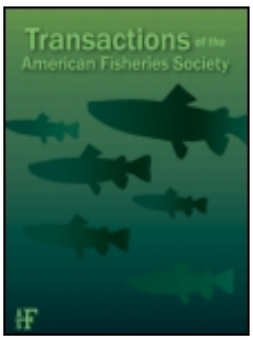

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ARTICLE

Nutrient Enrichment with Salmon Carcass Analogs in the Columbia River Basin, USA: A Stream Food Web Analysis

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Abstract

Anadromous fishes represent an important ecosystem linkage between marine and inland aquatic and terrestrial habitats. These fishes carry organic matter and marine-derived nutrient (MDN) subsidies across a vast landscape, often with profound influences on recipient ecosystem food web structure and function. In the Columbia River basin, century-long declines in the abundance of anadromous fish populations have focused attention on potential mitigation efforts to address MDN deficits. In this study, we evaluate components of the stream food web response (periphyton, macroinvertebrate, and fish) to pasteurized salmon carcass analog (SCA) treatments in 15 streams across the Columbia River basin. Periphyton standing crop, macroinvertebrate density, and salmonid fish growth rates and stomach fullness measures increased following the addition of SCA. We found no significant change in dissolved nutrient concentrations after treatment, suggesting that biological demand exceeded supply. Nitrogen stable isotope signatures confirmed trophic transfer from SCA to lower trophic levels but were noticeably weak in fish tissue samples despite our marked growth and stomach fullness measures. These data indicate that SCA has the potential to increase the productivity of nutrient-limited freshwater ecosystems and may provide a nutrient mitigation tool in ecosystems where MDNs are severely limited or unavailable.

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The Columbia River basin in western North America was historically one of the world's largest producers of wild anadromous salmonids; however, contemporary populations have declined following periods of intense commercial harvest, hydrosystem development, hatchery production, and habitat loss (Nehlsen et al. 1991; Lichatowich 1999). In California, Oregon, Idaho, and Washington, Pacific salmon *Oncorhynchus* spp. have been eliminated from about 40% of their historical range (NRC 1996). Furthermore, many spawning and rearing streams in the Pacific Northwest (PNW) are nutrient-limited (Thomas et al. 2003; Sanderson et al. 2009). The reduction or complete loss of anadromous fish populations across the landscape has had enormous cultural, economic, and ecological ramifications (Gende et al. 2002). Such declines contribute to "cultural oligotrophication" (Stockner et al. 2000; Anders and Ashley 2007) and have reduced the transport of marine-derived nutrients (MDN) to freshwater tributaries (Gresh et al. 2000).

A large body of evidence supports the idea that salmon can influence the food webs, trophic structure, nutrient budgets, and productivity of aquatic and terrestrial ecosystems (Gende et al. 2002). Spawning salmon contribute to the nitrogen (N) and phosphorus (P) loading in salmon-bearing watersheds (Gresh et al. 2000), and even small inputs of nutrients and carbon (C) may be important to the maintenance of trophic productivity (Larkin and Slaney 1997). A positive feedback loop process has been described whereby returning salmon function to enhance freshwater productivity (Wipfli et al. 1998; Naiman et al. 2002). Marine-derived nutrients may be essential for maintaining the productivity of rearing habitat for future generations of salmon (Larkin and Slaney 1997), and increases in freshwater productivity can ultimately lead to changes in fish growth, survival, and production (Bilby et al. 1996, 1998; Larkin and Slaney 1997; Wipfli et al. 2003, 2004). Subsidies of MDN are incorporated into the freshwater trophic system via two primary pathways: (1) direct consumption of gametes and carcass materials by fish and invertebrates and (2) indirect uptake of nutrients released from fish during spawning (i.e., excretion and egestion) or carcass decomposition following death and the subsequent utilization and trophic transfer of bioavailable nutrients into stream food-web communities (e.g., biofilm, invertebrates, and fish) (Naiman et al. 2002).

Our understanding of ecosystem linkages (marine–freshwater), nutrient dynamics, riverine food webs, and the specific trophic processes and pathways that affect the productivity of salmon-rearing habitats has progressed over time (Vannote et al. 1980; Lamberti et al. 2010; Mulholland and Webster 2010; Wipfli and Baxter 2010). It is now widely accepted that stream ecosystem response to spawning salmon is characterized by great complexity. However, researchers are evaluating how salmon-derived nutrients influence freshwater productivity across multiple trophic levels (Wipfli et al. 2003, 2004) and continue to investigate the potential sources of variability (Wipfli et al. 1999; Janetski et al. 2009).

Many freshwater habitats across the Columbia River basin now receive diminished subsidies of C, nutrients, and energy in the form of spawning salmon and steelhead *O. mykiss* (anadromous rainbow trout) (Nehlsen et al. 1991; Gresh et al. 2000; Thomas et al. 2003; Scheuerell et al. 2005). Achord et al. (2003) found evidence of density-dependent mortality at population sizes well below historical levels, suggesting nutrient deficits as a limiting factor capable of reducing stream-rearing carrying capacities. Declining returns of anadromous fishes in the Columbia River basin, where numerous stocks of salmon and steelhead are listed as threatened or endangered under the U.S. Endangered Species Act, have focused attention and research on nutrient mitigation strategies. The relevance of MDN to salmon recovery efforts has prompted volunteer groups and local, state, federal, and tribal agencies to add supplemental nutrients, usually hatchery carcasses or inorganic nutrients, into riverine and lacustrine habitats, especially in salmon-depleted watersheds. However, the efficacy of nutrient enhancement efforts may vary across the landscape, and the response of an aquatic ecosystem to nutrient enrichment should be considered in an experimental setting before large-scale management practices occur (Compton et al. 2006).

Salmon carcass analogs (SCA) represent a potential source of pathogen-free, marine-derived carbon and nutrients that could be used to stimulate primary productivity and food availability in blocked habitats (e.g., above dams without fish passage), or habitats with chronically depressed salmon and steelhead populations and low access to carcasses from hatcheries. Nutrient enrichment of streams using pasteurized SCA may be a viable alternative to planted carcasses and inorganic nutrient additions as a salmon restoration tool. For example, the use of raw carcass material for restoration of MDN in streams has consistently presented problems of availability, storage, transportation, distribution, and pathogen introduction (Pearsons et al. 2007), and inorganic nutrients do not contain carbon-based macromolecules (Wipfli et al. 2010). Salmon carcass analogs provide an organic input of nutrients and carbon-based compounds that could mimic the addition of salmon carcasses to streams while eliminating many of the associated problems. The manufacturing process for SCA kills pathogens present in the parent material and produces a compact, low-moisture pellet that is readily stored and transported (Pearsons et al. 2007). Benefits may include direct consumption by juvenile salmonids (Pearsons et al. 2007), a trophic pathway not provided by inorganic nutrients (Kiernan et al. 2010). Other advantages include the ability to produce large amounts of SCA for dispersal into areas where hatchery carcass placement is unwarranted owing to access (e.g., roadless areas), availability (e.g., low hatchery returns), or potential pathogen and contaminant issues (i.e., fish pathogens). It is worth noting that potential contaminants (e.g., mercury, PCBs) in the salmon carcass source material used to produce SCA warrants circumspection prior to use in research or management applications (Compton et al. 2006). For a

detailed description of the development process and initial testing of SCA see Pearsons et al. (2007).

Research investigating the potential utility of SCA has been limited to short-term responses by using experimental stream channels (Wipfli et al. 2004) and small-scale natural stream experiments, usually focusing on lower trophic levels (Kohler et al. 2008; Kohler and Taki 2010; but see Wipfli et al. 2004). In southeast Alaska, Wipfli et al. (2004) found that SCA enhanced the growth of juvenile salmonids in mesocosms and in a natural stream comparable to salmon carcass inputs. In central Idaho streams of the upper Salmon River, Kohler et al. (2008) reported that periphyton chlorophyll *a*, ash-free dry mass, and macroinvertebrate biomass were significantly higher in stream reaches treated with SCA, and Kohler and Taki (2010) observed spatial ordination shifts in macroinvertebrate communities associated with increased relative abundances following SCA treatments in the same streams. These studies represent evaluations at different trophic levels and across diverse landscapes, providing preliminary evaluations of the efficacy of SCA as a management tool.

The present evaluation represents a form of meta-analysis that draws from coordinated, semi-independent studies that employed nearly identical experimental designs and examined the same conceptual hypotheses (i.e., the same null hypotheses). Our approach was to integrate data collected in 2001–2006 from 15 streams in the Columbia River basin: four streams in the upper Salmon River subbasin (central Idaho), six streams in the Yakima River subbasin (central Washington), three streams in the Klickitat River subbasin (south-central Washington), and two streams in the Wind River subbasin (southwest Washington). We used a meta-analysis concept to estimate the stream food-web response and average effect of SCA treatments across a large spatial (i.e., 15 streams) and temporal (i.e., 3 years per stream) scale. Our specific objectives were to investigate the response to SCA in study streams by measuring (1) water chemistry, (2) periphyton accrual and macroinvertebrate density, (3) salmonid growth rates and stomach fullness, and (4) stream food-web nitrogen and carbon stable isotopes. We hypothesized that SCA additions would increase stream food-web productivity by providing a source of marine-derived C, N, and P to freshwater study streams. Our analysis assesses physicochemical and stream food-web response to SCA treatments over a large spatial scale. Our results contribute to a broader understanding of SCA in natural stream settings and expose knowledge gaps that should be addressed by future research efforts and considered by natural resource managers before adopting nutrient mitigation strategies using this type of nutrient subsidy.

METHODS

Study area.—We included 15 streams from the upper Salmon River, Middle Fork Salmon River, Yakima River, Klickitat River, and Wind River subbasins in our assessment (Figure 1). Upper and Middle Fork Salmon River tributaries included Elk Creek (treatment), Valley Creek (control), Cape Horn Creek (treatment), and Marsh Creek (control). The parent geology of Salmon River tributaries is dominated by Cretaceous granite, quartz diorite, and Idaho batholith (Omernik 1987); hill-slope vegetation is primarily lodgepole pine *Pinus contorta*, with riparian areas supporting willows *Salix* spp., dogwood *Cornus sericea*, and alders *Alnus* spp. Yakima River tributaries included Cooke Creek (treatment), Coleman Creek (treatment), Pearson Creek (treatment), West Fork Teanaway River (treatment), Middle Fork Teanaway River (control), and Wilson Creek (control). Yakima basin tributaries are part of the Cascades ecoregion (Leland 1995; Cuffney et al. 1997) and are characterized by nonmarine sedimentary rocks and metamorphic and intrusive rocks (Leland 1995). There is no known bedrock source of inorganic N in these areas (Leland 1995). Riparian vegetation is a mix of conifers (Coniferae), alders, cottonwoods *Populus* spp., willows, hawthorns *Crataegus* spp., vine maple *Acer circinatum*, forbes, and grasses. Klickitat River tributaries included Trout Creek (treatment), Summit Creek (treatment), and Bear Creek (control). The parent geology of Klickitat River tributaries is dominated by the Columbia River basalts of the Eastern Cascades Slopes and Foothills ecoregion (Omernik 1987); hill-slope vegetation is largely ponderosa pine *Pinus ponderosa* and Douglas-fir *Pseudotsuga menziesii*, and riparian areas support alders and willows. Wind River tributaries included Martha Creek (treatment) and Cedar Creek (treatment). The parent geology of Wind River tributaries is dominated by older volcaniclastic material (e.g., basalt and andesite) (Omernik 1987); hill-slope vegetation is primarily Douglas-fir, western hemlock *Tsuga heterophylla*, and grand fir *Abies grandis*, and riparian areas support bigleaf maple *Acer macrophyllum*, vine maple, and red alder *Alnus rubra* (Rawding 2000). Physical characteristics of the study streams are presented in Table 1.

Experimental design.—We used upstream–downstream and before–after comparisons (i.e., spatial and temporal control) in five control streams, and the experimental introduction of SCA in 10 treatment streams, to investigate the stream food web response to artificial nutrient enrichment across a broad spatial scale. Study streams were divided into 1-km upstream and 1-km downstream reaches with the exception of Wind River tributaries, where 500-m reaches were used. Salmon carcass analogs were applied to the downstream reaches of randomly selected treatment streams. Response variable measurements were collected before and after SCA additions in all study streams.

We acknowledge explicitly some shortcomings of our experimental design. Although standard data collection methods were employed among streams, response variable data were not consistently collected in all study streams and for all periods. In addition, although 80% of our treatment streams received equal SCA loading rates, 20% of our streams (i.e., Wind River tributaries) were loaded at higher rates. We refer readers interested in more detailed, within-subbasin methods and evaluations to individual reports by Pearsons et al. 2003 (Yakima River streams), Zendt and Sharp 2006 (Klickitat River streams), Mesa et al.

