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Transfer of Nutrients from Spawning Salmon to Riparian Vegetation in Western Washington

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Abstract.—The extent to which nutrients from Pacific salmon are transported to riparian areas may be influenced by differences in spawning behavior among species. Chum salmon *Oncorhynchus keta*, pink salmon *O. gorbuscha*, and sockeye salmon *O. nerka* typically spawn in dense aggregations, while species like steelhead *O. mykiss* and coho salmon *O. kisutch* spawn at lower densities. The contribution of nutrients to riparian vegetation was compared at two watersheds in western Washington, Griffin Creek (used by coho salmon) and Kennedy Creek (used by chum salmon). Salmonberry *Rubus spectabilis* foliage was collected at the channel edge above and below barriers to spawning salmon and at 20, 50, and 100 m upslope from the stream and analyzed for nitrogen stable isotope ratio ($\delta^{15}N$, an indicator of salmon-derived nitrogen), total nitrogen (N), and phosphorus (P) content. Cover, plant density, and the species richness of shrub and understory vegetation were compared between sites with and without salmon. The $\delta^{15}N$ values in salmonberry leaves were higher at sites with salmon than at corresponding distances from the channel at sites without salmon at Kennedy Creek but not Griffin Creek. Salmonberry foliage adjacent to salmon spawning reaches possessed significantly higher levels of total N and P in both watersheds. Nitrogen content was positively associated with $\delta^{15}N$ values at the Kennedy Creek sites but not at the Griffin Creek sites. At Kennedy Creek, shrub species diversity and understory plant density and species diversity were higher at sites with salmon than at sites without salmon. These results suggest that areas bordering streams utilized by high-density-spawning species like chum salmon receive a substantial nutrient contribution from the fish and that this subsidy influences the vegetation. We did not see clear evidence for a similar nutrient contribution from coho salmon.

Anadromous salmonids *Oncorhynchus* spp. play a key role in the nutrient and trophic dynamics of aquatic ecosystems in watersheds tributary to the northern Pacific Ocean (Kline et al. 1990, 1994; Bilby et al. 1996; Johnston et al. 1997). More than 95% of the body mass of Pacific salmon is accumulated in the marine environment (Groot and Margolis 1991). This material is transported to the streams, rivers, and lakes where the salmon spawn and die. The importance of this nutrient and organic matter subsidy has long been recognized for lakes supporting sockeye salmon *O. nerka* (Juday et al. 1932). More recent research has demonstrated that the eggs and carcasses deposited in streams and rivers by spawning salmon make a significant contribution to the nutrient capital (Kline et al. 1990; Johnston et al. 1997) and biological productivity (Bilby et al. 1998; Wipfli et al. 1999) of these systems as well.

Nutrients from salmon are transported to terrestrial ecosystems as well. Several studies have used analysis of stable isotope ratios to demonstrate that nitrogen (N) derived from the carcasses of salmon is found in the foliage of riparian plants (Bilby et al. 1996; Ben-David et al. 1998; Helfield and Naiman 2001). Examination of the spatial distribution of salmon-derived N in riparian ecosystems on Chichagof Island, Alaska, revealed its presence at considerable distances from the edge of the channel (Ben-David et al. 1998). The extent of upslope distribution varied by site and plant species and was influenced by the presence of piscivorous predators. However, evidence of salmon-

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derived N was found in some plant species up to 200 m from the channel edge. There has been no evaluation of the upslope distribution of salmon-derived nutrients to terrestrial vegetation south of Alaska. Owing to regional differences in the hydrologic regime, density of salmon, and abundance and types of piscivorous predators and scavengers, the extent of salmon nutrient movement into Pacific Northwest forests may be considerably different.

The magnitude of nutrient contributions to terrestrial ecosystems may also be influenced by the species of salmon. In Washington, chum salmon *O. keta*, pink salmon *O. gorbuscha*, and sockeye salmon often spawn at densities exceeding 10,000 fish/km (Washington Department of Fish and Wildlife and Western Washington Treaty Indian Tribes 1993). In contrast, species like coho salmon *O. kisutch*, steelhead *O. mykiss*, and sea-run cutthroat trout *O. clarki* typically spawn at densities well below 1,000 fish/km, and in the case of steelhead and cutthroat trout, not all the adults die after spawning. Therefore, the contribution of nutrients from species exhibiting these different spawning strategies may be very different. Nearly all the evaluations of salmon-derived nutrient contributions to riparian vegetation have been conducted along stream reaches supporting species of salmon that typically spawn at very high densities (Ben-David et al, 1998; Helfield and Naiman 2001).

Increased availability of nutrients may influence plant community composition and production (Huston 1994), suggesting that salmon may alter the characteristics of riparian vegetation. Trees grow more rapidly along stream reaches supporting pink salmon in southeast Alaska (Helfield and Naiman 2001). However, only one study to date has compared the characteristics of riparian understory vegetation at sites with and without salmon (Bartz 2001).

We examined riparian areas along stream reaches in two watersheds, one supporting chum salmon and the other coho salmon. Riparian areas adjacent to sites used by the salmon were compared with nearby riparian areas along stream reaches inaccessible to anadromous fishes. Our objectives were to compare the nutrient contributions to riparian vegetation by chum and coho salmon, to determine the extent to which salmon-derived nutrients were transported upslope, and to determine whether the characteristics of shrub and understory vegetation were associated with the presence of spawning fish.

