

Response of nutrients, biofilm, and benthic insects to salmon carcass addition

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Abstract: Salmon carcass addition to streams is expected to increase stream productivity at multiple trophic levels. This study examined stream nutrient (nitrogen, phosphorus, and carbon), epilithic biofilm (ash-free dry mass and chlorophyll *a*), leaf-litter decomposition, and macroinvertebrate (density and biomass) responses to carcass addition in three headwater streams of southwestern Washington State, USA. We used stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to trace incorporation of salmon-derived (SD) nutrients into stream food webs. SD nutrients were assimilated by biofilm, benthic insects (Perlidae and Limnephilidae spp.), and age-1 steelhead (*Oncorhynchus mykiss gairdneri*). SD nutrients peaked ~2 weeks after carcass addition for insects and fish feeding on carcasses, but indirect uptake of SD nutrients by biofilm and insects was delayed by ~2 months. A strong stable isotope signal did not always correspond with measurable biological change. At reaches 10–50 m downstream from carcasses, ammonium concentration, leaf-litter decomposition, and benthic insect density all increased relative to upstream control sites. The strongest responses and greatest SD-nutrient uptake were observed 10 m from decomposing carcasses, with effects generally decreasing to undetectable levels 250 m downstream. Carcass addition to headwater streams can have a transient effect on primary and secondary trophic levels, but responses may be limited to specific taxa near carcass locations.

Résumé : L'addition de carcasses de saumons dans les cours d'eau doit augmenter, croit-on, la productivité du milieu à plusieurs niveaux trophiques. Notre étude examine les réactions des nutriments du cours d'eau (azote, phosphore et carbone), du biofilm épilithique (masse sèche sans les cendres et chlorophylle *a*), de la décomposition de la litière de feuilles et des macroinvertébrés (densité et biomasse) à l'addition de carcasses dans trois cours d'eau d'amont du sud-ouest de l'état de Washington, É.-U. Nous utilisons les isotopes stables ($\delta^{13}\text{C}$ et $\delta^{15}\text{N}$) pour suivre l'incorporation des nutriments dérivés des saumons (nutriments SD) dans les réseaux alimentaires des cours d'eau. Les nutriments SD sont assimilés par le biofilm, les insectes benthiques (des espèces de Perlidae et de Limnephilidae) et les truites arc-en-ciel anadromes (*Oncorhynchus mykiss gairdneri*) d'âge 1. Les nutriments SD atteignent un sommet ~2 semaines après l'addition des carcasses chez les insectes et les poissons qui se nourrissent de carcasses, mais l'incorporation indirecte des nutriments SD par le biofilm et les insectes est retardée de ~2 mois. Un fort signal d'isotopes stables ne correspond pas toujours à un changement biologique mesurable. Dans des secteurs 10–50 m en aval des carcasses, les concentrations d'ammonium, la décomposition de la litière de feuilles et la densité des insectes benthiques augmentent toutes par rapport aux sites témoins d'amont. Les réactions les plus fortes et l'incorporation la plus importante de nutriments SD s'observent à 10 m des carcasses en décomposition et les effets décroissent généralement à des niveaux non décelables 250 m en aval. L'addition de carcasses dans les cours d'eau d'amont peut avoir un effet transitoire sur les niveaux trophiques primaire et secondaire, mais les effets peuvent se limiter à des taxons particuliers près de l'emplacement des carcasses.

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Introduction

Restoration techniques in human-disturbed Pacific streams may include salmon carcass addition to increase nutrient supply and productivity. Pacific salmon (*Oncorhynchus* spp.) migrating from the ocean to freshwater to spawn subsidize streams with salmon-derived (SD) nutrients during gamete

release, waste excretion, and carcass decomposition (Cederholm et al. 2001). Spawning salmon can increase dissolved nutrient concentrations in stream water columns (Richey et al. 1975; Mitchell and Lamberti 2005) and can be important sources of nitrogen and carbon for freshwater aquatic organisms (Kline et al. 1990; Johnston et al. 1997). In the Pacific Northwest, where freshwater ecosystems are

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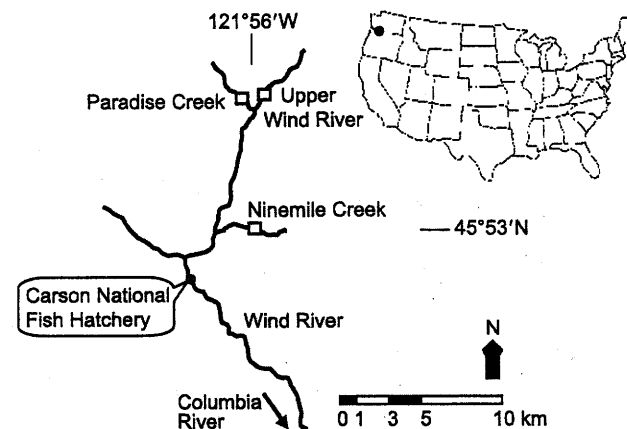
generally oligotrophic (Gregory et al. 1987), SD nutrient enrichment may enhance ecological processes and biota.

The consistency, timing, and magnitude of response to SD nutrients vary considerably among studies. Epilithic biofilm, measured as ash-free dry mass (AFDM) or chlorophyll *a*, can increase in response to salmon presence (Mathisen 1972; Chaloner et al. 2004; Johnston et al. 2004). However, other studies observed no change in chlorophyll *a* (Minshall et al. 1991) or gross primary production (Ambrose et al. 2004). Moreover, variable chlorophyll response can occur among streams and between years (Mitchell and Lamberti 2005). Dissolved nutrients from salmon carcasses may stimulate microbial and invertebrate shredder activity leading to faster leaf decomposition. High nutrient levels can increase microbial biomass and leaf processing by microbes (Meyer and Johnson 1983) and, subsequently, the abundance or size of invertebrate shredders (Robinson and Gessner 2000). Macroinvertebrate abundance can increase in response to salmon presence (Wipfli et al. 1998, 1999), whereas total biomass may show little difference in areas with and without salmon (Chaloner et al. 2004). Positive response by chironomid larvae (Diptera) to carcass addition may reflect their dispersal ability, rapid growth and reproduction, and broad food and habitat preferences (Wipfli et al. 1999; Chaloner et al. 2004). Grazing insects may respond positively to increased biofilm production, although a change in biofilm composition could negatively impact specialized grazers (Wipfli et al. 1999). Increased secondary production should, in turn, provide more food resources to juvenile salmonids, thereby increasing their growth and abundance (Groot and Margolis 1991). Response variability is likely caused by system-specific factors, such as nutrient concentrations, organic matter retention, light levels, water temperature, and flow regimes (Wipfli et al. 1999).

Some macroinvertebrates and juvenile salmonids consume salmon tissue or eggs (Bilby et al. 1998; Chaloner et al. 2002; Minakawa et al. 2002). Salmon carcasses can provide consumers with a high-quality organic food resource (Cederholm et al. 2001). However, colonization of salmon carcasses by invertebrates is not ubiquitous (Minshall et al. 1991; Johnston et al. 2004), suggesting that insect colonization may be influenced by local community composition or by the availability, timing, and quality of other food resources.

