

Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity

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Spawning Pacific salmon (*Onchorhynchus*) transport marine-derived nutrients into streams and rivers. Subsequently, these marine-derived nutrients are incorporated into freshwater and terrestrial food webs through decomposition and predation. In this study, we investigated the influence of spawning Pacific salmon on terrestrial vegetation using stable isotope analysis. We hypothesized that terrestrial vegetation near streams or in areas with activity of piscivorous predators will show higher $\delta^{15}\text{N}$ values compared with the same species growing elsewhere. The influence of spawning Pacific salmon as observed in elevated $\delta^{15}\text{N}$ in terrestrial consumers was also investigated. Data collected from five species of plants in 18 transects from the stream to the upland forest (0 to 1000 m) indicated that a significant decrease in $\delta^{15}\text{N}$ values occurred with increase in distance and relative elevation from the stream in three of the five plant species sampled. Values of $\delta^{15}\text{N}$ in plants at sites actively used by piscivorous predators were higher than those of the same plants growing elsewhere, and similar to values measured near the stream. A decrease in values of $\delta^{15}\text{N}$ and increase in values of $\delta^{13}\text{C}$ in muscles of small mammals, with increase in distance from the stream, indicated that this signature was not a result of direct consumption of salmon carcasses but rather an indirect assimilation of marine-derived nitrogen through terrestrial vegetation. These results indicate that salmon carcasses contribute to the nitrogen pool available to riparian vegetation. The spatial distribution of the marine-derived nitrogen is apparently determined by flooding and the activity patterns of piscivorous predators. The importance of these nitrogen additions to the riparian zone, however, will depend on whether nitrogen is a limiting factor to plant growth in this system, and requires further investigation.

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Spawning Pacific salmon (*Onchorhynchus*) transport marine-derived nutrients into streams and rivers through migration to their natal spawning grounds. Subsequently, a large fraction of these marine-derived nutrients is incorporated into freshwater and terrestrial food webs through decomposition and predation (Richey et al. 1975, Cederholm et al. 1989, Kline et al. 1989, 1993, Piorkowski 1995, Ben-David et al. 1997a, b). This flux of nutrients can have a significant contri-

bution to the freshwater ecosystem. Several studies have demonstrated increased concentrations of dissolved organic nitrogen and NH_4^+ , increase in phosphorus concentrations, elevated autotrophic production as well as increase in heterotrophic activity in salmon streams and lakes, compared with those lacking salmon in the same geographic areas (Donaldson 1967, Brickell and Goering 1970, Richey et al. 1975, Mathisen et al. 1988, Kline et al. 1989, 1993, Piorkowski 1995, Bilby et

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al. 1996). Similarly, spawning Pacific salmon have affected the community structure of stream macroinvertebrates, as well as growth rate and production of freshwater fish (Kline et al. 1989, 1993, Piorkowski 1995, Bilby et al. 1996).

Carbon and nitrogen are key elements in nature, and the stable isotope ratios $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ (expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are widely used as natural tracers in ecosystem studies (Ehleringer and Rundel 1988). Recent investigations of food webs have demonstrated that stable isotope ratios of carbon and nitrogen are correlated with trophic level and can provide dietary information when tissues of consumer and food are compared (Schoeninger and DeNiro 1984, Fry and Sherr 1988, Schell et al. 1988, Gearing 1991, Hobson and Montevecchi 1991). Spawning Pacific salmon contain higher proportions of the heavier carbon and nitrogen isotopes ($\delta^{13}\text{C} = -18.65\text{‰} \pm 0.18$ (mean \pm SE) and $\delta^{15}\text{N} = 13.01\text{‰} \pm 0.13$; Ben-David et al. 1997a) than most temperate terrestrial plants, thus providing a natural marker to the transfer of nutrients from the carcasses to the terrestrial system (Kline et al. 1989, 1993, Piorkowski 1995, Bilby et al. 1996, Ben-David et al. 1997a, b, 1998). Studies using stable isotope analysis have shown that biota in streams and lakes had significantly higher $\delta^{15}\text{N}$ values compared with the same species in streams and lakes without salmon (Kline et al. 1989, 1993, Piorkowski 1995, Bilby et al. 1996). Similarly, terrestrial and semi-aquatic predators such as brown bears (*Ursus arctos*), river otters (*Lutra canadensis*), mink (*Mustela vison*), and marten (*Martes americana*) inhabiting areas with salmon streams show seasonal and annual changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in response to the availability of salmon (Hilderbrand et al. 1996, Ben-David et al. 1997a, 1998). For example, stable isotope analysis revealed that in years of low abundance of small mammals, salmon carcasses constituted about 30% of the diet of martens in southeast Alaska (Ben-David et al. 1997b).

