

Salmon Decay and Nutrient Contributions to Riparian Forest Soils

Abstract

Empirical evidence links salmon-derived nutrients to riparian vegetation production and quality, but mechanisms regulating transformation of salmon tissues into plant tissues are still largely unknown. We measured salmon carcass nutrient contributions to riparian soils of Kennedy Creek, WA, a coastal rainforest system. We used ion exchange resins to estimate cumulative bioavailability of major ions in soils, and soil extracts to examine timing and lateral movement of ammonium (NH_4^+) and nitrate (NO_3^-) from carcasses. Over the period of skeletonization (76 days), bioavailability of NH_4^+ was ~250x, soluble P (primarily PO_4^{2-}) was ~2x, and sulfur (SO_4^{2-}) was ~5.5x higher than baseline within 20 cm of carcasses, while availability of other ions was not affected. Maximum NH_4^+ and NO_3^- within 10 cm of carcasses occurred at ~240 degree days (dd; 56 days). NO_3^- and NH_4^+ maxima 20 and 50 cm from carcasses occurred between 300 dd (70 days) and 600 dd (150 days). When protected from large scavengers, an average minimum of 49.3% of total carcass N was contributed to soils, and NH_4^+ and NO_3^- moved through soils laterally at least 50 cm. Approximately 97% of salmon N is in quickly decaying soft tissues, while 88% of Ca and 50% of P is in the slowly decaying skeleton. Different lag-times in bioavailability of nutrients result; NH_4^+ becomes bioavailable within weeks, NO_3^- within months, and P and Ca^{+2} over months to years. These findings provide a potential timing mechanism for feedbacks between salmon and riparian vegetation in the context of local conditions.

Introduction

Pacific salmon (*Oncorhynchus* spp.) carry nutrients and energy from the ocean to the streams where they spawn and die. Fates and influences of salmon nutrients have been the focus of much research in recent years (reviewed by Willson et al. 1998, Naiman et al. 2002), resulting in a growing appreciation for the importance of salmon to freshwater and riparian systems. Salmon are now thought to play a role in supplying nutrients to riparian forests that surround spawning streams, systems that play important roles in the larger landscape as centers of biodiversity, nutrient retention and transformation, and regulation of microclimatic conditions (Naiman et al. 2000, 2005).

Salmon-derived nutrients move from streams to riparian forests via several pathways—carcasses are carried into the forest by floods and predators (Ben-David et al. 1998), excreta of predators and scavengers consuming salmon are deposited in the forest (e.g., Hilderbrand et al. 1999), and the products of salmon metabolism and carcass decay dissolved in stream water can be transferred via hyporheic flow (e.g., O’Keefe and Edwards 2003) and diffusion. Uptake and use of salmon-

derived nutrients by riparian vegetation have been demonstrated empirically; salmon contributions have been associated with higher nitrogen (N) content of riparian vegetation (Bilby et al. 2003), and several studies have shown that foliage along salmon streams is isotopically enriched relative to reference sites without salmon (e.g., Ben-David et al. 1998, Helfield and Naiman 2001, Bilby et al. 2003). Isotopic enrichment of plant N may result from the direct uptake of (enriched) salmon-derived N, or uptake of soil N enriched by microbial processes (e.g., denitrification, Pinay et al. 2003), rates of which can be increased by salmon nutrient contributions. The influence of salmon has also been linked to tree growth rates (Drake et al. 2002, Helfield and Naiman 2001), and characteristics of understory communities (Bartz and Naiman in press, Bilby et al. 2003). The collective evidence suggests that riparian forests and salmon production are linked by positive feedbacks—salmon-derived nutrients encourage the growth of some riparian trees and vegetation, which provide shading, bank stabilization, and, ultimately, large woody debris to streams, thereby improving habitat for freshwater life stages of salmon. The body of research, however, lacks a mechanistic description of the dynamics of salmon-derived nutrients in soils. The quantity, timing, and form in which salmon-derived nutrients are made available to riparian vegetation are unknown.

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Our objectives here were to better understand the dynamics and fate of salmon carcass nutrients in soils. The onset of decomposition in animals is governed by autolysis (Vass et al. 2002). As cells are deprived of oxygen, blood CO_2 increases, pH decreases, and wastes accumulate, poisoning cells. Cellular enzymes begin to dissolve cells from the inside, which eventually rupture and release nutrient-rich fluids, including dissolved organic nitrogen. As these become available, microbial decay (an aerobic process) and putrefaction (an anaerobic process) begin. These microbial processes are primarily regulated by temperature, and secondarily by moisture. The products of decay and putrefaction are mineralized nutrients (e.g., NH_4^+ , CO_2 , and organic wastes). Insects, vertebrate scavengers, plants, and soil microorganisms compete for the energy and nutrients in salmon carcasses deposited in the riparian forest. Carcass nutrients are also potentially lost via physical processes such as leaching and volatilization.

