

The effects of salmon carcasses on soil nitrogen pools in a riparian forest of southeastern Alaska

Scott M. Gende, Amy E. Miller, and Eran Hood

Abstract: Long-term studies in Alaska have demonstrated that bears may capture and carry to the riparian forest a large number of salmon that return to spawn in small freshwater streams. Most of the carcasses are partially consumed, resulting in a large amount of salmon nutrients in the form of biomass deposited on the forest floor. Using an experimental approach, we examined how these carcasses may influence the spatial and temporal dynamics of soil C and N in a riparian forest in southeastern Alaska. At their peak, ammonium ($\text{NH}_4^+\text{-N}$) concentrations in soil 10 cm from carcasses were as much as several orders of magnitude greater than soils in adjacent control plots without carcasses and remained elevated until the onset of winter. Nitrate ($\text{NO}_3^-\text{-N}$) and $\delta^{15}\text{N}$ concentrations also increased coincident with maximum $\text{NH}_4^+\text{-N}$ concentrations. However, soil N concentrations were only moderately elevated 20 cm from carcasses and closely resembled background concentrations at 30 cm. These results suggest that salmon carcasses, via bear foraging activities, can dramatically influence soil N pools, although the impacts appear to be highly localized and largely dependent on the spatial distribution of carcasses in the riparian forest.

Résumé : Des études à long terme réalisées en Alaska ont démontré que les ours peuvent capturer et transporter vers la forêt riveraine un grand nombre de saumons qui reviennent frayer dans les petits ruisseaux d'eau douce. La plupart des carcasses sont partiellement consommées entraînant le dépôt d'une grande quantité de nutriments sous forme de biomasse sur le parterre forestier. À l'aide d'une approche expérimentale, nous avons examiné comment ces carcasses peuvent influencer la dynamique spatiale et temporelle du C et de N du sol dans une forêt riveraine du sud-est de l'Alaska. À son maximum, la concentration d'ammonium ($\text{NH}_4^+\text{-N}$) dans le sol à 10 cm des carcasses était jusqu'à plusieurs ordres de grandeur plus élevée que dans le sol de parcelles témoins adjacentes sans carcasses et est demeurée élevée jusqu'au début de l'hiver. Les concentrations de nitrate ($\text{NO}_3^-\text{-N}$) et de $\delta^{15}\text{N}$ ont aussi augmenté en même temps que la concentration maximum de $\text{NH}_4^+\text{-N}$. Cependant, la concentration de N dans le sol était seulement modérément élevée à 20 cm des carcasses et ressemblait étroitement à la concentration normale à 30 cm. Ces résultats indiquent que les carcasses de saumon, via les activités des ours pour trouver de la nourriture, peuvent avoir une influence énorme sur les pools d'azote bien que les impacts semblent très localisés et largement dépendants de la distribution spatiale des carcasses dans la forêt riveraine.

[Traduit par la Rédaction]

Introduction

The annual return of spawning Pacific salmon (genus *Oncorhynchus*) can have a dramatic effect on the nutrient capital and productivity of recipient freshwater ecosystems (Mathiesen et al. 1988; Kline et al. 1997; Wipfli et al. 1998). Salmon-derived nutrients (SDN) are made available to stream food webs via metabolic waste products, as gametes, or in the form of carcasses following senescent death (Gende et al. 2002). Consequently, concentrations of stream nutrients, such as ammonium, soluble reactive phosphorus, and nitrate may increase by an order of magnitude during the spawning season (Sugai and Burrell 1984; Kline et al. 1993; O'Keefe and Edwards 2003; Johnston et al. 2004; Sarica et al. 2004). These nutrients may be utilized by primary producers, which can result in elevated productivity of freshwater food webs via bottom-up processes (Gende et al. 2002; Johnston et al. 2004).

However, not all of the SDN are retained within the freshwater systems. Salmon attract aggregations of brown bears (*Ursus arctos* L., 1758) and black bears (*Ursus americanus* Pallas, 1780) (Frame 1974; Collins et al. 2005) that may capture a large fraction of the returning fish. Streams surveyed for more than 10 years in southwestern Alaska revealed mean predation rates of over 30% of the total salmon run, with rates in some streams in some years exceeding 90% (Quinn et al. 2003). This can equate to thousands of salmon being killed by bears in relatively small (≤ 2 km) stream systems (Quinn et al. 2003). Furthermore, following capture, bears often carry the salmon from the stream (Reimchen 2000; Gende and Quinn 2004; Willson et al. 2004) and only partially consume the carcasses. In over 20 000 salmon carcasses surveyed in Alaska, bears consumed a mean of only 37% of the total biomass of each fish (Gende et al. 2001). Consequently, up to 50% or more of the salmon biomass that returns to spawn in a stream may