Bilby et al. (1996) reported a significant contribution of marine-derived nitrogen to riparian foliage along salmon streams compared with streams lacking salmon. Three potential pathways exist for the transfer of marine-derived nitrogen from streams to the riparian vegetation: (1) During flush-floods, which are characteristic to flooding in the Pacific Northwest coast (Cederholm et al. 1989, Pollock 1995), spawned carcasses are deposited on stream banks. These decomposing carcasses can then act as fertilizers to the riparian vegetation. (2) Dissolved organic and inorganic nitrogen from the stream filter into the ground water (hyporheic zone) and thus can be taken up by riparian vegetation (Lowrence et al. 1984, Peterjohn and Correll 1984, Triska et al. 1989, Valett et al. 1990). (3) Terrestrial and semi-aquatic predators such as brown bears, black bears (*U. americanus*), bald eagles (*Haliaeetus leucocephalus*), river otters, mink and marten carry

carcasses into the riparian forest (Cederholm et al. 1989, Ben-David et al. 1997a, b), where many carcasses are cached, for example under large trees. In addition, these animals may travel long distances upland, after consuming salmon, and deposit their feces away from the streams.

In this study, we investigated the influence of spawning Pacific salmon on terrestrial vegetation using stable isotope analysis. In particular, we were interested in establishing the distance in which fertilization by salmon can be detected in relation to flooding and the activity of piscivorous predators. We hypothesized that terrestrial vegetation will show higher $\delta^{15}\text{N}$ values in the frequently flooded areas near salmon streams compared with the same species growing away from streams. We also hypothesized that plants growing away from streams, but in close proximity to sites with activity of piscivorous predators will have higher $\delta^{15}\text{N}$ values than those growing in areas with little or no predator activity. In addition, the transfer of marine-derived nutrients originating from spawning Pacific salmon to primary consumers in the terrestrial system was also tested using stable isotope analysis.

Methods

Study area

Our study area was located on Chichagof Island in southeast Alaska, USA (Tenakee Springs at $57^{\circ}52' \text{N}$, $135^{\circ} 18' \text{W}$; Fig. 1). The island, one of the three large

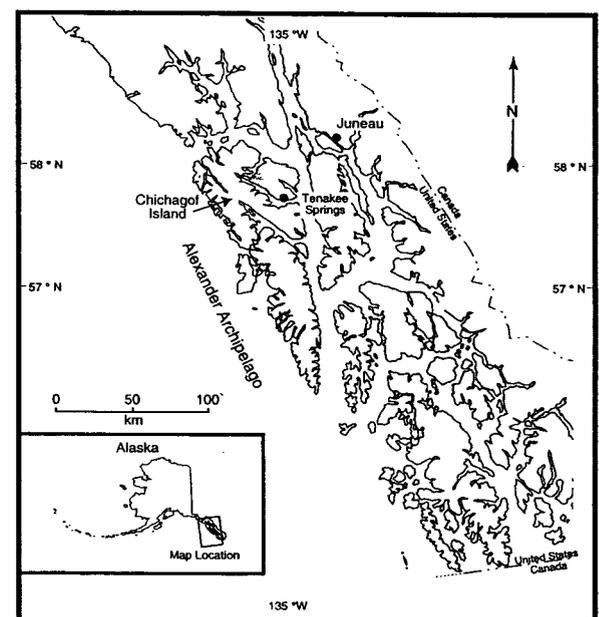


Fig. 1. Location of study area (shaded) on Chichagof Island, southeast Alaska, USA.

Table 1. Definitions for sites with activity of piscivorous predators observed during late summer 1993 and 1994 on Chichagof Island, southeast Alaska.

Activity	Definition
Brown bear	Accumulation of ≥ 5 feces within the 10-m radius of site
Bald eagle	Excreta cover of at least half of the 10-m radius of site
River otter	Accumulation of ≥ 10 feces within the 10-m radius of site
Other	At least 2 salmon carcasses showing evidence of consumption

northern islands of the Alexander Archipelago, is part of the Tongass National Forest. The archipelago has a maritime climate; summers are cool and wet, and winters are characterized by deep snow (236 cm annual precipitation). The snow-free period extends from early May to late November at lower elevations. Vegetation at higher elevations is typically alpine tundra, and in lower elevations coastal, old-growth forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with well-developed understory (mainly *Oplopanax horridus*, *Vaccinium* spp., *Menziesia ferruginea*, and *Rubus* spp.). The study area encompasses six streams (Kadashan, Tonalite, West Kadashan, Indian River, Trap Creek, and Salt Lake Creek) that support an annual run of approximately 800,000 spawning Pacific salmon (*Onchorhynchus gorbuscha*, *O. keta*, and *O. kisutch*), from early July to late November.

