

## Restoring Productivity of Salmon-Based Food Webs: Contrasting Effects of Salmon Carcass and Salmon Carcass Analog Additions on Stream-Resident Salmonids

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**Abstract.**—We tested the hypotheses that salmon carcasses and salmon carcass analogs (dried, processed hatchery salmon) increase the condition factor, production, and whole-body lipid content of stream-resident salmonids and that stream shading affects responses to enrichment. Two enrichment treatments (salmon carcass, salmon analog) and a control, each with and without simulated riparian shading (95% shade), were replicated six times in once-through artificial channels (mesocosms). Each channel was stocked with three live young-of-the-year coho salmon *Oncorhynchus kisutch*. The experiment spanned 30 July through 18 September 2002. Production and lipid content significantly increased in both carcass and analog treatments. Condition was generally unchanged. Stream shading significantly reduced the magnitude of production and lipid responses. In addition, in a small stream where salmon carcasses and analogs were added to two separate tributaries, cutthroat trout *O. clarki* had higher mean condition, production, and lipid content than fish in stream sections that were not enriched (6 August to 20 September 2002). Furthermore, coho salmon production was also higher in an analog-enriched reach than in control reaches. This study illustrates that marine subsidies from salmon spawners and salmon analogs increase condition, production, and lipid concentrations of resident and anadromous salmonids. Larger and more lipid-rich fish may subsequently have higher survival and reproduction, thereby elevating freshwater and marine salmonid production. Salmon analogs appear to hold promise for restoring nutrients and productivity to freshwater ecosystems suffering reduced salmon runs and may prove to be a useful, albeit temporary, tool for improving aquatic productivity.

Ocean-derived biomass enters freshwater ecosystems each year when anadromous fishes return to their natal habitats to spawn (Mathisen et al. 1988; Gende et al. 2002). Fishes such as Pacific salmon *Oncorhynchus* spp. and eulachon *Thaleichthys pacificus* hatch in freshwater but spend most of their lives in salt water, sequestering nutrients and carbon derived from or produced in the ocean (Levy 1997; Willson et al. 1998). After returning to freshwater as reproductively mature adults, they mate, spawn, and die; in the process, they deposit nutrients and energy-rich carbon in the same habitats their young will soon occupy. The ecological benefits of this marine subsidy can be dramatic, not only for the plants and animals already occupying these habitats, but also for subsequent generations of their own deme that will

eventually rear there (Schmidt et al. 1998; Wipfli et al. 1998; Cederholm et al. 1999; Naiman et al. 2002; Wipfli et al. 2003).

This resource subsidy from the ocean has important ecological consequences for the members of freshwater food webs, including fishes. Bilby et al. (1996) showed that stream-resident salmonids consumed salmon eggs and tissue in two Washington streams, and that marine-derived nitrogen and carbon were subsequently taken up by these fishes, as evidenced by the presence of <sup>15</sup>N and <sup>13</sup>C in body tissues. Chaloner et al. (2002) found that stream-resident salmonids in southeastern Alaska, as well as lower trophic levels including biofilm and several species of aquatic insects, incorporated marine N (up to 73%) and C (up to 52%) in their tissues. These marine nutrients appear to increase food web productivity, elevating stream biofilm and chlorophyll-*a* levels (Wipfli et al. 1999), invertebrate densities and growth rates (Wipfli et al. 1998; Minakawa and Gara 1999; Chaloner et al. 2002; Chaloner and Wipfli 2002), and fish growth rates and biomass (Bilby et al. 1998; Wipfli et al. 2003). Fish health also appears

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to be affected by salmon runs. Heintz et al. (2004) found elevated levels of triacylglycerides (energy reserves) and marine-derived fatty acids (omega-3 fatty acids) in juvenile coho salmon *O. kisutch* exposed to salmon carcasses, which could lead to increased survival, reproduction, and overall performance (Adams 1998; Olsen 1998).

While Alaska, Yukon, and parts of British Columbia still support relatively high runs of salmon (Baker et al. 1996; Slaney et al. 1996), many river systems in southern British Columbia, California, Idaho, Oregon, and Washington have experienced salmon population declines over recent decades, especially in wild stocks (NRC 1996; Schoonmaker et al. 2003; Thomas et al. 2003). Reductions in salmon runs result in lower inputs of marine biomass that historically provided nutrients and carbon to these oligotrophic systems (Ashley and Slaney 1997; Gresh et al. 2000; Thomas et al. 2003). The effects of losing marine subsidies in freshwater food webs could potentially be profound. Food web productivity across multiple trophic levels could decrease, as was observed in Washington and Alaska streams that received few, if any, returning salmon (Bilby et al. 1998; Wipfli et al. 1998; Minakawa and Gara 1999; Wipfli et al. 2003).

The concept and practice of restoring nutrients and food web productivity in freshwater systems suffering depressed salmon runs and nutrient deficits continue to gain momentum in the Pacific Northwest (Ashley and Slaney 1997; Stockner 2003). Addition of P and N fertilizers to lakes has increased aquatic productivity and sockeye salmon *O. nerka* production in Alaska and British Columbia (Stockner and MacIsaac 1996; Kyle et al. 1997). Applications of these fertilizers to selected oligotrophic streams in British Columbia also appear to elevate productivity, where bottom-up effects often reach upper trophic levels (Ashley and Slaney 1997; Wilson et al. 2003). Although N and P fertilizers can stimulate primary producers (Borchardt 1996), they lack the carbon and carbon-based compounds, such as lipids and proteins, that salmon carcasses contain (Mathisen et al. 1988; Gende et al. 2002). These carbon-based compounds may be critical to other species and trophic levels in streams. They provide lateral-in effects, whereby consumers ingest the carbon directly from the spawners, as opposed to bottom-up effects, in which carbon produced by primary producers (i.e., algae) reaches consumers indirectly (Wipfli et al. 1998; Gende et al. 2002).

Fish carcass analogs (e.g., those made from

hatchery salmon) are also being produced and marketed as a way to restore lost nutrients and productivity through emulating the chemical makeup, stoichiometry, and dissolution rates of decomposing fish (Dennis Roley, Bio-Oregon, Inc., personal communication). Because they are often manufactured from hatchery salmon, which achieve most of their biomass in the ocean, analogs theoretically contain the same or a similar compliment of naturally occurring nutrients, carbon, and carbon-based compounds as is found in naturally returning salmon. Because they are compositionally (chemically) similar to salmon carcasses, salmon carcass analogs may provide the same benefits to food webs when added to streams. How the effects of these dried fish pellets actually compare with salmon carcasses in influencing stream food webs has not been determined.

