**Working title:** Mixed effects of long-term enrichment of riparian areas with salmon carcasses on inorganic soil nitrogen pools, nitrogen transformations, and stable isotopic ratios.

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**Abstract** *(350 words for ecology)*

**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) and is a textbook case of cross-ecosystem nutrient subsidies (sensu, Polis et al. 2004). Salmon derived nutrients enter freshwater and terrestrial food webs through two pathways: direct consumption by predators on salmon or their eggs, and recycling of nutrients as salmon carcasses decay and are incorporated into the food web via primary production (Gende et al. 2002). Dozens of studies have identified the presence of marine derived nutrients (MDN), particularly nitrogen (N) from salmon, as crossing the ecosystem boundaries of rivers, lakes, and streams into the terrestrial environment. The large body of research focused on the contributions of salmon to surrounding ecosystems is primarily based on nitrogen stable isotope analysis (15N/14N). Salmon are enriched in 15N relative to 14N when compared to watershed-derived nitrogen; as such, the elevated abundance of the heavier isotope can be used to trace the presence of MDN (Schindler et al. 2003). These analyses have shown significant contribution of salmon N to total N via the direct-consumption pathway. For example, the proportion of N derived from salmon ranges from 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. 1997; 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 throughout their range (Schindler et al 2013). Carcasses and roe are documented prey for over 22 species of mammals and birds (Cenderholm et al. 1989), and invertebrates (Minakawa et al. 2002, Winder et al. 2005). It is important to note presence of MDN derived from stable isotope analysis should not be conflated with importance and demonstrating the presence and distribution of MDN does not elucidate its effect on ecosystem dynamics. Nonetheless it is well documented MDN is both present and important for direct consumers in terrestrial and freshwater ecosystems. Bear population density, body size, and reproductive output have been correlated with increased MDN (Hilderbrand et al. 1999). Increased salmon carcasses generally result in elevated growth rates of both invertebrates and juvenile salmonids (Minakawa et al. 2002, Wipfli et al. 2002). In aquatic ecosystem higher salmon returns are correlated with enriched 15N in lower trophic levels including zooplankton and periphyton (Finney et al. 2000; Holtgrieve et al. 2010). Density, condition factors, and size increases for juvenile coho salmon with the addition of salmon carcasses, and is correlated with an increase of MDN estimated by stable isotope analysis (Bilby et al. 1998).

Stable isotope analysis has been used in a similar manner to trace the presence of MDN in primary producers and thus track its incorporation into the food web via nutrient recycling. Via this bottom up pathway, algae and bacteria uptake dissolved nutrients which are then consumed by predators and transferred through the food web. It has been posited salmon increase primary and subsequently secondary production by providing limited nutrients (N and P) (Holtgrieve and Schindler 2011). Reduction of two-thirds of MDN by commercial fisheries in fresh water lakes in Alaska resulted in a 3-fold decline in algal production (Schindler et al. 2005). This indicates MDN plays an important role for providing nutrients that support primary production in freshwater lakes. In stream ecosystems, salmon abundance increases dissolved inorganic nutrients such as phosphorus and NH4+. These nutrients have positive effects on epilithon growth (bacteria and algae), though the magnitude of this response is dependent on other growth limiting factors such as sunlight and disturbance (Johnston et al. 2004, Mitchell and Lamberti 2005, Chaloner et al. 2007, Janetski et al 2009).

In the terrestrial realm, the presence of MDN from salmon is well documented in both consumers and producers. Studies across much of the North American range where salmon are abundant have shown anywhere from X to Y percent of N in riparian plants and general correlations with salmon abundance and distance from the salmon spawning location (a bunch of papers here including Hocking and Reynolds, Science). Direct evidence as to the importance of MDN for ecosystem function is much less clear however. Helfield and Naiman (2001) measured tree growth increments in areas with and without salmon and found higher growth in one species in areas where salmon nutrients were present, although these findings and later contested based on statistical grounds () and have yet to be replicated (need to double check this is true). Hocking and Reynolds () observed some trends in understory plant community composition with salmon abundance, with a decrease in overall diversity and increases in a single N tolerant species. 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 an overriding trend for increased tree growth in the last 20 years (likely due to climate warming).