Study Sites

We compared the chemical and biological characteristics of plant communities in areas bordering stream reaches where salmon spawn with those of plant communities at comparable, nearby riparian sites upstream of a barrier to anadromous fish. We conducted this study in watersheds tributary to Puget Sound in Washington. Six riparian sites were sampled in the Kennedy Creek watershed (47°05′N, 123°08′W), three of which were adjacent to areas where salmon spawn and three upstream from a 15-m waterfall. All six sites were within 3 km of one another and were underlain by the Crescent Formation, a combination of marine sedimentary and volcanic rock (Logan 1987). Soils at these sites are of the Schneider series, a gravelly loam formed from basaltic colluvium (Pringle 1990). A large population of chum salmon spawns in Kennedy Creek, which drains into southern Puget Sound. Small numbers of coho and chinook salmon *O. tshawytscha* also spawn in this system but make a negligible contribution of carcass biomass compared with the chum salmon. Chum salmon runs have averaged several thousand fish per kilometer in the reach accessible to anadromous fishes since 1980 but have frequently exceeded 10,000 fish/km over the last decade (Washington Department of Fish and Wildlife, unpublished data).

Four riparian sites adjacent to channel reaches used by coho salmon for spawning were sampled in the Griffin Creek watershed (47°30′N, 121°46′W). Four sites without salmon were sampled along Tokul Creek, the watershed immediately to the south of Griffin Creek. Nearly all of Tokul Creek is inaccessible to salmon due to a series of impassable waterfalls just upstream from its mouth. All sample sites were within 5 km of one another and were underlain by glacial recessional outwash deposits of sand and gravel (Booth 1990). Tokul series soils, a coarse loam formed of glacial till and volcanic ash were present at all the sample sites (Goldin 1992). Both streams are tributary to the Snoqualmie River, which flows into central Puget Sound. The Griffin and Tokul Creek sites will hereafter be referred to collectively as Griffin Creek. Griffin Creek was selected for study because relatively large numbers of coho salmon (several hundred per kilometer) spawn in this system (Washington Department of Fish and Wildlife, unpublished data).

The riparian sites sampled at both Griffin and Kennedy creeks bordered stream reaches with sim-

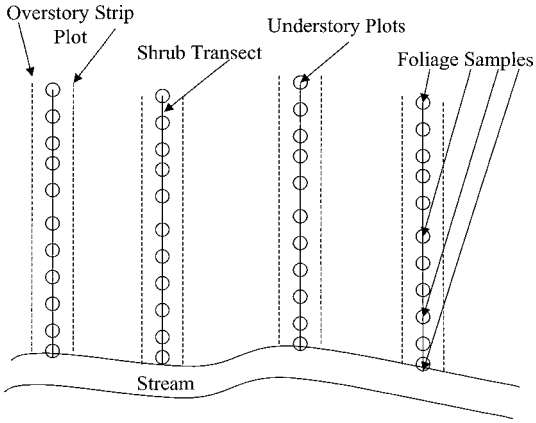

FIGURE 1.—Schematic representation of the sampling design at each riparian site.

ilar physical characteristics. The channels ranged from 4 to 10 m in bank-full width, with gradients less than 4%. The streambed substrate at all sites was composed primarily of cobbles and gravel.

All of the sampled sites were logged approximately 50–70 years ago. We selected sample sites with overstories dominated by conifers, the most common being western hemlock *Tsuga heterophylla*, Douglas-fir *Pseudotsuga menziesii*, and western redcedar *Thuja plicata*. Sites with an overstory that was predominantly red alder *Alnus rubra* were avoided. Red alder is a very common riparian species in this region and fixes nitrogen, which might mask the influence of salmon-derived nutrients. The average proportion of red alder in the overstory at our riparian sites ranged from 0% to 30%, although three of the individual strip plots at Kennedy Creek (there were four strip plots per site) did contain more than 50% red alder. These plots were omitted from comparisons of N content in foliage at sites with and without salmon (see below) but were included in all other comparisons.

Methods

The Washington Department of Fish and Wildlife counts spawning salmon at selected stream reaches in the Kennedy Creek and Griffin Creek watersheds. Surveys are conducted approximately every 10 d during the period of spawning, and all live and dead fish are counted. We used live fish counts and the area-under-the-curve method of Ames (1984) to estimate the density of spawning salmon in each watershed during autumn 1996, the autumn prior to sample collection.

Each riparian sample site was 400 m long and extended 100 m upslope from the channel edge.

TABLE 1.—Representation of riparian landforms at the study sites in Washington with and without spawning salmon. Values indicate the proportions of understory vegetation plots that were assigned to each landform category. Landform definitions are provided in the text.

	Griffin Creek		Kennedy Creek	
Landform	No Salmon	Salmon	No Salmon	Salmon
Floodplain	17.8	24.1	19.5	20.8
Low terrace	35.0	38.3	42.7	31.7
High terrace	30.5	24.4	24.7	35.0
Slope	16.7	13.2	13.1	12.5

Four transects were established perpendicular to the stream channel at each of the 14 sample sites (Figure 1). One transect was located within each of the four 100-m segments of the 400-m site. The transect origin was located randomly within each 100-m segment. The vegetation along each transect was sampled by means of several standardized methods (Bonham 1989). Overstory composition was characterized with a 10-m-wide strip plot centered on each transect. The species and diameter at breast height (DBH) of each tree within the strip plot with a DBH of 10 cm or more was recorded. Shrub species composition and cover were measured along the transect using a line-intercept method. A tape was extended 100 m upslope from the transect origin at the channel edge, and the species of all shrubs 1−3 m tall intersecting the plane defined by the tape were noted as well as the length of the transect intersected by each shrub. Circular plots with an area of 1 m^2 were established at the channel edge and at 10-m intervals along each transect (11 per transect) to characterize understory vegetation (less than 1 m tall). All species of vascular plants in each plot were identified, and the percent cover by each species was estimated. The canopy cover above each understory plot was measured with a moosehorn densiometer (Cook et al. 1995).

Riparian landforms have been postulated to explain some variation in riparian plant community composition (Rot 1995). We assigned each understory plot to one of four landform categories established by Rot (1995): (1) floodplain (less than 1 m above the level of bank-full flow); (2) low terrace (1−3 m above bank-full flow); (3) high terrace (more than 3 m above bank-full flow); and (4) slope (hill slopes greater than 20%). The representation of riparian landforms was comparable at sites with and without salmon for both Kennedy and Griffin creeks (Table 1).