Light regime can also play a major role in the response of certain trophic levels to the presence or absence of nutrient or food additions. Biofilm production is often higher in streams with less shading (Hill et al. 1995); more food is thus provided for grazing invertebrates, potentially increasing prey resources for fishes. Additionally, increased light levels may help drift-feeding fishes detect and capture prey more proficiently (Young et al. 1997; Vogel and Beauchamp 1999). An understanding of how food webs respond to nutrient supplements (e.g., via salmon carcasses or salmon analogs) under various stream shading scenarios would help unveil the potential management options, including nutrient supplementation and riparian canopy thinning, for small, forested, salmonid-rearing streams in Alaska and other regions.

The objective of this study was to compare the relative effects of salmon carcasses and manufactured salmon carcass analogs (salmon cakes) on stream-resident salmonids. We specifically wanted to decipher the relative influence of salmon carcasses and salmon analogs on juvenile coho salmon and cutthroat trout *O. clarki* condition, production, and lipid levels in southeastern Alaska. We also tested the effects of stream shading on the outcome of salmon carcass and carcass analog additions to determine whether enrichment effects (carcasses, analogs, or both) on fish differed in shaded versus unshaded streams. This information should be valuable for determining the utility of fish carcass or analog applications under different riparian canopy conditions for elevating aquatic productivity and restoring freshwater ecosystems

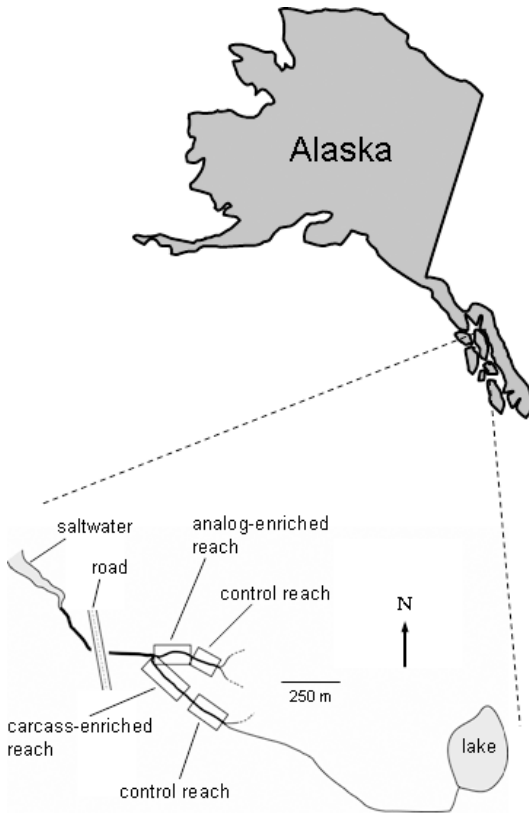


FIGURE 1.—Study reaches in Bridget Cove Creek, Alaska, where the effects of salmon carcass and carcass analog enrichment on juvenile salmonid condition, production, and lipid levels were studied during 2002.

in the Pacific Northwest and other places targeted for recovery.

### Methods

**Study sites.**—Studies were conducted in artificial (mesocosm) and natural streams near Juneau, Alaska, during summer 2002 ( $58^{\circ}37'16''\text{N}$ ,  $134^{\circ}56'11''\text{W}$ ; Figure 1). The mesocosm experiment was conducted from 30 July to 18 September 2002 in artificial streams constructed along Sheep Creek, about 10 km south of Juneau. The natural stream experiment extended from 6 August to 20 September 2002 in Bridget Cove (BC) Creek, a second-order stream about 40 km north of Juneau. The mesocosm experiment provided the statistical rigor commonly lacking in natural stream experiments. The natural stream experiment, in spite of lacking true replication, provided an opportunity to determine whether patterns documented in the

mesocosm experiment could also be observed in a natural setting.

**Mesocosm experiment.**—The mesocosm contained 36 once-through stream channels; six channels were situated on each of six platforms. The mesocosm operation and water supply system are described by Wipfli et al. (1998). Channels ( $294 \times 18 \times 23$  cm) were constructed of plywood with pine board sidewalls. Each channel was divided into three sections: an upstream pool ( $102 \times 18 \times 20$  cm) to which treatments (salmon carcasses or analogs) were applied, a riffle ( $66 \times 18$  cm) for sampling macroinvertebrates and biofilm, and a downstream pool ( $118 \times 18 \times 7$  cm) that served as habitat for age-0 coho salmon. The riffle consisted of five plastic substrate baskets ( $13 \times 18 \times 4$  cm) constructed of plastic mesh (6-mm openings). Each basket was lined with fiberglass mesh (2-mm openings) and filled with 250 mL of small (1–3 cm) stream gravel and 170 mL of large (3–5 cm) gravel. Three unglazed clay tiles ( $5 \times 5$  cm) were placed on the surface of the three center baskets to sample biofilm and invertebrates for another study; the two outer (upstream, downstream) baskets served as buffers to reduce potential edge effects. The riffle was elevated (6–16 cm) and sloped (15%) to create rapid flow across the gravels and thus minimize sediment accumulation. The downstream pool was filled with 5.5 L of gravel (approximately 2.5-cm diameter) and was divided into three reaches by attaching two wood blocks ( $19 \times 8 \times 4$  cm) to alternate sides of the channel. Blocks protruded about halfway (8 cm) across the channel, creating sinuous flow. Three stones (approximately  $13 \times 7 \times 5$  cm) were placed into each reach to provide cover for the coho salmon. Perforated aluminum plates at each end of the pool prevented coho salmon from escaping.

Salmon analogs used for treatments were manufactured from Chinook salmon *O. tshawytscha* and marine fish bone meal (Bio-Oregon, Inc., Warrenton, Oregon). Bone meal in the analogs supplied additional P that was diluted by the gelatin binder, which only added N (Dennis Roley, Bio-Oregon, Inc., personal communication). The 6-g analog pellets contained 2.3% P, 10.9% N, 14.6% fat, and 67.9% protein by mass.

Platforms were covered with Plexiglas (4.4 mm thick) to prevent tampering by vertebrates. Although these clear plastic covers might have affected the input of solar radiation into the channels, all treatments were treated equally (i.e., they all had the same cover). Discharge through channels was maintained at 0.4–0.6 L/s during the ex-

TABLE 1.—Salmon carcass and salmon carcass analog treatments applied to artificial channels in the mesocosm experiment in southeastern Alaska during 2002. Treatments are as follows: CN = control, no shade; AN = analog, no shade; SN = salmon carcass, no shade; CS = control, shade; AS = analog, shade; SS = salmon carcass, shade.

