Effects of salmon inputs to soil nitrogen pools, transformations, and stable isotope ratios: implications for marine derived nutrient subsidies to riparian areas

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Abstract

Marine-derived nitrogen (MDN) enters terrestrial and freshwater ecosystems when Pacific salmon (*Oncorhynchus* spp.) return to spawn and die. The ecological importance of salmon tissue for direct consumers is well established; however, many studies examining the broader role of salmon nutrients document the presence of MDN without evaluating its ecological importance. Uncertainty around the ecological importance of MDN is particularly pronounced in terrestrial riparian systems. To test the long-term importance of salmon nutrients to riparian ecosystems, a 20-year manipulation was performed where salmon carcasses were systematically removed from one bank and deposited on the opposite bank along the full length of a 2 km stream in southwestern Alaska. We examined the effect of this manipulation on riparian soil fertility. Soil core samples were taken from 9 paired transects along the stream at distances 1m, 3m, 6m, 10m, and 20m from the bank and measured for organic and inorganic nitrogen ($[NH_4^+]$, $[NO_3^-]$, $[N_{Org}]$) and nitrogen transformation rates (net mineralization and net nitrification). The presence of MDN was also documented using stable isotope ratios of nitrogen ($^{15}N/^{14}N$) for bulk soils as well as NH_4^+ and NO_3^- soil pools. Stable isotope analyses confirmed MDN was elevated on the salmon enhanced bank compared to the salmon depleted bank. The presence of MDN did not, however, produce measurable biogeochemical responses in soil nitrogen concentrations and transformations during peak vegetative growth season, despite long-term annual enrichment with a high level of salmon, raising questions about ecosystem uptake and loss of MDN pulses. These results suggest variations in soil fertility may be more dependent on other landscape level factors rather than salmon presence. Our findings also document $\delta^{15}N$ values of plant-available soil nitrogen that exceed salmon $\delta^{15}N$ inputs, highlighting additional nitrogen isotope fractionation that raises significant methodological issues with previous MDN assessments.

Introduction

The migration of Pacific salmon (*Oncorhynchus* spp.) from marine environments to freshwater spawning grounds contributes substantial nutrients and organic material to inland coastal ecosystems (Gende et al. 2002, Schindler et al. 2003). Salmon migration is a textbook case of cross-ecosystem nutrient subsidies and dozens of studies have identified the presence of marine derived nitrogen (MDN) from salmon as crossing ecosystem boundaries from oceans to freshwaters and into the terrestrial environment (sensu, Polis et al. 2004). Salmon derived nutrients enter 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}N) relative to the light isotope (^{14}N) when compared to watershed-derived nitrogen, which has been used to quantitatively trace the presence of marine derived nitrogen (MDN) from salmon into watersheds (Schindler et al. 2003). For example, the proportion of N derived from salmon ranges from approximately 30%-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 (Hilderbrand et al. 1999; Hicks et al. 2005; 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). Carcasses and roe are documented prey for over 22 species of mammals, birds (Cenderholm et al. 1989), and invertebrates (Minakawa et al. 2002, Winder et al. 2005). Bear population density, body size, and reproductive output have been related to increased MDN (Hilderbrand et al. 1999). In aquatic ecosystems, salmon carcass abundance has been correlated with elevated growth rates of invertebrates and size, density, and

condition factor of juvenile salmonids, (Minakawa et al. 2002, Wipfli et al. 2003, Bilby et al. 1998).

The presence of MDN has been documented in aquatic primary producers, though its overall ecological importance remains ambiguous. Higher salmon returns are correlated with MDN signatures in lower trophic levels including zooplankton and periphyton (Finney et al. 2000; Holtgrieve et al. 2010). Via this bottom-up pathway, MDN supplies a critical limiting nutrient (N) to increase primary and/or bacterial productivity, which are subsequently transferred to consumers and up through the food web (Holtgrieve and Schindler 2011, Chaloner et al. 2002, Wipfli et al. 1998, Richey et al. 1975). Both direct ecological and paleolimnological evidence suggests MDN plays an important role providing nutrients to lakes (Moore et al. 2007). For example, commercial fisheries remove upwards of two-thirds of MDN to freshwater lakes in Alaska which has resulted in a 3-fold decline in algal production with no apparent effect on the number of returning salmon (Schindler et al. 2005). In stream ecosystems, the decomposition of salmon increases dissolved organic and inorganic nutrients, including highly available forms such as orthophosphate (PO_4^{3-}) and ammonia/ammonium (NH_3/NH_4^+). These nutrients can stimulate epilithon growth (bacteria and algae), though the magnitude of this response is dependent on other growth limiting factors such as sunlight and disturbance that may reduce any positive growth effects from MDN (Holtgrieve et al. 2010, Johnston et al. 2004, Mitchell and Lamberti 2005, Chaloner et al. 2007, Janetski et al 2009, Wipfli et al. 1998).