Sampling

Samples of berries from blueberries (*Vaccinium ovalifolium*: $n = 63$ and *V. alaskaense*: $n = 5$), salmonberries (*Rubus spectabilis*), and devil's club (*Oplopanax horridus*), and seeds of Sitka spruce and skunk cabbage (*Lysichitum americanum*) were collected from 18 transects extending from the river to the upland forest in July 1993 and July 1994. Transects were 1000 m long and were set perpendicular to the stream using a compass. The start point of each transect along the stream was selected at random and sampling stations were set at 0, 50, 100, 200, 300, 400, 500 and 1000 m away from the stream. At each station, the berries and seeds of the five species of plants were collected within 10 m radius, the absence/presence of sign of predator activity (Table 1) was recorded, and relative elevation above the stream was calculated using an inclinometer. Where elevations above the stream were between 0 and 1 m we arbitrarily assigned these stations a value of 1 m. Because spruce and salmonberry were in low abundance at 1000 m, additional samples of berries and seeds were collected at five other random locations at

distances ≥ 1000 m from the streams. Relative elevations for these samples was determined from a digital elevation model (GIS) obtained from the USDA Forest Service, Tongass National Forest. Isotope analysis of these samples indicated that values for these plants did not significantly differ from those obtained in our 1000-m transect stations (Mann-Whitney, $P = 0.8$). Therefore, we pooled the data from the five random locations with the transect data and present it in the 1000-m category. Similarly, because no significant difference (Mann-Whitney, $P = 0.9$) was detected between the samples of *Vaccinium ovalifolium* ($n = 63$) and *V. alaskaense* ($n = 5$) collected at stations of the same distance, we combined data for these plants and termed them *Vaccinium* spp. in further discussions.

Muscle samples from Keen's deer mice (*Peromyscus keeni*), long-tailed voles (*Microtus longicaudas*), common shrews (*Sorex cinereus*), and red squirrels (*Tamiasciurus hudsonicus*), were collected for stable isotope analysis, from small rodents trapped in two companion studies by R. W. Flynn (ADFG, Wildlife Conservation, Douglas, Alaska) and T. A. Hanley (for details see Ben-David et al. 1997b). The remainder of each carcass was prepared as a museum specimen (including frozen tissues) and archived at the Univ. of Alaska Museum. All methods used in this study were approved by an independent Animal Care and Use Committee at the Univ. of Alaska Fairbanks.

Analysis of stable isotope ratios

Samples of muscle tissues and vegetation samples were kept frozen until preparation for determination of stable isotope ratios. Samples were dried at 60° to 70°C for 48 h and then ground to fine powder using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, IL). Subsequently, a subsample (1–1.5 mg for animal tissues and 8–10 mg for plant tissues) was weighed into a miniature tin cup (4 by 6 mm) for combustion. We used a Europa C/N continuous flow isotope ratio mass spectrometer (CFIRMS) to obtain the stable isotope ratios, as well as values of percent carbon (%C) and nitrogen (%N). Each sample was analyzed in duplicate and results were accepted only if the variance between the duplicates did not exceed that of the peptone standard ($\delta^{13}\text{C}_{\text{std}} = -15.8$, $\delta^{15}\text{N}_{\text{std}} = 7.0$, $\text{CV} = 0.1$).

Statistical analysis

To test our hypothesis that plants growing in the vicinity of streams will show higher values of $\delta^{15}\text{N}$, and due to small sample sizes, we used a Kruskal-Wallis test with multiple comparisons (Zar 1984; SPSS for Windows), with distance from stream as the grouping variable. Similarly, we used a Kruskal-Wallis test with

multiple comparisons to investigate the effects of distance from streams on values of $\delta^{13}\text{C}$, %C and %N in the plant samples. To test whether relative elevation had an effect on $\delta^{15}\text{N}$ values of plants, in those cases in which distance had a significant effect, we used Spearman rank correlation analysis (Zar 1984; SPSS for Windows) between the isotope values and relative elevation. We used a Mann-Whitney test (Zar 1984; SPSS for Windows) to explore the hypothesis that plants growing in close proximity to sites with activity of piscivorous predators will have higher $\delta^{15}\text{N}$ values than those growing in areas with little or no predator activity at each station. To test our hypothesis that primary consumers trapped in the vicinity of streams will show higher values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, we used a Kruskal-Wallis test with multiple comparisons (Zar 1984; SPSS for Windows) with distance from stream as the grouping variable.

Results and discussion

Elevation and flooding

Relative elevation increased with distance from the river in an exponential fashion in all transects. Variation in elevation increased with distance as a result of the differences in microtopographic characteristics at each transect (Figs 2–6). The relation between distance and elevation was similar for all species, except that elevation of stations in which blueberries were collected increased within the first 50 m of the river, while those of skunk cabbage did not significantly increase in elevation until 500–1000 m distance from the river. Blueberries are characteristic of elevated well drained microsites, whereas skunk cabbage tends to grow in low, wet microsites (Klinka et al. 1989).

Pollock (1995) studied relations between flooding and plant community composition, in our study area, concurrent with our field work. He found that areas < 1.5 m higher than the stream channel flood frequently, 6–12 times per year, while areas > 1.5 m higher than the channel flood only infrequently, 1–2 times per year. Pollock (1995) also found that floods of the stream bank were short in duration, usually lasting less than 48 h. Therefore, our transect stations at < 50 m distance were subject to frequent flooding, while those at ≥ 50 m distance and beyond flooded only infrequently (except in the case of skunk cabbage, which tends to grow in the microtopographic depressions and back channels). Flooding was most frequent in fall (Pollock 1995), which coincides with the later salmon runs and follows the peak salmon biomass in our study area. Cederholm et al. (1989) found that 10 of 25 radiotagged salmon were deposited as carcasses on the floodplain of their study area in Washington State. While most salmon carcasses in our study area occurred in or

near the stream channel, a large number were deposited on the floodplain as well. We counted > 100 salmon carcasses at distances > 20 m from the river following a flood in October 1993 while checking mink and marten traplines in our study area (7 km along the Kadashan and Tonalite rivers; Ben-David et al. 1997a, b); the corresponding number of carcasses at distances < 20 m, though, was at least an order of magnitude greater than that.