We used ion-exchange resins as a proxy to estimate availability of nutrients to roots over the process of salmon decay, and we measured NH_4^+ and NO_3^- in soil extracts to quantify the composition, timing, and lateral movement of N from decaying salmon carcasses into riparian soils. These issues are of particular interest in the context of the currently fashionable practice of placing carcasses along streams in the interest of “nutrient enhancement,” an attempt to increase salmon production. For example, ~30,000 salmon carcasses are distributed over a 32 km reach of the South Fork Skokomish River, WA and tributaries annually (Olympic Provenance Advisory Committee 2002). Since conditions that drive salmon carcass decay and soil processes vary with season, climate, local biota, and soil characteristics, we present this work as a case study using chum salmon (*Oncorhynchus keta*) on Kennedy Creek, WA. The results, however, contain implications for the fate of salmon-derived nutrients in streamside forests throughout the region.

Methods

Site Description

Kennedy Creek is ~12 km northwest of Olympia, WA (47°05'N, 123°08'W). The climate is typical of the Pacific Coastal Ecoregion: mean annual precipitation is ~250 cm and the mean annual air temperature range is ~4-20° C (Western Re-

gional Climate Center records at www.wrcc.dri.edu/summary/climsmwa.html). Kennedy Creek is small, with a mean daily flow of ~18.5 m³/sec (average for 1990-1999). However, it supports a large chum salmon population: escapement averaged 41,000 adults per year from 1992-2001, and the entire population spawns within a 5.2 km reach (Washington Department of Fish and Wildlife, unpublished data). Upstream migration and spawning occurs from mid-October through December. Kennedy Creek is surrounded by a second growth (~80 year-old) Douglas-fir (*Pseudotsuga menziesii*) forest. At the study site, western redcedar (*Thuja plicata*) is replacing fir within 20 m of the river, and scattered bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) are also present, especially near the riverbank. Sword fern (*Polystichum munitum*) and several mosses dominate the understory, but vine maple (*Acer circinatum*) and salmonberry (*Rubus specabilis*) are also common. The soil is loamy sand of the Indianola Series, deep and well-drained, and formed in sandy glacial drift (Pringle 1990). Soils are rich in organic matter with a 4.1 cm O horizon and a 14 cm A horizon with 18% organic matter, and mean soil pH (top 10 cm of soil combined) is 5.9 +/- 0.3 (Drake unpublished data).

The study site was on a flat terrace ~1.5 m (vertical) and 5-15 m (horizontal) from the active channel. We conducted the study from 30 October 2003 to 1 April 2004 (154 days). Most herbaceous plants were dormant during this period.

Field and Laboratory Methods

Ion exchange resins (IERS) are commonly used in agriculture to measure the availability of mineralized nutrients over time (Skogley and Dobermann 1996), and are gaining acceptance in forest soil research (e.g., Lajtha et al. 1999, Sheppard et al. 2001). IERS provide a proxy for nutrient uptake by roots by continually adsorbing nutrient ions that come into contact with resins via diffusion or bulk flow over days to months. We used pre-fabricated IER capsules (PST-1, Unibest Inc). The surface area of each capsule (radius = 1 cm) is 12.56 cm², and the absorption capacity is ~7.5 meq (3.75 meq cations and 3.75 meq anions; Martin Moore, Unibest Inc, personal communication). The order of cation affinity in PST resins is $\text{Ca}^{+2} > \text{Fe}^{+2/+3} > \text{Mg}^{+2} > \text{K}^+ > \text{Mn}^{+2} > \text{NH}_4^+$, and relative anion affinity is $\text{NO}_3^- > \text{HSO}_4^- > \text{NO}_2^- > \text{HSO}_3^- > \text{SO}_4^{-2} > \text{HPO}_4^{-2}$ (only ions of interest are listed). We also

chemically extracted exchangeable NH_4^+ and NO_3^- from soil samples collected over the period of decay. Soil extract and IER data complement each other. IERs provide estimates of nutrient bioavailability integrated over time, and better account for nutrient release and transport kinetics (Quian and Schoenau 2002). Static soil extract data provide estimates of extractable nutrients at points in time and are not subject to problems reported for IERs such as differential ion affinity and leaching (e.g., Kjønnaas 1999).

One month before we began the experiment (2 October 2003), we deployed IERs in 3 arrays, each consisting of two sets of capsules arranged in perpendicular transects at 0, 10, 20, 40, 80, and 160 cm (Fig. 1). We also deployed 3 IERs ~50 m from the carcasses. We buried the IERs 3-5 cm deep, at the interface between the O (organic) and A (mineral) horizons, where fine roots of redcedar were most abundant. We attempted to minimize soil disturbance during IER installation; a hand trowel was inserted to the O-A interface and pulled to a slight angle, the capsule was then dropped into the opening, and the top layer of soil replaced whole and tamped lightly.

