Salmon Carcasses Increase Stream Productivity More than Inorganic Fertilizer Pellets: A Test on Multiple Trophic Levels in Streamside Experimental Channels

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Abstract.—Inorganic nutrient amendments to streams are viewed as possible restoration strategies for re-establishing nutrients and stream productivity throughout the western coast of North America, where salmon runs and associated marine-derived nutrient subsidies have declined. In a mesocosm experiment, we examined the short-term (6 weeks) comparative effects of artificial nutrient pellets and salmon carcasses, alone (low and high amounts) and in combination, on stream food webs. Response variables included dissolved nutrient concentrations, biofilm ash-free dry mass (AFDM) and chlorophyll-a levels, macroinvertebrate density, growth and body condition of juvenile coho salmon Oncorhynchus kisutch, and whole-body lipid content of invertebrates and juvenile coho salmon. Most of the response variables were significantly influenced by carcass treatment; the only response variable significantly influenced by fertilizer pellet treatment was soluble reactive phosphorus (SRP) concentration. Ammonium-nitrogen concentration was the only response variable affected by both (low and high) levels of carcass treatment; all others showed no significant response to the two carcass treatment levels. Significant treatment $\times$ time interactions were observed for all responses except nitrate; for most responses, significant treatment effects were detected at certain time periods and not others. For example, significantly higher SRP concentrations were recorded earlier in the experiment, whereas significant fish responses were observed later. These results provide evidence that inorganic nutrient additions do not have the same ecological effects in streams as do salmon carcasses, potentially because inorganic nutrient additions lack carbon-based biochemicals and macromolecules that are sequestered directly or indirectly by consumers. Salmon carcasses, preferably deposited naturally during spawning migrations, appear to be far superior to inorganic nutrient amendments for sustaining and restoring stream productivity, including fish production, and should be chosen over artificial nutrient additions when feasible and practical.

Stream ecosystems throughout western North America are often nutrient limited, at least at basal trophic levels (see Ashley and Slaney 1997; Murphy 1998). Primary production can be controlled by phosphorus...
Juvenile coho salmon (Mundie et al. 1983) and the growth rates of increased biomass and densities of benthic invertebrates in streams often leads to increased production, growth, or densities of upper trophic levels, including fishes (Peterson et al. 1993; Perrin and Richardson 1997). Stream food webs that respond to nutrient additions are usually nutrient-limited, open-canopied systems that receive ample solar radiation (see Stevenson et al. 1996; Ambrose et al. 2004; Wilzbach et al. 2005).

Alternatively, carbon from allochthonous inputs can be the primary driver of stream productivity, especially in small streams (Vannote et al. 1980; Bisson and Bilby 1998; Wallace et al. 1999). Riparian litter that falls into streams is often the main source of energy for aquatic heterotrophs and invertebrates in low-order, forested streams in the Pacific Northwest and elsewhere (Cummins et al. 1989; Wallace et al. 1997; Suberkropp 1998). Supplements of organic carbon to streams increased biomass and densities of benthic invertebrates (Mundie et al. 1983) and the growth rates of juvenile coho salmon Oncorhynchus kisutch (Mason 1976) on Vancouver Island, British Columbia, suggesting that these systems may be at least partly carbon limited. Conversely, Bilby and Bisson (1992) found that both autotrophic and heterotrophic pathways were important for salmonid production in selected tributaries in Washington under both closed- and open-canopied conditions. Autotrophic pathways were most important for salmonid production in spring and summer in these small streams, whereas heterotrophic processes were dominant in fall and winter.

Allochthonous inputs from the ocean in the form of returning adult salmon supply both nutrients and carbon to many coastal freshwater ecosystems (Gende et al. 2002). This biomass influx elevates biofilm ash-free dry mass (AFDM), biofilm chlorophyll \( a \), and invertebrate densities in streams (Wipfli et al. 1998, 1999; Johnston et al. 2004; Mitchell and Lamberti 2005) as well as increasing juvenile salmonid biomass and growth rates (Bilby et al. 1998; Wipfli et al. 2003; Scheuerell et al. 2007). Although it is not clear what specifically is controlling food web responses to this marine subsidy, evidence suggests that both nutrients (e.g., nitrogen and phosphorus) and carbon may be important (Perrin et al. 1987; Johnston et al. 1990, 2004; Ashley and Slaney 1997; Wipfli et al. 1998; Pearsons et al. 2007). Wipfli et al. (1999) found that although biofilm mass increased markedly from salmon carcasses in Alaska streams, very little chlorophyll \( a (<0.006\%) \) was present in the biofilm, suggesting that a large portion of it consisted of heterotrophs. Gende et al. (2002) suggested that lateral inputs (i.e., allochthonous carbon) rather than bottom-up controls (i.e., nutrients) may be more important in salmon-based riverine food webs. These lateral inputs were shown to be important trophic pathways for aquatic invertebrates (Minakawa and Gara 1999; Chaloner and Wipfli 2002) and vertebrates (Cederholm et al. 1989; Willson et al. 1998; Hicks et al. 2005) in salmon-based systems. Chaloner and Wipfli (2002) demonstrated that selected invertebrates increased their growth rates when given salmon tissue. Juvenile salmonids also feed directly on salmon tissue and eggs (Bilby et al. 1996), and their body size, growth rates, and whole-body lipid concentrations increased in the presence of salmon carcasses (Wipfli et al. 2003, 2004; Heintz et al. 2004, 2010; Giannico and Hinch 2007). This supports the notion that inputs of carbon can be important drivers of stream communities.

