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Source: Journal of the North American Benthological Society, 29(2) : 690-710

Published By: Society for Freshwater Science

URL: https://doi.org/10.1899/09-091.1

J. N. Am. Benthol. Soc., 2010, 29(2):690–710

DOI: 10.1899/09-091.1

Macroinvertebrate response to salmon carcass analogue treatments: exploring the relative influence of nutrient enrichment, stream foodweb, and environmental variables

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Abstract. In Pacific Northwest (USA) streams, historical levels of marine-derived subsidies of C, N, and P from spawning salmon and steelhead are either greatly diminished or no longer present. A novel nutrient enrichment form, pasteurized salmon carcass analogue (SCA), has been developed as a management tool to increase freshwater productivity. We analyzed macroinvertebrate assemblages in 4 central Idaho (USA) streams to explore the relative influence of reach-scale SCA treatments on macroinvertebrate assemblages. We stratified study streams into upstream (control) and downstream (treatment) reaches and applied a single SCA treatment in mid-September to the downstream reaches of 2 treatment streams. We measured chemical, physical, and biological variables in all study streams and used nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate communities to illustrate relationships to foodweb and environmental variables. Macroinvertebrate assemblages differed significantly among streams ($p < 0.001$) and between treated and control reaches in treatment streams ($p < 0.030$). No reach-level differences were found in control streams ($p > 0.458$) or in treatment streams before SCA additions ($p > 0.130$). Variables that were significantly and positively correlated with NMDS ordination scores and suggested an SCA response included presence of SCA, elevated periphyton and macroinvertebrate δ^{15}N, increased periphyton ash-free dry mass, and increased relative abundances of dipterans, collectors, and Chironomidae. A weaker autotrophic response in 1 treatment stream relative to the other appeared to be explained partially by differences in canopy shading, as indicated by periphyton autotrophic index values. Increased autotrophic productivity and the absence of major shifts in treatment stream macroinvertebrate community composition and structure suggest that SCA is a viable nutrient-enrichment strategy.

Key words: Nutrient subsidies, freshwater productivity, macroinvertebrate community, nonmetric multidimensional scaling, multivariate ordination.

Sizable amounts of marine-derived C, N, and P enter freshwater aquatic and terrestrial ecosystems when large populations of anadromous salmonids (*Oncorhynchus* spp.) spawn and die (Kline et al. 1990, Larkin and Slaney 1997, Cederholm et al. 1999, Bilby et al. 2003). These marine-derived nutrients stimulate primary production and increase freshwater productivity and the growth and survival of stream-dwelling salmonids (Wipfli et al. 2003). Thus, anadromous fishes are an important vector of marine-derived nutrients and organic materials to inland aquatic and terrestrial ecosystems. In the absence of abundant anadromous fishes, freshwater productivity and the rearing capacities of freshwater streams for juvenile salmonids could decline from a lack of available nutrients and organic materials. Therefore, attention has focused on nutrient enrichment as a mitigation measure to facilitate salmon recovery efforts (Scheuerell et al. 2005).

Numerous studies have investigated the response of freshwater food webs to nutrient additions. These studies include delivery of nutrients to aquatic systems via direct application of inorganic liquid or slow-release pellet fertilizer (Kline et al. 1990, Gulis and Suberkropp 2003), natural spawning events of semelparous salmon and manipulative carcass additions and exclusions (Minshall et al. 1991, Wipfli et al. 1998, Ambrose et al. 2004, Chaloner et al. 2004, Lang et al. 2006), and use of pasteurized salmon carcass analogue (SCA) (Wipfli et al. 2004, Pearsons et al. 2007, Kohler et al. 2008). These investigations encompass a variety of trophic transfer pathways and demonstrate unique and variable responses in auto-

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trophic, heterotrophic microorganism, and macroinvertebrate and fish consumer communities across a range of lotic and lentic environments.

In southeastern Alaska (USA) streams, total macroinvertebrate densities and densities of Chironomidae midges, *Baetis* and *Cinygmula* mayflies, and *Zapada* stoneflies were higher in carcass-enriched than in control areas (Wipfli et al. 1998). In a similar study in southeast Alaska, biomass of chironomid midges was elevated in stream reaches with salmon spawners, whereas biomass of *Epeorus* spp. and *Rhithrogena* spp. mayflies was significantly higher in stream reaches lacking spawners (Chaloner et al. 2004). Natural spawning events cause significant habitat modification, which might explain differential taxonomic responses (Moore et al. 2004, Honea and Gara 2009). In southwest Washington (USA) streams, Heptageniidae, Chironomidae, and Elmidae densities were higher near carcass additions than in upstream control sites (Claeson et al. 2006).