On 30 October 2003 we placed one, spawned-out chum salmon from Kennedy Creek, dead for less than 24 hours, on the soil directly over the 0 point of each of the three IER arrays (Fig. 1). Dorsal-ventral widths of the fish were ~15 cm, so the 10 cm capsules were 2-5 cm from the edge of the carcasses, i.e., 10 cm from the center of the fish. Two of the carcasses were whole upon placement, and ~30% of the last salmon had been consumed. Average carcass weight was 3.19 kg. We placed a mesh cage (1 cm² plastic-coated wire) over each carcass as protection from large scavengers. Carcasses were exposed to ambient temperature, precipitation, air circulation and sunlight, and insects had free access to them.

We retrieved the IERs at the point of skeletonization (76 days). We immediately rinsed them in deionized water and shipped them to Unibest Inc., Kennewick, WA for analyses. The IERs were extracted with 50 ml 2 N HCl. Extracts were then neutralized to pH 5.0-9.0 with 2 N NaOH, and NO_3^- -N and NH_4^+ -N were determined using a Skalar SanFlow Segmented Flow Analyzer. Concentrations of all other nutrients in extracts were determined on a Perkin Elmer Optima 3000 radial ICP.

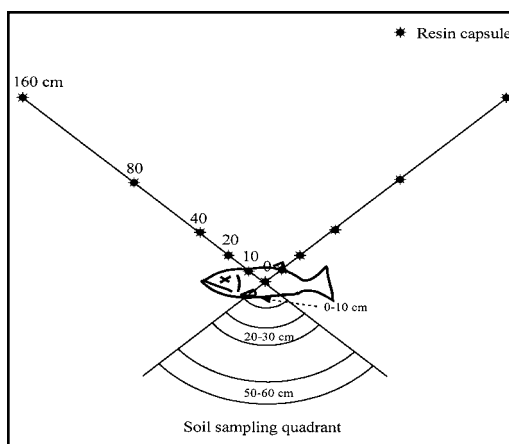


Figure 1. Arrangement of IER capsule arrays and soil sampling relative to salmon carcasses. Carcasses were centered on the 0 point IER capsule. Soil cores were collected 0-10 cm and 50-60 cm from the edge of the carcasses.

We collected soil samples (cores) at 0-10 cm, 20-30 cm and 50-60 cm from the edge of each carcass at the time of IER placement, and 8 additional times over the following 10 weeks (Table 1) until the carcasses were completely skeletonized (270 dd, 76 days). Although we originally planned to end the experiment upon skeletonization, extractable N was still clearly changing at the end of the experiment, so we collected additional soil samples at 135 and 154 days. Soil within 10 cm of the carcasses had been disturbed by IER removal, so we were only able to collect soil samples at 20 and 50 cm on the last two dates.

Soil cores were 10 cm in depth (including the organic layer), 2.5 cm in diameter, and were collected in the quadrant opposite the IERs to avoid disturbing the surrounding soil (Fig. 1). We also collected and analyzed soil samples from two additional sites ~50 m from the carcasses for a related study, and the results are included here as a reference. We passed the soil samples through a 4-mm sieve and removed all roots. Subsamples (~10 g) were dried at 80°C for 48 hours to determine water content and ashed at 550°C for 1 hour to determine organic matter content. Additional subsamples (~12 g) were extracted for 30 minutes in 100 ml 2M potassium chloride (KCl) solution (after Robertson et al. 1999) for NH_4^+ and NO_3^- determination. We stored the soil samples in a refrigerator, and performed KCl extractions within 7 days of sample collection. We stored all extracts

TABLE 1. Site factors regulating microbial decay of carcasses: soil sample collection dates (time), expressed in the text as days after carcass placement, degree days (lower threshold = 1°C) from the time of carcass placement (temperature), and soil water.

Date	Days after carcass placement	Degree days (dd) °C	Soil Moisture (% water by weight +/- stdev)
10/1/03	pre-experiment	pre-experiment	18.5 (4.3)
10/30/03	0	0.0	29.9 (3.2)
10/31/03	1	7.7	30.7 (2.6)
11/2/03	3	10.7	33.6 (7.9)
11/5/03	6	17.4	28.7 (3.0)
11/12/03	13	54.2	33.2 (3.5)
11/26/03	27	117.8	36.3 (2.9)
12/15/03	46	199.4	31.6 (4.5)
12/30/03	61	239.5	34.2 (4.5)
1/14/04	76	267.6	36.7 (3.5)
3/13/04	135	571.6	45.6 (9.8)
4/1/04	154	712.1	43.2 (6.6)

frozen until analysis, and determined NH_4^+ and NO_3^- in KCl extracts using colorimetric analyses (modified from Mulvaney 1996).

Skeletons of two salmon had been scattered by the end of the experiment. The remaining complete skeleton was collected, dried, weighed and ashed at 550°C for 3 hours for bone mineral estimation.