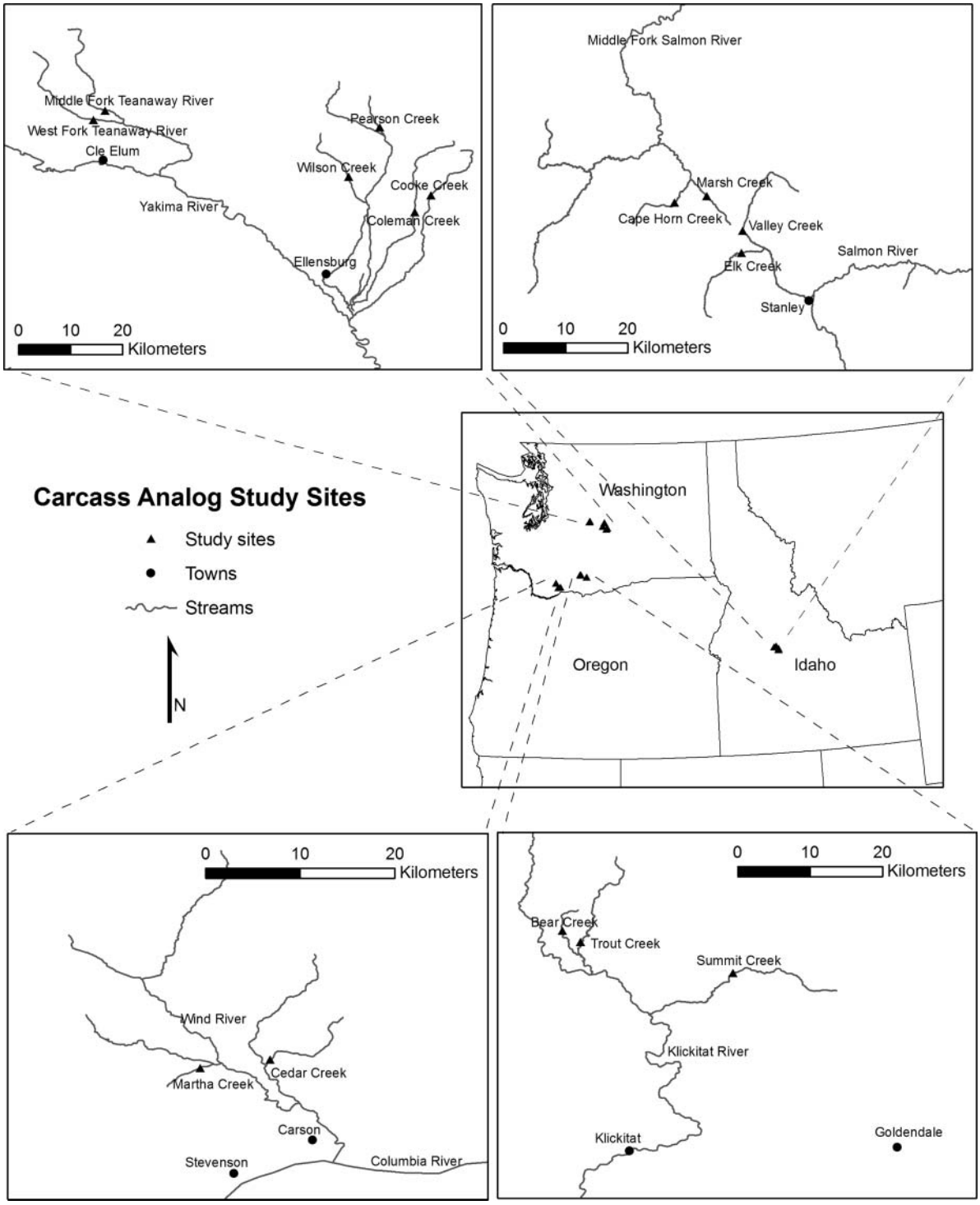

FIGURE 1. Location of study streams in the Columbia River basin in the Pacific Northwest.

2007 (Wind River streams), and Kohler et al. 2008 (Salmon River streams).

Salmon carcass analog treatment.—Streams were treated with SCA produced from fall Chinook salmon *O. tshawytscha* carcasses and marine fish bone meal (Bio-Oregon, Warrenton, Oregon) in August–October. The 11-g, 2.5-cm-diameter SCA pellets contained approximately 54.5% crude protein, 13.5% crude fat, 8.7% N, and 3.9% P by mass. Salmon River, Yakima River, and Klickitat River SCA stocking densities were based on N stable isotope data from Bilby et al. (1996) and were

TABLE 1. Physical characteristics of study streams in the Salmon (Salmon and Middle Fork Salmon) River subbasin, the Yakima River subbasin, the Klickitat River subbasin, and the Wind River subbasin in the Columbia River basin; MF = Middle Fork, WF = West Fork, NA = data not available.

Stream	Subbasin	Treatment or control	Catchment area (km^2)[a]	Gradient (%)	Discharge (m^3/s)[b]	Water temperature (°C)[b]	Bankfull channel width (m)	Canopy cover (%)[c]
Elk Creek	Salmon	Treatment	71	1.4	1.1 (0.2–3.2)	10.1 (0.1–19.8)	8.2	42 (27–53)
Valley Creek	Salmon	Control	51	0.9	1.3 (0.1–2.8)	10.3 (0.8–19.9)	7.6	42 (25–60)
Cape Horn Creek	MF Salmon	Treatment	52	0.6	0.9 (0.1–3.4)	7.7 (0.5–15.3)	9.2	9 (0–20)
Marsh Creek	MF Salmon	Control	122	0.4	1.5 (0.1–4.9)	10.7 (0.9–20.5)	10.3	1 (0–5)
Cooke Creek	Yakima	Treatment	38	3.6	0.05 (NA)[d]	5.2 (0.2–10.2)[e]	5.8	NA
Coleman Creek	Yakima	Treatment	48	3.0	0.03 (NA)[d]	5.8 (0.2–12.5)[e]	5.3	NA
Pearson Creek	Yakima	Treatment	16	6.1	0.02 (NA)[d]	4.2 (0.1–9.8)[e]	4.9	NA
WF Teanaway River	Yakima	Treatment	75	1.0	0.04 (NA)[d]	6.0 (2.0–11.0)[e]	15.7	NA
MF Teanaway River	Yakima	Control	73	1.9	0.08 (NA)[d]	5.8 (2.0–10.9)[e]	17.6	NA
Wilson Creek	Yakima	Control	22	5.7	0.05 (NA)[d]	5.1 (1.2–10.6)[e]	5.5	NA
Trout Creek	Klickitat	Treatment	84	1.5	0.3 (0.2–0.6)	13.0 (4.5–21.5)	9.1	34 (17–52)
Summit Creek	Klickitat	Treatment	57	1.7	0.7 (0.6–1.0)	9.6 (4.3–16.2)	6.4	23 (3–43)
Bear Creek	Klickitat	Control	17	2.8	0.2 (0.1–0.4)	11.7 (4.2–18.4)	4.8	68 (4–99)
Martha Creek	Wind	Treatment	NA	2.6	0.003 (NA)	8.9 (0.4–19.9)	3.6	54 (0–100)
Cedar Creek	Wind	Treatment	16	3.4	0.04 (NA)	8.4 (1.4–15.2)	4.6	NA

[a]Catchment area represents watershed drainage area upstream of study sites only.
[b]Average (range); values from period June to October.
[c]Average (range); values estimated using a spherical densitometer.
[d]Discharge measured once during base flows in 2001.
[e]Average (range); values from period September to October.

stocked with analog material at 0.03 kg/m^2 of bankfull channel width. Wind River tributary SCA stocking densities were based on target carcass levels developed from Wipfli et al. (2003) and stocked at 0.15 kg/m^2 (Martha Creek) and 0.30 kg/m^2 (Cedar Creek). Bio-Oregon pasteurized and tested SCA material for common fish pathogens prior to application. Refer to Pearsons et al. (2007) for details regarding the development and initial testing of SCA.

Stream water chemistry measures.—Water samples were collected from upstream and downstream reaches in all study streams ($n = 15$) before and after SCA treatments. Water was sampled from the thalweg and filtered as necessary following standard methods (APHA 1995). All water samples were processed by an analytical laboratory certified in water chemistry analyses. Dissolved nutrient concentrations (μg/L) were determined for nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), and soluble reactive phosphorus (SRP) as phosphate (PO_4) by certified water quality laboratories. Dissolved inorganic nitrogen (DIN) was calculated by summing inorganic nitrogen species.

Periphyton measures.—Periphyton samples were collected from upstream and downstream reaches of Salmon River and Wind River study streams ($n = 5$) before and after SCA treatments. Periphyton accrual was measured from samples collected on unglazed ceramic tiles (Salmon River, Yakima River, and Klickitat River streams) and natural substrate (Wind River streams) as chlorophyll *a* (mg/m^2), or ash-free dry mass (AFDM) (g/m^2), or both. Sample collection and analysis followed methods described in Steinman and Lamberti (1996) and Moulton et al. (2002) for artificial and natural substrata.

Macroinvertebrate measures.—Macroinvertebrate samples were collected from upstream and downstream reaches of Salmon River and Wind River ($n = 5$) study streams before and after SCA treatments. Salmon River samples were collected with a modified Hess sampler (500 μm mesh) and Wind River samples were collected with a Slack sampler (500 μm mesh). Three subsamples were collected from randomly, or haphazardly, chosen riffles in upper, middle, and lower strata locations within upstream and downstream reaches in respective study streams. Subsamples were composited at each riffle and used to estimate reach level densities. Pretreatment samples were collected in July and posttreatment samples were collected approximately 4 weeks after SCA treatments in October. Sample collection, preservation, and enumeration followed methods described in Hauer and Resh (1996).

Fish measures.—Electrofishing surveys were conducted in Yakima, Klickitat, and Wind river tributaries ($n = 9$) to estimate salmonid population abundance, growth, and diet measures (Yakima and Klickitat river tributaries only) before and after SCA treatments. Electrofishing surveys were not conducted in the Salmon River tributaries because of difficulty obtaining sampling permits under the Endangered Species Act and logistical challenges associated with sampling fish in wide streams. Salmonid population abundance was estimated by using multiple removal methods. In each stream, three 100-m (blocked) transects were surveyed in upstream and downstream reaches. Population estimates were calculated by using the programs Capture (White et al. 1982) and MicroFish (Van Deventer and Platts 1989). A Peterson method with a Chapman modification was used for population estimation in Wind River tributaries (Seber 2002). Salmonid fish abundance (density) was measured before the first and second year of SCA treatments and 1 year after the second year of SCA applications. Growth rates were assessed from length and mass measurements of recovered rainbow trout that were marked with passive integrated transponder (PIT) tags. Instantaneous growth was determined for all recaptured PIT-tagged fish. The instantaneous growth rate (IGR) for length and mass of individual fish was calculated by using the following formula (Ricker 1975):

$$\text{IGR} = (\log_e Y_2 - \log_e Y_1)/(t_2 - t_1),$$

where Y_2 = the mass (g) or fork length (mm) at the end of the period, Y_1 = the mass (g) or fork length (mm) at the beginning of the period, and $t_2 - t_1$ = the number of days between capture and tagging and subsequent recapture. Stomach content samples collected via gastric lavage were used to estimate percent stomach fullness for rainbow trout and cutthroat trout *O. clarkii* in Yakima River tributaries and for rainbow trout in Klickitat River tributaries by using methods described in Herbold (1986). To minimize confounding issues related to fish movement between reaches, reach-level growth was estimated by using data from fish captured and recaptured in the same reach over time (i.e., 14–365 d).

Carbon and nitrogen stable isotope measures.—Stable isotopes ratios of C ($^{13}C/^{12}C$; $\delta^{13}C$) and N ($^{15}N/^{14}N$; $\delta^{15}N$) were calculated from periphyton, invertebrate, and fish samples collected in control and treatment streams before ($n = 13$), 1 month after ($n = 13$), and 1 year after ($n = 9$) the first year of SCA treatments, and before ($n = 9$), 1 month after ($n = 3$), and 1 year after ($n = 3$) the second year of SCA treatments. Sample locations and sizes were influenced by budget constraints. Periphyton samples were scrubbed from streambed rocks in riffle habitat by using stiff-bristle brushes and a small volume of river water. The resulting slurry was filtered through pre-ashed, glass fiber filters and held in a freezer. Macroinvertebrates were sampled in riffle habitat by using D-frame kick nets and Hess samplers. Following sample collections, macroinvertebrates were held alive for 24 h to allow for gut evacuation. Samples from scraper taxa, mostly Ephemeroptera, were then segregated and frozen for later analysis. Salmonid fish samples were collected during electrofishing efforts (outside of areas used to estimate salmonid population abundance). A sample of approximately 10 g of dorsal muscle tissue was removed from individual fish, rinsed with distilled water, and freeze-dried for later analysis. Periphyton, macroinvertebrate, and fish samples were shipped to the National Marine Fisheries Service Northwest Fisheries Science Center (Seattle, Washington) for processing and subsequently sent to the University of Alaska Stable Isotope Facility, Fairbanks, for isotope analysis. Sample $\delta^{13}C$ and $\delta^{15}N$ values were calculated by using the following formula:

$$\delta^{15}\text{N or } \delta^{13}\text{C} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1{,}000,$$

where R_{sample} = the stable isotope ratio in the sample and R_{standard} = the stable isotope ratio in the standard. The standard for N is atmospheric N, and for C is Peedee Belemite, a calcareous rock from a formation in South Carolina (Peterson and Fry 1987).