Although Pacific salmon bring back huge amounts of nutrients and energy to aquatic ecosystems each year when they spawn and die (Levy 1997; Gende et al. 2002; Naiman et al. 2002), many aquatic systems along the western coast of North America could be suffering from a nutrient deficit because of dramatic decreases in spawner densities over the past decades (Cederholm et al. 1999; Gresh et al. 2000). This loss of marine-derived biomass may be causing large declines in aquatic and riparian productivity (Gende et al. 2002; Naiman et al. 2002). Attempts to restore lost nutrients and productivity in streams have included adding hatchery salmon carcasses, carcass analogs, and artificial fertilizers (nutrient pellets) to streams (Ashley and Slaney 1997; Levy 1997; Cederholm et al. 1999; Wipfli et al. 2004; Pearsons et al. 2007; Kohler et al. 2008). While artificial nutrient additions and fertilization programs have been successful at increasing aquatic productivity and fish production in some cases (Stockner and Shortreed 1978; Johnston et al. 1990; Peterson et al. 1993; Ashley and Slaney 1997; Stockner 2003), the comparative effects of enrichment from artificial nutrient additions versus salmon carcasses have not been investigated. Artificial nutrient amendments lack carbon, which may explain the breadth and magnitude of stream food web responses to salmon carcasses (Wipfli et al. 2003, 2004; Pearsons et al. 2007). Lipids, protein, and other carbon-based macromolecules may be critically important for the nutritional health and productivity of aquatic ecosystems (Heintz et al. 2004, 2010).

The objectives of this study were to measure the comparative responses of multiple food web compo-
nents (nutrients, biofilm, invertebrates, and fish) to salmon carcasses and inorganic nutrient pellets in streamside experimental channels. We wanted to (1) compare stream food web effects from slow-release fertilizer pellets containing nitrogen and phosphorus with effects from salmon carcasses and (2) determine when effects occurred over a period of 6 weeks. We measured ammonium-nitrogen (NH$_4^+$-N), nitrate-nitrogen (NO$_3^-$-N), and soluble reactive phosphorus (SRP); biofilm AFDM and chlorophyll a; benthic invertebrate density; juvenile coho salmon growth and body condition; and invertebrate and coho salmon whole-body lipid content. Information gained in this study will (1) further our understanding of ecological effects of marine subsidies in freshwater ecosystems, (2) help clarify the role nutrients (e.g., nitrogen or phosphorus) and carbon play in stream productivity, (3) aid in marine and freshwater ecosystem management, and (4) provide guidance for salmon protection and restoration (Ashley and Slaney 1997).

**Methods**

The experiment was conducted during 23 July–4 September 2001 in 36 experimental stream channels constructed along Sheep Creek near Juneau, Alaska. Stream water containing naturally occurring invertebrates, organic detritus, sediment, and nutrients from Sheep Creek (upstream of a barrier to salmon migration) was gravity-fed through two polyethylene pipes (15 cm in diameter × 90 m long) to a plastic head tank (1,900 L) and from the head tank to each channel through 36 polyethylene pipes (3-cm diameter) fitted with controllable T-valves. Nylon nets (9-mm mesh) filtered coarse detritus from water entering the head tank to prevent debris from clogging valves.

The 36 channels (each 294 cm long × 18 cm wide × 23 cm tall) were constructed of plywood, with six channels to a platform on six platforms. Each channel was divided into three sections: an upstream pool (102 cm long × 18 cm wide × 20 cm deep) to which carcass or fertilizer treatments were applied, a mid-channel riffle (66 cm long × 18 cm wide × 2 cm deep) for sampling macroinvertebrates and biofilm, and a downstream pool (118 cm long × 18 cm wide × 7 cm deep) that served as habitat for juvenile coho salmon. The riffle contained five plastic substrate baskets (13 cm long × 18 cm wide × 4 cm deep) constructed of plastic mesh (6-mm openings); each basket was lined with fiberglass mesh (2-mm openings) and filled with 200 mL of small (1–3-cm) stream gravel and 160 mL of large (3–5-cm) stream gravel. The three center baskets were sampled for macroinvertebrates, while the outer two served as buffers to reduce possible edge effects. The fiberglass liners helped prevent invertebrates from escaping when baskets were removed from channels during sampling. Three unglazed clay tiles (5 × 5 cm) were placed on the surface of the four downstream baskets for sampling biofilm. The riffle was elevated (6–16 cm) off the channel bottoms with an impervious layer and was sloped (15%) to create rapid flow across the gravels and minimize sediment accumulation in substrate baskets. The downstream pool was filled with 3.7 L of gravel (about 3 cm in diameter) and was divided into three subreaches by attaching two wooden blocks (8 cm long × 9 cm wide × 4 cm thick) to alternate sides of the channel. Blocks protruded about halfway (8 cm) across the channel, creating sinuous flow. Three stones (~13 × 7 × 5 cm) were placed in each pool subreach to provide cover for the small coho salmon. Perforated aluminum plates at each end of the pool prevented coho salmon from escaping.

All 36 channels were covered with clear Plexiglas (4.4 mm thick) to prevent tampering by vertebrates and shade cloth (55% shade) to simulate typical light conditions present in salmon spawning streams of southeastern Alaska. Discharge through channels was maintained at 0.6 L/s during the experiment, and stream water passage through channels began 4 d before the experiment started. Water temperature in the head tank was logged every hour with an Optic Stowaway and averaged 7.4°C (range = 6.2–9.3°C).

The upstream pool in each channel received one of six treatments (all applied at the start of the experiment) according to a Latin square design (Montgomery 1991): low concentration of salmon tissue, high concentration of salmon tissue, low concentration of fertilizer, high concentration of fertilizer, a combination of low concentrations of tissue and fertilizer, and no fertilizer or tissue (Table 1). The six treatments were each replicated (blocked) across the six tables (6 treatments × 6 blocks = 36 channels). Salmon tissue consisted of carcass chunks and eggs from female chum salmon O. keta. Chunks were transverse sections (184–741 g wet mass) from between the pectoral fin and anus; eggs were single or in skeins. Fertilizer (16-30-0 N-P-K) consisted of slow-release, 8-g nutrient pellets (“silver bullets” as used in other studies; Ashley and Slaney 1997) manufactured by Lesco, Inc. Fertilizer contained 16.0% nitrogen as urea (4.0%) and magnesium ammonium phosphate (12.0%), phosphoric acid (30.0%; 13.1% as phosphorus), magnesium (11.0%), and vegetable oil (2.0%). Analysis of fertilizer by an independent laboratory showed that pellets contained 14.7% nitrogen and 36.7% phosphoric acid (16.0% as phosphorus) and thus were slightly higher in nitrogen than the formulation used by Ashley and Slaney (1997). Our intent was to match the amount of
phosphorus released from fertilizer pellets to that of carcasses for both low and high concentrations of each (Table 1). Pre-experiment trials and previous studies (Ashley and Slaney 1997; Wipfli et al. 1998, 1999) indicated that we could expect about 50% less phosphorus release into stream water from the carcasses than from the nutrient pellets over the course of this experiment, which would translate into roughly the same amount of phosphorus release into stream water between the two treatment types at the given treatment levels, and this turned out to be very close (Table 1). Nutrient stocking densities were determined from past studies (Wipfli et al. 1998, 1999) to reflect natural runs of salmon in area streams. To simulate the natural physical breakdown of salmon carcasses in streams, carcass chunks (50% of the original amount added) in each channel were hand-macerated after 2 and 4 weeks. Carcass maceration and suspension of tissue fragments caused tissue to drift into riffle and pool substrates as observed in natural streams from normal physical breakdown processes (authors’ personal observation). Some tissue drifted out of the channels during and immediately after physical disturbance. We conducted the experiment for 6 weeks because previous studies demonstrated that this would be ample time to capture most food web responses from a single-pulse nutrient treatment (Wipfli et al. 1998, 2003, 2004).

