

# Riparian soil nitrogen cycling and isotopic enrichment in response to a long-term salmon carcass manipulation experiment

MEGAN L. FEDDERN<sup>1,†</sup> ,<sup>1,†</sup> GORDON W. HOLTGRIEVE,<sup>1</sup> STEVEN S. PERAKIS,<sup>2</sup> JULIA HART,<sup>1</sup> HYEJOO RO,<sup>1</sup> AND THOMAS P. QUINN<sup>1</sup>

<sup>1</sup>*School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA*

<sup>2</sup>*Forest and Rangeland Ecosystem Science Center, US Geological Survey, Corvallis, Oregon, USA*

**Citation:** Feddern, M. L., G. W. Holtgrieve, S. S. Perakis, J. Hart, H. Ro, and T. P. Quinn. 2019. Riparian soil nitrogen cycling and isotopic enrichment in response to a long-term salmon carcass manipulation experiment. *Ecosphere* 10(11): e02958. 10.1002/ecs2.2958

**Abstract.** Pacific salmon acquire most of their biomass in the ocean before returning to spawn and die in coastal streams and lakes, thus providing subsidies of marine-derived nitrogen (MDN) to freshwater and terrestrial ecosystems. Recent declines in salmon abundance have raised questions of whether managers should mitigate for losses of salmon MDN subsidies. To test the long-term importance of salmon subsidies to riparian ecosystems, we measured soil nitrogen cycling in response to a 20-yr manipulation where salmon carcasses were systematically removed from one bank and deposited on the opposite bank along a 2-km stream in southwestern Alaska. Soil samples were taken at different distances from the stream bank along nine paired transects and measured for organic and inorganic nitrogen concentrations, and nitrogen transformation rates. Marine-derived nitrogen was measured using  $^{15}\text{N}/^{14}\text{N}$  for bulk soils, and  $\text{NH}_4^+$  and  $\text{NO}_3^-$  soil pools. Stable isotope analyses confirmed  $^{15}\text{N}/^{14}\text{N}$  was elevated on the salmon-enhanced bank compared to the salmon-depleted bank. However,  $^{15}\text{N}/^{14}\text{N}$  values of plant-available inorganic nitrogen exceeded the  $^{15}\text{N}/^{14}\text{N}$  of salmon inputs, highlighting nitrogen isotope fractionation in soils that raises significant methodological issues with standard MDN assessments in riparian systems. Surprisingly, despite 20 yr of salmon supplementation, the presence of MDN did not cause a long-term increase in soil nitrogen availability. This finding indicates the importance of MDN to ecosystem nitrogen biogeochemistry, and riparian vegetation may be overestimated for some systems. Given that essential nutrients can also be pollutants, we urge more critical analyses of the role of MDN to inform compensatory mitigation programs targeting salmon nutrient enhancement.

**Key words:** Alaska; boreal forest; marine-derived nitrogen; riparian; salmon; soil biogeochemistry; stable isotopes.

**Received** 24 September 2019; **accepted** 7 October 2019. <sup>a</sup>Corresponding Editor: Debra P. C. Peters.

**Copyright:** © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

<sup>†</sup> **E-mail:** mfeddern@uw.edu

## INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) migration from marine environments to freshwater spawning grounds is a textbook case of cross-ecosystem nutrient subsidies. Dozens of studies have identified the presence of marine-derived nitrogen (MDN) from salmon cross-ecosystem boundaries from oceans to freshwaters and into the terrestrial environment (sensu Polis et al. 2004, Gende

et al. 2002, Schindler et al. 2003). Declines in Pacific salmon populations in many areas, caused by human activities (overharvest, habitat degradation, dams; Gustafson et al. 2007), and the concern over loss of MDN to coastal watersheds have made restoration of salmon nutrients a focal point for many management and mitigation strategies. For example, in the Columbia River Basin where Pacific salmon populations have declined, legislation requiring

compensatory mitigation has led to nutrient enhancement programs, on the foundation that habitats have lost critical nutrients from salmon, and therefore, augmentation is necessary to maintain ecosystem function (Collins et al. 2015).

Salmon bring nutrients, including phosphorus (P) and other compounds in addition to nitrogen (N), into freshwater and terrestrial food webs through two pathways: (1) direct consumption of tissues by predators and scavengers, and (2) autotrophic or heterotrophic assimilation of nutrients released as salmon spawn, die, and eventually decay (Gende et al. 2002). Salmon are enriched in the heavy isotope of nitrogen ( $^{15}\text{N}$ ) relative to the light isotope ( $^{14}\text{N}$ ) when compared to terrestrial and watershed-derived N. This isotopic enrichment has been used to quantitatively trace the presence of salmon-derived nutrients into watersheds (Schindler et al. 2003). For example, the proportion of N derived from salmon ranges from approximately 30% to 75% in fish and aquatic invertebrates (Naiman et al. 2002), 10–90% in piscivorous mammals such as bears, and 20–40% in piscivorous fishes near salmon spawning grounds (Bilby et al. 1996, Hilderbrand et al. 1999, Chaloner et al. 2002, Claeson et al. 2006).

The annual return of this predictable and abundant, yet temporally limited, high-quality resource drives the foraging ecology of both terrestrial and aquatic consumers (Schindler et al. 2013, Quinn 2018). Carcasses and roe are documented food sources for over 22 species of mammals, birds (Cederholm et al. 1989), fishes (Scheuerell et al. 2007), and invertebrates (Minakawa et al. 2002, Meehan et al. 2005, Winder et al. 2005). Bear population density, body size, and reproductive output have been correlated with meat (primarily salmon) consumption, with piscivorous populations having 55 times higher density than their meat-limited counterparts (Hilderbrand et al. 1999). In aquatic ecosystems, salmon carcass abundance has been correlated with elevated growth rates of invertebrates, and with size, density, and condition factor of juvenile salmonids (Bilby et al. 1998, Minakawa et al. 2002, Wipfli et al. 2003).

The presence of MDN has been documented in aquatic primary producers, though its overall ecological importance remains ambiguous. Via this bottom-up pathway, salmon supply critical

limiting nutrients that can increase primary and/or bacterial productivity, which are subsequently transferred to consumers and up through the food web (Wipfli et al. 1998, Chaloner et al. 2002, Holtgrieve and Schindler 2011). Higher salmon returns are correlated with MDN signatures in lower trophic levels including zooplankton and periphyton (Kline et al. 1993, Finney et al. 2000, Holtgrieve et al. 2010). Both direct ecological evidence and paleolimnological evidence suggest MDN and P positively influence primary production in lakes (Moore et al. 2007). For example, commercial fisheries remove upwards of two-thirds of MDN, which would otherwise enter some freshwater lakes in Alaska, resulting in a threefold decline in algal production (Schindler et al. 2005). In stream ecosystems, the decomposition of salmon increases dissolved organic and inorganic nutrients, including highly available forms such as orthophosphate ( $\text{PO}_4^{3-}$ ) and ammonia/ammonium ( $\text{NH}_3/\text{NH}_4^+$ ). These nutrients can stimulate epilithon growth (bacteria and algae), though the magnitude of this response is highly variable and dependent on other growth limiting factors such as sunlight and disturbance (Johnston et al. 2004, Mitchell and Lamberti 2005, Janetski et al. 2009).

In the terrestrial realm, bottom-up effects of MDN from salmon are also thought to be ecologically important, though this has been difficult to demonstrate rigorously. Studies across the range of salmon in North America have inferred that up to 26% of foliar N in riparian plants is marine-derived, with foliar N levels often correlating with salmon abundance and distance from the salmon spawning location (e.g., Hocking and Reynolds 2012, Reimchen and Fox 2013). While MDN is clearly present in terrestrial producers, direct evidence of the importance of MDN for ecosystem function and productivity is much less evident. Helfield and Naiman (2001) measured tree growth increments in areas with and without salmon and found higher growth in one species (Sitka spruce) in areas where salmon nutrients were present, although these findings were later contested on statistical grounds (Kirchhoff 2003). Hocking and Reynolds (2012) observed decreased understory plant diversity with increasing salmon abundance, though this pattern was largely attributed to increased dominance of a single N-tolerant species

(salmonberry). Reimchen and Fox (2013) suggested that salmon abundance increased tree growth, but tree ring  $^{15}\text{N}/^{14}\text{N}$  values were not related to salmon abundance; other growth limiting factors such as temperature and location were important covariates. Most recently, Quinn et al. (2018) examined tree growth increments in the riparian zone of a small Alaskan stream before and after a 20-yr, >200,000 kg, salmon carcass manipulation. In the two decades prior to manipulation, white spruce (*Picea glauca*) on average grew faster on one bank compared to the other. The subsequent decades of carcass manipulation enriched the naturally slower growing side and were associated with increased growth. However, the growth effect of the carcasses was smaller than the natural side-to-side variation, and other important site and landscape factors such as forest demography, climate, aspect, and water availability were not fully considered, a common trend in MDN studies of riparian vegetation.

