

Nitrogen uptake by plants subsidized by Pacific salmon carcasses: a hierarchical experiment

Morgan D. Hocking and John D. Reynolds

Abstract: Bears (*Ursus* spp.) and other predators can capture and transport large numbers of Pacific salmon (*Oncorhynchus* spp.) to riparian areas beside small coastal streams, a process that may affect site productivity and local plant communities. We used a novel experimental manipulation of salmon carcasses to analyze understory plant uptake of salmon-derived N. A hierarchical before–after, control–impact design was used with the addition of chum salmon (*Oncorhynchus keta* (Walbaum in Artedi, 1792)) carcasses to forest sites along 11 streams on the central coast of British Columbia, Canada. Eight months after carcass placement, the foliar %N and $\delta^{15}\text{N}$ in three herbaceous and one moss species had increased by an average of 14%–60% (%N) and 0.5–3.3‰ ($\delta^{15}\text{N}$) at treatment carcass sites versus control sites. Treatment effects for %N were typically greater than for $\delta^{15}\text{N}$. Nitrogen isotope signatures at carcass sites were highly variable ($\delta^{15}\text{N}$ range = 30.1‰) and were mediated by plant species, stream salmon density, carcass mass, and individual plant foliar %N. These results show that understory plants use N from salmon during an important period of plant growth many months after carcasses were deposited in riparian areas. However, they also indicate that habitat variation across spatial scales from individual plants to streams needs to be considered when estimating the contribution of salmon to plant nutrition.

Résumé : Les ours (*Ursus* spp.) et autres prédateurs peuvent capturer et transporter un grand nombre de saumons du Pacifique (*Oncorhynchus* spp.) dans les zones riveraines le long de cours d'eau côtiers, un processus qui pourrait influencer la productivité du site et les communautés végétales locales. Nous avons utilisé une nouvelle manipulation expérimentale des carcasses de saumon pour analyser le prélèvement de N provenant du saumon par les plantes du sous-bois. Un plan expérimental hiérarchique avant–après avec témoin a été utilisé avec l'ajout de carcasses de saumon kéta (*Oncorhynchus keta* (Walbaum in Artedi, 1792)) dans des stations forestières le long de 11 cours d'eau sur la côte centrale de la Colombie-Britannique, au Canada. Huit mois après avoir placé les carcasses, %N et $\delta^{15}\text{N}$ dans les feuilles de trois espèces d'herbacées et une espèce de mousse avaient augmenté en moyenne de 14 % – 60 % (%N) et de 0,5 ‰ – 3,3 ‰ ($\delta^{15}\text{N}$) dans les stations traitées avec des carcasses versus les stations témoins. Les effets du traitement étaient typiquement plus importants sur le %N que sur $\delta^{15}\text{N}$. La signature isotopique de N dans les stations avec des carcasses était très variable (écart de $\delta^{15}\text{N}$ = 30,1 ‰) et était influencée par les espèces végétales, la densité de saumon dans le cours d'eau, le poids des carcasses et le %N dans le feuillage de chaque plante. Ces résultats montrent que les plantes de sous-bois utilisent le N des saumons pendant une importante période de leur croissance plusieurs mois après que les carcasses aient été déposées dans les zones riveraines. Cependant, ils indiquent également qu'on doit tenir compte de la variation de l'habitat aux échelles spatiales allant des plantes individuelles au cours d'eau pour estimer la contribution du saumon à la nutrition des plantes.

[Traduit par la Rédaction]

Introduction

Anadromous Pacific salmon (*Oncorhynchus* spp.) affect biodiversity and ecosystem processes in streams throughout the Pacific Rim. Salmon are born in freshwater, with most populations migrating as juveniles to the ocean where they obtain >95% of their full body mass. As adults, salmon return to their natal streams to spawn and die, delivering marine-derived nutrients to aquatic and terrestrial habitats that are often resource limited (Willson and Halupka 1995; Gende et al. 2002; Naiman et al. 2002). Stream nutrient concentrations, such as NH_4^+ , NO_3^- , and soluble reactive P, can be elevated during the spawning season, which subsequently affects the productivity of freshwater food webs (Johnston et al. 2004; Verspoor et al. 2010).

The retention of salmon nutrients in watersheds varies with the extent of stream disturbance by salmon themselves (Moore et al. 2007) and through shifts in stream substrate, forest harvesting and site slope (Tiegs et al. 2008; Holtgrieve et al. 2010) but also with the rate of salmon predation and terrestrial nutrient transfer by bears (*Ursus* spp.), wolves (*Canis lupus* Linnaeus, 1758), and other vertebrates (Reimchen 2000; Gende et al. 2001; Quinn et al. 2009). In small coastal streams, or in tributaries of larger rivers and lakes, vertebrate predators can transfer more than 50% of the spawning salmon to streamside areas (Helfield and Naiman 2006; Hocking and Reimchen 2006; Quinn et al. 2009). This creates hotspots of nutrient release that may be accessed by riparian plants (Gende et al. 2007; Holtgrieve et al. 2009).

Received 14 November 2011. Accepted 12 February 2012. Published at www.nrcresearchpress.com/cjfr on xx April 2012.

M.D. Hocking and J.D. Reynolds. Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.

Corresponding author: Morgan D. Hocking (e-mail: mhocking@sfu.ca).

Along with other pathways of salmon nutrient entry into terrestrial food webs, such as flooding and hyporheic water flow, salmon subsidies may ultimately affect riparian plant diversity (Wilkinson et al. 2005; Hocking and Reynolds 2011).

Correlational studies of the role of salmon nutrients in riparian plant nutrition have typically found increasing stable isotope ratios of heavy to light N ($\delta^{15}\text{N}$) in plant leaves across natural gradients in salmon spawning density (Bilby et al. 2003; Bartz and Naiman 2005; Nagasaka et al. 2006; Hocking and Reimchen 2009). This suggests that salmon provide an important source of N to streamside plants and is attributed to the fact that salmon carcasses have higher $\delta^{15}\text{N}$ (~12‰) than terrestrial sources of N (~0‰). However, confounded with this $\delta^{15}\text{N}$ -source-based approach is the fact that plant $\delta^{15}\text{N}$ can also reflect site productivity, which itself may be influenced by salmon abundance (Pinay et al. 2003; Hocking and Reynolds 2011). For example, plant leaf $\delta^{15}\text{N}$ broadly reflects the available N sources, rates of N cycling, and plant–mycorrhizal associations, which all influence N isotopic fractionation (Hogberg 1997; Evans 2001; Morris et al. 2005). Thus, simple correlations among locations between leaf N and numbers of salmon may be confounded by correlated differences in site productivity, which may amplify or obscure the true impacts of salmon on plant nutrient uptake.

Here, we use the first experimental approach with understory plants and salmon carcasses, based on a before–after, control–impact design, to analyze plant uptake of salmon-derived N. Chum salmon (*Oncorhynchus keta* (Walbaum in Arty, 1792)) carcasses were placed along forest transects parallel to the stream channel in 11 watersheds on the central coast of British Columbia, Canada, intended to mimic natural salmon carcass transfer by wildlife that is widespread in this region (Hocking and Reimchen 2006; Darimont et al. 2008). Previous experiments in soils have shown that decaying salmon carcasses create biogeochemical hotspots including localized increases in soil NO_3^- and NH_4^+ concentrations, higher soil $\delta^{15}\text{N}$, and greater fluxes of N_2O gas (Drake et al. 2005; Gende et al. 2007; Holtgrieve et al. 2009).