Every 2 weeks during the 6-week experiment, we measured ammonium-nitrogen, nitrate-nitrogen, and SRP concentrations; biofilm AFDM and chlorophyll a; macroinvertebrate density; and juvenile coho salmon growth and condition. Macroinvertebrates (for density) and biofilm (for AFDM and chlorophyll a) were sampled from one of the middle three baskets during each period as determined by a Latin square design. Whole-body lipid content in coho salmon and macroinvertebrates was measured at the end of the experiment.

Triplicate water samples for analysis of ammonium, nitrate, and SRP were collected from each channel. Water samples were taken from the upstream pool outlet using a 60-mL syringe and were filtered in the field through a syringe filter holder fitted with a Whatman GF/F filter (0.7 μm). Nitrate and SRP samples were stored frozen at −20°C and usually analyzed within 1 week of sampling. Nitrates were analyzed using the hydrazine reduction method adapted from Kamphake et al. (1967). The SRP was analyzed using the ascorbic acid method with a spectrophotometer cell (10-cm path length; APHA 1992). Ammonium was analyzed immediately after sampling using the fluorometric ammonium analysis technique (Holmes et al. 1999).

Each sampling period, three tiles from each riffle were placed in individual plastic bags with stream water and transported to the laboratory for analysis of biofilm AFDM chlorophyll-a levels (mass/unit area). The upper surface of each tile was scrubbed with a toothbrush, and the biofilm was pooled into one sample for each channel. Samples were filtered onto pre-ashed Gelman AE glass fiber filters and stored in dark film canisters at −20°C until analyzed (within the next few days). Chlorophyll a was extracted in 90% buffered acetone for 24 h at 4°C and was determined spectrophotometrically and corrected for phaeopigments (APHA et al. 1999). After the chlorophyll-a analysis, the entire sample was transferred to an

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**Table 1.** Salmon carcass (from chum salmon) and fertilizer (nutrient pellet) treatments in experimental stream channels near Sheep Creek, Alaska. Treatments are control, low carcass (LC), low fertilizer (LF), high carcass (HC), high fertilizer (HF), and carcass plus fertilizer combination (CF).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>LC</th>
<th>LF</th>
<th>HC</th>
<th>HF</th>
<th>CF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total P added to channels (g)a</td>
<td>0</td>
<td>11.2</td>
<td>22.1</td>
<td>22.4</td>
<td>44.2</td>
<td>33.3</td>
</tr>
<tr>
<td>Total P added to channels (g/m²)</td>
<td>0</td>
<td>21.1</td>
<td>41.7</td>
<td>42.3</td>
<td>83.4</td>
<td>62.8</td>
</tr>
<tr>
<td>P released into stream water (g)b</td>
<td>NA</td>
<td>4.2</td>
<td>3.2*</td>
<td>5.5</td>
<td>6.5</td>
<td>8.9</td>
</tr>
<tr>
<td>Percent P &quot;loss&quot; during experiment</td>
<td>NA</td>
<td>37.3</td>
<td>14.3</td>
<td>24.6</td>
<td>14.7</td>
<td>22.6</td>
</tr>
<tr>
<td>Total N added to channels (g)</td>
<td>0</td>
<td>117.4</td>
<td>20.1</td>
<td>234.8</td>
<td>40.2</td>
<td>137.5</td>
</tr>
<tr>
<td>Total N added to channels (g/m²)</td>
<td>0</td>
<td>221.5</td>
<td>37.9</td>
<td>443.0</td>
<td>75.8</td>
<td>259.4</td>
</tr>
<tr>
<td>Carcass mass (kg)</td>
<td>0</td>
<td>3.6</td>
<td>7.2</td>
<td>1.6</td>
<td>3.6</td>
<td>0.9</td>
</tr>
<tr>
<td>Estimated carcass dry mass (kg)</td>
<td>0</td>
<td>0.9</td>
<td>1.9</td>
<td>1.6</td>
<td>6.0</td>
<td></td>
</tr>
<tr>
<td>Carcass concentration (kg wet mass·L⁻¹·s⁻¹)</td>
<td>0</td>
<td>6.0</td>
<td>12.0</td>
<td>6.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carcass mass (kg wet mass/m² of streambed area)</td>
<td>0</td>
<td>6.8</td>
<td>13.6</td>
<td>6.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carcass density (carcasses/m²)</td>
<td>0</td>
<td>1.6</td>
<td>3.2</td>
<td>1.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*a Total P in carcass tissue was estimated using unpublished data for percent P in muscle and eggs of "fresh or entry" chum salmon (Gende et al. 2004). The P content of fertilizer was determined by an independent laboratory.

* Calculated from stream water chemistry data. The water source passed an additional 3.8 g of P through each channel during the 6-week experiment.

* P loss calculated from fertilizer analysis was 5.8 g in the LF treatment.
aluminum weigh pan, dried, and analyzed for AFDM (Steinman et al. 2006).

