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The nutrient legacy left by salmon tissue on riparian soils in Southeast Alaska

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Abstract

Salmon-derived nutrients (SDN) are a distinctive aquatic subsidy to terrestrial ecosystems. Streamwater nutrient increases in response to SDN have been documented but uncertainties about the magnitude and persistence of their effects in riparian areas remain. A key research gap is the response of specific soil types to the nutrient subsidy over time. To address this question, an Entisol and a Spodosol commonly found in riparian zones of Southeast Alaska were delineated adjacent to streams with abundant spawning salmon for experimental nutrient additions. Salmon nutrient additions were applied to track the fate of N and P through time to investigate the patterns of nutrient retention and loss in the Entisol and Spodosol. Salmon additions to Entisols across eight watersheds revealed a large and consistent residual concentration of available NH_4^+–N but a high variability in NO_3^-–N after a 30-d incubation. A comparison of Entisols and Spodosols in two watersheds tracked salmon tissue additions for ∼1 yr, where nutrient concentrations at 240 d decreased relative to 30 d but a flush of available nutrients occurred at 340 d, with higher values in the salmon-amended soils. The magnitudes of extractable N and P retained in the extractable fraction were similar in the Entisol and Spodosol but dissolved N loss measured via resin beads at the base of the measurement cores indicated higher leaching of NO_3^-–N from the surface in Entisols. Identification of specific soil types can advance the understanding of nutrient processing, uptake, and loss from SDN additions on riparian landforms.

1 | INTRODUCTION

Adult Pacific salmon (*Oncorhynchus* spp.) can provide a significant ecosystem resource subsidy to freshwater ecosystems when they return from the ocean to spawn (Schindler & Smits, 2016; Willson, Gende, & Marston, 1998). Multiple studies have shown that aquatic organisms use the energy and nutrients (especially N and P) associated with salmon runs, as reflected in increased stream productivity and biomass (Levi, Tank, Tiegs, Chaloner, & Lamberti, 2013; Ruegg et al., 2012) and altered stable isotope composition (Reisinger, Chaloner, Ruegg, Tiegs, & Lamberti, 2013). Large numbers of dead fish are also deposited on adjacent riparian areas (Fellman, Hood, Edwards, & D'Amore, 2008; Gende, Edwards, Willson, & Wipfli, 2002). Through this deposition in riparian areas, the SDN subsidy has also been linked to increased terrestrial productivity (Ben-David, Hanley, & Schell, 1998; Helfield & Naiman, 2001; Bilby, Beach, Fransen, Walter, & Bisson, 2003). Connecting SDN to terrestrial nutrient cycles has been supported by mixing models that use the natural abundance of N isotopes ($\delta^{15}N$)(Drake, Naiman, & Bechtold, 2006; Gende, Miller, & Hood, 2007). However, the natural abundance

Abbreviations: SDN, salmon-derived nutrients; SRP, soluble reactive P.

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of $\delta^{15}N$ is confounded by denitrification within soils that alter $\delta^{15}N$ in the absence of SDN (Högberg, 1997), leading to potentially misleading soil enrichment values (Cross & Perakis, 2011; D'Amore, Bonzey, Berkowitz, Ruegg, & Bridgham, 2011).

Riparian soils with very different physical and chemical attributes are found in close association along alluvial landforms adjacent to salmon streams (D'Amore et al., 2011). These soils vary laterally across the riparian zone with proximity to the stream and vertically within a single soil type as a result of soil horizon development during soil genesis (Jenny, 1941). Varying time scales have resulted in well-developed terrace Spodosols and younger floodplain Entisols (D'Amore et al., 2011). The development of spodic soil horizons in the terrace soils compared with the less-developed floodplain Entisols suggests that the SDN will be retained and processed differently within each soil type. In addition, salmon can spawn during the latter part of the growing season, when falling temperatures and lower solar radiation result in plant senescence. Thus deposited nutrients are less likely to be taken up by plants or incorporated into microbial biomass. However, there is evidence that western redcedar (*Thuja plicata* Donn ex D. Don) responded to SDN additions (Drake et al., 2006). It is worth noting that redcedar and yellow-cedar [*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little] have a more plastic growth response than other co-occurring conifer species (Grossnickle & Russell, 2006) and do not exhibit strong cold-hardiness over the fall and winter (Schaberg, D'Amore, Hennon, Halman, & Hawley, 2011). Therefore, the cedars may benefit from off-season SDN additions in riparian zones. In order to be of ecological significance, nutrients need to be stored in the soil matrix for use by plants and microbes in the subsequent growing season. Despite this potential for storage and the important function that SDN may play in terrestrial systems, there has been no consideration of the soil nutrient loading provided by SDN with a detailed treatment of nutrient dynamics across space and time in specific soils. Further, there is a distinct pattern to the alluvial landscape along salmon streams where two soils co-occur on the floodplain and terrace landforms (D'Amore et al., 2011). Therefore, characterization of this soil variation is needed in order to fully understand the effect that salmon nutrients could have on riparian ecosystems. Studies that establish a clear response within specific soil types to the presence of SDN over time are important, given that some have argued that SDN are important for the succession of streams and associated riparian areas after glaciers receded in Southeast Alaska [see Milner & Robertson (2010)].

We implemented two companion studies to provide information on both the variability of SDN applications across the landscape in near-stream Entisols and provide an understanding of how the concentration of SDN changes over time within two soil types. We identified Entisols within eight independent watersheds and measured the impact of SDN additions during a 30-d time period to determine the extent of spatial variability in the processing of SDN across space. We also identified an Entisol and Spodosol in two watersheds where we tracked the SDN additions over 340 d. This study examined how N and P concentrations in soils on two landscape positions changed through time after SDN was encountered. We used a uniform application of salmon tissue material to replicate soil cores, followed by measurements of soil nutrient content over time to determine the extractable (i.e., available) N and P in the soil. In the intensive study, we also used an adsorbing resin placed at the bottom of each core to capture any N and P that leaked from the core to assess the mobility of N and P over time. The intensive experiment was conducted for the annual cycle from the time that salmon spawners were present in fall, through the winter, and up to the next cycle of salmon spawning. We designed our study to test the two following hypotheses: (a) SDN will be retained in floodplain soils across varying watershed locations, and (b) the magnitude of retention and loss of SDN will vary between floodplain (Entisols) and terrace (Spodosols) because of differences in soil horizonation.