Although carcass addition is a current restoration technique in the Pacific Northwest, the effects of this practice are little studied and few in situ studies have been documented. In this study, we experimentally added salmon carcasses to three streams in Washington State, USA, to determine if SD nutrients resulted in increased density and biomass standing stock in the primary and secondary trophic levels. We used stable isotope analysis of nitrogen (^{15}N : ^{14}N) and carbon (^{13}C : ^{12}C) to determine which food web components assimilate SD nutrients. Before and after carcasses were added, we measured benthic biofilm and macroinvertebrate density and biomass and monitored dissolved organic and inorganic nutrient concentrations in the water column. Our objectives were (i) to quantify changes in nutrient concentrations, epilithic biofilm, leaf-litter decomposition, and benthic macroinvertebrates, (ii) to determine the incorporation of SD nutrients by different trophic levels, and (iii) to

Fig. 1. Location of study reaches (□) in the Wind River basin of southwest Washington State, USA.



measure spatial and temporal dynamics in measured responses relative to carcass locations. We hypothesized that (i) adding salmon carcasses to streams would increase nutrient concentrations in the water column and SD nutrients in the food web and (ii) these additional nutrients would stimulate biofilm and macroinvertebrate density and biomass and speed leaf decomposition. Lastly, responses were expected to decrease with distance downstream from carcasses and also decrease in magnitude through time.

Materials and methods

Study area

The study took place in the Wind River basin (Gifford Pinchot National Forest) in southwestern Washington State, USA (Fig. 1). The maritime climate is characterized by cool, wet winters and warm, dry summers. Currently, steelhead and spring Chinook salmon (*Oncorhynchus tshawytscha*) spawn in the Wind River basin; however, steelhead populations were federally listed as threatened in 1998 and are quite small. The study was replicated in three forested, second-order streams: Upper Wind River (UW), Paradise Creek (PR), and Ninemile Creek (NM) (Fig. 1). Douglas fir (*Pseudotsuga menziesii*) was the dominant overstory vegetation, with some vine maple (*Acer circinatum*) and N_2 -fixing red alder (*Alnus rubra*) also present in the riparian. Chinook spawn in the mainstem of the Wind River beginning in mid-July. Our experiment spanned 21 July 2003 through 15 October 2003, ending with the onset of winter rains.

A 300 m reach was chosen within each stream. Stream reaches differed somewhat in size and discharge but were otherwise physically similar and largely undisturbed (Table 1). Drainage area (hectares) for each reach was estimated from 30 m digital elevation maps using ArcInfo® (ESRI, Redlands, California). Instantaneous discharge ($\text{L}\cdot\text{s}^{-1}$) was calculated bimonthly by multiplying depth- and time-averaged water velocity flow (measured with a Marsh-McBirney® meter, Frederick, Maryland) with stream depths and widths (measured over at least 10 equal increments across stream width). Discharge was high in July from snowmelt and in October from rain and was lowest in early September. Stream gradient (%) was estimated with a cli-

Table 1. Physical characteristics of the three study reaches from July to October 2003.

	Upper Wind	Paradise	Ninemile
Drainage area (ha)	37.4	19.9	10.6
Discharge (L·s ⁻¹)	119 (83–154)	40 (20–72)	14 (4–33)
Bankfull width (m)	14	12	8
Gradient (%)	4	4	5
Gravel–cobble (%)	79	84	77
Water temperature (°C)	12.8 (8.9–15.4)	11.9 (9.1–14.0)	11.4 (9.3–13.0)
Solar flux (mJ·m ⁻² ·day ⁻¹)	4.6 (2.1–7.8)	2.5 (0.5–3.6)	2.3 (0.2–5.5)
Riparian vegetation ^a	Psme/Thpl	Psme/Thpl	Psme/Alru
Background SRP (µg·L ⁻¹)	17 (15–19)	8 (7–9)	24 (22–30)
Background TDN (mg·L ⁻¹)	0.07 (0.05–0.08)	0.07 (0.03–0.11)	0.10 (0.06–0.21)
Bedrock	Andesite	Andesite	Lapilli/Breccia
Elevation (m)	457	466	427

Note: Discharge, water temperature, solar flux, soluble reactive phosphorus (SRP), and total dissolved nitrogen (TDN) values are means with their range in parentheses (minimum to maximum).

^aDominant overstory vegetation: *Pseudotsuga menziesii* (Psme, Douglas fir), *Thuja plicata* (Thpl, western red cedar), *Alnus rubra* (Alru, red alder).

nometer. To characterize substrates, we used a modified Wolman pebble count consisting of 500 randomly stratified points classified as sand, gravel, cobble, boulder, bedrock, or wood. During the study period, daily mean temperatures were averaged from temperatures recorded each hour by submerged iButtons® (Maxim Integrated Products, Sunnyvale, California). Solar flux (mJ·m⁻²·day⁻¹) at the study areas was estimated with a Solar Pathfinder™ (Linden, Tennessee). Water temperature and solar flux decreased from July through October.

Experimental design

Frozen hatchery Chinook carcasses, adult male and female (some with eggs), were obtained from a local hatchery and tested for diseases (a slit was made in each ripe carcass to remove a small section of skein for disease testing). Carcasses were added to each stream on 30–31 July 2003 and were evenly distributed among streams by sex and presence of eggs. Carcasses were retained within a 5 m long reach, centered at the 0 m site, using chicken wire and rebar to group carcasses and keep them submerged and from floating downstream. Each stream received approximately the same amount of wet carcass tissue per streambed surface area (1.5 kg·m⁻² within a 5 m long reach × bankfull width): 104 kg of carcasses in Upper Wind, 88 kg of carcasses in Paradise, and 58 kg of carcasses in Ninemile. Within each stream, four sampling sites were located downstream from the carcasses. Each site was 10 m long and centered at 10, 50, 150, and 250 m from the carcasses, respectively. Effective loading rates at the downstream sites were 0.75 kg·m⁻² at the 10 m site, 0.15 kg·m⁻² at the 50 m site, 0.05 kg·m⁻² at the 150 m site, and 0.03 kg·m⁻² at the 250 m site. A control site was located 50 m upstream of the carcasses (~50 m site). We assumed that carcasses did not affect trophic processes upstream of the treatments. Responses measured from each downstream site were compared with the corresponding stream's control site.

Water chemistry

Stream water chemistry was sampled on 28 July, 6 August, 2 September, and 15 October 2003. One water sample

was collected from each of the five sites per stream, in addition to collecting a sample 1 m downstream from the carcasses. Total dissolved nitrogen (TDN) was determined using persulfate digestion (Cabrera and Beare 1993), followed by measurement of nitrate. Ammonium (NH₄-N), nitrate (NO₃-N), nitrite (NO₂-N), and soluble reactive phosphorus (SRP) levels were determined with an automated colorimetric continuous flow autoanalyzer (Lachat Instruments Flow Injection Autoanalyzer, Hach Instruments, Loveland, Colorado). Dissolved organic nitrogen (DON) was calculated as TDN minus ammonium-N, nitrate-N, and nitrite-N. Dissolved organic carbon (DOC) was determined by automated UV-persulfate oxidation followed by infrared spectrophotometry (Dohrmann TOC analyzer, Teledyne Tekmar, Mason, Ohio). Detection limits for these analyses were determined within the laboratory and are 0.001 mg NO₃-N·L⁻¹, 0.002 mg NH₄-N·L⁻¹, 1 µg PO₄-P·L⁻¹, and 0.1 mg DOC·L⁻¹ (Erway et al. 2001).