In the terrestrial realm, bottom-up effects of MDN from salmon is also thought to be ecologically important, though in some cases is difficult to resolve. Studies across the range of salmon in North America have shown up to 26% of foliar N in riparian plants is marine derived, and percent foliar MDN generally correlates with salmon abundance and distance from the salmon spawning location (Hocking and Reynolds 2012, Reimchen and Fox 2013).

While MDN is clearly present in terrestrial producers, direct evidence as to 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 based on statistical grounds (Kirchoff 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) determined salmon abundance did increase tree growth, but tree ring ^{15}N signature was 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 Alaska before and after a 20-year, 250,000 kg, salmon carcass manipulation to find elevated growth with MDN, but the effect was smaller than natural site-to-site variation and did not consider important landscape factors such as forest demography, aspect and water availability.

Interpreting the contributions of MDN to terrestrial producers using stable isotopes is also challenging, as variability of N sources and overall N availability can conflate 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 $^{15}N/^{14}N$ 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 $^{15}N/^{14}N$ of salmon (12.62 ± 0.31 per mil for sockeye salmon) is typically used (S2). Inherent assumptions with these models therefore include: 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. Given nitrogen

101 cycling in soils is strongly controlled by position in the landscape and contains a number of
102 steps which strongly fractionate nitrogen isotopically (Högberg 1997, Figure 1), it is unlikely
103 these assumptions are valid.

104 Experiments examining the contributions of MDN are often limited by short
105 timescales, and relatively few experiments investigate changes in plant-available soil nitrogen
106 pools important to plant nutrient uptake and growth (Collins et al. 2015). Studies examining
107 spatial and temporal impacts of salmon on soil inorganic nitrogen have identified highly
108 localized responses (effects only observed less than 30 cm from carcasses) where soil
109 ammonium (NH_4^+) and nitrate (NO_3^-) increase for weeks to months (Gende et al. 2007; Drake
110 et al. 2005, Holtgrieve et al. 2009). In addition, experiments typically examine the
111 contributions of MDN by nutrient addition not nutrient removal, which is important for
112 understanding the effects of lower numbers of salmon returning to coastal watersheds due to
113 fishing, habitat reduction, and climate change. To resolve the extent to which salmon
114 carcasses contribute MDN to plant-available N pools and the ecological response of this
115 subsidy, we present the results of a 20-year fertilization experiment in southwestern Alaska.
116 We use this system to assess the importance of MDN to riparian ecosystems by 1) evaluating
117 the presence of MDN in soils through bulk stable isotope analysis of N, 2) quantifying the
118 response of plant-available nitrogen pools ($[NH_4^+]$ and $[NO_3^-]$) and their rate of supply via
119 mineralization and nitrification to MDN, and 3) considering how changes in $^{15}N/^{14}N$ of plant-
120 available NH_4^+ may impact mixing model results. This research fills key knowledge gaps by
121 examining inorganic nitrogen pools and both salmon addition and removal on relatively long-
122 time scales.

Methods

Site Description and Sample Collection

This study was conducted on Hansen Creek, a ~2 km long, 2nd order tributary to Lake Aleknagik in the Wood River system of Bristol Bay, AK. An average of 10,853 sockeye salmon return to the stream annually. Overstory vegetation is dominated by white spruce *(Picea glauca)* and paper birch (*Betula papyrifera*), and unlike other watersheds in the region, it has a low density of symbiotic N_2-fixing alder (*Alnus spp.*). From 1997-2017 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, and tossed onto the river left bank. Thus, the right side of the stream was manipulated for depletion of MDN and the left bank was enhanced in MDN. Approximately 108,530 individual fish were translocated over the 20-year period representing 222,420 kg of salmon, 6,672.6 kg of N and 889.68 kg of phosphorus (P) (Quinn et al. 2018).

Soil samples were collected from the riparian zone on July 13th 2017 along nine sets of paired transect sites. Three sets of transect sites were evenly nested within three equal sized stream reaches, across both the river left and river right banks. Transects covered the full 2 km length of the stream and were selected to be representative of typical riparian vegetation and high spawning intensity. Each transect included sampling sites at 1m, 3m, 6m, 10m, and 20m from the bank-full point. Sampling occurred during peak growing season (maximum normalized difference vegetation index (NDVI); Kasischke and French 1995), when plant transpiration and growth most actively remove available N from soil, approximately 1week prior to salmon return in the creek. Thus, our sampling captured the long-term legacy of MDN manipulations. A 5cm x 5cm x 10cm 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 hours prior to processing.