Core ideas

- Alluvial soils mediate the loss of salmon-derived nutrients (SDN) through an annual cycle.
- Distinguishing soil types is important for understanding the fate of SDN in riparian zones.
- The fate of SDN in riparian zones varies with soil type.

2 | MATERIALS AND METHODS

2.1 | Site description and selection

Study sites were located on Prince of Wales Island in Southeast Alaska (Figure 1). The climate of this region of Southeast Alaska is maritime cool and moist with annual precipitation of 2347 mm yr^{-1} and an average temperature of 7.5°C (Alaska Climate Research Center, 2020). The watersheds (Indian, Maybeso, Nossuk, Rio Roberts, Trocadero, Slide, Twelve Mile, and Upper Slide) were chosen as part of a larger study of SDN in streams across a range of watersheds (Figure 1) (Ruegg et al., 2012; Tiegs et al., 2008). Specific soil sample locations along similar large floodplain stream reaches were chosen where soil mapping units adjacent to the stream contained floodplain and terrace geomorphic units (Map Unit 10) as identified in the Tongass soil resource inventory (USDA Forest Service, 1997). Within this soil map

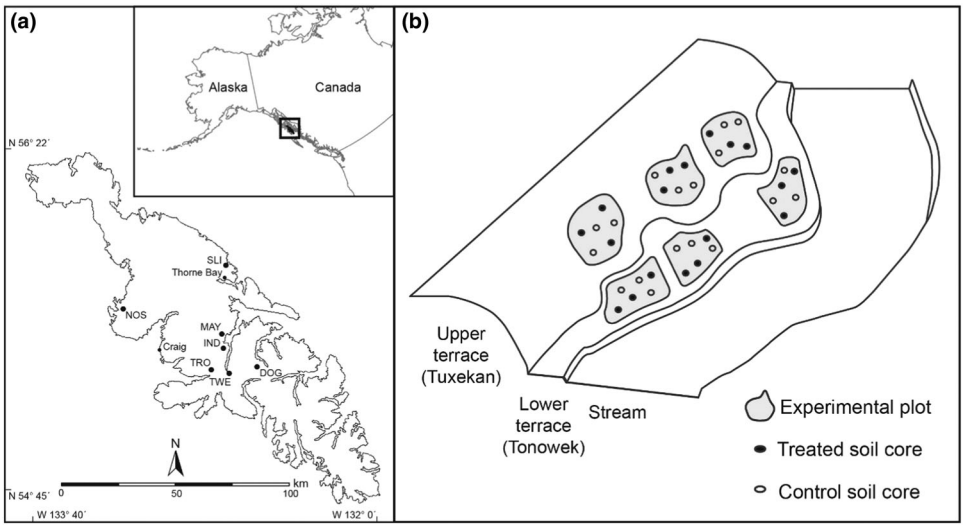

FIGURE 1 Regional location of the study. (a) Watershed locations on Prince of Wales Island in Southeast Alaska: IND, Indian; MAY, Maybeso; NOS, Nossuk; ROB, Rio Roberts; SLI, Slide; TRO, Trocodero; TWE, Twelve Mile; USL, Upper Slide. (b) Schematic of soil locations and core placements corresponding to the Tuxekan soils on terrace landforms and Tonowek soils located on floodplain and terrace landforms adjacent to salmon-bearing streams

unit, the toposequence of the Tonowek (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, nonacid Typic Cryofluvents) and Tuxekan (coarse-loamy over sandy or sandy-skeletal, mixed, superactive Typic Humicryods) soil series generally extends outward perpendicular to the stream bank. Once the soil types were confirmed by site surveys at each location, soil profile descriptions were completed for each site (Soil Survey Division Staff, 1999). The study sites were dominated by Sitka spruce [*Picea sitchensis* (Bong.) Carrière] and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], along with occasional red alder (*Alnus rubra* Bong.). Redcedar (*T. plicata*) and yellow-cedar (*C. nootkatensis*) are not common in riparian zones in Southeast Alaska because of the disturbance history that has formed the terrace and floodplain landforms. Streams are dominated by pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*), with smaller numbers of coho salmon (*Oncorhynchus kisutch*) at several sites (Tiegs et al., 2008). All sites contained the Tonowek soil series (Inceptisol; Typic Cryofluvent) within the riparian zone immediately adjacent to the stream. The soil surface is usually finer in texture than the coarse-gravelly C horizon (D'Amore et al., 2011). At two of the sites (the Twelve Mile and Indian watersheds), the Tuxekan soils series (Spodosol; Typic Humicryod) were also examined on the terrace landform. These soils have a spodic horizon and usually, though not always, an E horizon. Surface organic horizons can be up to 10 cm thick, but are usually thinner, depending on the microsite position of the soil (D'Amore et al., 2011). A soil series delineation was conducted at each site to identify three replicate sample plots for either Tonowek or Tuxekan soils within each watershed (Figure 1).