Given plants dominantly assimilate soil inorganic nitrogen (NH4+ and NO3-) that has been converted in soil rather than direct uptake of nutrients from salmon, fractionation in soils and nitrogen availability must be accounted for when considering mixing model end members. This is important for calculating the relative contribution of MDN to terrestrial communities via pathways that do not involve direct consumption of salmon. Studies using δ15N as an MDN tracer for plants typically assume nitrogen from salmon is directly assimilated by plants by using salmon δ15N as a mixing model end member, an assumption that is demonstrably false. The nitrogen cycle in soils contains a number of potentially fractionating steps (Figure 1). Organic material from decomposing salmon must undergo depolymerization, the conversion of organic matter to monomers, and mineralization, the conversion of organic compounds to ammonium by nitrogen fixing microbes. Ammonium then is converted to nitrate (NO3-) by nitrifying bacteria. Depolymerization, mineralization, and nitrification control plant available nitrogen pools and ultimately its corresponding δ15N (Schimel and Bennett 2004). These conversions also have the potential to enrich nitrogen pools in 15N (Gende et al. 2002; Schindler et al. 2003) which is likely to provide misleading over-estimates of the contributions of MDN to terrestrial vegetation. Nitrification and denitrification transformations have been shown to preferentially favor light isotopes and can impart stable isotope signatures as large as 15-35‰ and 30‰ respectively (Hogberg 1997), far exceeding the 12‰ salmon end member typically used in mixing models. Additionally, there is evidence δ15N and nitrogen availability are correlated, with foliar δ15N becoming more enriched when plant available nitrogen is abundant. Therefore, foliar δ15N is a signature of both the source δ15N of inorganic nitrogen in soils and nitrogen availability (Craine et al. 2009). Soil δ15N of organic material is also correlated to carbon and nitrogen availability (Craine et al. 2015).

Experiments examining the contributions of MDN are often limited by short timescales and few experiments investigate plant available nitrogen pools. Collins et al. 2015 demonstrated the need to evaluate ecosystem responses over longer periods of time to understand the magnitude and timescale of the effects of salmon on ecosystems. Studies examining spatial and temporal impacts of salmon on inorganic nitrogen pools have identified responses are highly localized (effects only observed less than 30 cm from carcasses), and NH4+ and NO3- become biologically available on the order of weeks to months respectively (Gende et al. 2007; Drake et al. 2005). Predator exclosure experiments determined impacts to soil N processing only persist for a year (Holtgrieve et al. 2009). If salmon do not arrive to ecosystems until after peak growing season of terrestrial vegetation, and plant available nitrogen sources do not persist for more than a year, the contributions of MDN to plant growth is likely minimal. In addition, experiments typically examine the contributions of MDN by nutrient addition not nutrient removal. This research contributes to these knowledge gaps by examining inorganic nitrogen pools, and both salmon addition and removal on long time scales.

To resolve the extent to which salmon carcasses impact plant available nitrogen pools (NH4+ and NO3-) and the rate of supply of these pools (via nitrification and mineralization), we present the results of a long-term fertilization experiment in southwestern Alaska. We also evaluate the impacts of soil nitrogen conversions on δ15N by examining the δ15N of NH4+ and NO3- in soils. Finally, we assess the relationship between nitrogen availability on stable isotope signatures of inorganic nitrogen pools.

**Methods**

*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. And average of XXX salmon return to the stream annually and, unlike some watersheds in the region, the watershed has a low density of alder (*Alnus crispa*), which can be a significant source of nitrogen via symbiotic fixation of atmospheric N2. For the last 20 years, the stream was surveyed daily during the annual sockeye salmon (*Oncorhynchus nerka*) run and all dead salmon were removed from the creek and its river right bank, and tossed on the river left bank. Thus, the right (no-salmon) side of the stream was manipulated for depletion of MDN, while the left bank was enriched. In total, YYY individual fish were translocated, representing XXXX kg of salmon, ZZZ kg of N and YYY kg of phosphorus (P).