Variable	Treatment					
	CN	AN	SN	CS	AS	SS
Total P added to channels (g/m <sup>2</sup> ) <sup>a</sup>	0.0	44.4	22.2	0.0	44.4	22.2
Total N added to channels (g/m <sup>2</sup> )	0.0	211.2	222.3	0.0	211.2	222.3
Carcass/analog wet mass (kg)	0.0	1.1	3.6	0.0	1.1	3.6
Estimated carcass dry mass (kg)			0.9			0.9
Concentration (kg wet mass·L <sup>-1</sup> ·s <sup>-1</sup> ) <sup>b</sup>		2.2	7.2		2.2	7.2
Mass density (kg wet mass/m <sup>2</sup> )		2.1	6.8		2.1	6.8
Carcass density (no. carcasses/m <sup>2</sup> )			1.6			1.6

<sup>a</sup> Total P in carcass tissue was estimated based on unpublished data for the percentage P in the muscle and eggs of “fresh or entry” chum salmon (Scott Gende, personal communication). The P content of the analog was determined by an independent laboratory.

<sup>b</sup> Estimated average discharge was 0.5 L/s.

periment. Stream water was passed through the channels for 21 d before the experiment began. Water temperature in the head tank, logged every hour with an Optic Stowaway, averaged 7.2°C (range: 5.7–9.1°C).

Treatments consisted of two types of enrichment (salmon analogs, salmon carcasses) and two light levels (no shade, 95% shade) (Table 1). Treatments were applied to the six channels in each platform according to a Latin square design. The unshaded treatment, which was exposed to late-morning and full-afternoon sunlight (direct), was intended to simulate open canopies, and the 95% shade treatment simulated dense, young-growth canopies in southeastern Alaska (McGowan 1998). Salmon carcasses consisted of salmon carcass chunks (skin, muscle, bone) and eggs from female chum salmon *O. keta*. We made transverse sections of chum salmon from between the pectoral fin and anus to produce carcass chunks weighing about 500 g (wet mass); eggs were single or in skeins. We attempted to keep total P levels in analog and carcass treatments equal (Table 1). Although we recognized that P from carcasses (i.e., in bone tissue) might be immediately less labile and less biologically available than that of analogs, total P was the most practical means of standardizing treatments. To simulate the natural physical breakdown of salmon carcasses in streams, we hand-macerated carcass chunks (50% of the original amount added) in each channel after 2 and 4 weeks. Analog fragments into small particles shortly after placement in the pools and were covered with sediment over time. At the same time carcasses were macerated, we agitated the analog-sediment mixture, which exposed and suspended the analog fragments. Analog and carcass fragments were re-

suspended by hand once during weeks 5 and 6 to simulate the natural breakdown and drift of material in natural streams (Wipfli et al. 2003). Agitation of the analog-sediment mixture and maceration of carcasses caused analog and tissue fragments to drift into the riffle and downstream pool substrates. We observed fish feeding on both types of fragments. Some fragments drifted out of the channels. On 22 August, an additional 540 g of analog in mesh bags was added to each analog-treated channel because water chemistry analyses indicated that the analog material was no longer leaching nutrients.

Juvenile (age-0) coho salmon from a nearby stream were captured with baited minnow traps and separated into three size-classes (mean wet mass ± SD): small (0.54 ± 0.08 g), medium (0.85 ± 0.16 g), and large (1.41 ± 0.27 g). Age-0 coho salmon were used in this experiment because they were the most reliably available of the fishes present (i.e., species and size-class). One individual from each size-class was anesthetized with Finquel, measured for wet mass (nearest 0.01 g) and fork length (nearest 0.5 mm), and released into each channel. Large and medium individuals were given upper and lower caudal fin clips, respectively, for identification. Fish were released into the channels 1 d before treatment with salmon analogs and carcass tissue. Individuals found dead during the experiment were replaced with similar-sized individuals and were excluded from statistical analyses. After 2 and 5 weeks, we captured, anesthetized, re-measured, and returned each fish to its channel. After 7 weeks, each fish was killed, measured, and placed in a freezer. The percentage change in body condition (Fulton condition factor  $K = \text{mass}/\text{length}^3$ ) and production were calculated

TABLE 2.—Water temperature, discharge, and physical habitat measurements in two tributaries of Bridget Cove Creek, Alaska, where the effect of salmon carcass enrichment (right fork) and carcass analog enrichment (left fork) was studied in 2002. Ranges are given in parentheses.

Variable	Left fork	Right fork
Mean water temperature (°C)	9 (7–11)	10 (7–12)
Mean discharge (m <sup>3</sup> /s)	27 (5–118)	41 (12–129)
<b>Enriched stream reach</b>		
Channel length (m)	166	264
Channel area (m <sup>2</sup> )	339	483
Pool area (m <sup>2</sup> )	206	177
Number of pools	25	26
<b>Unenriched stream reach</b>		
Channel length (m)	108	125
Channel area (m <sup>2</sup> )	229	239
Pool area (m <sup>2</sup> )	147	107
Number of pools	13	12

for each fish after 2, 5, and 7 weeks. Production was calculated as the mean change in wet mass per channel (mg/d). Original surviving salmon from each channel were combined into one sample, placed in a  $-20^{\circ}\text{C}$  freezer for 2 months, and shipped frozen to the Food Products Laboratory, Portland, Oregon, for percent lipid determination (acid extraction, gas chromatography analysis). Storing fish tissue samples at  $-20^{\circ}\text{C}$  for 2 months prior to lipid extraction may have resulted in some loss of lipids (Bligh and Scott 1966; Braddock and Dugan 1972; Hardy et al. 1979; Refsgaard et al. 2000; Heintz et al. 2004). Although colder temperatures are preferable for sample storage, we did not have the requisite facilities.

*Natural stream experiment.*—The natural stream experiment included the same enrichment treatments (control, analog, salmon carcass) as the mesocosm experiment, and the two experiments were conducted nearly concurrently. Unlike the mesocosm experiment, the shading effect was not tested. The lower reaches of BC Creek are accessible to anadromous fishes and contain coho salmon, pink salmon *O. gorbuscha*, cutthroat trout, Dolly Varden *Salvelinus malma*, and sculpins *Cottus* spp. at various times of the year. The experiment was conducted in two second-order tributaries (BC-left and BC-right), each divided into unenriched (control) and enriched (treated) reaches (Figure 1; Table 2). The control reach was located immediately upstream of the treated reach in each tributary.

