 2003; Wondzell 2011), each of which may facilitate increased size and longevity of old growth trees. Yet, there remains ambiguity in these associations as multiple biophysical attributes can differ among these geographically diverse watersheds such as precipitation and temperature that are independent of salmon nutrients. However, my data address much of this ambiguity as the DBH was about 50% larger

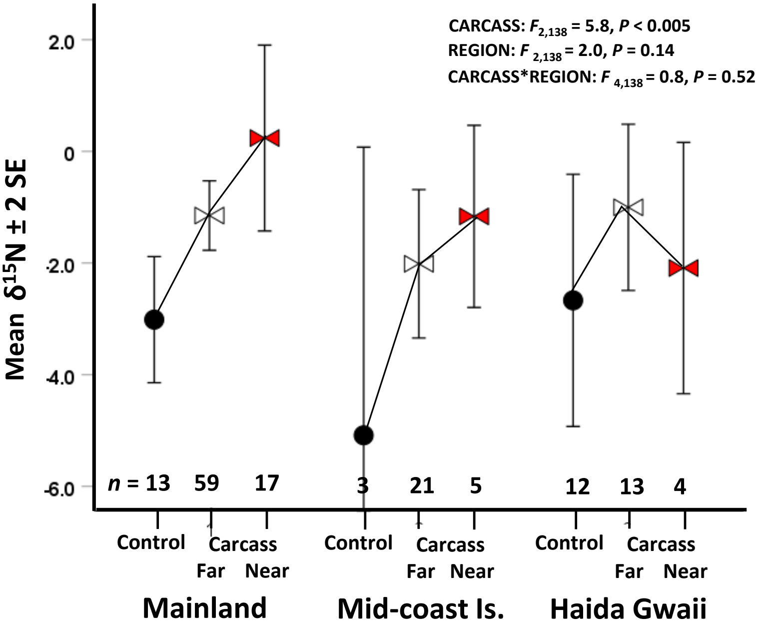

FIGURE 9. Average δ^{15}N signatures for tree rings of riparian Sitka Spruce (*Picea sitchensis*) heartwood (1950–1954, 1975–1979) among regions in relation to salmon carcass occurrence. *n* = number of trees.

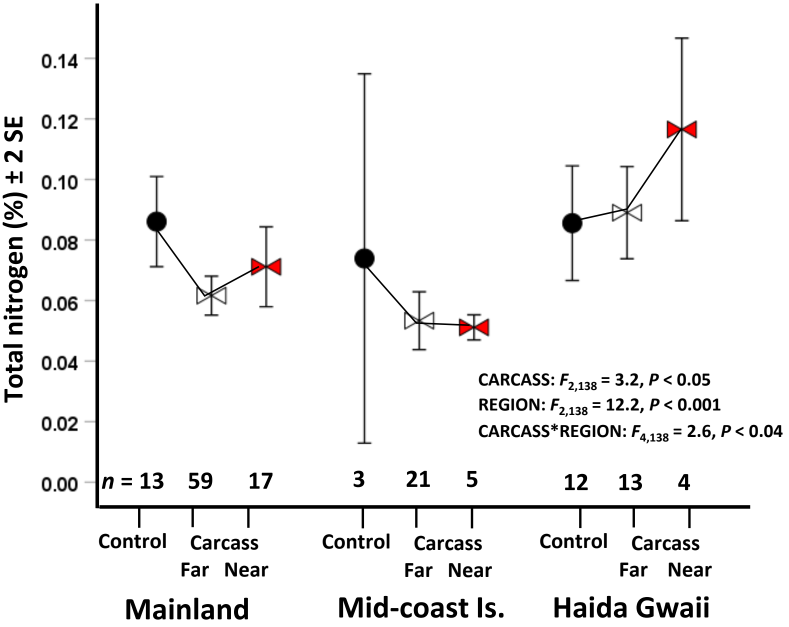

FIGURE 10. Total nitrogen for tree rings of riparian Sitka Spruce (*Picea sitchensis*) heartwood (1950–1954, 1975–1979) among regions in relation to salmon carcass occurrence. *n* = number of trees.

in carcass zones relative to adjacent control trees and in two of three regions, DBH was higher in carcass-near trees as opposed to carcass-far trees. Furthermore, while the close proximity of the control trees to the carcass trees does not remove the microspatial edaphic conditions that occur in these riparian zones, they greatly minimize the differences compared to the 2–25 km distances that have been used in previous