148 *Soil nitrogen concentrations and transformations*

149 Soil NH_4^+ and NO_3^- concentration and N transformations were measured according to
150 Holtgrieve and Schindler 2009. Briefly, we extracted 10 to 12 g of field-moist sieved (< 2
151 mm) soil with 100 mL of 2 M potassium chloride (KCl) by shaking for 60 s, followed by
152 settling for 24 hours prior to filtration through pre-leached Whatman #1 filter papers.
153 Approximately 8 mL of filtered extracts were frozen and later analyzed colorimetrically for
154 [NH_4^+] and [NO_3^-] with an Auto-Analyzer 500 Model (Perstorp Analytical Co, Analytical
155 Service Station, Seattle, WA, USA). The remaining extract was frozen prior to stable isotope
156 analyses (see below). To estimate inorganic N transformation rates, a second 10 to 12 g soil
157 subsample was incubated aerobically in the dark for 15 days at 20°C prior to extraction,
158 filtration, and analysis as above. Net mineralization was calculated as the total change in
159 inorganic [NH_4^+] and [NO_3^-] divided by the incubation duration, and net nitrification was
160 calculated as the change in [NO_3^-] over the incubation duration (Hart 1994). [N_{org}] was
161 calculated by taking total soil N concentration determined by mass spectrometry (see below)
162 and subtracting [NH_4^+] and [NO_3^-]. All soil N values were corrected for gravimetric soil
163 water content (g H_2O/g dry soil) determined by drying 50 to 100 g of field-moist soil at
164 105°C for 48 hours (Gardner, 1986).

165 *Stable isotope analysis*

166 Fresh soil was freeze dried for 48 hours and ground into a uniform powder (< 212
167 μm) using a ball mill prior to analysis for nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) stable
168 isotope ratios at the University of Washington's IsoLab using a Costech Elemental Analyzer,
169 Conflo III MAT253 for continuous flow-based measurements. This procedure also provided
170 C and N concentrations of the soil samples. Data are reported using standard delta notation,
171 which describes the per mil deviation in the ratio of heavy to light isotope relative to accepted

172 international standards, in this case air and Vienna Pee Dee Belemite (VPDB) for N and C
173 respectively (Schoeninger et al. 1983).
174 For $^{15}N/^{14}N$ stable isotope analysis of NH_4^+ and NO_3^-, KCl extracts were placed in
175 Erlenmeyer flasks for diffusion using modified methods from Sigman et al. (1997) and
176 Holmes et al. (1998). To retrieve NH_4^+ as gaseous NH_3, 300 mg of MgO and an acid trap (1
177 cm glass fiber filter treated with $KHSO_4$ and sealed in Teflon) were added to each flask,
178 immediately stoppered, sealed with parafilm, and shaken for six days prior to removal of acid
179 traps to a desiccator for 3 to 4 days. The same extracts were then shaken uncovered for one
180 day to remove any remaining NH_4^+. To retrieve NO_3^- as NH_3, another 300 mg of MgO were
181 added to each extract and immediately followed with 75 mg of Devarda's alloy and an acid
182 trap, then processed as above. Samples were run in four separate batches, for each batch three
183 blanks (KCl with no soil extract) and three reference standards, NH_4Cl and KNO_3 with
184 known $^{15}N/^{14}N$, were also run. Batch blanks showed quantifiable N from the KCl; therefore, a
185 two-source mixing model correction was applied to both samples and reference standards
186 using equation 1:
187 **(1)** $\delta^{15}N_{\text{Blank Corrected}} = (\delta^{15}N_{\text{measured}} * (N_{\text{blank},x} + N_{\text{extracted}}) \ (\delta^{15}N_{\text{blank},x} * N_{\text{Blank},x}))/ N_{\text{extracted}}$
188 Where *x* represents an individual batch, $N_{\text{Blank},x}$ is the average measured mass (µg) of
189 nitrogen in a blank for a given batch, and $\delta^{15}N_{\text{Blank},x}$ is the average measured $\delta^{15}N$ of blanks
190 for a given batch. $\delta^{15}N_{\text{measured}}$ is the $\delta^{15}N$ value for a given sample, and $N_{\text{extracted}}$ is the mass of
191 nitrogen (µg) measured in the sample. A standard correction was then applied to the blank
192 corrected measurements where:
193 **(2)** $\delta^{15}N_{\text{Corrected}} = \delta^{15}N_{\text{Blank Corrected}} - (\text{Standard}_{\text{Measured},x} - \text{Standard}_{\text{true}})$
194 Where $\text{Standard}_{\text{measured},x}$ is the average measured value of the standard for a given batch. All
195 reported $\delta^{15}N$ of NH_4^+ and NO_3^- values are expressed as the $\delta^{15}N_{\text{corrected}}$, where a blank and
196 standard correction has been applied. C:N ratios were calculated from bulk isotope data by

dividing %C by %N and converting to the molar ratio of C:N. The internal standard of the $\delta^{15}N$ of 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, $\delta^{15}N$ of NO_3^- data are not reported here.