Interpreting the contributions of MDN to terrestrial producers using stable isotopes is often highly simplified, and does not consider how variability of N sources and overall N availability may confound results. MDN analyses apply simple two-source mixing models to infer the proportion of total N derived from salmon. When applied to terrestrial vegetation, the terrestrial end-member for the mixing models is typically determined by sampling the  $^{15}\text{N}/^{14}\text{N}$  of the same species of plant either laterally away from the stream (where MDN contribution is expected to be small), upstream of barriers to salmon migration, or in watersheds without salmon. For the salmon end-member, a single value equal to the average  $^{15}\text{N}/^{14}\text{N}$  of salmon ( $12.62 \pm 0.31$  per mil for sockeye salmon) is typically used (Appendix S1: Eq. S1). Inherent assumptions with these models therefore include the following: (1) reference sites are biogeochemically similar to salmon sites, and (2) the isotopic signature of salmon is unchanged in the soils prior to plant uptake. N cycling in soils is strongly controlled by position in the landscape and contains a number of chemical reactions that fractionate N isotopically (Högberg 1997, Wheeler et al. 2014; Fig. 1); therefore, these assumptions may not be valid.

Experiments examining the contributions of MDN are often limited by short timescales, and

relatively few experiments investigate changes in plant-available soil N pools important to plant nutrient uptake and growth (Collins et al. 2015). Studies examining spatial and temporal impacts of salmon on soil inorganic N have identified highly localized responses (effects only observed <30 cm from carcasses) where soil ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ) increase for weeks to months (Drake et al. 2005, Gende et al. 2007, Holtgrieve et al. 2009) and rarely consider long-term N retention in the system. Experiments typically examine the contributions of MDN by nutrient addition not nutrient removal; however, nutrient removal is important for understanding the effects of lower numbers of salmon returning to coastal watersheds due to fishing, habitat reduction, and climate change. In addition, previous research observed a strong effect of watershed slope on  $^{15}\text{N}/^{14}\text{N}$  in riparian plants and attributed this to topography concentrating carcasses near streams (Hocking and Reynolds 2012). However, watershed topography also influences soil water content and N cycling, which affect N isotopes (Högberg 1997) and therefore complicate MDN assessments.

To resolve the extent to which salmon carcasses contributed MDN to plant-available N pools and the long-term ecological response to this subsidy, we present a second study of the 20-yr carcass manipulation experiment described in Quinn et al. (2018). While Quinn et al. focused on tree growth before and after the manipulation, the objective of this work was to determine whether prolonged enhancement and reduction of salmon subsidies altered long-term soil N cycling, similar to that documented in forests receiving N fertilizer additions (Prescott et al. 1992, 1995, Lu et al. 2010). If long-term changes in N availability due to salmon enhancement or reduction were observed, compensatory nutrient subsidies may be valuable for maintaining critical ecosystem functions in riparian areas with reduced salmon returns. If not, then the addition of nutrients as a management response to low salmon returns may have unintended negative consequences (sensu Compton et al. 2006). Specifically, the importance of MDN to riparian ecosystems was assessed by (1) evaluating the presence of MDN in soils enhanced and depleted in salmon carcasses through bulk stable isotope analysis of N, (2) quantifying the response of

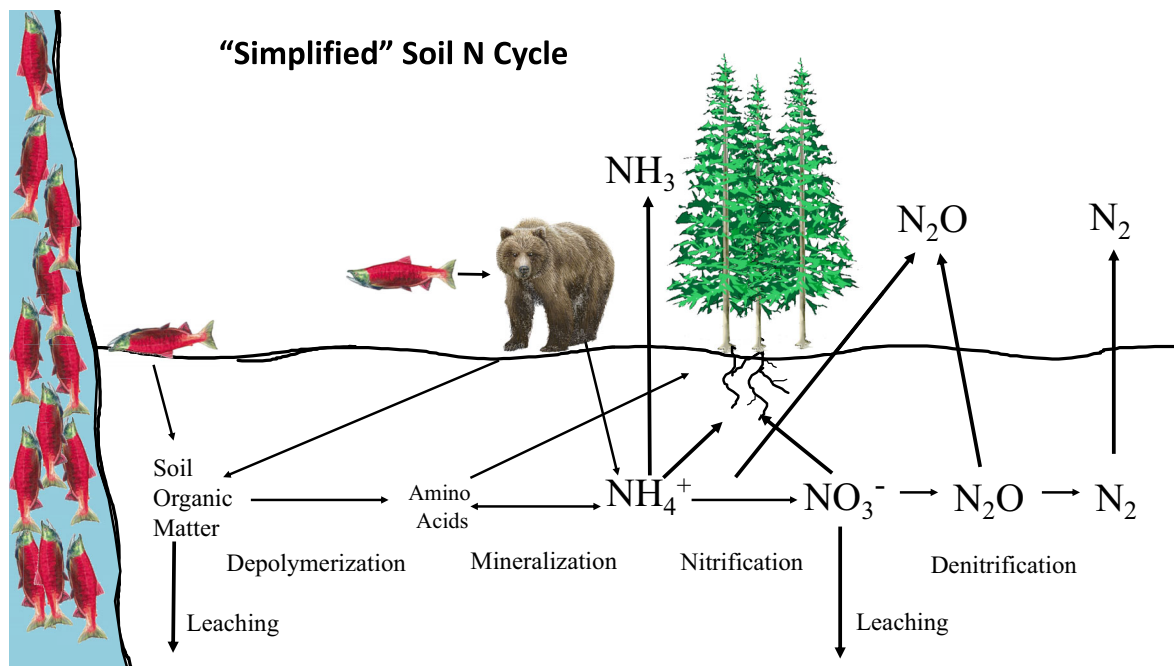


Fig. 1. Nitrogen pathways in soil where marine-derived nitrogen enters terrestrial systems via decay of salmon organic tissues or excretion from direct salmon consumers such as bears. Arrows represent conversion pathways with the potential to impart isotopic fractionations on plant-available nitrogen ( $\text{NH}_4^+$  or  $\text{NO}_3^-$ ).

plant-available N pools ( $[\text{NH}_4^+]$  and  $[\text{NO}_3^-]$ ) and their rate of supply via mineralization and nitrification, (3) considering how fractionation in soils may impact mixing model results by measuring  $^{15}\text{N}/^{14}\text{N}$  of  $\text{NH}_4^+$ , and (4) comparing these results to the vegetation responses measured by Quinn et al. 2018 at the same site. This research fills key knowledge gaps by examining the long-term legacy of inorganic N pools, both salmon addition and removal, and considering site variability that may impact the assumption of biogeochemical similarity between test and control sites, following a 20-yr manipulation.

## METHODS

### Site description and sample collection

This study was conducted on Hansen Creek, a ~2 km long, second-order tributary to Lake Aleknagik in the Wood River system of Bristol Bay, AK, and uses the same carcass manipulation described in Quinn et al. (2018). Briefly, from 1997 to 2016 an average of 10,853 sockeye salmon returned to the stream annually. Overstory vegetation is dominated by white spruce and paper

birch (*Betula papyrifera*), and unlike many other watersheds in the region, it has a low density of symbiotic  $\text{N}_2$ -fixing alder (*Alnus* spp. Helfield and Naiman 2002). From 1997 to 2016, the stream was surveyed daily during the annual sockeye salmon (*Oncorhynchus nerka*) run and all dead salmon were removed from the creek and the river right bank to a distance of about 5 m and tossed onto the river left bank. To avoid double-counting carcasses on the river left bank, carcasses naturally occurring on the river left bank were also relocated to a distance of about 5 m; thus, all carcasses (with the exception of those moved by wildlife; see Quinn et al. 2018) were located between 3 and 6 m on the river left bank. Therefore, the right side of the stream experienced a reduction in carcass density (depletion), while the left bank received an increase in carcasses (enhancement). Quinn et al. (2018) calculated that prior to manipulation, the both banks averaged 4545.6 kg of salmon annually and that after manipulation, the river left bank averaged 13,381 kg of salmon and the river right bank averaged 2,260 kg of salmon annually, a 9.6-fold difference. Approximately 108,530 individual



fish (in many cases partially consumed by bears) were translocated over the 20-yr period representing a total of 267,620 kg of salmon, 8,028 kg of N, and 1,356 kg of phosphorus (P; Quinn et al. 2018). To estimate the mass of nitrogen added per m<sup>2</sup>, we assumed all salmon were tossed within 6 m of the creek's edge along the entire 2-km creek, thus within a 12,000-m<sup>2</sup> area.

Soil samples were collected from the riparian zone on 13 July 2017 (prior to arrival of salmon and any carcass manipulation that season) along nine sets of paired transect sites. Paired transects were used to control for naturally occurring salmon density. Transects covered the full 2 km length of the stream and were selected to represent typical riparian vegetation and high annual carcass abundance. Each transect included sampling sites at 1, 3, 6, 10, and 20 m from the bank-full point. Sampling occurred during peak growing season (i.e., during the typical time of maximum normalized difference vegetation index [NDVI]; Kasischke and French 1995), approximately one week prior to the arrival of the first salmon in the creek. Thus, our sampling was intended to capture the long-term legacy of MDN manipulations and to avoid short-term pulses following salmon return that may not represent a system-level change in N availability, retention, and recycling in soils, which has already been documented in multiple short-term studies. A 5 × 5 × 10 cm soil column was taken for each sample site, and the litter layer was removed before storing at 4°C in airtight plastic bags for 48 h prior to processing. Nitrogen cycling decreases dramatically with depth, sampling at this depth includes the O and A horizons where a majority of nitrogen cycling occurs (Sparks et al. 1996).