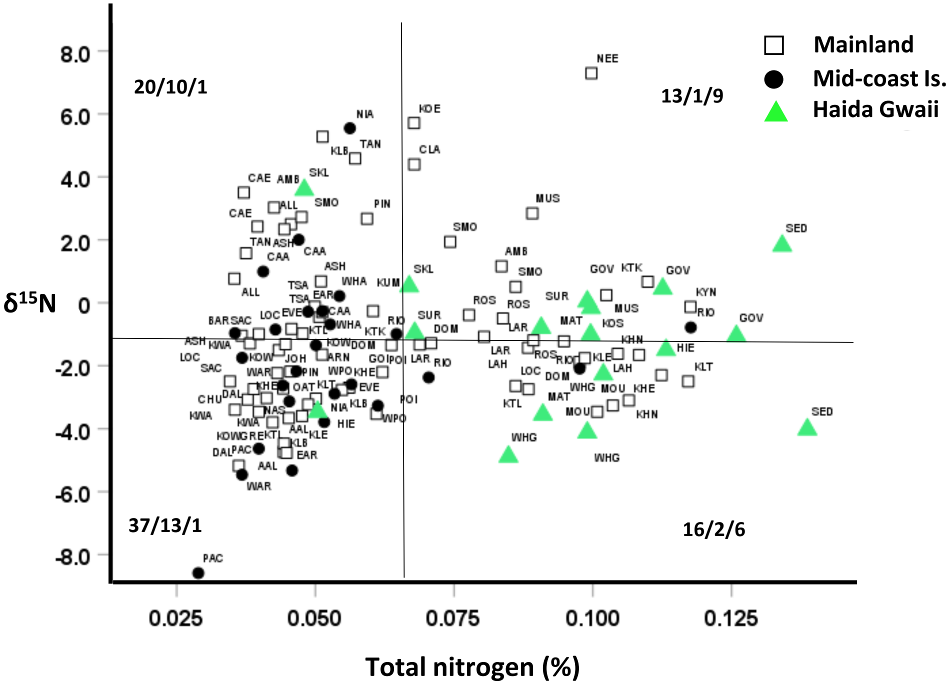

Figure 11. Bivariate plot of δ^{15}N data against total nitrogen (TN) for each Sitka Spruce (*Picea sitchensis*) tree from the salmon carcass zones, separated by region. Stream labels shown adjacent to each value (see Table S1 for full names). Sets of three values in each quadrat indicate total number of trees from that quadrat for each region. Note the disproportionate number of Mid-coast Islands trees in the low δ^{15}N and low TN quadrat.

studies (e.g., Drake and Naiman 2007).

Quantifying radial growth was my primary interest and I found that BAI did not differ between carcass-near trees and carcass-far trees. These trees averaged 100% greater growth than adjacent control trees and ranged from 70% greater on Haida Gwaii to 240% greater on the Mid-coast Islands. These differences persisted over much of the five decades of yearly data. Although less informative, I also examined RW which was also similar between carcass-near and carcass-far trees with both averaging about 60% greater growth than adjacent control trees, ranging from 10% greater on Haida Gwaii to 125% greater on the Mid-coast Islands. Other biophysical factors co-varied with the presence or absence of carcasses and may have contributed to the observed differences in growth. For example, I found that annular growth was lower on older trees (see Cherubini *et al.* 1998; Peters *et al.* 2014), lower on those from steeper slopes, and lower on those further from the stream. However, when I statistically corrected for these effects, the relative BAI growth enhancement (marginal means) for presence/absence of carcasses ranged from 55% to 150% dependent on region. These estimates, derived from 282 trees in 79 watersheds, are much larger than previously reported (Reimchen and Arbellay 2019) from 13 trees in five watersheds where there was an average 19% greater growth in carcass trees. Four of these five watersheds, including Salmon River, had unusually high carcass density and bear activity (T.E.R. pers. obs.) and I suspected that even 'control' sites in these watersheds could be positively influenced by nutrient uploading. This would reduce the growth differential between carcass and control trees. Elevated isotopic signatures in control trees in one of these watersheds (Salmon River, Haida Gwaii) are consistent with this interpretation. Previous tree ring studies have also identified positive responses to nutrient loading and salmon abundance in comparisons with control sites (Helfield and Naiman 2001; Drake and Naiman 2007). However, the distances between salmon sites and control sites were large, averaging 6 km (maximum 25 km). Tree age and distance from the stream were not compared and as such, the differences between these may involve multiple habitat differences unrelated to salmon abundance and cannot provide a reliable proxy for historical signatures of salmon.