Nitrogen in plants

The expected pattern of $\delta^{15}\text{N}$ enrichment near the river occurred in three of the five plant species. Values of $\delta^{15}\text{N}$ for fruits of blueberries were significantly greater at 0 and 50 m than at > 50 m from the river (Kruskal-Wallis, $P < 0.001$; Fig. 2). Spruce seed $\delta^{15}\text{N}$ was more variable than that of blueberries but exhibited a similar decline with distance ($P = 0.030$; Fig. 3). Values of $\delta^{15}\text{N}$

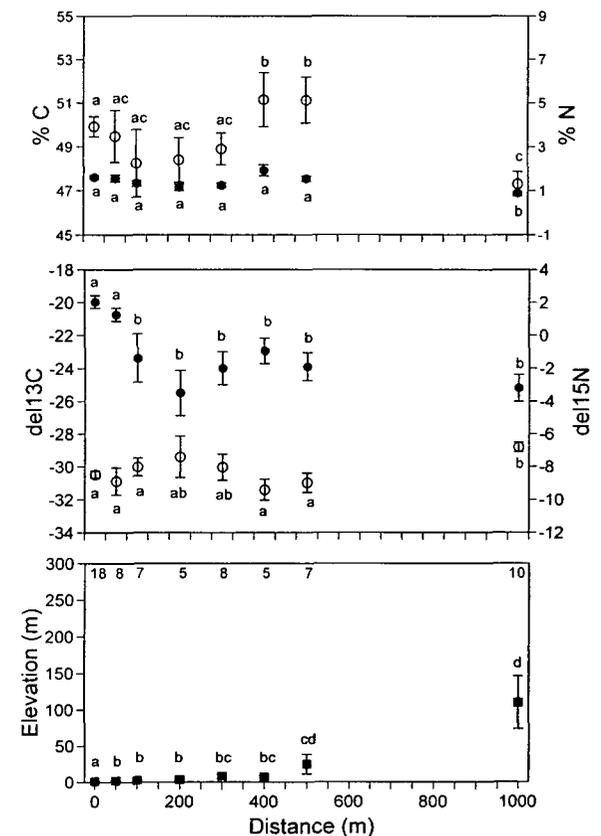


Fig. 2. Relative elevation (m), values of $\delta^{15}\text{N} \pm \text{SE}$ (\bullet), values of $\delta^{13}\text{C} \pm \text{SE}$ (\circ), %N $\pm \text{SE}$ (\bullet), and %C $\pm \text{SE}$ (\circ) plotted against distance from stream (m) for fruits of blueberries (*Vaccinium* spp.) collected from 18 transects on Chichagof Island, southeast Alaska summer 1993 and summer 1994. Letters represent statistical difference at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons). Sample sizes of stations where berries were collected are given above relative elevation.

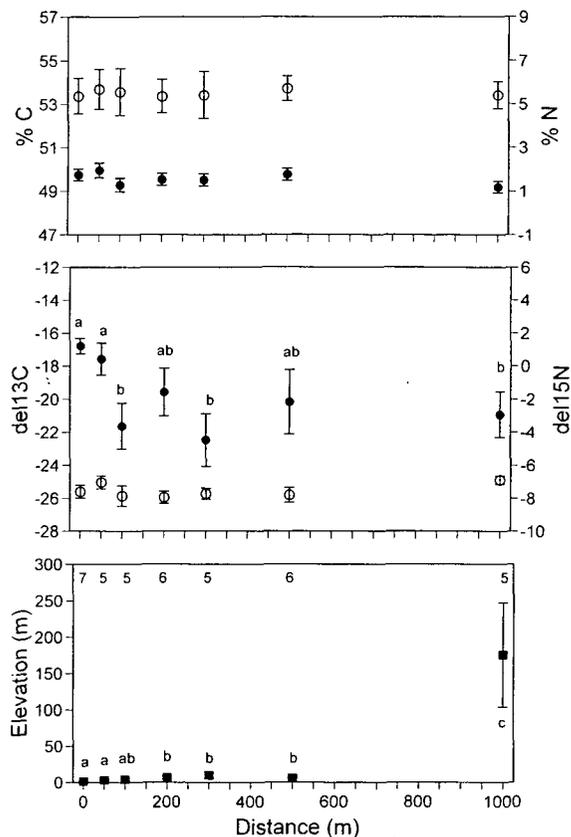


Fig. 3. Relative elevation (m), values of $\delta^{15}\text{N} \pm \text{SE}$ (●), values of $\delta^{13}\text{C} \pm \text{SE}$ (○), %N \pm SE (●), and %C \pm SE (○) plotted against distance from stream (m) for seeds of spruce (*Picea sitchensis*) collected from 18 transects on Chichagof Island, southeast Alaska summer 1993 and summer 1994. Letters represent statistical difference at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons). Sample sizes of stations where seeds were collected are given above relative elevation.