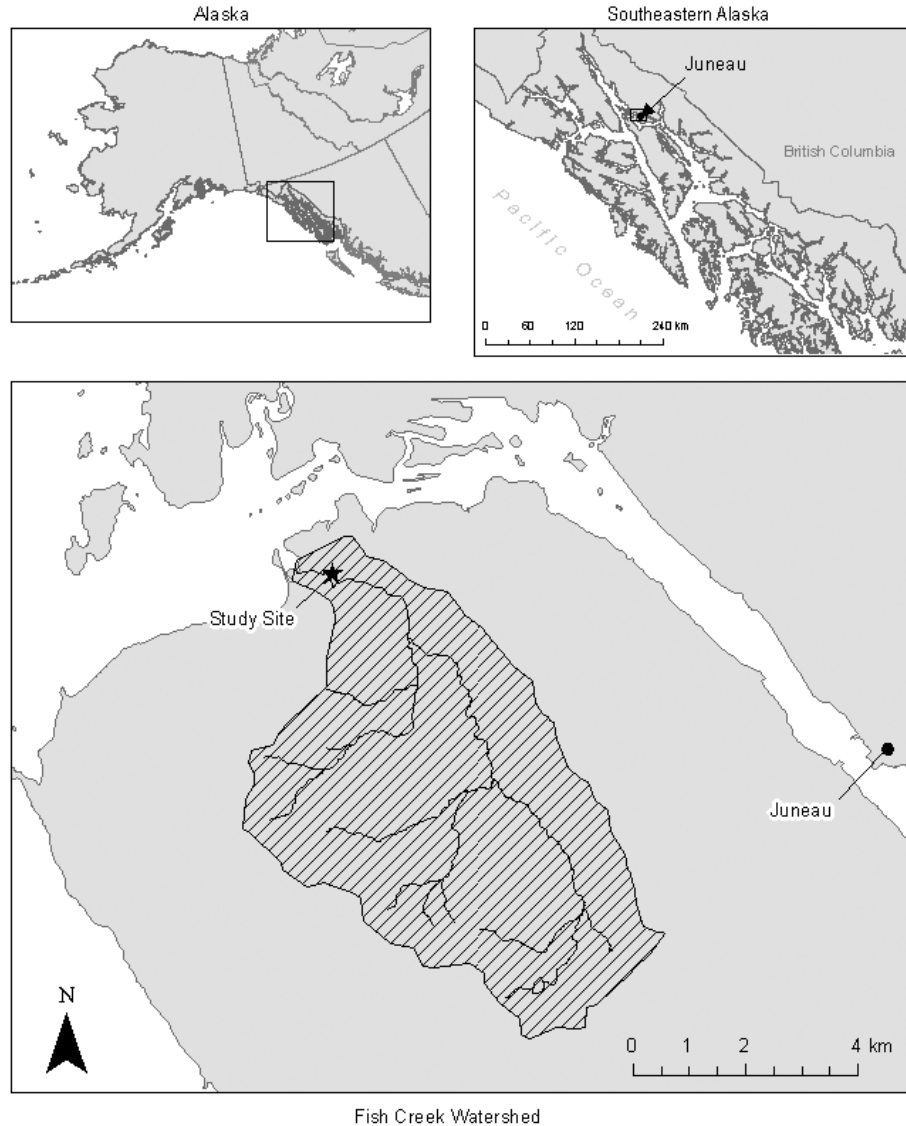
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Fig. 1. Location of study plots in the lower Fish Creek watershed near Juneau, Alaska.

ultimately end up on the riparian forest floor as a result of bear foraging activities (Gende et al. 2004a; Johnston et al. 2004).

Given that SDN can influence the nutrient capital and productivity in stream ecosystems and that bears can transfer large numbers of salmon to riparian forests, it follows that salmon, via bear foraging activities, may influence the nutrient capital and productivity of riparian ecosystems. To date, a number of studies have demonstrated that riparian plants, including trees, understory shrubs, mosses, and liverworts, utilize SDN as evidenced by elevated isotopic signatures of N in aboveground tissue (Bilby et al. 1996; Helfield and Naiman 2002; Bilby et al. 2003; Wilkinson et al. 2005). However, these studies rarely show a direct relationship between $\delta^{15}\text{N}$ enrichment and nutrient loading, possibly because $\delta^{15}\text{N}$ enrichment in plants is not solely proportional to N utilization but may be a function of a suite of factors, including substrate, plant species composition, mycorrhizal uptake, and physiological mechanisms within the plant (Garten 1993; Chang and Hanley 2000; Evans 2001).

Clearly, more studies are needed to clarify the relationship between salmon carcasses, soil nutrient dynamics, and utilization by riparian plants.

Here, we experimentally examine the effects of salmon carcasses on soil N pools along a salmon stream in southeastern Alaska. Our specific goal was to describe the spatial and temporal effects of salmon carcasses on plant-available N, total soil C and N, and bulk soil $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, with the larger goal of gaining insight into the importance of SDN on watershed processes.

Materials and methods

Study area

Our study site was in the Fish Creek watershed on Douglas Island near Juneau, in southeastern Alaska (Fig. 1). Juneau has a maritime climate, characterized by frequent cloud cover, high relative humidity, cool temperatures, and high precipitation. Mean annual temperature recorded at the Juneau airport, directly across Gastineau channel from Fish

Creek, was 4.9 °C and mean annual precipitation was 1430 mm, much of which falls as rain and snow in autumn. Fish Creek represents a typical mid-sized stream in south-eastern Alaska supporting small runs of coho (*Oncorhynchus kisutch* (Walbaum)) and chinook salmon (*Oncorhynchus tshawytscha* (Walbaum)) and at times substantial runs of pink (*Oncorhynchus gorbuscha* (Walbaum)) and chum salmon (*Oncorhynchus keta* (Walbaum)). Salmon spawning typically begins in late June and extends through September with a peak in mid-August. Run size varies among species and years but is supplemented by fish from the Douglas Island Pink and Chum (DIPAC) salmon hatchery in Juneau.