On 6–7 August, we used G-type minnow traps baited with salmon eggs to capture cutthroat trout and juvenile coho salmon from pools within each tributary. Traps were set three times for 1–2 h per set. Each fish was anesthetized, measured for fork

length and wet mass, and injected with a passive integrated transponder (PIT) tag in the abdominal cavity. Individuals too small to tag were anesthetized and measured for length and wet mass only. Fish were returned to the tributary and reach from which they were captured. We tagged 75 cutthroat trout from BC-right and 63 cutthroat trout from BC-left (64–124 mm fork length); 7 juvenile coho salmon were tagged from BC-right and 24 juvenile coho salmon were tagged from BC-left (74–92 mm fork length). We sacrificed four cutthroat trout from each reach (16 fish total) to determine pre-enrichment lipid content. Fish were transported to the laboratory on ice and measured for fork length, and the stomach contents were removed by use of a gastric lavage technique. A 10% sample of flesh was removed from each fish for stable isotope analysis for a separate study, and the remaining carcass was frozen. Samples for lipid analyses were sent to the Food Products Laboratory as described above.

Salmon analogs were added to the enriched reach of BC-left, and pink salmon carcasses were added to the enriched reach of BC-right. Salmon carcasses and analogs were applied over several days, from 11 to 15 August in BC-left and from 9 to 16 August in BC-right. Adult pink salmon (mean wet mass = 1.42 kg, male:female ratio = 60:40 by wet mass) were collected from main-stem BC Creek and from BC-right, given a blow to the head, then sexed, weighed, and anchored to the bottom of pools with nails. Most (>95%) salmon taken from BC-right were removed prior to spawning so that disturbance to the streambed was minimal. During the first week, salmon carcasses removed by bears *Ursus* spp. were replaced with

TABLE 3.—Analysis of variance design for the mesocosm experiment on the effect of salmon carcass or carcass analog enrichment of artificial channels that were either 95% shaded or unshaded and statistical inference testing ( $\alpha = 0.05$ ) for the effects of salmon carcasses, analogs, and shading through time.

Source of error	df
Table	5
Treatment	5
Nonorthogonal contrasts <sup>a</sup>	
No shade	
Control vs. salmon carcass	1
Control vs. analog	1
Salmon carcass vs. analog	1
No shade vs. shade	
Control	1
Salmon carcass	1
Analog	1
Error (table $\times$ treatment)	25
Time	2
Treatment $\times$ time	10
Error (table $\times$ time + table $\times$ treatment $\times$ time)	60
Total	107

<sup>a</sup> Testing for nonorthogonal contrast used an  $\alpha$  value of 0.05/6 or 0.0083.

carcasses of similar mass and sex to maintain 0.54 kg of fish material/m<sup>2</sup> (equivalent to 4 g P/m<sup>2</sup>). This carcass density was within the range of previous salmon enrichment experiments (Wipfli et al. 1999, 2003). After 7 d, lost salmon were not replaced, so as to avoid further disturbance to the stream prior to sampling for biofilm, invertebrates, and fish. Salmon carcass fragments were observed in BC-right until 16 September (Dominic Chaloner, personal communication).

Salmon analogs were placed inside plastic mesh bags (0.45 kg/bag) that were anchored in the stream to prevent them from floating out of the study reach. Analog pellet loading averaged 0.20 kg/m<sup>2</sup> (equivalent to 4 g P/m<sup>2</sup>). On 13 August, a spate apparently washed most of the pellets from the mesh bags. Because analog material was likely not incorporated into the food web prior to the spate and most material appeared to have been flushed from the study reach, a second dose was applied to the reach on 15 August. Although high water occurred after the second dose, a thick microbial coating on the mesh bags retained most of the analog material. Analog material was observed in BC-left until 2 October (Dominic Chaloner, personal communication). We recognize that the subsequent additions of carcasses (following losses from bears) and analogs (following losses from the spate) may have affected the targeted equal-P treatments (analog versus salmon carcasses), but we believe this was still the most reasonable approach under the circumstances.

A small number of naturally returning pink

salmon were observed in and removed from some of the experimental reaches. Adults returning to BC-right (all but one found in the carcass-enriched reach) and the three adults returning to BC-left (all in the analog-enriched reach) were immediately removed and became part of the treatment that was applied to the salmon carcass-enriched reach. Because very few naturally returning adults occurred in these stream reaches, and because the ones that were there were quickly removed, there was probably little if any enrichment effects from these returning fish.

On 19 and 20 September, we used baited minnow traps to capture fish in both tributaries and measured PIT-tagged individuals to obtain length and wet mass. For each reach and species, we calculated the mean percent change in condition and mean production (of PIT-tagged fish) as described above. In addition, four cutthroat trout from each reach (16 fish total) were sacrificed and processed to determine lipid content.

Of the 63 cutthroat trout tagged in BC-left and the 76 cutthroat trout tagged in BC-right, 33% and 13%, respectively, were recaptured at the end of the experiment. Eleven of 24 (46%) tagged coho salmon were recaptured in BC-left; none of the seven coho salmon tagged in BC-right were recaptured.

*Experimental design and analyses.*—The mesocosm experiment was a randomized complete block design with repeated measures (Table 3). Individual channels were the experimental unit to which treatments were applied. Treatments in-