SCA was developed by Pearsons et al. (2007) and is a novel approach to nutrient enrichment with several beneficial attributes: SCA is a pasteurized product that reduces the chance of pathogen transfer, contains nutrients and C-based compounds similar to those in naturally spawning salmon, and is easily manufactured, stored, and transported. SCAs slowly release nutrients and particulates similar to naturally decomposing salmon. Juvenile salmonids potentially could consume SCA material directly (Pearsons et al. 2007). Condition, production, and lipid concentrations of stream-resident cutthroat trout (*Oncorhynchus clarki*) and production and lipid content of young-of-the-year coho salmon (*Oncorhynchus kisutch*) increased in natural and artificial stream channels following SCA treatment (Wipfli et al. 2004). Kohler et al. (2008) demonstrated a positive stream foodweb response to SCA additions. The responses included elevated periphyton chlorophyll *a* and ash-free dry mass (AFDM), macroinvertebrate density and biomass, periphyton and macroinvertebrate stable isotope (δ^{15}N) values, and increased leaf decomposition rates in a stream reach containing SCA.

An important knowledge gap is the effect of SCA addition on invertebrate community composition, which might shift in response to changes in periphyton biomass and species composition. Kohler et al. (2008) demonstrated gross stream foodweb responses to SCA treatment, but ecologically meaningful effects on macroinvertebrate assemblages might have gone undetected. Macroinvertebrate communities represent a potentially important vector of marine-derived nutrients to aquatic and terrestrial consumers and warrant closer examination.

Our study is a follow-up to the study by Kohler et al. (2008) and focuses on the macroinvertebrate community response to SCA treatment in 2 central Idaho streams. We examined macroinvertebrate community characteristics and potential correlations with biological and physicochemical attributes. Comparing these effects with results of previous studies will highlight the similarities and differences between interim strategies like SCA and more sustainable forms of nutrient delivery ideally represented by healthy populations of Pacific salmon and steelhead.

The potential for differential stream foodweb responses to natural (i.e., spawning anadromous fishes) and artificial (e.g., SCA) nutrient enrichment strategies is of particular concern. For example, does SCA treatment truly mimic nutrient enrichment pathways represented by naturally spawning salmon and steelhead? Are the effects of SCA treatment on stream macroinvertebrate communities analogous to observations in natural systems with spawning fishes or those that receive carcass additions? How do environmental and stream foodweb variables interact with SCA additions and spawning fishes to deliver marine-derived nutrients to freshwater ecosystems? Answers to these questions require a thorough understanding of the interactions between nutrient subsidies and the biological and physicochemical characteristics of aquatic environments.

The specific objective of our study was to evaluate macroinvertebrate community response to SCA treatment using multivariate ordination and to explore the relationship between macroinvertebrate assemblages and measured stream foodweb and environmental variables with correlation analysis. We used multivariate techniques to illustrate and determine patterns of macroinvertebrate community assemblage before and after SCA treatment and joint plots to explore relationships to SCA treatment in control and treatment streams. We investigated 3 principal research questions. First, do control and treatment stream macroinvertebrate community assemblages differ in ordination space (within-stream and between-stream differences)? Second, do measured stream foodweb and environmental variables correlate with macroinvertebrate assemblages in control and treatment streams? Third, is macroinvertebrate community response to SCA treatment similar to responses observed in studies of alternative nutrient enrichment strategies and naturally spawning and decomposing fishes?

We expected that SCA treatment might affect macroinvertebrate assemblages by stimulating primary productivity and subsequently increasing the relative abundance of Ephemeroptera scrapers and