Macroinvertebrates were sampled from substrate baskets after the removal of tiles. Baskets were removed with a net (250-μm mesh) held downstream to capture dislodged macroinvertebrates. Removed baskets were immediately replaced with another substrate basket. Macroinvertebrates were washed from the net, basket, and substrates, filtered onto a 250-μm sieve, and placed in 70% ethyl alcohol. In the laboratory, macroinvertebrates from whole samples or subsamples (50% or 25% depending on sample quantity) were counted and identified under a dissecting microscope (20–40× magnification). Invertebrates from substrate baskets and the downstream pool were collected for lipid analysis at the end of the experiment. The most abundant taxa (chironomids, mayflies Baetis spp., and stoneflies Zapada spp.) from each channel sampled were placed in individual plastic bags and stored at −80°C until lipid extraction and analysis.

Juvenile (age 0+) coho salmon from a nearby stream were captured with baited minnow traps and visually separated into four size-classes: small (mean wet mass $\pm$ SD = 0.51 ± 0.09 g), small-medium (0.78 ± 0.09 g), medium-large (1.12 ± 0.15 g), and large (1.74 ± 0.40 g). One individual from each size-group was anesthetized (with Finquel), wet mass (nearest 0.01 g) and fork length (nearest 0.5 mm) were measured, and the fish was released into the lower pool habitat in each channel (total of 4 fish/channel). The pool habitat closely mimicked the natural stream rearing habitat of juvenile coho salmon, and stocking density was within the normal range seen in area streams (Wipfli et al. 2010). Coho salmon (four per channel, one from each size category) were released into channels 1 d after treatment (platforms 1–3) and 2 d (platforms 4–6) after treatment. Time periods were subunits within channels and analyzed with a split-plot analysis of variance (ANOVA; $\alpha$ = 0.05). Responses included nitrate-nitrogen, ammonium-nitrogen, and SRP concentrations; biofilm AFDM and chlorophyll-$a$ levels; macroinvertebrate density; and juvenile coho salmon growth and $K$. Statistical tests included a treatment effect, time effect, and treatment × time interaction (SAS Institute 1989). Planned contrasts were: (1) control versus average low and high carcass, (2) control versus average low and high fertilizer, (3) low carcass versus high carcass, (4) low fertilizer versus high fertilizer, (5) average low and high carcass versus average low and high fertilizer, and (6) low carcass versus low carcass–fertilizer combination. Since the six contrasts were not orthogonal, $\alpha$ was adjusted from 0.05 to 0.0083 ($\alpha/6$) according to Sokal and Rohlf (1995). We adjusted the critical $\alpha$ value for each contrast using the Bonferroni correction, which maintains a constant familywise error rate by adjusting the critical $\alpha$ based on the number of hypotheses being tested (Sokal and Rohlf 1995). For those responses with a significant treatment × time interaction, contrasts were tested again within each time period to better understand how treatment effects varied through time. Macroinvertebrate density data were positively
skewed and the variance was heterogeneous; therefore, the data were log transformed to meet ANOVA normality and homogeneity of variance assumptions. Log-transformed data were checked for normality with normal plots and the Shapiro–Wilk test for normality (Shapiro and Wilk 1965). Homogeneity of variances was examined using Bartlett’s test (Snedecor et al. 1989). Untransformed data are presented in the figures.

Contrasts 1 and 2 above allowed us to test for carcass and fertilizer effects, respectively. Contrasts 3 and 4 provided a test for treatment loading (for both carcass and fertilizer). Contrast 5 allowed us to compare responses between carcass and fertilizer treatments, and contrast 6 allowed us to investigate the effects of adding fertilizer to a low background carcass density. This last contrast provided the opportunity to test whether adding fertilizer to streams with a “suppressed” salmon return (i.e., lower carcass density) significantly elevated responses beyond the low carcass effect level.

Lipid content was measured within a smaller subset of responses due to the high costs associated with lipid analyses. Percent lipid content in macroinvertebrates was measured for three treatments (control, high carcass, and high fertilizer) within four platforms (1, 3, 5, and 6) for the last time period. Percent lipid content in coho salmon was measured in the same manner except that we used six platforms (replicates) instead of four. These data were analyzed with a two-way ANOVA (α = 0.05), with platforms serving as completely randomized blocks. Planned contrasts were (1) control versus high carcass, (2) control versus high fertilizer, and (3) high carcass versus high fertilizer. Since the three contrasts were not orthogonal, α was adjusted from 0.05 to 0.0167 (i.e., α/3). These three contrasts allowed us to test for and compare carcass and fertilizer effects.

**Results**

There was a significant overall treatment effect for SRP, ammonium-nitrogen, density of invertebrates other than chironomids, and coho salmon growth (wet mass), K, and lipids (Tables 2, 3; \( P < 0.0083 \) and \( P < 0.0167 \) for analyses in Tables 2 and 3, respectively). Nearly all of the response variables were significantly influenced by carcass addition, whereas the only one influenced by the fertilizer treatments was SRP. Ammonium-nitrogen was the only response variable that was significantly greater for the high versus low carcass treatments (\( P < 0.0083 \)); all other response variables showed no significant differences between the two carcass levels (\( P > 0.0083 \)). There was no effect between the two levels of artificial nutrients added across all response variables. There was a significant treatment × time interaction for all responses except nitrate (Table 2; \( P < 0.05 \)). Depending upon response, significant effects were detected at some time periods and not others. For example, SRP differences were detectable early on in the experiment, whereas biofilm, invertebrate, and fish responses were generally seen later.

Specific nutrient responses were variable (Figure 1). Concentrations of SRP were significantly higher for carcass and nutrient pellet treatments than for the control treatment during most of the sampling times (\( P < 0.0083 \)), while nitrate-nitrogen showed no response to any of the carcass or fertilizer treatments (\( P > 0.05 \); Table 2). On the other hand, ammonium-nitrogen was significantly higher in the carcass treatments than in the control and fertilizer treatments, was significantly higher in the high carcass treatment than in the low carcass treatment at each individual period (2, 4, and 6 weeks; \( P < 0.0083 \)), but showed no response to fertilizer treatments (\( P > 0.05 \)).

Although biofilm AFDM and chlorophyll a did not show overall treatment effects (\( P > 0.05 \)), there was a significant treatment × time interaction. Significant interaction effect was due to carcass effects during the last time period (6 weeks) for chlorophyll a (\( P = 0.002 \); Figure 2). There were no fertilizer effects on chlorophyll a (\( P > 0.05 \)). There was a significant treatment × time interaction effect for biofilm AFDM (\( P < 0.05 \)). Effects were significantly higher in the carcass treatment than in the control treatment at 4 and 6 weeks and were also higher in the carcass treatment than in the fertilizer treatment at 6 weeks (\( P < 0.0083 \)). No other significant responses for biofilm were detected with the remaining contrasts (\( P > 0.05 \)).