in berries of devil's club dropped significantly at distances beyond 200 m from the stream (Kruskal-Wallis; $P = 0.019$, Fig. 4). Salmonberry and skunk cabbage $\delta^{15}\text{N}$, on the other hand, exhibited no relation to distance from the river (Kruskal-Wallis; $P = 0.899$, Fig. 5; $P = 0.420$, Fig. 6, respectively). Relative elevation and $\delta^{15}\text{N}$ values were negatively correlated in blueberries, devil's club berries, and spruce seeds (Spearman's $r = -0.647$, -0.540 , and -0.480 , respectively; all $P \leq 0.002$), reflecting the positive correlation between elevation and distance from the river.

Skunk cabbage was a problematic species in two major respects: first, because it occurred in low-elevation microsites ("pits" and back-channels), we were unable to obtain much variation in elevation in relation to distance from river. Second, such microsites contain high levels of soil organic matter from decaying leaves of skunk cabbage (Klinka et al. 1989). Skunk cabbage tissues contain high levels of nitrogen (Fig. 6) and the

decaying leaves may contribute to high localized nutrient cycling and enrichment in nitrogen and $\delta^{15}\text{N}$ levels. Under such conditions soil fertilization by salmon is likely to be unimportant. In retrospect, sampling seeds from this species may have been an ill choice.

Similarly, values of $\delta^{15}\text{N}$ salmonberry exhibited no relation to distance from the river. The only explanation we can offer for this observation is that our results represent a bias due to small sample sizes. Supporting this are the $\delta^{15}\text{N}$ signatures of salmonberry at 500 m with and without predator activity (Table 2). In sites with predator activity, salmonberry $\delta^{15}\text{N}$ were enriched by about six ‰ compared with salmonberries growing in sites without predator activity. This suggests that under certain conditions of fertilization, salmonberries can take up nitrogen derived from salmon carcasses, and therefore the lack of significant difference in $\delta^{15}\text{N}$ with distance from the stream is likely a result of sampling bias.

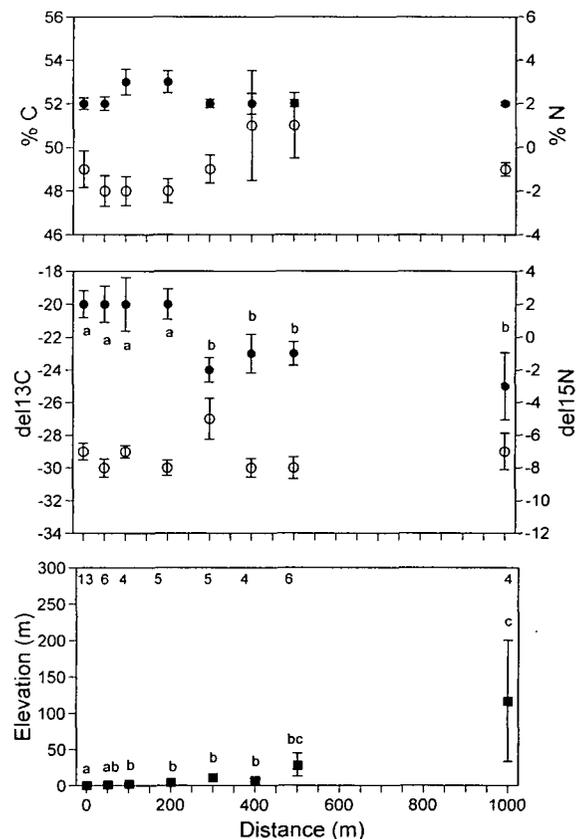


Fig. 4. Relative elevation (m), values of $\delta^{15}\text{N} \pm \text{SE}$ (●), values of $\delta^{13}\text{C} \pm \text{SE}$ (○), %N \pm SE (●), and %C \pm SE (○) plotted against distance from stream (m) for fruits of devil's club (*Oplopanax horridus*) collected from 18 transects on Chichagof Island, southeast Alaska summer 1993 and summer 1994. Letters represent statistical difference at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons). Sample sizes of stations where berries were collected are given above relative elevation.