Epilithon and leaf decomposition

Epilithic biofilm was collected from streambed rocks at each site for AFDM and chlorophyll *a* measurements. Epilithon appeared to be primarily diatoms with little green algae observed. Each sample was a composite of biofilm scraped, with a metal brush, from three randomly collected, cobble-sized rocks (20 cm² area of biofilm per rock). Three composite samples were collected at each site on 21–23 July, 19–21 August, 16–18 September, and 13–15 October 2003. Each composite sample was mixed, split in half, and filtered through glass-fiber filters (Whatman® GF/F, Clifton, New Jersey) for analysis of AFDM (mg·cm⁻²) and chlorophyll *a* (mg·cm⁻²). Prewashed and preweighed filters for AFDM were oven-dried, weighed, ashed at 500 °C, and reweighed (Steinman and Lamberti 1996). The difference in weights was an estimate of AFDM. Chlorophyll *a* was extracted from the filter in 90% buffered acetone for 24 h, measured spectrophotometrically, and corrected for phaeopigments (Steinman and Lamberti 1996).

Leaf decomposition rates were measured by calculating the average dry mass lost per day from preweighed leaf packs (Benfield 1996). Leaf packs were composed of red al-

der (3.0 ± 0.1 g dry mass) and vine maple (2.0 ± 0.1 g dry mass) leaves that had recently fallen from riparian trees. Oven-dried leaves were weighed and secured together in large-mesh bags (10 mm $\times$ 4 mm mesh). In each stream, six leaf packs were randomly spaced within each site, excluding the 250 m site. Leaf packs were accessible to microbes, aquatic macroinvertebrates, and some physical abrasion by flowing water. Leaf packs were removed after 1 month, on 25 September 2003, with a 500 μ m net. Leaves and remaining leaf fragments were removed from mesh bags, swirled in water, and visually inspected to remove macroinvertebrates. Oven-dried leaves and fragments were weighed, their weights were subtracted from predecomposed weights, and the difference was divided by the number of days in the stream.

Benthic macroinvertebrates

Six macroinvertebrate samples were randomly collected at each site in each stream on the same dates as biofilm collections. Macroinvertebrates were collected with a Surber sampler (250 μ m mesh, 0.09 m²) and stored in 70% ethyl alcohol. In the laboratory, the six samples per site were pooled together and subsampled with a zooplankton splitter for a minimum of 500 individuals, usually one-eighth of the total sample. Aquatic insects were counted and identified generally to genus, except Chironomidae, which were identified to subfamily or tribe (Merritt and Cummins 1996). Non-insects were identified to order. To estimate insect biomass (mg·m⁻²), length – dry mass regressions at the family or order level (Smock 1980; Benke et al. 1999) were used after the body length of each insect was measured with a microscope micrometer. Subsample counts and biomass were divided by the fraction subsampled to obtain full-sample estimates.

Stable isotopes

Riparian litterfall, epilithic biofilm, benthic macroinvertebrates, fish, and carcass tissue were sampled for analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Five riparian litterfall baskets (0.6 m²) were placed in the riparian along each stream in August and September 2003 to collect material entering the stream (generally red alder leaves, vine maple leaves, cedar twigs, and hemlock or fir needles). Baskets were combined to form one sample per stream per month. We assumed that the added carcasses did not affect riparian vegetation during the short duration of this study. Litterfall was collected to represent the riparian input of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ into each stream.

Epilithic biofilm was scraped from streambed rocks as described above. Three biofilm samples were collected per site and stream, excluding the 250 m site, on 24 July, 12 August, and 21 September 2003. Biofilm samples were freeze-dried and homogenized before analysis. Benthic macroinvertebrates were collected with a 500 μ m dip net from the same sites and dates. We targeted common macroinvertebrates representing three functional feeding groups (FFG): scraper-collectors *Ecclisomyia* (Trichoptera: Limnephilidae), shredders *Pteronarcys* (Plecoptera: Pteronarcyidae), and predators Perlidae spp. (Plecoptera) (Merritt and Cummins 1996). Multiple individuals of the same taxa were combined into one sample to provide sufficient mass for isotopic analysis. Macroinvertebrates were oven-dried at 50 °C, were not acid-washed, and were homogenized before analysis.

Juvenile steelhead (age-0 and age-1+) and sculpins were collected from each stream on 12 August and 21 September 2003 via electroshocking. Three fish per taxa and age group were collected at least 150 m upstream from the carcasses (0 m site), above summertime natural fish blockages (i.e., above debris dams or places of intermittent surface flow), and 1–25 m downstream of the carcasses. For analysis, upstream fish were placed in the –50 m sites and downstream fish were grouped in the 10 m sites. All fish were killed by a quick blow to the head and stomach contents were removed. Whole bodies were used for isotopic analysis because their small size (fork length: 36–157 mm) made it difficult to separate muscle from other tissues. One sample of Chinook carcass tissue was collected per stream on 12 August 2003 for isotope analyses. Fish samples were oven-dried at 50 °C and homogenized before analysis.

Samples were analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ by continuous-flow isotope ratio mass spectrometry (Thermo Finnigan Delta Plus XP mass spectrometer, Waltham, Massachusetts). Separate runs were conducted for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Isotope enrichment between successive trophic levels occurs as the heavier isotope accumulates in the consumer with each trophic transfer: an average of 2.3‰ for ^{15}N and 0.5‰ for ^{13}C (McCutchan et al. 2003). Higher delta values indicate higher proportions of the heavy isotope (^{15}N vs. ^{14}N , ^{13}C vs. ^{12}C) in a sample. Mass-balance equations were used to provide estimates of the percent SD nutrient assimilated by organisms (Johnston et al. 1997):

$$(1) \quad \text{SD-nutrient enrichment (\%)} = (\delta X_{\text{se}} - \delta X_{\text{c}}) / ((\delta X_{\text{s}} + (\text{TL} \cdot \delta X_{\text{e}})) - \delta X_{\text{c}}) \times 100$$

where X refers to the element of interest (C or N), δX_{se} is the isotope ratio of the organism in areas enriched with salmon carcasses, δX_{c} is the isotope ratio of the organism in areas without carcasses, δX_{s} is the isotopic ratio of salmon tissue, and δX_{e} is the isotope enrichment factor per trophic level. TL is the trophic level correction factor: 1 for primary consumers (grazing and shredding insects), 2 for secondary consumers (predatory insects), and 3 for fish. These calculations would underestimate an organism's use of SD nutrients if they actually fed at a lower trophic level.