#### Soil nitrogen concentrations and transformations

Soil [NH<sub>4</sub><sup>+</sup>], [NO<sub>3</sub><sup>-</sup>], and N transformations were measured according to Holtgrieve et al. (2009). Briefly, we extracted 10–12 g of field-moist sieved (<2 mm) soil with 100 mL of 2 mol/L potassium chloride (KCl) by shaking for 60 s, followed by settling for 24 h prior to filtration through pre-leached Whatman #1 filter papers. Approximately 8 mL of filtered extracts was frozen and later analyzed colorimetrically for [NH<sub>4</sub><sup>+</sup>] and [NO<sub>3</sub><sup>-</sup>] with an Auto-Analyzer 500 Model (Perstorp Analytical, Analytical

Service Station, Seattle, Washington, USA). The remaining extract was frozen prior to stable isotope analyses (see *Stable isotope analysis*). To estimate inorganic N transformation rates, a second 10–12 g soil subsample was incubated aerobically in the dark for 15 d at 20°C prior to extraction, filtration, and analysis as above. Net mineralization was calculated as the sum of the change in [NH<sub>4</sub><sup>+</sup>] and [NO<sub>3</sub><sup>-</sup>] divided by the incubation duration, and net nitrification was calculated as the change in NO<sub>3</sub><sup>-</sup> over the incubation duration and represents the conversion of NH<sub>4</sub><sup>+</sup> to NO<sub>3</sub><sup>-</sup> (Hart et al. 1994). [N<sub>org</sub>] was calculated by taking total soil N concentration, [N<sub>tot</sub>] determined by elemental analysis (see *Stable isotope analysis*), and subtracting [NH<sub>4</sub><sup>+</sup>] and [NO<sub>3</sub><sup>-</sup>]. All soil N values were corrected for gravimetric soil water content (g H<sub>2</sub>O/g dry soil) determined by drying 50–100 g of field-moist soil at 105°C for 48 h (Gardner 1986).

#### Stable isotope analysis

Fresh soil was freeze-dried for 48 h and ground into a uniform powder (<212 μm) using a ball mill prior to analysis for nitrogen (<sup>15</sup>N/<sup>14</sup>N) and carbon (<sup>13</sup>C/<sup>12</sup>C) stable isotope ratios at the University of Washington's IsoLab using a Costech Elemental Analyzer, ConFlo III, MAT253 for continuous flow-based measurements. This procedure also provided total carbon and nitrogen concentrations, [C<sub>tot</sub>] and [N<sub>tot</sub>], and percent C and N, of the soil samples. Data are reported using standard delta notation, which describes the per mil deviation in the ratio of heavy to light isotope relative to accepted international standards, in this case, air and Vienna Pee Dee Belemnite for N and C, respectively (Schoeninger et al. 1983).

For <sup>15</sup>N/<sup>14</sup>N stable isotope analysis of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>, KCl extracts were placed in Erlenmeyer flasks for diffusion using modified methods from Sigman et al. (1997) and Holmes et al. (1998). To retrieve NH<sub>4</sub><sup>+</sup> as gaseous NH<sub>3</sub>, 300 mg of MgO and an acid trap (1-cm glass fiber filter treated with KHSO<sub>4</sub> and sealed in Teflon) were added to each flask, immediately stoppered, sealed with parafilm, and shaken for six days prior to removal of acid traps to a desiccator for 3–4 d. The same extracts were then shaken uncovered for one day to remove any remaining NH<sub>4</sub><sup>+</sup>. To retrieve NO<sub>3</sub><sup>-</sup> as NH<sub>3</sub>, another 300 mg of MgO was added to each extract and

immediately followed by 75 mg of Devarda's alloy and an acid trap, then processed as above. Samples were run in four separate batches, for each batch, three blanks, KCl with no soil extract, and three reference standards,  $\text{NH}_4\text{Cl}$  and  $\text{KNO}_3$  with known  $^{15}\text{N}/^{14}\text{N}$ , were also run. Batch blanks showed quantifiable N from the KCl; therefore, a two-source mixing model correction was applied to both samples and reference standards to calculate the blank corrected value,  $\delta^{15}\text{N}_{\text{bl},x}$ , using Eq. 1:

$$\delta^{15}\text{N}_{\text{bl},x} = \frac{\delta^{15}\text{N}_x(\text{N}_{\text{bl},b} + \text{N}_x) - (\delta^{15}\text{N}_{\text{bl},b} \times \text{N}_{\text{bl},b})}{\text{N}_x} \quad (1)$$

where  $b$  represents an individual batch, and  $x$  represents an individual sample;  $\text{N}_{\text{bl},b}$  is the average measured mass ( $\mu\text{g}$ ) of nitrogen in a blank for a given batch; and  $\delta^{15}\text{N}_{\text{bl},b}$  is the average measured  $\delta^{15}\text{N}$  of blanks for a given batch.  $\delta^{15}\text{N}_x$  is the  $\delta^{15}\text{N}$  value for a given sample, and  $\text{N}_x$  is the mass of nitrogen ( $\mu\text{g}$ ) measured in the sample. A standard correction was then applied to the blank corrected measurements using Eq. 2:

$$\delta^{15}\text{N}_c = \delta^{15}\text{N}_{\text{bl},x} - (\text{standard}_{\text{m},x} - \text{standard}_t) \quad (2)$$

where  $\text{standard}_{\text{m},x}$  is the average measured value of the standard for a given batch, and  $\text{standard}_t$  is the true value of the standard. All reported  $\delta^{15}\text{N}$ - $\text{NH}_4^+$  and  $\text{NO}_3^-$  values are expressed as the  $\delta^{15}\text{N}_c$ , where a blank and a standard correction have been applied. The internal standard of the  $\delta^{15}\text{N}$  of  $\text{NO}_3^-$  had a  $-23.6\%$  to  $9.6\%$  deviation from its true value, indicating a significant methodological issue. Given there was not enough sample to refine these methods and the potential for standard corrections of this magnitude to be misleading,  $\delta^{15}\text{N}$  of  $\text{NO}_3^-$  data are not reported here.

C:N ratio, percent nitrification, and percent carbon were also calculated to evaluate N availability and retention across the sites. C:N ratios were calculated on a mass basis. Percent nitrification was calculated as:

$$\% \text{ Nitrification} = 100 \times \frac{\text{Net Nitrification}}{\text{Net Mineralization}} \quad (3)$$

### Statistical analyses

We used multi-model selection procedures via Akaike's information criterion (AIC) to identify how salmon carcass treatment governed a suite of response variables using the stats v3 and lme4 packages in R. These response variables were  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of bulk soil,  $\delta^{15}\text{N}$  of  $\text{NH}_4^+$ ,  $[\text{NH}_4^+]$  and  $[\text{NO}_3^-]$ , net mineralization and net nitrification,  $[\text{N}_{\text{org}}]$ , gravimetric water content (GW), and C:N. For all response variables, candidate models (Appendix S1: Table S1) included bank (left vs. right) and distance from river's edge. A linear and quadratic interaction structure for bank and distance was fit for each response variable, and these interaction terms allowed the effect of distance to vary by bank and the effect of bank to vary by distance. A  $\log_e$  transformation was used for the distance. Gravimetric water was considered as a covariate for all response variables, soil  $[\text{NH}_4^+]$  was considered as a covariate for net nitrification, and soil  $[\text{N}_{\text{org}}]$  was considered as a covariate for net mineralization, given  $[\text{N}_{\text{org}}]$  and  $[\text{NH}_4^+]$  function as the substrate for mineralization and nitrification, respectively.  $[\text{N}_{\text{tot}}]$  was considered as a covariate for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of bulk soil, and for  $\delta^{15}\text{N}$  of  $\text{NH}_4^+$ . The best model was selected from the candidate model set using AIC for each response variable.

Two model parameters—bank (left vs. right) and distance from the stream—were used to test salmon carcass and site variability impacts to soil N cycling. Changing the number of salmon carcasses on each bank was the primary goal of the manipulation; however, the two banks potentially differ in aspect, soil type, and drainage, which can affect nutrient cycling and generate a bank effect unrelated to salmon manipulation (Chapin et al. 2011). Notably, the salmon-enhanced bank has a northwest-facing slope approximately 20 m of the creek edge. Distance from the stream reflects the magnitude of salmon manipulation because carcasses were placed primarily 3–6 m from the stream's edge. Other factors such as vegetation, soil type, and water availability can also change with distance laterally from the stream edge, though such changes are expected to be more continuous, rather than focused on the same 3- to 6-m band where salmon were placed. These differences in expected lateral patterns in soil properties due to salmon (focused at 3–6 m) verse other factors (more

continuous) provide a means to test whether salmon significantly altered soil patterns in our experiment.