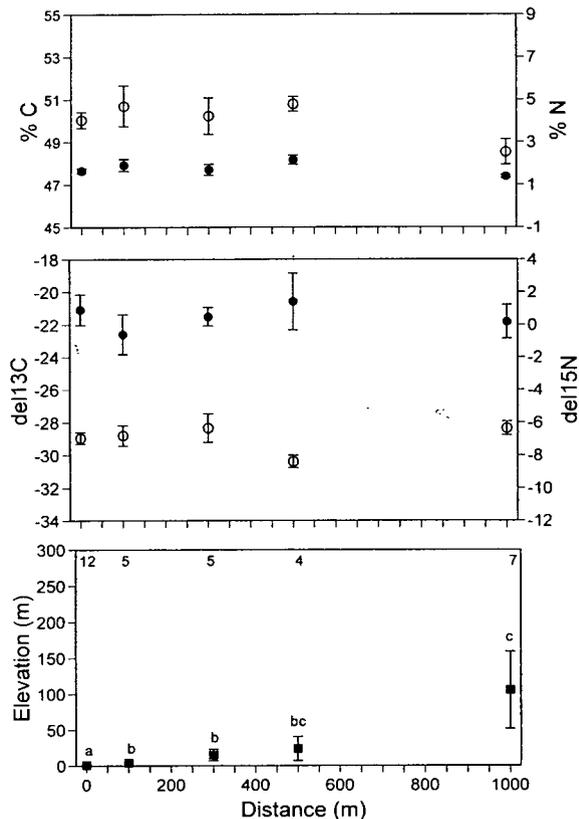


Fig. 5. Relative elevation (m), values of $\delta^{15}\text{N} \pm \text{SE}$ (●), values of $\delta^{13}\text{C} \pm \text{SE}$ (○), $\% \text{N} \pm \text{SE}$ (●), and $\% \text{C} \pm \text{SE}$ (○) plotted against distance from stream (m) for fruits of salmonberries (*Rubus spectabilis*) collected from 18 transects on Chichagof Island, southeast Alaska summer 1993 and summer 1994. Letters represent statistical difference at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons). Sample sizes of stations where berries were collected are given above relative elevation.

Values of $\delta^{15}\text{N}$ from plant samples collected in relation to activity of piscivorous predators were generally higher in active than in non-active sites for all species except skunk cabbage (Table 2). The values from sites with predator activity, regardless of distance from river, were in all cases (except skunk cabbage) similar to the values at the river edge, regardless of activity. This follows the expected pattern from nitrogen fertilization by salmon carcasses and provides evidence that fertilization by salmon carcasses occurs at the river edge. Nonetheless, other explanations for elevation in $\delta^{15}\text{N}$, such as anoxic soil conditions related to flooding (Klingsmith and Van Cleve 1993, Nadelhoffer and Fry 1994, Hogberg 1997, Hedin et al. 1998) or rooting depth (i.e. access to the hyporheic zone; Nadelhoffer and Fry 1988, Hogberg 1997) cannot be dismissed with our data. Further research into the interaction between nitrogen inputs from salmon carcasses and the effects of flooding on nitrification and denitrification processes

in soil, will enhance our understanding of these important ecosystem processes.

Only blueberries showed any significant differences in total nitrogen content as a percentage of dry weight (Kruskal-Wallis; $P = 0.052$), and that difference was small (only 0.2% less at 1000 m distance from river than from all other sites; Fig. 2). Several studies documented an increase in nitrogen contents in foliage as response to fertilization by animals (Bazley and Jefferies 1985, Iason et al. 1986, Inouye et al. 1987, Swihart 1991, Molvar et al. 1993). On the other hand, Bryant (1987) noted that fertilization had an inconsistent effect on total nitrogen concentration in shoots, suggesting that high growth rate of fertilized plants can reduce the nitrogen concentration in those tissues. Salmon carcasses may be a significant source of nitrogen added to floodplains, as each carcass contains on average 74 g of nitrogen (Mathisen et al. 1988). Nonetheless, nitrogen derived from salmon carcasses may be undetected as percent of dry matter, because growth and other allocation processes can in-

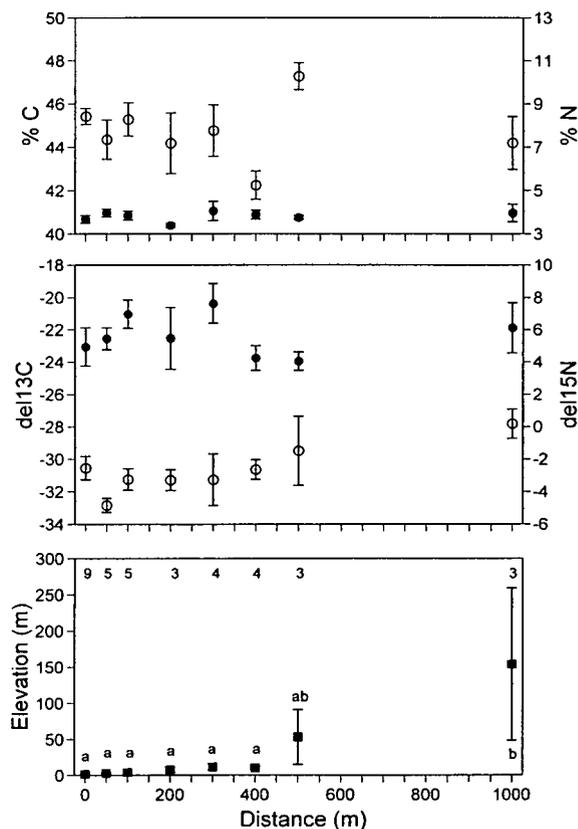


Fig. 6. Relative elevation (m), values of $\delta^{15}\text{N} \pm \text{SE}$ (●), values of $\delta^{13}\text{C} \pm \text{SE}$ (○), $\% \text{N} \pm \text{SE}$ (●), and $\% \text{C} \pm \text{SE}$ (○) plotted against distance from stream (m) for seeds of skunk cabbage (*Lysichitum americanum*) collected from 18 transects on Chichagof Island, southeast Alaska summer 1993 and summer 1994. Letters represent statistical difference at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons). Sample sizes of stations where seeds were collected are given above relative elevation.