Statistical analyses.—We considered samples collected from sites within reaches as subsamples and used multiple sites to estimate mean response variable values for each stream reach. We used mean reach values for stream water chemistry, periphyton, macroinvertebrate, fish, and stable isotope measures to facilitate comparisons between treatment and control streams. We applied a multiple before–after, control–impact (MBACI) design following that of Keough and Quinn (2000) to response variable data represented by the difference between the mean response of the downstream and upstream reaches (i.e., treatment reach mean minus control reach mean for treatment streams and downstream reach mean minus upstream reach mean for control streams). We used streams as replicates and analyzed a treatment by period (i.e., before–after) interaction effect with a multilevel model (MIXED) ANOVA (PROC MIXED; SAS Institute, 2003). The ANOVA model had two main factors of interest: (1) SCA addition or treatment (T; two levels, treatment and control) and (2) before–after SCA addition or period (BA; two levels). In addition, the model had streams (S) nested within T with year and S specified as random factors. The final ANOVA model included the terms T, BA, T × BA, Basin (i.e., Salmon, Yakima, Klickitat, and Wind), and Basin × T × BA. The term of most interest was T × BA, which measured any relative change in a response variable associated with SCA treatment. We used ANOVA P-values (alpha = 0.10) to indicate statistical significance in study stream interaction effects (hereafter overall interaction) and adjusted Tukey–Kramer P-values (alpha = 0.10) to evaluate significant differences in the least-squares-means interaction effects for treatment stream (hereafter treatment stream interaction). To test for response variable interactions over time (i.e., among periods), we used a mixed model repeated-measures ANOVA (RMANOVA) and tested for a T by time interaction (T × time; alpha = 0.10). The mixed model approach allows for the improved estimation of fixed and random effects and may be preferable when an

unbalanced design is used (Wagner et al. 2006). Mixed models are also robust to the departures of normality often seen in ecological data (Anderson and Braak 2003). We tested standard assumptions of normality and homogeneity of variance with Shapiro–Wilk and Levene's tests. Data that did not meet standard assumptions were log transformed prior to parametric statistical evaluations. Finally, we summarized effect size by comparing the percent difference relative to upstream reference reach conditions in control streams receiving no SCA treatments and treatment streams receiving SCA treatments.

RESULTS

Response variable effect sizes, expressed as percent differences, are presented in Figure 2, and ANOVA results used to test for a discrete change in response variable means following SCA addition are presented in Table 2 and Figures 3–6, while interaction effects between SCA treatment and time are presented in Table 3. We also present summarized results by response variable categories and temporal periods relative to stream-specific SCA applications. As such, we have five sampling periods: (1) samples collected before the first year of SCA treatments (Figure 2a; Table A.1 in the appendix), (2) samples collected after the first year of SCA treatments (Figure 2b; Table A.1), (3) samples collected before the second year of SCA treatments (Figure 2c; Table A.1), (4) samples collected after the second year of SCA treatments (Figure 2d; Table A.1), and (5) samples collected 1 year after the second year of SCA treatments (Figure 2e; Table A.1).

Stream Water Chemistry

A significant overall interaction effect (ANOVA: $P = 0.056$; Table 2) was detected in total nitrogen; N concentrations were highest in the downstream reaches of treatment streams before SCA additions (Figure 2a). Total N was 113.1 and 110.3 μg/L in upstream and downstream reaches, respectively, of control streams, and 132.9 and 163.3 μg/L in upstream and downstream reaches, respectively, of treatment streams (Table A.1). No other measured stream water chemistry variables showed significant responses to SCA (Tables 2 and 3).

Periphyton

There was a significant treatment stream interaction effect (Table 2; Figure 4) with periphyton chlorophyll *a* (ANOVA: $P = 0.099$) and AFDM (ANOVA: $P = 0.079$). Periphyton chlorophyll *a* and AFDM were 214% and 178% greater in downstream treatment reaches, respectively, relative to upstream controls in streams that received SCA applications (Figure 2b). Periphyton chlorophyll *a* was 1.5 and 2.1 mg/m^2 in upstream and downstream reaches, respectively, of control streams, and 4.0 and 12.6 mg/m^2 in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1). Mean AFDM was 0.6 and 0.4 g/m^2 in upstream and downstream reaches, respectively, of control streams, and 0.7 and 2.0 g/m^2 in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1). A significant Basin × T × BA interaction effect (ANOVA: $P = 0.093$) indicated differences among basins in periphyton AFDM response. Salmon River streams had a stronger response to SCA additions relative to Yakima and Wind river streams. We also found a significant treatment stream interaction effect (ANOVA: $P < 0.001$; Table 2; Figure 6) in periphyton δ^{15}N. Periphyton δ^{15}N was 296% (Figure 2b) and 51% (Figure 2d) greater in downstream treatment reaches relative to upstream controls in streams that received SCA applications. Periphyton δ^{15}N was 1.5‰ and −0.9‰ after the first year of SCA additions and 2.3‰ and 1.1‰ after the second year of SCA additions in upstream and downstream reaches, respectively, of control streams; and 0.9‰ and 3.4‰ after the first year of SCA additions and 1.7‰ and 2.5‰ after the second year of SCA additions in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1).

Macroinvertebrates

We found significant overall (ANOVA: $P = 0.079$; Table 2), treatment stream (ANOVA: $P = 0.007$; Table 2; Figure 4), and treatment by time interaction effects (RMANOVA: $P = 0.072$; Table 3) in macroinvertebrate density. Macroinvertebrate density was 158% greater in downstream treatment reaches relative to upstream controls in streams that received SCA (Figure 2b). Mean macroinvertebrate density was 911.3 and 829.1 individuals (ind.)/0.1 m^2 in upstream and downstream reaches, respectively, of control streams, and 454.2 and 1,171.6 (ind./0.1 m^2) in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1). There was also a significant treatment stream interaction effect (ANOVA: $P = 0.012$; Table 2; Figure 6) in macroinvertebrate δ^{15}N. Macroinvertebrate δ^{15}N was 100% (Figure 2b) and 48% (Figure 2d) greater in downstream treatment reaches relative to upstream controls in streams that received SCA applications following the first and second years of SCA treatment, respectively. Macroinvertebrate δ^{15}N was 2.6‰ and 2.7‰ after the first year of SCA additions and 4.1‰ and 4.3‰ after the second year of SCA additions in upstream and downstream reaches, respectively, of control streams; and 3.0‰ and 6.0‰ after the first year of SCA additions and 2.8‰ and 4.1‰ after the second year of SCA additions in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1).

Fish

We found significant overall (ANOVA: $P = 0.019$; Table 2), treatment stream (ANOVA: $P = 0.051$; Table 2; Figure 5), and treatment by time (RMANOVA: $P < 0.001$; Table 3) interaction effects in fish stomach fullness. Stomach fullness was 315% (Figure 2b) and 167% (Figure 2d) greater in downstream treatment reaches relative to upstream controls in streams that received SCA applications following the first and second years

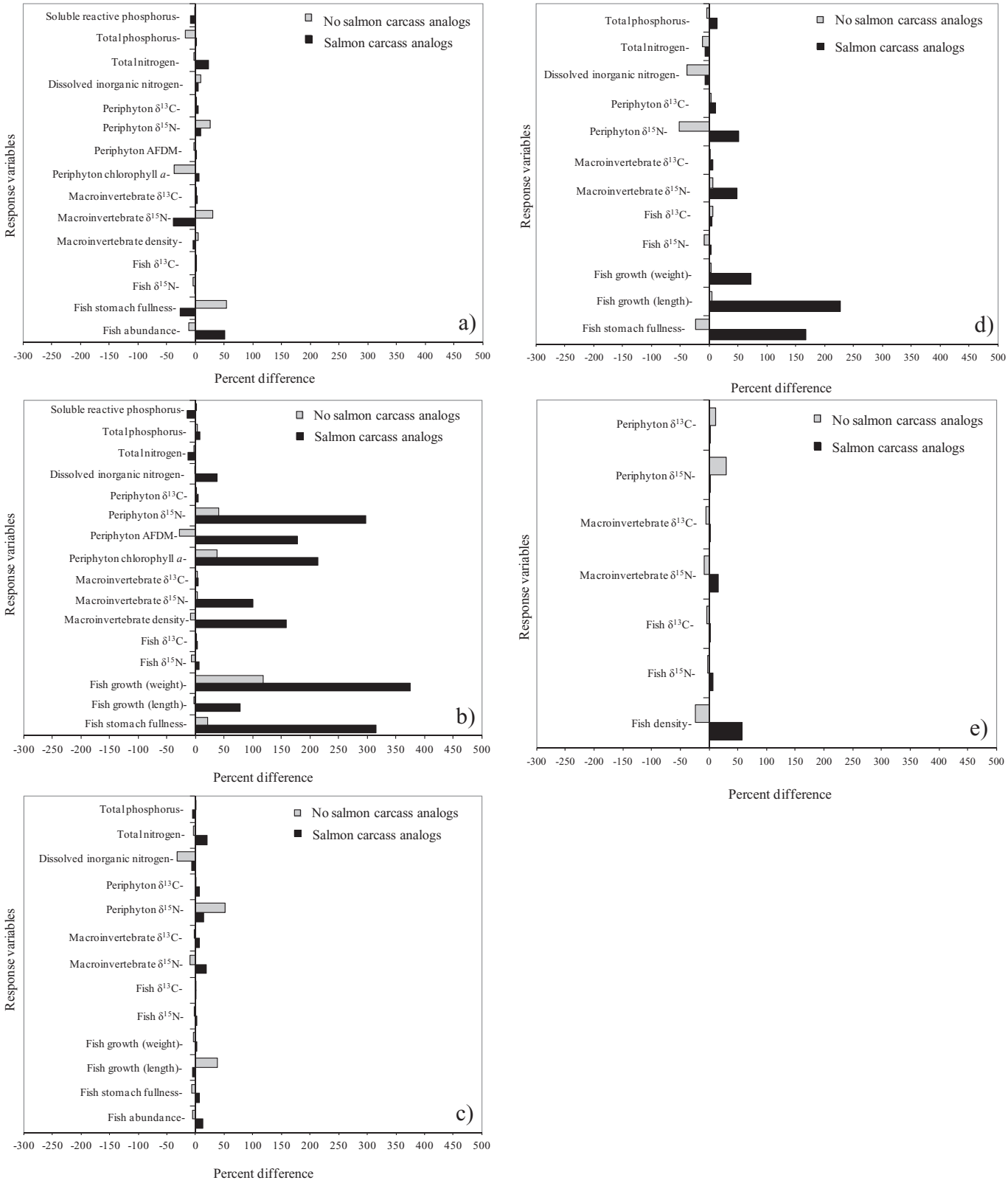

FIGURE 2. Percent difference relative to upstream control reach conditions in control streams receiving no salmon carcass analog (SCA) treatments and treatment streams receiving SCA treatments. (**a**) Data collected before the first year of SCA treatments; (**b**) data collected after the first year of SCA treatments; (**c**) data collected before the second year of SCA treatments; (**d**) data collected after the second year of SCA treatments; (**e**) data collected 1 year after the second year of SCA treatments.

TABLE 2. Analysis of variance PROC MIXED model for effects of salmon carcass analog (SCA) treatment (with and without carcass analogs) and period (before and after salmon carcass analog treatment) and interactions on stream water chemistry, periphyton, macroinvertebrate, and fish response variables. See text for an explanation of experimental design and statistical details. *P*-values in bold italics indicate a statistically significant difference at a probability of alpha = 0.10 for the overall treatment by period (T × BA) interaction effect and the treatment stream least-squares-means (LSM) T × BA interaction effect following SCA treatment. T = treatment, BA = before–after SCA addition, TN = total N, TP = total P, DIN = dissolved inorganic N, SRP = soluble reactive P, AFDM = ash-free dry mass.

Dependent variable	Effect	Numerator df	Denominator df[a]	*F*-value	*P*-value	LSM *P*[b]
		Stream water chemistry				
TN (μg/L)	T	1	18	0.23	0.633	
	BA	1	18	1.32	0.265	
	T × BA	1	18	4.17	***0.056***	0.136
	Basin	3	18	0.59	0.628	
	Basin × T × BA	7	18	1.09	0.409	
TP (μg/L)	T	1	8	0.95	0.359	
	BA	1	10	3.82	0.080	
	T × BA	1	10	2.23	0.167	0.406
	Basin	3	6	0.64	0.614	
	Basin × T × BA	7	13	1.82	0.170	
DIN (μg/L)	T	1	17	<0.01	0.945	
	BA	1	17	0.01	0.931	
	T × BA	1	17	0.10	0.750	0.353
	Basin	3	1	0.09	0.957	
	Basin × T × BA	7	17	0.07	0.999	
SRP (μg/L)	T	1	15	<0.01	0.980	
	BA	1	15	0.02	0.885	
	T × BA	1	15	<0.01	0.945	0.699
	Basin	2	1	0.59	0.678	
	Basin × T × BA	4	15	0.04	0.996	
		Periphyton				
Chlorophyll *a* (mg/m^2)	T	1	3	1.69	0.285	
	BA	1	5	1.78	0.245	
	T × BA	1	5	0.81	0.412	***0.099***
	Basin	1	2	1.55	0.326	
	Basin × T × BA	1	5	2.69	0.168	
AFDM (g/m^2)	T	1	7	2.82	0.135	
	BA	1	7	4.11	0.082	
	T × BA	1	10	0.86	0.376	***0.079***
	Basin	2	7	2.18	0.185	
	Basin × T × BA	2	11	2.96	0.093	
δ^{15}N (‰)	T	1	21	2.41	0.135	
	BA	1	22	1.81	0.193	
	T × BA	1	21	1.83	0.191	<***0.001***
	Basin	2	4	1.53	0.322	
	Basin × T × BA	6	21	0.65	0.690	
δ^{13}C (‰)	T	1	20	<0.01	0.972	
	BA	1	22	0.87	0.360	
	T × BA	1	20	0.11	0.742	0.614
	Basin	2	1	0.10	0.916	
	Basin × T × BA	6	21	0.21	0.969	
		Macroinvertebrate				
Density (ind./0.1 m^2)	T	1	4	0.96	0.393	
	BA	1	5	3.84	0.105	

TABLE 2. Continued.