Fish Creek supports old-growth riparian forest typical of the area, characterized by a mix of large Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) with a well developed understory of salmonberry (*Rubus spectabilis* Pursh), blueberry (*Vaccinium* spp.), and devil's club (*Oplopanax horridum* (J.E. Smith) Miq.). Although a popular stream for sport fishing, black bears frequent Fish Creek to feed on salmon.

Because of the cool wet maritime climate in southeastern Alaska, decomposition is often slow, resulting in the persistence of recalcitrant forms of organic material and, in many areas, thick organic soil horizons (Kramer et al. 2003). Although the Fish Creek watershed includes a mixture of poorly drained spodosols (Typic Cryaquods) and riverine soils (Cryofluvents), the riparian zone where the salmon carcass plots were located is characterized by deep, well-drained alluvial soils in the Tonowek series. Soils in the plots ranged from O over C to OAC with an O horizon ranging between 0 and 2 cm. The bulk density (0.84 ± 0.02 g/cm³; mean \pm SE) was estimated from the dry mass of five intact soil cores taken from the top 10 cm of soil (Blake and Hartge 1986).

Study design

Eight sets of paired 1 m² plots were established in the riparian zone along Fish Creek in August 2004, when salmon were present in the stream. Plot pairs consisted of a "carcass" treatment that contained two chum salmon, placed side by side lengthwise, and a control plot (no carcass) that bordered the carcass plot. Chum salmon, acquired from the DIPAC salmon hatchery, were collected mature but unspawned to mimic the nutrient levels of many of the bear-killed salmon (Gende et al. 2004b). Plot pairs were spaced 7–100 m apart along the lower reaches of the stream where most of the spawning occurs. Plots were placed one to several metres from the stream bank, on level ground, where fish are most likely to be carried by bears (Willson et al. 2004). Carcasses had a mean length of 55 cm, a mean width of 15 cm, and weighed between 3.0 and 4.9 kg (mean 3.8 kg), which equates to a range of 102–167 g N/fish (Gende et al. 2004a).

Soil samples were collected in the study plots on five occasions between August and early November 2004. Sampling on the first date in August occurred immediately before the placement of the salmon carcasses, and then 4, 29, 44, and 79 days following carcass placement, with sampling on the last date in November occurring just before soils froze for the winter. Sampling frequency represented a

trade-off between disturbing the soils within the plots and capturing the temporal variability in nutrient concentrations.

At each set of paired plots, three soil cores (2 cm diameter, 10 cm depth) were collected at 10, 20, and 30 cm from the edge of the long axis of carcasses or from the centre of the adjacent control plots. Thus, a total of 12 cores were collected from each set of paired plots during each sampling date. Following removal of vegetation and the surface organic horizon (moss, litter), soil cores from each sampling point were composited and immediately returned to the laboratory. The <2 mm fraction was processed within 12 h of collection for determination of K₂SO₄-extractable ammonium (NH₄⁺-N) and nitrate (NO₃⁻-N). Approximately 10 g dry mass equivalent of soil was extracted in 25 mL of 0.5 mol/L K₂SO₄ at room temperature for 2 h. Extracts were filtered through preleached Whatman No.1 filters and frozen until analysis. Nitrate was determined using a Dionex DX 500 ion chromatograph with an IonPac AS4A-SC Analytical Column and ammonium was determined on a Lachat QuikChem 4000 Flow Injection Analyzer at the University of Colorado, Boulder, Colorado. Bulk soil samples (mineral horizon) were dried at 55 °C, ground to a fine powder, and analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, and total C and N, at the University of California, Davis, California. Instrument precision was 0.04% and 0.004% for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively.

Statistics and loading calculations

To test for the effect of salmon carcasses on soil nutrient dynamics, we used ANOVA with a randomized complete block design with repeated measures (programmed using split plots in time; SAS general linear models procedure; SAS Institute Inc., Cary, N.C.). We used the interaction of plot \times treatment as the error term to test for an effect of treatment (carcasses) on the different response variables (NH₄⁺-N, NO₃⁻-N, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, C/N). If a treatment effect (carcass) was significant, we used a paired *t* test to examine differences in nutrient concentration during the first and last sampling date to assess whether nutrient concentrations were still elevated at last sampling (30 August vs. 17 November; a total of 79 days).

We also estimated the total minimum loading (g/m²) of inorganic N around each carcass based on our instantaneous measurements of soil inorganic N pools. Nitrogen loading at each plot was estimated as the difference in exchangeable inorganic N pools between carcass and control plots on each sampling date at two different distances: 0–10 cm from the perimeter of the carcasses (or the centre of control plots) and at 10–20 cm. These distances were chosen because the exchangeable N pools within 10 cm of carcasses were much higher than pools at 10–20 cm, whereas soils >20 cm from the carcasses had similar inorganic N concentrations to control plots (see below).