We inferred that salmon significantly influenced a soil property when that soil property met the following conditions: The property (1) differed between the study banks, (2) varied with distance from the stream edge, and (3) displayed a peak response at 3–6 m on the salmon addition bank. All conditions (1, 2, 3) are required to infer that salmon significantly altered the soils on the treatment bank. In contrast, we inferred that support for only one of these parameters demonstrates underlying site variability in the system. Effect of natural site variability on soil properties is also an important component to test. Control sites are typically assumed to be biogeochemically similar to carcass sites without validating this assumption, despite control sites often being located at different stream reaches or on different streams altogether. For each of the nine response variables, three competing hypotheses were compared, that the differences in response variables were due to (H1) a bank and/or distance effect that does not demonstrate a peak response between 3 and 6 m indicating site variability not caused by salmon manipulation, (H2) a bank and distance effect as a quadratic interaction with a peak between 3 and 6 m indicating a response to salmon manipulation, or (H3) no difference caused by distance and bank indicating support for the other covariates tested. These hypotheses were tested by categorizing each candidate model into one of the three hypotheses (Table 1; Appendix S1: Table S1) and considering the hypothesis categorization for the model with the most support, and any additional competing models with relative support ( $\Delta\text{AIC}$  value of  $<2$ ; Burnham and Anderson 2002) for each response variable (e.g.,  $[\text{NH}_4^+]$ ,  $[\text{NO}_3^-]$ ,  $\delta^{15}\text{N}$ ). If models showed support for H2, the effect of salmon was confirmed by examining whether the response variable peaked at the salmon-enhanced bank between 3 and 6 m. If this did not occur, the response is due to site variability and not salmon.

## RESULTS

Bulk soil stable isotope analysis indicated that salmon carcasses enriched the N isotope pools

(Table 1).  $\delta^{15}\text{N}$  values peaked between 3 and 6 m from the stream edge, which was the distance salmon were typically relocated to during the experiment and declined at distances greater than 6 m. Maximum  $\delta^{15}\text{N}$  of bulk soils was 11.8‰ for the salmon-enhanced bank and 11.6‰ for the salmon-depleted bank, and no observations exceeded the sockeye salmon end-member value of 12.6‰ (Fig. 2a).  $\delta^{13}\text{C}$  was more enriched at greater distances from the bank and on average was highest at 20 m (Fig. 2b).  $\delta^{13}\text{C}$  was primarily governed by distance, with some evidence  $[\text{N}_{\text{tot}}]$  and bank also had an effect (Table 1).

Salmon carcass manipulation also enriched  $\delta^{15}\text{N}$  of soil  $\text{NH}_4^+$ . Stable isotope values were enriched at 3 m from the stream edge on the salmon-enhanced bank and declined at distances  $>3$  m. On the salmon-depleted bank,  $\delta^{15}\text{N}$  of soil  $\text{NH}_4^+$  was most enriched at 1 m and declined with distance (Fig. 2c). The only model with support contained a quadratic interaction of distance and bank, which provides strong evidence that  $\delta^{15}\text{N}$  of  $\text{NH}_4^+$  was affected by salmon (Table 1). In contrast to bulk soil N,  $\delta^{15}\text{N}$  values of  $\text{NH}_4^+$  exceeded the salmon end-member of 12.6‰ for 23% of all observations ( $n = 21$ ).

Inorganic nitrogen concentrations were primarily governed by bank and GW (Table 1). The salmon-enhanced bank had a higher mean  $[\text{NH}_4^+]$  and  $[\text{NO}_3^-]$  compared to the salmon-depleted bank (Fig. 3a, b). The most supported models for both  $[\text{NH}_4^+]$  and  $[\text{NO}_3^-]$  showed evidence for H1 that observed differences were not caused by salmon. For  $[\text{NH}_4^+]$ , there was substantial model uncertainty, with six competing models receiving relative support ( $\Delta\text{AIC} < 2$ ; Table 1), but none of the competing models supported a salmon effect. Two competing models for  $[\text{NO}_3^-]$  supported a site variability effect, and one competing model supported a salmon effect (Table 1), and all three contained gravimetric water content as a covariate. This indicates  $[\text{NH}_4^+]$  was driven by site factors unrelated to salmon, while  $[\text{NO}_3^-]$  was driven by gravimetric water content with some support for salmon enhancement.

Nitrogen transformation rates were unaffected by salmon carcass manipulation. Both net nitrification and net mineralization models with relative support contained N substrate ( $[\text{NH}_4^+]$  and  $[\text{N}_{\text{org}}]$ , respectively), and the models with the

Table 1. Competing models with relative support ( $\Delta AIC < 2$ ) using Akaike's information criterion (AIC) analysis for each response variable, where the models with the most support are shown in bold.

Response variable	Model hypothesis	$\Delta AIC$	Covariates included in models with relative support
Bulk $\delta^{15}N$	<b>2</b>	<b>0.00</b>	<b>Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance)<sup>2</sup></b>
	2	0.41	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance) <sup>2</sup> , [N <sub>tot</sub> ]
Bulk $\delta^{13}C$	<b>1</b>	<b>0.00</b>	<b>ln(Distance)</b>
	1	0.22	Bank, ln(Distance)
	1	0.62	ln(Distance), [N <sub>tot</sub> ]
	1	1.23	Bank, ln(Distance), [N <sub>tot</sub> ]
$\delta^{15}N$ of $NH_4^+$	<b>2</b>	<b>0.00</b>	<b>Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance)<sup>2</sup></b>
	1	0.00	<b>Bank, ln(Distance)</b>
[NH <sub>4</sub> <sup>+</sup> ]	1	0.69	Bank, ln(Distance), Bank:ln(Distance)
	1	0.69	Bank
	1	0.95	Bank, GW
	1	1.10	Bank, ln(Distance), GW
	1	1.87	Bank, ln(Distance), Bank:ln(Distance), GW
	1	1.87	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance) <sup>2</sup> , GW
[NO <sub>3</sub> <sup>-</sup> ]	<b>1</b>	<b>0.00</b>	<b>Bank, GW</b>
	1	1.72	Bank, ln(Distance), GW
	2	1.87	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance) <sup>2</sup> , GW
	2	1.87	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance) <sup>2</sup> , GW
Net mineralization	<b>3</b>	<b>0.00</b>	<b>[N<sub>org</sub>]</b>
	3	0.61	GW, [N <sub>org</sub> ]
	1	0.74	Bank, [N <sub>org</sub> ]
	1	1.61	Bank, GW, [N <sub>org</sub> ]
Net nitrification	<b>3</b>	<b>0.00</b>	<b>[NH<sub>4</sub><sup>+</sup>], GW</b>
	1	1.02	Bank, [NH <sub>4</sub> <sup>+</sup> ], GW
[N <sub>org</sub> ]	<b>1</b>	<b>0.00</b>	<b>ln(Distance), GW</b>
	1	0.22	Bank, ln(Distance), Bank:ln(Distance), GW
	2	0.33	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance) <sup>2</sup> , GW
	1	1.94	Bank, ln(Distance), GW
Gravimetric water content (GW)	<b>1</b>	<b>0.00</b>	<b>ln(Distance), Bank</b>
	1	1.00	ln(Distance)
	1	1.80	Bank, ln(Distance), Bank:ln(Distance)

Note: Reported are  $\Delta AIC$  and the hypothesis supported by each model: (1) a bank and/or distance effect caused by site variability and not salmon, (2) a bank and distance effect as a quadratic interaction indicating a response to salmon manipulation, and (3) no difference caused by distance and bank indicating support for the other covariates tested.

most support did not include distance or bank. Net mineralization had some model uncertainty, with four models receiving relative support; however, all of the competing models supported either H1 or H3 with no support for a salmon effect. [N<sub>org</sub>] was the only covariate included in all of the competing models, indicating [N<sub>org</sub>] was the most important covariate tested for determining net mineralization. Net nitrification had greater model certainty, and both models that received relative support contained [NH<sub>4</sub><sup>+</sup>] and gravimetric water content. Similar to net mineralization, these models supported H1

and H3 with no support for H2, the salmon effect, though net nitrification was slightly higher on average between 3 and 6 m on the salmon-enhanced bank (Table 1; Appendix S1: Table S2). Overall, these results demonstrated the manipulation of salmon carcasses did not have clearly detectable effects on N transformation rates.