Dependent variable	Effect	Numerator df	Denominator df[a]	*F*-value	*P*-value	LSM *P*[b]
	T × BA	1	5	4.74	***0.079***	***0.007***
	Basin	1	3	0.01	0.920	
	Basin × T × BA	1	5	0.07	0.805	
δ^{15}N (‰)	T	1	11	0.81	0.386	
	BA	1	16	1.61	0.223	
	T × BA	1	16	0.97	0.340	***0.012***
	Basin	2	11	0.16	0.851	
	Basin × T × BA	6	18	0.05	0.999	
δ^{13}C (‰)	T	1	11	0.26	0.624	
	BA	1	15	1.23	0.285	
	T × BA	1	14	0.06	0.804	0.428
	Basin	2	6	0.10	0.904	
	Basin × T × BA	6	18	0.40	0.872	
		Fish				
Density (ind./100 m^2)	T	1	5	0.72	0.409	
	BA	1	5	0.40	0.540	
	T × BA	1	5	0.80	0.387	0.638
	Basin	2	1	0.03	0.972	
	Basin × T × BA	4	5	24.77	0.001	
Stomach (% gut fullness)	T	1	23	5.80	0.024	
	BA	1	23	0.49	0.491	
	T × BA	1	23	6.41	***0.019***	***0.051***
	Basin	1	23	0.02	0.879	
	Basin × T × BA	3	23	2.50	0.085	
Specific growth (length)	T	1	8	0.05	0.834	
	BA	1	11	0.44	0.520	
	T × BA	1	10	2.18	0.170	***<0.001***
	Basin	2	6	0.71	0.529	
	Basin × T × BA	4	11	0.26	0.896	
Specific growth (weight)	T	1	12	0.19	0.669	
	BA	1	12	4.95	0.046	
	T × BA	1	12	0.83	0.380	***0.001***
	Basin	2	12	1.32	0.303	
	Basin × T × BA	4	12	1.85	0.185	
δ^{15}N (‰)	T	1	6	8.40	0.028	
	BA	1	14	0.23	0.638	
	T × BA	1	14	2.53	0.134	***0.024***
	Basin	1	6	2.85	0.143	
	Basin × T × BA	3	13	2.84	0.078	
δ^{13}C (‰)	T	1	5	0.10	0.762	
	BA	1	14	2.67	0.125	
	T × BA	1	14	0.62	0.445	***0.034***
	Basin	1	5	0.29	0.614	
	Basin × T × BA	3	9	1.14	0.386	

[a]The Satterthwaite approximation was used to estimate denominator df.
[b]Treatment stream *P*-value for the LSM T × BA interaction effect.

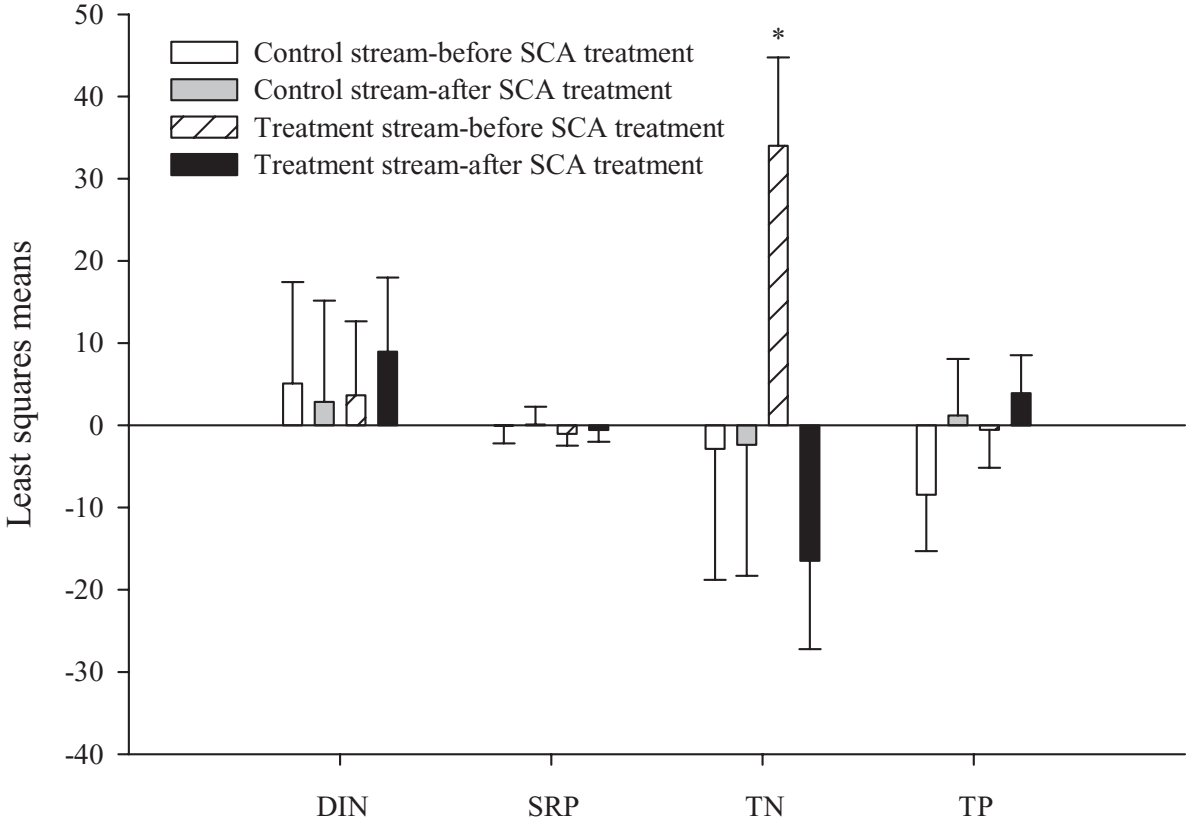

FIGURE 3. Water chemistry variable ANOVA least-squares means for the treatment by period interaction effect before and after salmon carcass analog treatment in control and treatment streams. Bars represent relative mean response across streams; error bars are SE. An asterisk indicates a significant ANOVA model treatment by period interaction effect. TN = total N, DIN = dissolved inorganic N, TP = total P, SRP = soluble reactive P.

of SCA treatment, respectively. Fish stomach fullness was 6.3% and 7.7% after the first year of SCA additions and 5.2% and 4.0% after the second year of SCA additions in upstream and downstream reaches, respectively, of control streams, and 8.5% and 35.1% after the first year of SCA additions and 8.9% and 23.9% after the second year of SCA additions in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1).

For specific growth in length and specific growth in weight we also found significant treatment stream (ANOVA: $P < 0.001$ and $P < 0.001$, respectively; Table 2; Figure 5) and treatment by time interaction effects (RMANOVA: $P = 0.075$ and 0.008, respectively; Table 3) . Specific growth (length) was 78% (Figure 2b) and 228% (Figure 2d) greater in downstream treatment reaches relative to upstream controls in streams that received SCA applications after the first and second years of SCA treatment, respectively. Specific growth (length) was 0.0004% and 0.0004% IGR after the first year of SCA additions and 0.0006% and 0.0006% IGR after the second year of SCA additions in upstream and downstream reaches, respectively, of control streams, and 0.0003% and 0.0005% IGR after the first year of SCA additions and 0.0003% and 0.0010% IGR after the second year of SCA additions in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1). Specific growth (weight) was 375% (Figure 2b) and 71% (Figure 2d) greater in downstream treatment reaches relative to upstream controls in streams that received SCA applications following the first and second years of SCA treatment, respectively. Specific growth (weight) was −0.0012% and 0.0002% IGR after the first year of SCA additions and 0.0018% and 0.0018% IGR after the second year of SCA additions in upstream and downstream reaches, respectively, of control streams, and was −0.0005% and 0.0013% IGR after the first year of SCA additions and 0.0007% and 0.0012% IGR after the second year of SCA additions in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1).

In addition, for $\delta^{15}N$ and $\delta^{13}C$ values in fish we found significant treatment stream effects (ANOVA: $P = 0.024$ and $P = 0.034$, respectively; Table 2; Figure 6). Fish $\delta^{15}N$ was 6% (Figure 2b) and 3% (Figure 2d) greater in downstream treatment reaches relative to upstream controls in streams that received SCA applications following the first and second years of SCA treatment, respectively. Fish $\delta^{15}N$ was 7.8‰ and 7.3‰ after the first year of SCA additions and 9.9‰ and 9.1‰ after the second year of SCA additions in upstream and downstream reaches,

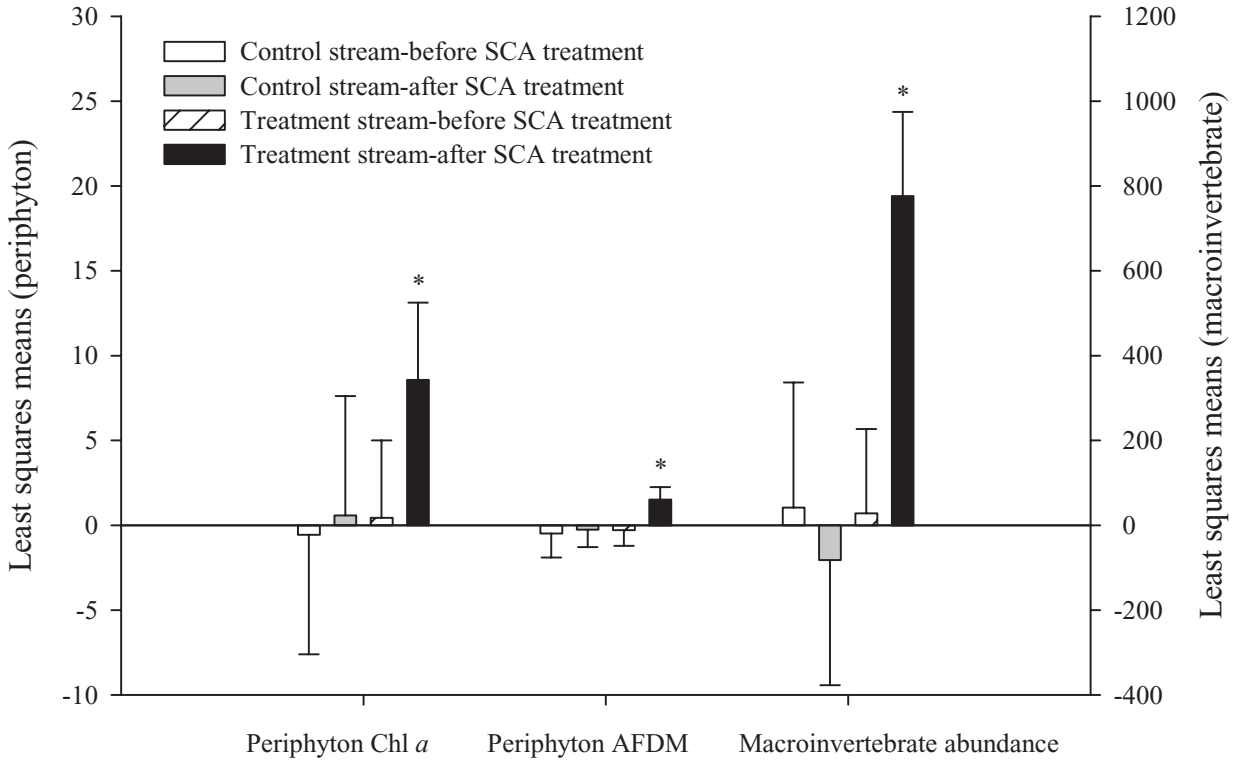

FIGURE 4. Periphyton and macroinvertebrate variables ANOVA least-squares means for the treatment by period interaction effect before and after salmon carcass analog treatment in control and treatment streams. Bars represent relative mean response across streams; error bars are SE. An asterisk indicates a significant ANOVA model treatment by period interaction effect. Chl *a* = periphyton chlorophyll *a*, AFDM = periphyton ash-free dry mass.