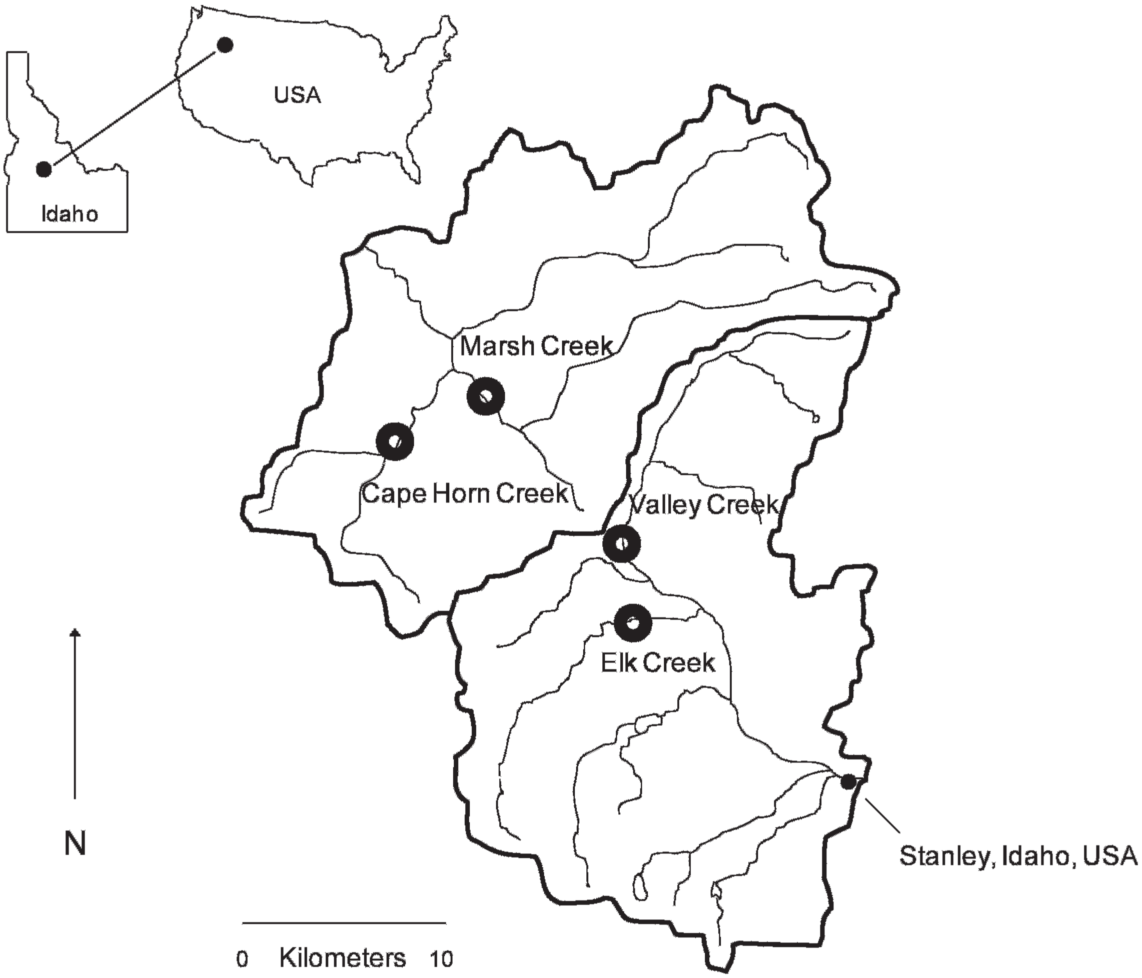

FIG. 1. Study area in central Idaho (USA) including control streams (Marsh Creek and Valley Creek) and treatment streams (Cape Horn Creek and Elk Creek).

Diptera collectors. Of particular concern was the potential for taxonomic shifts to invertebrates of poor quality for salmonid foraging after SCA additions. Understanding how macroinvertebrate communities respond to novel nutrient enrichment strategies like SCA will provide natural resource managers with valuable ecological information.

Methods

Study area

Our study streams are located in the Middle Fork Salmon River and upper Salmon River basins near Stanley, Idaho (Fig. 1). The streams are in 2 different drainages, but are spatially proximate and share characteristics common to the ecoregion. Study streams are on cretaceous granite, quartz diorite, and Idaho batholith (Omernik 1987) parent geology with upland vegetation consisting largely of lodgepole pine (*Pinus contorta*) and riparian vegetation dominated by willow (*Salix* spp.). N availability in central Idaho streams is limited by slow weathering of granitic parent material and a paucity of N-fixing riparian species (Henderson et al. 1978). Precipitation is largely in the form of winter snowfall. Peak stream flows generally occur during spring runoff in May and June, and base flows generally occur from July to April. We conducted aquatic habitat assessments following methods described in Bain and Stevenson (1999). Specific characteristics of the study streams are given in Table 1.

Experimental design

We divided 4 study streams into 1-km upstream and 1-km downstream reaches with no spatial separation between reaches. We applied a single SCA treatment to the downstream reach of 2 randomly selected study streams (Cape Horn Creek

TABLE 1. Mean (range) values for characteristics of the study streams.

Stream	Upstream catchment area (km^2)	Gradient (%)	Mean discharge[b] (m^3/s)	Mean water temperature[b] (°C)	Median particle size[c] (mm)	Mean % canopy cover[d]
Cape Horn Creek[a]	52	0.6	0.9 (0.1–3.4)	7.7 (0.5–15.3)	69.0 (63–79)	9.2 (0–20)
Marsh Creek	122	0.4	1.5 (0.1–4.9)	10.7 (0.9–20.5)	71.7 (60–82)	0.8 (0–05)
Elk Creek[a]	71	1.4	1.1 (0.2–3.2)	10.1 (0.1–19.8)	56.0 (51–70)	41.8 (27–53)
Valley Creek	51	0.9	1.3 (0.1–2.8)	10.3 (0.8–19.9)	60.2 (52–78)	52.2 (25–60)

[a] Salmon carcass analogue treatment stream
[b] June to October 2003
[c] From pebble counts ($n = 100$) at experimental units ($n = 6$)
[d] Measured in October 2003 with a spherical densitometer

[CHC] and Elk Creek [EC]) and left 2 streams (Marsh Creek [MC] and Valley Creek [VC]) untreated to serve as controls. We stratified stream reaches longitudinally into an upper, middle, and lower stratum, and in each stratum, we randomly selected a riffle habitat unit for sampling (Fig. 2). We considered riffle samples as subsamples and used them to estimate mean composite sample values. We did pretreatment sampling during July/August, applied SCA treatments in mid-September, and conducted posttreatment sampling in September/October.