We hypothesized that salmon-derived N would be detectable in understory plants during the period of spring plant growth, over 8 months after the deposition of salmon carcasses. First, we predicted that nutrients derived from salmon would increase the mean and the variance of foliar $\delta^{15}\text{N}$ and total N (%N) and that larger salmon carcasses would lead to increased N subsidies. Second, we predicted that plants in streams that had the lowest numbers of naturally spawning salmon would show the greatest increase in N uptake. Finally, we predicted that uptake by individual plants would depend on site productivity based on measures at the stream scale (salmon density, watershed size, and red alder density) and individual plant scale (foliar %N as a predictor of $\delta^{15}\text{N}$). For example, foliar %N is often positively correlated with foliar $\delta^{15}\text{N}$ because they both index soil N availability and turnover, site productivity and differences in N uptake through mycorrhizae (Tilman 1988; Hobbie et al. 2000; Wardle et al. 2004; Craine et al. 2009; Kranabetter and MacKenzie 2010). Thus, building plant %N into models of plant $\delta^{15}\text{N}$ may account for individual and microsite-level differences in these processes that are often difficult to determine and measure.

Materials and methods

Carcass experiment

We studied 11 small- to medium-sized streams (5–25 m bankfull width) on the central coast of British Columbia, Canada, near the Heiltsuk Nation village of Bella Bella (Table 1). Streams ranged from supporting no anadromous fish to high densities of spawning chum and pink salmon (*Oncorhynchus gorbuscha* (Walbaum, 1792)) and smaller numbers of coho salmon (*Oncorhynchus kisutch* (Walbaum, 1792)). This region receives some of the highest precipitation in North America (3000–4000 $\text{mm}\cdot\text{year}^{-1}$) and is classified within the Coastal Western Hemlock (CWH) biogeoclimatic zone (Pojar et al. 1987). Watersheds are accessible by boat only, and although some high-grade logging occurred in the 1930s and 1940s, human disturbances from road construction and forest harvesting remain minimal. Riparian plant communities are dominated by the shrubs salmonberry (*Rubus spectabilis* Pursh), false azalea (*Menziesia ferruginea* Sm.), salal (*Gaultheria shallon* Pursh), and blueberry (*Vaccinium* spp.), with a coniferous overstory of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), western redcedar (*Thuja plicata* Donn ex D. Don), and amabilis fir (*Abies amabilis* Douglas ex J. Forbes). Densities of the deciduous red alder (*Alnus rubra* Bong.) are generally fairly low (an exception is the Clatsop River: Table 1). Canopy community structure (stems per hectare) was assessed along six 10 m wide belt transects extending 40 m perpendicular to the stream (Hocking and Reynolds 2011). Stream catchment areas were calculated using iMapBC (Field and Reynolds 2011).

In October of 2006, we placed 9–10 chum salmon carcasses in the forest riparian zone of each watershed along a ~100 m transect parallel to each stream and within 10 m of the stream channel. Most of these carcasses had some carcass scavenging by vertebrates, although we chose fish that were largely intact rather than smaller remnants. Chum carcasses were weighed (grand mean = 3.5 ± 0.1 kg) and placed beside selected indicator plant species including lanky moss (*Rhytidiadelphus loreus* (Hedw.) Warnst.), bunchberry (*Cornus canadensis* L.), foamflower (*Tiarella trifoliata* L.), and false lily-of-the-valley (*Maianthemum dilatatum* (Alph. Wood) A. Nelson & J.F. Macbr.). Bunchberry, foamflower, and false lily-of-the-valley are all common understory perennial herbs with arbuscular mycorrhizae associations that facilitate plant access to N, P, and other nutrients (Kranabetter and MacKenzie 2010). Lanky moss forms the dominant ground cover across our sites and is hypothesized to be able to access nutrients through the soil substrate (Wilkinson et al. 2005) and via atmospheric deposition directly through the foliar tissues (Solga and Frahm 2006; Liu et al. 2008).

At the time of carcass placement, we took foliar samples from one plant individual for each indicator species present at the carcass site and also from a paired control site 2 m away. Each site had a lanky moss sample and had one or two of the three herbaceous indicator species. Carcass sites were marked and then monitored for a 2–3 week period to determine rates of disturbance of the carcasses. The majority of carcasses in our 11 watersheds were not disturbed (105/117), although we had originally used one additional watershed that we removed from the experiment because of re-

Table 1. Habitat and chum (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) population data (2006–2009) for the watersheds in this study.

Watershed	Spawning length (m)	Bankfull width (m)	Chum salmon mean	Pink salmon mean	Salmon index (kg·m ⁻¹)	Catchment area (km ²)	Red alder density (stems·ha ⁻¹)
Ada	435	11.1	1033	317	7.4	9.8	43
Bullock Square	296	8.4	233	140	2.5	2.8	38
Clatse	900	22.8	1688	8388	16.8	24.3	291
Fannie Left	1500	12.8	1094	4049	5.1	16.4	19
Kill	453	3.5	394	275	2.9	0.5	62
Mosquito Left	250	5.7	115	252	2.7	2.1	91
Neekas	2100	17.7	11489	29214	34.6	16.0	24
Ripley Bay	0	14.7	0	0	0.0	15.7	0
Roscoe Trib 1	250	14.1	361	844	8.8	8.5	62
Spiller Trib 1	80	7.7	9	73	1.5	2.3	24
Webster	800	16.5	1307	837	5.2	23.9	No data

peated carcass scavenging. Eight months later (June 2007), we returned and again collected foliar samples from indicator species at paired carcass and control sites. These were not the same individuals as from the sampling in the fall. Carcass sites were clearly discernable by bony remnants and by the N burning of the moss. Indicator samples were taken within 10 cm beyond the edge of the N burn. Due to early seasonal senescence, false lily-of-the-valley could only be sampled in the spring (June 2007).

Salmon population data

Fisheries and Oceans Canada monitors salmon spawning populations in two of our 11 study watersheds, with data extending 60 years to 1950. From fall 2006 to 2009, we partnered with the Heiltsuk Integrated Resource Management Department based in Bella Bella, British Columbia, to inventory salmon populations in small streams not consistently surveyed by Fisheries and Oceans Canada. This included the remaining eight streams supporting salmon populations from this study. Fish in all streams were counted during at least three separate years (seven of 10 streams had all four years). The area-under-the-curve estimation method was used for cases when three or more counts occurred for a stream in a given year (English et al. 1992). When we had one or two counts, or if salmon abundance was very low, the peak live plus dead estimate method was used (30 of 74 estimates). The method used did not affect population estimates. In cases when both methods were used, strong correlations were observed between area-under-the-curve and peak live plus dead estimates for both chum ($R^2 = 0.932$, $n = 37$) and pink salmon ($R^2 = 0.964$, $n = 23$), with no difference in means by method (paired t tests: $p > 0.18$). Stream residency times of 10 days (live chum salmon) and 20 days (live pink salmon) were assumed.

Based on counts from 2006 to 2009, we derived an index of salmon spawning density (SD) (kilograms of salmon biomass per metre of spawning length) for each stream:

$$[1] \quad SD = \frac{\sum(N_i \times W_i)}{SL}$$

where N is the number of adult salmon, i is the salmon species (chum or pink salmon), W is salmon mass (chum sal-

mon: 3.5 kg, pink salmon: 1.2 kg), and SL is the length of the stream in which salmon spawned (metres). The lengths of the spawning sections of streams were obtained from individual stream walks. Salmon spawning density was $\log(x + 1)$ transformed for the analysis.