The distribution of salmon-derived N upslope

from the stream was determined by comparing N stable isotope ratios in salmonberry *Rubus spectabilis* leaves at sites with and without salmon. Foliage samples were collected within the overstory strip plot at the channel margin as well as 20, 50, and 100 m from the edge of the channel. Salmonberry was very common at all riparian sites, enabling us to use a single species and avoid possible complications due to interspecific variation in isotopic values or nutrient content (Ben-David et al. 1998). We were able to collect salmonberry foliage at 90% (201 of 224) of the sample locations.

Stable N isotope ratios are expressed as $\delta^{15}N$ values, which represent the difference (‰) between the level of ^{15}N in the sample and that in the atmosphere N (Peterson and Fry 1987). Spawning salmon are enriched with ^{15}N relative to the other sources of N available in the watershed (Kline et al. 1990). Thus, the difference in $\delta^{15}N$ between sites with and without salmon provides an indication of the amount of salmon-derived N in salmonberry foliage at the salmon sites. Stable isotope analysis has previously been used to quantify the proportion of salmon-derived nutrients in riparian vegetation (Bilby et al. 1996; Ben-David et al. 1998) and stream ecosystems (Kline et al. 1990; Bilby et al. 1996, 1998; Johnston et al. 1997).

A total of 402 salmonberry foliage samples were analyzed for $\delta^{15}N$, 2 samples from each plot. In addition, dorsal muscle tissue samples from approximately 20 salmon carcasses were collected at each stream for N stable isotope analysis. Samples were kept cold in the field and frozen within 6 h of collection. Prior to analysis, samples were thawed, rinsed with distilled water, and dried at 50°C. Stable isotope analyses were performed at the University of Alaska, Fairbanks, following analytical procedures described in Ben-David et al. (1998). Samples were ground to a fine powder and 1–1.5 mg was combusted; the evolved N_2 gas was introduced into a continuous-flow isotope ratio mass spectrometer to determine $\delta^{15}N$ values.

Although foliage nutrient levels are not directly proportional to nutrient availability in the soil, these values do provide a relative indication of nutrient availability at a site (Aber and Melillo 1991). The concentration of total N and P in salmonberry foliage collected at the same locations as the stable isotope samples was also determined. A total of 201 samples were analyzed, one sample per plot. Nutrient analyses were performed at the Weyerhaeuser Analytical Chemistry Laboratory, Tacoma, Washington, using standard techniques (USEPA 1983). A 0.2-g subsample of the ground foliar tissue was digested using a Kjeldahl mixture with selenium dioxide catalyst. Simultaneous colorimetric determinations of this solution for ammonium nitrogen (Berthelot reaction) and total P (molybdenum blue reaction) were performed with a dual-channel flow-injection autoanalyzer. The results for N and P are reported as percentages of dry weight.

Analysis of variance (ANOVA) was used to evaluate the influences of distance from the channel and riparian landform on the stable isotope values and total N and P content of the salmonberry leaves. When significant effects were detected, differences between means were evaluated by means of a Tukey test. In cases in which distance and landform had no significant effect on the variable, values were compared between sites with and without salmon with a *t*-test. In addition, we compared regressions of N content against $\delta^{15}N$ values between sites with and without salmon. A relationship between N content and $\delta^{15}N$ values at sites with salmon but not at sites without salmon would indicate that the fish are in part responsible for the elevated level of N in salmonberry foliage.

Because it fixes nitrogen, red alder affects N levels in soils (Franklin et al. 1967). We omitted salmonberry foliage samples collected from transects where red alder constituted more than 50% of the trees in the overstory strip plot from the comparison of N content between sites with and without salmon. These transects were included in the comparisons of $\delta^{15}N$, however, as nitrogen fixation has relatively little impact on N stable isotope ratios (Hoering and Ford 1960; Delwiche and Steyn 1970; Kohl and Shearer 1980). The N content of foliage from transects at reference sites with more than 50% red alder was significantly greater than that at reference transects with less than 50% red alder (2.30% versus 2.09%; *t*-test; $P < 0.05$). Three of the overstory strip plots at Kennedy Creek (out of a total of 24) contained more than 50% red alder. Two of these transects were at sites without salmon and one was at a site with salmon. All other sampled strip plots contained less than 30% red alder, and no relationship between red alder and the N content of the salmonberry at the reference sites was seen. With the plots containing more than 50% alder omitted, the average proportion of red alder in the overstory at Kennedy Creek was 17.9% at the sites with salmon and 16.2% at the sites without salmon. None of the

TABLE 2.—Abundance of spawning salmon at the study sites and the contributions of organic matter, N, and P from carcasses. Average body weights are from Gresh et al. (2000). Estimates of nutrient deposition assume that N and P constituted 3.03% and 0.35%, respectively, of carcass wet weight (Larkin and Slaney 1997).

Variable	Griffin Creek	Kennedy Creek
Density of carcasses (fish/km)	260	22,000
Average wet weight (kg)	2.83[a]	4.63[b]
Biomass deposited (kg wet weight/km)	735	102,000
N deposited (kg/km)	22.3	3,090
P deposited (kg/km)	2.6	357

[a] Coho salmon.
[b] Chum salmon.

overstory strip plots at Griffin Creek contained more than 50% red alder.