We acknowledge explicitly the weaknesses of our experimental design. We would have preferred to apply SCA treatments to all 4 study streams. Instead, we treated only 2 streams. Pre- and posttreatment macroinvertebrate sampling occurred nearly 3 mo apart, so direct comparisons between sampling periods are confounded by seasonal changes in macroinvertebrate assemblages. Furthermore, comparisons of macroinvertebrate assemblages relied on the assumption that randomly chosen riffle habitat units were independent. This assumption might not be warranted and raises the issue of pseudoreplication (Hurlbert 1984). Therefore, we followed suggestions by Hurlbert (1984) and provided a diagram detailing the physical layout of the experiment, explicitly mentioned the weaknesses associated with the experimental design, and specifically detailed all statistical analyses.

The low replication and high variability typical of ecological experiments often means that only large responses are detected as statistically significant and that smaller, but perhaps biologically meaningful responses occur, but remain undetected (Francoeur 2001). Therefore, we used nonmetric multidimensional scaling (NMDS) ordination as a descriptive model for representing and understanding macroinvertebrate community data. Our experimental design used 2 levels of controls: streams that did not receive SCA treatments and the upstream reaches of treatment streams. Therefore, we separated control and treatment stream ordinations to facilitate interpretation of macroinvertebrate assemblage plots and associated stream foodweb and environmental variables before and after SCA additions. We presented spatial organization of macroinvertebrate assemblages within and between study streams graphically, with limited reliance on inferential statistics or direct comparisons between pre- and post-SCA treatment sampling periods. We used correlations of stream foodweb and environmental variables with NMDS axes to explore relationships between macroinvertebrate community structure and potential SCA treatment response.

Salmon carcass analogues

Salmon carcass analogue pellets (11 g; 2.5 cm) contained fall Chinook salmon (*Oncorhynchus tshawytscha*) carcasses and marine fish bone meal (Bio-Oregon, Inc., Warrenton, Oregon) with ~54.5% crude protein, 13.5% crude fat, 8.7% N, and 3.9% P by mass. We stocked pellets at densities of 30 g SCA material/m^2 of bankfull channel width throughout downstream treatment reaches in treatment streams. We used a target goal of 0.0063 kg P/m^2 of stream surface area to estimate loading densities (Wipfli et al. 2003). Pearsons et al. (2007) pasteurized and tested SCA for common fish pathogens prior to application (see Pearsons et al. 2007 for a detailed description of the development process).

Surface water chemistry

We collected water-chemistry samples from upper, middle, and lower strata in July, 1 wk before, and 2 wk after SCA treatment. We determined dissolved nutrient concentrations (µg/L) for NO_3^-, NO_2^-, NH_4^+, dissolved reactive P (DRP-PO_4), silicate (Si[OH]$_4$), total N (TN), and total P (TP) on a Technicon Autoanalyzer II segmented flow analyzer (SEAL