Stable isotope analysis

Plant indicator samples were dried and then ground into a fine powder with a heavy duty Wig-L-Bug grinder (Pike Technologies, Madison, Wisconsin). Ground plant samples (0.9–2.5 mg dry mass) collected in the fall were assayed for N and C isotope natural abundance using a Finnigan Delta Plus mass spectrometer interfaced via Conflo II to a NC2500 elemental analyzer at the Stable Isotope in Nature Laboratory (SINLAB) at the University of New Brunswick, Fredericton, New Brunswick. Ground plant samples (2.4–3.2 mg dry mass) collected in the spring were assayed for N and C isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California Davis Stable Isotope Facility. Isotopic signatures are expressed in delta notation (δ) as ratios in parts per mil (‰) deviations from known isotopic standards according to

$$[2] \quad \delta^{15}\text{N or } \delta^{13}\text{C (per mil)} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where R is the ratio of the heavy isotope (^{15}N or ^{13}C)/light isotope (^{14}N or ^{12}C). Ten plant samples from each of lanky moss, bunchberry, and foamflower (total $n = 30$ samples) processed at SINLAB were rerun at the University of California Davis and compared using repeated-measures ANOVA. Small but significant effects of lab were observed for $\delta^{15}\text{N}$, $\%N$, $\delta^{13}\text{C}$, and $\%C$. Significant lab \times species effects were observed for $\%N$ and $\delta^{13}\text{C}$. We therefore standardized SINLAB stable isotope data to University of California Davis data (Supplementary data Table S1).¹

Model selection

We use a model selection approach using the Akaike information criterion (AIC) to evaluate the relative importance of the candidate set of hypotheses for each dependent variable

¹Supplementary data are available with this article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/x2012-045>.

(%N and $\delta^{15}\text{N}$). AIC evaluates the predictive power of models with different combinations of variables based on the principal of parsimony, balancing optimal model fit with the number of parameters used (Burnham and Anderson 1998). We performed four analyses separated by indicator species groups and dependant variables: (1) lanky moss %N, (2) lanky moss $\delta^{15}\text{N}$, (3) herbaceous species %N, and (4) herbaceous species $\delta^{15}\text{N}$. Species separation was done because lanky moss and herbaceous arbuscular mycorrhizae plants are predicted to vary in their pathways of N uptake (Solga and Frahm 2006; Kranabetter and MacKenzie 2010) and because lanky moss has substantially lower foliar %N. Further, because false lily-of-the-valley was only sampled in the spring, herbaceous species models were simplified to include only spring data.

Mixed-effects models

Due to the hierarchical structure of the data set, we used mixed-effects modeling to account for the lack of independence and correlation structure among samples across different scales (McMahon and Diez 2007; Zuur et al. 2009). First, we chose the most parsimonious random structure using minimum AIC_c scores with a model that included the full set of fixed explanatory variables based on a priori hypotheses (Supplementary material Table S2). We excluded all three-way or greater interaction terms because none were predicted to be important. We set stream as a random effect and also applied a compound symmetry correlation structure among samples from carcass treatment – control pairs, nested within carcass sites, nested within streams. Because of observed heterogeneity in the residuals that violated assumptions of equal variances, we tested for the inclusion of variance identity parameters for carcass treatment and stream effects. Generally, we found higher variance in $\delta^{15}\text{N}$ and %N at treatment carcass sites versus control sites. The only exception was with lanky moss and %N as a dependent, where the top model included a variance identity parameter that accounted for large differences across streams (Supplementary material Table S3).

The second step of mixed-effects analysis is to choose the optimal fixed structure. Apart from the fixed effects of salmon carcass treatment, sampling season (fall and spring), and herbaceous species, our models included covariates at up to three scales: (1) salmon density and catchment area at the stream scale, (2) experimental carcass mass at the site scale, and (3) foliar %N at the individual plant scale (for $\delta^{15}\text{N}$ models). In initial analyses, red alder density was also used as a covariate at the stream scale. Because no relationships were observed between red alder density and plant $\delta^{15}\text{N}$ or %N, and because we were missing red alder density data from one stream, we removed red alder from the full final analyses.

We also hypothesized that several interaction terms would be important. Specific interactions tested included (a) treatment \times salmon density and treatment \times catchment area (plant N uptake from salmon carcasses varies across streams), (b) treatment \times carcass mass (larger carcasses provide greater N subsidies to plants), (c) treatment \times herbaceous species (some species can take up more N from salmon), (d) treatment \times %N ($\delta^{15}\text{N}$ –%N slopes become more positive with carcass addition), and (e) herbaceous species \times %N ($\delta^{15}\text{N}$ –%N

slopes vary by species). Starting with the full fixed models (Supplementary material Table S2), we used all model combinations and then assessed model performance using AIC_c (Zuur et al. 2009). Candidate models were computed using the maximum likelihood estimation method. Model weights and parameter likelihoods were calculated for models with $\Delta\text{AIC}_c < 4$. Models with $\Delta\text{AIC}_c < 2$ are shown in Supplementary material Table S4. The top model in each analysis was refit using restricted maximum likelihood to give parameter estimates. All analyses were conducted in R (R Development Core Team 2009) using the “nlme” package (Pinheiro et al. 2011).

Results

Effects of carcass addition

After 8 months, the addition of salmon carcasses led to increases in leaf %N by an average of 14%–60%, depending on plant species, compared with control sites (Fig. 1). We also observed elevated $\delta^{15}\text{N}$ signatures in the herbaceous species by 1.3‰–3.3‰. For lanky moss, we found only a marginal mean $\delta^{15}\text{N}$ increase of 0.5‰. Overall, the top models in each analysis explained 49%–69% of the variation in leaf %N or $\delta^{15}\text{N}$ (pseudo- R^2 values in Table 2).

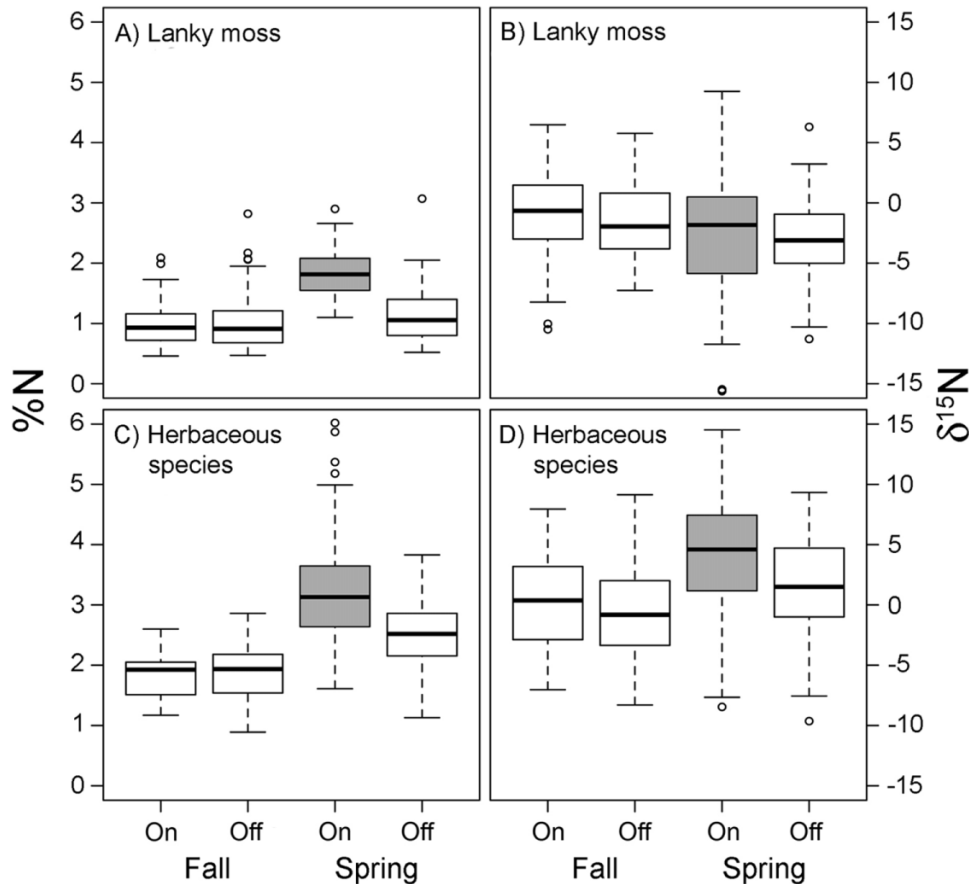
Carcass treatment effects were observed in all top models (Table 2). Significant coefficients for treatment were observed in the top model in both lanky moss analyses. In the herbaceous $\delta^{15}\text{N}$ model, treatment effects were greater in individuals with higher leaf %N (treatment \times foliar %N interaction). In the herbaceous %N models, a significant main effect of treatment was observed as well as treatment effects that varied by plant species (treatment \times plant species interaction).