Statistical analyses

We limited statistical analyses of multiple responses measured over time to five response indicators to reduce exaggeration of the type-I error rate from multiple comparisons (Zar 1984). Tested responses were chosen a priori to determine basic trophic level effects: ammonium concentrations, biofilm AFDM, biofilm chlorophyll a , total insect density, and total insect biomass. To control for natural changes in response levels over time and meet model assumptions of normality, response values were calculated as the log_e ratio of the response at a downstream site (10, 50, 150, or 250 m) to the upstream site (–50 m):

$$(2) \quad Y_{ijk} = \log_e(\text{Downstream}_{ijk} / \text{Upstream}_{i,k}) = \log_e(\text{Downstream}_{ijk}) - \log_e(\text{Upstream}_{i,k})$$

where i represents stream, j represents distance downstream from the carcasses, and k is month sampled.

We expected responses to change over time naturally and assumed that this seasonal change was the same among the five sites within each stream. We measured responses in July, before carcass placement, and assumed those values to be background, or inherent, differences between upstream and downstream sites (~ 0). Responses measured after carcass addition were then compared to July's precarcass levels.

Randomized block, repeated measures analysis of variance (ANOVA) (SAS 1999) were used on the $\log_e$ ratio of responses. Because analyses were limited by small sample sizes, we could not model both spatial autocorrelation of sites within a stream and temporal autocorrelation of samples collected over time. Therefore, our model considered the streams as blocks and assumed equal correlation among sites within blocks. Distance from carcasses was modeled as a continuous variable, with response variables at each site repeatedly measured four times (July, August, September, and October 2003). July values were used as the reference level. To determine the covariance structure over time, we ran 10 common covariance models and chose the one with the best fit using Akaike's information criterion corrected for small sample sizes for each response (ammonium and insect density used UN(4) models and AFDM, chlorophyll *a*, and insect biomass used Toep(1) models) (Wolfinger 1993). In effect, we ended up with a comparison of regression line models. We expected that precarcass differences among sites would be spatially constant and approximately zero, i.e., regressions of July's responses would have an intercept and slope equal to zero (H_0 : July = 0). After carcass addition, we hypothesized the greatest response to occur at the shortest distance from the carcasses, with the response decreasing downstream, i.e., post-July regressions would have intercepts and slopes differing from July.

Leaf-decomposition response values for each stream were calculated as the $\log_{10}$ ratio of the rates at a downstream site (10, 50, or 150 m) to the upstream site (~ 50 m). We used a one-tailed *t* test to make statistical comparisons (Zar 1984). No statistical analyses were conducted on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope values because of small sample sizes.

Results

Salmon carcasses

The carcasses, purposely kept under water to restrict birds and mammals from disturbing them, decomposed slowly. Caddisfly larvae, *Ecclisomyia*, were observed on carcasses within each stream, but only during early decomposition stages (2–3 weeks after carcass addition). They were distributed around the body and inside the gill cavities and mouth (~ 30 – 60 individuals per carcass). A thick mat of fungus covered most carcasses after 1 month of decomposition. No macroinvertebrates were seen on carcasses once the fungus developed.

After 2 months (late September), inner body tissues had decomposed with some skin and bones still intact. One week after the September sampling period, a black bear removed all the carcasses in Ninemile Creek. However, a large portion of the organic material probably had already leached from the carcasses, as the response pattern from Ninemile Creek in October was similar to those observed at the other

study streams in October (see below). Therefore, it appears that early removal of the carcasses did not affect the stable isotope, water chemistry, biofilm, or invertebrate responses measured in October.

Stable isotopes

Before the addition of carcasses in July, mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were similar for each taxonomic group among study sites (Table 2). Background $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, from sites upstream of carcasses, varied little from July through September 2003 (Table 2).

Carcass tissue was highly enriched in ^{15}N and ^{13}C (15.9‰ and -17.1 ‰, respectively), whereas leaf litter was relatively depleted (-3.1 ‰ and -29.2 ‰, respectively) (Table 2). Because pretreatment data indicated no spatial patterns in isotope ratios among sites within streams, an increase of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in August or September at the downstream sites compared with the upstream sites was attributed to the carcasses. In August, epilithon $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ increased relatively little at downstream sites compared with upstream sites (Fig. 2) (downstream sites were 5%–10% enriched with SD nitrogen (SDN) and 3%–5% enriched with SD carbon (SDC) compared with respective upstream site). In September, epilithon $\delta^{15}\text{N}$ showed more substantial ^{15}N enrichment (11%–16% SDN) and ^{13}C was inconsistently enriched or depleted (0%–9% SDC) (Table 2; Fig. 2).

Among insect feeding guilds, omnivorous *Ecclisomyia* caddisflies displayed the temporally most immediate and spatially greatest range in SDN uptake (Table 2; Fig. 2). In August, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of these limnephilids increased considerably at sites 10 m downstream of carcasses compared with upstream sites (36% SDN and 39% SDC). By September, limnephilid $\delta^{15}\text{N}$ increased at all downstream sites (12%–14% SDN), although $\delta^{13}\text{C}$ increased only slightly (2%–10% SDC). Neither shredding pteronarcid stoneflies nor predatory perlid stoneflies exhibited changes in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ at downstream sites in August (Fig. 2). Predatory perlid stoneflies exhibited a delayed response of increased $\delta^{15}\text{N}$ at downstream sites in September (8%–13% SDN) (Fig. 2).

Only age-1 steelhead assimilated SD nutrients (Table 2; Fig. 2); their $\delta^{15}\text{N}$ increased at downstream sites compared with upstream sites in August and September (12% and 14% SDN, respectively), as did $\delta^{13}\text{C}$ (15% and 14% SDC, respectively). Neither sculpins nor age-0 steelhead were enriched in August or September.

Water chemistry

Only ammonium concentrations increased in response to carcass addition. Significant concentration changes in ammonium may have been more easily detected than other nitrogen forms because ammonium had the lowest background concentration. Ammonium concentrations were similar between upstream and downstream sites before carcass addition in July (Fig. 3; Table 3). In August and September, ammonium concentrations were significantly higher at downstream sites most near the carcasses compared with upstream sites ($p = 0.002$ and $p < 0.001$, respectively) (Fig. 3; Table 3). Compared with July, ammonium concentrations in September significantly decreased with distance from the carcasses ($p = 0.001$). By October, am-

Table 2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰) isotope values for taxa collected from upstream (–50 m) and downstream (10, 50, 150 m) sites on 24 July, 12 August, and 21 September 2003.