Both [N<sub>org</sub>] and GW indicated there are site differences caused by distance and bank unrelated to salmon carcass manipulation. On average, [N<sub>org</sub>] was higher on the salmon-depleted bank than the salmon-enhanced bank. There was model support of H1 for both GW and [N<sub>org</sub>], indicating



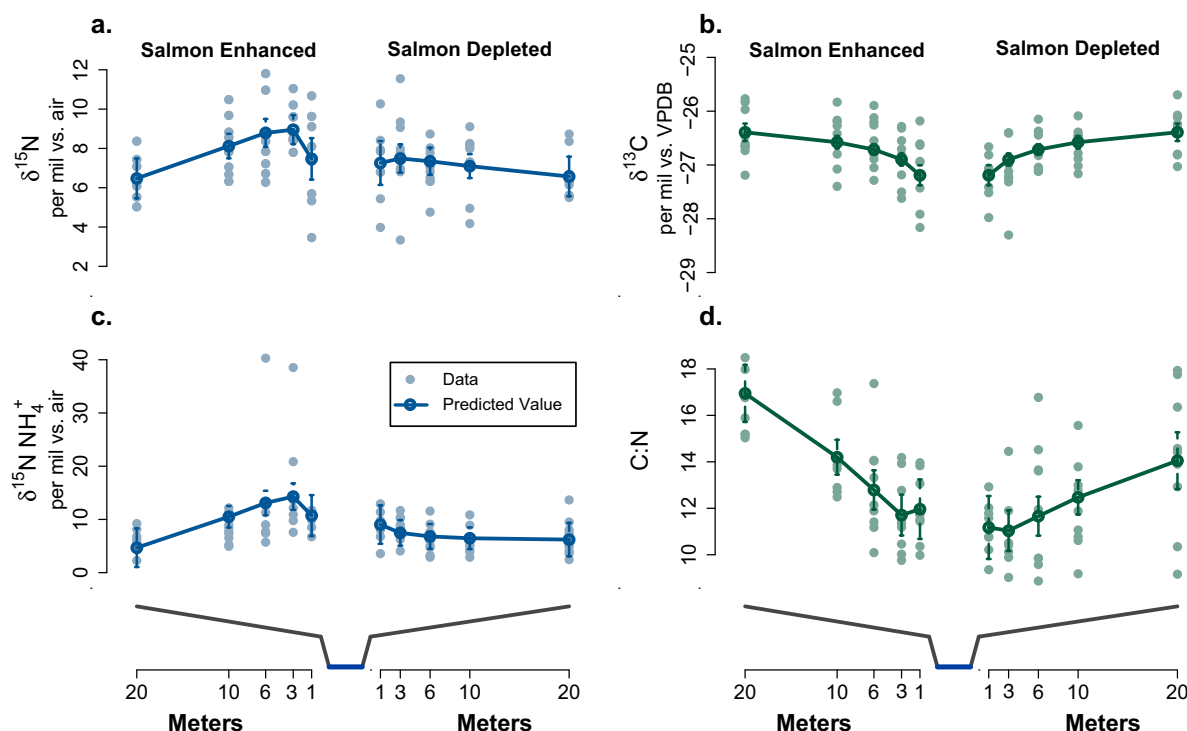


Fig. 2. Data (closed circles) and predicted values (open circles) for the model with the most support (bolded, Table 1) for soil organic  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  of  $\text{NH}_4^+$ , and C:N for both the salmon-enhanced and the salmon-depleted banks of Hansen Creek at 1, 3, 6, 10, and 20 m from the edge of the creek bed with 95% confidence intervals (dashed line) for predicted values. Blue (a and c) denotes measures of marine-derived nitrogen, and green (b and d) denotes site variable factors.

these variables decrease with distance (Table 1, Fig. 3e, f). While there was some evidence that there was both a distance and bank effect on GW, it was not caused by salmon as the salmon-enhanced bank does not show a peak GW at 3 and 6 m from the stream, which was where there was the highest observed isotopic enrichment and expected MDN. However, one competing model for  $[\text{N}_{\text{org}}]$  did support H2, indicating site factors and salmon may both affect  $[\text{N}_{\text{org}}]$ . However, the mean  $[\text{N}_{\text{org}}]$  for the salmon-enhanced bank was 18.42 mg/g and 18.97 mg/g for the salmon-depleted bank indicating salmon decrease  $[\text{N}_{\text{org}}]$ , if they affect it at all.

C:N, percent nitrification, and percent carbon indicate relatively high nitrogen availability across sampling sites in the Hansen Creek system. Mean percent carbon was 24.2 and 24.9 on the enhanced and depleted banks, respectively (Appendix S1: Table S2). Soil C:N of bulk isotopes was less than 20 for all sites, with a mean

of 15.8 (enhanced) and 14.2 (depleted). These values are well below the critical microbial C:N threshold of 29, demonstrating N is more available to meet microbial metabolic demands relative to C (Fig. 2d). In contrast, percent nitrification was relatively high with a mean of 64% and 62% on the enhanced and depleted banks (Appendix S1: Table S2).

## DISCUSSION

This study confirmed that MDN was both present in soils and increased on the bank enhanced with salmon carcasses for 20 yr. However, plant-available inorganic N pools and N transformation rates measured in soil during the peak growing season immediately prior to the annual return of salmon were largely unaffected by salmon enhancement. Even though the salmon-enhanced bank had increased net nitrification compared to the salmon-depleted bank, our

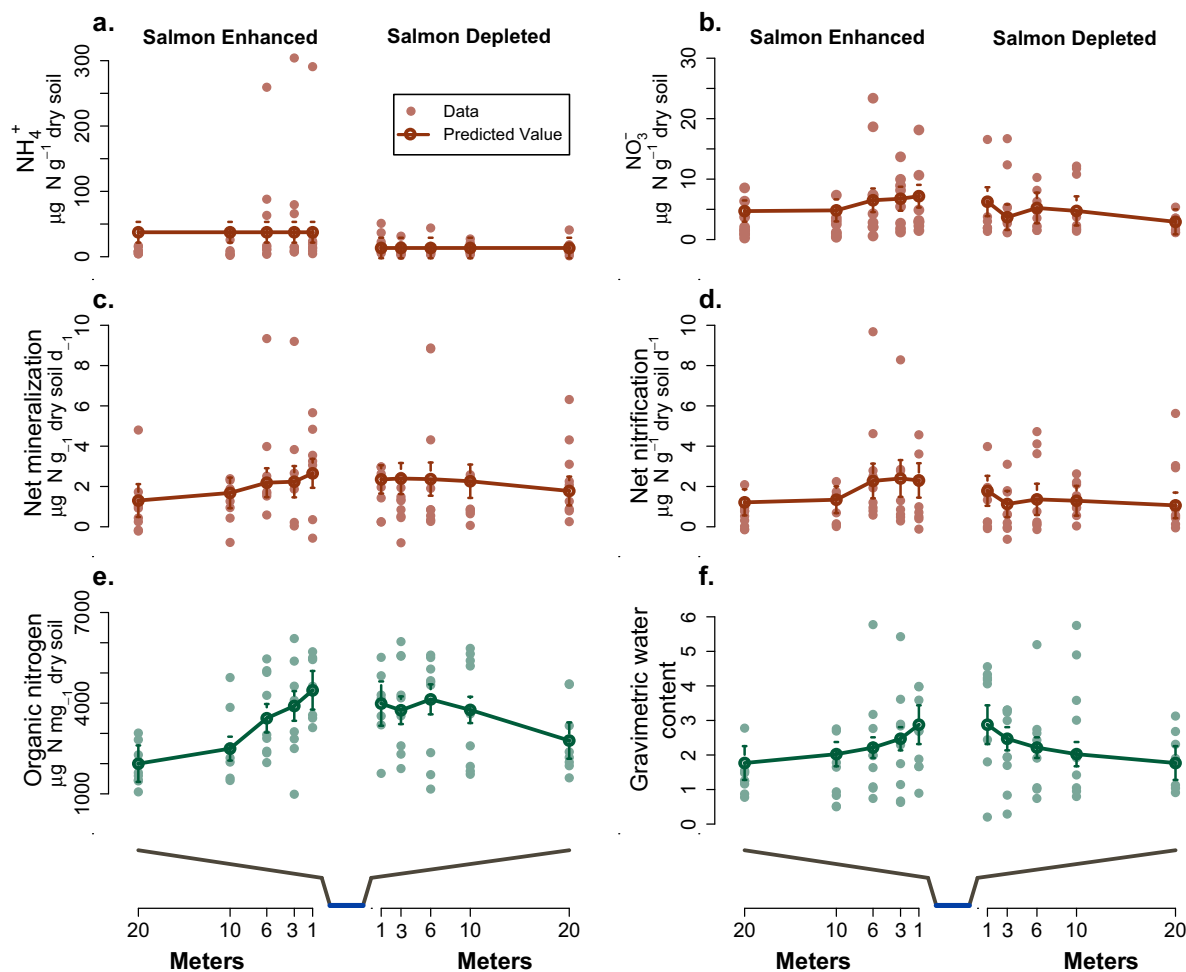


Fig. 3. Data (closed circles) and predicted values (open circles) for the model with the most support (bolded, Table 1) for  $[\text{NH}_4^+]$  and  $[\text{NO}_3^-]$ , net mineralization and nitrification,  $[\text{N}_{\text{org}}]$ , and gravimetric water content for both the salmon-enhanced and the salmon-depleted banks of Hansen Creek at 1, 3, 6, 10, and 20 m from the edge of the creek bed with 95% confidence intervals (dashed line) for predicted values. Red (a, b, c, d) denotes measures of soil productivity, and green (e and f) denotes site variable factors.

