**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 nutrients and organic material to freshwater and terrestrial ecosystems (Gende et al. 2002). Given a majority of salmon growth occurs in the ocean, these annual events provide an influx of marine derived nutrients (MDN). Carcasses and roe are prey for a variety of organisms, and this resource pulse is linked to variable responses in periphyton density, stream biofilms, freshwater nutrient concentration, and insect abundance (Mitchell and Lamberti 2005; Rüegg et al. 2011). The contributions of MDN are not restricted to aquatic environments and have been shown to contribute to terrestrial counterparts. Flooding, erosion, and sediment deposition can alter nutrient dynamics and soil composition in adjacent terrestrial ecosystems, including delivery of MDN (Naiman 1998; Naiman and Decamps 1997). In addition, transport of salmon carcasses by bears increases soil ammonium (NH4+) concentrations (Holtgrieve et al. 2009), and the spatial distribution of MDN in foliar material is linked to flooding and piscivorous predator activity (Ben-David et al. 1998).

The body of research focused on the contributions of MDN from anadromous, semelparous, fish species to surrounding ecosystems is primarily based on stable isotope analysis of δ15N (15N/14N). Salmon tend to be enriched in 15N relative to 14N when compared to freshwater nitrogen; this elevation of the heavier isotope can be used to trace the fate and distribution of MDN (Schindler et al. 2003). Stable isotope analysis is used to understand utilization of MDN by juvenile and adult salmon, plankton, and piscivorous predators (Hicks et al. 2005; Chaloner et al 2002; Claeson et al. 2006; Rinella et al. 2013)*.* For example, higher salmon returns have demonstrated elevated δ15N in zooplankton and periphyton (Finney et al. 2000; Holtgrieve et al. 2010). Salmon contributions to the terrestrial nitrogen pool support plant growth and distribution (Bilby et al. 2003; Helfield and Naiman 2001, 2006; Ben-David et al. 1998).

Given plants assimilate nitrogen 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 small stream flowing from a beaver pond to Lake Aleknagik in the Wood River system of Bristol Bay, AK. For the last 20 years adult spawned out sockeye salmon (*Oncorhynchus nerka*) were removed from Hansen Creek and its river right bank (decreasing salmon density) and tossed on the river left bank (increasing salmon density). Unlike some watersheds in the region, Hansen Creek has a low density of alder (*Alnus crispa*) which can be a source of nitrogen via symbiotic fixation of atmospheric N2, making it a useful system for studying MDN as the source of plant available nitrogen in soils.

Soil samples were collected from on July 13th 2017 along nine sets of paired transects on the river left and river right banks, and across 3 reaches of the creek at 1m, 3m, 6m, 10m, and 20m from the proper bank. Sampling was conducted during peak growing season when plants are removing the most nitrogen from soils thus incorporating available nitrogen. Studies examining the normalized difference vegetation index (NDVI) for boreal forests in Alaska indicate peak growing season of vegetation occurs during early July (Kasischke and French 1995). Sites were selected to be representative of typical riparian vegetation and high spawning intensity. An approximate 5cm x 5cm x 10cm soil column was taken for each sample and plant matter was removed from the samples. Samples were stored at 4 degrees C in airtight plastic bags for 48 hours prior to processing. To determine soil water content 50 – 100 g of soil (wet weight) were placed in a drying oven at 105°C until dry soil reached a constant mass, and gravimetric water content was calculated.

*Soil nutrient concentrations (NH4+ and NO3-) and N transformations*

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 24-48 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 12-16°C prior to extraction with KCl as above, and 8ml subsamples were 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.

*Stable isotope analysis*

Soil subsamples were freeze dried for 48 hours, sieved, and ground into a uniform powder (< 212 μm) using a ball mill grinder for bulk isotope analysis. 2 mg of soil were packed in tin capsules and analyzed for nitrogen stable isotope ratios (15N/14N) using Air-N2 for reference and carbon (13C/12C) stable isotope ratios using VPDB for reference. Samples were analyzed at University of Washington’s IsoLab using a Costech Elemental Analyzer, Conflo III MAT253 for continuous flow-based measurements. Measurements are reported as δ15N or δ13C which represent the per mil deviation in heavy isotope abundance from the isotopic standard (Schoeninger et al. 1983). Total nitrogen concentration was also calculated based on percent nitrogen from the isotope data. Percent nitrogen was converted to mg nitrogen per gram dry soil.

For inorganic stable isotope analysis of NH4+ and NO3-, total volume of formerly frozen filtered extracts were measured and placed in Erlenmeyer flasks. To retrieve NH4+,300 mg of MgO and an acid trap (1 cm glass fiber filter treated with KHSO4 and sealed in Teflon tape) 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 to remove remaining NH4+. To retrieve NO3-, 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 immediately stoppered, sealed with parafilm, and placed on a shaker table for six days before acid traps were removed and filters were packed as described above. For each batch blanks (KCl with no soil extract) and standards were also run. These samples were run in four separate batches and three blanks and three standards were run for each batch. To correct isotope data for analytical bias a mixing model was applied using equation 1:

(1) δ15NBlank Corrected = (Measured δ15N \* (Mass NBlank, x + Mass Nextracted) (δ15NBlank, x\*Mass NBlank, x))/ Mass Nextracted

Where x represents an individual batch so that Mass NBlank is the average measured mass (ug) of nitrogen in a blank for a given batch and δ15NBlank, x is the average measure δ15N of blanks for a given batch. Measured δ15N is the δ15N value for a given sample, and Mass Nextracted is the mass of nitrogen (ug) measured in the sample. A standard correction was then appied 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 used. Linear models and mixed effects models were fit to the data for each response variables: initial NH4+ and NO3- concentrations, net mineralization and net nitrification, δ15N and δ13C of bulk isotopes, and δ15N of NH4+ and NO3-. First, random effects structure was 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 and distance from rivers edge. Gravimetric water content was considered as a fixed effect, and NH4+ concentration was considered as a fixed effect for net nitrification, and organic nitrogen concentration was considered as a fixed effect for net mineralization, given NH4+ concentration and organic nitrogen concentration function as the substrate for the corresponding transformationss. 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.