Soil samples were collected from the riparian zone on July 13th 2017 along nine sets of paired transects, evenly nested within 3 equal sized stream reaches, across both the river left and river right banks. Transect location within reaches and covered the full length of the stream. Each transect included individual sampling sites at 1m, 3m, 6m, 10m, and 20m from the bank-full point. Sampling was targeted to occur during the peak growing season (maximum normalized difference vegetation index (NDVI); Kasischke and French 1995) when plants are removing the most nitrogen from soils thus incorporating available nitrogen and prior to the salmon run so as to consider long-term effects over short term. A 5cm x 5cm x 10cm soil column was taken for each sample site and the litter layer was removed before storing at 4 degrees C in airtight plastic bags for 48 hours prior to processing.

*Soil water content, nutrient concentrations (NH4+ and NO3-, and N transformations*

, (~ 48 hours). G as the change in mass divided by final dry mass (soil methods book)Soil nutrient concentration and N transformations were conducted according to Holtgrieve and Schindler 2009. Briefly, to determine the initial NH4+ and NO3- concentrations, subsamples (10-12 g wet weight) of sieved soils were extracted within 48 hours of collection in 100 ml of 2 M potassium chloride (KCl) (Hart et al. 1994). Soil extracts were shaken for 60 s then left to settle for 24 h before being filtered through Whatman #1 paper filters pre-leached with 100 ml of KCl. Approximately 8 ml of filtered extracts were frozen and later analyzed colorimetrically for NH4+ and NO3- with an Alpkem Flow Solution IV (OI Analytical, College Station, TX, USA). All leftover filtered extracts were frozen and stored for inorganic nitrogen stable isotope analysis. A second 10-12 g soil subsample was incubated aerobically in the dark for 15 days at ~20°C prior to extraction with KCl as above, and 8ml subsamples were similarly frozen and stored for colormetric analysis. Net mineralization calculated as the change in inorganic N concentration (NH4+ and NO3-) divided by the incubation duration, while net nitrification was calculated as the change in NO3- concentration over the incubation duration (Hart 1994).

*Stable isotope analysis*

Fresh soil subsamples were freeze dried for 48 hours, sieved, and ground into a uniform powder (< 212 μm) using a ball mill grinder. 2 mg samples of this ground soil were packed in tin capsules and analyzed for nitrogen (15N/14N) and carbon (13C/12C) stable isotope ratios at the University of Washington’s IsoLab using a Costech Elemental Analyzer, Conflo III MAT253 for continuous flow-based measurements. 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 Belemite (VPDB) for N and C respectively (Schoeninger et al. 1983). Total nitrogen concentration (mg N per gram dry soil) was also calculated based on percent nitrogen information obtained during the isotopic analysis.

For 15N/14N stable isotope analysis of NH4+ and NO3-, the total volume of formerly frozen filtered KCL extracts were measured and placed in Erlenmeyer flasks to undergo diffusion and capture using the methods of XXX. To retrieve NH4+ as gaseous NH3,300 mg of MgO and an acid trap (1 cm glass fiber filter treated with KHSO4 and sealed in Teflon) were added to each flask, which were immediately stoppered, sealed with parafilm, and placed on a shaker table. Samples shook continuously for six days after which acid traps were removed and stored in desiccator for 3-4 days before filters were removed and packed in tin capsules for analysis. Extracts were returned to the shaker table and left open to the atmosphere for one day to remove any remaining NH4+. To retrieve NO3- as NH3, another 300 mg of MgO were added to each extract and immediately followed with 75 mg of Devarda’s alloy and an acid trap. Extracts were then sealed and agitated on the shaker table for six more days before acid traps were removed and filters were packed as described above. Four each of batch blanks (KCl with no soil extract) and reference standards of NH4XX and KNO3 with known 15N/15N were also run. These samples were run in four separate batches and three blanks and three standards were run for each batch. Batch blanks showed quantifiable N from the KCl. Therefore, a two-source mixing model correction was applied to both samples and reference standards using equation 1:

(1) δ15NBlank Corrected = (δ15Nmeasured \* (Nblank, x + Nextracted) (δ15Nblank, x\*NBlank, x))/ Nextracted