Statistical analyses

To test the effect of salmon enhancement on soil nutrient concentrations, linear and mixed effects models were individually fit to the data for the following response variables: $\delta^{15}N$ and $\delta^{13}C$ of bulk soil, $\delta^{15}N$ of NH_4^+, $[NH_4^+]$ and $[NO_3^-]$, net mineralization and net nitrification, $[N_{org}]$, gravimetric water content (GW), and C:N. The random effects structure was initially tested using restricted maximum likelihood estimation where reach, site, and site nested within reach, were considered using the lme4 package in R. The random effects structure with the most support using Akaike's information criterion (AIC) was considered within the candidate model set. After determining the random effects structure, we used maximum likelihood to compare models with no random effects and the most supported random effects structure, and different fixed effects structures (Zuur et al. 2009). For all response variables, candidate models (S1) included the interaction between bank (left vs. right) and distance from rivers edge. This interaction term allows the effect of distance to vary, depending on whether the sample is collected from the left or right bank. A natural log transformation was used for the distance. GW content was considered as a fixed effect for all response variables, soil $[NH_4^+]$ was considered as a fixed effect for net nitrification, and soil $[N_{org}]$ was considered as a fixed effect for net mineralization, given $[NH_4^+]$ and $[N_{org}]$ function as the substrate for mineralization and nitrification respectively. The best model was selected from the candidate model set using AIC for each response variable. Under

circumstances where multiple models had a difference in AIC value of < 2 relative to the best model, the most parsimonious model was selected.

Two model parameters – bank (left vs. right) and distance from the stream – were used to test whether MDN from salmon carcasses impacts soil N cycling. Changing the number of salmon on each bank was the primary goal of the manipulation; however, the two banks potentially differ in aspect, soil type, and drainage, which can impact nutrient cycling and generate a bank effect unrelated to salmon manipulation (Chapin et al. 2002). Notably, the salmon enhanced bank has a northwest facing slope within 20m of the creek edge. Given salmon were only located within 3-6 meters from the stream edge after translocation, distance can also indicate an effect of salmon enrichment. However, vegetation, soil type, and water availability can also change with distance. Therefore, model support for both distance and bank parameters indicate an effect of salmon on the response variables, but support for only one of these parameters demonstrates underlying variability in the system. For each of the nine response variables, four competing hypotheses were compared, that the differences in response variables were due to H1) a bank effect not caused by salmon enhancement H2) a distance effect not caused by salmon enhancement H3) both a bank and distance effect indicating a response to salmon enhancement or H4) 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 four hypotheses (S1) and summing the AIC weights across all candidate models for each hypothesis. This generates an overall weight of evidence (Burnham and Anderson 2002; Hocking and Reynolds 2012) on a percentage scale for each hypothesis influencing the specific response variable under consideration (e.g., $[NH_4^+]$, $[NO_3^-]$, $\delta^{15}N$, etc.).

Results

There was model support to include reach as a random effect for C:N; for all other response variables there was insufficient model support to include random effects ($\Delta AIC < 2$) and only fixed effects were used for further analyses.

Bulk soil stable isotope analysis showed substantial support for H3, salmon enrich N isotope pools, demonstrating increased MDN on the salmon enhanced bank (Table 1). $\delta^{15}N$ values peaked at 3 meters from the stream edge, which is the distance salmon were typically relocated to during the experiment, and declined at distances greater than 3 meters. Maximum $\delta^{15}N$ 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‰ (Figure 2a). $\delta^{13}C$ was more enriched at greater distances from the bank and on average was highest at 20 meters (Figure 2b). The weight of evidence (70%) supported a model of $\delta^{13}C$ influenced by distance, but not by bank (Table 1).

$\delta^{15}N$ of NH_4^+ was most enriched at 3 meters from the stream edge on the salmon enhanced bank, and declined at distances greater than 3 meters. On the salmon depleted bank, $\delta^{15}N$ of NH_4^+ was most enriched at 1 meter and declined with distance (Figure 2c). The only model with sufficient support contained an interaction of distance and bank, which provides strong evidence that $\delta^{15}N$ of NH_4^+ was affected by salmon enhancement (Table 1, 2). In contrast to bulk soil N, $\delta^{15}N$ values of NH_4^+ exceeded the salmon endmember of 12.6‰ for 23% of all observations (n=21).

There was little model support that salmon enhancement increases inorganic N pools during peak growth season (H3). The salmon enhanced bank had a higher mean [NH_4^+] and [NO_3^-] compared to the salmon depleted bank (Figure 2d,e) but for [NH_4^+] there was substantial model uncertainty, with six competing models receiving relative support (Table 2). Similarly, a single hypothesis did not receive a substantial weight of evidence, and both H1 (39%) and H3 (46%) received comparable support (Table 2). These results demonstrate

that [NH_4^+] differs between the two banks, but whether that effect is attributed to salmon enhancement, or other biogeochemical factors that may vary between the two banks, is uncertain. The models of [NO_3^-] that received sufficient relative support contained both the bank parameter and gravimetric water content (Table 1). 63% of the weight of evidence supported H1, that [NO_3^-] was affected by bank but not distance (Table 2). While the salmon enhanced bank does have increased [NO_3^-] compared to the salmon depleted bank, lack of model support for a distance effect suggests that this result is caused by bank characteristics unrelated to salmon carcass density.