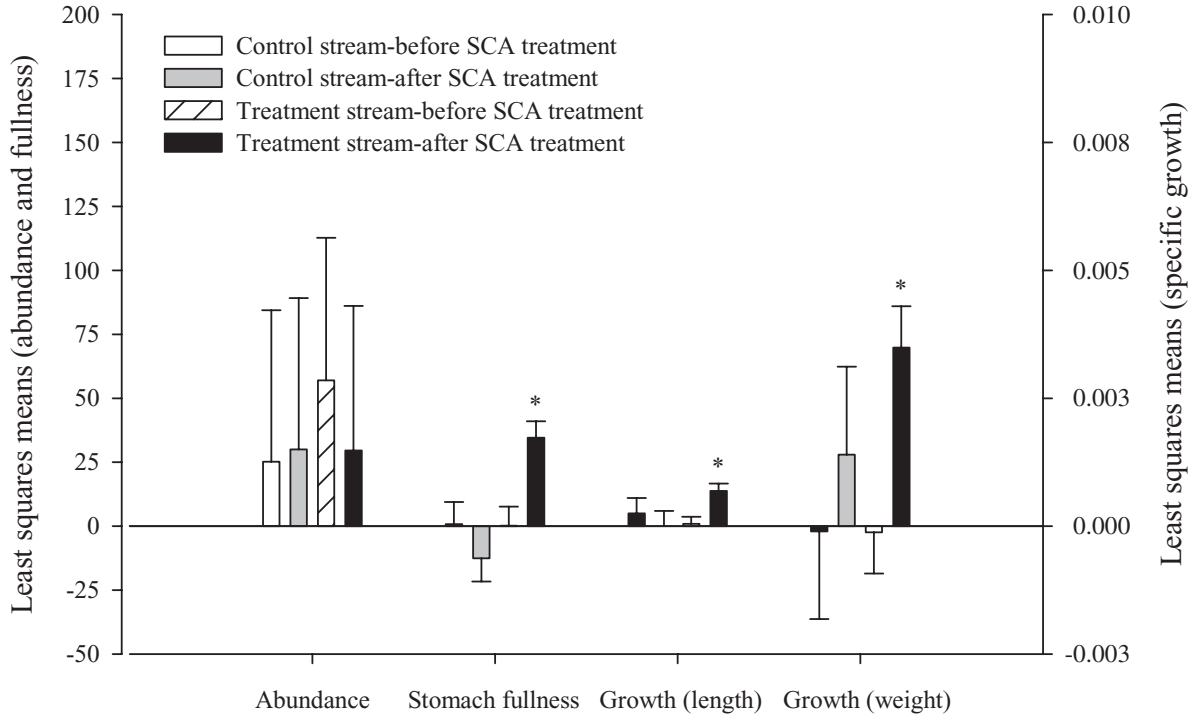

FIGURE 5. Fish variable ANOVA least-squares means for the treatment by period interaction effect before and after salmon carcass analog treatment in control and treatment streams. Bars represent relative mean response across streams; error bars are SE. An asterisk indicates a significant ANOVA model treatment by period interaction effect.

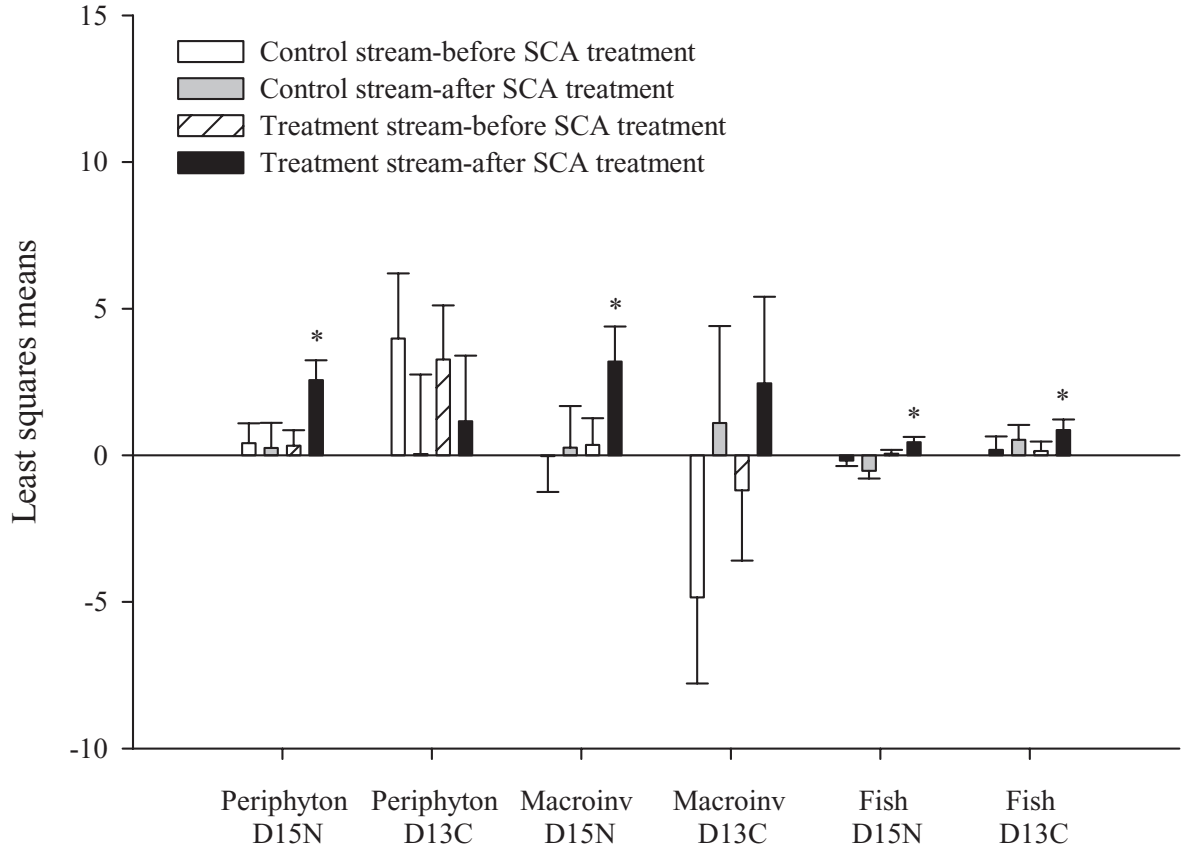

FIGURE 6. Periphyton, macroinvertebrate, and fish N and C stable isotope variable ANOVA least-squares means for the treatment by period interaction effect before and after salmon carcass analog treatment in control and treatment streams. Bars represent relative mean response across streams; error bars are SE. An asterisk indicates a significant ANOVA model treatment by period interaction effect. Macroinv = macroinvertebrate, D15N = δ^{15}N, D13C = δ^{13}C.

respectively, of control streams, and was 7.7‰ and 8.2‰ following the first year of SCA additions and 8.1‰ and 8.3‰ following the second year of SCA additions in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1). In addition, a significant Basin × T × BA interaction effect (ANOVA: $P = 0.078$) indicated differences between basins in δ^{15}N response. Yakima River streams showed increased δ^{15}N values after SCA additions relative to Klickitat River streams. Fish δ^{13}C was 4% (Figure 2b) and 6% (Figure 2 d) greater in downstream treatment reaches relative to upstream controls in streams that received SCA applications following the first and second years of SCA treatment, respectively. Fish δ^{13}C was −26.3‰ and −25.8‰ after the first year of SCA additions and −32.0‰ and −30.2‰ after the second year of SCA additions in upstream and downstream reaches, respectively, of control streams, and was −26.3‰ and −25.8‰ after the first year of SCA additions and −25.2‰ and −24.0‰ after the second year of SCA additions in upstream control and downstream treatment reaches, respectively, of treatment streams (Table A.1). No significant effects in salmonid fish abundance were detected with the exception of a Basin × T × BA interaction effect (ANOVA: $P = 0.001$; Table 2). Fish abundance varied between basins and did not respond to SCA treatments in a consistent manner.

DISCUSSION

Our study incorporates natural stream experiments conducted across a large spatial scale in the Columbia River basin and examines the response of physicochemical (dissolved nutrients), primary producer (periphyton), secondary consumer (macroinvertebrates and fish), and stream food web (C and N stable isotopes) responses to experimental SCA treatments. The physicochemical and stream food web response to SCA was varied and not altogether expected. Furthermore, the responses were not always consistent with what has been observed in studies that evaluated the effects of nutrient additions from spawning salmon. This, along with other evaluations of SCA, suggest that SCA is a potential tool for restoring nutrients to nutrient-limited systems, but key uncertainties indicate that additional large-scale studies could help inform management decisions. We recommend that nutrient mitigation using SCA be implemented within an experimental, adaptive management framework. We discuss our SCA treatment results specific to responses in

TABLE 3. Repeated-measures analysis of variance PROC MIXED model for effects of salmon carcass analog treatment (with and without carcass analogs) and interactions on stream water chemistry, periphyton, macroinvertebrate, and fish response variables over time. Time represents periods of data collection before and after 2 years of salmon carcass analog treatments. See text for explanation of experimental design and statistical details and Table 2 for definition of variable abbreviations. *P*-values in bold italics indicate a statistically significant difference at a probability of alpha = 0.10 for the overall treatment (T) by time (T × time) interaction effect.

Dependent variable	Effect	Numerator df	Denominator df	*F*-value	*P*-value
		Surface water chemistry			
TN (μg/L)	T	2	24	1.77	0.089
	T × time	2	24	1.47	0.155
TP (μg/L)	T	2	24	0.11	0.915
	T × time	2	24	0.13	0.897
DIN (μg/L)	T	2	24	0.66	0.525
	T × time	2	24	0.08	0.919
PO_4 (μg/L)	T	2	19	0.57	0.573
	T × time	2	19	0.07	0.949
		Periphyton			
Chlorophyll *a* (mg/m^2)	T	2	8	0.71	0.522
	T × time	2	8	0.11	0.896
AFDM (g/m^2)	T	2	8	0.92	0.437
	T × time	2	8	0.22	0.809
δ^{15}N (‰)	T	2	19	5.48	0.013
	T × time	2	19	1.36	0.280
δ^{13}C (‰)	T	2	19	1.79	0.195
	T × time	2	19	1.18	0.329
		Macroinvertebrate			
Density (ind./0.1 m^2)	T	2	8	2.04	0.192
	T × time	2	8	4.28	***0.072***
δ^{15}N (‰)	T	2	15	1.52	0.239
	T × time	2	15	0.19	0.827
δ^{13}C (‰)	T	2	15	0.74	0.494
	T × time	2	15	2.21	0.144
		Fish			
Density (ind./100 m^2)	T	2	14	0.05	0.951
	T × time	2	14	0.76	0.487
Stomach (% gut fullness)	T	2	19	47.49	<0.001
	T × time	2	19	30.56	<***0.001***
Specific growth (length)	T	1	6	5.61	0.056
	T × time	1	6	4.64	***0.075***
Specific growth (weight)	T	1	6	0.38	0.559
	T × time	1	6	15.42	***0.008***
δ^{15}N (‰)	T	2	14	7.95	0.005
	T × time	2	14	1.19	0.333
δ^{13}C (‰)	T	2	14	1.14	0.349
	T × time	2	14	0.49	0.620

water chemistry, periphyton, macroinvertebrates, and fish in the following sections.

Stream Water Chemistry Response to SCA Additions

We observed no effect of SCA additions on dissolved nutrient concentrations measured during the study period. These results are similar to previous SCA evaluations described in Kohler et al. (2008), but very different from studies that explored dissolved nutrient responses to spawning salmon or carcass additions. For example, significant increases in ammonium-nitrogen and soluble reactive phosphorus are commonly noted during and after salmon spawning (Minikawa and Gara 1999; Chaloner et al.

2004, 2007; Mitchell and Lamberti 2005; Cak et al. 2008; Janetski et al. 2009), which is probably the result of direct sources of metabolic waste products (via excretion), the physical disturbance of the streambed during spawning (via bioturbation) (Moore et al. 2004), and the decomposition of salmon organic matter following the spawning period. Differential response between inanimate SCA and live salmon spawner studies are more easily explained than differences observed following salmon carcass additions. Similar to live salmon spawners, carcass additions often elevate ammonium-nitrogen, soluble reactive phosphorus concentrations, or both (Claeson et al. 2006; Chaloner et al. 2007; Kiernan et al. 2010; Wipfli et al. 2010). Studies directly evaluating the dissolved nutrient response to inanimate salmon carcass and SCA additions under similar experimental settings are needed. We hypothesize that a strong biological demand and rapid biological uptake of dissolved nutrient subsidies provided by SCA additions in our study streams precluded any direct, measurable response in stream water nutrient concentrations. Inorganic forms of N and P, as well as dissolved organic matter, are rapidly utilized by biofilm (Freeman and Lock 1995) and sorbed onto stream sediments (Bilby et al. 1996). For example, salmon-derived ammonium and phosphorus moving in the hyporheic zone of a southwestern Alaska stream was removed, presumably by biofilm at the sediment surface, over short spatial distances (O'Keefe and Edwards 2003). Storage within biofilms and the eventual mineralization of MDN are hypothesized to become available to stream algae during subsequent growing seasons (Gende et al. 2002). These findings are invariably site-specific, and more long-term studies are needed to understand how alternative nutrient enrichment strategies affect nutrient dynamics in both autotrophic- and heterotrophic-based stream ecosystems.