We present time-dependent results in terms of degree days (dd) because microbial processes are regulated primarily by temperature (after Vass et al 1992). We calculated dd using a lower threshold = 1°C, and surface air temperatures measured at a weather station in Shelton, WA, about 10 km from the study site. We standardized all soil N extract data to bulk density (mg/g dry soil), for comparisons over time, and the results are expressed on an aerial basis. We used bulk density measurements from a related study (n = 40 measurements within 10 m of the carcasses), corrected for the relative depth of the organic layer, because it was not feasible to collect the large volumes of soils required for bulk density determination from under the carcasses.

Statistical Analyses

We compared IER nutrient accumulations to baseline values, i.e. mean accumulation values of all capsules at 160 cm (n = 6) from the carcasses. We averaged IER data for each ion by distance from the carcasses (3 capsules at 0 cm and 5-6 capsules each at 10, 20, 40 and 80 cm). Soil extract data

are a time series; therefore, baselines are mean pre-experiment values collected prior to carcass placement on 30 October 2004. We log transformed extractable N and IER nutrient data to improve normality, and used repeated measures ANOVA ($\alpha = 0.05$) to test for significant differences in IER nutrient accumulation over space, and soil extract data over time. We used Tukey tests for pairwise comparisons of baseline to experimental values (Zar 1984).

Results

Ion Exchange Resins (Spatial Patterns)

IERs accumulated significantly more NH_4^+ , SO_x (primarily as SO_4^{2-}), and soluble P (primarily as PO_4^{3-} , Martin Moore, Unibest, personal communication) within 20 cm of decaying carcasses relative to baseline accumulation over the period of skeletonization (~270 dd, Fig. 2, Table 2). Approximately 250x more NH_4^+ was accumulated by IERs at 0 and 10 cm relative to baseline ($P < 0.001$, Fig. 2a). Increased accumulation of other nutrients near the carcasses was less dramatic; SO_x was 5.5x higher ($P < 0.001$, Fig. 2c), and soluble P was 2x higher ($P < 0.05$, Fig. 2c) than baseline. NO_3^- and Fe accumulations were highly variable and were not significantly higher near carcasses, (Fig. 2b and 2e). Average accumulation of NO_3^- at 0 and 10 cm, however, was not much more variable than P and S, and the failure to detect a significant difference may be due to small sample size. IER accumulations of Ca^{2+} , Mg^{+2} , and Mn^{+2}