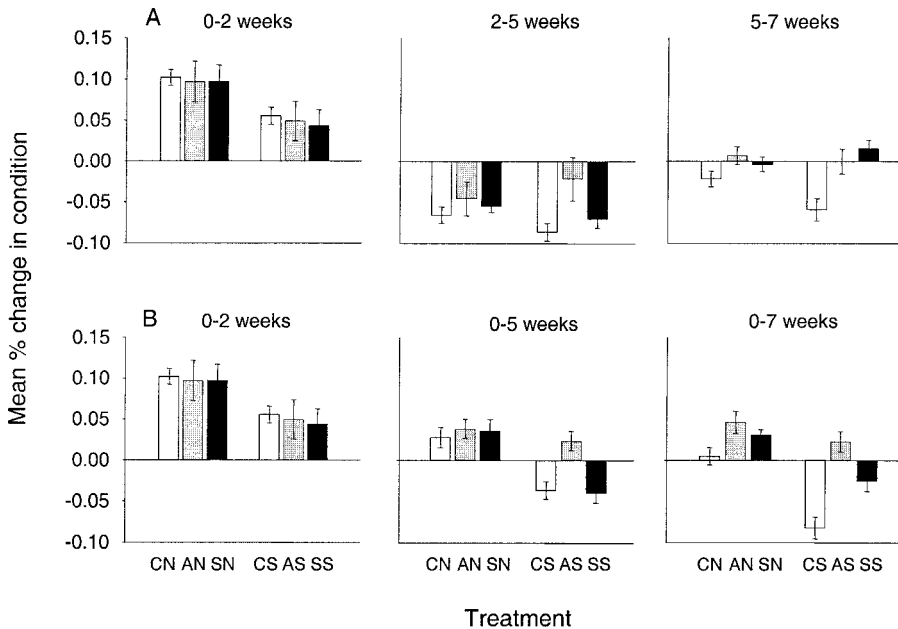


FIGURE 2.—Mean percent (A) incremental change and (B) cumulative change in condition of juvenile coho salmon in control, carcass-analog-enriched, and salmon-carcass-enriched channels with and without shade in an experimental mesocosm in southeastern Alaska. Treatments were as follows: control + no shade (CN), analog + no shade (AN), salmon carcass + no shade (SN), control + shade (CS), analog + shade (AS), and salmon carcass + shade (SS). Error bars indicate  $\pm 1$  SE.

cluded a control, salmon carcass enrichment, salmon analog enrichment, shade only, carcass enrichment plus shade, and analog enrichment plus shade. Response measures were coho salmon condition factor and production (and lipid, as discussed below). Statistical tests were calculated for treatment, time, and the treatment  $\times$  time interaction by use of a split-plot analysis of variance (ANOVA;  $\alpha = 0.05$ ) (SAS Institute 1989). Planned contrasts were as follows: (1) control versus salmon analog, (2) control versus salmon carcass, (3) salmon analog versus salmon carcass, (4) no shade versus shade, (5) salmon analog with no shade versus salmon analog with shade, and (6) salmon carcass with no shade versus salmon carcass with shade. Contrasts 1 and 2 tested for the effect of enriching streams with analogs and carcasses, contrast 3 tested for differences between analog and carcass enrichment, and contrasts 4–6 tested for interactive effects between enrichment and riparian canopy condition (i.e., shading). Because the six contrasts were not orthogonal, the significance level  $\alpha$  was adjusted from 0.05 to 0.0083 ( $\alpha/6$ ) for each contrast. The six planned contrasts were tested for each time period (2, 5, and 7 weeks) by use of a two-way ANOVA ( $\alpha = 0.0083$ ). Percent total

lipid of the coho salmon after 7 weeks was also analyzed for the six planned contrasts in a two-way ANOVA ( $\alpha = 0.0083$ ).

Two-tailed *t*-tests were performed on the BC Creek data (control versus analog, control versus carcass); PIT-tagged fish were used as pseudoreplicates. We were not able to establish true replicates (i.e., streams) due to the expense and logistics of replicating these treatments across multiple streams. Therefore, *t*-test results should not be extrapolated beyond the single stream reach at a single point in time, and do not mean that treatment differences, if detected, were necessarily due to treatments. Nonetheless, the natural stream experiment allowed us to see if responses observed in the mesocosm experiment were repeatable in a natural stream setting.

## Results

### Mesocosm Experiment

There was a significant overall treatment effect for all three responses (condition, production, total lipid) by the age-0 coho salmon in the mesocosm experiment ( $P < 0.001$ ) (Table 4). Significant treatment  $\times$  time interaction was also detected for

TABLE 4.—Analysis of variance output ( $P$ -values) for overall treatment effect, treatment  $\times$  time interaction, and individual a priori contrasts for the mesocosm experiment in which 95% shaded or unshaded artificial channels were enriched with salmon carcasses or carcass analogs to study the effect on juvenile coho salmon condition, production, and lipid levels. Bold italics type indicates a significant difference; NT = not tested.

Factor or contrast	Condition (cumulative)	Production (cumulative)	Percent total lipid
<b>Overall treatment effect (<math>\alpha = 0.05</math>)</b>			
Treatment	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
<b>Individual contrasts for all time periods (<math>\alpha = 0.0083</math>)</b>			
Control vs. analog	0.307	<b>&lt;0.001</b>	<b>0.002</b>
Control vs. carcass	0.528	<b>0.002</b>	<b>0.004</b>
Analog vs. carcass	0.690	0.010	0.723
No shade vs. shade (control)	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.103
No shade vs. shade (analog)	0.068	<b>&lt;0.001</b>	0.960
No shade vs. shade (carcass)	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.149
<b>Overall treatment <math>\times</math> time interaction (<math>\alpha = 0.05</math>)</b>			
Treatment $\times$ time	<b>0.006</b>	<b>&lt;0.001</b>	NT
<b>Individual contrasts at 2 weeks (<math>\alpha = 0.0083</math>)</b>			
Control vs. analog	0.843	0.035	NT
Control vs. carcass	0.844	0.631	NT
Analog vs. carcass	0.999	<b>0.002</b>	NT
No shade vs. shade (control)	0.072	0.029	NT
No shade vs. shade (analog)	0.066	0.012	NT
No shade vs. shade (carcass)	0.039	0.028	NT
<b>Individual contrasts at 5 weeks (<math>\alpha = 0.0083</math>)</b>			
Control vs. analog	0.516	<b>&lt;0.001</b>	NT
Control vs. carcass	0.628	<b>0.002</b>	NT
Analog vs. carcass	0.868	0.060	NT
No shade vs. shade (control)	<b>0.001</b>	<b>&lt;0.001</b>	NT
No shade vs. shade (analog)	0.367	<b>0.004</b>	NT
No shade vs. shade (carcass)	<b>&lt;0.001</b>	<b>&lt;0.001</b>	NT
<b>Individual contrasts at 7 weeks (<math>\alpha = 0.0083</math>)</b>			
Control vs. analog	0.028	<b>&lt;0.001</b>	NT
Control vs. carcass	0.157	<b>0.002</b>	NT
Analog vs. carcass	0.391	0.026	NT
No shade vs. shade (control)	<b>&lt;0.001</b>	<b>&lt;0.001</b>	NT
No shade vs. shade (analog)	0.197	<b>0.005</b>	NT
No shade vs. shade (carcass)	<b>0.004</b>	<b>&lt;0.001</b>	NT

the responses that could be tested for interaction effects: condition ( $P = 0.006$ ) and production ( $P < 0.001$ ). Five coho salmon died during the experiment, spread across three treatments and all from the smallest size-class, and were replaced with live, similarly sized coho salmon. These fish served as placeholders to maintain original fish density throughout the experiment, but were not included in the statistical analysis.