Where *x* represents an individual batch, NBlank, x is the average measured mass (µg) of nitrogen in a blank for a given batch, and δ15NBlank, x is the average measured δ15N of blanks for a given batch. δ15Nmeasured is the δ15N value for a given sample, and Nextracted is the mass of nitrogen (µg) measured in the sample. A standard correction was then applied to the blank corrected measurements where:

(2) δ15NCorrected = δ15NBlank Corrected – (StandardMeasured, x – Standardtrue)

Where Standardmeasured, x is the average measured value of the standard for a given batch. All reported δ15N of NH4+ and NO3- values are expressed as the δ15Ncorrected, where a blank and standard correction has been applied.

*Statistical analyses*

To test the effect of salmon enrichment on soil nutrient concentrations, linear and mixed effects models were individually fit to the data for the following response variables: NH4+ and NO3- concentrations, net mineralization and net nitrification, δ15N and δ13C of bulk soil, and δ15N of NH4+ and NO3-. The random effects structure was initially tested using restricted maximum likelihood estimation where reach, site, and site nested within reach were considered. The random effects structure with the most support using Akaike’s information criterion (AIC) was then considered within the candidate model set.

An ordinary likelihood structure was then applied to compare models with different fixed effects structures, no random effects, and the most supported random effects structure (Zuur et al. 2009). For all response variables, candidate models (supplementary material 1—need to add) included the interaction between bank (left vs. right) and distance from rivers edge. Gravimetric water content was considered as a fixed effect, and soil NH4+ concentration was considered as a fixed effect for net nitrification, and soil organic nitrogen concentration was considered as a fixed effect for net mineralization, given NH4+ and organic nitrogen function as the substrate for mineralization and nitrification respectively. The best model was selected from the candidate models 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 examined to assess the hypothesis that MDN provided by salmon carcasses impacts soil N cycling. Changing the number of salmon on each bank was the primary goal of the manipulation and therefore is the most direct indicator of a salmon effect. from the stream-6 stream after translocation, soils, and available water For both the bank and distance model parameters, the weighted sum of all AIC supported models (AIC < 2) that included these parameters calculated to generate an overall effect size on a scale from 0 to 1. The effect of nitrogen availability on stable isotope signature was also tested by including mass of nitrogen as a covariate in the candidate model set for δ15N of NH4+, NO3-, and organic nitrogen, and similar weighted across all models for an overall effect size. Effect sizes of bank or distance greater than XXX were considered to be strong model support for the presence of salmon influencing the specific response variable under consideration (e.g., [NH4+], [NO3-], δ15N, etc.).

To test the utility of 12‰ as a mixing model end member, the proportion of observations for δ15N of NH4+, NO3-, and organic nitrogen that exceeded 12‰ was calculated.

**Results**

*Effect of salmon enrichment*

Multiple response variables indicated relative support for multiple models within the candidate model set (Table 1). Given this result, using cumulative weights of models that include a certain parameter, such as a bank effect, is the most useful way to interpret results. Cumulative weights of 1 indicate strong support within the supported models for the inclusion of a parameter, while cumulative weights of 0 indicate no support.

Start with concentration data and follow with isotopes (which matches the figure). All supported models for δ15N of NH4+, NO3-, and organic nitrogen include an effect of creek bank with cumulative model weights of 1. All supported models of NO3- concentration also included a bank effect (Table 2; Figure 2). Both NH4+ concentration and net nitrification also had strong support for a bank effect, with cumulative weight if the bank effect of 0.88 and 0.82 respectively. There was little model support for a bank effect on δ13C or net mineralization (Table 2; Figure 2). \*\*\*I’m really confused. I struggle to see an effect in the figures but the model results seem to indicate a “YUGE” effect. I’m not sure what this effect size thing is really saying. Need to chat about it…\*\*\*

Cumulative weights show strong support for a distance effect for δ15N of NH4+, NO3-, and organic nitrogen, and δ13C of organic nitrogen. There was also relative support for a distance effect on NH4+ concentration and net nitrification with weights of 0.70 and 0.72 respectively. Models with relative support did not indicate relative support for a distance effect on net mineralization or NO3- (Table 2; Figure 2).