2.2 | Soil cores, analysis and resin beads

A series of polyvinyl chloride soil cores 25 cm deep (diameter = 7.62 cm) (Binkley and Hart, 1989) were inserted into the soil surfaces during late August 2007 (Figure 1). Six cores were installed in each Tonowek soil across eight watersheds as part of an extensive survey of short-term (30 d) nutrient yield. Three cores were randomly selected for treatment with salmon tissue; the remaining three cores were left untreated. An accompanying intensive installation at the Twelve Mile and Indian watersheds included both Tonowek and Tuxekan soils. Three plots with homogeneous soils were identified for placement of six paired cores, with one core of each pair randomly designated for treatment with salmon tissue. Therefore, the intensive sites had a total of 18 cores, with nine of these cores receiving salmon treatment. Fresh salmon additions of a fixed weight (mean fresh weight = 150 g) were placed in the treatment soil cores and allowed to decompose for 1 mo. All salmon additions were made from pink salmon from each study reach; the front and rear 30% of the fish was not used and all eggs were discarded prior to application. All cores were covered with coarse plastic mesh to prevent inadvertent displacement of the salmon tissue. An additional preliminary core was also taken to establish the initial conditions of the soils at each surface in both the extensive and intensive study sites. Three incubation periods were chosen to provide a standard mineralization timeframe (30 d, fall), the longest possible time before the next peak salmon spawning (340 d, summer), and a midpoint between the first and last sample (240 d, early spring). Following each incubation period (30 d for all sites; 240 and 340 d for Twelve Mile and Indian), a

randomly selected core from each treatment in the intensive study was removed from each plot (n = 3) at each watershed. Cores at the extensive study were removed after 30 d. Intact soil cores were transported to a field laboratory, then the soil was removed from the core and divided on the basis of soil horizon. Five grams of soil was extracted with 2 M KCl within 24 hr of collection. Soils for extraction were sieved while field-moist prior to analysis and triplicate extractions were performed with the A and C horizons (in Tonowek soils) and the O and B horizons (in Tuxekan soils). A subsample of soil was analyzed for water content to correct for the total dry mass of soil extracted. Because of the inconsistency and very narrow depth, the E horizon was not included in the analysis for Tuxekan soils. All solution samples were frozen for later nutrient analysis. Soluble reactive P (SRP), which is PO_4^-–P; ammonium (NH_4^+–N); and nitrate (NO_3^-–N) were measured with an Astoria II autoanalyzer (Astoria Pacific International, Clackamas, OR) via the phenate (Solorzano, 1969), cadmium reduction (Wood et al., 1967), and ascorbic acid methods (Murphy & Riley, 1962). All values are reported as μg extract per g dry soil.

The soil cores from surfaces in Tonowek and Tuxekan soils in the Twelve Mile and Indian watersheds that were used for the intensive study were fitted with circular mesh filled with XAD mixed-bed ion exchange resin beads (Amberlite, Supelco, Bellefonte, PA) inserted at the base of the cores. The purpose of inserting resin bags was to provide a relative estimate of nutrient flux through the soil core. After collection of the core, the mesh bags containing resin beads were removed and rinsed with deionized water to remove soil particles from the outside of the bag. The bags were then cut open to remove resin beads, which were placed in a small sieve and rinsed in DI water, then allowed to drain to remove excess water. The beads were placed in a 250-ml flask and 200 ml of a 2 M KCl extract solution was added to the flask. The flask was then shaken for 2 hr and then the extractant was collected and stored frozen until analyzed as described above.

2.3 | Statistical analyses

We assessed the effect of salmon tissue on riparian soils via linear and mixed linear models. For all models, the response variables were the concentrations of major nutrients (NH_4^+–N, NO_3^-–N, and SRP) measured from bulk soil cores or elutriated from resin beads. For Study Objective 1, we used a linear model to determine how nutrient concentration varied as a function of salmon amendment (present or absent), soil horizon (surface or subsurface), and watershed. For Study Objective 2 (the Tonowek–Tuxekan comparison), and Study Objective 3 (nutrient mobility), we fitted a linear mixed-effects model to determine whether nutrient concentrations differed as a function of salmon tissue (present or absent), soil type (Tonowek or Tuxekan), soil horizon (upper or lower), incubation period (30, 240, or 340 d), and the random effect of watershed (Indian or Twelve Mile). Watershed was considered to be a random effect because sites lacked independence because the same sites were sampled multiple times. Statistical inference was determined by applying a Kenward–Roger approximation to determine the denominators' degrees of freedom to calculate F-statistics and P-values to determine the significance of fixed effects (Kenward & Roger, 1997; Ziter & MacDougall, 2013). All nutrient concentration data were log-normally distributed and a log+1 transformation was conducted prior to model fitting to meet the assumption of normality (Zar, 2010). A significance level of .05 was used for all statistical tests. Analyses were conducted via the lmer and lmerTest package in R (Crawley, 2007; Bates, Mächler, Bolker, & Walker, 2010).

3 | RESULTS

3.1 | Variation in nutrient concentrations across watersheds

Differences in nutrient concentrations were evident in Tonowek soils across multiple watersheds after the 30-d incubation period (Figure 2). The salmon amendment resulted in an average 99% increase in NH_4^+–N concentrations ($F_{(1, 67)}$ = 666.5; P < .001). However, the magnitude of this effect also depended upon the watershed ($F_{(7, 67)}$ = 2.2; P = .046), the interaction between salmon amendment and soil horizon ($F_{(1, 67)}$ = 5.8; P = .020), and the interaction between soil horizon and watershed location ($F_{(1, 67)}$ = 2.8; P = .01). The salmon × horizon and horizon × watershed interactions appear to be strongly driven by variations in background surface and subsurface nutrient concentrations across watersheds in amended cores (Figure 2).

The salmon amendment resulted in an average increase of 56% in NO_3^-–N concentrations ($F_{(1, 67)}$ = 48.5; P < .001). There was a wide range in the effect of SDN on NO_3^-–N, from 6% lower in the Nossuk watershed to 94% higher in the Maybeso watershed (Figure 2). However, this variation was also influenced by watershed location ($F_{(7, 67)}$ = 5.6; P < .001) and the salmon amendment × watershed interaction ($F_{(7, 67)}$ = 7.1; P < .001).

The salmon amendment resulted in an average increase of 76% in PO_4^- concentrations (Figure 2; $F_{(1, 67)}$ = 93.5; P < .001). The response in PO_4^- concentrations was also related to watershed location ($F_{(7, 67)}$ = 5.5; P < .001) and the salmon amendment × soil horizon interaction ($F_{(1, 67)}$ = 37.4; P < .001).