Based on the planned contrasts, we detected no significant effects of either salmon analog enrichment or carcass enrichment on age-0 coho salmon body condition ( $P > 0.0083$ ; Table 4). Condition of fish in all treatments improved most dramatically during the first 2 weeks of the experiment, then declined the most during the next 3 weeks (Figure 2). Condition continued to decline after that for fish

in control channels, but leveled off or increased slightly in both enrichment treatments during the final 2 weeks (weeks 5–7; Figure 2A). However, after 5 and 7 weeks, body condition of coho salmon in control and carcass-enriched channels without shade was significantly higher than that of fish in shaded channels ( $P < 0.001$ ; Table 4; Figure 2). Although we noticed the same pattern with the analog treatments, differences between the shade and no shade treatments were not statistically significant ( $P = 0.068$ ; Table 4; Figure 2).

Coho salmon production was significantly higher in enriched channels (analog  $P < 0.001$ ; carcass  $P = 0.002$ ) than in control channels (Table 4; Figure 3). Production was greatest in all treatments during the first 2 weeks and declined thereafter, especially in control channels (Figure 3A). Production was

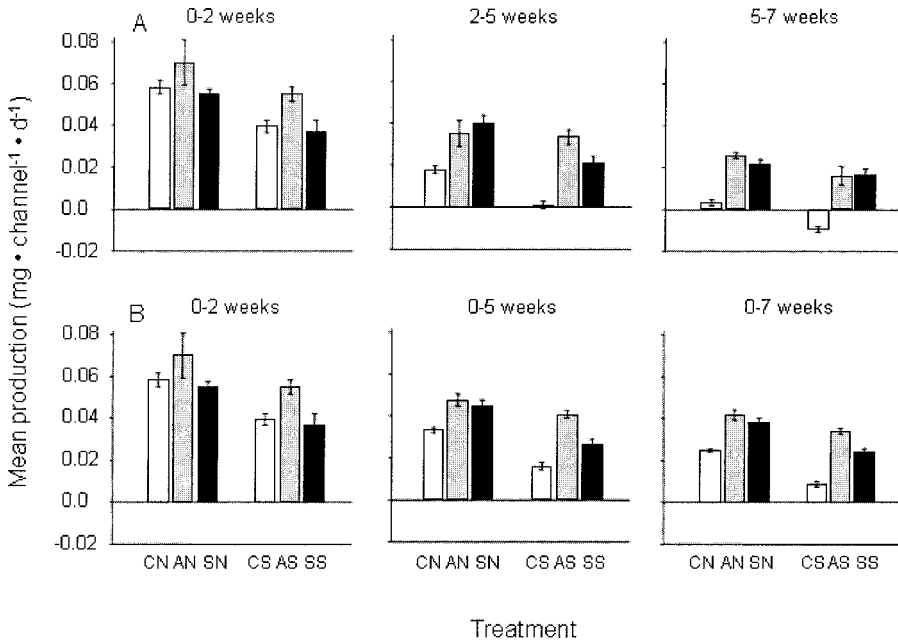


FIGURE 3.—Mean (A) incremental change and (B) cumulative change in production of juvenile coho salmon in control, carcass-analog-enriched, and salmon-carcass-enriched channels with and without shade in an experimental mesocosm in southeastern Alaska. See the caption to Figure 2 for treatment codes. Error bars indicate  $\pm 1$  SE.

significantly higher in both enrichment treatments than in controls during the last two sampling periods ( $P \leq 0.002$ ) but not during the first sampling period ( $P > 0.0083$ ) (Table 4; Figure 3). There was no significant difference between analog and carcass

treatment effects on coho salmon production ( $P > 0.0083$ ). Shade had a negative effect on production in all three treatments (control, analog, carcass), and effects were most prominent during the latter part of the experiment ( $P \leq 0.005$ ) (Table 4; Figure 3). Final cumulative production was positive for fish in all treatments, but was greatest for fish in unshaded analog-enriched and carcass-enriched channels and lowest for fish in the shaded control treatment (Figure 3B).

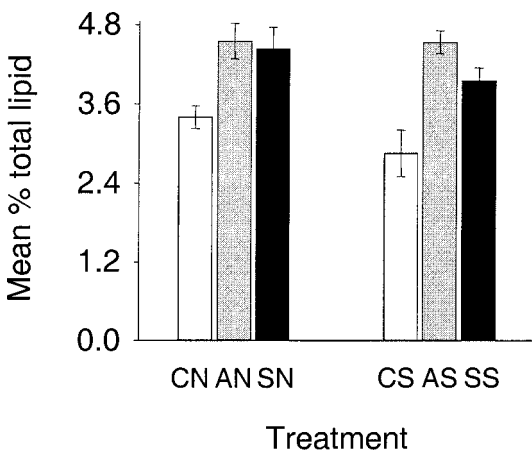


FIGURE 4.—Mean percent total lipid of juvenile coho salmon after 7 weeks in control, carcass-analog-enriched, and salmon-carcass-enriched channels with and without shade in an experimental mesocosm in southeastern Alaska. See the caption to Figure 2 for treatment codes. Error bars indicate  $\pm 1$  SE.

Lipid levels were significantly higher in coho salmon within the enrichment treatments (analog  $P = 0.002$ ; carcass  $P = 0.004$ ) than in those from the control treatment (Table 4; Figure 4). There was no difference in percent total lipid between coho salmon in the analog-enriched treatment and those in the carcass-enriched treatment ( $P > 0.0083$ ). Unlike condition and production, lipid levels were not significantly affected by shading ( $P > 0.0083$ ).

*Natural Stream Experiment*

Patterns in fish responses in BC Creek were generally similar to those recorded in the mesocosm experiment but were much more variable. Cutthroat trout condition was significantly higher in both analog-enriched ( $P = 0.017$ ) and carcass-en-

TABLE 5.—Mean (SE) percent change in condition and production ( $\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) of cutthroat trout and juvenile coho salmon in carcass-analog- and salmon-carcass-enriched reaches and in unenriched (control) reaches of Bridget Cove Creek, Alaska. Bold italics indicates a significant  $P$ -value ( $t$ -test).