The proportion of salmon-derived N in salmonberry foliage was estimated when the N stable isotope value for leaves from locations with salmon was significantly higher than that at corresponding locations without salmon. A simple isotopic mixing model was used to derive this estimate. The proportion of salmon-derived N was computed as

$$(\delta^{15}\text{N foliage below} - \delta^{15}\text{N foliage above}) \div (\delta^{15}\text{N carcass} - \delta^{15}\text{N foliage above}),$$

where δ^{15}N foliage below is the stable isotope value of salmonberry foliage at sites used by salmon, δ^{15}N foliage above is the stable isotope value of salmonberry foliage at sites above blockages to salmon, and δ^{15}N carcass is the stable isotope value of salmon carcasses for that site. This model has been applied to derive similar estimates in other studies (Kline et al. 1990; Bilby et al. 1996). We assumed that no fractionation occurred during the uptake of N by the salmonberry. However, plants will preferentially utilize the lighter N isotope ^{14}N when N is abundant (Peterson and Fry 1987). Therefore, our assumption is conservative in that if fractionation did occur at our sites our estimate of the contribution of N from salmon would be low.

We deliberately selected study areas with similar riparian forests to minimize differential overstory effects on the shrub and understory plant communities. The similarity of the overstory characteristics was determined by comparing canopy cover, stem density, and average diameter between sites with and without salmon at Kennedy and Griffin creeks by means of a *t*-test. We could not evaluate the effect of salmon-derived nutrients on overstory characteristics. Precise information on the age of the trees at each sample location was not collected. In addition, the method of regeneration (e.g., planting, seeding, or natural) and the initial stand density were unknown. Without this information it was not possible to determine whether nutrients from salmon contributed to any differences in tree size or density.

The influences of distance from the channel and riparian landform on the vegetative cover, number of plant species, and number of plants per understory plot were evaluated using ANOVA. Understory vegetation data were transformed ($\log_e[n + 1]$) to achieve normality. Variables not significantly influenced by landform and distance from the channel were compared between sites with and without salmon using *t*-tests, as described above. Shrub cover and the number of shrub species per transect were normally distributed, so these data were not transformed. Otherwise, shrub characteristics were compared using the same approach as for understory vegetation. All comparisons were considered to be significantly different at $P \leq 0.05$.

Results

There was a very large difference in the density of salmon spawning at the study watersheds in 1996 (Table 2). Although the density of spawning coho salmon at Griffin Creek is among the highest for this species in Puget Sound, that of chum salmon at Kennedy Creek was two orders of magnitude higher. As chum salmon are larger than coho salmon, the difference between the two watersheds in terms of the amount of carcass biomass and nutrients deposited was even more pronounced (Table 2).

Most of the measured overstory characteristics were comparable between sites with and without salmon (Table 3). However, at Griffin Creek, tree density was greater at locations without salmon and average stem diameter was greater at sites with salmon. Stand density and tree diameter were not different at the Kennedy Creek sites with and without salmon. Percent canopy cover and the proportion of the stand composed of red alder did not

TABLE 3.—Characteristics of the overstory forest at the Kennedy Creek and Griffin Creek study sites. Values are averages for all transects (16 for each Griffin Creek value and 12 for each Kennedy Creek value) ± 1 SE. The acronym DBH stands for diameter at breast height; % red alder is the percentage of stems of this species. Asterisks indicate significant differences between sites with and without salmon (*t*-test; $P \leq 0.05$).

Site	Stand density (trees/ha)	Average DBH (cm)	% red alder	Average canopy cover (%)
Griffin Creek				
With salmon	277 ± 47*	45.6 ± 14.0*	9.0 ± 10.8	81.8 ± 16.4
Without salmon	452 ± 67*	34.4 ± 3.5*	13.9 ± 7.3	82.8 ± 17.6
Kennedy Creek				
With salmon	318 ± 74	43.1 ± 4.1	21.7 ± 12.9	73.3 ± 26.0
Without salmon	333 ± 64	41.1 ± 9.2	30.5 ± 21.8	79.6 ± 20.9

differ between sites with and without salmon at either Griffin Creek or Kennedy Creek. Overstory cover was comparable at sites with and without salmon in each watershed. Therefore, it is unlikely that the differences in shrub and understory characteristics between sites with and without salmon were due to differences in light levels.

The $\delta^{15}N$ values in salmon muscle tissue samples taken from carcasses at the Kennedy and Griffin Creek sites were much higher than those observed in the salmonberry foliage samples collected from these sites. Chum salmon at Kennedy Creek exhibited an average $\delta^{15}N$ of 12.6‰ (SE = 0.36; $n = 20$), and the average $\delta^{15}N$ for coho salmon at Griffin Creek was 14.1‰ (SE = 0.43; $n = 17$). The $\delta^{15}N$ in vegetation samples ranged from about −5.0‰ to 4.0‰ (Figure 2). Therefore, incorporation of salmon-derived N by riparian vegetation should result in elevated $\delta^{15}N$ levels.

The N stable isotope ratios in salmonberry foliage at the Kennedy and Griffin Creek sites both with and without salmon decreased significantly with distance from the channel (Figure 2). Stable isotope ratios did not vary by riparian landform type. At the Griffin Creek sites without salmon, $\delta^{15}N$ values decreased from about −1.0‰ at the channel edge to −4.0‰ 100 m from the stream. The $\delta^{15}N$ values at the Kennedy Creek sites without salmon declined from −1.0‰ at the channel margin to −2.5‰ at 100 m.

At Griffin Creek, there was no significant difference in $\delta^{15}N$ values in salmonberry foliage between sites with and without salmon (Figure 2). At Kennedy Creek, however, salmonberry at sites with salmon exhibited a $\delta^{15}N$ value significantly greater than that at sites without salmon at all distances from the channel. The difference in $\delta^{15}N$ between sites with and without salmon at Kennedy Creek decreased with distance from the channel, from 2.8‰ at the channel edge to 0.8‰ at 100 m.