	$\delta^{15}\text{N}$ (‰)				$\delta^{13}\text{C}$ (‰)			
	Upstream		Downstream sites		Upstream		Downstream sites	
	–50 m	10 m	50 m	150 m	–50 m	10 m	50 m	150 m
July — 1 week before carcass addition								
Epilithic biofilm	–1.2 (0.3)	–1.3 (0.2)	–1.3 (0.5)	–1.2 (0.3)	–32.5 (2.0)	–33.8 (1.4)	–33.1 (1.1)	–32.1 (2.3)
Limnephilidae	–0.5 (0.3)	0.1 (0.2)	–0.1 (0.3)	–0.1 (0.4)	–27.8 (0.6)	–26.8 (1.0)	–28.8 (1.1)	–28.4 (0.4)
Pteronarcyidae	–0.4 (0.1)	–0.3 (0.1)	–0.2 (0.1)	–0.3 (0.1)	–27.9 (0.2)	–27.9 (0.2)	–28.3 (0.1)	–27.9 (0.3)
Perlidae	1.9 (0.1)	1.8 (0.2)	1.9 (0.3)	2.0 (0.2)	–31.1 (1.4)	–30.9 (1.0)	–31.2 (1.5)	–31.1 (1.1)
August — 2 weeks after carcass addition								
Leaf litterfall ^a	–3.1 (0.4)				–29.2 (0.2)			
Epilithic biofilm	–1.1 (0.3)	0.6 (0.8)	–0.2 (0.4)	–0.1 (0.2)	–32.0 (2.9)	–31.6 (3.5)	–31.6 (2.5)	–31.2 (3.8)
Limnephilidae	0.0 (0.4)	6.7 (1.4)	0.5 (0.2)	0.5 (0.3)	–27.7 (1.3)	–23.4 (0.6)	–28.2 (1.7)	–25.8 (3.1)
Pteronarcyidae	–0.3 (0.1)	0.2 (0.3)	0.0 (0.2)	–0.2 (0.1)	–27.9 (0.2)	–27.8 (0.5)	–28.0 (0.4)	–28.2 (0.3)
Perlidae	2.1 (0.1)	2.2 (0.2)	2.2 (0.3)	2.1 (0.2)	–30.9 (1.5)	–31.1 (1.6)	–30.5 (1.3)	–30.8 (1.2)
Sculpin	4.1 (0.4)	3.5 (0.2)		–29.0 (1.4)	–27.9 (1.2)			
Steelhead age-0	5.0 (0.4)	5.7 (0.5)		–26.7 (1.0)	–26.2 (0.9)			
Steelhead age-1	5.5 (0.3)	7.6 (2.0)		–27.1 (0.2)	–25.4 (2.1)			
Carcass tissue		15.9 (0.1)				–17.1 (0.3)		
September — 8 weeks after carcass addition								
Leaf litterfall ^a	–3.1 (0.6)				–29.0 (0.3)			
Epilithic biofilm	–1.1 (0.3)	1.5 (0.5)	1.1 (0.7)	0.7 (0.3)	–30.0 (2.4)	–31.1 (2.5)	–28.9 (3.9)	–32.2 (3.2)
Limnephilidae	–0.4 (0.3)	2.2 (1.4)	1.9 (0.8)	2.2 (1.3)	–26.9 (3.0)	–26.6 (2.6)	–25.8 (2.5)	–26.1 (2.1)
Pteronarcyidae	–0.2 (0.2)	0.8 (0.1)	0.7 (0.1)	0.2 (0.1)	–27.4 (0.6)	–27.4 (0.4)	–27.9 (0.2)	–27.9 (0.1)
Perlidae	2.0 (0.3)	4.3 (0.8)	3.4 (0.3)	3.4 (0.2)	–29.1 (2.0)	–28.9 (0.9)	–30.2 (2.0)	–28.8 (1.3)
Sculpin	4.3 (0.5)	4.5 (0.5)		–27.9 (1.4)	–28.1 (1.6)			
Steelhead age-0	5.2 (0.3)	6.3 (0.6)		–26.2 (1.5)	–26.2 (1.0)			
Steelhead age-1	5.6 (0.4)	8.0 (1.4)		–27.0 (0.7)	–25.3 (1.3)			

Note: Values are the mean (+1 standard error in parentheses) of three streams. Isotope values in bold demonstrate taxa that assimilated at least 10% SD nutrients.

^aLeaf litterfall samples represent an entire stream, formed from a composite of five samples per stream.

Fig. 2. Isotope signatures of representative trophic level taxa (mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) collected from upstream (–50 m) and downstream (10, 50, 150 m) sites among the three study streams: (a) 12 August and (b) 21 September 2003. Taxa collected: upstream sites, open symbols; 10 m sites, solid symbols; 50 m sites, lightly shaded symbols; and 150 m sites, medium shaded symbols. Symbols: leaf litter and biofilm, squares; insects, circles, fish and carcass tissues, diamonds.

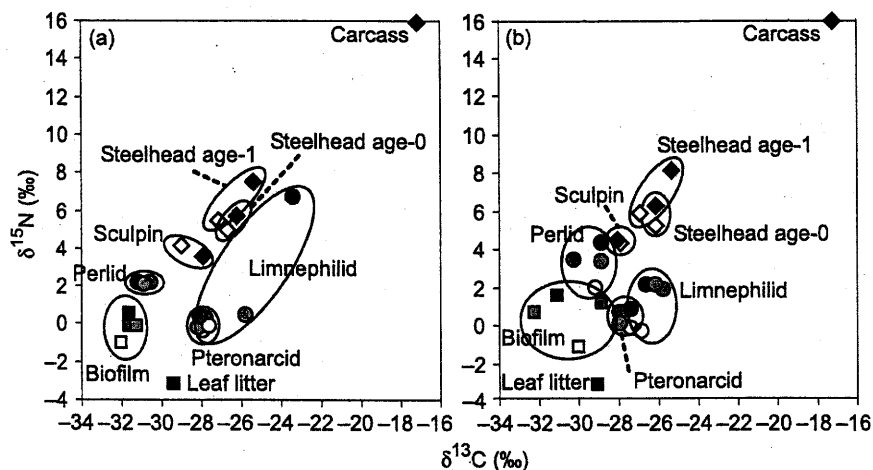


Fig. 3. Ammonium ($\text{NH}_4\text{-N}$) concentrations ($\mu\text{g}\cdot\text{L}^{-1}$) from upstream (-50 m) and downstream (1, 10, 50, 150, 250 m) sites: (a) 28 July, (b) 6 August, (c) 2 September, and (d) 15 October 2003. Bars show the mean $\pm$ 1 standard error of three streams. Open bars represent concentrations before or upstream of carcass addition; solid bars represent concentrations after or downstream of carcass addition.