Nitrogen transformation rates were similarly unaffected by salmon enhancement. Both net nitrification and net mineralization models with relative support contained N substrate ([NH_4^+] and [N_{org}] respectively). Net mineralization had high model uncertainty, with five models receiving similar relative support (Table 1). [N_{org}] was the only covariate included in all of the supported models, indicating [N_{org}] was the most important covariate tested for determining net mineralization. While no hypothesis received a substantial proportion of the weight of evidence, H3 only received 13% of the weight, demonstrating the enhancement of salmon carcasses is unlikely to impact net mineralization. Net nitrification had greater model certainty and both models that received relative support contained [NH_4^+] and gravimetric water content (Table 1). There was no model support for a distance effect, and most of the weight of evidence supported H4; covariates tested other than distance and bank effect were better predictors of net nitrification (Table 2).

Both [N_{org}] and GW indicate there are differences caused by distance and bank unrelated to salmon enhancement. On average [N_{org}] was higher on the salmon depleted bank than the salmon enhanced bank. There was some support for both H2 and H3 indicating [N_{org}] decreases with distance (Table 2). While there is some evidence (57%) that there is both a distance and bank effect on [N_{org}] it is unlikely caused by salmon, as the salmon

enhanced bank does not show a peak [N_{org}] at 3m from the stream, which is where there was the highest observed isotopic enrichment and thus the most MDN. GW had evidence of H2 and H3 (Table 2), indicating differences between the two banks and with distance from the stream; however, it is unlikely this result is related to salmon density as GW declined with distance. Additionally, the salmon enhanced bank had greater molar C:N ratio of bulk soils compared to the depleted bank; however, it is unlikely this is caused by salmon as terrestrial inputs such has wood have a higher C:N ratio relative to marine inputs(Fiugre 2).

Discussion

This study confirmed MDN was both present in soils and increased with 20 years of salmon enhancement. However, plant-available inorganic N pools and N transformation rates in soil during the peak growing season were largely unaffected by salmon enhancement. This latter result is unexpected, given numerous long-term fertilization experiments worldwide have shown a consistent pattern of elevated soil inorganic N pools and N transformations (Lu et al. 2010, Högberg 2006). Moreover, in boreal forests, plant productivity often increases with [NH_4^+] and [NO_3^-] (Nordin et al. 2001). The lack of increase in soil inorganic N concentrations and N mineralization that we observed following long-term salmon enhancement 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, but potential pre-treatment differences in forest growth and demography between salmon-enhanced and salmon-depleted banks may have complicated this analysis (Quinn et al. 2018). Indeed, white spruce growth response to recent warming across southwest Alaska depends strongly on tree density (Wright et al. 2018), and tree density is highly variable across our site, differing on average 60% between salmon-enhanced and salmon-depleted banks at our site (Quinn et al. 2018). Similar to studies of aquatic producers,

other growth limiting factors appear to be important for terrestrial response to MDN; the hierarchy of drivers of tree growth in this ecosystem appears to be landscape position (and associated forest demography) followed by climate and nutrients, despite soil enrichment by salmon corresponding to approximately 11.4 g/m^2 (114 kg/ ha) of N and 1.51 g/m^2 (15.1 kg/ha) of P over the past 20 years (Quinn et al. 2018).

Our ^{15}N stable isotope data raise further questions of assessing MDN subsidies to tree growth. Vegetation typically takes up only 17% of added ^{15}N to forests, with soils instead being the dominant N sink (Templer et al. 2012). Thus, elevated bulk soil ^{15}N in our study suggests a potentially significant MDN sink in soil. On the other hand, elevated bulk soil ^{15}N may also reflect increases in soil N fractionation during N cycling and loss under salmon. Highly localized N pulses (as occur with MDN) 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 ^{14}N and discriminate against ^{15}N (in some cases up to 30‰), and effects are strongest at high N availability, leading to high values of residual soil ^{15}N (Hogberg et al. 1997). Indeed, elevated N inputs from MDN are known to accelerate fractionating N losses from soil (Holtgrieve et al. 2009). However our finding that $\delta^{15}N$ of soil NH_4^+ was greater than bulk soil $\delta^{15}N$ 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. Such soil N fractionation may be widely important in MDN studies, but are rarely considered.

Accelerated soil N cycling and ^{15}N fractionation due to MDN may strongly influence plant available $\delta^{15}N$, with important implications for assessing salmon N subsidies to riparian forests. Increased soil N supply can increase the $\delta^{15}N$ of plant N uptake (Craine et al. 2009), and this is likely occurring. Our soil N data suggest that Hansen Creek is a site of intermediate fertility relative to other boreal forests, so that soil NH_4^+ (rather than organic N