Periphyton Response to SCA Additions

Autotrophic (algae) and heterotrophic (bacteria and fungus) epilithic biofilm responses to nutrient subsidies have been evaluated in numerous observational and manipulative studies across salmon habitat (Mathisen 1972; Chaloner et al. 2004, 2007; Wipfli et al. 2010). We documented a dramatic, short-term response on the standing crop of stream epilithic biofilm: the percent difference of chlorophyll *a* and AFDM measures collected in treatment stream reaches, relative to control streams, increased 214% and 178%, respectively, after SCA additions. These results are similar to previous studies investigating salmon carcass additions (Wipfli et al. 1998) in nutrient-limited, open-canopied streams (but see Ambrose et al. 2004). In contrast, results from studies investigating live salmon spawner influences on stream epilithic biomass appear to be highly variable and dependent on a suite of chemical (e.g., nutrient limiting status), physical (e.g., substrate size), and biological (e.g., spawner density and bioturbation) factors (see meta-analysis by Janetski et al. 2009). These differences indicate that inanimate SCA and carcass additions may not exactly mimic the ecological processes provided by nutrient subsidies in the form of live, spawning salmon, especially when considering short-term, basal resources directly influenced by the process of bioturbation. Long-term studies are needed to evaluate how these differences manifest across trophic levels within aquatic ecosystems.

Macroinvertebrate Response to SCA Additions

Salmon carcass analog additions increased macroinvertebrate densities following the first year of treatments. Short-term response in macroinvertebrate densities has been observed in streams receiving nutrient subsidies from spawning salmon (Minikawa 1997; Wipfli et al. 1998), carcass additions (Wipfli et al. 1998; Claeson et al. 2006), and SCA treatments (Kohler et al. 2008). However, it is important to note that dramatic differences (i.e., reductions) in short-term macroinvertebrate abundance have been observed with naturally spawning salmon when spawning densities are high (>0.1 salmon/m^2) (Moore and Schindler 2008) and substrate particle size is relatively small (<32 mm) (Janetski et al. 2009). Clearly, nutrient subsidies such as SCA and carcass additions do not mimic all of the ecological processes (e.g., bioturbation) provided by spawning salmon and specific biophysical contexts are important factors to consider when evaluating differential response to nutrient enrichment forms and trophic transfer pathways across the landscape (Tiegs et al. 2009). Studies that evaluate responses to nutrients in stream environments dominated by autotrophy as well as detritus-based systems are needed (Cross et al. 2006). In addition, simply measuring changes in density may obscure potential risks associated with nutrient enrichment, such as those described by Davis et al. (2010) where long-term dissolved, inorganic nutrient enrichment decoupled predator and prey production within macroinvertebrate communities in southern Appalachian streams. Alternatively, an evaluation of macroinvertebrate community composition and structure before and after SCA additions by Kohler and Taki (2010) did not reveal obvious negative responses, although this study was limited, used a different form of nutrient treatment (i.e., SCA), and did not represent a long-term data set. Long-term and large-scale studies evaluating the significance of these differences relative to the goals and objectives of alternative nutrient enrichment strategies like SCA will help inform scientists and natural resource managers.

Fish Response to SCA Additions

Marine-derived nutrients in the form of spawning salmon represent important subsidies to freshwater ecosystems and may fuel trophic level production and affect the growth, condition, and survival of stream- and lake-rearing juvenile salmonids (Bilby et al. 1996; Wipfli et al. 2003; Hyatt et al. 2004; Lang et al. 2006). In the presence of salmon eggs and carcass flesh, the majority of stream-dwelling salmonid stomach contents are composed of these materials (Bilby et al. 1998; although see Pearsons et al. 2008 for a contrast). We observed dramatic increases in stomach fullness and salmonid growth rates in both years after SCA treatments. These results are supported by the findings of Wipfli et al. (2004), who documented increased

condition, production, and lipid concentrations of resident and anadromous salmonids in salmon-carcass and SCA-enriched streams in Alaska. As suggested by Pearsons et al. (2007), our results provide strong evidence that a direct feeding pathway was provided to salmonid fishes from SCA; the majority of stomach content material after treatments was from SCA. Indirect benefits provided by SCA and transferred from basal food resources to salmonid fishes via bottom-up trophic transfer are less clear. The question remains: Are we simply feeding fish or are we providing both direct and indirect benefits over time? Evidence from lower trophic level production suggests that both pathways are influenced by SCA additions, but many uncertainties remain. For example, do benefits from SCA influence salmonid population abundance? Our abundance data, collected before and 1 year after SCA additions, is not conclusive. Furthermore, what are the consequences of nutrient enrichment on the population structure and dynamics of stream resident and anadromous fishes as described in Gende et al. (2002)? Will one group benefit at the other's expense? Will increasing growth rates influence pathways and relationships between smoltification and maturation similar to observations from natural systems with varied freshwater productivity (Wood 1995)? And finally, will increased growth translate to increased survival and production over time (Ward et al. 2003)? Answers to these questions are particularly important to resolve in locations that have low anadromous spawner abundance, diverse fish communities, and variable carrying capacities (Achord et al. 2003).

Periphyton, Macroinvertebrate, and Fish Stable Isotope Response to SCA

Natural abundance C and N stable isotope ratios have been used to identify trophic relationships and identify food resources in ecosystem studies (Peterson and Fry 1987; Mulholland et al. 2000). Bilby et al. (1996) and Chaloner et al. (2002) found biofilm, macroinvertebrate, and fish enriched with C and N stable isotopes in streams with spawning salmon. Similar to these studies and results from Kohler et al. (2008), we found elevated N stable isotope signatures in periphyton, macroinvertebrate, and fish biota following SCA additions. However, unlike Bilby et al. (1996, 1998) and Chaloner et al. (2002), who noted strongly enriched C and N in fish biota, presumably from direct pathways, our results are less clear. We present stable isotope data on the delta scale and, consistent with other response variables, use effect sizes expressed by percent differences. We suggest that direct comparisons among trophic levels be made using the delta scale results. In our study, a strong stable isotope signature did not always correspond with biological measurements. A weak N enrichment response suggests that the trophic transfer of MDN from SCA treatments to salmonid fishes was inefficient, despite growth and stomach fullness measures. These results may be germane to those of Shaff and Compton (2009), who found juvenile coho salmon *O. kisutch* enriched with N in streams supporting natural spawners, but not those planted with salmon carcasses. They reason that the restricted spatial and temporal distribution, general absence of eggs, and lack of bioturbation associated with inanimate carcasses are possible explanations for the difference. Do these same explanatory factors apply to SCA? An alternative explanation is found in Kline et al. (1997), where it is noted that N is subject to several microbial influenced processes (e.g., nitrification, denitrification) that can dramatically alter isotopic composition. Bottom-up forms of enrichment may be confounded, and therefore, using natural abundance N stable isotope composition to document MDN response in this context should be carefully evaluated (Gende et al. 2002).

CONCLUSIONS

We demonstrated dramatic, short-term stream food web response to SCA additions in study streams across a large spatial scale. Salmon carcass analog additions increased primary producer biomass (periphyton) and primary and secondary consumer densities (macroinvertebrates) and growth rates (fish). Indirect, bottom-up response to SCA treatment was clear in lower trophic level evaluations and less clear in salmonid fish response. Alternatively, a distinct, direct trophic pathway from SCA to salmonid fishes included the consumption of particulate SCA materials. These data contribute to our understanding of the potential effects of using pasteurized, salmon carcass materials as a form of nutrient enrichment in freshwater streams across the Columbia River basin. As mentioned above, many uncertainties and important research questions remain untested, and the adoption of SCA at larger spatial scales (i.e., stream segment or whole stream) should proceed with caution and only under experimental settings. In addition, the potential for negative consequences should be heeded (Compton et al. 2006; Wipfli et al. 2010) and the important differences between naturally spawning salmon and alternative forms of nutrient subsidies, such as SCA, noted. In the end, restoring the nutrient cycle to aquatic and terrestrial ecosystems via naturally spawning anadromous fishes is the most desirable long-term solution. Salmon carcass analogs should not be considered a substitute for live salmon and steelhead. However, SCA may provide an important interim tool to address large-scale nutrient deficits where salmon and steelhead populations have been extirpated or are severely reduced.

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REFERENCES

Achord, S., P. S. Levin, and R. W. Zabel. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? Ecology Letters 6:335–342.

Ambrose, H. E., M. A. Wilzbach, and K. W. Cummins. 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. Journal of the North American Benthological Society 23: 701–712.

Anders, P. J., and K. I. Ashley. 2007. The clear-water paradox of aquatic ecosystem restoration. Fisheries 32:125–128.

Anderson, M., and C. T. Braak. 2003. Permutation tests for multi-factorial ANOVA. Journal of Statistical Computation and Simulation 73:85–113.

APHA (American Public Health Association). 1995. Standard methods for the examination of water and wastewater, 19th edition. APHA, Washington, D.C.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53:164–173.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Cak, A. D., D. T. Chaloner, and G. A. Lamberti. 2008. Effects of spawning salmon on dissolved nutrients and epilithon in coupled stream-estuary systems of southeastern Alaska. Aquatic Sciences 70:169–178.

Chaloner, D. T., G. A. Lamberti, A. D. Cak, N. L. Blair, and R. T. Edwards. 2007. Inter-annual variation in responses of water chemistry and epilithon to Pacific salmon spawners in an Alaskan stream. Freshwater Biology 52:478–490.

Chaloner, D. T., G. A. Lamberti, R. W. Merritt, N. L. Mitchell, P. H. Ostrom, and M. S. Wipfli. 2004. Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. Freshwater Biology 49:587–599.

Chaloner, D. T., K. M. Martin, M. S. Wipfli, P. H. Ostrom, and G. A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. Canadian Journal of Fisheries and Aquatic Sciences 59:1257–1265.

Claeson, S. M., J. L. Li, J. E. Compton, and P. A. Bisson. 2006. Response of nutrients, biofilm, and benthic insects to salmon carcass addition. Canadian Journal of Fisheries and Aquatic Sciences 63:1230–1241.

Compton, J. E., C. P. Andersen, D. L. Phillips, J. R. Brooks, M. G. Johnson, M. R. Church, W. E. Hogsett, M. A. Cairns, P. T. Rygiewicz, B. C. McComb, and C. D. Shaff. 2006. Ecological and water quality consequences of nutrient addition for salmon restoration in the Pacific Northwest. Frontiers in Ecology and the Environment 4:18–26.

Cross, W. F., J. B. Wallace, A. D. Rosemond, and S. L. Eggert. 2006. Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. Ecology 87:1556–1565.

Cuffney, T. F., M. R. Meador, S. D. Porter, and M. E. Gurtz. 1997. Responses of physical, chemical, and biological indicators of water quality to a gradient of agricultural land use in the Yakima River basin, Washington. Environmental Monitoring and Assessment 64:259–270.

Davis, J. M., A. D. Rosemond, S. L. Eggert, W. F. Cross, and J. B. Wallace. 2010. Long-term nutrient enrichment decouples predator and prey production. Proceedings of the National Academy of Sciences of the USA 107: 121–126.

Freeman, C., and M. A. Lock. 1995. The biofilm polysaccharide matrix: a buffer against changing organic substrate supply? American Society of Limnology and Oceanography 40:273–278.

Gende, S. M., E. D. Edwards, M. F. Wilson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917–928.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25(1):15–21.

Hauer, R. F., and V. H. Resh. 1996. Benthic macroinvertebrates. Pages 339–369 *in* R. F. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Academic Press, San Diego, California.

Herbold, B. 1986. An alternative to the fullness index. Pages 315–320 *in* C. A. Simenstad and G. M. Cailliet, editors. Contemporary studies on fish feeding: the proceedings of GUTSHOP' 84. Dr W. Junk, Dordrecht, The Netherlands.

Hyatt, K. D., D. J. McQueen, K. S. Shortreed, and D. P. Rankin. 2004. Sockeye salmon (*Oncorhynchus nerka*) nursery lake fertilization: review and summary of results. Environmental Review 12:133–162.

Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. Oecologia 159:583–595.

Keough, M. J., and G. P. Quinn. 2000. Legislative vs. practical protection of an intertidal shoreline in southeastern Australia. Ecological Applications 10:871–881.

Kiernan, J. D., B. N. Harvey, and M. L. Johnson. 2010. Direct versus indirect pathways of salmon-derived nutrient incorporation in experimental lotic food webs. Canadian Journal of Fisheries and Aquatic Sciences 67:1909–1924.

Kline, T. C., Jr., J. J. Goering, and R. J. Piorkowski. 1997. The effect of salmon carcasses on Alaskan freshwaters. Pages 179–204 *in* A. M. Milner and M. W. Oswood, editors. Freshwaters of Alaska, ecological syntheses. Springer-Verlag, New York.

Kohler, A. E., A. Rugenski, and D. Taki. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho, U.S.A. streams. Freshwater Biology 53:446–460.

Kohler, A. E., and D. Taki. 2010. Macroinvertebrate response to salmon carcass analogue treatments: exploring the relative influence of nutrient enrichment, stream food web, and environmental variables. Journal of the North American Benthological Society 29:690–710.

Lamberti, G. A., D. T. Chaloner, and A. E. Hershey. 2010. Linkages among aquatic ecosystems. Journal of the North American Benthological Society 29:245–263.

Lang, D. W., G. H. Reeves, J. D. Hall, and M. S. Wipfli. 2006. The influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on growth and production of juvenile coho salmon rearing in beaver ponds on the Copper River delta, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 63:917–930.