To test the hypothesis MDN provided by salmon carcasses impacts plant available nitrogen, the weight of all supported models (del AIC < 2) that included a bank effect were calculated and summed across all models to generate an effect size of the bank parameter. Strong model support for the inclusion of a bank parameter indicates the presence of salmon has an effect on the response variable. The cumulative effect of the distance parameter was also considered, as most salmon are located within 3 meters of the creek edge. However, this parameter is a less direct measure of the effect of MDN on response variables as other factors change with distance from the bank including vegetation and contributions terrestrial verse aquatic sources of nutrients. 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. Similarly, its weight was summed across all models for an effect size. 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.

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).

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+ exceeded values of salmon or 12‰ 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** | **delAIC** | **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 a fractionation on plant available nitrogen (NH4+ or NO3-).

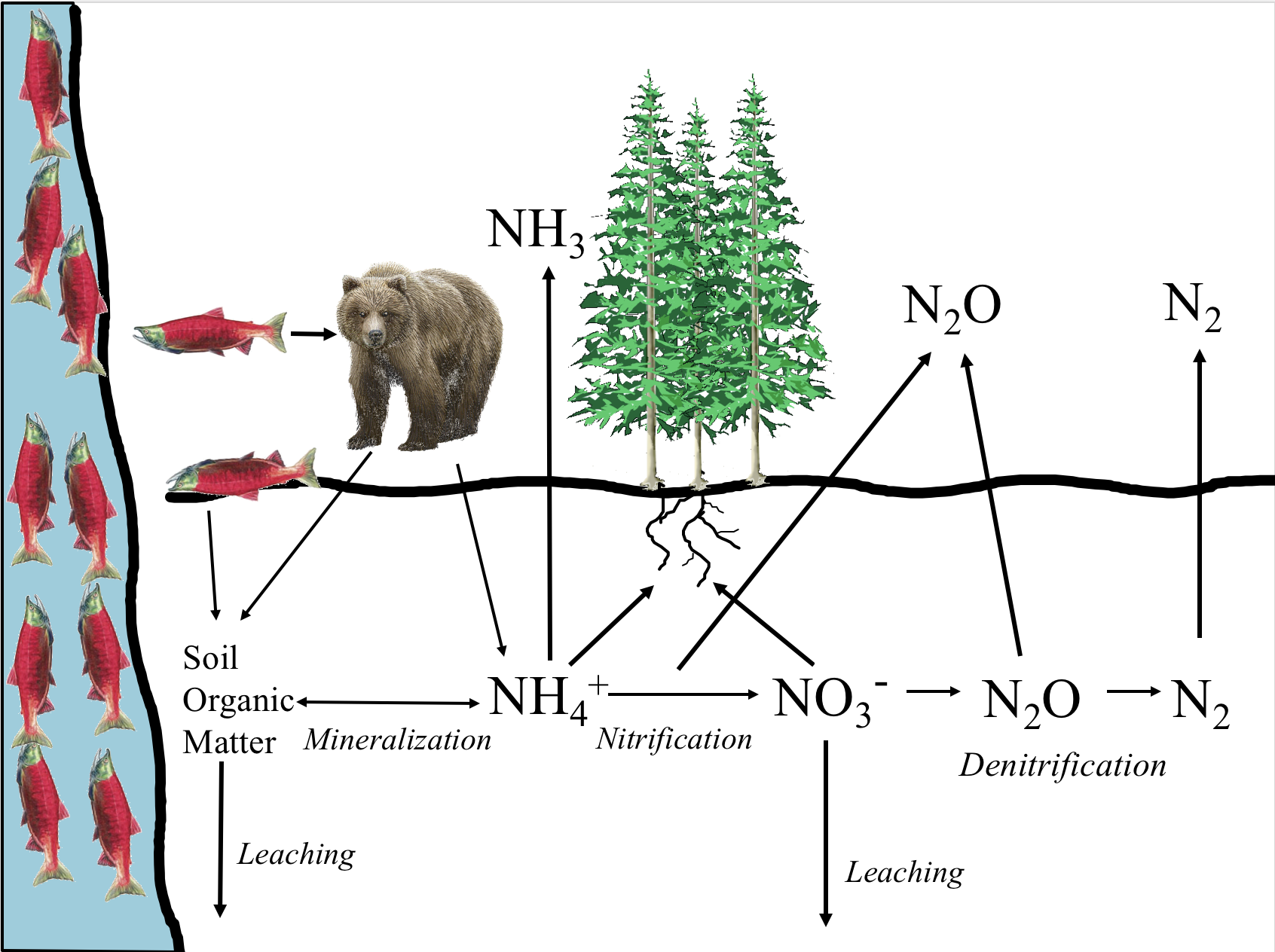
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Figure 2: Data (grey) and predicted (black) values of NH4+ and NO3- concentration, and net mineralization and nitrification, δ15N and δ13C of organic material, and δ15N of NH4+ and NO3- for both the salmon enriched and the non-salmon enriched banks 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** |