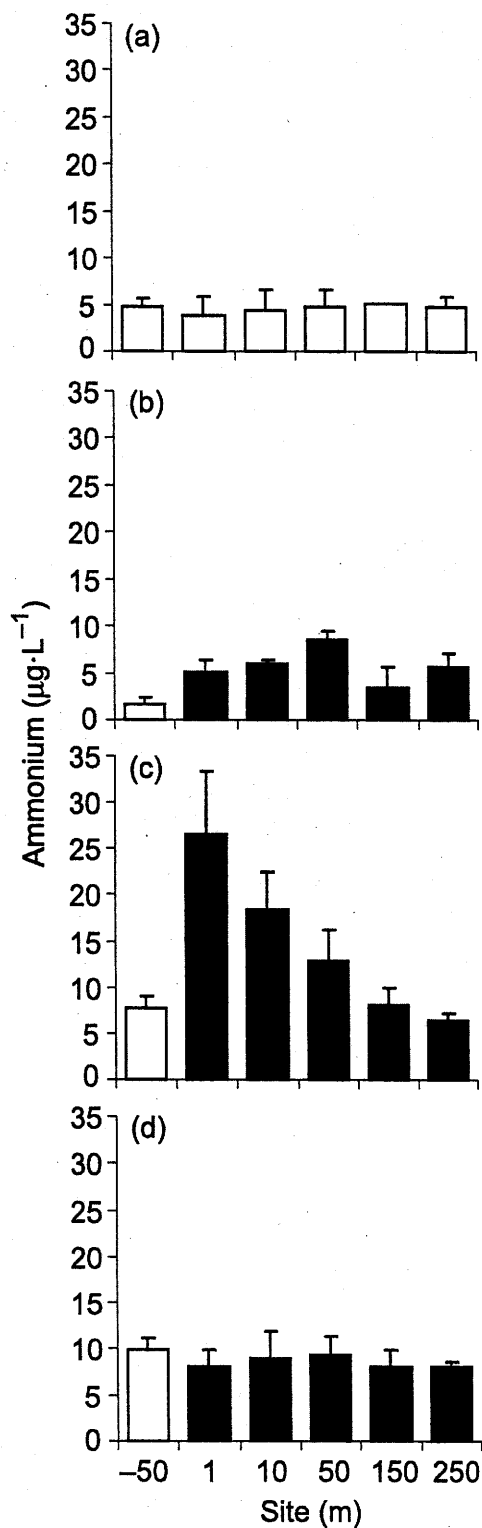


Fig. 4. Chlorophyll *a* levels ($\mu\text{g}\cdot\text{cm}^{-2}$) from upstream (-50 m) and downstream (10, 50, 150, 250 m) sites: (a) 22 July, (b) 20 August, (c) 17 September, and (d) 14 October 2003. Bars show the mean $\pm$ 1 standard error of three streams. Open bars represent levels before or upstream of carcass addition; solid bars represent levels after or downstream of carcass addition.

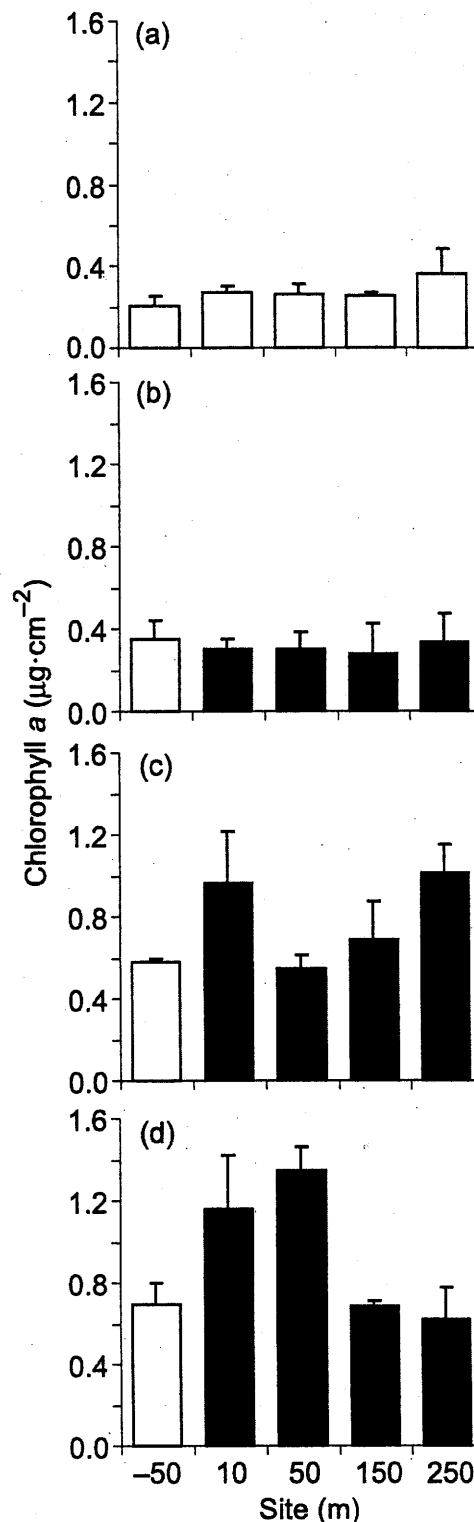


Table 3. Linear-fit regressions from repeated measures analysis of variance of response change as functions of distance downstream from carcasses for each month.

Month	Ammonium intercept, slope	AFDM intercept, slope	Chlorophyll <i>a</i> intercept, slope	Insect density intercept, slope	Insect biomass intercept, slope
July	-0.318, 0.002	-0.017, <0.001	-0.170, <0.001	-0.336, 0.001	-0.578, <0.001
<i>p</i> value	NS, NS	NS, NS	NS, NS	NS, NS	NS, NS
August	1.062 , -0.001	0.110, <-0.001	-0.137, <-0.001	-0.052, <-0.001	0.396, <-0.001
<i>p</i> value	0.002 , NS	NS, NS	NS, NS	NS, NS	NS, NS
September	0.824 , -0.004	0.167, <0.001	0.131, 0.001	0.693 , -0.002	0.131, -0.003
<i>p</i> value	<0.001 , 0.001	NS, NS	NS, NS	0.002 , NS	NS, NS
October	-0.144, <-0.001	-0.091, <0.001	0.570, -0.003	0.319, -0.002	-0.644, -0.002
<i>p</i> value	NS, NS	NS, NS	0.076, 0.022	NS, NS	NS, NS

Note: Intercept and slope estimates are log₁₀(downstream/upstream) ratios. Responses measured in July (before carcass addition) show background differences between upstream and downstream sites. Responses measured in August, September, and October show differences attributed to the carcass addition. Intercept or slope estimates in bold are significantly different from the null hypothesis ($p < 0.05$). NS indicates nonsignificant, $p > 0.10$. AFDM, ash-free dry mass.

monium concentrations returned to before carcass addition and upstream levels. Our data suggest that the peak ammonium release occurred in September, approximately 8 weeks after carcass addition.

Epilithon and leaf decomposition

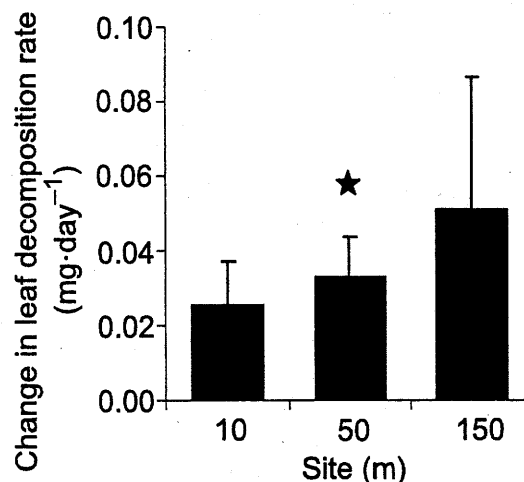
In July, before carcasses were added to the study streams, epilithon AFDM and chlorophyll *a* levels were similar between sampling locations. After carcass addition, chlorophyll responses were highly variable and not significantly different between sites, yet there was a potentially biologically meaningful increase at sites downstream of carcasses compared with upstream in October, particularly at Ninemile and Paradise creeks ($p = 0.076$) (Fig. 4; Table 3). Chlorophyll responses significantly decreased with distance from carcasses ($p = 0.022$). AFDM did not respond to carcass addition. Given the large AFDM and chlorophyll standard errors and a significance level of <0.05 , mean levels at downstream sites had to be 2 times and 1.4 times greater than upstream sites, respectively, to be significantly different from levels before carcass addition. Mean leaf-pack decomposition was faster at sites downstream than upstream of carcasses (Fig. 5), but responses were significant only at the 50 m site ($p = 0.010$).