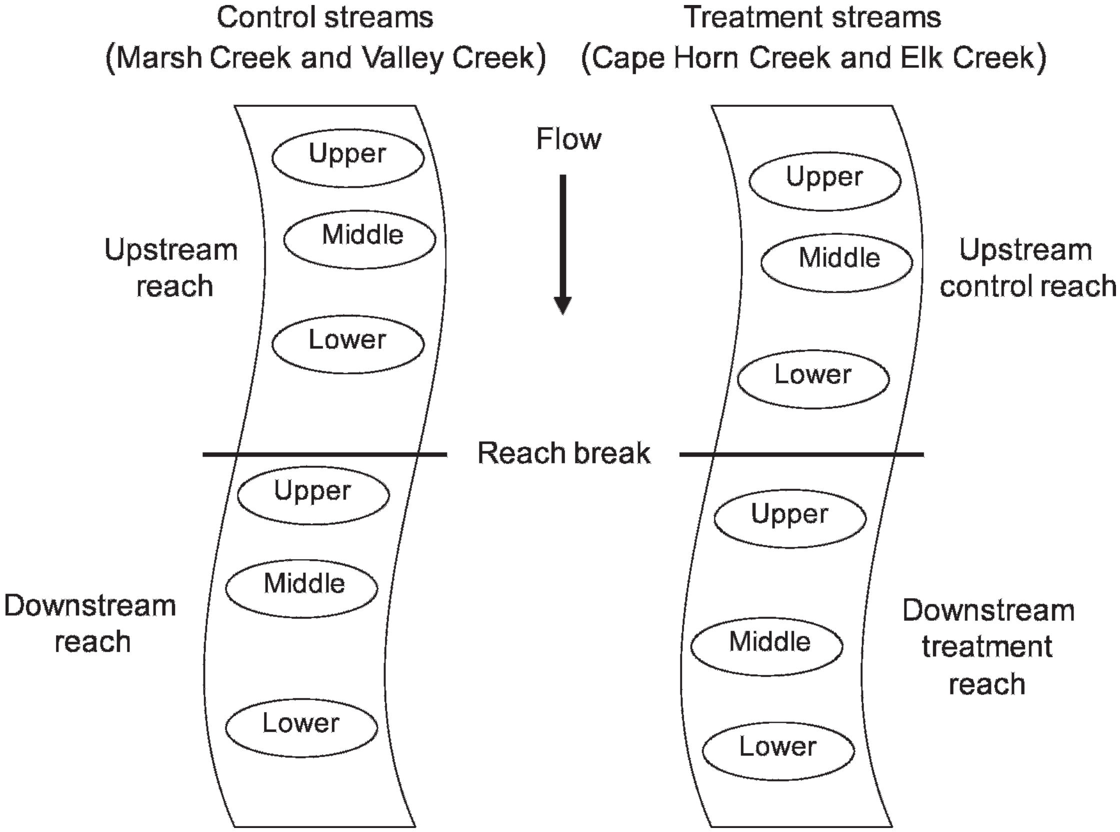

FIG. 2. Diagram of the study design depicting reach-level sampling locations in 4 study streams. Macroinvertebrate, stream foodweb, and environmental response variables were collected from randomly chosen upper, middle, and lower riffle habitat units in 1-km-upstream and 1-km-downstream reaches.

Analytical, Inc., Mequon, Wisconsin) (UNESCO 1994, Valderrama 1981). We measured dissolved organic C (DOC) with a Shimadzu model TOC5000® high temperature combustion C analyzer (Shimadzu Scientific Instruments, Inc., Columbia, Maryland) and with the high temperature catalytic oxidation method (Sharp et al. 2002). We calculated dissolved inorganic N (DIN) by summing inorganic N species (NO_2^-+ NO_3^-+ NH_4^+).

Periphyton sampling

We incubated ceramic tiles in stream reaches after spring freshets in July and again in mid-September concurrent with SCA treatments. We placed unglazed ceramic tiles in stream riffles for 30 (±2) d to standardize periphyton sampling substrate and incubation periods. We measured, scraped, brushed, rinsed, and filtered periphyton from 6 to 12 tiles onto glass-fiber filters (0.45 μm) at each riffle sampling site. We froze filters after sampling and analyzed for chlorophyll *a* and AFDM with standard laboratory methods (APHA 2005). We investigated the heterotrophic nature of the periphyton community by calculating an autotrophic index (Crossey and La Point 1988).

Macroinvertebrate sampling

We collected macroinvertebrate samples before SCA additions in July and 30 d after SCA treatments in October. We used a modified Hess sampler (363 μm) and standard effort (3 min) and disturbance depth (10 cm) to collect macroinvertebrates. We collected 3 subsamples from each riffle, the composite of which was considered a sample. We collected 3 replicate macroinvertebrate composite samples in each reach (n = 6/stream). We rinsed, stored in 70% ethanol, and identified all macroinvertebrates to the lowest feasible taxonomic level without subsampling. We identified macroinvertebrates with keys in Merritt and Cummins (1996) and assigned functional feeding groups according to Cummins and Klug (1979).

Stable isotope analyses

We measured periphyton and macroinvertebrate stable isotope ($\delta^{15}N$) values in control and treatment

TABLE 2. Summary characteristics of nonmetric multidimensional scaling ordinations of macroinvertebrate assemblages. MC = Marsh Creek, VC = Valley Creek, CHC = Cape Horn Creek, EC = Elk Creek.

Period	Streams	Solution	Iterations	Final stress	Final instability
Pretreatment	CHC, EC	2-dimensional	41	5.33999	0.00009
	MC, VC	2-dimensional	38	10.04243	0.00009
Posttreatment	CHC, EC	2-dimensional	72	3.68312	0.00007
	MC, VC	2-dimensional	40	6.84030	0.00007

streams. We scraped, rinsed, and brushed periphyton from a known area of unglazed ceramic tiles and filtered the slurry onto glass-fiber filters (0.45 μm). We then transferred periphyton samples in dark coolers to a laboratory freezer for storage. We collected macroinvertebrate samples using a modified Hess sampler (363 μm). We sorted a subset of scraper/grazer taxa and held them in freshwater for 24 h to allow gut evacuation and eventual stable isotope analysis. We sent frozen, desiccated samples to the University of Alaska Fairbanks Stable Isotope Facility for analysis. Stable isotope samples were analyzed using a Costech elemental analyzer and a Finnigan MAT ConFlo interface with a Delta + XL mass spectrometer (Thermo Finnigan MAT GmbH, Inc., Bremen, Germany).