Treatment	$n$	Condition (% change)	Production (% change)
<b>Cutthroat trout</b>			
Analog			
Enriched	9	6.5 (1.7)	0.4 (0.1)
Unenriched	12	-0.2 (1.8)	0.1 (0.0)
$P$ -value		<b><i>0.017</i></b>	<b><i>&lt;0.01</i></b>
Carcass			
Enriched	5	10.1 (1.6)	0.3 (0.1)
Unenriched	5	0.6 (2.4)	0.2 (0.1)
$P$ -value		<b><i>0.012</i></b>	0.502
<b>Coho salmon</b>			
Analog			
Enriched	4	7.8 (1.2)	0.2 (0.0)
Unenriched	7	11.0 (4.5)	0.1 (0.0)
$P$ -value		0.617	<b><i>0.004</i></b>
Carcass			
Enriched		No data	No data
Unenriched		No data	No data

riched ( $P = 0.012$ ) reaches relative to the upstream control reaches (Table 5; Figure 5A), suggesting a possible treatment effect. We observed no pattern in coho salmon condition ( $P = 0.617$ ), and we were not able to recapture any PIT-tagged coho salmon in the carcass-enriched tributary, BC-right (Table 5; Figure 5B).

Cutthroat trout production was also higher in the analog-enriched reach than in the control reach ( $P < 0.001$ ) (Figure 6) but was not higher in the carcass-enriched reach ( $P = 0.502$ ). A similar pattern was seen for juvenile coho salmon in reaches with analog additions (Figure 6), but because we recaptured no PIT-tagged coho salmon in the carcass-enriched tributary, we were unable to determine differences between enrichment methods.

Whole-body lipid levels were higher in fish from the enriched reaches than in those from the control reaches. Percent total lipid in cutthroat trout inhabiting the carcass-enriched reach after treatment application was about three times higher than pre-treatment levels, and about twice as high as that of control fish during the posttreatment period (Figure 7). Lipid levels differed little between cutthroat trout collected from the analog-enriched reach and the upstream control reach. As expected, lipid levels of fish inhabiting the control reaches

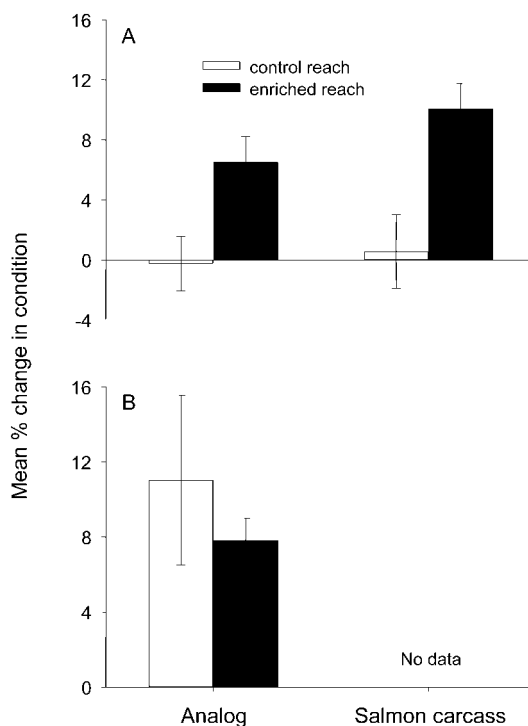


FIGURE 5.—Mean percent change in condition of (A) cutthroat trout and (B) coho salmon in control, carcass-analog-enriched, and salmon-carcass-enriched reaches of Bridget Cove Creek, Alaska. Error bars indicate  $\pm 1$  SE.

did not differ significantly between pre- and post-treatment periods in both tributaries (Figure 7).

## Discussion

This study showed that salmon carcasses and analogs can increase condition, lipid levels, and production of stream-resident salmonids. Responses from the artificial and natural streams corrob-

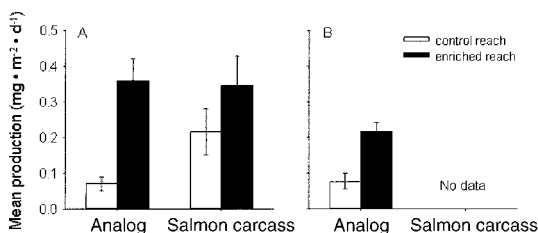


FIGURE 6.—Mean production of PIT-tagged (A) cutthroat trout and (B) coho salmon in control, carcass-analog-enriched, and salmon-carcass-enriched reaches of Bridget Cove Creek, Alaska. Error bars indicate  $\pm 1$  SE.

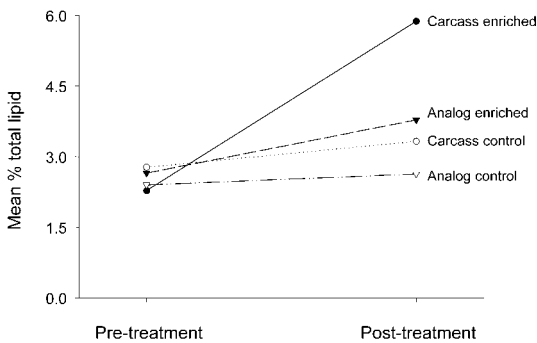


FIGURE 7.—Mean percent total lipid of cutthroat trout in control, carcass-analog-enriched, and salmon-carcass-enriched reaches of Bridget Cove Creek, Alaska, before and after treatment in 2002.

orated fairly well, with the exception of some from BC Creek (i.e., coho salmon condition in the analog treatment, cutthroat trout production in the carcass treatment). This could be due to several factors. First, the few naturally returning pink salmon in the system immediately before the experiment began could have differentially influenced background levels of nutrients in some of the study reaches, masking or exaggerating treatment effects. However, compared to the relatively high densities of carcasses and analogs added to enriched reaches, naturally returning salmon probably had negligible enrichment effects in those reaches. Second, runs from previous years could also have contributed nutrients and carbon to certain stream reaches differentially, also influencing treatment effects. Third, the small lake upstream of BC-right could have played a role in nutrient dynamics and concentrations. Background differences between the two tributaries, including underlying local geology or riparian vegetation cover as well as other naturally occurring factors, could have also influenced responses to treatments. Again, we emphasize that treatments were not randomly applied to these tributaries, nor were they replicated across streams; thus, the responses we ultimately detected did not necessarily indicate treatment effects or a lack thereof. However, the fact that we detected many patterns in the natural stream that were consistent with those measured in the statistically rigorous mesocosm experiment suggests that fish may be responding similarly to enrichment in both the natural and mesocosm settings.