Leaf %N and $\delta^{15}\text{N}$ values were more variable at sites where we added carcasses than at control sites that lacked carcasses (all $F > 1.5$, all $p < 0.015$; exception is lanky moss %N: $F_{[97,293]} = 0.82$, $p = 0.25$) (Fig. 1). In all species and across all watersheds, $\delta^{15}\text{N}$ signatures from spring carcass sites varied from -15.6‰ to 14.5‰ (range = 30.1‰), while control sites varied from -11.3‰ to 9.3‰ (range = 20.6‰). Leaf %N values varied from 1.1% to 6.0% (range = 4.9%) at experimental carcass sites and from 0.5% to 3.8% (range = 3.3%) at control sites. Increased %N and $\delta^{15}\text{N}$ variation at carcass sites compared with control sites means that these models perform better when a parameter that accounts for unequal variances is included (see Materials and methods).

Effects of foliar %N at the individual plant scale

We observed positive relationships between %N and $\delta^{15}\text{N}$ in all species, with $\delta^{15}\text{N}$ model performance increasing when individual plant foliar %N was included as a predictor (Fig. 2; Table 2). In lanky moss, the relationship between %N and $\delta^{15}\text{N}$ did not differ when carcasses were added. In the herbaceous models, %N and $\delta^{15}\text{N}$ values varied by plant species, and there were strong plant species \times %N and treatment \times %N interactions. Foamflower and false lily-of-the-valley typically had higher mean %N and $\delta^{15}\text{N}$, stronger treatment effects on %N and $\delta^{15}\text{N}$, and shallower control slopes of $\delta^{15}\text{N}$ –%N compared with bunchberry. For all herba-

Fig. 1. Foliar (A and C) %N and (B and D) $\delta^{15}\text{N}$ values in (A and B) lanky moss (*Rhytidiadelphus loreus*) and (C and D) herbaceous understory plants from chum salmon (*Oncorhynchus keta*) carcass site pairs (on/off carcass) in the fall immediately before carcass placement and in the spring 8 months after carcass decay. Shading indicates treatment effect. The horizontal line in each box is the median, the boxes define the 25%–75% quartile range, and the lines extend 2 standard deviations from the mean. Circles may be considered outliers.



ceous species, $\delta^{15}\text{N}$ –%N slopes were steeper at experimental carcass sites compared with control sites.

Effects of experimental carcass mass at the site scale

In lanky moss, higher %N and $\delta^{15}\text{N}$ values were observed from larger experimental carcasses (significant treatment \times carcass mass interactions) (Fig. 3; Table 2). For example, some $\delta^{15}\text{N}$ values at small experimental carcasses were highly depleted in $\delta^{15}\text{N}$ (–5 to –15‰), while $\delta^{15}\text{N}$ values from large carcasses were enriched (up to +10‰). In the herbaceous species, relationships between carcass mass and %N or $\delta^{15}\text{N}$ were weak and were not present in the top models.

Effects of salmon density and catchment area at the stream scale

Leaf %N and $\delta^{15}\text{N}$ values were higher at streams that had higher densities of spawning salmon (kilograms of salmon biomass per metre of spawning length) (Fig. 4; Table 2). Differences in stream salmon density also affected the impacts of carcass additions on total N uptake. Plants at streams with lower salmon densities showed greater increases in %N with carcass addition than streams with higher salmon density (treatment \times salmon spawning density interactions). In contrast, important treatment \times salmon spawning density interactions for $\delta^{15}\text{N}$ were not observed.

Strong effects of catchment area and treatment \times catchment area were not observed in this data set. All main effects and interactions with catchment area had p values >0.2 and thus were not present in the top models. For example, using a weighted parameter likelihood approach, where all possible models with a $\Delta\text{AIC}_c < 4$ are considered, catchment area parameter likelihood was low and ranged from 0.16 to 0.40 depending on the analysis. In comparison, salmon density occurred in all possible models with a $\Delta\text{AIC}_c < 4$ across each of the four analyses.

Discussion

Our experiments provide evidence of salmon nutrient uptake in four common riparian plant species during a period of late spring plant growth 8 months after salmon carcass placement. Using a hierarchical design, significant variation in leaf %N and $\delta^{15}\text{N}$ was accounted for by including differences among streams in background densities of spawning salmon, the mass of the carcasses that were added, the plant species, and, for $\delta^{15}\text{N}$, individual plant foliar %N. These experimental results complement previous correlational studies on the role of salmon in riparian plant nutrition and account for several compounding variables that are discussed below.

Our experiment shows that salmon nutrient addition can affect total N cycling to plants at multiple scales. At the

Table 2. Parameter estimates (\pm SE) for the top models in each analysis.

Analysis	Parameter	Value	SE	df	<i>t</i>	<i>p</i>
Lanky moss foliar %N ($R^2 = 0.69$)	Intercept	0.80	0.15	290	5.34	<0.001
	Treatment	0.55	0.11	290	4.80	<0.001
	Season	0.14	0.03	290	4.64	<0.001
	Salmon density	0.21	0.07	9	3.03	0.014
	Carcass mass	-0.0001	0.00002	86	-3.14	0.002
	Treatment \times salmon density	-0.10	0.030	290	-3.41	<0.001
	Treatment \times carcass mass	0.0001	0.00003	290	3.18	0.002
Lanky moss foliar $\delta^{15}\text{N}$ ($R^2 = 0.50$)	Intercept	-5.03	1.03	290	-4.87	<0.001
	Treatment	-3.90	1.43	290	-2.73	0.007
	Season	-2.27	0.33	290	-6.86	<0.001
	Salmon density	1.16	0.39	9	3.01	0.015
	Foliar %N	1.37	0.47	290	2.92	0.004
	Carcass mass	0.0001	0.0002	86	0.74	0.46
	Treatment \times carcass mass	0.001	0.0004	290	2.68	0.008
Herbaceous species foliar %N ($R^2 = 0.49$)	Intercept	1.80	0.18	198	10.22	<0.001
	Treatment	0.53	0.20	198	2.69	0.008
	Salmon density	0.29	0.09	8	3.10	0.015
	Species: false lily-of-the-valley	0.18	0.16	198	1.10	0.271
	Species: foamflower	0.45	0.18	198	2.50	0.013
	Treatment \times salmon density	-0.20	0.11	198	-1.74	0.083
	Treatment \times false lily-of-the-valley	0.87	0.27	198	3.26	0.001
Treatment \times foamflower	0.30	0.28	198	1.06	0.292	
Herbaceous species foliar $\delta^{15}\text{N}$ ($R^2 = 0.58$)	Intercept	-8.95	2.68	197	-3.34	0.001
	Treatment	-2.34	1.88	197	-1.25	0.214
	Salmon density	2.72	0.88	8	3.07	0.015
	Foliar %N	3.28	0.96	197	3.41	<0.001
	Species: false lily-of-the-valley	2.98	2.44	197	1.22	0.222
	Species: foamflower	5.57	2.81	197	1.98	0.049
	Foliar %N \times false lily-of-the-valley	-2.57	1.06	197	-2.42	0.016
Foliar %N \times foamflower	-3.14	1.14	197	-2.76	0.006	
Treatment \times foliar %N	1.37	0.63	197	2.16	0.032	