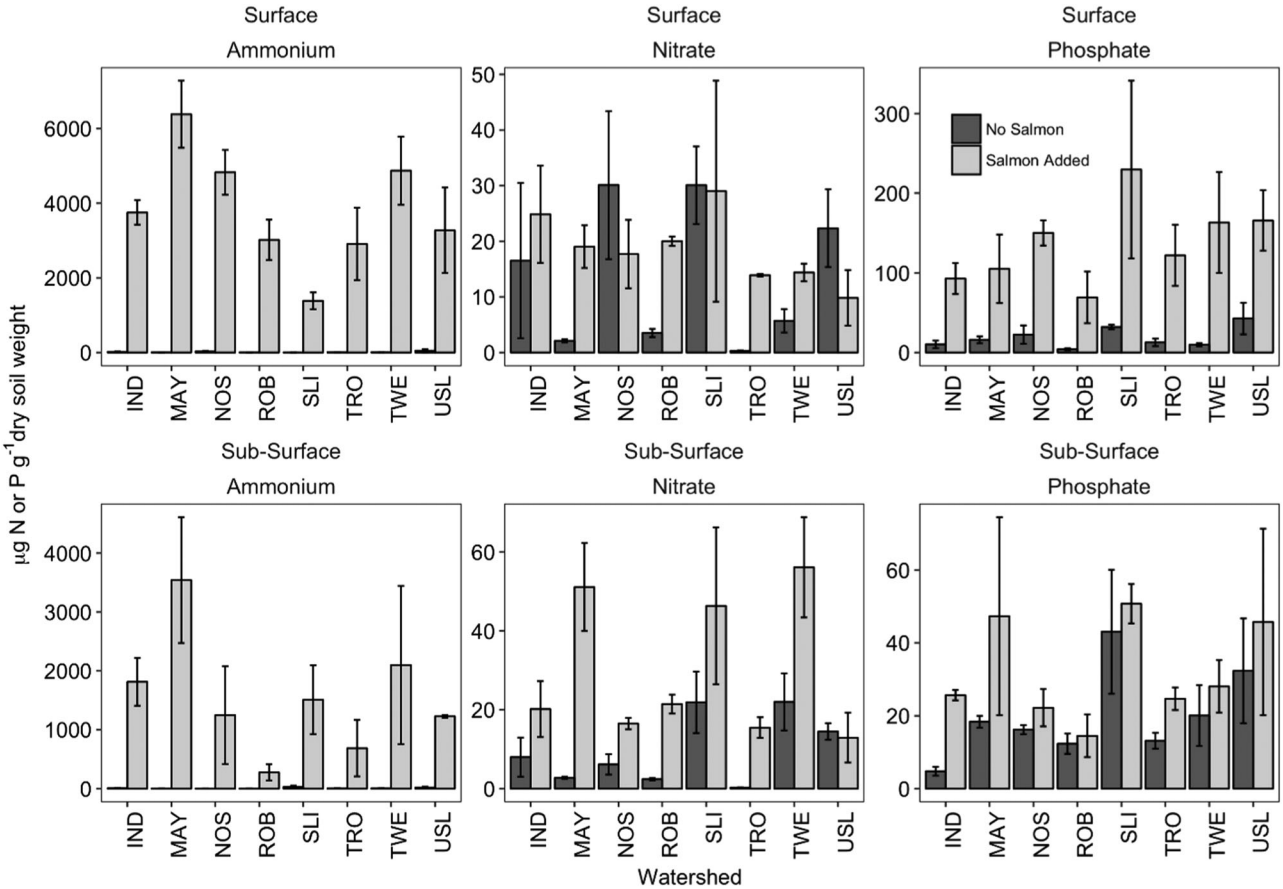

FIGURE 2 Mean extractable NH_4^+–N, NO_3^-–N, and PO_4^-–P from salmon-amended and nonamended soil cores located on floodplain (Tonowek) soils from surface and subsurface horizons at eight watershed locations on Prince of Wales Island, Southeast Alaska. The incubation period was 30 d. Note: For NH_4^+–N, the main effects of salmon amendment, soil horizon, watershed, salmon × horizon interaction, and horizon-watershed interaction were significant; for NO_3^-–N, the main effects of salmon amendment, watershed, and the salmon × watershed interaction were significant; for PO_4^-–P, the main effects of salmon amendment, watershed, and the salmon × horizon interaction were significant

3.2 | Variation in soil core nutrient dynamics

The experimental manipulation of Tonowek and Tuxekan soils in close association within two watersheds revealed varying effects of the salmon amendment in time and space. The concentration of NH_4^+–N was altered by salmon amendment ($F_{(2, 202)} = 191.6$; $P < .001$), incubation period ($F_{(2, 202)} = 7.4$; $P < .010$), soil horizon ($F_{(2, 202)} = 3.9$; $P = .048$), and the salmon amendment × incubation period interaction ($F_{(2, 202)} = 34.8$; $P < .001$). The salmon amendment × incubation period interaction is evident in that NH_4^+–N declined by 440% across incubation periods in salmon-amended soils and increased by 93% across incubation periods in nonamended soils (Figure 3). The concentration of NH_4^+–N was two orders of magnitude higher in salmon-amended cores than in nonamended cores averaged across treatments. The concentration of NH_4^+–N was 106% higher in surface soils than in subsurface soils and was fivefold higher under the 30-d incubation period than under the 340-d period. The concentration of NH_4^+–N did not vary between soil types ($F_{(2, 202)} = 3.5$; $P = .36$).

The concentration of soil NO_3^-–N differed with salmon amendment ($F_{(1, 202)} = 48.1$; $P < .001$) and incubation period ($F_{(2, 202)} = 6.7$; $P < .005$). The NO_3^-–N concentrations were 116% higher in salmon-amended soil cores and increased by 157% between the 30-d and 340-d incubation periods (Figure 3). The concentration of NO_3^-–N did not vary between soil types ($F_{(2, 202)} = 1.7$; $P = .35$).