Table 2. Values of $\delta^{15}\text{N}$ (‰) of fruits and seeds of plants from sites with and without predator activity. Samples were collected along linear transects at varying distances from the river to the upland during late summer 1993 and 1994 on Chichagof Island, southeast Alaska. Therefore, data are available only for those distances in which transects intersected sites with predator activity. Values of $\delta^{15}\text{N}$ from plants collected at sites with and without predator activity in each distance was compared using a Mann-Whitney test (Zar 1984; SPSS for Windows).

Species	Distance (m)	Without predator activity			With predator activity			Significance ($\alpha = 0.05$)
		<i>n</i>	$\delta^{15}\text{N}$	SE	<i>n</i>	$\delta^{15}\text{N}$	SE	
Blueberry	0	11	1.92	0.55	7	2.09	0.30	
	100	4	-4.31	0.58	3	2.50	1.06	*
	400	2	-2.70	0.76	3	0.23	0.25	
	500	4	-2.52	0.74	3	1.65	0.54	*
Spruce	0	3	1.70	1.10	4	0.86	0.26	
	100	2	-5.37	0.94	3	-2.47	2.15	
	500	3	-5.52	2.51	3	1.19	1.23	*
Devil's club	0	9	1.68	1.09	4	1.00	0.83	
	100	3	0.66	1.53	1	5.51	1.86	
	400	3	-1.70	1.22	1	1.55	1.86	
	500	5	-2.01	0.39	1	1.86	1.86	
Salmonberry	0	8	0.87	1.38	4	0.39	0.83	
	500	2	-1.56	0.66	2	4.37	0.39	
Skunk cabbage	0	5	6.57	1.64	4	2.91	1.18	
	100	2	7.30	1.06	3	6.74	1.48	
	400	3	4.26	1.10	1	4.19	1.48	

influence the distribution of nitrogen in certain plant tissues (Herms and Mattson 1992).

Carbon in plants

No differences in $\delta^{13}\text{C}$ were observed in relation to distance from the river for spruce seed (Kruskal-Wallis; $P = 0.357$, Fig. 3), devil's club berries ($P = 0.301$, Fig. 4), salmonberries ($P = 0.166$, Fig. 5), or skunk cabbage seed ($P = 0.116$, Fig. 6). Similarly, no differences in $\%C$ were observed in relation to distance from river for these species ($P > 0.2$). Blueberries, however, exhibited elevated $\delta^{13}\text{C}$ values at 1000 m from the river (Kruskal-Wallis; $P = 0.034$, Fig. 2), and elevated $\%C$ at 400 and 500 m distance ($P < 0.001$; Fig. 2). Nonetheless, we were unable to detect a trend in $\%C$ in relation to distance from streams (Fig. 2). The pattern of $\delta^{13}\text{C}$ follows our expectation of fertilization by salmon carcasses. Although salmon are enriched in $\delta^{13}\text{C}$ as well as $\delta^{15}\text{N}$, plants use atmospheric carbon rather than carbon derived from soil and therefore should show no relation between $\delta^{13}\text{C}$ and distance from the stream. That values of $\delta^{13}\text{C}$ increased only slightly with distance from streams or elevation indicates that plants in our study area did not suffer from significant water stress (Lajtha and Marshall 1994), which is to be expected, given the high average annual precipitation in the area. Alternatively, the increase in $\delta^{13}\text{C}$ in at 1000 m from the river may be due to lower temperature at higher altitudes. Michelsen et al. (1996) demonstrated an increase in $\delta^{13}\text{C}$ values in plants from non-warmed plots compared with those growing in warmed plots.

Isotope ratios in tissues of small mammals

Values of $\delta^{15}\text{N}$ decreased with distance from streams for deer mice (Kruskal-Wallis; $P < 0.001$), voles ($P = 0.037$), shrews ($P = 0.010$), and squirrels ($P = 0.001$; Fig. 7). Concurrently, values of $\delta^{13}\text{C}$ increased with distance from stream for deer mice (Kruskal-Wallis; $P < 0.001$), voles ($P < 0.001$), and squirrels ($P = 0.025$), but not for shrews ($P = 0.171$; Fig. 7). Because direct consumption of salmon tissues will result in enrichment in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ simultaneously, the opposing trends in the tissues of small mammals suggest that the increase in $\delta^{15}\text{N}$ close to the stream was not a result of direct consumption of salmon carcasses but rather tracking of the trend in the vegetation. Feeding trials with deer mice in our study area showed that the mice refused to feed on salmon tissues (Reese et al. 1997). The large area in which elevated values of $\delta^{15}\text{N}$ were detected in the small mammals possibly represent, the size of the foraging area of these animals. In a companion study on deer mice, we observed movements of individual animals of up to 1000 m within several-day intervals.