Note: R^2 values are derived from the linear relationship of observed versus model-fitted data for each analysis.

smallest scale near salmon carcasses, inorganic N inputs to soils can exceed $10 \text{ g N}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ (Gende et al. 2007), which we show can increase plant leaf %N by 14%–60% depending on plant species. In the herbaceous species, the greatest responses were observed in false lily-of-the-valley, and to a lesser extent foamflower, compared with bunchberry. Both false lily-of-the-valley and foamflower are nitrophilic, commonly found in nutrient-rich areas, and can capitalize on available N more effectively than bunchberry, which is a nutrient-poor indicator (Klinka et al. 1989; Morris et al. 2005; Kranabetter and MacKenzie 2010).

At larger scales across streams, %N values in control plants sampled from riparian areas showed an increase with spawning salmon density (kilograms per metre). While this pattern has been observed previously in correlational studies of $\delta^{15}\text{N}$ (Bilby et al. 2003; Nagasaka et al. 2006; Hocking and Reimchen 2009), this is one of the first demonstrations with %N. Foliar %N is known to scale strongly with soil nutrient status and overall site productivity (Hobbie et al. 2000; Craine et al. 2009; Kranabetter and MacKenzie 2010). With high rates of bear predation on salmon (e.g., 50% of the sal-

mon run), N inputs from the salmon–bear association can average over $2 \text{ g N}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ along each side of the stream and contribute roughly 25% of the riparian N budget (Helfield and Naiman 2006; Quinn et al. 2009). Thus, an across-stream gradient in productivity may be partly driven by salmon nutrient subsidies to riparian areas (Helfield and Naiman 2002; Drake and Naiman 2007; Hocking and Reynolds 2011). We recognize the limitations of our data set ($n = 11$ streams) when extrapolating to the stream scale, as there are likely to be many habitat factors that drive riparian productivity in addition to salmon density (e.g., large variation in Fig. 4). At a much larger scale, Hocking and Reynolds (2011) modeled the role of salmon and habitat across 50 streams in this same region and found that the physical features of watersheds such as stream size, slope, and canopy community mediate the effect of salmon subsidies on plant biodiversity. Our experimental approach supports these findings and provides evidence that N deficiencies can still remain in riparian areas that support high salmon abundance. For example, treatment and control curves of %N by salmon density fail to fully converge (see Fig. 4). In sites that are nu-

Fig. 2. Positive relationships between foliar $\delta^{15}\text{N}$ by %N vary by plant species, (A) lanky moss (*Rhytidiadelphus loreus*), (B) bunchberry (*Cornus canadensis*), (C) foamflower (*Tiarella trifoliata*), and (D) false lily-of-the-valley (*Maianthemum dilatatum*), and are often steeper at experimental carcass sites (solid circles, solid line) compared with control sites (open circles, broken line). Predicted lines are derived from top model parameter estimates (Table 2).