We detected no significant overall treatment effect on total invertebrate and chironomid densities (\( P > 0.05 \)), but we did detect an effect on nonchironomid invertebrates (\( P = 0.049 \); Figure 3). Invertebrate communities were largely dominated by Chironomidae (>90%), followed by Zapada (3%) and Baetis (3%), in proportions similar to those seen in natural streams of southeast Alaska (Wipfli et al. 1998, 1999; Lessard and Merritt 2006). We detected a significant treatment × time interaction (\( P < 0.001 \)) for all three invertebrate responses. Chironomid densities were significantly higher in carcass treatments than in control and fertilizer treatments at both 4 and 6 weeks. Low and high carcass treatments had similar effects on invertebrates, with no significant differences between the two treatments (\( P > 0.05 \)). There were no effects from fertilizer treatments relative to the control (\( P > 0.05 \)), but we did detect slightly higher nonchironomid invertebrate densities in the fertilizer treatments than in the carcass treatments (\( P = 0.006 \)); we attributed this result to increased Zapada
Table 2.—Analysis of variance output (P-values) for overall treatment effect, treatment × time interaction, and individual a priori contrasts for the addition of chum salmon carcasses or fertilizer to experimental streams (SRP = soluble reactive phosphorus; chl $a$ = chlorophyll $a$; AFDM = ash-free dry mass; NT = not tested). Significant differences are indicated by $P$-values in bold.

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Nitrate</th>
<th>SRP</th>
<th>Ammonium</th>
<th>Biofilm chl $a$</th>
<th>Biofilm AFDM</th>
<th>Density of all invertebrates</th>
<th>Chironomid-only density</th>
<th>Non-chironomid taxa density</th>
<th>Coho salmon condition</th>
<th>Coho salmon wet mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall treatment effect ($\alpha = 0.05$)</td>
<td>Overall treatment effect ($\alpha = 0.05$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual contrasts—all time periods ($\alpha = 0.0083$)</td>
<td>Control vs. carcass</td>
<td>0.412</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>0.865</td>
<td>0.866</td>
<td>0.604</td>
<td>0.711</td>
<td>0.049</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Low vs. high carcass</td>
<td>0.746</td>
<td>0.385</td>
<td>0.027</td>
<td>0.952</td>
<td>0.985</td>
<td>0.535</td>
<td>0.528</td>
<td>0.867</td>
<td>0.846</td>
<td>0.638</td>
</tr>
<tr>
<td>Control vs. fertilizer</td>
<td>0.285</td>
<td>$0.003$</td>
<td>0.145</td>
<td>0.833</td>
<td>0.698</td>
<td>0.777</td>
<td>0.794</td>
<td>0.696</td>
<td>0.945</td>
<td>0.620</td>
</tr>
<tr>
<td>Low vs. high fertilizer</td>
<td>0.107</td>
<td>0.056</td>
<td>0.830</td>
<td>0.929</td>
<td>0.988</td>
<td>0.531</td>
<td>0.560</td>
<td>0.411</td>
<td>0.435</td>
<td>0.496</td>
</tr>
<tr>
<td>Carcass vs. fertilizer</td>
<td>0.026</td>
<td>0.011</td>
<td>$&lt;0.001$</td>
<td>0.523</td>
<td>0.605</td>
<td>0.172</td>
<td>0.239</td>
<td>0.006</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Carcass + fertilizer vs. vs. low carcass</td>
<td>0.202</td>
<td>$0.003$</td>
<td>0.127</td>
<td>0.589</td>
<td>0.595</td>
<td>0.690</td>
<td>0.733</td>
<td>0.389</td>
<td>0.324</td>
<td>0.093</td>
</tr>
<tr>
<td>Overall treatment × time interaction ($\alpha = 0.05$)</td>
<td>Overall treatment × time interaction ($\alpha = 0.05$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual contrasts—2 weeks ($\alpha = 0.0083$)</td>
<td>Control vs. carcass</td>
<td>NT</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>0.006</td>
<td>0.850</td>
<td>0.007</td>
<td>0.014</td>
<td>$&lt;0.001$</td>
<td>0.051</td>
</tr>
<tr>
<td>Low vs. high carcass</td>
<td>0.715</td>
<td>$0.004$</td>
<td>0.069</td>
<td>0.056</td>
<td>0.251</td>
<td>0.223</td>
<td>0.364</td>
<td>0.146</td>
<td>0.199</td>
<td></td>
</tr>
<tr>
<td>Control vs. fertilizer</td>
<td>0.019</td>
<td>0.101</td>
<td>0.488</td>
<td>0.231</td>
<td>0.522</td>
<td>0.579</td>
<td>0.275</td>
<td>0.615</td>
<td>0.779</td>
<td></td>
</tr>
<tr>
<td>Low vs. high fertilizer</td>
<td>0.178</td>
<td>0.865</td>
<td>0.826</td>
<td>0.935</td>
<td>0.116</td>
<td>0.140</td>
<td>0.097</td>
<td>0.150</td>
<td>0.216</td>
<td></td>
</tr>
<tr>
<td>Carcass vs. fertilizer</td>
<td>0.062</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>0.216</td>
<td>0.010</td>
<td>0.017</td>
<td>0.002</td>
<td>0.070</td>
<td>0.007</td>
<td></td>
</tr>
<tr>
<td>Carcass + fertilizer vs. vs. low carcass</td>
<td>NT</td>
<td>0.033</td>
<td>0.106</td>
<td>0.255</td>
<td>0.713</td>
<td>0.203</td>
<td>0.156</td>
<td>0.396</td>
<td>0.592</td>
<td>0.132</td>
</tr>
<tr>
<td>Individual contrasts—4 weeks ($\alpha = 0.0083$)</td>
<td>Control vs. carcass</td>
<td>NT</td>
<td>$0.003$</td>
<td>$&lt;0.001$</td>
<td>0.021</td>
<td>0.005</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>0.101</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Low vs. high carcass</td>
<td>NT</td>
<td>0.027</td>
<td>$&lt;0.001$</td>
<td>0.158</td>
<td>0.124</td>
<td>0.038</td>
<td>0.031</td>
<td>0.784</td>
<td>0.897</td>
<td>0.823</td>
</tr>
<tr>
<td>Control vs. fertilizer</td>
<td>NT</td>
<td>$&lt;0.001$</td>
<td>0.587</td>
<td>0.432</td>
<td>0.276</td>
<td>0.485</td>
<td>0.455</td>
<td>0.752</td>
<td>0.446</td>
<td>0.178</td>
</tr>
<tr>
<td>Low vs. high fertilizer</td>
<td>NT</td>
<td>0.007</td>
<td>0.764</td>
<td>0.932</td>
<td>0.404</td>
<td>0.732</td>
<td>0.718</td>
<td>0.923</td>
<td>0.952</td>
<td>0.635</td>
</tr>
<tr>
<td>Carcass vs. fertilizer</td>
<td>NT</td>
<td>0.451</td>
<td>$&lt;0.001$</td>
<td>0.053</td>
<td>0.023</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>0.020</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Carcass + fertilizer vs. vs. low carcass</td>
<td>NT</td>
<td>$&lt;0.001$</td>
<td>0.297</td>
<td>0.643</td>
<td>0.662</td>
<td>0.261</td>
<td>0.271</td>
<td>0.511</td>
<td>0.503</td>
<td>0.095</td>
</tr>
<tr>
<td>Individual contrasts—6 weeks ($\alpha = 0.0083$)</td>
<td>Control vs. carcass</td>
<td>NT</td>
<td>0.421</td>
<td>$&lt;0.001$</td>
<td>0.002</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>0.002</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Low vs. high carcass</td>
<td>NT</td>
<td>0.827</td>
<td>$&lt;0.001$</td>
<td>0.148</td>
<td>0.026</td>
<td>0.038</td>
<td>0.284</td>
<td>0.258</td>
<td>0.486</td>
<td>0.145</td>
</tr>
<tr>
<td>Control vs. fertilizer</td>
<td>NT</td>
<td>$&lt;0.001$</td>
<td>0.696</td>
<td>0.190</td>
<td>0.115</td>
<td>0.485</td>
<td>0.737</td>
<td>0.750</td>
<td>0.677</td>
<td>0.951</td>
</tr>
<tr>
<td>Low vs. high fertilizer</td>
<td>NT</td>
<td>0.037</td>
<td>0.828</td>
<td>0.697</td>
<td>0.423</td>
<td>0.752</td>
<td>0.906</td>
<td>0.377</td>
<td>0.499</td>
<td>0.664</td>
</tr>
<tr>
<td>Carcass vs. fertilizer</td>
<td>NT</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>0.015</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Carcass + fertilizer vs. vs. low carcass</td>
<td>NT</td>
<td>0.045</td>
<td>0.303</td>
<td>0.028</td>
<td>0.031</td>
<td>0.261</td>
<td>0.202</td>
<td>0.182</td>
<td>0.140</td>
<td>0.120</td>
</tr>
</tbody>
</table>