The mean area covered by the carcasses was 1650 cm² (mean carcass length 55 cm, mean width 30 cm; two carcasses with a mean dorsal–ventral width of 15 cm placed together side by side). Thus, the amount of soil directly under the carcasses, plus 0–10 cm from the perimeter of the carcasses was 31 500 g (75 cm length \times 50 cm width \times 10 cm core depth \times mean soil bulk density of 0.84 g/cm³). Note that this loading volume includes the soil directly under the carcasses which were not sampled for inorganic N concen-

trations. Thus, these values represent minimum instantaneous loading estimates. The concentration of inorganic N ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$; $\mu\text{g N/g soil}$) was multiplied by the mass of soil within 10 cm of the carcasses to estimate inorganic N loading. Loadings of inorganic N were calculated in the same manner for the mass of soil 10–20 cm from the carcass (95 cm length \times 70 cm width \times 10 cm depth \times $0.84 \text{ g/cm}^3 - 31\,500 \text{ g} = 24\,360 \text{ g}$ of soil). The inorganic N loadings for each distance around the carcasses (0–10 cm and 10–20 cm) were then summed to achieve estimates of the total instantaneous loading of salmon-derived inorganic N around each carcass on every sample date. Although these estimates were measured on a volumetric basis, the actual loading occurred at the soil surface (95 cm \times 70 cm = 0.67 m^2), and thus, we present the data as grams inorganic N loaded per square metre.

Results

During the experiment, the study site experienced a total of 33 days of precipitation, with ambient air temperatures decreasing from a mean of $15.2 \text{ }^\circ\text{C}$ in August to $2.6 \text{ }^\circ\text{C}$ in November. Temperature and precipitation levels during the experiment were well within the 20 year average for this site. Carcasses generally decomposed from the inside out, with the skin becoming desiccated and shrinking to the bones. Although ovipositing flies were relatively uncommon, carrion beetles (*Necrophorus* spp.) were observed near the carcasses in several plots. Carcasses were left undisturbed by bears and other scavenging vertebrates, perhaps because of the abundance of carcasses naturally available near the stream bank. One plot was washed out during a flooding event halfway through the experiment, reducing the sample size to seven plots.

Inorganic N in soil pools

On the first sample date (just prior to carcass placement), bulk mineral soil samples collected from eight fish and eight control plots ($n = 16$) had a mean C content of 4.1% and a mean N content of 0.2% N. Carbon and N content did not differ significantly between carcass and control plots. Soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ concentrations in control and treatment plots were also virtually identical on the first sampling date (Fig. 2). Native $\text{NO}_3^-\text{-N}$ concentrations were approximately one-fourth as great as NH_4^+ concentrations, and neither N species showed marked spatial variation within the plots prior to carcass placement.

However, following carcass deposition, soil N concentrations 10 cm from carcasses increased rapidly (Fig. 2) and remained elevated over the course of the incubation ($\text{NH}_4^+\text{-N}$: $F = 15.48$, $p < 0.01$; $\text{NO}_3^-\text{-N}$: $F = 12.55$, $p = 0.01$, respectively). By late September (day 29), $\text{NH}_4^+\text{-N}$ concentrations had increased 60-fold over initial values, and by mid-October (day 44), $\text{NO}_3^-\text{-N}$ concentrations had approximately doubled. At peak concentrations, $\text{NO}_3^-\text{-N}$ pools 10 cm from the carcasses were roughly two orders of magnitude lower than maximum $\text{NH}_4^+\text{-N}$ pools.

However, the magnitude of nutrient response became less pronounced as the distance from carcasses increased. Over the course of the incubation, the increase in soil N concentration at 20 cm was significant for $\text{NH}_4^+\text{-N}$ ($F = 10.39$, $p =$

0.02) but not for $\text{NO}_3^-\text{-N}$ ($F = 3.1$, $p = 0.13$). Soil N pools at 20 cm increased from 1.6- ($\text{NO}_3^-\text{-N}$) to 8-fold ($\text{NH}_4^+\text{-N}$) over control levels but were highly variable and comparatively short lived. At 30 cm from the carcasses, soil N concentrations did not differ from controls over the course of incubation for either $\text{NH}_4^+\text{-N}$ ($F = 3.1$, $p = 0.14$) or $\text{NO}_3^-\text{-N}$ ($F = 1.95$, $p = 0.21$) (Fig. 2).

Although soil $\text{NO}_3^-\text{-N}$ and $\text{NH}_4^+\text{-N}$ concentrations showed similar spatial variation during the experiment, $\text{NO}_3^-\text{-N}$ appeared to lag $\text{NH}_4^+\text{-N}$ temporally. At 10 cm from the carcasses, $\text{NH}_4^+\text{-N}$ concentrations peaked 29 days after carcass placement and were not significantly different than control levels by the end of the incubation ($p > 0.12$). In contrast, $\text{NO}_3^-\text{-N}$ concentrations at 10 cm peaked on the last sampling date in mid-November and remained significantly elevated compared with the initial sample date (day 1 mean $1.18 \mu\text{g/g soil}$; day 79: mean 5.09 ; $t = 2.54$, $p = 0.03$). At 20 cm and 30 cm, $\text{NH}_4^+\text{-N}$ peaked 29 days after carcass placement but was not significantly different than control concentrations by the end of the incubation ($p > 0.21$). Although values of $\text{NO}_3^-\text{-N}$ in the carcass plots were significantly higher at the last sampling compared with the first sampling date at both 20 cm ($t = 3.26$, $p = 0.02$) and 30 cm ($t = 7.03$, $p < 0.01$), these values did not differ from controls, owing to concomitant increases in background concentrations. Background concentrations of $\text{NH}_4^+\text{-N}$ did not increase over the course of the experiment ($t = 1.06$, $p = 0.31$).