The concentration of PO_4^- differed by salmon amendment ($F_{(1, 175)} = 37.3$; $P < .001$), incubation period ($F_{(2, 175)} = 3.9$; $P = .025$), soil horizon ($F_{(1, 175)} = 26.3$; $P < .001$), the salmon amendment × incubation period interaction ($F_{(2, 175)} = 4.2$; $P = .016$), and the salmon amendment × soil horizon interaction ($F_{(1, 175)} = 15.1$; $P < .001$). The salmon amendment × soil horizon interaction reflects that PO_4^- concentrations were 80% higher in surface soils amended with salmon than in all other horizon–salmon amendment combinations (Figure 3). The salmon amendment × incubation period

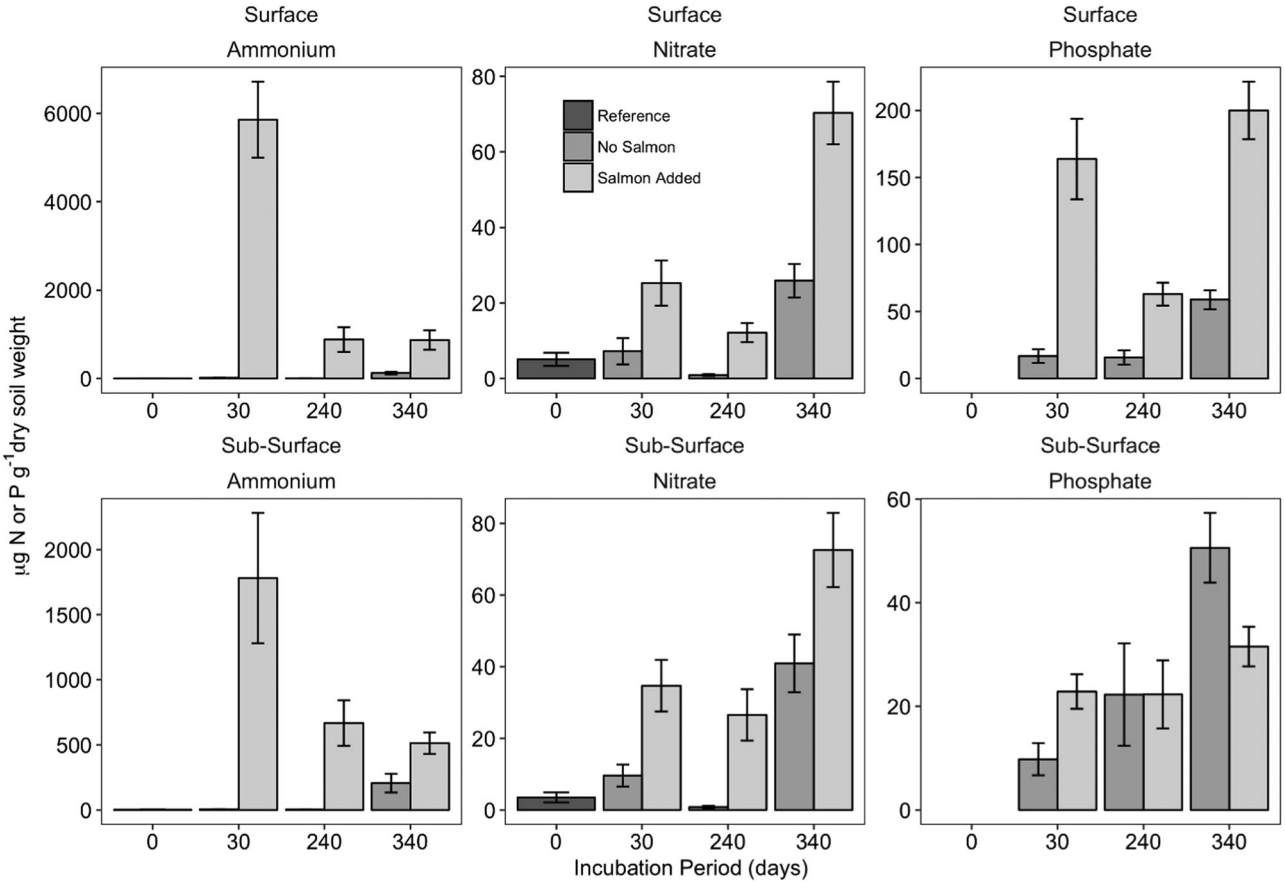

FIGURE 3 Mean extractable (±SE) NH_4^+–N, NO_3^-–N, and PO_4^-–P in salmon-amended and nonamended cores from surface and subsurface horizons in floodplain soils across an annual cycle (incubation period: 30, 240, or 340 d) at the Indian and Twelve Mile watersheds on Prince of Wales Island, Southeast Alaska. Note: For NH_4^+–N, the main effects of salmon amendment, incubation time, soil horizon, and the salmon × incubation interaction were significant; for NO_3^-–N, the main effects of salmon amendment and incubation time were significant; for PO_4^-–P, the main effects of salmon amendment, incubation time, soil horizon, the salmon × incubation interaction, and the salmon × horizon interaction were significant; Time 0 indicates the reference conditions of soil prior to the salmon treatments being applied. Reference samples were unavailable for PO_4^-–P. No difference was found between floodplain soil types

interaction reflects that soil PO_4^- concentrations declined by 52% between the 30- and 240-d incubation periods but increased by 158% between the 240- and 340-d incubation period in salmon-amended soils (Figure 3). However, soil PO_4^- concentrations were 315% higher between the 30- and 340-d incubation period in nonamended soils (Figure 3). Similar to NO_3^-–N and NH4$^+$–N, the concentration of PO_4^- did not vary between soil types ($F_{(2, 202)} = 1.7$; $P = .35$).