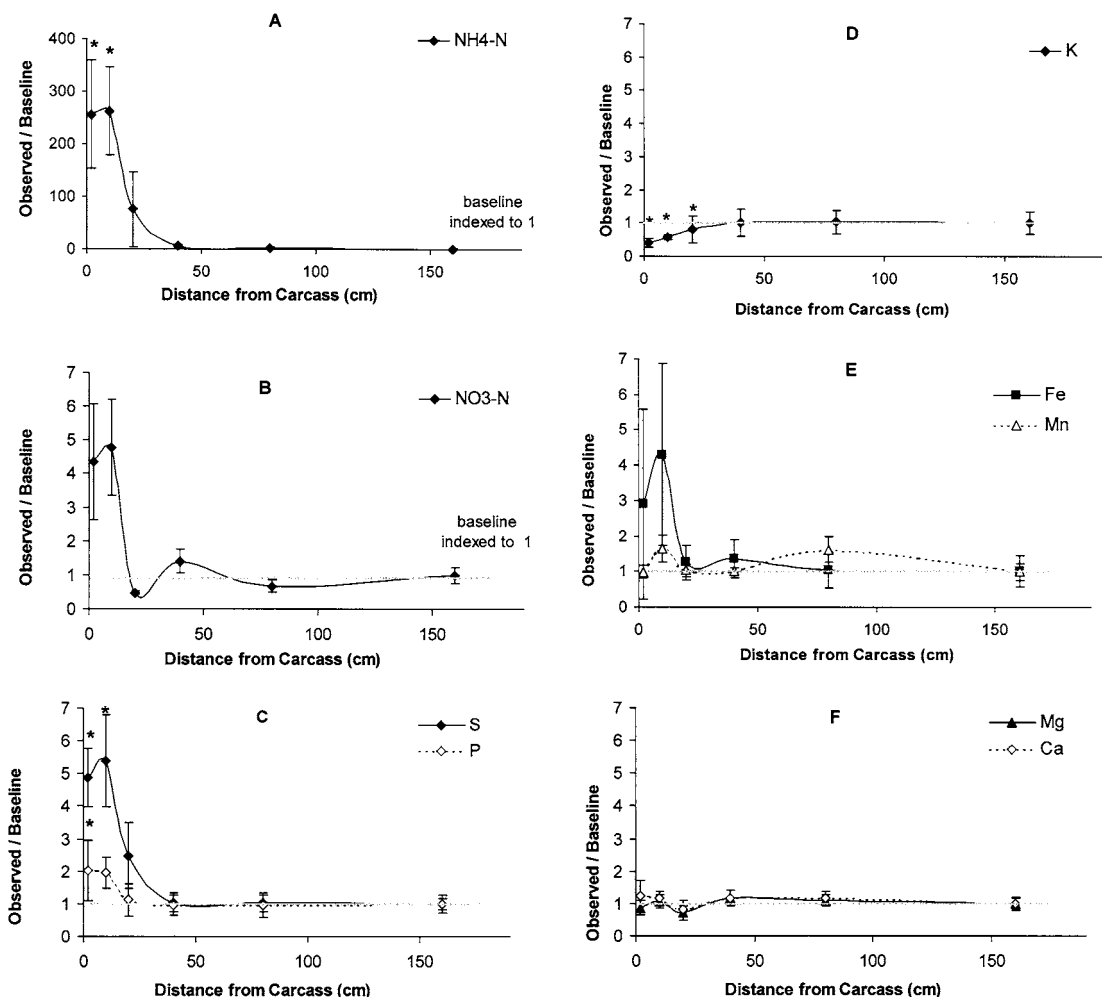


Figure 2a-f. Relative abundance of mineral nutrients (+/- standard error) with distance from decaying salmon carcasses (indexed to average values at 160 cm). At 0 cm and baseline $n = 3$, all other distance $n = 5$ or 6.

ions were approximately equal at all distances from the carcasses (Fig. 2e and 2f). IER accumulation of K^+ was significantly ($\sim 50\%$) lower within 20 cm of the carcasses ($P < 0.01$, Fig. 2d).

Three resin capsules deployed at 50 m from the carcasses accumulated $\sim 1.5 - 4.5x$ more of all nutrients than IERs 160 cm from carcasses (Table 2), demonstrating high variability of soil nutrient availability over 10s of meters.

Soil Extracts (Temporal Patterns)

Extractable NH_4^+ and NO_3^- in soil surrounding the carcasses rose dramatically over the experiment (Fig. 3). Maximum extractable NH_4^+ and NO_3^- at

0-10 cm occurred at ~ 240 dd, while at 20-30 and 50-60 cm extractable NH_4^+ and NO_3^- maxima occurred later, between 270 dd and 570 dd, (between data points, Fig.3). NO_3^- concentrations began to rise significantly approximately 100 dd later than NH_4^+ . At the time of carcass placement, one carcass had been partially consumed by birds (the skin was torn, muscle and organ tissues were exposed). NH_4^+ rose more quickly near this carcass, beginning to increase ~ 40 dd (7 d) earlier than the other carcasses, and appears to have peaked ~ 150 dd (~ 30 days) earlier than concentrations associated with whole carcasses. This was expected since mechanical injury is known to increase the decay rate of large mammals

TABLE 2. Mean mass of resin capsule accumulation of elements over 154 days (+/- stdev) with distance from the salmon carcasses.

	distance from carcasses (cm)						
	0	10	20	40	80	160	50,000
	mass (mg)						
NO ₃ -N	0.119 (0.181)	0.110 (0.191)	0.011 (0.007)	0.032 (0.047)	0.016 (0.0240)	0.023 (0.030)	0.091 (0.111)
NH ₄ -N	53.300 (28.181)	41.116 (29.4140)	11.862 (27.070)	0.840 (1.131)	0.476 (0.492)	0.157 (0.078)	0.343 (0.288)
Ca	10.823 (6.484)	9.012 (3.503)	6.486 (5.020)	8.996 (4.120)	8.922 (3.572)	7.758 (3.771)	11.052 (0.702)
Fe	0.058 (0.085)	0.079 (0.105)	0.023 (0.022)	0.025 (0.022)	0.019 (0.021)	0.018 (0.018)	0.041 (0.036)
K	1.143 (0.554)	1.476 (0.401)	2.128 (2.632)	2.686 (2.337)	2.712 (2.029)	2.642 (1.998)	3.019 (0.266)
Mg	2.151 (0.919)	2.493 (1.133)	1.658 (0.006)	2.697 (0.004)	2.573 (0.012)	2.335 (0.008)	3.395 (0.002)
Mn	0.012 (0.005)	0.025 (0.013)	0.016 (0.006)	0.015 (0.004)	0.025 (0.012)	0.015 (0.008)	0.021 (0.002)
P	0.380 (0.231)	0.286 (0.159)	0.164 (0.177)	0.139 (0.099)	0.139 (0.125)	0.145 (0.091)	0.183 (0.039)
S	5.764 (1.431)	5.038 (2.914)	2.320 (4.236)	0.966 (0.617)	0.953 (0.527)	0.934 (0.351)	1.518 (0.997)
number of capsules (n)	3	5	6	5	6	6	3