The difference in stable isotope values in salmonberry leaves between sites with and without salmon at Kennedy Creek suggests that salmon provide about 22% of the N in salmonberry leaves at the edge of the channel (Figure 3). This proportion declines with distance from the stream. The differences in $\delta^{15}N$ values between sites with and without salmon at 100 m from the channel were statistically significant but small. Small differences in the rates of N isotopic fractionation between sites with and without salmon could have contributed to or caused this difference. If salmon-derived N caused the differences in $\delta^{15}N$ values at 100 m, the fish would have accounted for only about 4% of the N in the foliage. Thus the majority of salmon-derived N at this site appears to be distributed relatively close to the channel.

The total N and P in salmonberry foliage did not exhibit a significant relationship with distance from the channel or riparian landform at either Griffin Creek or Kennedy Creek. At both creeks, the average N and P content of salmonberry leaves was significantly greater at sites with salmon than at sites without salmon (Table 4).

The N content in salmonberry leaves increased with increasing $\delta^{15}N$ values at the Kennedy Creek sites with salmon, but no relationship was found at the reference sites (Figure 4). There was no relationship between $\delta^{15}N$ values and N content in foliage samples at the Griffin Creek sites.

Average shrub cover at the Griffin Creek sites was more than 30% higher along streams with salmon than without, a significant difference (Table 5). There were no differences between sites with and without salmon in the average number of shrub species per transect at the Griffin Creek sites. Shrub cover at the Kennedy Creek sites with and without salmon was nearly identical (Table 5). However, shrub species richness was significantly

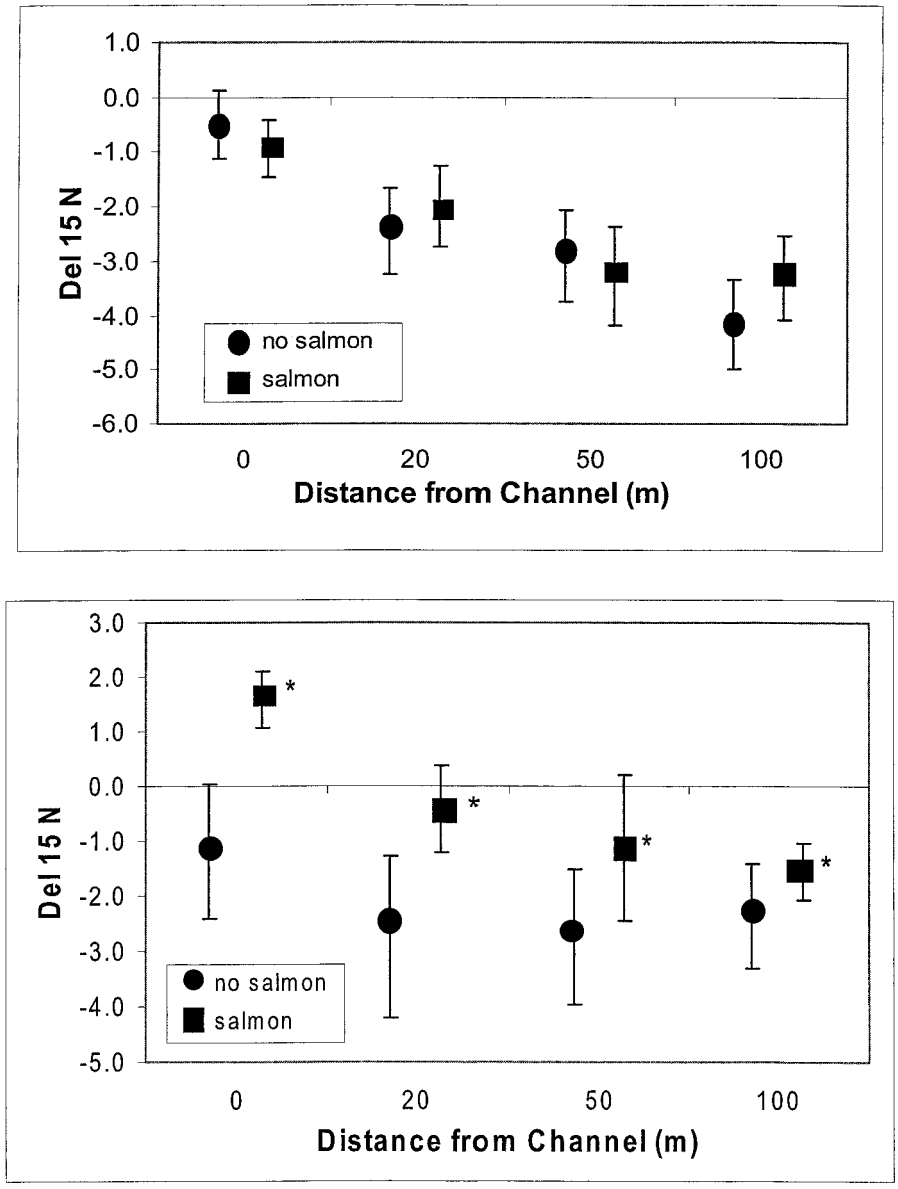

FIGURE 2.—Values of $\delta^{15}N$ at sites with and without salmon at Griffin Creek (upper panel) and Kennedy Creek (lower panel) by distance from the channel. Values are shown ± 1 SE. Instances in which a site with salmon is significantly ($P \leq 0.05$) different from the corresponding site without salmon are indicated by asterisks. The numbers of samples represented by the different points are as follows: Griffin Creek without salmon: 0 m (32), 20 m (32), 50 m (26), and 100 m (28); Griffin Creek with salmon: 0 m (32), 20 m (28), 50 m (28), and 100 m (28); Kennedy Creek without salmon: 0 m (22), 20 m (22), 50 m (20), and 100 m (20); Kennedy Creek with salmon: 0 m (22), 20 m (22), 50 m (18), and 100 m (22).

greater at Kennedy Creek sites with salmon than at sites without salmon (Table 5).