The models with relative support did not indicate an effect of mass of nitrogen on δ15N of NH4+ or organic nitrogen, however there was strong support for an effect of nitrogen on δ15N of NO3- (Table 2: Figure 2). It was also observed δ15N values of NH4+ exceeded12‰ (the average value of sockeye salmon) for 23% of all observations (n=21). Similarly, δ15N values of NO3- exceeded values of salmon for 21% of all observations (n=19). There were no observation of δ15N of organic nitrogen values exceeding 12‰.

**Discussion**

These results confirmed the presence of MDN in soils and that salmon enrichment increases nitrogen concentration in soils. Models with relative support demonstrated the salmon enriched bank had elevated total nitrogen concentration and all three tested nitrogen pools (NH4+, NH3-, and organic nitrogen) had enriched δ15N. Given soils were sampled prior to the return of salmon for the year, these results indicate elevated nitrogen and δ15N persist through the winter and are available even when salmon are not present in the system. δ15N was the most enriched at 3m from the edge of the enriched edge and with distance, indicating the presence of MDN is somewhat localized to areas where salmon carcasses are placed.

Despite increased total nitrogen concentration, fertilization from salmon carcasses did not increase all plant available nitrogen pools and transformation rates during peak vegetative growing season. Given vegetation incorporates the largest quantities of nitrogen during the growing season, these results indicate long term fertilization does not increase nitrogen sources that are seasonally accessible to plants. While models with relative support indicate carcass fertilization increases net nitrification, and NH4+ and NO3- , they did not demonstrate carcass fertilization increases net mineralization rates. While vegetation in salmon enriched areas may demonstrate elevated stable isotope signatures, this reflects the presence of MDN and not necessarily the contributions MDN has made to vegetation.

Stable isotope measurements of inorganic nitrogen sources had values that exceeded salmon stable isotope end members commonly used in plant MDN mixing models. This indicates soil nitrogen pathways can enrich stable isotope values beyond their organic inputs. While our results did indicate an effect of salmon enrichment on δ15N of NH4+ and NO3-, observations also excided the δ15N of organic nitrogen in the soil demonstrating fractionation is likely occurring through microbial pathways. As a result, using a mixing model end member of 12‰ to represent a nitrogen signature 100% derived from salmon is inaccurate, as under some circumstances plant available nitrogen pools can exceed that value. This demonstrates incorporating isotopic enrichment associated with nitrogen transformations in soils is important and necessary to accurately assess the contributions of MDN to plants. If these transformations are not considered, it is likely calculations may overstate the importance of MDN to plants. Understanding the relative importance of all plant available nitrogen pools, including NH4+, NO3- and amino acids, and their corresponding isotope signature will be important for determining accurate mixing model end members and thus contributions of MDN to terrestrial vegetation.

Global declines in Pacific salmon populations caused by anthropogenic impacts (overharvest, habitat degradation, hydropower dams) and the preservation of this ecosystem service and has been a focal point for many management and mitigation strategies (Collins et al. 2015; Lichatowich 1999). It has been established salmon provide supplementary nutrients to aquatic systems and direct consumers, however the necessity of MDN for plant communities and their consumers is less certain. While these results support the presence of MDN in soils, the utility of these nutrients as represented by δ15N is dependent on what nutrients are limiting to plant growth, and whether they are available during the growing season. The relationship between fractionation and nitrogen concentration, and the fractionation caused by nitrogen transformations has the potential to mislead results linking MDN to growth.