346 or NO_3^-) is most likely the dominant N source taken up by plants (Chapin et al. 2011).
347 Typical MDN mixing models assume 1) the isotopic signature of salmon is unchanged in the
348 soils prior to plant uptake, and 2) reference sites are biogeochemically similar to salmon sites.
349 However, our data suggest that both of these assumptions are likely violated at Hansen Creek.
350 First, we observed that $\delta^{15}N$ of NH_4^+, the dominant form of inorganic N in our soils,
351 exceeded the 12.6‰ salmon end-member for 26% of our observations for the salmon
352 enriched bank and 9% of observations for the salmon depleted bank, thus violating
353 assumption (1) above. Second, our data on [N_{Org}], C:N, $\delta^{13}C$, and GW vary with distance
354 from the stream independent of salmon enhancement. This presents a challenge for selecting
355 control sites, as key N cycling factors vary longitudinally away from streams and simply
356 selecting reference sites that are beyond the reach of salmon likely violate the mixing model
357 assumption of biogeochemical similarity. Violation of these assumptions can lead to
358 significant bias in mixing model calculations of MDN sources.
359 To illustrate this point, we applied a typical mixing model framework to our
360 maximum observed $\delta^{15}N$ of NH_4^+ values to calculate the percent MDN contribution of
361 salmon to NH_4^+. Assuming soil processes have no effect on the isotopic signature, we get the
362 impossible result of 298% MDN contribution. To account for isotopic fractionation in soils,
363 we applied our average observed $\delta^{15}N$ of soil NH_4^+ at the 3-meter distance (19.25‰) as the
364 marine endmember to mean foliar $\delta^{15}N$ data from Quinn et al. (2018) and estimate 59.24%
365 MDN on the salmon bank, which is 27.4% lower than the original estimates using salmon
366 $\delta^{15}N$ as the marine endmember. Repeating this with our max observed value for $\delta^{15}N$ of NH_4
367 (41.2‰), we estimate only 28.9% of foliar N on salmon enhanced bank is MDN. This
368 demonstrates that failure to account for isotopic enrichment associated with soil N
369 transformations can lead to overestimates of MDN contributions to plants, and that observed
370 variability in $\delta^{15}N$ of NH_4^+ can produce a wide range of MDN estimates.

371 Our study is comprehensive in terms of the number of ecosystems factors considered,
372 but limited in that it includes only one seasonal timeframe. While MDN inputs do not affect
373 the N pools and transformation rates during the summer growth period based on our results, it
374 is possible N concentrations and transformations may be elevated in this system on shorter
375 timescales (weeks to months after salmon return). As much as 40% of the annual inorganic N
376 flux is released during the eight-month dormant season (September-May) and it has been
377 posited spring and fall may be important for many biogeochemical processes in boreal forests
378 (Chapin et al. 2006; Hobbie and Chapin 1996). Given plant growth still occurs during these
379 seasons and the potential for salmon to elevate inorganic N pools on shorter timescales, it is
380 possible salmon contribute to this system beyond the scope of this study. Understanding this
381 knowledge gap will enhance our understanding of ecosystem response to MDN.
382 Global declines in Pacific salmon populations caused by human activities
383 (overharvest, habitat degradation, dams) and the concern over loss of MDN to coastal
384 watersheds has made restoration of salmon nutrients a focal point for many management and
385 mitigation strategies (Collins et al. 2015; Lichatowich 1999). While it is well established that
386 salmon provide critical food resources to myriad consumers (Cederholm et al. 1999, Gende et
387 al. 2002, Schindler et al. 2013), the evidence that MDN stimulate terrestrial primary
388 production is less certain. The salmon enrichment experiment described here and in Quinn et
389 al. (2018) represents an extreme case of MDN addition and depletion to riparian areas with
390 generally equivocal results for both soils and trees. Simultaneously, other recent changes to
391 boreal forest systems, such as moisture and temperature, appear to have a greater potential
392 than MDN to alter biogeochemical pathways and primary production in these systems
393 (Chapin et al. 2006, Lloyd et al. 2010, Yarie 2008, Wright et al. 2018). Altogether, while
394 MDN has clear benefits for consumers, we believe that management of salmon populations
395 based on terrestrial productivity response to MDN inputs requires more rigorous analysis.

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574

575 Table 1: Weight of evidence supporting each competing hypothesis. Shown are the AIC
576 weights for each hypothesis summed across the candidate model set where H1 is a bank
577 effect not caused by salmon enhancement, H2 is a distance effect not caused by salmon
578 enhancement, H3 is both a bank and distance effect indicating a response to salmon
579 enhancement and H4 indicates support for the other covariates tested. Weights of evidence
580 greater than 50% are bolded.

Response Variable	1. Bank	2. Distance	3. Bank and distance	4. No bank or distance
Bulk $\delta^{15}N$	3%	1%	**95%**	0%
Bulk $\delta^{13}C$	0%	**70%**	30%	0%
$\delta^{15}N$ of NH_4^+	0%	0%	**100%**	0%
$[NH_4^+]$	39%	12%	46%	3%
$[NO_3^-]$	**63%**	0%	36%	0%
Net Mineralization	30%	11%	13%	46%
Net Nitrification	28%	2%	21%	49%
$[N_{Org}]$	0%	40%	**57%**	2%
GW	13%	49%	37%	0%
C:N	0%	0%	**100%**	0%

581

582 Table 2: Models with relative support using AIC analysis for each response variable where
583 models with the most support are shown in bold.