The increased production after enrichment in this study suggests that both salmon carcasses and

salmon analogs can increase fish production in freshwater ecosystems. Fish likely benefit through two distinct trophic pathways: direct feeding on carcass (and egg) and analog fragments, and indirectly through bottom-up effects from nutrients and carbon that are sequestered by the microbial community and transferred up through the food web (Wipfli et al. 1998). Bilby et al. (1998) discovered that stream-resident salmonids ingest salmon eggs and carcass tissue in selected Washington streams. Wipfli et al. (1998, 1999) found that lower trophic levels (biofilm and invertebrates) responded strongly to the presence of salmon runs. Biofilm mass and invertebrate densities in southeastern Alaska streams sharply increased following enrichment from salmon carcasses and eggs; more aquatic invertebrates, especially chironomid midges, a key prey category, were provided for stream-resident cutthroat trout, coho salmon, and Dolly Varden (Wipfli 1997). The elevated production in our study was a reflection of higher growth rates in fish within the confined mesocosm and PIT-tagged fish in BC Creek. Because of increased lipid concentrations, these larger fish could be expected to survive and perform better than fish that lack access to either salmon carcasses or analogs (Adams 1998).

Data on effects from carcass analog enrichment have not been reported before, and our results suggest that analogs evoke similar responses in freshwater-rearing salmonids as do salmon carcasses when added to streams at about the time salmon runs are taking place. This is not surprising, given that the analogs were manufactured from salmon freshly stripped of eggs and milt early in their inevitable physiological and biological decay process. Therefore, the fish used in analogs contained nutrient and carbon levels similar to those of salmon soon after freshwater entry (Dennis Roley, Bio-Oregon, Inc., personal communication). The analogs would be expected to have a biochemical composition very similar to that of natural salmon carcasses, and likewise should have similar effects on stream fishes, provided that material fragmentation and utilization by fishes (e.g., consumption of drifting fragments) mimic those of natural carcasses (Bilby et al. 1996). Because the fish consume tissue fragments directly, we attribute some of the responses by fish in this study to carbon compounds in the carcasses and analogs. Fragments of carcass and analog material were seen drifting down through the channels and were ingested by the young coho salmon, serving as a

direct trophic transfer mechanism from carcasses or analogs to consumers.

The significant negative effects of shading on fish condition and production in this study could have been the result of several factors. Possible explanations include reduced bottom-up effects, where primary producers are less stimulated under lower light conditions (Hill et al. 1995), or reduced feeding efficiency under the lower light levels (Young et al. 1997; Vogel and Beauchamp 1999). Shading effects were detected in the control as well as the enrichment treatments. If the reduction in bottom-up effects was the actual cause of reduced fish responses, our data suggest that at a given level of nutrient concentration (i.e., background levels of the controls, or elevated levels of the enriched treatments), stream canopy will ultimately govern how the stream community responds. Many of the smaller salmonid-bearing tributaries in southeastern Alaska commonly have dense, young-growth canopies, a result of timber clear-cutting along these streams over three decades ago. These canopies range from pure conifer to nearly pure red alder *Alnus rubra*, with various mixtures of the two canopy types. Hetrick et al. (1998a, 1998b) found that multiple trophic levels were stimulated in southeastern Alaska streams that had their young-growth riparian canopies removed. Stream shading of 95% in our study was reflective of the relatively dense canopy and shade that young, even-aged forests provide (McGowan 1998). When vegetation management is an option in riparian zones, managers who wish to stimulate aquatic production might consider partially thinning dense, young-growth forest canopies that prevent suitable light levels from reaching streams, if their goal is to maximize productivity of stream food webs and fish (Chapman and Knudsen 1980). However, increased light levels could also increase predation efficiency on salmonids (Vogel and Beauchamp 1999). Additional tradeoffs from stand thinning, such as potentially lower future wood recruitment to streams and higher stream temperatures, need to be balanced with the potential positive food web effects. Information on interactions between enrichment, shading, and fishes is needed to allow definitive statements on the role of riparian shading to be made prior to the initiation of thinning projects.

The primary strengths and weaknesses of this study warrant a brief discussion. The use of concurrent natural stream and artificial stream experiments is an effective research strategy that offers both the authenticity of a natural stream experi-

ment and the high replication and statistical power of a mesocosm experiment when an adequate number of natural stream replicates are not available (Wipfli et al. 2003). This dual experimental approach provides the opportunity to rigorously test whether patterns observed in an under-replicated or pseudoreplicated natural stream experiment are also occurring in a controlled, adequately replicated mesocosm experiment. Another strength was the semi-natural features of the outdoor mesocosm, which was supplied with natural stream water (e.g., natural nutrient, organic matter, sediment, and drifting invertebrate levels, and ambient water temperature) and ambient light. However, though the mesocosm provides the opportunity to test specific treatments in the absence of other factors (e.g., constraints on foraging) that often add variability, lack of such factors may also make extrapolation to natural streams more tenuous. The mesocosm probably demonstrates what is possible under ideal conditions. Results in an adequately replicated, natural stream experiment could be different in the presence of these natural forces. Another potential weakness was the necessity of storing the fish tissue samples at  $-20^{\circ}\text{C}$  for 2 months prior to lipid extraction. Evidence is inconclusive about whether lipid will hydrolyze at this temperature (Bligh and Scott 1966; Braddock and Dugan 1972; Hardy et al. 1979; Refsgaard et al. 2000; Heintz et al. 2004), but our storage method could have affected the total amount of lipid detected in fish. If lipid did partially hydrolyze, losses should have been proportionate across treatments, thereby affecting each treatment to the same degree. Nonetheless, we did detect treatment differences in fish lipid levels in this study. Another weakness, as addressed previously, was the lack of replication in the natural stream experiment. Clearly, replicated stream studies are needed before solid conclusions can be drawn about the effects of analogs, carcasses, and stream shading on stream-resident salmonids.

A growing body of literature indicates increased productivity of multiple trophic levels in streams that receive salmon runs (Kline et al. 1997; Bilby et al. 1998; Wipfli et al. 1998, 2003). Salmon analogs appear to be a reasonable, temporary substitute for marine subsidies in systems that have lost their salmon runs or are experiencing reduced runs. Because we wanted to directly compare the effectiveness of the analogs and carcasses of naturally returning salmon, stream enrichment in this study coincided with salmon returns in late summer and fall. Different and probably more dramatic

effects would be anticipated from enrichment treatments (both salmon carcasses and analogs) added in spring and summer, when water temperature and day length are both greater, and when a longer period of growing season remains after enrichment. Furthermore, analogs should be regarded as a short-term tool for helping restore stream food web productivity and fish communities in systems where nutrient or carbon deficits are believed to limit production.

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