I found that over the five decades, there were major yearly oscillations in BAI that were often concordant among geographical regions, including reduced growth in the 1950s and higher growth in the mid-1960s, in 1978, and in 1993. These common coast wide responses presumably indicate common climatic effects and/or nutrient pulses. Spruce growth is optimal on moist sites with rich soil nutrient regimes (Farr and Harris 1979; Farrelly *et al.* 2011), environmental conditions that largely characterize salmon watersheds of the Pacific Northwest. However, globally climatic variables tend to be poorly associated with Sitka Spruce growth (Blyth and MacLeod 1981; Worrell and Malcolm 1990; Feliksik and Wilczyński 2008; Hadley and Knapp 2011). That the major growth oscillations I observed in carcass forests were positively correlated with those from adjacent control sites suggest broader climatic influences largely independent of salmon numbers entering the streams.

If annular tree growth is responding directly to salmon abundance, then one predicts that the extensive yearly variability in abundance of salmon in British Columbia (NuSEDS 2019) should result in higher variability in annular tree growth relative to adjacent control trees of similar size. My data are consistent with this prediction for the Mainland and the Mid-coast Islands but not for Haida Gwaii, although for the latter the major exceptions are 2/19 control trees that have elevated variance. Longer term trends in growth have been used to estimate salmon abundance in past centuries (Starheim *et al.* 2013).

Positive correlations between salmon abundance and radial growth with a time lag from one to six years were initially reported for conifers in Alaska and Oregon (Drake and Naiman 2007) and in British Columbia (Reimchen and Fox 2013). In experimental fertilization studies, uptake of enriched nitrogen occurred one year after application (Hart and Classen 2003). In the current study, there were multiple oscillations in BAI over 50 years that were associated with salmon biomass that lagged from one to eight years; shorter lags (1–3 years) were the most common, consistent with more detailed studies at several of these watersheds (Reimchen and Arbellay 2019). Longer lags might reflect a more complex cycling of nutrients in the soils prior to uptake by old-growth trees (Simard *et al.* 2012).

Quantification of δ^{15}N signatures in annular growth rings was initially reported by Poulson *et al.* (1997) using full ring mass of felled trees and subsequently by Drake *et al.* (2002, 2011), Reimchen *et al.* (2003), and Saurer *et al.* (2004) using increment cores. Further investigations allowed historical insight into nutrient cycling using isotopic signatures of tree rings in salmon watersheds (Drake and Naiman 2007; Reimchen and Fox 2013; Reimchen and Arbellay 2018, 2019) and in seabird colonies (Holdaway *et al.* 2007; Reimchen *et al.* 2013). Holdaway *et al.* (2007) found marine nutrients did not influence conifers, presumably because enriched nutrients do not by themselves translate to elevated growth when other parameters (moisture, phosphorus, etc.) are limiting in seabird colonies. I found that the presence/absence of carcasses were better predictors of δ^{15}N in tree rings than salmon spawning biomass. Trees with carcasses near their base had about 3‰ isotopic enrichment relative to adjacent control trees, indicative of highly localized spatial heterogeneity in nutrient uptake in these riparian zones. These sharp gradients in marine-derived nutrients and corresponding large differences in tree ring δ^{15}N are inconsistent with conclusions and predictions (Handley *et al.* 1999; Amundson *et al.* 2003) that precipitation and temperature will be the major predictors of δ^{15}N in temperate latitudes, at least with respect to rainforests of western North America.

I observed multiple exceptions to these isotopic associations with salmon carcasses including marked deficiency of tree ring δ^{15}N in some watersheds where salmon spawning migrations were large as well as occasional high isotopic signatures in control sites. At least some of these exceptions are associated with differences in activity of the major predators. Black Bear (*Ursus americanus*) and Grizzly Bear (*Ursus arctos*) are dominant transfer vectors of salmon carcasses from the stream to the forests in western North America (Reimchen 1994, 2000, 2017; Hilderbrand *et al.* 1999) but are absent from multiple watersheds. For example, on the Mid-coast Islands and Haida Gwaii, smaller islands with salmon streams commonly have no evidence of carcass transfer due to the absence or very low density of bears or other transfer vectors. As well, high stream banks and deep channels on some of the larger salmon rivers on the Mainland limit or exclude movement of bears from the stream channel into the riparian zone also resulting in low isotopic signatures. I cannot account for why control sites occasionally had enriched isotopic signatures. Diverse mechanisms are probably involved as isotopic nitrogen is an integrator of nutrient cycling in the complex edaphic interactions occurring in forests (Robinson 2001; Craine *et al.* 2009). Transfer vectors, other than bears, such as canopy-roosting seabirds (Christie and Reimchen 2008) or nesting raptors (Anthony *et al.* 1982), may also contribute. Furthermore the extended historical use of these riparian forests by Indigenous Peoples, whose cultures were based on marine resources, may account for such elevated signatures in what I classified as 'control' sites.