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**Tables**

Table 1: Models with relative support using AIC analysis for each response variable

|  |  |  |  |
| --- | --- | --- | --- |
| **Response Variable** | **AIC Weight** | **AIC** | **Models with Relative Support** |
| Bulk δ15N | **0.17** | 2.0 | δ15N = bank\*log10(distance) + I(log10(distance)2)\*bank + organic nitrogen + mass total nitrogen + (1|site) + ε |
| **0.36** | 0.46 | δ15N = bank\*log10(distance) + I(log10(distance)2)\*bank + ε |
| **0.44** | 0.00 | δ15N = bank\*log10(distance) + I(log10(distance)2)\*bank + mass total nitrogen + ε |
| Bulk δ13C | 0.23 | 0.75 | δ13C = log10(distance)+ mass nitrogen+ ε |
|  | 0.35 | 0.00 | δ13C = log10(distance) + ε |
| NO3- concentration | **0.58** | 0.00 | NO3- concentration = bank + GW + ε |
| NH4+ concentration | **0.12** | 1.11 | NH4+ concentration = bank\*log10(distance) + GW + ε |
| **0.20** | 0.07 | NH4+ concentration = bank\*log10(distance) + ε |
| **0.09** | 1.58 | NH4+ concentration = bank\*log10(distance) + I(log10(distance)2)\*bank + ε |
| 0.08 | 1.75 | NH4+ concentration = log10(distance) + ε |
| **0.21** | 0.00 | NH4+ concentration = bank + GW + ε |
| Net Mineralization | 0.27 | 0.00 | Net Mineralization = organic nitrogen + ε |
| **0.22** | 0.48 | Net Mineralization = bank + organic nitrogen + ε |
| 0.10 | 1.96 | Net Mineralization = log10(distance) + organic nitrogen + ε |
| Net Nitrification | **0.22** | 0.00 | Net Nitrification = bank + NH4+ concentration + gravimetric water content + (1|site) +ε |
| 0.14 | 0.93 | Net Nitrification = log10(distance ) + NH4+ concentration + GW + (1|site) +ε |
| **0.12** | 1.19 | Net Nitrification = bank\*log10(distance) + I(log10(distance)2)\*bank + GW + NH4+ concentration + ε |
| **0.11** | 1.39 | Net Nitrification = bank\*log10(distance) + I(log10(distance)2)\*bank + GW + NH4+ concentration + (1|site) + ε |
| **0.10** | 1.58 | Net Nitrification = bank + NH4+ concentration + ε |
| **0.09** | 1.82 | Net Nitrification = I(log10(distance)2)\*bank + GW + NH4+ concentration + (1|site) + ε |
| δ15N of NO3- | **0.42** | 0.00 | δ15N of NO3- = bank\*log10(distance)+ mass nitrogen + (1|reach) + ε |
|  | **0.18** | 1.64 | δ15N of NO3- = bank\*log10(distance)+ mass nitrogen + GW + (1|reach) + ε |
|  | **0.16** | 1.97 | δ15N of NO3- = bank\*log10(distance) + I(log10(distance)2)\*bank + mass nitrogen + (1|reach) + ε |
| δ15N of NH4+ | **0.72** | 0 | δ15N of NH4+ = bank\*log10(distance) + I(log10(distance)2)\*bank + ε |

Table 2: Cumulative weights of covariates on response variables.

|  |  |  |  |
| --- | --- | --- | --- |
| **Response Variable** | **Bank Weight** | **Distance Weight** | **Mass Nitrogen Weight** |
| Bulk δ15N | 1.0 | 1.0 | 0.45 |
| Bulk δ13C | 0.0 | 1.0 | - |
| NO3- concentration | 1.0 | 0.0 | - |
| NH4+ concentration | 0.88 | 0.70 | - |
| Net Mineralization | 0.37 | 0.17 | - |
| Net Nitrification | 0.82 | 0.72 | - |
| δ15N of NO3- | 1.0 | 1.0 | 1.0 |
| δ15N of NH4+ | 1.0 | 1.0 | 0.0 |