Data analysis

We used cluster analysis and NMDS ordination to investigate the response of macroinvertebrate assemblages to SCA treatment in control and treatment streams before and after SCA additions. Multivariate analyses commonly are used to illustrate patterns of community structure and are useful for inferring species–environment relationships (Cao et al. 2002). NMDS illustrates community patterns with an iterative process that searches for an ordination of samples that best represents a similarity matrix (Clarke 1993), is an appropriate ordination method for ecological community data, and provides an effective way to represent community relationships graphically (McCune and Grace 2002).

We did cluster analysis based on a Sørenson (Bray–Curtis) distance measure and a group average linkage method. We describe NMDS analytical procedures and outputs in Table 2. We used $\log_{10}(x + 1)$-transformed family-level macroinvertebrate abundance to ordinate the sample × taxon matrix with rare species (<5% frequency of occurrence) omitted as recommended by Gauch (1982). Family-level taxonomic data compares favorably with studies at the genus or species level when used to determine community structure and assess taxon–environment relationships (Bailey et al. 2001). We generated dendrograms and NMDS ordination and joint plots with PC-ORD (Mather 1976, McCune and Mefford 1999).

We explored research questions about potential differences between streams and between reaches within streams for sample units in taxonomic space (NMDS ordination) with rank-transformed multiresponse permutation procedures (MRPP). Rank-transformed MRPP results are theoretically analogous to those from NMDS and are more similar to Analysis of Similarity (ANOSIM) (Clarke and Green 1988, Clarke 1993) than is MRPP using raw distances (McCune and Grace 2002). We calculated correlations between NMDS ordination axis scores and family-level macroinvertebrate and environmental variables with SigmaStat® (version 3.5) (Systat Software, Inc., Point Richmond, California). We used horizontally reflected ordination scores and variable vectors to facilitate graphical interpretation. We interpreted within-stream macroinvertebrate assemblage variability along NMDS axis 1 and between-stream macroinvertebrate assemblage variability along NMDS axis 2 based on MRPP results and spatial observations of ordination points along axes. We showed stream foodweb and physicochemical variables as vectors correlated with macroinvertebrate assemblage ordinations in control and treatment streams following SCA additions.

Results

Macroinvertebrate community cluster analysis and NMDS ordination before and after SCA treatment

Before SCA additions, ordination points for control and treatment streams showed no clear evidence of within-stream reach-level differences (MRPP, p = 0.130–0.901; Fig. 3A, B). Ordination points for upstream control and downstream treatment reaches clustered with minimal spatial separation along NMDS axis 1, which explained 6.8% and 5.8% of the variance in control and treatment streams, respectively. Ordination points for control and treatment streams showed clear evidence for between-stream differences in macroinvertebrate communities

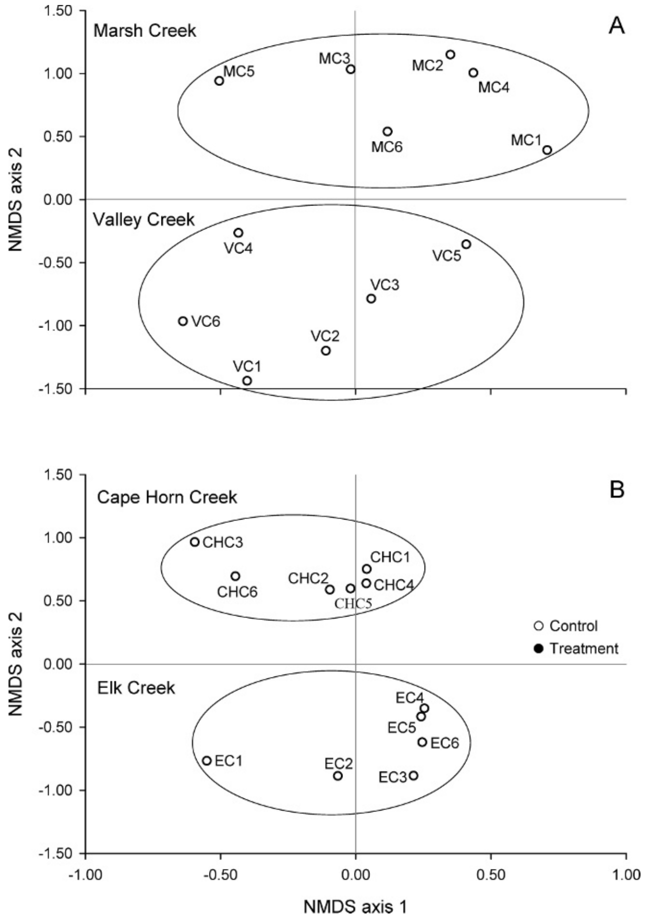

FIG. 3. Pretreatment nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate assemblages at control (Marsh Creek [MC] and Valley Creek [VC]) (A) and treatment (Cape Horn Creek [CHC] and Elk Creek [EC]) (B) streams. Sampling units were collected from riffles and represent a composite of 3 random subsamples. 1 = upper control, 2 = middle control, 3 = lower control, 4 = upper treatment, 5 = middle treatment, 6 = lower treatment (Fig. 2).