From our loading estimates, we calculated that exchangeable inorganic N in the carcass plots ranged from 0.7–6.9 g N/m² (Fig. 3). $\text{NH}_4^+\text{-N}$ accounted for more than 90% of the exchangeable soil N pool, and thus the maximum loading was coincident with the high $\text{NH}_4^+\text{-N}$ concentrations in late September (day 29).

Stable isotopes and C/N ratios

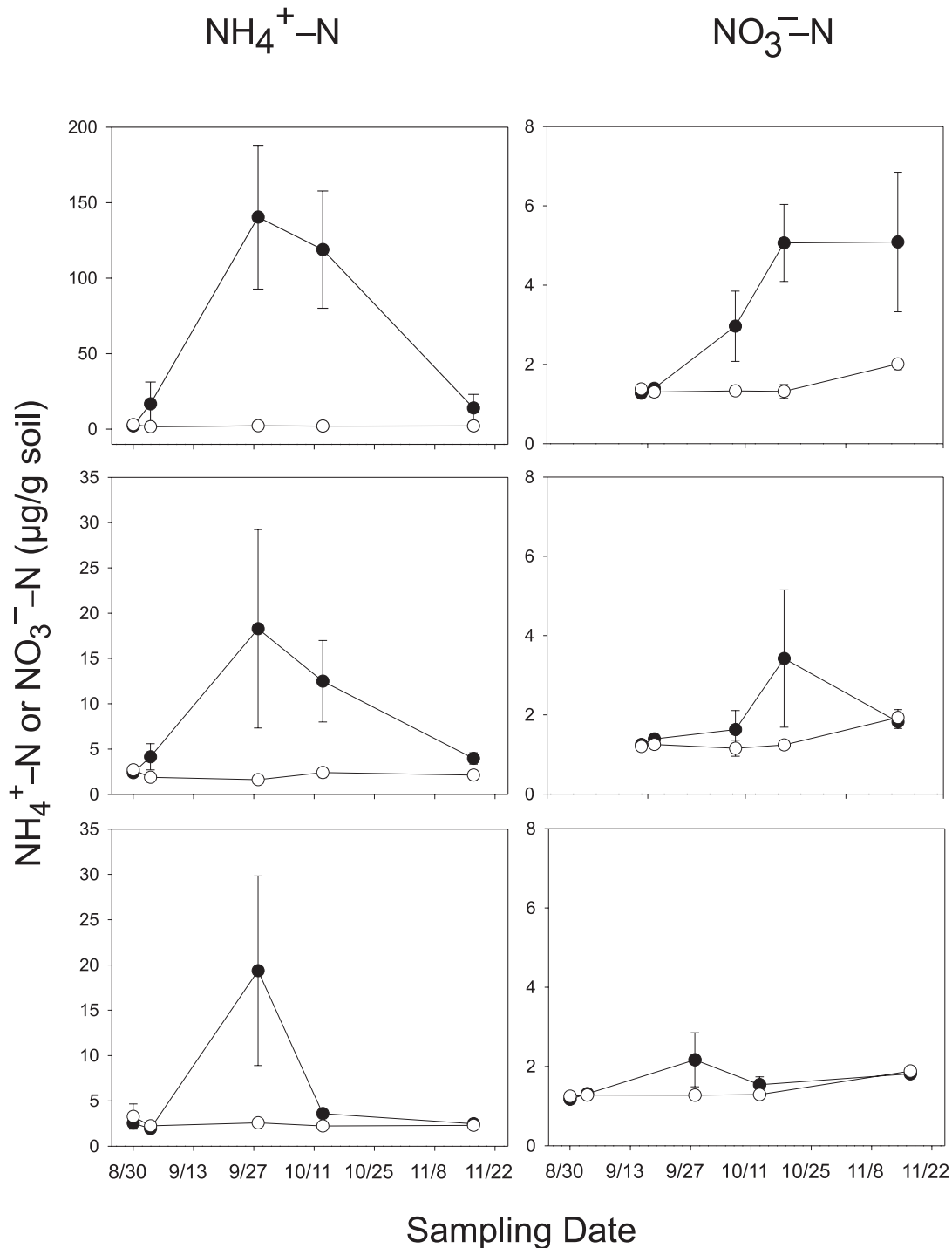
Soil $\delta^{15}\text{N}$ measured at 10 cm from carcasses was significantly enriched relative to control plots only on day 44 (carcass mean 5.31 ; control mean 3.91 ; $t = 6.68$, $p = 0.04$) (Fig. 4). Soil $\delta^{13}\text{C}$ values did not differ between carcass and control plots and did not vary with sample date (Fig. 4). The increase in soil N associated with carcasses appeared to result in lower soil C/N ratios in carcass plots than in controls, but this difference was not significant across sample dates ($F = 2.04$, $p = 0.07$) (Fig. 5).

Discussion

Soil N pools

Our goal was to better understand the effects of salmon carcasses on soil N pools, and our results clearly demonstrate dramatic temporal and spatial variability in exchangeable N over the course of carcass decay. Inorganic N pools in soils changed rapidly following carcass placement, with maximum concentrations occurring approximately 1 month following deposition. These effects were highly localized and ephemeral but, nevertheless, appeared to influence soil $\delta^{15}\text{N}$, suggesting that potentially much larger reservoirs of salmon-derived N were held in soil organic matter (SOM). The sustained increase in $\text{NO}_3^-\text{-N}$ concentrations over the course of the incubation indicated that nitrification continued well after $\text{NH}_4^+\text{-N}$ levels had declined. Although final

Fig. 2. Mean extractable $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ concentrations in soils at 10 cm (top graphs), 20 cm (middle graphs), and 30 cm (bottom graphs) from carcass in carcass plots (solid circles) and the centre of control plots (open circles). Error bars are SEs. Note the different ranges of values among graphs.