Understory vegetation cover, species richness, and plant density were not influenced significantly by distance from the channel or riparian landform. However, all understory variables differed between sites with and without salmon at Griffin Creek (Table 6). Total cover was 15% greater and species richness and plant density were greater at sites with salmon at Griffin Creek. Total under-

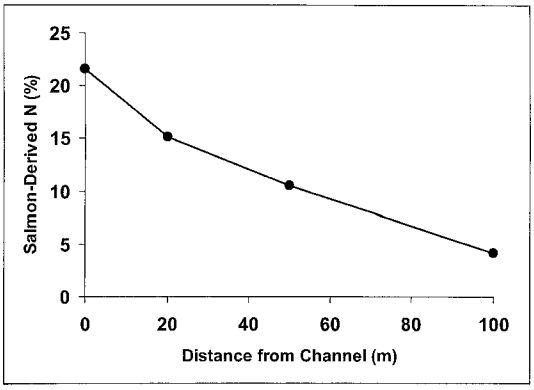

FIGURE 3.—The proportion of salmon-derived N in salmonberry foliage at Kennedy Creek by distance from the channel.

story cover was not significantly different between sites with and without salmon at Kennedy Creek. However, species richness and plant density were significantly higher at riparian sites bordering salmon-bearing stream reaches.

TABLE 4.—Concentration (% dry weight) of N and P in salmonberry leaves at study sites. Values presented are averages ± 1 SE; sample sizes are given in parentheses. Asterisks indicate significant differences between sites with and without salmon (*t*-test; $P \leq 0.05$).

Site	N	P
Griffin Creek		
With salmon	2.58 ± 0.34 (58)*	0.20 ± 0.05 (58)*
Without salmon	2.23 ± 0.39 (57)*	0.15 ± 0.03 (57)*
Kennedy Creek		
With salmon	2.31 ± 0.28 (40)*	0.22 ± 0.08 (44)*
Without salmon	2.10 ± 0.26 (34)*	0.14 ± 0.02 (42)*

Discussion

Factors other than contributions of N from spawning salmon can cause elevation in $\delta^{15}N$ values in riparian vegetation. This fact is illustrated by the decline in $\delta^{15}N$ with distance from the channel edge at all sites at Griffin and Kennedy creeks, including sites without spawning salmon (Figure 2). Denitrification near the channel likely contributed to this pattern. Because this process utilizes

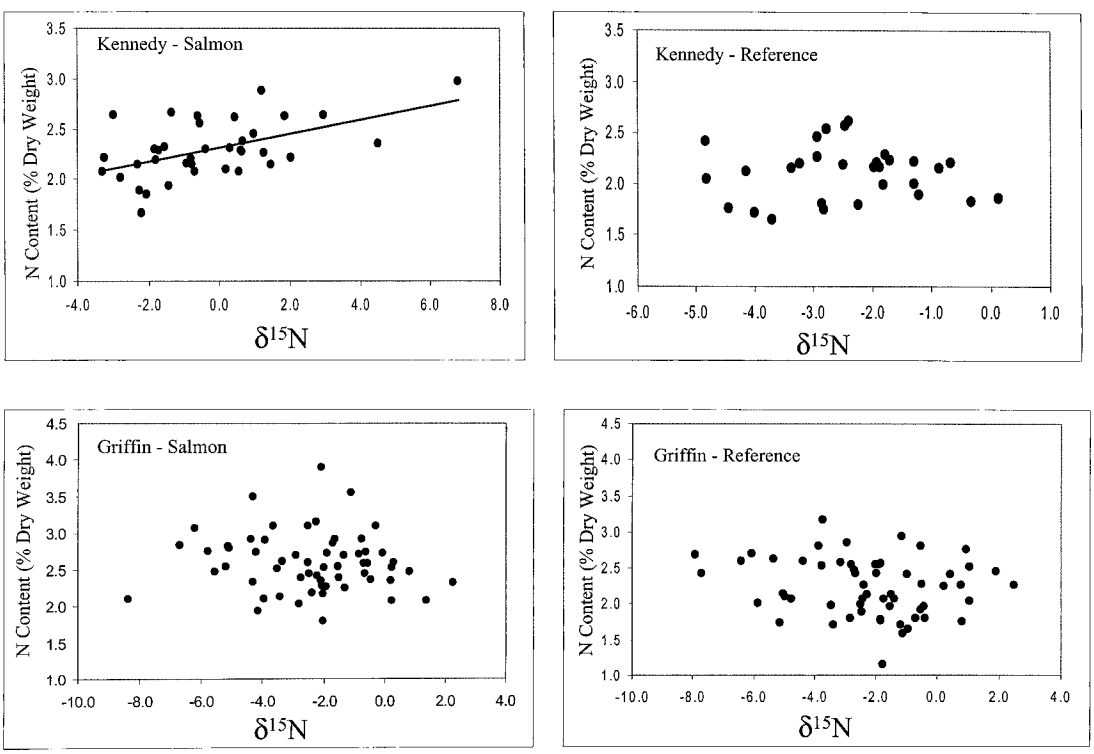

FIGURE 4.—Relationships between nitrogen concentrations and $\delta^{15}N$ values in salmonberry foliage at Griffin Creek and Kennedy Creek sites with and without salmon. The estimated equation for Kennedy Creek sites with salmon was as follows: $y = 0.079x + 2.28$ ($R^2 = 0.28$; $P \leq 0.05$); no significant relationships were found for the other locations.

TABLE 5.—Comparison of shrub community characteristics at the study sites. Shrubs were defined as plants between 1 and 3 m tall. Values are averages for all transects (16 each for the Griffin Creek values and 12 each for the Kennedy Creek values) ± 1 SE. Canopy cover was measured above each understory sample plot. Asterisks indicate significant differences between sites with and without salmon (*t*-test; $P \leq 0.05$).