3.3 | Soil nutrient mobility

Resin beads revealed the mobility of NH_4^+–N and NO_3^-–N within Tonowek and Tuxekan soils. The concentration of NH_4^+–N in resin beads was significantly increased by salmon amendment ($F_{(1, 41)} = 72.9$; $P < .001$). No other factor, including time of incubation ($F_{(1, 41)} = 0.1$; $P = .780$) and soil type ($F_{(1, 41)} = 0.3$; $P = .600$), was significant. The concentration of NH_4^+–N was 97% higher in salmon-amended soils than in nonamended soils. This pattern was consistent between soil types and incubation periods, suggesting the higher mobility of N and potential leakage from the soil after SDN amendments (Figure 4). The concentration of NO_3^-–N in resin beads was significantly related to salmon amendment ($F_{(1, 41)} = 14.9$; $P < .001$), time of incubation ($F_{(1, 41)} = 31.4$; $P < .001$), and soil type ($F_{(1, 41)} = 16.5$; $P < .001$) and exhibited a three-way interaction among salmon amendment, time of incubation, and soil type. ($F_{(1, 41)} = 8.7$; $P < .005$). Tonowek soils amended with salmon accumulated 67% more NO_3^-–N than soils that were not amended (Figure 4). However, this pattern varied strongly among incubation periods, with 76% more NO_3^-–N accumulated in the 240-d period than in the 30-d incubation period (Figure 4).

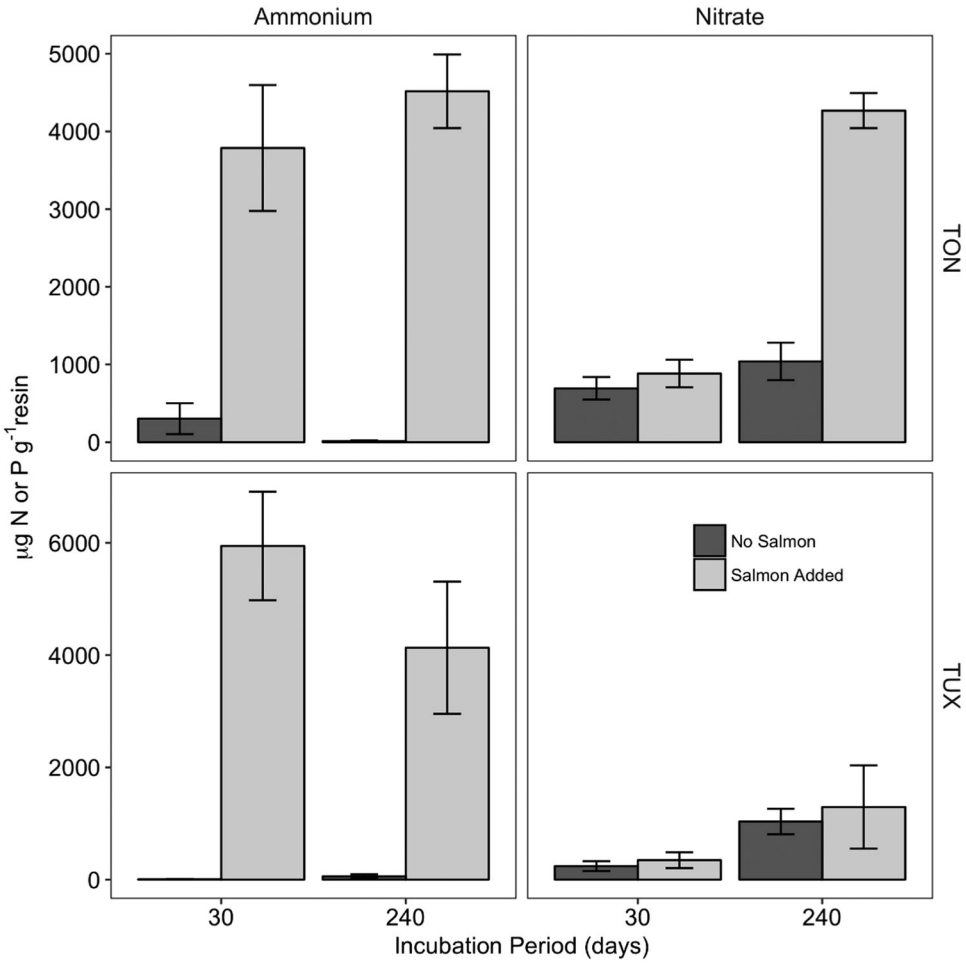

FIGURE 4 Mean extractable NH_4^+–N and NO_3^-–N from resin beads placed at the bottom of salmon-amended and nonamended soil cores from surface and subsurface horizons in floodplain [Tonowek (TON)] and terrace [Tuxekan (TUX)] soils across an annual cycle (incubation period: 30 or 240 d) at the Indian and Twelve Mile watersheds on Prince of Wales Island, Southeast Alaska. Note: For NH_4^+–N, only salmon amendment was significant (incubation time and soil type were shown to demonstrate the persistence of the salmon effect); for NO_3^-–N, the main effects of salmon amendment, incubation, soil type, and a three-way salmon amendment × time of incubation × soil type interaction were significant

4 | DISCUSSION

4.1 | Legacy of SDN on riparian soils

The presence of large quantities of salmon material in streams and associated riparian areas has been considered indicative of its importance as a nutrient subsidy to terrestrial ecosystems (Gende et al., 2002; Naiman, Bilby, Schindler, & Helfield, 2002). However, scientific evidence linking deposition of SDN on terrestrial surfaces and the subsequent ecological significance of this nutrient subsidy is still lacking (Schindler & Smits, 2016). Fundamentally, resolving this uncertainty requires a more nuanced and detailed understanding of the soil mechanisms that mediate the retention and transformation of SDN from organic to elemental forms of N and P that can be used by plants and microbial communities. Although the delivery of SDN to riparian zones is evident, the nutrient benefit to plants depends on subsidy timing and the characteristics of the recipient soils. The temporal pattern of SDN is dominated by a large initial period of deposition, with the annual spawning of salmon in late July through August during the growing season in northern latitudes. Therefore, initial efforts to determine the benefit of SDN in the terrestrial environment focused on the redistribution of nutrients derived from fish to plants as a mechanism by which nutrients are captured and stored (Ben-David et al., 1998; Bilby et al., 2003; Helfield & Naiman, 2001). Elevated soil nutrient levels returned to reference levels before the next spawning event in repeated observations in natural systems (Drake, Smith, & Naiman, 2005; Gende et al., 2007; Holtgrieve, Schindler, & Jewett, 2009).