Response Variable	AIC Weight	ΔAIC	Models with Relative Support
Bulk $\delta^{15}N$	**0.52**	**0.00**	**$\delta^{15}N$ = bank*ln(distance) + I(ln(distance)^2)*bank + ε**
	0.42	0.41	$\delta^{15}N$ = bank*ln(distance) + I(ln(distance)^2)*bank + mass total nitrogen + ε
Bulk $\delta^{13}C$	**0.40**	**0.00**	**$\delta^{13}C$ = ln(distance) + ε**
	0.29	0.62	$\delta^{13}C$ = ln(distance) + mass nitrogen + ε
	0.15	1.97	$\delta^{13}C$ = bank*ln(distance)+ mass nitrogen + ε
$\delta^{15}N$ of NH_4^+	**0.72**	**0.00**	**$\delta^{15}N$ of NH_4^+ = bank*ln(distance) + I(ln(distance)^2)*bank + ε**
$[NH_4^+]$	**0.23**	**0.00**	**$[NH_4^+]$= bank + ε**
	0.23	0.00	$[NH_4^+]$= bank*ln(distance) + ε
	0.20	0.26	$[NH_4^+]$= bank+ GW + ε
	0.13	1.19	$[NH_4^+]$= bank*ln(distance) + GW + ε
	0.10	1.60	$[NH_4^+]$ = bank*ln(distance) + I(ln(distance)^2)*bank + ε
	0.10	1.78	$[NH_4^+]$= ln(distance) + ε
$[NO_3^-]$	**0.72**	**0.00**	**$[NO_3^-]$ = bank + GW + ε**
	0.28	1.87	$[NO_3^-]$ = bank*ln(distance) + I(ln(distance)^2)*bank + GW + ε
Net Mineralization	**0.31**	**0.00**	**Net Mineralization = [organic nitrogen] + ε**
	0.23	0.61	Net Mineralization = GW + [organic nitrogen] + ε
	0.21	0.74	Net Mineralization = bank + [organic nitrogen] + ε
	0.14	1.61	Net Mineralization = bank+ [organic nitrogen] + ε
Net Nitrification	**0.62**	**0.00**	**Net Nitrification = $[NH_4^+]$ + GW + ε**
	0.37	1.00	Net Nitrification = bank + $[NH_4^+]$ + GW + ε
[Organic N]	**0.40**	**0.00**	**[Organic N] = ln(distance) + GW + ε**
	0.31	0.53	[Organic N] = bank*ln(distance) + GW + ε
	0.26	0.86	[Organic N] = bank*ln(distance) + I(ln(distance)^2)*bank + GW + ε
GW	**0.49**	**0.00**	**GW = $\log_{10}$(distance) + ε**
	0.33	0.81	GW = bank*ln(distance) + ε
C:N	**0.81**	**0.00**	**C:N = bank*ln(distance) + I(ln(distance)^2)*bank + GW + (1|Reach) + ε**

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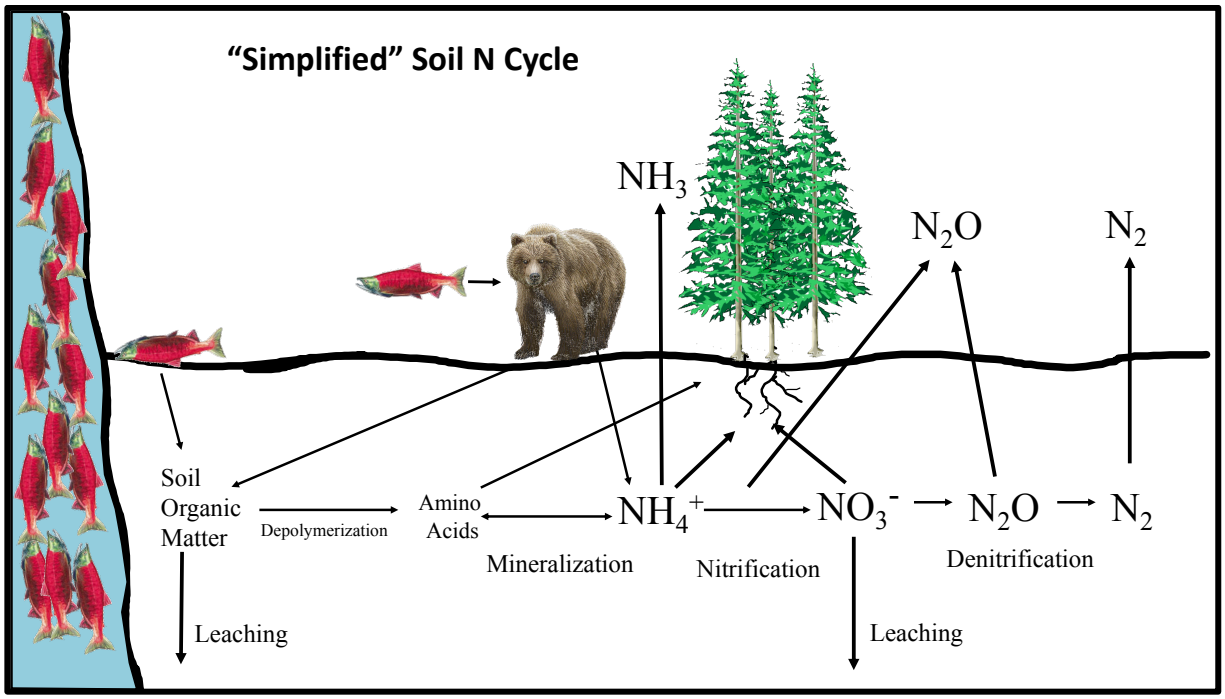
585

Figures

Figure 1: Nitrogen pathways in soil where MDN 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 (NH_4^+ or NO_3^-).