I also evaluated the TN in the rings predicting that this could give insight to the general availability of soil nutrients. Total nitrogen in conifer heartwood is characteristically low relative to sapwood or foliar tissues and has thus received limited attention in tree-ring studies. Heartwood TN values averaged 0.03% in Red Spruce (*Picea rubens* Sargent) from eastern North America (Doucet *et al.* 2011), 0.05% in Norway Spruce (*Picea abies* (L.) H. Karsten) in Switzerland (Saurer *et al.* 2004), and 0.01% in hybrids between Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh) and Red Spruce (Martin *et al.* 2015). In my study of Sitka Spruce, coast-wide average TN value was about 0.07% in carcass zones and about 0.08% in adjacent control trees, approximately double that observed in other geographical regions. These results differ from those of Reimchen and Arbellay (2019) who reported an average 0.02% increase in TN in five control trees relative to eight adjacent carcass trees, data also included in the current analyses of 282 trees, and suggestive of the asymmetric number of trees.

There were regional differences in the extent of co-variation between TN and $\delta^{15}N$. When partitioning the data into quadrats separated by coast-wide averages for TN and $\delta^{15}N$, the majority of carcass trees from Haida Gwaii had greater TN values, but average $\delta^{15}N$ values, while the Mid-coast Islands watersheds had both low TN and low $\delta^{15}N$. These trends occurred in both partial and full datasets. The Mid-coast Islands also had the lowest average salmon biomass, the lowest BAI growth throughout the five decades, the largest differences in BAI between control trees and carcass zone trees as well as a substantial number of positive lags between salmon biomass and BAI. This might indicate that the control sites on the Mid-coast Islands are particularly nutrient-deficient, possibly from limited soil depth, emphasizing the particular importance of salmon spawning migration to the riparian zones in these small watersheds.

Conclusions

I show that across a broad geographical region of coastal British Columbia, bear-mediated transfer of salmon carcasses to riparian zones results in an approximate doubling of annual radial growth of mature Sitka Spruce relative to adjacent control trees. Enrichment of nitrogen isotope signatures in growth rings among trees with salmon carcasses at their base confirm the uptake of these marine-derived sources. Major yearly fluctuations in radial growth over five decades (1945–1999) are concordant among geographical regions and within watersheds between carcass trees and adjacent control trees indicative of broad climatic influences. However, the yearly growth variance is greater in carcass trees and is associated with a one to four year lag in the major yearly oscillations in salmon biomass entering the streams. My data confirm and greatly extend previous studies of the 'salmon forest' and emphasize the substantive contribution of vectors such as bears to riparian primary productivity.

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SUPPLEMENTARY MATERIALS:

TABLE S1. Watersheds surveyed in coastal British Columbia to examine the relationship between salmon carcasses and Sitka Spruce (*Picea sitchensis*) growth.

TABLE S2. General linear model analyses (full dataset) of basal area increment (BAI; 1945–1999) of old-growth Sitka Spruce (*Picea sitchensis*) against tree age (AGE), riparian slope (SLOPE), and carcass condition (CARCASS) for three geographical regions.

FIGURE S1. Partial data set ($n = 282$ trees). Regional and temporal (1945–1999) trends of Sitka Spruce (*Picea sitchensis*) ring width (RW) in relation to salmon carcass trees against adjacent control trees.

FIGURE S2. Full data set ($n = 502$ trees) of regional and temporal (1945–1999) trends for basal area increment (BAI) on Sitka Spruce (*Picea sitchensis*) in relation to salmon carcass trees against adjacent control trees.

FIGURE S3. Full dataset ($n = 502$ trees) of relationship between mean basal area increment (BAI; 1945–1999) for each core in relation to tree age of Sitka Spruce (*Picea sitchensis*) separated for region and carcass occurrence.

FIGURE S4. Full dataset ($n = 247$) of average $\delta^{15}N$ signatures for tree rings of riparian Sitka Spruce (*Picea sitchensis*) heartwood (1950–1954, 1975–1979) among regions in relation to salmon carcass occurrence.

FIGURE S5. Full dataset ($n = 247$) of average total nitrogen for tree rings of riparian Sitka Spruce (*Picea sitchensis*) heartwood (1950–1954, 1975–1979) among regions in relation to salmon carcass occurrence.

FIGURE S6. Full dataset ($n = 247$) of bivariate plot of $\delta^{15}N$ data against total nitrogen (TN) for each Sitka Spruce (*Picea sitchensis*) tree and separated by region.