Site	% cover by shrubs	Shrub species per transect
Griffin Creek		
With salmon	78.4 ± 21.6*	9.3 ± 2.8
Without salmon	46.2 ± 29.2*	7.9 ± 3.3
Kennedy Creek		
With salmon	71.8 ± 32.3	11.8 ± 2.5*
Without salmon	74.2 ± 19.1	9.5 ± 2.3*

^{14}N more readily than ^{15}N (Delwiche and Steyn 1970), denitrification may elevate $\delta^{15}N$ values in riparian soils. Denitrification rates increase under water-saturated, low-oxygen conditions, which are common at locations immediately adjacent to streams, especially those with riparian area of low relief, as was the case at our sites. Thus, dentrification likely contributes to the pattern of declining $\delta^{15}N$ in salmonberry foliage with distance from the channel edge irrespective of the presence of salmon carcasses. The lack of a relationship between landform and $\delta^{15}N$ suggests that proximity to the channel has a greater influence on stable isotope ratios than landform.

By using paired locations with and without salmon, we were able to separate the influence of salmon on the $\delta^{15}N$ value of salmonberry foliage from enrichment associated with other causes. This approach to accounting for nonsalmon effects on the degree of ^{15}N in the foliage of riparian plants has been taken in other studies (Helfield and Naiman 2001) and is a common way to examine the contributions of nutrients from spawning salmon to aquatic systems (Kline et al. 1990; Bilby et al. 1996). The N stable isotope values in the salmonberry foliage samples collected at Kennedy Creek suggest that small amounts of salmon-derived N were distributed as far as 100 m upslope from the channel. The proportion of salmon-derived N in riparian plant tissues declined with increasing distance from the channel, as indicated by the decreasing difference in $\delta^{15}N$ between sites with and without salmon at progressively greater distances from the channel (Figure 2). Griffin Creek did not exhibit a difference in $\delta^{15}N$ between sites with and without salmon at any distance from the channel. Thus, we found no evidence that salmon were providing N to the riparian plants in that watershed. The lack of response is likely due to the small amount of salmon carcass tissue deposited at the Griffin Creek sites compared with that at Kennedy Creek (Table 2); the biomass of salmon carcasses deposited at the Griffin Creek sites in 1996 was less than 1% of that of carcasses deposited at Kennedy Creek.

The elevated levels of N and P in salmonberry foliage at the Kennedy Creek sites with salmon suggest that salmon may be contributing enough nutrients to those sites to influence its availability to the plants (Table 4). This point is supported by the observation that salmon-derived N comprised 22% of the N in the salmonberry leaves at the edge of the channel at Kennedy Creek (Figure 3). In addition, the relationship between N content in the foliage and the $\delta^{15}N$ values at the Kennedy Creek sites with salmon (Figure 4) also suggests that the salmon are influencing N availability. The elevated nutrient content in the foliage along stream reaches supporting large salmon populations may have ecological consequences beyond its direct influence on the plants. Higher nutrient concentration in the foliage of riparian plants and the litter they produce enhances the nutritional quality of this material for terrestrial herbivores (Oh et al. 1970) and aquatic invertebrates (Triska and Buckley 1978).

TABLE 6.—Characteristics of the understory vegetation at the sampled sites. Values are averages for all plots ± 1 SE; sample sizes are given in parentheses. Asterisks indicate significant differences between sites with and without salmon (*t*-test; $P \leq 0.05$).

Site	Cover (%/plot)	Species richness (species/plot)	Density (plants/plot)
Griffin Creek			
With salmon	40.5 ± 2.5 (176)*	4.2 ± 0.8 (176)*	18.1 ± 3.1 (176)*
Without salmon	25.0 ± 4.1 (176)*	3.3 ± 1.0 (176)*	10.5 ± 3.4 (176)*
Kennedy Creek			
With salmon	50.7 ± 5.4 (132)	4.8 ± 0.9 (132)*	18.5 ± 3.2 (132)*
Without salmon	55.1 ± 5.0 (131)	4.1 ± 0.9 (131)*	14.0 ± 3.1 (131)*

We did not observe a decline in the N and P content of salmonberry foliage with distance from the channel at Kennedy Creek, despite stable isotope evidence of higher contributions from salmon closer to the channel. Higher levels of denitrification (which could affect N levels) and leaching (which could affect both N and P levels) nearer the channel may explain this pattern in nutrient concentration.

We also found significant differences in the N and P concentrations in salmonberry leaves between the Griffin Creek sites with and without salmon, despite the lack of isotopic evidence indicating a substantial N contribution from the fish. In fact, the N levels in leaves were higher at the Griffin Creek sites with salmon than at the Kennedy Creek sites with salmon (Table 4; *t*-test; $P \leq 0.05$). The reason for the difference in nutrient content between Griffin Creek sites with and without salmon could not be determined from our data. As we saw no difference in $\delta^{15}N$ values, there is no evidence that salmon caused the difference. However, it is possible that the salmon are contributing to elevated N levels at the Griffin Creek sites but that it is not reflected in the isotope values. Plants do not discriminate between the heavy and light isotopes of N when N is in limited supply (Peterson and Fry 1987). However, when N is not limiting, the lighter isotope is taken up preferentially. Therefore, the lack of elevated $\delta^{15}N$ values at Griffin Creek sites with salmon may have been an artifact of the high N availability at these sites (Table 4). If this were the case, salmon could be contributing N to riparian vegetation but the stable isotope signature of this contribution would be masked. However, we have no evidence that this was in fact occurring at Griffin Creek.