$\text{NO}_3^-\text{-N}$ concentrations were equivalent to only 3% of the maximum $\text{NH}_4^+\text{-N}$ pool, continued, rapid immobilization and cycling of $\text{NO}_3^-\text{-N}$ through the soil microbial pool could have accounted for much greater N turnover than our instantaneous pool measurements suggest (cf. Stark and Hart 1997).

We did not measure microbial uptake or turnover rates, and thus, the amount of inorganic N released directly from carcasses versus that mineralized from organic constituents

and released to the soil cannot be determined directly from this study. However, the >2‰ increase in soil $\delta^{15}\text{N}$ in some plots following carcass placement was concurrent with the increase in soil $\text{NH}_4^+\text{-N}$ concentrations and was likely due to a combination of carcass-derived N (direct N inputs) and soil N processes that occurred in response to the added N (e.g., indirect effects on N turnover and loss). An increase in soil $\delta^{15}\text{N}$ has also been observed in riparian forests bor-

Fig. 3. Mean loading of inorganic N to soil available N pools in a 70 cm × 95 cm rectangle around the carcasses (20 cm from the edge of the 30 cm × 55 cm area covered by the carcasses). Error bars are SEs.

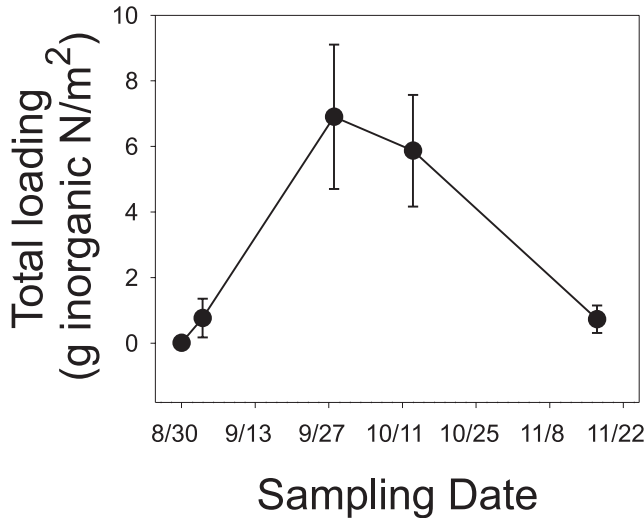


Fig. 4. Time series of mean soil $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 10 cm from carcasses in carcass plots (solid circles) and the centre of control plots (open circles). Error bars are SEs.

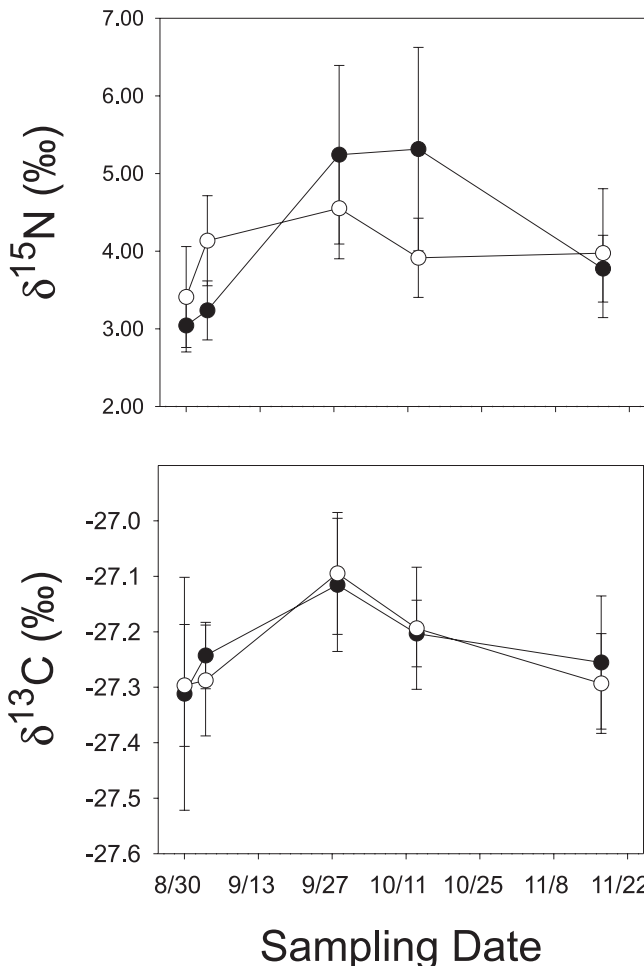
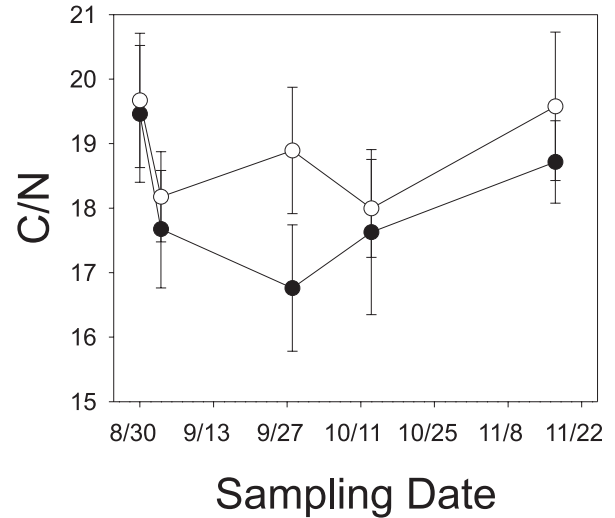