Benthic macroinvertebrates

Insect densities were similar between upstream and downstream sites in July, before carcass additions. Throughout the study, Diptera (primarily Chironomidae) and Ephemeroptera (primarily Baetidae and Heptageniidae) were the most abundant orders. Insect biomass was greater at sites upstream than downstream of carcasses in July. Plecoptera (primarily large-bodied Pteronarcyidae and Perlidae species) and several genera of Trichoptera constituted the greatest insect biomass. Non-insects (primarily water mites, worms, and snails) represented a small portion of the benthic macroinvertebrates collected per stream (9%–13%).

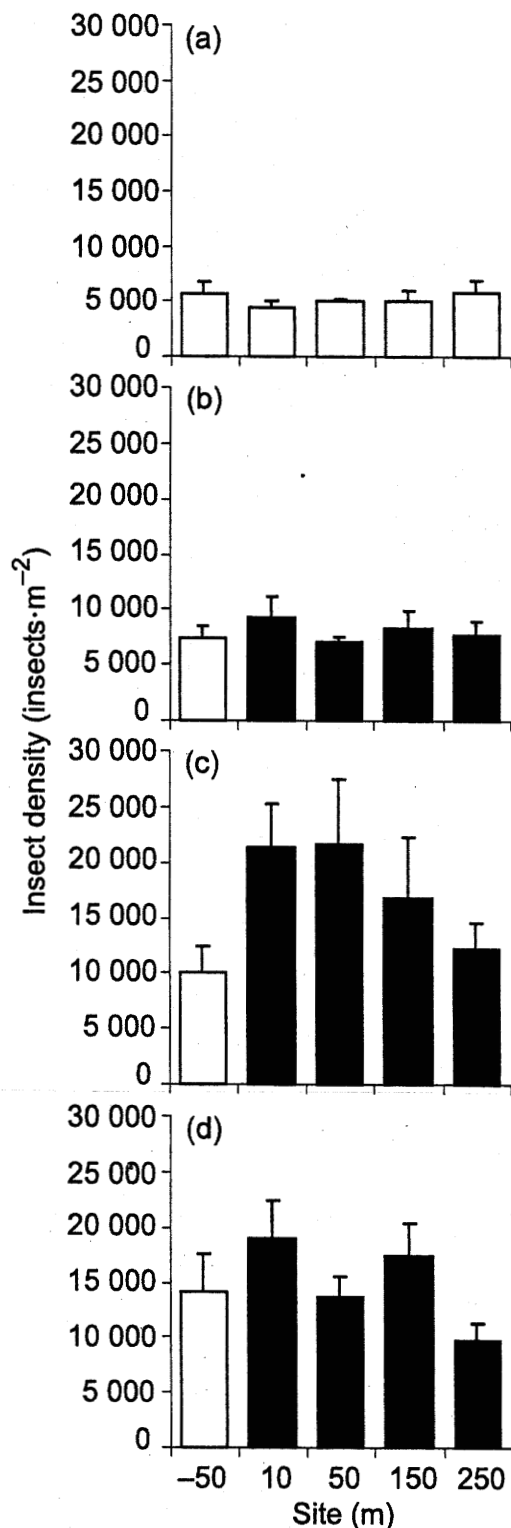
Macroinvertebrate responses to carcass addition were mixed, but certain taxa were more abundant near carcasses. In September, total insect abundance was significantly greater at sites downstream than upstream of carcasses ($p = 0.002$) (Fig. 6; Table 3). Heptageniidae (*Cinygmula*, *Rhithrogena*, *Epeorus*, and *Ironodes*) and Chironomidae (*Tanytarsini* and *Orthocladiinae*) larvae contributed most to

Fig. 5. Leaf decomposition response: difference in log₁₀-transformed decomposition rates (mg·day⁻¹) between respective downstream (10, 50, 150 m) and upstream (-50 m) sites. The decomposition study ran between 28 August and 25 September 2003. The star indicates a significant difference from zero. Bars show the mean + 1 standard error of three streams.



increased densities in September; heptageniid density increased by an average of 298% (mean of 4693 individuals·m⁻² at the 10 m sites compared with 1574 individuals·m⁻² at the upstream sites), and chironomid density increased by an average of 249% (mean of 7769 individuals·m⁻² at the 10 m sites compared with 3124 individuals·m⁻² at the upstream sites). The density of elmids (*Heterolimnium*), ubiquitous but less numerous at each site, increased by an average of 186% (mean of 321 individuals·m⁻² at the 10 m sites compared with 172 individuals·m⁻² at the upstream sites) in September. Unlike other insect groups, chironomid density continued to increase at sites downstream of carcasses in October, compared with sites upstream, with an average increase of 268% (mean of 8985 individuals·m⁻² at the 10 m sites compared with 3358 individuals·m⁻² at the upstream sites). Heptageniidae, Elmidae, and Chironomidae larval densities declined with distance downstream, and their densities 250 m downstream from carcasses were not different from upstream sites. Densities of other common insect taxa, in-

Fig. 6. Benthic insect density (insects·m⁻²) from upstream (–50 m) and downstream (10, 50, 150, 250 m) sites: (a) 22 July, (b) 20 August, (c) 17 September, and (d) 14 October 2003. Bars show the mean + 1 standard error of three streams. Open bars represent insects collected before or upstream of carcass addition; solid bars represent insects collected after or downstream of carcass addition.



cluding the mayflies Baetidae, stoneflies Pteronarcyidae, Perlidae, Perlodidae, and Nemouridae, and caddisflies Limnephilidae, Lepidostomatidae and Hydropsychidae, did not display different abundance patterns along spatial or temporal distributions.

Insect biomass was highly variable among sampling locations and over time. No significant changes in total biomass, biomass of insect groups (order, family, or genera level), or abundance of different size classes were detected from carcass addition. Downstream total biomass needed to be five times greater than upstream biomass to be significantly different from levels before carcass addition, based on observed standard errors and a significance level of <0.05. In contrast to responses in insect abundance, carcass addition did not significantly affect insect biomass.

Discussion

This study tested the direct and indirect effects of decomposing salmon carcasses on primary producers and secondary consumers longitudinally downstream of introduced carcasses. SD nutrients were incorporated into the stream food web at all trophic levels. As in other studies, we observed higher ammonium and variable chlorophyll *a* levels in response to carcass addition (Chaloner et al. 2004; Mitchell and Lamberti 2005). Greater macroinvertebrate abundance, a response also reported in southeastern Alaska (Wipfli et al. 1998, 1999), was driven primarily by Chironomidae and Heptageniidae in these western Washington streams. Our examination of longitudinal effects downstream of carcass introductions suggested that changes to stream chemistry and biota tended to be transient and most apparent within 50 m of carcasses.