Numerous interacting mechanisms are responsible for the distribution of marine-derived nutrients into riparian ecosystems (Gende et al. 2002). Ben-David et al. (1998) identified three pathways by which nutrients from salmon carcasses may be transported into the terrestrial environment. First, freshets may deposit carcasses in riparian areas, where they decompose and the released nutrients become available to plants (Cederholm et al. 1989). Overbank floods are common during the period (November–January) when salmon carcasses are present at Griffin and Kennedy creeks. We observed numerous carcasses along the edge of stream channels and in riparian vegetation following high flows. Second, nutrients released from decomposing carcasses in the stream water may be transported into the hyporheic zone beneath the riparian area and become available to terrestrial vegetation where the roots of the plants extend into this zone (Triska et al. 1989). Floodplain and low-terrace landforms are common along streams in both watersheds, accounting for more than 50% of the area sampled at our sites (Table 1). These landforms were less than 3 m above the bank-full channel level, and the roots of riparian vegetation could easily have extended into the hyporheic zone at these locations. Third, piscivorous predators and scavengers may remove salmon from the stream and carry them into the riparian area, where they are consumed or cached for later use (Ben-David et al. 1997a, 1997b). Cederholm et al. (1989) found that 40% of the coho salmon carcasses in several small Olympic Peninsula streams were removed from the water by scavengers. Many of these carcasses were partially consumed, with the remainder being deposited in the riparian area. Elimination of waste products by animals eating the carcasses can further distribute salmon-derived nutrients to the forest. Although we did not quantify wildlife use at our study sites, there were clear indications (e.g., feces, tracks, and partially consumed carcasses) of numerous species at the sites with salmon, including gulls *Larus* spp., bald eagle *Haliaeetus leucocephalus*, black bear *Ursus americanus*, raccoon *Procyon lotor*, coyote *Canis latrans*, and cougar *Felis concolor*. An additional mechanism of transport is litterfall, which can progressively move salmon-derived nutrients incorporated by riparian plants upslope. We believe that all of these pathways contributed to the transport of salmon-derived nutrients from the stream to riparian plants at the Kennedy Creek sites.

We did observe differences in shrub and understory vegetation between sites with and without salmon, including greater cover, species diversity, and plant density at sites with salmon. Overstory cover was similar at transects with and without salmon in both watersheds (Table 3), so light levels were not responsible for the observed differences in the understory and shrub community. Interactions between frequency of disturbance and productivity have been found to be the primary determinants of riparian plant diversity in southeast Alaska (Pollock et al. 1998), with the highest diversity occurring at intermediate levels of productivity and disturbance. Thus, a moderate increase in productivity caused by the nutrients provided by salmon could have contributed to the increase in shrub and understory species diversity that we observed. Total N and P levels were higher at sites with salmon than without in both watersheds (Ta-

ble 4), and an increase in the productivity of riparian trees has been associated with spawning salmon (Helfield and Naiman 2001). Thus, it is possible that elevated nutrient availability contributed to the observed differences in vegetation. However, any effect of elevated nutrient levels on the plant community can be attributed to salmon only at the Kennedy Creek sites.

Another factor that may have influenced understory and shrub characteristics was a greater abundance of wildlife at the salmon sites, although this was not quantified. As indicated above, scavengers distribute nutrients from the salmon by carrying carcasses into the riparian forest to consume them and by depositing urine and feces containing salmon-derived nutrients. The animals may have trampled or otherwise disturbed understory vegetation and shrubs in the process. An increased level of disturbance could have provided enhanced conditions for seedling establishment, thus contributing to the increased number of species and higher density of individual plants observed at sites with salmon. In Olympic National Park, the disturbance of riparian vegetation by ungulates has been associated with greater understory plant diversity (Woodward et al. 1994). Disturbance by wildlife could have influenced riparian vegetation at both of our study sites, as the scavenging of carcasses was observed at both.

Our results suggest that a significant amount of nutrients may be transported from salmon to riparian areas at sites where salmon spawn at very high densities. Previous work in Alaska also has demonstrated this point (Ben-David et al. 1998; Helfield and Naiman 2001). However, we did not find any clear evidence that a significant amount of salmon-derived N was transported into riparian areas along stream reaches supporting only coho salmon. Because coho salmon tend to spawn at lower densities than mass-spawning species like chum, pink, or sockeye salmon, their contribution may not be as ecologically important to terrestrial ecosystems. However, there may be locations in watersheds supporting coho salmon at which a significant amount of nutrient transfer to riparian systems occurs, such as sites where the stream flow concentrates a large number of carcasses. Our Kennedy Creek results indicate that vegetation bordering stream reaches supporting large numbers of chum salmon receives a contribution of nutrients from the fish.

We also saw an indication that increased nutrient levels, possibly coupled with increased wildlife use, alter the characteristics of the riparian plant community. Nutrients contributed by spawning salmon have been related to increased tree growth (Helfield and Naiman 2001) and alterations of understory plant communities (Bartz 2001) in Alaska. Restoration of riparian vegetation is an important element of the effort to restore productive aquatic ecosystems in the Pacific Northwest (National Research Council 1996). The potential effect of marine-derived nutrients on the vegetation in riparian areas along sites supporting large populations of spawning fish is not usually considered in riparian restoration projects. Over the last several years sufficient evidence has been amassed to suggest that this component of riparian system function should be considered when designing projects to restore riparian systems. In some cases, fertilizer applications to mitigate for the loss of salmon-derived nutrients have been suggested. However, the vegetation at a given site may or may not respond to the application of nutrients, depending on the initial nutrient status of the site. Fertilization of riparian areas should be conducted only at locations where nutrients have been demonstrated to limit plant growth. Even in cases where this approach appears warranted, field experiments are required to determine appropriate application levels and evaluate the impacts on water quality. However, fertilizer applications cannot replace all the ecological services provided by spawning salmon. The contribution of salmon-derived nutrients to riparian areas and the importance of spawning salmon to aquatic ecosystems (Kline et al. 1990; Bilby et al. 1996; Johnston et al. 1997) and wildlife (Cederholm et al. 1989; Ben-David et al. 1997a, 1997b) indicate that the ecological role salmon play in watersheds should be considered in formulating salmon management policies.

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