Larkin, G. A., and P. A. Slaney. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. Fisheries 22(11):16–24.

Leland, H. V. 1995. Distribution of phytobenthos in the Yakima River basin, Washington, in relation to geology, land use, and other environmental factors. Canadian Journal of Fisheries and Aquatic Sciences 52:1108–1129.

Lichatowich, J. A. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C.

Mathisen, O. A. 1972. Biogenic enrichment of sockeye salmon lakes and stock productivity. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 18:1089–1095.

Mesa, M. G., C. D. Magie, T. C. Robinson, E. S. Copeland, and P. J. Connoly. 2007. Nutrient assessment in the Wind River watershed: report of phase

III activities in 2006. U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, Cook, Washington.

Minikawa, N. 1997. The dynamics of aquatic insect communities associated with salmon spawning. Doctoral dissertation. University of Washington, Seattle.

Minikawa, N., and R. I. Gara. 1999. Ecological effects of chum salmon (*Oncorhynchus keta*) spawning run in a stream of the Pacific Northwest. Journal of Freshwater Ecology 14:327–335.

Mitchell, N. L., and G. A. Lamberti. 2005. Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. American Society of Limnology and Oceanography 50:217–227.

Moore, J. W., and D. E. Schindler. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. Journal of Animal Ecology 77:275–284.

Moore, J. W., D. E. Schindler, and M. D. Scheuerell. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. Oecologia 139: 298–308.

Moulton, S. R., J. G. Kennen, R. M. Goldstein, and J. A. Hambrook. 2002. Revised protocols for sampling algal, invertebrate, and fish communities as part of the national water quality assessment program. U.S. Geological Survey, Open-File Report 02-150, Reston, Virginia.

Mulholland, P. J., J. L. Tank, D. N. Sanzone, W. M. Wollheim, B. J. Peterson, J. R. Webster, and J. L. Meyer. 2000. Food resources of stream macroinvertebrates determined by natural-abundance stable C and N isotopes and a ^{15}N tracer addition. Journal of the North American Benthological Society 19:145–157.

Mulholland, P. J., and J. R. Webster. 2010. Nutrient dynamics in streams and the role of *J-NABS*. Journal of the North American Benthological Society 29:100–117.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(3):4–21.

NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

O'Keefe, T. C., and R. T. Edwards. 2003. Evidence for hyporheic transfer and removal of marine-derived nutrients in a sockeye stream in southwest Alaska. Pages 99–107 *in* J. G. Stockner, editor. Nutrients in salmonid ecosystems: sustaining production and biodiversity. American Fisheries Society, Symposium 34, Bethesda, Maryland.

Omernik, J. M. 1987. Aquatic ecoregions of the conterminous United States. Annals of the Association of American Geographers 77:118–125.

Pearsons, T. N., C. L. Johnson, M. R. Schmuck, T. D. Webster, D. D. Roley, and R. E. Bilby. 2003. Influences of stocking salmon carcass analogs on salmonids in Yakima River tributaries. 2000–2002 Progress Report to the Bonneville Power Administration, Portland, Oregon.

Pearsons, T. N., C. L. Johnson, and G. M. Temple. 2008. Spring Chinook salmon interactions indices and residual/precocious male monitoring in the upper Yakima basin. 2007–2008 Annual Report to the Bonneville Power Administration, DOE/BP-106760, Portland, Oregon.

Pearsons, T. N., D. D. Roley, and C. L. Johnson. 2007. Development of a carcass analog for nutrient restoration in streams. Fisheries 32:114–124.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

Rawding, D. 2000. Wind River subbasin summary. Northwest Power Planning Council, Report, Portland, Oregon.

Ricker, W. E. 1975. Comparison of ocean growth and mortality of sockeye salmon during their last two years. Journal of the Fisheries Research Board of Canada 19:531–560.

Sanderson, B. L., H. J. Coe, C. D. Tran, K. H. Macneale, D. L. Harstad, and A. B. Goodwin. 2009. Nutrient limitation of periphyton in Idaho streams: results from nutrient diffusing substrate experiments. Journal of the North American Benthological Society 28:832–845.

Scheuerell, M. D., P. S. Levin, R. W. Zabel, J. G. Williams, and B. L. Sanderson. 2005. A new perspective of marine-derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 62:961–964.

Seber, G. A. F. 2002. The estimation of animal abundance and related parameters. Blackburn Press, Caldwell, New Jersey.

Shaff, C. D., and J. E. Compton. 2009. Differential incorporation of natural spawners vs. artificially planted salmon carcasses in a stream food web: evidence from δ^{15}N of juvenile coho salmon. Fisheries 34:62–72.

Steinman, A. D., and G. A. Lamberti. 1996. Biomass and pigments of benthic algae. Pages 295–313 *in* R. F. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Academic Press, San Diego, California.

Stockner, J. G., E. Rydin, and P. Hyenstrand. 2000. Cultural oligotrophication: causes and consequences for fisheries resources. Fisheries 25(5):7–14.

Thomas, S. A., T. V. Royer, G. W. Minshall, and E. Synder. 2003. Assessing the historic contribution of marine-derived nutrients to Idaho streams. Pages 41–55 *in* J. G. Stockner, editor. Nutrients in salmonid ecosystems: sustaining production and biodiversity. American Fisheries Society, Symposium 34, Bethesda, Maryland.

Tiegs, S. D., E. Y. Campbell, P. S. Levi, J. Ruegg, M. E. Benbow, D. C. Chaloner, R. W. Merritt, J. L. Tank, and G. A. Lamberti. 2009. Separating physical disturbance and nutrient enrichment caused by Pacific salmon in stream ecosystems. Freshwater Biology 54:1864–1875.

Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data—user's guide for MicroFish 3.0. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, General Technical Report INT-254, Ogden, Utah.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Wagner, T., D. B. Hayes, and M. T. Bremigan. 2006. Accounting for multilevel data structures in fisheries data using mixed models. Fisheries 31: 180–187.

Ward, B. R., D. J. F. McCubbing, and P. A. Slaney. 2003. Evaluation of the addition of inorganic nutrients and stream habitat structures in the Keogh River watershed for steelhead trout and coho salmon. Pages 127–147 *in* J. G. Stockner, editor. Nutrients in salmonid ecosystems: sustaining production and biodiversity. American Fisheries Society, Symposium 34, Bethesda, Maryland.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal estimates for sampling closed populations. U.S. Department of Energy, Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35:373–387.

Wipfli, M. S., J. P. Hudson, and J. P. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1503–1511.

Wipfli, M. S., J. P. Hudson, and J. P. Caouette. 2004. Restoring productivity of salmon-based food webs: contrasting effects of salmon carcass and salmon carcass analog additions on stream-resident salmonids. Transactions of the American Fisheries Society 133:1440–1454.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132:371–381.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, N. L. Mitchell, J. L. Lessard, R. A. Heintz, and D. T. Chaloner. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic levels in streamside experimental channels. Transactions of the American Fisheries Society 139:824–839.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Caouette. 1999. The influence of salmon spawner densities on stream productivity in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.

Wood, C. C. 1995. Life history variation and population structure in sockeye salmon. Pages 195–216 *in* J. L. Nielsen and D. A. Powers, editors. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Zendt, J., and B. Sharp. 2006. Influences of stocking salmon carcass analogs on salmonids in Klickitat River tributaries. 2001–2005 Completion Report to the Bonneville Power Administration, Project 200105500, Portland, Oregon.

Appendix 1: Summary of Reach Level Response Variable Data Collected

TABLE A.1. Sample size (n = number of streams), mean, standard error (SE), and range for reach level response variable measurements collected in study streams before and after salmon carcass analog treatments. Abbreviations are as follows: SCA = salmon carcass analog, T = treatment, BA = before–after SCA addition, TN = total N, TP = total P, DIN = dissolved inorganic N, SRP = soluble reactive P, AFDM = ash-free dry mass, NA = data not available.

	Upstream control reach				Downstream treatment reach			
Class, period, treatment, and response variable	*n*	Mean	SE	Range	*n*	Mean	SE	Range
Water chemistry measures								
Before SCA (year 1)								
Control stream								
TN (μg/L)	5	113.1	21.3	54.5–184.6	5	110.3	13.3	74.9–150.4
TP (μg/L)	5	51.2	22.6	11.2–137.8	5	42.8	14.4	12.0–94.7
DIN (μg/L)	5	18.4	9.6	1.8–54.2	5	20.3	10.2	2.6–58.2
SRP (μg/L)	4	7.5	6.0	0.9–25.6	4	7.5	6.1	1.1–25.7
Treatment stream								
TN (μg/L)	10	132.9	17.0	63.2–220.0	10	163.3	22.1	58.7–264.1
TP (μg/L)	10	45.8	8.1	13.2–87.3	10	46.1	8.2	13.1–85.5
DIN (μg/L)	10	32.5	12.0	2.1–113.6	10	34.3	11.9	1.3–111.0
SRP (μg/L)	8	15.7	4.7	1.2–32.1	8	14.4	4.6	0.8–32.8
After SCA (year 1)								
Control stream								
TN (μg/L)	5	105.6	20.3	57.9–156.8	5	103.3	27.1	56.3–203.9
TP (μg/L)	5	39.9	15.6	11.0–86.7	5	41.1	18.4	11.6–109.1
DIN (μg/L)	5	20.7	11.1	1.6–57.0	5	20.3	11.2	0.9–55.7
SRP (μg/L)	4	6.6	5.2	1.0–22.2	4	6.7	5.3	0.8–22.4
Treatment stream								
TN (μg/L)	10	120.3	11.4	70.2–184.0	10	105.2	15.2	52.2–180.0
TP (μg/L)	10	39.6	8.4	16.7–81.8	10	42.6	11.9	7.0–123.7
DIN (μg/L)	10	27.7	10.6	3.3–101.9	10	38.1	19.1	3.6–191.0
SRP (μg/L)	8	13.2	3.8	1.4–25.0	8	11.3	3.7	1.4–25.9
Before SCA (year 2)								
Control streams								
TN (μg/L)	1	97.9	NA	NA	1	93.9	NA	NA
TP (μg/L)	1	122.0	NA	NA	1	122.6	NA	NA
DIN (μg/L)	1	34.3	NA	NA	1	23.1	NA	NA
Treatment stream								
TN (μg/L)	2	125.4	43.7	81.8–169.1	2	126.5	40.6	85.9–167.1
TP (μg/L)	2	102.6	4.4	98.2–107.0	2	100.3	3.9	96.4–104.2
DIN (μg/L)	2	47.3	41.4	5.9–88.7	2	44.2	38.5	5.7–82.7
After SCA (year 2)								
Control stream								
TN (μg/L)	1	103.4	NA	NA	1	91.2	NA	NA
TP (μg/L)	1	55.1	NA	NA	1	53.0	NA	NA
DIN (μg/L)	1	55.3	NA	NA	1	34.2	NA	NA

(Continued on next page)

TABLE A.1. Continued.

Class, period, treatment, and response variable	Upstream control reach				Downstream treatment reach			
	n	Mean	SE	Range	*n*	Mean	SE	Range
Treatment stream								
TN (μg/L)	3	117.9	36.0	50.5–173.4	3	109.2	34.6	54.4–173.1
TP (μg/L)	3	34.7	11.4	13.0–51.3	3	39.5	7.4	26.0–51.6
DIN (μg/L)	3	54.5	34.5	3.9–120.4	3	50.9	33.2	4.4–115.2
Periphyton measures								
Before SCA (year 1)								
Control stream								
Chlorophyll *a* (mg/m^2)	2	1.5	1.2	0.4–2.7	2	1.0	0.6	0.4–1.6
AFDM (g/m^2)	2	0.7	0.4	0.3–1.1	2	0.7	0.3	0.3–1.0
Periphyton δ^{15}N (‰)	5	1.3	0.7	(–1.1)–3.1	4	1.7	0.5	0.7–3.2
Periphyton δ^{13}C (‰)	5	–28.4	2.8	(–37.7)–(–21.4)	4	–28.2	2.1	(–32.6)–(–22.9)
Treatment stream								
Chlorophyll *a* (mg/m^2)	4	3.9	2.0	0.6–9.5	4	4.2	2.0	0.6–9.2
AFDM (g/m^2)	4	2.5	1.5	0.6–6.9	4	2.5	1.7	0.4–7.4
Periphyton δ^{15}N (‰)	7	1.5	0.5	(–0.8)–3.1	5	1.7	0.4	0.8–2.8
Periphyton δ^{13}C (‰)	7	–29.2	0.4	(–30.0)–(–28.2)	5	27.7	1.1	(–30.4)–(–24.8)
After SCA (year 1)								
Control stream								
Chlorophyll *a* (mg/m^2)	2	1.5	1.2	0.4–2.7	2	2.1	1.9	0.2–3.9
AFDM (g/m^2)	4	0.6	0.2	0.2–1.1	4	0.4	0.2	0.1–1.1
Periphyton δ^{15}N (‰)	5	1.5	0.8	(–0.9)–3.7	5	2.1	0.5	1.0–3.9
Periphyton δ^{13}C (‰)	5	–29.2	2.0	(–34.9)–(–23.4)	5	–29.0	2.0	(–35.9)–(–23.8)
Treatment stream								
Chlorophyll *a* (mg/m^2)	4	4.0	2.2	0.1–10.2	4	12.6	8.8	0.8–38.2
AFDM (g/m^2)	8	0.7	0.2	0.1–1.9	8	2.0	1.1	0.5–9.3
Periphyton δ^{15}N (‰)	8	0.9	0.5	(–2.1)–2.0	8	3.4	0.8	(–1.1)–6.0
Periphyton δ^{13}C (‰)	8	–27.2	1.1	(–32.0)–(–23.7)	8	–25.7	1.1	(–31.3)–(–19.9)
Before SCA (year 2)								
Control streams								
Periphyton δ^{15}N (‰)	3	3.5	0.4	2.9–4.3	3	5.3	0.7	4.5–6.7
Periphyton δ^{13}C (‰)	3	–26.0	2.7	(–31.0)–(–21.7)	3	–25.6	2.7	(–31.0)–(–21.8)
Treatment stream								
Periphyton δ^{15}N (‰)	6	3.8	1.0	(–0.3)–6.2	6	4.4	1.6	(–1.4)–9.7
Periphyton δ^{13}C (‰)	6	–25.6	0.7	(–28.7)–(–23.9)	6	–23.8	0.3	(–24.8)–(–22.9)
After SCA (year 2)								
Control stream								
Periphyton δ^{15}N (‰)	1	2.3	NA	NA	1	1.1	NA	NA
Periphyton δ^{13}C (‰)	1	–32.3	NA	NA	1	–31.1	NA	NA
Treatment stream								
Periphyton δ^{15}N (‰)	2	1.7	2.1	(–0.5)–3.8	2	2.5	2.0	0.6–4.5
Periphyton δ^{13}C (‰)	2	–21.7	0.9	(–22.6)–(–20.8)	2	–19.2	1.6	(–20.8)–(–17.6)
One year after 2nd year SCA								
Control streams								
Periphyton δ^{15}N (‰)	1	1.5	NA	NA	1	1.9	NA	NA
Periphyton δ^{13}C (‰)	1	–33.0	NA	NA	1	–29.3	NA	NA