(MRPP, $p < 0.001$; Fig. 3A, B). Ordination points for control and treatment streams were spatially segregated on axis 2, which explained 90.2% and 87.9% of the variance in control and treatment streams, respectively (Fig. 3A, B).

After SCA additions, ordination points for control streams showed significant between-stream differences (MRPP, $p < 0.001$) along axis 2, which explained 86.4% of the variance, but no significant differences between reaches within streams (MRPP, $p > 0.641$) along axis 1, which explained 6.6% of the variance (Fig. 4A). Ordination points for treatment streams clustered with clear evidence of within-stream reach-level differences (MRPP, $p < 0.030$; Fig. 4B). Ordination points for upstream control and downstream

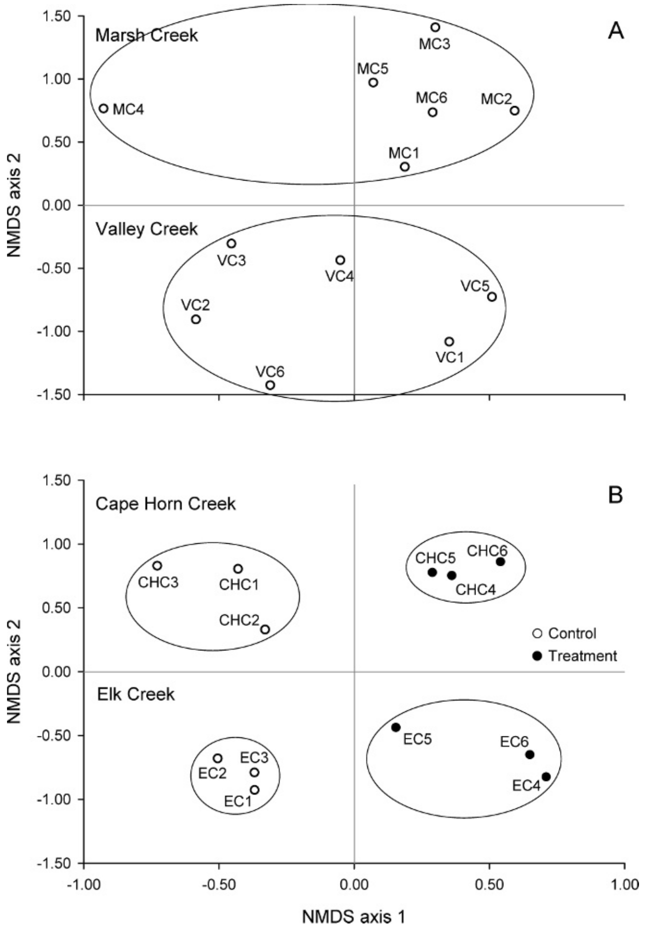

FIG. 4. Posttreatment nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate assemblages at control (Marsh Creek [MC] and Valley Creek [VC]) (A) and treatment (Cape Horn Creek [CHC] and Elk Creek [EC]) (B) streams. Samples were collected above and below the salmon carcass analogue treatment in downstream (treatment) reaches. Sampling units are identified as in Fig. 3.

treatment reaches clustered with distinct spatial separation along NMDS axis 1, which explained 29.5% of the variance. A between-stream difference was illustrated along NMDS axis 2 (MRPP, $p < 0.001$), which explained 65.4% of the variance (Fig. 4B). Cluster analysis supported the results from the NMDS ordination. Dendrograms showed separation between streams and separation between control and treatment reaches after SCA treatments in treatment streams, but not in control streams (Fig. 5).

NMDS ordination following SCA treatment and stream foodweb and environmental variable relationships

We found no significant correlations between stream foodweb and environmental variables and NMDS axis 1 and no within-stream reach-level