analysis found no pattern with distance from the stream, suggesting that elevated nitrification was caused by bank characteristics unrelated to salmon carcass density. Given numerous conventional long-term fertilization experiments worldwide have shown a consistent pattern of elevated soil inorganic N pools and N transformations (Högberg et al. 2006, Lu et al. 2010), it was surprising that 20 yr of MDN inputs did not clearly accelerate soil N cycling in our study. Soils are the dominant (>70%) sink for added N in forests worldwide (Templer et al. 2012), and tree growth in high-latitude conifer forests is

often strongly N-limited (Nordin et al. 2001), both of which should have fostered retention of salmon N inputs to our site. Indeed, the 20 yr of cumulative salmon N additions in the zone near the stream in our study (~6690 kg N/ha) greatly exceeded typical riparian surface soil N pools (500–2500 kg N/ha; Walker 1989, Morris and Stanford 2011, Perry et al. 2017), suggesting that even partial retention of salmon N inputs in soils should have increased soil  $[\text{N}_{\text{org}}]$ . The lack of increase in soil  $[\text{N}_{\text{org}}]$  due to salmon that we observed is consistent with the lack of increase in N availability, because soil  $[\text{N}_{\text{org}}]$  fuels long-term

changes in N availability and recycling via plant uptake, litterfall, and decomposition (Chappell et al. 1999, Perakis and Sinkhorn 2011, Perakis et al. 2012). Combined with observations of low C:N and high percent nitrification, this indicates N from salmon subsidies is not being retained in this system. Overall, the lack of increase in soil organic and inorganic N concentrations and N transformations that we observed following 20-yr salmon manipulation raises questions of whether plant growth responses should be expected at our site.

Prior work at Hansen Creek inferred that MDN stimulated white spruce growth based on tree ring analyses (Quinn et al. 2018). However, substantial salmon enhancement corresponding to approximately 669 g/m<sup>2</sup> (6690 kg/ha) of N and 113 g/m<sup>2</sup> (1130 kg/ha) of P over the past 20 yr was unable to overcome pre-treatment differences in forest growth between banks. For reference, it is estimated white spruce in floodplain stands require approximately 1.35 g·m<sup>-2</sup>·yr<sup>-1</sup> of N (Chapin et al. 2006), which was far exceeded by the mean change of 33.45 g·m<sup>-2</sup>·yr<sup>-1</sup> of N added from this manipulation. Additionally, fertilization experiments apply N on the order of 100–1000 kg/ha with clear results (Chappell et al. 1999), a much lower application rate than in this study. Factors such as climate, stand demography, and site variability also must affect tree growth in this system. Indeed, white spruce growth response to recent warming across southwest Alaska depends strongly on tree density (Wright et al. 2018). Basal area density is highly variable across our site, differing on average 40% between salmon-enhanced and salmon-depleted banks, although the difference was not statistically significant (Quinn et al. 2018). Ultimately, the hierarchy of drivers of tree growth in this ecosystem appears to be landscape position (site variability and associated forest demography) followed by climate, and thirdly, nutrients. All told, a lack of long-term changes in soil nutrient dynamics and only marginal response in tree growth (Quinn et al. 2018) indicates that salmon nutrients are not a strong bottom-up force in northern riparian forest dynamics.

Our <sup>15</sup>N/<sup>14</sup>N stable isotope data raise further questions of assessing MDN subsidies to tree growth. Vegetation typically takes up only 17% of added N to forests, with soils instead being

the dominant N sink (Templer et al. 2012). Thus, elevated bulk soil <sup>15</sup>N/<sup>14</sup>N in our study suggests a potentially significant MDN sink in soil. On the other hand, elevated bulk soil <sup>15</sup>N/<sup>14</sup>N may also reflect increases in soil N fractionation during N cycling and loss under salmon. Highly localized N pulses (as occur with MDN and other N subsidies) temporarily exceed plant and soil N sinks, leading to accelerated N loss via ammonia volatilization, nitrification and nitrate leaching, and/or denitrification (Perakis 2002). All of these N loss pathways favor <sup>14</sup>N and discriminate against <sup>15</sup>N (in some cases with a fractionation up to 30‰), and effects are strongest at high N availability, leading to high values of residual soil <sup>15</sup>N (Högberg 1997). Prior work has shown that MDN inputs accelerate N losses from soil, particularly gaseous N losses (Holtgrieve et al. 2009) that are associated with large isotope fractionation (Högberg 1997). Our finding that δ<sup>15</sup>N of soil NH<sub>4</sub><sup>+</sup> was greater than bulk soil δ<sup>15</sup>N for 95% of observations on the salmon-enhanced bank and 84% of observations on the salmon-depleted bank further confirms that isotopic fractionation is important at Hansen Creek and likely elsewhere.

There is a global trend for higher foliar δ<sup>15</sup>N with increased soil N supply (Craine et al. 2009), indicating accelerated soil N cycling and δ<sup>15</sup>N fractionation due to exogenous N (from salmon or elsewhere) will alter plant foliar δ<sup>15</sup>N. This has important implications for using two-source mixing models to assess salmon N subsidies to riparian forests. Typical MDN mixing models assume (1) the isotopic signature of salmon is unchanged in the soils prior to plant uptake, and (2) reference sites are biogeochemically similar to salmon sites. However, our data suggest that both of these assumptions are violated at Hansen Creek and are likely violated at all salmon-influenced riparian ecosystems. First, we observed that δ<sup>15</sup>N of NH<sub>4</sub><sup>+</sup>, the dominant form of inorganic N in our soils, exceeded the 12.6‰ salmon end-member for 26% of our observations from the salmon-enhanced bank and 9% of observations from the salmon-depleted bank, thus violating assumption (1) above. Our soil N data indicate Hansen Creek is a site of intermediate fertility relative to other boreal forests, so that soil NH<sub>4</sub><sup>+</sup> (rather than organic N or NO<sub>3</sub><sup>-</sup>) is most likely the dominant N source taken up by plants (Chapin et al. 2011).

Second,  $[N_{org}]$ , C:N,  $\delta^{13}C$ , and GW varied with distance from the stream independent of salmon enhancement indicating site variability is a dominant driver of N cycling in this system. This presents a challenge for selecting control sites to calculate terrestrial end-members, as key N cycling factors vary longitudinally away from streams and simply selecting reference sites that are beyond the reach of salmon would likely violate the mixing model assumption of biogeochemical similarity. Additionally, observations of  $\delta^{13}C$  increasing and GW decreasing from the creek edge are consistent with higher water use efficiency and less  $^{13}C$  discrimination by vegetation, resulting in higher  $\delta^{13}C$  in soil due to litter-fall (Gabriel and Phillip 2016). These data identify systematic differences between salmon-enhanced vs. salmon-depleted banks that cannot be attributed to salmon and which likely reflect landscape or soil differences. Previous studies examining contributions of MDN to riparian vegetation have not tested biogeochemical similarity across sites, an assumption that is violated beyond Hansen Creek specifically.

Violation of mixing model assumptions can lead to significant bias in calculations of MDN sources. To illustrate this point, we applied a typical mixing model framework to our maximum observed  $\delta^{15}N$  of  $NH_4^+$  values to calculate the percent MDN contribution of salmon to  $NH_4^+$  for the most extreme observation, representing the greatest possible bias in calculations. Assuming soil processes have no effect on the isotopic signature yielded impossible result of 298% MDN contribution. To account for isotopic fractionation in soils, we applied our mean observed  $\delta^{15}N$  of soil  $NH_4^+$  at the 3 m distance (19.25‰) as the marine end-member to mean foliar  $\delta^{15}N$  data at the same site from Quinn et al. (2018) and estimate 59.24% MDN on the salmon bank, which is 27.6% lower than the original estimate of 86.8% using salmon  $\delta^{15}N$  as the marine end-member. Repeating this with our maximum observed value for  $\delta^{15}N$  of  $NH_4$  (41.2‰), we estimate only 28.9% of foliar N on salmon-enhanced bank was MDN (a 57.9% reduction from Quinn et al. 2018 estimates). Thus, failure to account for isotopic enrichment associated with soil N transformations can lead to overestimates of MDN contributions to plants, and observed variability in  $\delta^{15}N$  of  $NH_4^+$  can produce a wide range of MDN estimates not previously

considered. Given that our elevated  $\delta^{15}N$  of  $NH_4^+$  values are consistent with expected changes during soil N transformation (Högberg 1997), there is a distinct possibility that previous MDN studies have overestimated the amount of MDN by not considering the effects of  $^{15}N/^{14}N$  fractionation in mixing model calculations. Wheeler and Kavanagh (2017) found similar results in a semiarid ecosystem of central Idaho, where accounting for fractionation from decomposition resulted in a 16% reduction in estimated N deposition rates from salmon carcasses. The effects of fractionation on soil N pools are occurring in both of these systems, and likely elsewhere, and need to be considered when applying mixing models to MDN data to avoid overestimations of salmon N contributions to riparian systems.