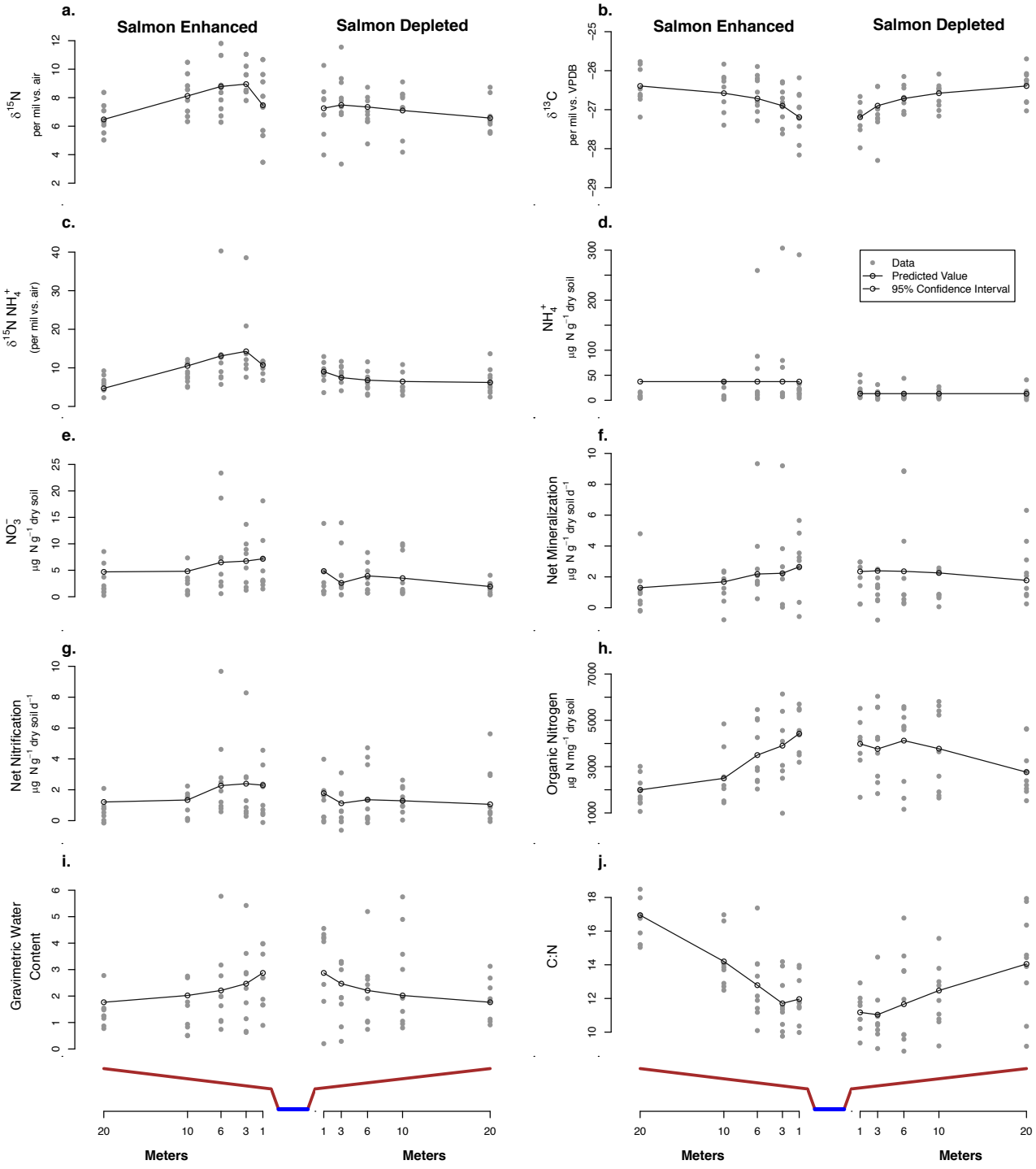


Figure 2: Data (grey) and predicted (black) values of NH_4^+ and NO_3^- concentration, and net mineralization and nitrification, $\delta^{15}N$ and $\delta^{13}C$ of organic material, and $\delta^{15}N$ of NH_4^+ and NO_3^- for both the salmon enriched and the non-salmon enriched banks of Hansen creek at 1m, 3m, 6m, 10m, and 20m from the edge of the creek bed with 95% confidence intervals for predicted values.