In our study, Tonowek and Tuxekan soils clearly retained a large quantity of plant-available NH_4^+–N after the initial dose of salmon tissue. In addition, the NH_4^+–N permeated the soil rooting zone (~25 cm), further enhancing the ability of plants to access the labile nutrient pool. Perhaps more

important to the nutrient subsidy is the addition of SRP via SDN. Soil P can be tightly bound over time (Walker and Syers, 1976) but SDN can alleviate P deficiency by providing a labile source of inorganic P as well as a supply of organic P for mineralization over time. The capacity of the soils to retain inorganic N and P as NH_4^+–N and SRP during the observation period confirms that SDN remains available in the soil matrix for riparian microbial and plant consumption beyond the salmon spawning period. Such a legacy effect of salmon subsidies has been alluded to before in terrestrial ecosystems (Gende et al., 2007; Helfield & Naiman, 2001). The retention and transformation of SDN in the soils over the annual observation period highlights the capacity of the soils to distribute out the nutrient delivery to plants and soil organisms over months (including during the growing season following SDN delivery), thereby supporting the concept of SDN as a potential source of labile N and P over time in riparian zones. However, this still requires an appreciation and understanding of the heterogeneity of soil surfaces, especially in riparian zones.

4.2 | Prediction of SDN through soil maps

Spatial resolution in SDN studies has relied on landform designations. Soil information has been included as a generalized description of site conditions, although sampling has occurred across landforms (Bartz & Naiman, 2005; Bilby et al., 2003; Gende et al., 2007). Different landforms have different soil types, highlighting the importance of soil designations as reaction surfaces in SDN research in riparian zones. Salmon material usually accumulates close to streams [~10 m; Willson, Gende, & Bisson (2004)] because of bear (*Ursus* spp.) feeding (Ben-David et al., 1998; Gende et al., 2002) and overbank flooding (Fellman et al., 2008). Therefore, soils that occupy floodplain and terrace alluvial landforms are important hotspots for transformation and retention of the SDN nutrient subsidy and interaction with plant communities because of their proximity to the stream edge. The presence of identifiable and distinct alluvial landform features provides a powerful tool for extrapolation of SDN effects across riparian areas. Landscape evolution in the perhumid coastal rainforest region has promoted a common landscape association of Holocene terrace and floodplains at the distal portions of large watersheds (D'Amore et al., 2011). Information on these landforms and soils in the field has been facilitated by extensive soil mapping efforts and the development of soil resource inventories in both Canada (Canadian Soil Information Service, 2018) and the United States (USDA-NRCS, 2018). The Tonowek soil series (Typic Cryofluvent) and the Tuxekan soil series (Typic Humicryod) represent common soil types found on Holocene floodplains and terraces throughout salmon spawning grounds of coastal British Columbia and Southeast Alaska and thus they serve as models for SDN-affected soils throughout the region. The soil mapping information provides a means for reducing the uncertainty in the potential fate of SDN on near-stream soil surfaces for soils in close association with the majority of salmon spawning that occurs across this region.

4.3 | Alluvial soils vary in reaction paths for nutrients

Comparison of the spatial patterns of extractable nutrients between the two riparian soil types does not suggest differences in the retention of N and P between Tonowek and Tuxekan soils. This finding is surprising, given the physicochemical differences in the soils (Table 1). It is possible that different mechanisms are responsible for retention within each soil. For example, the surface horizon of Tonowek contains approximately 15% clay, which could provide reactive surfaces for the retention of N. The low C concentration may inhibit the microbial immobilization of N in the soil matrix as well, along with curtailing denitrification. The low pH could play a role in the complexation of P in the soil matrix, enhancing P retention despite the low cation exchange capacity and clay content. Tuxekan soils have abundant reactive surfaces, as indicated by the CEC values, along with high silt and clay fractions compared with sand. The presence of the O horizon may also play a large role in retaining both N and P because of the abundance of reactive surface area, as indicated by CEC (Table 1). However, the somewhat higher pH in the B horizons may lead to a reduction in the overall retention of P, narrowing the difference between the P retention values between the two soils. The transformation of SDN appears to take different trajectories both within the Tonowek soil series across watersheds and between the two soil types, providing an incentive for mapping of the riparian soils at higher resolution, with a focus on the physicochemical attributes associated with nutrient retention.

The larger relative amount of NO_3^-–N extracted from resin beads at the bottom of the Tonowek cores compared with the Tuxekan cores suggests that more N is leached from the surface of Tonowek soils than from Tuxekan soils, which partly supports our hypothesis that the soils will not respond to SDN additions similarly. The large decrease in NH_4^+–N over time in the cores is not matched by a proportional increase in NO_3^-–N, which would be expected if the majority of the excess N was nitrified (Stark & Hart, 1997). The soil attributes provide evidence that the higher pH and larger concentration of C may promote conditions that are more favorable to denitrification in Tuxekan than in Tonowek soil. The lack of a large pulse of NO_3^-–N differs from previous observations in riparian soils, where increases in nitrate concentration were coincident with the maximum NH_4^+–N concentrations

TABLE 1 Summary of physical and chemical variables for Tonowek and Tuxekan soils in Southeast Alaska[a]