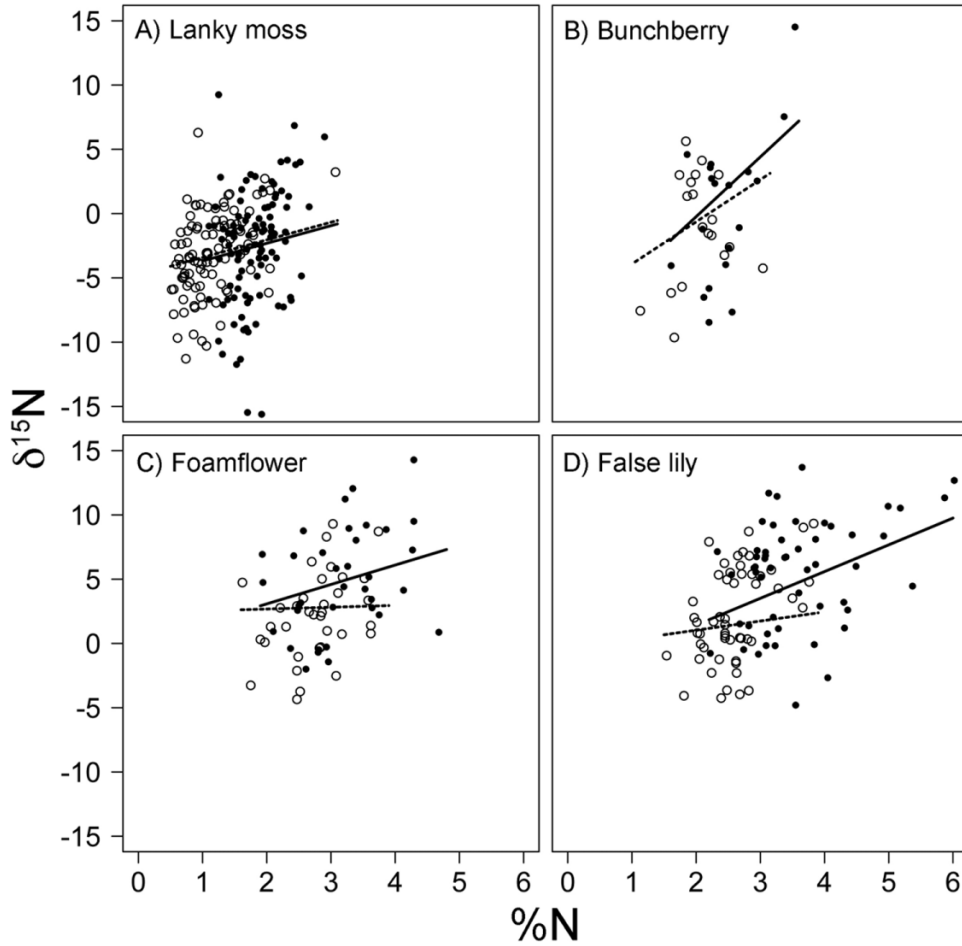
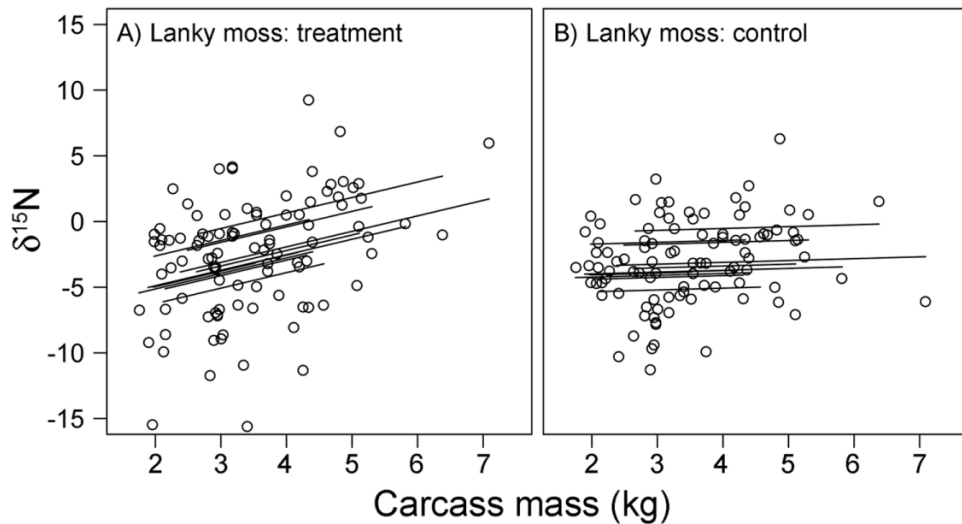
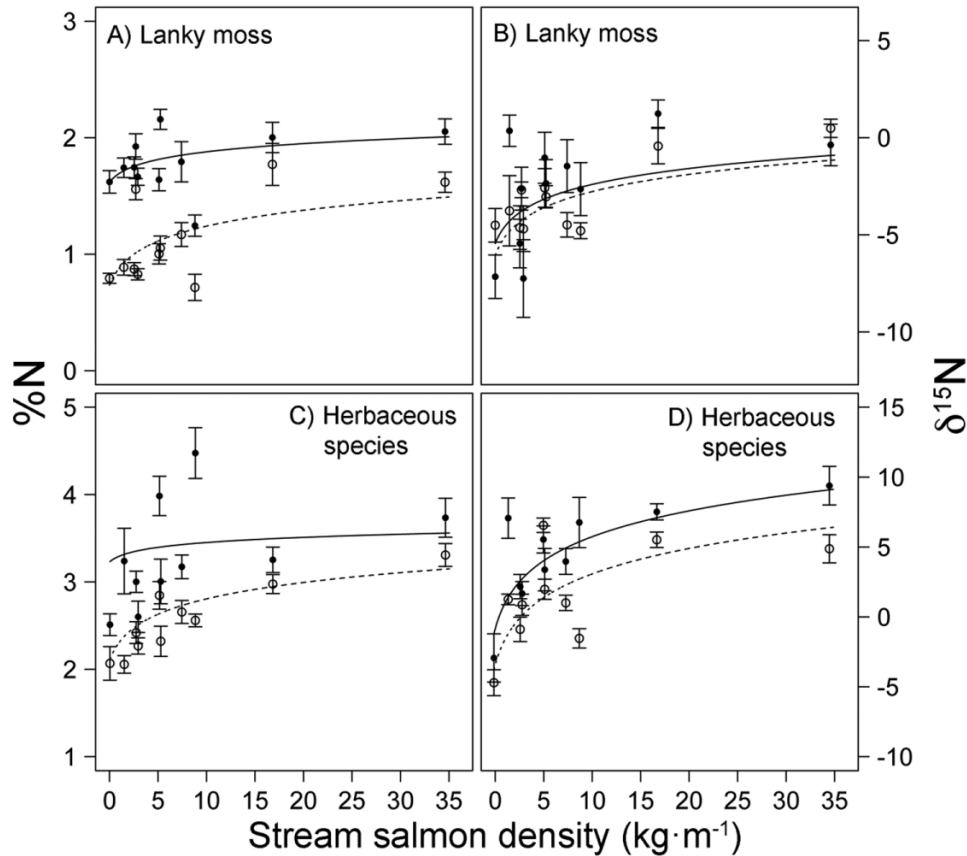


Fig. 3. Foliar $\delta^{15}\text{N}$ values in lanky moss (*Rhytidiadelphus loreus*) increase with experimental chum salmon (*Oncorhynchus keta*) carcass mass at (A) carcass treatment sites but not at (B) control sites. Multiple lines represent the predicted relationships for each watershed (random intercept by watershed).



Can. J. For. Res. Downloaded from www.nrcresearchpress.com by Simon Fraser University on 04/17/12
For personal use only.

Fig. 4. Mean (\pm SE) foliar (A and C) %N and (B and D) $\delta^{15}\text{N}$ in (A and B) lanky moss (*Rhytidiadelphus loreus*) and (C and D) herbaceous understory plants from spring treatment chum salmon (*Oncorhynchus keta*) carcass sites (solid circles) and spring control sites (open circles) in watersheds that vary by salmon density (per metre of spawning length). Predicted lines are derived from the top model parameter estimates (Table 2) where solid lines represent treatment and broken lines represent control. Note the differences in the %N and $\delta^{15}\text{N}$ scales.



trient limited, pulsed nutrient inputs can cause rapid microbial responses that transform existing soil organic materials into forms (e.g., NO_3^- and NH_4^+) that are more readily available to plants (Wardle 2002; Kranabetter et al. 2005; Gende et al. 2007). This may partially explain our greater treatment effects on leaf %N than on $\delta^{15}\text{N}$. For example, Bump et al. (2009) observed rapid foliar %N responses to wolf-killed moose carcasses and lagged increases in foliar $\delta^{15}\text{N}$.

We observed substantial variability in N isotopes, especially at salmon carcass sites ($\delta^{15}\text{N}$ range = 30.1‰) compared with control sites ($\delta^{15}\text{N}$ range = 20.6‰) and approaching the $\delta^{15}\text{N}$ range observed in a global data set of vascular plant species (Craine et al. 2009). Plant $\delta^{15}\text{N}$ variation reflects the range of soil N sources, plant–mycorrhizal associations, and fractionation processes during N transformations in ecosystems (Hogberg 1997; Hobbie et al. 2000; Evans 2001). Beside salmon streams, the wide range in plant $\delta^{15}\text{N}$ will partly reflect the mosaic and long-term legacy of the pinpoint nutrient deposits from salmon carcasses. However, interpreting plant $\delta^{15}\text{N}$ in correlational studies of salmon ecosystems is challenging because higher rates of gaseous N losses at sites with higher productivity can also lead to soil $\delta^{15}\text{N}$ enrichments (Hogberg 1997; Pinay et al. 2003). Furthermore, at sites that are N limited, there is increased dependence on mycorrhizal fungi, which transfer isotopically depleted N to their host plants (Hobbie et al. 2000; Kranabetter and MacKenzie 2010). Both processes result in

variable soil to plant N isotopic fractionation that confounds estimates of salmon-derived N in plants (e.g., Morris et al. 2005). We suggest that one way to account for these processes is to include %N as a predictor of $\delta^{15}\text{N}$. Positive correlations between foliar %N and $\delta^{15}\text{N}$ suggest that both %N and $\delta^{15}\text{N}$ can be used as indicators of site primary productivity (Kahmen et al. 2008; Craine et al. 2009). We show a significant positive slope between %N and $\delta^{15}\text{N}$ that varies by plant species and is steeper with the addition of salmon carcasses. The positive slope in bunchberry at control sites and the absence of this relationship in false lily-of-the-valley and foamflower at control sites suggest that mycorrhizal fungi may play a greater role in transferring N to bunchberry than to the other herb species. This result parallels observations by Morris et al. (2005) in a nearby salmon-bearing watershed who found that false lily-of-the-valley leaf $\delta^{15}\text{N}$ was similar to soil $\delta^{15}\text{N}$, while bunchberry leaf $\delta^{15}\text{N}$ was highly depleted relative to soil. Thus, while our experiments confirm that plants take up N derived from salmon carcasses, we caution against quantifying the amount of N contributed from salmon using $\delta^{15}\text{N}$ measurements alone. This means that previous estimates of percent salmon-derived or marine-derived N in plants that use constant marine and terrestrial end-members may be incorrect. Here, observed increases in $\delta^{15}\text{N}$ across the index of salmon density probably reflect a combination of increasing site productivity and long-term salmon subsidies with a $\delta^{15}\text{N}$ -enriched salmon source of N.