Fig. 5. Time series of soil C/N ratios 10 cm from carcasses in carcass plots (solid circles) and the centre of control plots (open circles). Error bars are SEs.



dering salmon streams in other studies, with up to 3‰ enrichment (based on linear two-member mixing models; Kline et al. 1993) observed in organic and upper mineral horizons relative to non-salmon streams (Bartz and Naiman 2005). We can also use a linear two-member mixing model for calculating the contribution of SDN to soils:

$$\text{SDN (\%)} = \left(\frac{\text{SAM} - \text{TEM}}{\text{MEM} - \text{TEM}} \right) \times 100$$

where SDN is the percentage of salmon-derived N in the carcass plots, SAM is the observed $\delta^{15}\text{N}$ of sample soils from the carcass plots, TEM is the terrestrial end member, and MEM is the marine end member. If we used the average of published values of $\delta^{15}\text{N}$ for salmon muscle tissue (range: 11%–14%; Chaloner et al. 2002; Morris et al. 2005) and the mean of observed $\delta^{15}\text{N}$ values for soils in our carcass and control plots, we estimate that the contribution to soils from salmon-derived N would be approximately 15% of the bulk soil N pool, assuming negligible fractionation.

As a check against this value, we used our loading estimate derived from the instantaneous soil N pools and the observed percent N in bulk soil to calculate the expected contribution of salmon-derived N in the carcass plots. Using this approach, the calculated contribution of exchangeable SDN to the total soil N pool was approximately 4%, substantially less than our estimate of 15% above. Again applying a two-member mixing model to derive an expected enrichment for $\delta^{15}\text{N}$ values in carcass plots based on our measured loadings of inorganic N generates an estimated enrichment of 0.3‰ over control values, four- to five-fold lower than our observed $\delta^{15}\text{N}$ enrichment in carcass plots. These values suggest that approximately 20%–25% of the SDN in these plots was located in the exchangeable inorganic N pool. It is likely that a large proportion of the N released from salmon carcasses (e.g., in the form of soluble proteins and amino acids), was incorporated into SOM and, thus, was not included in the exchangeable inorganic N pool. A smaller fraction may have entered directly into the soluble organic N pool.

It is also possible that the $\delta^{15}\text{N}$ of the bulk soil N pool was enriched through fractionation associated with N mineralization, nitrification, and leaching of SDN, as well as through other processes, including ammonia volatilization and immobilization (Shearer et al. 1974; Kendall and McDonnell 1998). In studies where soils or vegetation have been used to infer the terrestrial end-member, and salmon $\delta^{15}\text{N}$ has been used as the marine end-member, fractionation associated with N transfer through trophic levels may lead to overestimation of SDN (Morris et al. 2005). However, in the Morris et al. (2005) study, the $\delta^{15}\text{N}$ of SDN (transferred via bear feces) was not altered during decomposition, suggesting that little fractionation occurred in soils. We expect that the transfer of nutrients from salmon carcasses to the soil in our study would be analogous, and the $\delta^{15}\text{N}$ of salmon tissue is the appropriate choice for the marine end member.

Substrate availability drives N mineralization, as demonstrated by the positive correlation between total soil N and gross N mineralization across a range of environments (Booth et al. 2005) and by numerous studies that show a stimulation of N processing with increased N inputs (Ledgard et al. 1998; Hall and Matson 1999; Fisk and Fahey 2001). Thus, the addition of carcass N likely enhanced turnover of slower cycling pools (e.g., SOM), as well as providing direct inputs of labile N into the soil. The combination of increased N turnover and potentially increased rates of N leaching may have resulted in the elevated $\delta^{15}\text{N}$ we observed in carcass plots. In contrast, the lack of response in bulk soil $\delta^{13}\text{C}$ in carcass plots, and the lack of change in soil C/N, indicates that the organic soil C pool was sufficiently large to be unimpacted by salmon inputs. However, for the 1%–2% of the soil C pool that is actively cycling, salmon inputs may have been significant. If so, the large pulse in labile carbon may have enhanced the capacity of these soils to immobilize N, resulting in greater N retention than would be expected with direct inputs of inorganic N alone.