**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 (NH4+ or NO3-).

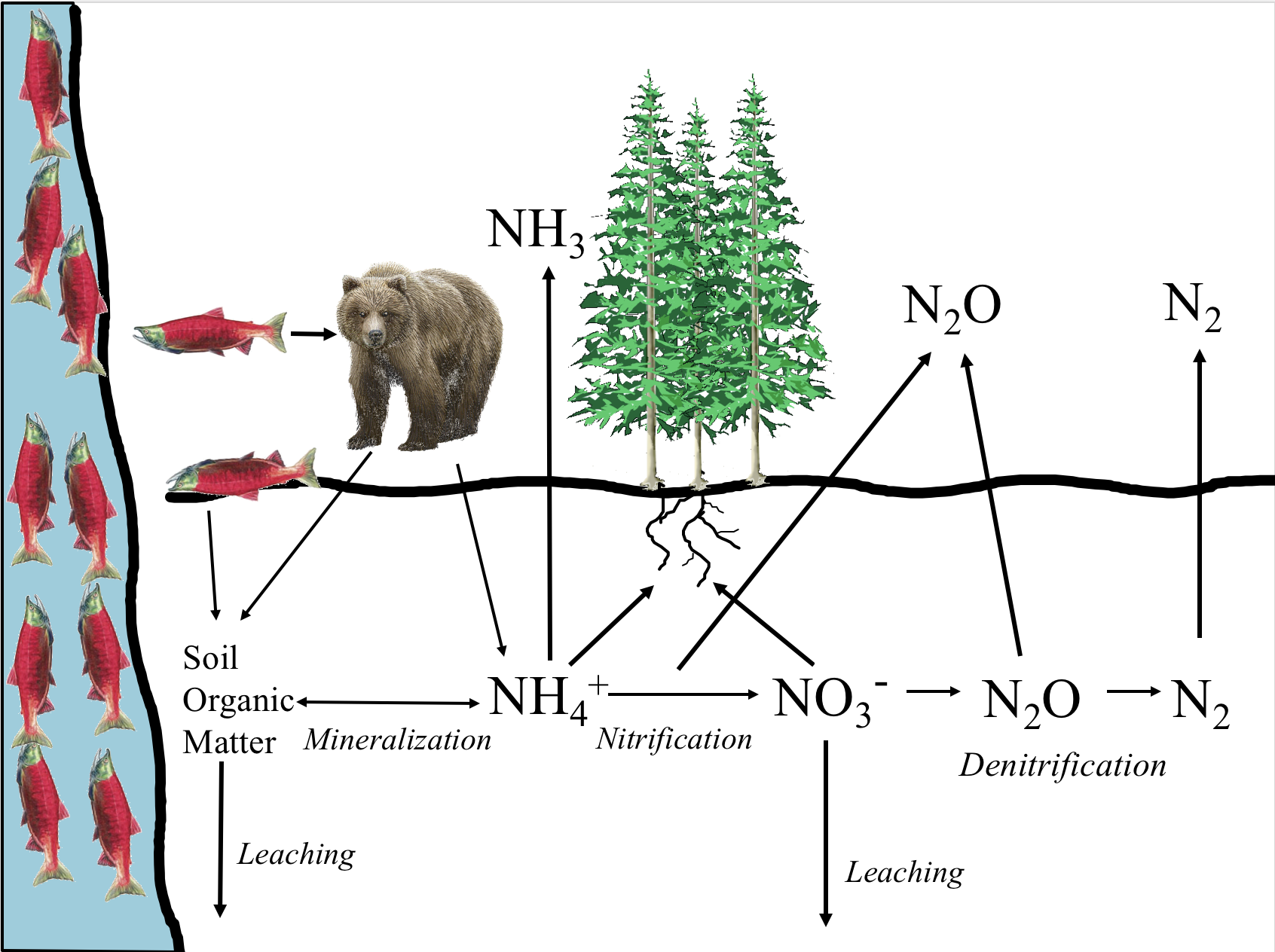
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Figure 2: Data (grey) and predicted (black) values of NH4+ and NO3- concentration, and net mineralization and nitrification, δ15N and δ13C of organic material, and δ15N of NH4+ and NO3- for both the salmon enriched and the non-salmon enriched banks of Hansen creek at 1m, 3m, 6m, 10m, and 20m from the edge of the creek bed with 95% confidence intervals for predicted values.





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**Supplementary Material**

SI 1: The candidate model set tested for each response variable using AIC analysis. \* denotes a mixed effects model where reach and site are random effects and all other variable are fixed effects. All other candidate models are linear models. For net nitrification and net mineralization, NH4+ concentration and organic nitrogen concentration were considered as fixed effects respectively.

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| **Candidate Model Set** |