Another complexity to interpreting $\delta^{15}\text{N}$ involves the dual N uptake pathways of some nonvascular plants, shown here by the $\delta^{15}\text{N}$ variation in lanky moss. Many species of mosses can take up N not only from the substrate but also by absorption from the air directly through the leaf surface (Solga and Frahm 2006; Liu et al. 2008). We hypothesize that some lanky moss samples were highly enriched in $\delta^{15}\text{N}$ (e.g., +10‰) due to substrate N uptake, while others were highly depleted (e.g., -15‰) due to foliar uptake of volatilized NH_3 , which is $\delta^{15}\text{N}$ depleted (Hogberg 1997). NH_3 volatilization is likely an important process during the decay of salmon carcasses (Gende et al. 2007; Holtgrieve et al. 2009).

In conclusion, we provide the first experimental evidence that salmon carcasses shift N use in plants during an important period of spring plant growth many months after carcasses were deposited in forest areas, including substantial increases in total N (%N) in leaf tissues. Increasing foliar % N (and declining C/N ratio) is associated with greater plant palatability and litter quality, faster N cycling, and a shift in plant resource allocation towards stem and leaf growth rather than root development and foliar defense (Tilman 1988; Wardle et al. 2004). These patterns are consistent with shifts towards higher total N, increased tree growth, and nutrient-rich plant communities across larger-scale gradients in salmon spawning density where salmon subsidies ultimately influence riparian productivity (Helfield and Naiman 2006; Drake and Naiman 2007; Hocking and Reynolds 2011). However, we also caution that these impacts can be spatially restricted to salmon carcass locations and will vary across spatial scales with habitat and the productivities of plant species, sites, and watersheds. A substantial proportion of variation in leaf $\delta^{15}\text{N}$ was not explained by carcass addition or longer-term salmon spawning density. Thus, we do not recommend using plant $\delta^{15}\text{N}$ values alone to quantify the contribution of salmon to terrestrial communities. While Pacific salmon certainly play a significant role in structuring coastal ecosystems, the challenge that remains is how to integrate this information into ecosystem-based management.

Acknowledgements

We thank the Heiltsuk Nation, the Raincoast Conservation Foundation, and Fisheries and Oceans Canada for field support and salmon population data. In particular, we thank Mike Reid, Randy Carpenter, Jeff McConnachie, and Walter Campbell from the Heiltsuk Integrated Resource Management Department, Misty MacDuffee and Nicola Temple from the Raincoast Conservation Foundation, and Ralph Nelson, Matt Mortimer, and Dan Wagner from Fisheries and Oceans Canada. Thanks also to Eric Nelson and Mark Spoljaric for field assistance and Doug Braun, Andy Cooper, Emily Darling, Rachel Field, Joel Harding, Jennifer Linton, Michelle Nelson, Morgan Stubbs, and Jan Verspoor from Simon Fraser University. Funding was provided by a Natural Sciences and Engineering Council of Canada postdoctoral fellowship to M.D.H., Natural Sciences and Engineering Council of Canada discovery and accelerator grants to J.D.R., the Mountain Equipment Co-op, and the Tom Buell Research Chair partnership between the Pacific Salmon Foundation, the BC Leading Edge Fund, and Simon Fraser University.

References

- Bartz, K.K., and Naiman, R.J. 2005. Effects of salmon-borne nutrients on riparian soils and vegetation in Southwest Alaska. *Ecosystems* (N.Y.), **8**(5): 529–545. doi:10.1007/s10021-005-0064-z.
- Bilby, R.E., Beach, E.W., Fransen, B.R., Walter, J.K., and Bisson, P. A. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. *Trans. Am. Fish. Soc.* **132**(4): 733–745. doi:10.1577/T02-089.
- Bump, J.K., Peterson, R.O., and Vucetich, J.A. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecology*, **90** (11): 3159–3167. doi:10.1890/09-0292.1. PMID:19967871.
- Burnham, K.P., and Anderson, D.R. 1998. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science + Business Media Inc., New York.
- Craine, J.M., Elmore, A.J., Aidar, M.P.M., Bustamante, M., Dawson, T.E., Hobbie, E.A., Kahmen, A., Mack, M.C., McLaughlan, K.K., Michelsen, A., Nardoto, G.B., Pardo, L.H., Penuelas, J., Reich, P. B., Schuur, E.A.G., Stock, W.D., Templer, P.H., Virginia, R.A., Welker, J.M., and Wright, I.J. 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytol.* **183**(4): 980–992. doi:10.1111/j.1469-8137.2009.02917.x. PMID:19563444.
- Darimont, C.T., Paquet, P.C., and Reimchen, T.E. 2008. Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. *BMC Ecol.* **8**: 14. doi:10.1186/1472-6785-8-14. PMID:18764930.
- Drake, D.C., and Naiman, R.J. 2007. Reconstruction of Pacific salmon abundance from riparian tree-ring growth. *Ecol. Appl.* **17** (5): 1523–1542. doi:10.1890/06-1200.1. PMID:17708226.
- Drake, D.C., Smith, J.V., and Naiman, R.J. 2005. Salmon decay and nutrient contributions to riparian forest soils. *Northwest Sci.* **79**: 61–71.
- English, K.K., Bocking, R.C., and Irvine, J.R. 1992. A robust procedure for estimating salmon escapement based on the area-under-the-curve method. *Can. J. Fish. Aquat. Sci.* **49**(10): 1982–1989. doi:10.1139/f92-220.
- Evans, R.D. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends Plant Sci.* **6**(3): 121–126. doi:10.1016/S1360-1385(01)01889-1. PMID:11239611.
- Field, R.D., and Reynolds, J.D. 2011. Sea to sky: impacts of residual salmon-derived nutrients on estuarine breeding bird communities. *Proc. Biol. Sci.* **278**(1721): 3081–3088. doi:10.1098/rspb.2010.2731. PMID:21325324.
- Gende, S.M., Quinn, T.P., and Willson, M.F. 2001. Consumption choice by bears feeding on salmon. *Oecologia* (Berl.), **127**(3): 372–382. doi:10.1007/s004420000590.
- Gende, S.M., Edwards, R.T., Willson, M.F., and Wipfli, M.S. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience*, **52**(10): 917–928. doi:10.1641/0006-3568(2002)052[0917:PSIAAT]2.0.CO;2.
- Gende, S.M., Miller, A.E., and Hood, E. 2007. The effects of salmon carcasses on soil nitrogen pools in a riparian forest of southeastern Alaska. *Can. J. For. Res.* **37**(7): 1194–1202. doi:10.1139/X06-318.
- Helfield, J.M., and Naiman, R.J. 2002. Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. *Oecologia* (Berl.), **133**(4): 573–582. doi:10.1007/s00442-002-1070-x.
- Helfield, J.M., and Naiman, R.J. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems* (N.Y.), **9**(2): 167–180. doi:10.1007/s10021-004-0063-5.
- Hobbie, E.A., Macko, S.A., and Williams, M. 2000. Correlations