To date, only one other study has experimentally examined the impacts of salmon carcass decay on soil nutrient pools. Using ion exchange resin capsules and soil extracts to estimate plant-available N from carcasses, Drake et al. (2005) found high rates of soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ loading associated with salmon carcasses, nutrient concentrations that persisted over several months, and $\text{NO}_3^-\text{-N}$ concentrations that generally lagged $\text{NH}_4^+\text{-N}$. In both our study and the Drake et al. (2005) study, soil N concentrations were highly localized, with soils only 30 cm from carcasses bearing little indication of elevated nutrient loading. The consistency with our results is striking given that the Drake et al. (2005) study was conducted in second-growth forest dominated by alder, whereas alder, an N-fixer that may impact microbial processes as well as nutrient pools (e.g., Selmants et al. 2005), was largely absent at our old-growth site. Together, these results suggest that (i) the influence of salmon carcasses will primarily be a function of the spatial distribution of the carcasses (a function of bear behaviour) rather than migration of the nutrients leaching from those carcasses and (ii) at fine scales, salmon-derived N may overwhelm N inputs due to N fixation. Because most of the salmon captured by bears are carried less than 10 m from the high water bank (Willson et al. 2004), N loading is expected to

be much higher near the stream channel compared with locations further from the stream, a conclusion largely consistent with elevated levels of SDN in streamside vegetation (Ben-David et al. 1998; Hilderbrand et al. 1999; Bartz and Naiman 2005).

Implications for SDN in riparian systems

Several early studies have documented the high density of salmon carcasses carried to the forest by bears and hypothesized that the salmon nutrients may act as a fertilizer to riparian zone vegetation (Ben-David et al. 1998; Willson et al. 1998). Our results demonstrated that the maximum inorganic N loadings in soils within 20 cm of salmon carcasses were on the order of 6–7 g N/m². This loading exceeds typical silvicultural application rates of 3–5 g N·m⁻²·year⁻¹ (Thomas et al. 1999), and are similar in magnitude to experimental application rates that have yielded measurable growth responses in coastal Douglas-fir (*Pseudotsuga menziesii* (MIRB.) Franco) and western hemlock stands (Weetman et al. 1993; Brown 2003) and in riparian shrubs (Binkley et al. 1995). Moreover, assuming a turnover time on the order of a day (Stark and Hart 1997), the seasonal range of inorganic N loadings that we recorded would imply that approximately two-thirds of the N in a salmon carcass enters the plant-available N pool in soils during the course of carcass decomposition, suggesting that the loading would even be much higher. In comparison, N inputs to forested systems in the western United States range from 4 to >20 g N·m⁻²·year⁻¹ resulting from N deposition, and ≥ 100 g N·m⁻²·year⁻¹ resulting from N₂ fixation (Fenn et al. 1998). If our loading estimates were increased by one-third, which is likely given that our loading estimates were instantaneous values and turnover rates would be high, SDN could add as much as 10.5 g N·m⁻²·year⁻¹ to soils, comparable with rates of atmospheric N deposition that have resulted in N saturation in other ecosystems (Fenn et al. 1998). Clearly, the salmon are providing nitrogen to soils immediately adjacent to the carcasses over the course of several months at concentrations that may influence plant growth.

However, our experiments also demonstrate that N loadings from salmon carcasses are highly localized and somewhat ephemeral and that their overall effect on soils and riparian plants may be highly spatially constrained. For example, Gende and Quinn (2004) found that, during the spawning run in 2000, the riparian zone in the Bear Creek watershed on Chichagof Island, a stream with size, salmon, riparian vegetation, and watershed characteristics similar to Fish Creek, received an equivalent loading of 140 chum salmon (200 partially consumed salmon) as a result of bear foraging activities. Assuming that two-thirds of the N in these salmon entered soil available N pools, the mean loading to the 9000 m² riparian zone bordering the spawning reach (450 m reach of stream, 10 m on either side of the creek) would be 12.7 kg N. This would equate to approximately 1.4 g N/m² if we averaged the loading across the defined riparian zone. However, individual carcasses influence inorganic N pools only within an area of less than 1 m² surrounding the carcass. Even if we assumed that each of the 140 carcasses were spaced evenly throughout the riparian zone (a spurious assumption given that bears tend to carry

carcasses consistently to some areas; Helfield and Naiman 2002; Gende and Quinn 2004), the area influenced by salmon carcasses would equate to less than 2% of the defined riparian zone, with very high loadings (on the order of 5–20 g/m²; see also Drake et al. 2005) of inorganic N immediately adjacent to those carcasses. Of course, other processes will further “distribute” SDN, such as scavenging by invertebrates (e.g., Meehan et al. 2005; Hocking et al. 2006), hyporheic flow of dissolved nutrients (O’Keefe and Edwards 2003), and defecation of digested fish waste (Hilderbrand et al. 1999). However, our results clearly demonstrate that the extent to which leaching from the nutrient shadow around salmon carcasses impacts the larger riparian zone deserves further attention.

Finally, in the context of watershed retention of salmon-derived nitrogen, the rapid decomposition of salmon carcasses and relatively short duration of the nutrient pulse at a time when plant uptake is expected to be decreasing (fall senescence) suggests the potential for nutrient loss. Although the dominant overstory species in this system appear well adapted to exploit seasonal pulses of NH₄⁺ (Kronzucker et al. 1996, 1997), low uptake rates suggest that forest sequestration of SDN could be limited in the short term, even in younger stands. Relatively low recovery of ¹⁵N in forest trees following a late-season tracer addition and rapid immobilization of ¹⁵N by SOM suggest that soils may play a critical role in uptake and turnover of SDN, particularly when nutrients become available in the latter half of the growing season and are accompanied by a large pulse of labile C (Drake et al. 2006). Thus, it is likely that N retention in this system, as in other forested systems, is tied to the capacity of soils to serve as a reservoir for salmon-derived N and to the capacity of plants to exploit that N as it is re-released from SOM (Currie and Nadelhoffer 1999; Nadelhoffer et al. 1999; Perakis et al. 2005).

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