and $Baetis$ densities. Chironomid and total invertebrate densities for the combination treatment (carcass + fertilizer) were close to those recorded for the low carcass treatment, with no differences detected between these two treatments ($P > 0.05$).

Juvenile coho salmon $K$ dropped for all treatments at 2 and 4 weeks relative to that recorded at the start of the experiment, but $K$ then rebounded by the end of the experiment for those treatments that contained salmon carcasses—the low carcass, high carcass, and carcass–

Table 3.—Analysis of variance output (P-values) for overall treatment effect and individual a priori contrasts for lipid levels in invertebrate and fish tissue in response to the addition of chum salmon carcasses or fertilizer to experimental streams. Bold font indicates a significant difference; $\alpha$ is 0.05 for the main treatment effect and 0.0167 for paired contrasts.

<table>
<thead>
<tr>
<th>% Lipid</th>
<th>All invertebrate taxa</th>
<th>Chironomidae</th>
<th>$Baetis$</th>
<th>Zapada</th>
<th>Coho salmon fry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall treatment effect</td>
<td>0.672</td>
<td>0.119</td>
<td>0.612</td>
<td>0.085</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Control vs. high carcass</td>
<td>0.805</td>
<td>0.086</td>
<td>0.389</td>
<td>0.042</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Control vs. high fertilizer</td>
<td>0.547</td>
<td>0.853</td>
<td>0.426</td>
<td>0.778</td>
<td>0.325</td>
</tr>
<tr>
<td>High carcass vs. high fertilizer</td>
<td>0.405</td>
<td>0.066</td>
<td>0.942</td>
<td>0.058</td>
<td>$&lt;0.001$</td>
</tr>
</tbody>
</table>
fertilizer combination treatments (Figure 4). Condition factor for these fish was significantly higher in the carcass treatments than in the control treatment for the last two time periods ($P < 0.0083$). Condition factor was equally low for the fertilizer treatments as was recorded in the control treatment, with no significant differences between the two treatments ($P > 0.05$). Fish also grew faster in the carcass treatments, with significantly greater growth recorded for fish at the 4- and 6-week intervals ($P < 0.0083$). The combination carcass–fertilizer treatment produced roughly the same result as the low carcass treatment. The coho salmon also grew faster in the carcass treatments than in the fertilizer treatments ($P < 0.0083$). Fish in the fertilizer treatments did not grow faster than those in the control treatments ($P > 0.05$). Of the 11 fish that died or were missing during the experiment, three-fourths were from channels without salmon tissue.

There were no significant treatment (fertilizer or carcass) effects on invertebrate lipid levels ($P > 0.05$; Table 3; Figure 5). We did detect significantly higher lipid levels in the coho salmon exposed to salmon carcasses than in fish exposed to the control or fertilizer treatment ($P < 0.001$). There were no significant fertilizer effects on coho salmon lipids ($P > 0.05$).