Soil type	Horizon	Db[b]	Sand	Silt	Clay	C	N	C/N ratio	CEC[c]	pH[c]
		g cm^{-3}	%			%			cmol kg^{-1}	
Tonowek	A	0.47 (0.06)	66.87 (0.04)	18.26 (0.04)	14.87 (0.01)	6.71 (0.83)	0.38 (0.04)	17.91 (1.31)	19.6	4.5
	C	0.52 (0.05)	75.20 (0.04)	14.52 (0.03	10.28 (0.01)	1.99 (0.34)	0.11 (0.02)	17.64 (0.93)	26.9	4.9
Tuxekan	O	0.12 (0.02)	0.91 (0.01)	0.02 (0.01)	0.08 (0.01)	42.03 (6.54)	1.64 (0.11)	25.42 (3.47)	166.65	3.6
	E	ND[b]	46.00 (0.03)	36.00 (0.05)	18.00 (0.02)	2.63 (2.03)	0.13 (0.09)	18.49 (2.60)	18.10	4.1
	Bhs–Bs	0.38 (0.02)	38.24 (0.09)	42.45 (0.07)	19.31 (0.02)	3.37 (0.41)	0.17 (0.03)	21.69 (2.22)	49.67	5.3

[a]Data were compiled from D'Amore et al. (2011); data on soil pedons have been taken from the USDA-NRCS database. Values are means ± SE, with the SE shown in parentheses. [b]Db, bulk density; CEC, cation exchange capacity; ND, no data available. [c]CEC and pH were obtained from NRCS laboratory data (https://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey; verified 16 Apr. 2020).

(Gende et al., 2007). Given that one of the major loss pathways for excess N in riparian soils is through denitrification (Gregory, Swanson, McKee, & Cummins, 1991; Pinay, O'Keefe, Edwards, & Naiman, 2000), it is reasonable to assume that this is a potential loss vector for N in the present study. There is specific evidence for the impact of SDN on denitrification where large, ephemeral excursions of N_2O were observed in streams where bears feed on salmon (Holtgrieve et al., 2009). The lack of increased NO_3^-–N concentrations relative to NH_4^+–N could be explained by the potential for substantial denitrification in Tuxekan soils, which have soil texture and moisture conditions that promote oxic–anoxic zones for the nitrification–denitrification pathways to coexist and process N (Seitzinger et al., 2006; Table 1). We can surmise that there is then either a more intense denitrification pathway in Tuxekan soils or that the N is immobilized within the soil matrix by microbial assimilation, similar to a range of soils in the perhumid coastal rainforest region (Bisbing & D'Amore, 2018).

Larger losses of N through denitrification in Tuxekan soils relative to Tonowek soil could also explain the discrepancy in isotopic N fractionation within the two alluvial soils (D'Amore et al., 2011), where higher natural abundance of $\delta^{15}N$ was not consistent with proximity to the stream (Bilby et al., 2003). This phenomenon could be explained by discrimination against the heavier N isotope through denitrification (Högberg, 1997). The evidence of a different loss vector for NO_3^-–N between the two soils observed in the present study supports this conclusion, as well as highlighting the need to delineate soils in order to determine the overall fate of SDN in riparian zones accurately. The difference in the age and horizon development of the two soils is consistent with two distinct reaction pathways in the two soil types that influence N processing (Table 1). The A–C horizon sequence of Tonowek soils facilitates the movement of material through a soil matrix that is dominated by sand size particles. In addition, these soils have a lower exchange capacity because of the low clay content, C concentration, narrow C/N ratio, and lower CEC in the C horizon (Table 1). Tuxekan soils have B horizons with colloidal metal–organic complexes and highly reactive amorphous material in the Bh–Bs horizons with higher CEC, more clay, and higher C concentrations (Table 1), which can attenuate the movement of N through the soil matrix (Heilman & Gass, 1974). Tuxekan soils are probably able to retain NO_3^-–N in the matrix longer than Tonowek soils, resulting in denitrification once the soils begin to warm. Tuxekan soils' structure may also promote a more vigorous denitrification potential within the soil matrix, given adequate soil moisture, abundant N, and active denitrifying microbial communities. The residence time of N evident in our study would facilitate the interaction with microbial communities, as they are active throughout the year (Nikrad, Kerkhof, & Haggblom, 2016). The microbial community could facilitate both the immobilization of N by incorporation into biomass (Giblin, Nadelhoffer, Shaver, Laundre, & McKerrow, 1991) and the denitrification process (Holtgrieve et al., 2009).

4.4 | Salmon-derived nutrients as a surrogate for fertilization

The flush of mineralized N during the final sampling period observed in Tonowek and Tuxekan soils, in both treated and untreated cores, illustrates the potential for N and P mineralization from organic matter in the soils. The mineralization potential demonstrated in the untreated cores provides evidence for the high nutrient potential of alluvial soils. These sites may exhibit less nutrient limitation than the adjacent upland soils. The source of the nutrient capital could be caused by the N fixation of red alder, or legacy SDN from previous salmon runs followed by release of stored N and P through organic matter turnover. (Barrie & Conway, 2002; Gharrett and Finney, 2008). Reconciling the source of the legacy storage pool of N in riparian soils should be a priority for future research looking to understand the influence of salmon and salmon nutrients in the context of riparian ecosystems. In part, this will be helped by a deeper understanding of the soils in this region as bioreactors for nutrient retention and transformation. Assuming an effect on vegetation growth similar to fertilizer applications designed to enhance growth on N-limited sites provides some insights. However, fertilizer

applications are not as effective on more fertile forest sites compared with nutrient-limited sites (Miller & Fight, 1979). Consequently, the impact of SDN fertilization is likely to be more limited on the alluvial landforms because of their higher inherent fertility than on upland landforms and the impact of the SDN is likely to be limited to a small spatial extent in the riparian zone.

5 | CONCLUSIONS

The linkage between soil biogeochemical cycling with specific mapped soil units in riparian zones undertaken in our study has advanced the understanding of soil nutrient dynamics associated with the presence of SDN through a detailed consideration of nutrient dynamics across time and space in two specific soil types. The persistence of extractable N and P through time supports the idea that SDN provides a nutrient subsidy in riparian soils that may benefit terrestrial ecosystems. The overall loading of N and P did not vary between soil types but the processing of the material did appear to vary by soil type. Therefore, nutrient cycling models for SDN need to identify soil types by using existing soil mapping to elucidate the input, processing, uptake, and loss of N and P within riparian landforms.

CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

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