- between foliar $\delta^{15}\text{N}$ and nitrogen concentrations may indicate plant–mycorrhizal interactions. *Oecologia* (Berl.), **122**(2): 273–283. doi:10.1007/PL00008856.
- Hocking, M.D., and Reimchen, T.E. 2006. Consumption and distribution of salmon (*Oncorhynchus* spp.) nutrients and energy by terrestrial flies. *Can. J. Fish. Aquat. Sci.* **63**(9): 2076–2086. doi:10.1139/f06-110.
- Hocking, M.D., and Reimchen, T.E. 2009. Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. *Oikos*, **118**(9): 1307–1318. doi:10.1111/j.1600-0706.2009.17302.x.
- Hocking, M.D., and Reynolds, J.D. 2011. Impacts of salmon on riparian plant diversity. *Science*, **331**(6024): 1609–1612. doi:10.1126/science.1201079. PMID:21442794.
- Hogberg, P. 1997. Tansley Review No. 95: ^{15}N natural abundance in soil–plant systems. *New Phytol.* **137**(2): 179–203. doi:10.1046/j.1469-8137.1997.00808.x.
- Holtgrieve, G.W., Schindler, D.E., and Jewett, P.K. 2009. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. *Ecol. Res.* **24**(5): 1125–1135. doi:10.1007/s11284-009-0591-8.
- Holtgrieve, G.W., Schindler, D.E., Gowell, C.P., Ruff, C.P., and Lisi, P.J. 2010. Stream geomorphology regulates the effects on periphyton of ecosystem engineering and nutrient enrichment by Pacific salmon. *Freshw. Biol.* **55**(12): 2598–2611. doi:10.1111/j.1365-2427.2010.02489.x.
- Johnston, N.T., MacIsaac, E.A., Tschaplinski, P.J., and Hall, K.J. 2004. Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Can. J. Fish. Aquat. Sci.* **61**(3): 384–403. doi:10.1139/f03-172.
- Kahmen, A., Wanek, W., and Buchmann, N. 2008. Foliar $\delta^{15}\text{N}$ values characterize soil N cycling and reflect nitrate or ammonium preference of plants along a temperate grassland gradient. *Oecologia* (Berl.), **156**(4): 861–870. doi:10.1007/s00442-008-1028-8.
- Klinka, K., Krajina, V.J., Ceska, A., and Scagel, A.M. 1989. Indicator plants of coastal British Columbia. University of British Columbia Press, Vancouver, B.C.
- Kranabetter, J.M., and MacKenzie, W.H. 2010. Contrasts among mycorrhizal plant guilds in foliar nitrogen concentration and $\delta^{15}\text{N}$ along productivity gradients of a boreal forest. *Ecosystems* (N.Y.), **13**(1): 108–117. doi:10.1007/s10021-009-9304-y.
- Kranabetter, J.M., Banner, A., and de Groot, A. 2005. An assessment of phosphorus limitations to soil nitrogen availability across forest ecosystems of north coastal British Columbia. *Can. J. For. Res.* **35**(3): 530–540. doi:10.1139/x04-192.
- Liu, X.Y., Xiao, H.Y., Liu, C.Q., Li, Y.Y., and Xiao, H.W. 2008. Atmospheric transport of urban-derived NH_x : evidence from nitrogen concentration and $\delta^{15}\text{N}$ in epilithic mosses at Guiyang, SW China. *Environ. Pollut.* **156**(3): 715–722. doi:10.1016/j.envpol.2008.06.011. PMID:18644666.
- McMahon, S.M., and Diez, J.M. 2007. Scales of association: hierarchical linear models and the measurement of ecological systems. *Ecol. Lett.* **10**(6): 437–452. doi:10.1111/j.1461-0248.2007.01036.x. PMID:17498143.
- Moore, J.W., Schindler, D.E., Carter, J.L., Fox, J., Griffiths, J., and Holtgrieve, G.W. 2007. Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. *Ecology*, **88**(5): 1278–1291. doi:10.1890/06-0782. PMID:17536413.
- Morris, A.E.L., Stark, J.M., and Gilbert, B.K. 2005. Evaluation of isotopic fractionation error on calculations of marine-derived nitrogen in terrestrial ecosystems. *Can. J. For. Res.* **35**(7): 1604–1616. doi:10.1139/x05-094.
- Nagasaka, A., Nagasaka, Y., Ito, K., Mano, T., Yamanaka, M., Katayama, A., Sato, Y., Grankin, A.L., Zdorikov, A.I., and Boronov, G.A. 2006. Contributions of salmon-derived nitrogen to riparian vegetation in the northwest Pacific region. *J. For. Res.* **11**(5): 377–382. doi:10.1007/s10310-006-0226-7.
- Naiman, R.J., Bilby, R.E., Schindler, D.E., and Helfield, J.M. 2002. Pacific salmon, nutrients and the dynamics of freshwater and riparian ecosystems. *Ecosystems* (N.Y.), **5**(4): 399–417. doi:10.1007/s10021-001-0083-3.
- Pinay, G., O’Keefe, T.C., Edwards, R., and Naiman, R.J. 2003. Potential denitrification activity in the landscape of a western Alaska drainage basin. *Ecosystems* (N.Y.), **6**(4): 336–343. doi:10.1007/s10021-002-0169-6.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Development Core Team. 2011. nlme: linear and non-linear mixed-effects models. R package version 3.1-100. Available from www.R-project.org.
- Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manage.* **22**(1–2): 119–154. doi:10.1016/0378-1127(87)90100-9.
- Quinn, T.P., Carlson, S.M., Gende, S.M., and Rich, H.B., Jr. 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Can. J. Zool.* **87**(3): 195–203. doi:10.1139/Z09-004.
- R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from www.R-project.org.
- Reimchen, T.E. 2000. Some ecological and evolutionary aspects of bear–salmon interactions in coastal British Columbia. *Can. J. Zool.* **78**(3): 448–457. doi:10.1139/z99-232.
- Solga, A., and Frahm, J.P. 2006. Nitrogen accumulation by six pleurocarpus moss species and their suitability for monitoring nitrogen deposition. *J. Bryol.* **28**(1): 46–52. doi:10.1179/174328206X104552.
- Tiegs, S.D., Chaloner, D.T., Levi, P., Ruegg, J., Tank, J.L., and Lamberti, G.A. 2008. Timber harvest transforms ecological roles of salmon in southeast Alaska rain forest streams. *Ecol. Appl.* **18**(1): 4–11. doi:10.1890/07-0655.1. PMID:18372551.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J.
- Verspoor, J.J., Braun, D.C., and Reynolds, J.D. 2010. Quantitative links between Pacific salmon and stream periphyton. *Ecosystems* (N.Y.), **13**(7): 1020–1034. doi:10.1007/s10021-010-9371-0.
- Wardle, D.A. 2002. Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton, N.J.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., and Wall, D.H. 2004. Ecological linkages between aboveground and belowground biota. *Science*, **304**(5677): 1629–1633. doi:10.1126/science.1094875. PMID:15192218.
- Wilkinson, C.E., Hocking, M.D., and Reimchen, T.E. 2005. Uptake of salmon-derived nitrogen by mosses and liverworts in coastal British Columbia. *Oikos*, **108**(1): 85–98. doi:10.1111/j.0030-1299.2005.13277.x.
- Willson, M.F., and Halupka, K.C. 1995. Anadromous fish as keystone species in vertebrate communities. *Conserv. Biol.* **9**(3): 489–497. doi:10.1046/j.1523-1739.1995.09030489.x.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer Science + Business Media, New York.