Conclusions

Our results are consistent with the growing body of evidence that nitrogen from salmon carcasses contributes to the nitrogen pool utilized by members of freshwater and terrestrial ecosystems (Donaldson 1967, Brickell and Goering 1970, Richey et al. 1975, Mathisen et al. 1988, Kline et al. 1989, Piorkowski 1995, Bilby et al. 1996, Ben-David et al. 1997a): We found that although nitrogen from salmon seems to be utilized by a

range of terrestrial plants (three of the five species sampled), it may not be used by all. Studies investigating salmon fertilization of terrestrial vegetation, therefore, should include a variety of plant species. We also found a gradient of fertilization, with nitrogen inputs declining with distance from the stream, as would be expected to coincide with the distribution of salmon carcasses by floods. Nonetheless, because of the confounding effects of anoxic conditions in soil due to flooding, and the effects of rooting depth, further research is needed to firmly establish the importance of fertilization of riparian vegetation by salmon carcasses. Preferably, streams with and without salmon runs should be compared and the $\delta^{15}\text{N}$ signatures of nitrogen pools of soil and ground-water should be identified. This, in turn, will elucidate the importance of each of the three potential pathways of assimilation of salmon-derived nutrients to the terrestrial vegetation (i.e., flooding, ground-water filtration, and predator activity).

Piscivorous predators may also affect the spatial distribution of fertilization by salmon carcasses away from the stream environment. These effects, however, may be limited to localized areas. Better quantification of the area affected by these predators will be useful in determining the importance of this phenomenon. We also found that nitrogen derived from salmon carcasses can be detected through the food web with all four of the small mammal species (including the insectivorous shrew) showing the same gradient in $\delta^{15}\text{N}$

with distance from the river as was found in the vegetation.

Therefore, spawning Pacific salmon appears to be an important source of nutrients and may play a significant role in the productivity of terrestrial riparian ecosystems. Where large numbers of salmon return to spawning streams each year (as in our study area), their effects on the terrestrial ecosystem may be quite large. The magnitude of such effects, and their actual importance, however, remains uncertain. Understanding the limiting nature of nutrients on productivity and the relative contribution of salmon to those nutrient pools will be essential for management and restoration of riparian systems in the Pacific Northwest. If, for example, nitrogen is superabundant relative to other limiting effects such as available sunlight in riparian forests, then the uptake of salmon-derived nitrogen may be of little significance to system productivity. Evidence, such as ours, that terrestrial vegetation and animals utilize salmon-derived nitrogen can be regarded as the first step in this investigation.

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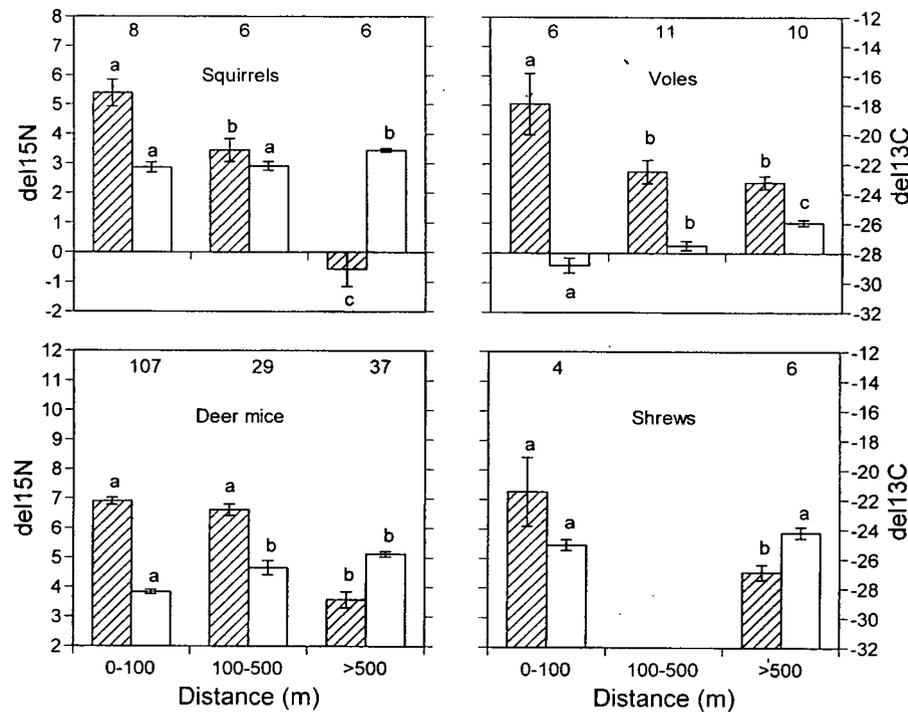


Fig. 7. Values of $\delta^{15}\text{N} \pm \text{SE}$ (hatched bars) and $\delta^{13}\text{C} \pm \text{SE}$ (open bars) plotted against distance from stream (m) for small mammals collected on Chichagof Island, southeast Alaska late summer and autumn 1992, 1993 and autumn 1994. Letters represent statistical difference at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons). Sample sizes are given above error bars.

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