Our study is comprehensive in terms of the number of ecosystems factors considered but limited in that it includes only one seasonal time frame. As much as 40% of the annual inorganic N flux is released during the eight-month dormant season (September–May), and it has been posited spring and fall may be important for many biogeochemical processes in boreal forests (Hobbie and Chapin 1996, Chapin et al. 2006, Drake et al. 2006). While MDN inputs do not affect the N pools and transformation rates during the summer growth period based on our results, N concentrations and transformations may be elevated in this system on shorter time-scales (weeks to months after salmon return). The objective of this study was to identify the long-term legacy of salmon subsidies; short-term effects were both beyond the scope of this study and have been previously investigated in this system (Holtgrieve et al. 2009). Considering long-term effect of N subsidies as opposed to short-term effect provides new information on sustained N use and retention in the ecosystem and whether these salmon nutrients have lasting impacts on ecosystem function meaningful in a restoration context.

While this study is limited to one system, the results that N transformations cause a fractionation that can bias MDN mixing model estimates and that landscape factors are the primary driver of long-term N retention and use are relevant to other systems where anadromous, semelparous salmon are abundant (Pacific, Atlantic, Great Lakes; Quinn 2018). This result also agrees with



related research examining fractionation of mineralization and nitrification (Högberg 1997), and fertilization studies (Lu et al. 2010). Additionally, it demonstrates salmon N subsidies may have a short-term and likely small spatial scale (Drake et al. 2005) legacy in soils. While the importance of site variability relative to salmon subsidies may vary by system, this work demonstrates the importance of considering site variability and demonstrating biogeochemical similarity when selecting control sites for riparian MDN studies.

Salmon provide critical food resources to many of terrestrial and aquatic consumers (Cederholm et al. 1999, Gende et al. 2002, Schindler et al. 2003), but the evidence that MDN stimulates terrestrial primary production is less certain. The salmon carcass manipulation experiment described here and in Quinn et al. (2018) represents an extreme case of carcass addition and depletion to riparian areas, as measured by bulk  $\delta^{15}\text{N}$ , and estimated percent contribution was approximately twice that of previous studies for both trees and soils (Helfield and Naiman 2002, Bartz and Naiman 2005). Generally, results of this manipulation were equivocal for soils and had a statistically significant but ecologically small effect on trees (Quinn et al. 2018). Simultaneously, other recent changes to boreal forest systems, such as moisture and temperature, appear to have a greater potential than MDN to alter biogeochemical pathways and primary production in these systems (Chapin et al. 2006, Yarie 2008, Lloyd et al. 2013, Wright et al. 2018). This study also demonstrates the importance of testing biogeochemical and site similarity between experimental and control sites in nutrient subsidy studies, as even banks on the same creek can have landscape and soil variability that alter N concentrations, transformations, and thus vegetative growth. Altogether, while salmon have clear benefits for consumers, management of salmon populations or application of compensatory restoration strategies based on terrestrial productivity response to salmon inputs may be unfounded for some systems, and at least, hard to predict.

## ACKNOWLEDGMENTS

We thank the Alaska Salmon Program at the University of Washington for facilitating access to the field site,

and specifically Jackie Carter, Katie McElroy, and Max Ramos for help with field sampling and logistics. The long-term research in Bristol Bay has been funded by many entities, but we especially thank the seafood processing industry for their consistent support over many decades. More recently, the Alaska Salmon Program as a whole also received support from the NSF BioComplexity, the Coupled Natural and Human Systems programs, the Gordon and Betty Moore Foundation, the Alaska Department of Fish and Game, and other sponsors. The daily surveys and carcass manipulation (by 3–5 people) have involved far more individuals than we can name, but we specifically thank Gregory Buck, Harry Rich, Jr., Curry Cunningham, Chris Boatright, Jackie Carter, and the undergraduate students in the Aquatic Ecological Research in Alaska classes. We also thank Eric Ward for his insight into the statistical methods used in this analysis, Washington SeaGrant for their support, and the feedback from our anonymous reviewers. Any use of trade names does not imply endorsement by the US Government.

## LITERATURE CITED

- Bartz, K. K., and R. J. Naiman. 2005. Effects of salmon-borne nutrients on riparian soils and vegetation in southwest Alaska. *Ecosystems* 8:529–545.
- Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:164–173.
- Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern WA, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1909–1918.
- Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multi-Model Inference, A Practical Information—Theoretic Approach. Second edition. Springer-Verlag, New York, New York, USA.
- Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1347–1355.
- Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibani. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* 24:6–15.
- Chaloner, D. T., K. M. Martin, M. S. Wipfli, P. H. Ostrom, and G. A. Lamberti. 2002. Marine carbon

- and nitrogen in southwestern Alaska stream food webs: evidence from artificial and natural streams. *Canadian Journal of Fisheries and Aquatic Science* 59:1257–1265.
- Chappell, H. N., C. E. Prescott, and L. Vesterdal. 1999. Long-term effects of nitrogen fertilization on nitrogen availability in coastal Douglas-fir forest floors. *Soil Science Society of America Journal* 63:1448–1454.
- Chapin, F. S., P. A. Matson, and P. M. Vitousek. 2011. *Principles of terrestrial ecosystem ecology*. Second edition. Springer Berlin Heidelberg, New York, New York, USA.
- Chapin, F. S., M. W. Oswood, K. Van Cleve, L. A. Vier-  
eck, and D. L. Verbyla. 2006. *Alaska's changing  
boreal forest*. Oxford University Press, New York,  
New York, USA.
- Claeson, S. M., J. L. Li, J. E. Compton, and P. A. Bisson.  
2006. Response of nutrients, biofilm, and benthic  
insects to salmon carcass addition. *Canadian Jour-  
nal of Fisheries and Aquatic Science* 63:1230–1241.
- Collins, S. F., A. M. Marcarelli, C. V. Baxter, and M. S.  
Wipfli. 2015. A critical assessment of the ecological  
assumptions underpinning compensatory mitiga-  
tion of salmon- derived nutrients. *Environmental  
Management* 56:571–586.
- Compton, J. E., et al. 2006. Ecological and water qual-  
ity consequences of nutrient addition for salmon  
restoration in the Pacific Northwest. *Frontiers in  
Ecology and the Environment* 4:18–26.
- Craigne, J. M., et al. 2009. Global patterns of foliar nitro-  
gen isotopes and their relationships with climate,  
mycorrhizal fungi, foliar nutrient concentrations,  
and nitrogen availability. *New Phytologist*  
183:980–992.
- Drake, D. C., R. J. Naiman, and J. S. Bechtold. 2006.  
Fate of nitrogen in riparian soils and trees: an  $^{15}\text{N}$   
tracer study simulating salmon decay. *Ecology*  
87:1256–1266.
- Drake, D. C., J. V. Smith, and R. J. Naiman. 2005. Sal-  
mon decay and nutrient contributions to riparian  
forest soils. *Northwest Science* 79:61–71.
- Finney, B. P., I. Gregory-Eaves, J. Sweetman, M. S. V.  
Douglas, and J. P. Smol. 2000. Impacts of climatic  
change and fishing on Pacific salmon abundance  
over the past 300 years. *Science* 290:795–799.
- Gabriel, S., and G. Phillip. 2016. Carbon isotope dis-  
crimination by *Picea glauca* and *Populus tremuloides*  
is related to the topographic depth to water index  
and rainfall. *Canadian Journal of Forest Resources*  
46:1225–1233.
- Gardner, W. H. 1986. Water content. Pages 493–544 in  
A. Klute, editor. *Methods of Soil Analysis: Part 1—  
Physical and Mineralogical Methods*. Soil Science  
Society of America Book Ser. 5.1. Soil Science  
Society of America, American Society of Agron-  
omy, Madison, Wisconsin, USA.
- Gende, S. M., R. T. Edwards, M. F. Willson, and  
M. S. Wipfli. 2002. Pacific salmon subsidize  
freshwater and terrestrial ecosystems through sev-  
eral pathways, which generates unique manage-  
ment and conservation issues but also provides  
valuable research opportunities. *BioScience* 52:917–  
928.
- Gende, S. M., A. E. Miller, and E. Hood. 2007. The  
effects of salmon carcasses on soil nitrogen pools in  
a riparian forest of southeastern Alaska. *Canadian  
Journal of Forest Resources* 37:1194–1202.
- Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weit-  
kamp, G. J. Bryant, O. W. Johnson, and J. J. Hard.  
2007. Pacific salmon extinctions: quantifying lost  
and remaining diversity. *Conservation Biology*  
21:1009–1020.
- Hart, S. C., J. M. Stark, E. A. Davidson, and M. K. Fire-  
stone. 1994. Nitrogen mineralization, immobiliza-  
tion, and nitrification. Pages 985–1018 in R. W.  
Weaver, S. Angle, P. Bottomly, B. Bezdicek, S.  
Smith, A. Tabatabai, and A. Wollum, editors. *Methods  
of soil analysis, Part 2. Microbiological and bio-  
chemical properties*. Soil Science Society of  
America, Madison, Wisconsin, USA.
- Helfield, J. M., and R. J. Naiman. 2001. Effects of sal-  
mon-derived nitrogen on riparian forest growth  
and implications for stream productivity. *Ecology*  
82:2403–2409.
- Helfield, J. M., and R. J. Naiman. 2002. Salmon and  
alder as nitrogen sources to riparian forests in a  
boreal Alaskan watershed. *Oecologia* 133:573–582.
- Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M.  
E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servh-  
een. 1999. The importance of meat, particularly sal-  
mon, to body size, population productivity, and  
conservation of North American brown bears.  
*Canadian Journal of Zoology* 77:132–138.
- Hobbie, S. E., and F. S. Chapin. 1996. Winter regulation  
of tundra litter carbon and nitrogen dynamics. *Bio-  
geochemistry*. 35:327–338.
- Hocking, M. D., and J. D. Reynolds. 2012. Nitrogen  
uptake by plants subsidized by Pacific salmon car-  
casses: a hierarchical experiment. *Canadian Journal  
of Forest Research* 42:908–917.
- Högberg, P. 1997. Tansley review No. 95  $^{15}\text{N}$  natural  
abundance in soil-plant systems. *New Phytologist*  
137:179–203.
- Högberg, P., H. Fan, M. Quist, D. Binkley, and C. O.  
Tamm. 2006. Tree growth and soil acidification in  
response to 30 years of experimental nitrogen load-  
ing on boreal forest. *Glob Change Biology* 12:489–  
499.