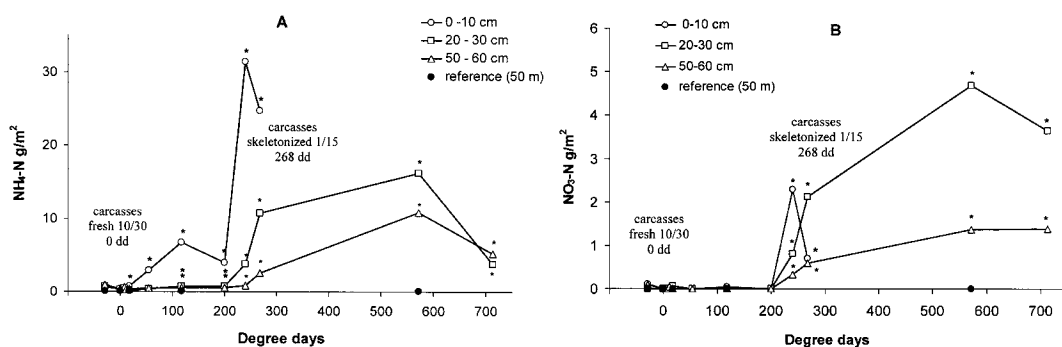


Figure 3. Extractable NH₄⁺ (A) and NO₃⁻ (B) over 270 dd (76 days) in surface soils 0-10 cm from carcasses, over 700 dd (154 days) in surface soils 20-30 cm and 50-60 cm from carcasses, and at reference sites ~ 50 m from the carcasses. n = 3 at each point, and * denotes values significantly higher than baseline NH₄⁺ and NO₃⁻ (averaged for 10/1/03 and 10/30/03), $\hat{\alpha} = 0.05$.

(Micozzi 1986). Extractable NH_4^+ and NO_3^- in the reference samples (from ~50 m away) showed the same underlying pattern in pre-experimental samples (a slight decrease in extractable NH_4^+ between 2 October and 30 October), but did not increase during the winter months.

The Fate of Carcass N

We estimate, using soil extract data, that an average minimum of ~50% of total carcass N became available in mineral form in surrounding soils (Table 3). The remaining ~50% of carcass N may have been consumed by small scavengers such as fly maggots (observed on the carcasses during decay), immobilized by soil microbes, leached into deeper soils, or persisted in soils as dissolved organic nitrogen. Soil extract N results demonstrate lateral movement of NH_4^+ and NO_3^- at least 50-60 cm from the carcasses; extractable N maxima occurred later in soils further from the carcasses (Fig. 3). Extractable NO_3^- continued to increase after skeletonization (at 76 days). NH_4^+ maxima at 20 and 50 cm occurred after skeletonization, but earlier than the NO_3^- maxima.

Bone and Soft Tissue Nutrients

The skeleton contains about 88% of the Ca and 50% of the P in a whole salmon (Table 4). The skeleton of fish 2 weighed 67.6 g (dry weight, 154 days after death); this is <2% of the total fresh carcass weight. Using published nutrient content values for fish tissue and bone (Table 4), we estimate that ~50% of total P and ~88% of total Ca is bound in the skeleton, while about ~97% of total

TABLE 3. Estimated minimum soil N contribution (g) from chum salmon carcasses. Estimates are deviations from background values of $\text{NH}_4\text{-N} = 0.75 \text{ g/m}^2$, and $\text{NO}_3\text{-N} = 0.015 \text{ g/m}^2$, summed over the area of known influence (up to 60 cm from the salmon carcasses). Estimates are corrected for area and soil bulk density. % N estimates are based on chum salmon at senescent death (male and female %N are both 2.5%; Gende et al. 2004).

	Fish 1	Fish 2	Fish 3
Fresh weight (g)			
10/30/04	3650	3580	2340
N content (g)	91.25	89.50	58.50
Date of max soil N content	1/15/04	3/15/04	12/30/03
Soil N (g) over background ($\text{NO}_3^- + \text{NH}_4^+$)	45.35	56.27	20.66
% of total carcass N contributed to soil	49.7%	62.9%	35.3%

N and S is bound in soft tissues. The skeleton of fish 2 did not decay noticeably before collection (bones were not broken, scattered, or gnawed), although by 700 dd (154 days) some leaching presumably had occurred.

Discussion

The heterogeneity of riparian soils is both extreme and largely invisible (Naiman et al. in press). We must re-emphasize that this work is a case study; we used a small number of salmon carcasses to

TABLE 4. Nutrient content of a 3.58 kg spawned-out whole salmon, and the skeleton alone, which weighed 44.16 g after ashing. The total and skeletal weights from fish 2 were used because its skeleton was the most complete at the end of the experiment.