The addition of carcasses to increase nutrients has the potential to conflict between water quality and salmon restoration objectives. However, if carcass addition does not overstimulate algal growth, but increases stream secondary production, then salmon restoration objectives would be satisfied without compromising the intent of water quality goals. Carcass addition in Wind River streams did not strongly alter water chemistry or cause substantial algal blooms. We conducted this study during summer low-streamflow conditions, which should maximize any effects on water chemistry. Only ammonium levels responded to carcass addition. Following elevated levels in August, peak ammonium release occurred in September. In these montane, low-order streams, effects from carcass addition on stream chemistry appear minimal. Although highly variable, algal biomass, measured as chlorophyll *a*, tended to increase downstream of carcasses in October. This temporal lag in nutrient release and uptake was detected particularly in herbivores. Biofilm volumes were not apparently influenced by carcass addition, but biofilm production may have been masked by increased grazing. Measures of AFDM and chlorophyll *a* estimate standing stock and do not account for grazing by macroinvertebrates.

As chlorophyll *a* levels increased at some sites, densities of scraping (Heptageniidae) and collecting (Chironomidae and Elmidae) insects increased 2 months after carcass addition. Scrapers may have benefited from an increase in the quality or quantity of biofilms. Collectors may have bene-

fitted from increased organic particles from the breakdown of carcass tissues or from carcass fragments dislodged by foraging insects and water current. Predatory insects did not increase in density or biomass as expected, although perlid stoneflies had enhanced levels of $\delta^{15}\text{N}$, suggesting potential indirect effects in higher trophic levels. Increased macroinvertebrate densities within the treatment reaches may have resulted from a net increase per stream or, more likely, from invertebrates drifting into the carcass-treated reaches.

We hypothesized that decomposing salmon carcasses would stimulate microbial and invertebrate activity on leaf litter, leading to faster leaf decomposition. Leaf packs composed of alder and vine maple leaves decomposed significantly faster at the site 50 m downstream from carcasses compared with upstream sites. Average decomposition rates were also faster at 10 and 150 m sites, but these were more variable and not significantly different from the control site. Shredding insects did not increase in density or biomass in response to carcass addition. The shredder *Pteronarcys* did not assimilate SD nutrients, suggesting that the increase in decomposition rates resulted from an increase in microbial activity rather than by macroinvertebrates. In an artificial pond study, the addition of alewife carcasses caused microbial production and respiration on leaf litter to increase, indicating faster leaf processing by microbes (Durbin et al. 1979). Contrary results were observed when SD nutrients enhanced biofilm on wood debris but did not influence wood decomposition (Fisher-Wold and Hershey 1999). In our study, the addition of carcasses enhanced leaf litter breakdown, but we were not able to verify the biological agent causing the increase.

SD nutrients were incorporated into the stream food web through both direct (i.e., consumption of carcass tissues or eggs) and indirect (i.e., nutrients leached from the carcasses) pathways. The timing of changes in isotope ratios reflected the mechanistic differences between these pathways. Limnephilidae caddis larvae were observed feeding directly on salmon carcasses in early August, likely explaining their high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Age-1 steelhead were also observed to feed directly on carcasses, and salmon eggs were found in their stomachs during collection for isotope samples in August and September. Both organisms showed large increases in $\delta^{13}\text{C}$, indicating direct consumption of an enriched food source. Age-0 steelhead had no increased isotope activity and appeared to consume unenriched food resources. Sculpin also may have consumed unenriched prey. Unlike juvenile steelhead, the slow growth of sculpins may cause slow tissue turnover rates, resulting in a longer interval for tissues to change isotopic composition in response to changes in food (Hesslein et al. 1993).

As carcasses decomposed, observable direct consumption diminished and indirect nutrient pathways developed. SD nutrients were detected in September, 2 months after carcass addition, in epilithic biofilm, Perlidae stoneflies, and Limnephilidae caddisflies. Caddis larvae may have been exploiting ^{15}N derived from epilithon, as no insects were seen on carcasses in September, or possibly consuming dislodged carcass fragments within the stream substrate. Carcass biofilm may inhibit invertebrates from colonizing salmon carcasses and is not unique to the Wind River basin (Minshall et al. 1991; Johnston et al. 2004). Predatory

stoneflies probably consumed enriched prey. SD-nutrient transfer via direct carcass consumption began quickly, whereas evidence of SD nutrients transferred indirectly required at least 2 months.

Measurable responses of secondary consumers, and to some extent primary producers, were seen at sites close to carcasses (1–50 m) and declined with increasing distance from the carcasses. Most effects were undetectable 250 m downstream from carcasses. However, SD nutrients were incorporated by some organisms (biofilm, Limnephilidae, and Perlidae) collected 150 m downstream from carcasses. SD nutrients may spiral downstream at levels detectable by isotope analysis, but measurable changes in the benthic community, which are more difficult to detect, may only occur in carcass-rich areas.

Adding frozen carcasses to streams and caging carcasses in wire mesh may have slowed fish decomposition by preventing some movement, resulting in fragmentation and possibly increasing the lag time observed in some responses. Nevertheless, dissolved ammonium concentrations increased significantly just 1 week after carcass addition, indicating that decomposition was well underway. Confining carcasses to one place and adding them at one time is somewhat different from the typically haphazard method of adding carcass to streams. It should be noted that streams receiving a single influx of salmon carcasses from manual addition may exhibit different responses than a stream that receives spawners annually and repeatedly over a spawning cycle. Local populations not adapted to or not present when carcasses are added may be limited by life history or morphology to take advantage of the new food source. Unlike natural spawning, supplementing carcasses omits substrate disturbance caused by redd excavation (Peterson and Foote 2000) and the slow release of nutrients through waste excretion (Braband et al. 1990).

Stream communities studied in the Wind River basin, although upstream of salmon spawning areas, exhibited many of the same biological responses observed from carcass addition elsewhere (Wipfli et al. 1999; Mitchell and Lamberti 2005). Our results differed in that we detected increased scraping mayflies (unlike Wipfli et al. 1998) but not significant increases in epilithic biofilm. Likewise, primary production was not measurably enhanced by rainbow trout addition in an Idaho stream (Minshall et al. 1991) or by salmon carcass addition in northern California streams (Ambrose et al. 2004). Thus, carcass supplementation in headwater streams may have a transient effect on lower trophic levels that could be readily consumed by secondary consumers. Detectable responses may be limited to select taxa or be limited by physical controls (e.g., sunlight, high gradient).

Carcass supplementation has become a popular, although unproven, method of adding marine-derived nutrients to headwater streams (Cederholm et al. 2001). Our study emphasizes the need for more research in natural streams. We found that relatively few significant changes in selected response variables could be differentiated from background variation and that these changes were observed only in close proximity to the carcasses. Although we were able to detect significant differences in ammonium concentrations and total insect densities, smaller and undetected effects may have

had biologically meaningful consequences. Stable isotope analyses are useful for detecting more subtle responses in the food web, but as shown here, a strong stable isotope signal may not correspond with biological change. A variety of stream settings should be studied to understand the potential range of trophic responses to salmon carcasses at different densities so that scientists and managers can anticipate with greater certainty where carcass supplementation will have a demonstrated beneficial effect.

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