**Discussion**

Most of the stream water chemistry and food web components sampled in this study responded to salmon carcass addition, which is consistent with other marine-derived nutrient (MDN) studies conducted throughout the Pacific Northwest. Biofilm, invertebrates, and fishes have generally responded strongly to MDN from salmon runs, carcass additions to streams, and carcass analog additions (Bilby et al. 1998; Wipfli et al. 1998, 2003, 2004; Minakawa and Gara 1999; Giannico...
and Hinch 2007; Pearsons et al. 2007; Scheuerell et al. 2007). Also, marine signatures of carbon and nitrogen have been observed in aquatic invertebrate and fish tissue, indicating that this marine-derived biomass is sequestered by freshwater fauna (Kline et al. 1990; Bilby et al. 1996, 2001; Chaloner et al. 2002a; Hicks et al. 2005).

Food web components exhibited no effect from the additional increment of carcass material in this study (6.8 versus 13.6 kg of wet mass/m² of streambed area), a finding consistent with that recorded by Wipfli et al. (1999), where additional increments of salmon tissue (range = 3.2–16.1 kg/m²) did not result in higher invertebrate densities. However, our results were inconsistent with biofilm responses in the Wipfli et al. (1999) study, where more AFDM was observed at the higher carcass densities. Wipfli et al. (2003) also detected a significant carcass-loading effect (range = 1.9–7.4 kg/m²) on juvenile coho salmon growth, but Chaloner et al. (2002a) did not observe a simple relationship between carcass loading and marine nitrogen and carbon uptake by the fish. Johnston et al. (1997) also did not observe any marine carbon uptake by stream salmonids in British Columbia, but they did find significant uptake of marine nitrogen by the fish up to a carcass loading density of about 4 kg/m². The response of aquatic communities to carcass loading may vary among trophic levels as well as among streams, with the latter being due to system-specific differences in physical, chemical, and biological features (Wipfli et al. 1999).

Conversely, the fertilizer additions in this study did not result in significant responses in any of the food web components, in spite of higher stream water SRP and ammonium concentrations from fertilizer treatments versus the control. Nitrate and SRP concentrations in stream water were roughly equal for both carcass and fertilizer treatments, and SRP concentrations were significantly higher for these two treatments relative to the control treatment, yet we recorded no significant effects of fertilizer treatments on food web components, in contrast to the results for carcass treatments. Therefore, our results suggest that this stream system, or at least biofilm development, was not limited by phosphorus but was potentially limited by something else, such as ammonium or carbon. Ammonium concentrations were significantly increased from carcass treatments but not from fertilizer pellets, and the three trophic levels tested all responded similarly, suggesting that ammonium from the rotting carcasses may have played a role in food web responses. Artificial nutrient addition studies in British Columbia have shown positive responses by biota, including patterns of increased fish growth and smolt...
production, but those studies were generally conducted over a much longer time period (years), they had multiple or semicontinuous applications of nutrients over a range of concentrations, and they were often unreplicated due to their natural stream settings (Ashley and Slaney 1997; Stockner 2003). Carbon (i.e., energy) from carcasses appeared to affect stream food webs in our study as much as or possibly even more than nutrients (e.g., nitrogen or phosphorus). This could be a function of the short-term duration of the study, where longer time frames may show food web effects from inorganic nutrients (Stockner 2003), and carbon may be providing a quicker consumer response than nutrients. Albeit limited, the literature suggests that stream food webs along the west coast of North America may be, at least in part, carbon limited.

Marine carbon was detected in multiple food web components in Alaskan systems receiving salmon runs (Kline et al. 1990; Chaloner et al. 2002a; Hicks et al. 2005). Cereal grain and soybean Glycine max meal added to stream troughs on Vancouver Island, British Columbia, increased count and biomass densities of aquatic invertebrates (Mundie et al. 1983), and juvenile coho salmon growth rates and overall biomass increased in response to the addition of euphausiid prey to another small Vancouver Island stream (Mason 1976), an example of lateral inputs in the form of carbon (i.e., food). Others have also demonstrated the important role of carbon in stimulating energy pathways in streams (Vannote et al. 1980; Wallace et al. 1997; Gende et al. 2002), including possibly through carcass analog additions (Wipfli et al. 2004;
However, if heterotrophic processes are the main energy flow pathways in this study, this phenomenon (carbon production) is still fundamentally an autotrophic process. In this case (i.e., marine subsidies from salmon runs in freshwater ecosystems), autotrophic pathways in the ocean gave rise to adult salmon biomass. This ocean-based carbon production is transferred from the marine ecosystems to freshwater ecosystems, ultimately subsidizing the land-based food webs (Bilby et al. 1998; Wipfli et al. 1998, 2003). Such lateral inputs (Gende et al. 2002) of carbon may partly override the consequences of oligotrophy in these aquatic ecosystems (Ashley and Slaney 1997), allowing for increased food web production in spite of limited instream primary production. Although carbon appears to be playing a large role in regulating this food web, we do not know the mechanism (i.e., dissolved organic matter uptake by heterotrophs, particulate organic matter ingestion by invertebrates and fish) or the form of carbon that is most important (e.g., proteins, amino acids, lipids; Gende et al. 2002). Furthermore, research on insect secondary production in southeast Alaska streams indicates important interactions between spawning disturbance and MDN enrichment, which regulates benthic community responses to MDN (Lessard et al. 2009) and may partly drive the enrichment mechanisms used by juvenile salmonids. For example, juvenile salmonids in streams dominated by fall runs of pink salmon _O. gorbuscha_ and chum salmon may rely on direct tissue and egg consumption for MDN transfer during the primary carcass decomposition period, while bottom-up pathways could provide additional MDN from short-lived multivoltine invertebrate taxa alone (e.g., chironomids; Chaloner and Wipfli 2002; Chaloner et al. 2002a; Hicks et al. 2005; Lessard and Merritt 2006; Lessard et al. 2009).