Element	% by weight of whole salmon (spawned-out)	mg in 3.58 kg salmon	% by weight in bone	% (whole fish) in bone
N	2.50a	89.50	6.25d	3.08
P	0.43a	15.39	17.30e	49.63
Ca	0.50b	17.90	35.60e	87.83
K	0.14b	5.01	0.36e	3.30
S	0.10c	3.58	0.10c	1.23
Mg	0.03b	1.07	0.61e	44.16
Fe	0.003b	0.11	0.007e	44.00
Mn	0.002b	0.01	0.003e	43.17

^a values from Gende et al. (2004), ^b estimated from Shearer et al. (1994), ^c estimated from published values of other vertebrate tissues, ^d values based on N:P ratios from Sterner and Elser (2002), ^e values estimated from Hamada et al. (1994).

estimate nutrient contributions to riparian soils on one creek. Climate, vegetation and soil characteristics such as texture, pH, cation exchange capacity all potentially affect the dynamics, movement, and cycling of salmon nutrients in riparian ecosystems.

Time-lags in Nutrient Bioavailability

Salmon bones can persist in riparian forests for at least one year. The slow decay of salmon skeletons clearly releases Ca^{+2} , Mg^{+2} , and soluble P more slowly than highly seasonal inputs of N and S from soft tissues. Annual salmon inputs, then, may release a relatively steady supply of bone nutrients over the year, while salmon-derived N and S are delivered as pulse lasting several months during and after salmon spawning. Annual nutrient contributions from salmon bones are probably small relative to native ions in Kennedy Creek soils; average native (extractable) ions in the top 10 cm of Kennedy Creek soils are 1820 kg/ha Ca^{+2} , 82 kg/ha Mg^{+2} , and 200 kg/ha soluble P (Drake unpublished data). Calculation of relative bone nutrient contributions would require estimates of the amount of bone deposited in the riparian forest annually and the area over which bones are distributed, which are currently unavailable. Over thousands of years, however, salmon bones may constitute an important source of some nutrients.

The initial nitrogenous product of carcass dissolved organic nitrogen mineralization is clearly NH_4^+ . At Kennedy Creek, NH_4^+ in soil solution began to rise significantly about 20 dd (6 days) after carcass placement, while NO_3^- didn't increase until ~100 dd (27 days), demonstrating almost immediate availability of NH_4^+ and a short-term lag in the availability of NO_3^- . In the well-drained soils of Kennedy Creek, a high rate of denitrification is unlikely, and nitrate immobilization is probably minimal as soil heterotrophs prefer NH_4^+ as a N source (Jones and Richards 1977). We conclude that the lag in NO_3^- availability is a result of delayed nitrification. This delay may be a result of low initial populations of nitrifying microorganisms, allelopathic suppression of nitrifiers, or competition between heterotrophs and nitrifiers for another limiting nutrient (Vitousek et al. 1982). Elevated soil N persisted for at least 500 dd (~ 3.5 months) after skeletonization. Although NO_3^- and NH_4^+ are both taken up by vegetation, NO_3^- is more mobile in soils than NH_4^+ , and,

when present, may be more likely to come into contact with roots. Energetically, however, NH_4^+ is "preferred" by plants because NO_3^- must be reduced to NH_4^+ before it can be used. Cycling of NO_3^- through the soil microbial community is rapid relative to plant uptake, and microbial communities are thought to mediate plant N uptake in this way (Kaye and Hart 1997, Stark and Hart 1997). N contributions from decaying salmon, however, are ecologically unusual—carcasses can contribute relatively large quantities of N to small areas. This is very unlike other, more dispersed types of natural N loading such as litterfall. N from carcass decay is also accompanied by carbon and other nutrients, potentially shifting the dynamics of plant-microbe competition. The abundance of extractable N in soils near carcasses here suggest that the demands of both microbial populations and plants are saturated by carcass contributions at small scales, so that the regulation of soil N, as discussed by Kaye and Hart (1997) and Stark and Hart (1997), may not apply to salmon carcass decay.

Relative Importance of Salmon Nutrients to Kennedy Creek Soils

Over the period of skeletonization (76 days), IER accumulation of N (250x baseline) near carcasses was much higher than accumulation of soluble P (2x baseline) and SO_x (5.5x baseline), although all were significantly higher than baseline. N is the most abundant nutrient in salmon; the molar N:P ratio of whole, dead, spawned-out salmon (including bones) is 12.9, and the molar N:S is 68.6. N is also relatively more abundant than P in soft tissues; molar N:P is 24.8. The molar N:S ratio of bone is the same as soft tissue, ~ 57.1. Soil ion dynamics are complex—in forest soils P is tightly cycled and conserved in organic horizons. Salmon P may have been taken up or immobilized quickly by surface soils, before reaching the IERs. Additionally, a large fraction of total salmon P (50%) is bound in slowly decaying bones, which helps explain the relatively modest increase in soluble P accumulation near carcasses. IER accumulation of N relative to S (molar N:S = 47.2) was similar to the molar N:S of salmon tissues (57.1).