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TABLE A.1. Continued.

Class, period, treatment, and response variable	Upstream control reach				Downstream treatment reach			
	n	Mean	SE	Range	*n*	Mean	SE	Range
Treatment stream								
Periphyton $\delta^{15}N$ (‰)	2	1.4	0.7	(–0.3)–3.1	2	1.4	1.6	(–0.2)–3.0
Periphyton $\delta^{13}C$ (‰)	2	–24.8	0.7	(–25.5)–(–24.0)	2	–24.3	2.2	(–26.5)–(–22.2)
Macroinvertebrate measures								
Before SCA (year 1)								
Control stream								
Density (ind./0.1 m^2)	2	771.7	411.0	360.7–1,182.7	2	813.4	370.9	442.4–1,184.3
Macroinvertebrate $\delta^{15}N$ (‰)	4	1.4	0.9	(–0.9)–3.7	4	1.8	0.7	0.2–3.1
Macroinvertebrate $\delta^{13}C$ (‰)	4	–29.5	2.7	(–34.5)–(–22.0)	4	–29.2	2.1	(–33.3)–(–25.4)
Treatment stream								
Density (ind./0.1 m^2)	4	305.1	58.1	143.4–412.2	4	292.3	84.4	132.9–529.9
Macroinvertebrate $\delta^{15}N$ (‰)	6	3.8	0.4	3.2–4.6	8	2.4	0.6	(–1.1)–4.2
Macroinvertebrate $\delta^{13}C$ (‰)	6	–29.3	2.0	(–32.6)–(–25.6)	8	–28.1	1.0	(–33.2)–(–25.2)
After SCA (year 1)								
Control stream								
Density (ind./0.1 m^2)	2	911.3	479.8	431.6–1,391.1	2	829.1	331.8	497.3–1,160.9
Macroinvertebrate $\delta^{15}N$ (‰)	5	2.6	0.9	0.1–5.5	5	2.7	1.0	(–0.5)–5.6
Macroinvertebrate $\delta^{13}C$ (‰)	5	–29.5	1.4	(–32.0)–(–24.0)	5	–28.7	1.2	(–32.1)–(–25.1)
Treatment stream								
Density (ind./0.1 m^2)	4	454.1	48.5	364.3–589.6	4	1171.6	418.7	192.9–2,008.1
Macroinvertebrate $\delta^{15}N$ (‰)	8	3.0	0.6	0.1–5.5	7	6.0	0.2	5.6–7.2
Macroinvertebrate $\delta^{13}C$ (‰)	8	–28.7	0.7	(–31.1)–(–25.8)	7	–27.2	0.6	(–29.8)–(–24.7)
Before SCA (year 2)								
Control streams								
Macroinvertebrate $\delta^{15}N$ (‰)	3	4.0	0.4	3.3–4.6	3	3.7	0.6	2.8–4.7
Macroinvertebrate $\delta^{13}C$ (‰)	3	–28.4	1.3	(–30.4)–(–26.1)	3	–28.5	1.2	(–30.2)–(–26.2)
Treatment stream								
Macroinvertebrate $\delta^{15}N$ (‰)	6	4.6	1.9	0.5–13.3	6	5.4	2.4	0.5–16.5
Macroinvertebrate $\delta^{13}C$ (‰)	6	–28.7	0.9	(–32.4)–(–26.1)	6	–26.9	0.9	(–29.4)–(–24.5)
After SCA (year 2)								
Control stream								
Macroinvertebrate $\delta^{15}N$ (‰)	1	4.1	NA	NA	1	4.3	NA	NA
Macroinvertebrate $\delta^{13}C$ (‰)	1	–31.7	NA	NA	1	–31.6	NA	NA
Treatment stream								
Macroinvertebrate $\delta^{15}N$ (‰)	2	2.8	1.6	1.2–4.3	2	4.1	0.7	3.4–4.8
Macroinvertebrate $\delta^{13}C$ (‰)	2	–27.9	0.3	(–28.2)–(–27.5)	2	–26.2	0.7	(–26.9)–(–25.5)
One year after 2nd year SCA								
Control streams								
Macroinvertebrate $\delta^{15}N$ (‰)	1	5.6	NA	NA	1	5.1	NA	NA
Macroinvertebrate $\delta^{13}C$ (‰)	1	–31.5	NA	NA	1	–33.1	NA	NA
Treatment stream								
Macroinvertebrate $\delta^{15}N$ (‰)	2	3.6	1.7	1.9–5.3	2	4.2	1.4	2.8–5.6
Macroinvertebrate $\delta^{13}C$ (‰)	2	–27.1	0.8	(–27.8)–(–26.3)	2	–26.7	0.1	(–26.7)–(–26.6)

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TABLE A.1. Continued.

Class, period, treatment, and response variable	Upstream control reach				Downstream treatment reach			
	n	Mean	SE	Range	*n*	Mean	SE	Range
Fish measures								
Before SCA (year 1)								
Control stream								
Abundance (ind./100 m^2)	3	65.6	9.9	52.3–85.0	3	58.2	9.3	40.0–70.7
Stomach (% gut fullness)	3	4.8	0.7	3.6–5.9	3	7.5	0.8	6.1–8.7
Fish $\delta^{15}N$ (‰)	3	7.6	1.2	5.8–9.8	3	7.3	1.0	5.6–9.2
Fish $\delta^{13}C$ (‰)	3	–26.5	2.3	(–30.6)–(–22.8)	3	–26.2	2.1	(–30.4)–(–23.9)
Treatment stream								
Abundance (ind./100 m^2)	8	78.2	17.2	26.0–167.0	8	118.7	40.9	41.7–393.7
Stomach (% gut fullness)	4	8.6	2.0	4.9–14.2	4	6.3	0.3	5.6–7.0
Fish $\delta^{15}N$ (‰)	6	7.8	0.5	6.3–9.3	6	7.7	0.6	5.4–9.6
Fish $\delta^{13}C$ (‰)	6	–24.7	0.4	(–26.2)–(–23.1)	6	–24.5	0.5	(–26.1)–(–22.6)
After SCA (year 1)								
Control stream								
Growth (length)	2	0.0004	0.0004	(0.0000)–0.0007	2	0.0004	0.0004	(0.0000)–0.0007
Growth (weight)	2	–0.0012	0.0015	(–0.0027)–0.0003	2	0.0002	0.0010	(–0.0008)–0.0012
Stomach (% gut fullness)	3	6.3	0.5	5.3–7.2	3	7.7	1.0	6.4–9.5
Fish $\delta^{15}N$ (‰)	3	7.8	1.2	5.8–10.0	3	7.3	1.1	5.4–9.2
Fish $\delta^{13}C$ (‰)	3	–26.3	2.3	(–30.7)–(–22.9)	3	–25.8	2.5	(–30.8)–(–22.9)
Treatment stream								
Growth (length)	4	0.0003	0.0001	0.0001–0.0007	5	0.0005	0.0003	0.0000–0.0015
Growth (weight)	4	–0.0005	0.0004	(–0.0013)–0.0006	5	0.0013	0.0007	(–0.0002)–0.0034
Stomach (% gut fullness)	6	8.5	1.1	4.7–11.1	6	35.1	5.8	17.6–55.4
Fish $\delta^{15}N$ (‰)	6	7.7	0.6	5.7–9.7	6	8.2	0.6	6.0–9.7
Fish $\delta^{13}C$ (‰)	6	–24.6	0.4	(–26.0)–(–23.8)	6	–23.8	0.4	(–25.5)–(–22.4)
Before SCA (year 2)								
Control streams								
Abundance (ind./100 m^2)	3	57.0	9.7	38.0–69.7	3	54.4	15.1	31.0–82.7
Growth (length)	2	0.0006	<0.0001	0.0006–0.0007	2	0.0009	0.0002	0.0007–0.0010
Growth (weight)	2	0.0022	0.0005	0.0017–0.0026	2	0.0021	0.0005	0.0016–0.0026
Stomach (% gut fullness)	3	8.1	2.8	2.5–11.4	3	7.6	2.4	3.1–11.3
Fish $\delta^{15}N$ (‰)	3	7.8	1.2	5.6–9.8	3	7.7	1.0	6.1–9.6
Fish $\delta^{13}C$ (‰)	3	–27.0	2.2	(–31.0)–(–23.4)	3	–27.0	2.1	(–31.0)–(–23.8)
Treatment stream								
Abundance (ind./100 m^2)	6	65.2	14.5	29.7–120.0	6	73.9	19.3	22.3–131.0
Growth (length)	5	0.0008	<0.0001	0.0007–0.0009	4	0.0008	0.0001	0.0005–0.0010
Growth (weight)	5	0.0023	0.0002	0.0019–0.0028	4	0.0024	0.0003	0.0017–0.0030
Stomach (% gut fullness)	6	8.7	2.4	1.4–17.5	6	9.3	1.9	4.9–17.2
Fish $\delta^{15}N$ (‰)	6	7.9	0.6	6.3–9.7	6	8.1	0.5	6.4–9.8
Fish $\delta^{13}C$ (‰)	6	–25.3	0.3	(–26.5)–(–24.2)	6	–25.2	0.4	(–26.5)–(–23.9)
After SCA (year 2)								
Control stream								
Growth (length)	1	0.0006	NA	NA	1	0.0006	NA	NA
Growth (weight)	1	0.0018	NA	NA	1	0.0018	NA	NA
Stomach (% gut fullness)	3	5.2	1.4	3.8–8.0	3	4.0	1.52	1.2–6.4

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TABLE A.1. Continued.

Class, period, treatment, and response variable	Upstream control reach				Downstream treatment reach			
	n	Mean	SE	Range	*n*	Mean	SE	Range
Fish δ^{15}N (‰)	1	9.9	NA	NA	1	9.1	NA	NA
Fish δ^{13}C (‰)	1	–32.0	NA	NA	1	–30.2	NA	NA
Treatment stream								
Growth (length)	4	0.0003	0.0001	0.0001–0.0006	4	0.0010	0.0003	0.0005–0.0018
Growth (weight)	4	0.0007	0.0012	(–0.0015)–0.0037	4	0.0012	0.0007	(–0.0007)–0.0024
Stomach (% gut fullness)	6	8.9	1.0	6.9–13.5	6	23.9	3.9	9.1–34.3
Fish δ^{15}N (‰)	2	8.1	1.8	6.2–9.9	2	8.3	1.5	6.8–9.9
Fish δ^{13}C (‰)	2	–25.2	0.7	(–25.9)–(–24.5)	2	–24.0	0.4	(–24.5)–(–23.6)
One year after 2nd year SCA								
Control streams								
Abundance (ind./100 m^2)	1	71.0	NA	NA	1	54.0	NA	NA
Fish δ^{15}N (‰)	1	9.1	NA	NA	1	8.9	NA	NA
Fish δ^{13}C (‰)	1	–29.7	NA	NA	1	–30.9	NA	NA
Treatment stream								
Abundance (ind./100 m^2)	2	58.5	18.5	40.0–77.0	2	92.0	31.0	61.0–123.0
Fish δ^{15}N (‰)	2	7.8	1.8	6.1–9.6	2	8.4	1.4	7.0–9.8
Fish δ^{13}C (‰)	2	–24.3	0.7	(–24.9)–(–23.6)	2	–24.3	0.2	(–24.5)–(–24.1)