Given the preceding discussion, it is timely to consider the experimental environment. In spite of the strong food web responses and clear MDN effects measured in this study, it is important to keep in mind that this investigation took place in a mesocosm. To its credit, the study took advantage of many of the natural field conditions (i.e., experiments were conducted outdoors and streamside; channels received natural stream water containing the natural baseline water temperature, chemistry, particulates, and macroinvertebrates; and channels contained natural stream substrate), but applying the findings to natural streams needs to be done with caution. Although mesocosm

![Figure 4](image-url)

_Figure 4._ Mean (±SE) percent change in condition factor and growth (percent change in wet mass) of age-0 coho salmon at 2, 4, and 6 weeks after salmon carcass and nutrient pellet (fertilizer) additions to experimental stream channels. Treatment codes are defined in Figure 1.
studies can provide appropriately controlled experimental conditions and high replication of treatments, as was the case in this study, their application to natural settings still has limits. Nonetheless, these results do provide important clues about what can be expected in natural streams if adequate and true replication (problematic in many natural stream studies and case studies to date) proves feasible in subsequent natural stream studies. Ultimately, treatment contrasts and dose–responses need to be investigated in replicated natural streams to further determine whether these findings are supported beyond the small-scale mesocosm responses measured here. Ideally, concurrent natural stream studies (albeit potentially unreplicated) containing naturally returning and spawning salmon, coupled with mesocosm studies (highly replicated) that incorporate to the extent possible a broad suite of natural conditions (Wipfli et al. 1998; Chaloner et al. 2002a), will help move us towards a better understanding of salmon and nutrient effects in streams and on riverine food webs.

Community nutrition is undoubtedly a key component of healthy stream ecosystems (Meyer 1997) and in many cases may largely revolve around the subsidy of carbon found in a variety of forms, such as proteins, lipids, carbohydrates, and other macromolecules, that are essential for sustaining life (Adams 1998; Olsen 1998). These biochemicals may be critically important for maintaining productive stream food webs. Heintz et al. (2004, 2010) showed that omega-3 : omega-6 fatty acid ratios were much higher in young coho salmon that had access to food webs enriched with salmon carcasses, as these fish prepared themselves for their migration from freshwater to salt water, and the higher ratios apparently increased the likelihood of successful migration. Stored energy reserves (i.e., lipids) also were higher in salmonids that had access to salmon carcass-enriched stream food webs, as was found in this study. The rapid mass and lipid gains in the coho salmon in this short-term study probably indicate that fish would glean even greater benefits over longer periods, especially in the cases where returns of multiple salmon species are spread out over more of the year (Groot and Margolis 1991), leading to greater survival and eventual smolt production (Stockner 2003). Compensatory growth in fish not receiving as much MDN benefits might in part alleviate growth and lipid discrepancies the subsequent winter and spring (Wipfli et al. 2003), but the extent to which that might occur remains to be tested. Nonetheless, evolution of these aquatic ecosystems to the annual and predictable biomass from the ocean in the form of returning salmon may be the cornerstone of the systems’ historically productive nature (i.e., salmon production), and

![Graph showing invertebrate and age-0 coho salmon mean (±SE) percent whole-body lipid measured 6 weeks after salmon carcass and nutrient pellet (fertilizer) additions to experimental stream channels. Treatment codes are defined in Figure 1.](image)
sustaining this nutritionally balanced carbon and nutrient source may be the key to the long-term health, productivity, and sustainability of such systems.

This study illustrates the potential importance of carbon (and associated macromolecules) in the productivity and nutrition of salmon-based stream food webs. Clearly, nutrients (e.g., nitrogen and phosphorus) are also important for stream ecosystems (Stockner and Shortreed 1978; Bothwell 1989; Peterson et al. 1993; Borchardt 1996; Naiman et al. 2002; Sanderson et al. 2009). Both autotrophic and heterotrophic processes are likely to play a role in sustaining stream health and food web productivity (Meyer 1997; Meyer and Wallace 2001), as was illustrated by Bilby and Bisson (1992) for small streams in Washington. Comprehensive food web studies that aim to understand the broader short-, intermediate-, and long-term consequences of both carbon and nutrients on biodiversity, productivity, community nutrition, and species demographics and interactions are needed to help us better understand ecosystems and subsequently manage natural resources. Watersheds and stream food webs probably respond uniquely to salmon runs depending upon many system-specific physical, chemical, and biological conditions (Wipfli et al. 1999). Knowing what factors (i.e., nutrients, carbon, habitat, or other) limit salmon-based food webs and the magnitude of that limitation (i.e., degree of oligotrophy) on an ecoregion-by-ecoregion basis or even a watershed-by-watershed basis will help us understand the ecological significance of salmon returns.

These findings not only illustrate the need to better understand the ecological consequences of salmon carcasses, carbon, and nutrients in streams, they may also provide some clues for better aquatic ecosystem management. This study suggests that artificial inorganic nutrients, at least in the form of slow-release nutrient pellets, may not benefit salmon-based food webs in the same way as natural salmon runs. We caution against the well-intentioned practices of adding commercial fertilizers to streams for nutrient and food web rehabilitation purposes. The human fixation on and obsession with quick technological fixes to “repair” or “restore” natural processes, with the intent of substituting for nature, may lead us down the wrong path and may not be as beneficial as the real thing (i.e., naturally spawning salmon), or worse yet, may be harmful. Additions of only nutrients may promote prey species that are less desirable or less preferred by fishes and other consumers (Wipfli 1997). Consequences of adding only artificial nutrients may be that autotrophic pathways are stimulated when in fact the heterotrophic pathways may be as important as or more important than the autotrophic pathways. Salmon provide both nutrients and carbon along with critical macromolecules and other biochemicals that are not present in inorganic nutrients. Alternatively, both autotrophic and heterotrophic pathways may be important in these salmonid-rearing streams depending upon the time of year (Bilby and Bisson 1992), and the addition of both carbon and nutrients in the biologically suitable stoichiometric composition (Elser and Urabe 1999) provided by returning salmon may be the best remedy for keeping these aquatic ecosystems nutritionally healthy, productive, and biologically diverse. Further, carcasses provide a substrate (as well as a food source) for many invertebrates (Kline et al. 1997; Minakawa and Gara 1999): invertebrate densities can reach several thousand individuals per single salmon carcass (Chaloner et al. 2002b). These salmon-based communities may have evolved around the reliable annual input of marine subsidies from salmon runs, and attempts to replace this biochemically complex biomass with artificial nutrients may be short-sighted. Finally, this study highlights the need to better understand the comparative ecological effects of salmon runs and the various commercially available products being considered for restoring nutrients to salmonid ecosystems. While these replacements may hold some value in helping restore salmon runs in some regions, they appear to be vastly subordinate to the inputs from the biomass of naturally occurring salmon runs.

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