Accumulation of several nutrients, most notably Ca^{+2} , was essentially equal in all of the IERs, irrespective of distance from the carcasses. The lack of a spatial pattern in Ca^{+2} attributable to carcass inputs suggests that Ca^{+2} in Kennedy Creek soils

is not immediately affected by salmon inputs. Most salmon Ca is bound in bones (~88%), which decay slowly. Additionally, Kennedy Creek soils are relatively high in native Ca^{+2} (~1820 kg/ha extractable Ca^{+2} in the top 10 cm; Drake unpublished data), presumably overwhelming any Ca^{+2} from decay of soft tissues. Significantly lower accumulation of K^+ near the carcasses (~50% of baseline) was unexpected, especially because the cation exchange resins have a higher affinity for K^+ than NH_4^+ . As resins approach adsorption capacity towards the outsides of the capsules, however, ions with lower affinity can still displace those with higher affinity if present in a much higher concentration. Adsorption of other cations may also have been affected by high NH_4^+ , but the anions (NO_3^- , and most of the soluble P and SOx) are adsorbed by anion exchange resins and are unaffected by cation dynamics.

Salmon bones may play an important ecological role in supplying nutrients (especially Ca^{+2} , Mg^{+2} , and K^+) to riparian forests low in native ions. Acid soils in particular tend to lose cations over time; anions are more abundant at lower pH, and bond with cations to form neutral compounds, which leach quickly into deeper soils. Additionally, cation exchange capacity decreases with pH (Brady and Weil 1999), reducing availability of adsorbed cations to roots. Western redcedar, the dominant tree species at the study site, may influence soil properties, thereby contributing base cations to surface soils. Cedars can function as Ca biocyclers, moving Ca^{+2} from deep in the soil profile to surface layers, resulting in higher soil cation exchange capacities, pHs, and exchangeable Ca (Alban 1969). Western redcedar foliar Ca content is 2-5 times that of Douglas-fir and western hemlock (*Tsuga heterophylla*), while foliar N and P of the three species are comparable (Radwan and Harrington 1986).

Modes of Nutrient Transfer and Their Implications

Each salmon carcass influenced nutrient availability in riparian soils in a ~2.5 m² area, moving via diffusion and bulk flow through soils. If not protected from large scavengers, the carcasses would undoubtedly have been partially consumed and moved, decreasing the amount of tissue available to decay but speeding the decay process and distributing the nutrients over a larger area. Carcass consumption and distribution depends on the type

and abundance of predators and scavengers present. Bears, known to play a major role in catching and distributing salmon in other systems (Hilderbrand et al. 1999), are not common at Kennedy Creek (Jauquet et al. 2003, Jeff Cederholm, Washington State Department of Natural Resources, personal communication). Instead, smaller species more likely to consume carcasses in place or move only small portions of the carcasses [e.g. fly maggots (unknown species), gulls (*Larus spp.*), American crows (*Corvus brachyrhynchos*), raccoons (*Procyon lotor*) and river otter (*Lutra canadensis*)] disperse salmon-derived nutrients into the forest (Jauquet et al. 2003). N isotope data provide evidence that salmon N is distributed as far as 100 m from Kennedy Creek (Bilby et al. 2003). Given the relatively low abundance of bears and prevalence of smaller predators and scavengers, salmon nutrients are more likely to be moved into the Kennedy Creek riparian forest as excreta than as whole or partial carcasses. Flooding may deposit whole carcasses in the forest in some years, but not in 2003-2004; high flows occurred after a storm in November 2003, but few carcasses were distributed laterally as a result.

This case study highlights a number of important considerations for understanding interactions between salmon and riparian soil-plant systems. The timing of salmon migration and spawning, and therefore the temperature and precipitation during decay, will determine decay rate and regulate the physiological activity of soil microbes and roots. The timing of salmon nutrient delivery may then confer an advantage to plants with roots that are physiologically active during and soon after the upstream migration of salmon [e.g., roots of cedar, but not the dominant herbaceous species (sword ferns), grow vigorously at Kennedy Creek over the winter]. Salmon carcass decay leaves small islands of nutrient-rich soils, which may contribute to small-scale heterogeneity in plant and microbial communities. Plants with extensive root systems and a large capacity for nutrient storage, such as trees, are better able to take advantage of patchily-distributed resources and may benefit from salmon contributions more consistently than small or short-lived plants. Our findings also suggest a timing mechanism for feedbacks between salmon and riparian vegetation in the context of native soils and nutrient-limitation. N-limited vegetation may respond at a relatively short time scale (one growing season), as almost all salmon N is

delivered during the decay of soft tissues. Vegetation in systems with acid soils low in cations may respond to nutrients that leach from bones over longer periods, such as decadal-scale variation in salmon populations or the anthropogenic decline of Pacific salmon over the last century. The mode of salmon nutrient delivery may also be tied to soil microbial and plant communities; the nutrients in whole carcasses (such as those distributed via flooding) are delivered over longer periods and smaller areas than nutrients in carcasses partially consumed by predators, while salmon-derived nutrients in excreta are almost immediately available to plants and microbes, and are more widely distributed. Ongoing research will add to our understanding of these processes and feedbacks that subtly shape the ecology of salmon rivers and their riparian forests.

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