- Holmes, R. M., J. W. McClelland, D. M. Sigman, B. Fry, and B. J. Peterson. 1998. Measuring  $15\text{N-NH}_4$  in marine, estuarine and fresh waters: an adaption of the ammonium diffusion method for samples with low ammonium concentrations. *Marine Chemistry* 60:235–243.
- Holtgrieve, G. W., and D. E. Schindler. 2011. Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology* 92:373–385.
- Holtgrieve, G. W., D. E. Schindler, C. P. Gowell, C. P. Ruff, and P. J. Lisi. 2010. Stream geomorphology regulates the effects on periphyton of ecosystems engineering and nutrient enrichment by Pacific salmon. *Freshwater Biology* 55:2598–2611.
- Holtgrieve, G. W., D. E. Schindler, and P. K. Jewett. 2009. Large predators and biogeochemical hotspots: Brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. *Ecological Research* 24:1125–1135.
- Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia* 159:583–595.
- Johnston, N. T., E. A. MacIsaac, P. J. Tschaplinski, and K. J. Hall. 2004. Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Canadian Journal of Aquatics and Fisheries Science* 61:384–403.
- Kasischke, E. S., and N. H. F. French. 1995. Locating and estimating the areal extent of wildfires in Alaskan boreal forests using multiple-season AVHRR NDVI composite data. *Remote Sensing of Environment* 51:263–275.
- Kirchhoff, M. D. 2003. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity: comment. *Ecology* 84:3396–3399.
- Kline, T. C. J., J. J. Goering, O. A. Mathisen, P. Poe, P. L. Parker, and R. S. Scanlan. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  evidence in the Kvichak River watershed, Bristol Bay, Southern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2350–2365.
- Lloyd, A. H., P. A. Duffy, and D. H. Mann. 2013. Non-linear responses of white spruce growth to climate variability in interior Alaska. *Canadian Journal of Forest Research* 43:331–343.
- Lu, M., Y. Yang, Y. Luo, C. Fang, X. Zhou, J. Chen, X. Yang, and B. Li. 2010. Responses of ecosystem nitrogen cycle to nitrogen addition: a meta-analysis. *New Phytologist* 189:1040–1050.
- Meehan, E. P., E. E. Seminet-Reneau, and T. P. Quinn. 2005. Bear predation on Pacific salmon facilitates colonization of carcasses by fly maggots. *American Midland Naturalist* 153:142–151.
- Minakawa, N., R. I. Gara, and J. M. Honea. 2002. Increased individual growth rate and community biomass of stream insects associated with salmon carcasses. *Journal of North American Benthological Society* 21:651–659.
- Mitchell, N. L., and G. A. Lamberti. 2005. Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. *Limnology and Oceanography* 50:217–227.
- Moore, J. W., D. E. Schindler, J. L. Carter, J. M. Fox, J. Griffiths, and G. W. Holtgrieve. 2007. Biotic control of stream ecosystem fluxes: spawning salmon drive nutrient matter and export. *Ecology* 88:1278–1291.
- Morris, M. R., and J. A. Stanford. 2011. Floodplain succession and soil nitrogen accumulation on a salmon river in southwestern Kamchatka. *Ecological Monographs* 81:43–61.
- Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399–417.
- Nordin, A., P. Högborg, and T. Nasholm. 2001. Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient. *Oecologia* 129:125–132.
- Perakis, S. S. 2002. Nutrient limitation, hydrology and watershed nitrogen loss. *Hydrological Processes* 16:3507–3511.
- Perakis, S. S., J. J. Matkins, and D. E. Hibbs. 2012.  $\text{N}_2$ -fixing red alder indirectly accelerates ecosystem nitrogen cycling. *Ecosystems* 15:1182–1193.
- Perakis, S. S., and E. R. Sinkhorn. 2011. Biogeochemistry of a temperate forest nitrogen gradient. *Ecology* 92:1481–1491.
- Perry, L. G., P. B. Shafroth, and S. S. Perakis. 2017. Riparian soil development linked to forest succession above and below dams along the Elwha River, Washington, USA. *Ecosystems* 20:104–129.
- Polis, G., M. E. Power, and G. R. Huxel. 2004. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois, USA.
- Prescott, C. E., J. P. Corbin, and D. Parkinson. 1992. Immobilization and availability of N and P in the forest floors of fertilized Rocky Mountain coniferous forests. *Plant and Soil* 143:1–10.
- Prescott, C. E., B. E. Kischchuck, and G. F. Weetman. 1995. Long-term effects of repeated N fertilization and straw application in a jack pine forest 3. Nitrogen availability in the forest floor. *Canadian Journal of Forest Resources* 25:1991–1996.

- Quinn, T. P. 2018. *The Behavior and Ecology of Pacific Salmon and Trout*. Second edition. University of Washington Press, Seattle, Washington, USA.
- Quinn, T. P., J. Helfield, C. S. Austin, R. Hovel, and A. G. Bunn. 2018. A multidecade experiment shows that fertilization by salmon carcasses enhanced tree growth in the riparian zone. *Ecology* 99:2433–2441.
- Reimchen, T. E., and C. H. Fox. 2013. Fine-scale spatiotemporal influences of salmon on growth and nitrogen signatures of Sitka spruce tree rings. *BMC Ecology* 13:38.
- Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. *Freshwater Biology* 52:1944–1956.
- Schindler, D. E., J. B. Armstrong, K. T. Bentley, K. Janowski, P. J. Lisi, and L. X. Payne. 2013. Riding the crimson tide: Mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters* 9:20130048.
- Schindler, D. E., P. R. Leavitt, C. S. Brock, S. P. Johnson, and P. D. Quay. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. *Ecology* 86:3225–3231.
- Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment* 1:31–37.
- Schoeninger, M. J., M. J. DeNiro, and H. Tauber. 1983. Stable nitrogen isotope ratios of bone collagen reflect marine mammal and terrestrial components of prehistoric human diet. *Science* 220:1381–1383.
- Sigman, D. M., M. A. Altabet, R. Michener, D. C. McCorkle, B. Fry, and R. M. Holmes. 1997. Natural abundance-level measurement of nitrogen isotopic composition of oceanic nitrate: an adaptation of the ammonia diffusion method. *Marine Chemistry* 57:227–242.
- Sparks, D. L., A. L. Page, P. A. Helmke, and R. H. Loeppert, editors. 1996. *Methods of Soil Analysis Part 3—Chemical Methods*. Soil Science Society of America Book Series. 5.3. Soil Science Society of America, American Society for Agronomy, Madison, Wisconsin, USA.
- Templer, P. H., et al. 2012. Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of <sup>15</sup>N tracer field studies. *Ecology* 93:1816–1829.
- Walker, L. R. 1989. Soil nitrogen changes during primary succession on a floodplain in Alaska, USA. *Arctic and Alpine Research* 21:341–349.
- Wheeler, T. A., and K. L. Kavanagh. 2017. Soil biogeochemical responses to the deposition of anadromous fish carcasses in inland riparian forests of the Pacific Northwest. *Canadian Journal of Forest Research* 47:1506–1516.
- Wheeler, T. A., K. L. Kavanagh, and S. A. Daanen. 2014. Terrestrial salmon carcass decomposition: nutrient and isotopic dynamics in central Idaho. *Northwest Science* 88:106–119.
- Winder, M., D. E. Schindler, J. W. Moore, S. P. Johnson, and W. J. Palen. 2005. Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? *Canadian Journal of Fisheries and Aquatic Sciences* 62:2285–2293.
- Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1503–1511.
- Wipfli, M. S., J. P. Hudson, and J. P. Caouquette. 2003. Marine subsidies in freshwater ecosystems: Salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society* 132:371–381.
- Wright, M., R. L. Sherriff, A. E. Miller, and T. Wilson. 2018. Stand basal area and temperature interact to influence growth in white spruce in southwest Alaska. *Ecosphere* 9:e02462.
- Yarie, J. 2008. Effects of moisture limitation on tree growth in upland and floodplain forest ecosystems in interior Alaska. *Forest Ecology and Management* 256:1055–1063.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2958/full>