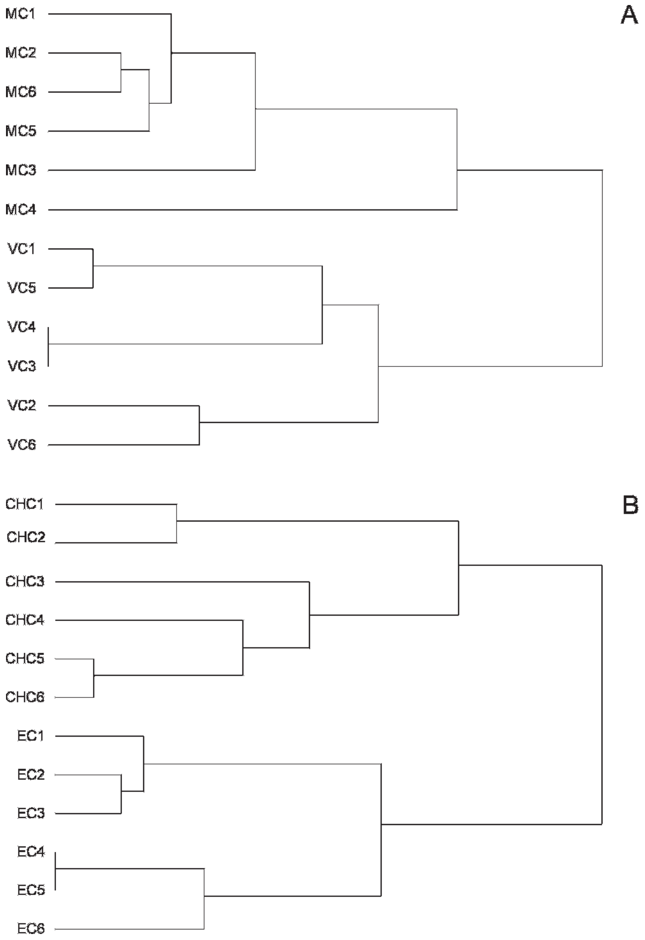

FIG. 5. Posttreatment Bray–Curtis cluster analysis of macroinvertebrate assemblages using group average linkage of sampling units from control (Marsh Creek [MC] and Valley Creek [VC]) (A) and treatment (Cape Horn Creek [CHC] and Elk Creek [EC]) (B) streams. Samples were collected above and below the salmon carcass analogue treatment in downstream (treatment) reaches. Sampling units are identified as in Fig. 3.

differences (MRPP, $p > 0.652$) in control stream macroinvertebrate assemblages (Fig. 6A, Table 3). In treatment streams, we found significant and positive correlations between periphyton AFDM, periphyton $\delta^{15}N$, macroinvertebrate $\delta^{15}N$, and the presence of SCA and NMDS axis 1, indicating an association with within-stream reach-level differences (MRPP, $p < 0.001$) in macroinvertebrate assemblages (Fig. 6B, Table 3).

Stream foodweb and environmental variables were significantly correlated with NMDS axis 2, indicating associations with between-stream differences (MRPP, $p < 0.001$) in macroinvertebrate assemblages in all study streams (Fig. 6A, B, Table 3). Correlated control stream variables included periphyton chlorophyll *a*, periphyton AFDM, periphyton autotrophic index, periphyton $\delta^{15}N$, macroinvertebrate $\delta^{15}N$, DIN, TN, TP, DIN:DRP, conductivity, median particle size, embeddedness, and % canopy shading. Correlated treatment stream variables included periphyton chlorophyll *a*, periphyton AFDM, periphyton autotrophic index, macroinvertebrate $\delta^{15}N$, TN, DRP, DOC, conductivity, median particle size, embeddedness, and % canopy shading. Stream foodweb and physicochemical variable means, 95% confidence intervals, and ranges are shown in Appendix 1.

NMDS ordination following SCA treatment and family-level macroinvertebrate metric relationships

Collector and scraper functional feeding group(s) (FFG), Ephemeroptera, Plecoptera, Trichoptera (EPT) and total taxonomic richness were significantly correlated with NMDS axis 1 in control streams (Fig. 7A, Table 4). We found no significant within-stream reach-level differences (MRPP, $p > 0.642$) in macroinvertebrate assemblages in control streams. Therefore, significant correlations with NMDS axis 1 do not appear to reflect significant within-stream reach-level differences. Strongly overlapping mean variable ranges illustrate natural variability and do not suggest within-stream reach-level differences (Appendix 2). In treatment streams, % Diptera and the collector FFG were significantly correlated with NMDS axis 1, illustrating associations to within-stream reach-level differences (MRPP, $p < 0.030$; Fig. 7B, Table 4) and a potential SCA treatment response.

Variables that were strongly correlated with NMDS axis 2 in control streams appeared to be associated with significant between-stream differences (MRPP, $p < 0.001$) in macroinvertebrate assemblages. Correlated variables included Shannon–Wiener diversity, % Ephemeroptera, % Plecoptera, % Trichoptera, % filterer, % shredder, % EPT, and total taxon richness (Table 4). We also found significant correlations in treatment stream macroinvertebrate assemblages between % Plecoptera, % Trichoptera, % filterer, and % predator and NMDS axis 2, indicating associations with between-stream differences (MRPP, $p < 0.001$). Macroinvertebrate metric means, 95% confidence intervals, and ranges are shown in Appendix 2.

NMDS ordination following SCA treatment and family-level macroinvertebrate taxon relationships

We found no within-stream reach-level differences (MRPP, $p > 0.642$) in control stream macroinvertebrate assemblages (Fig. 8A). Overlapping mean ranges illustrate natural variability and do not imply

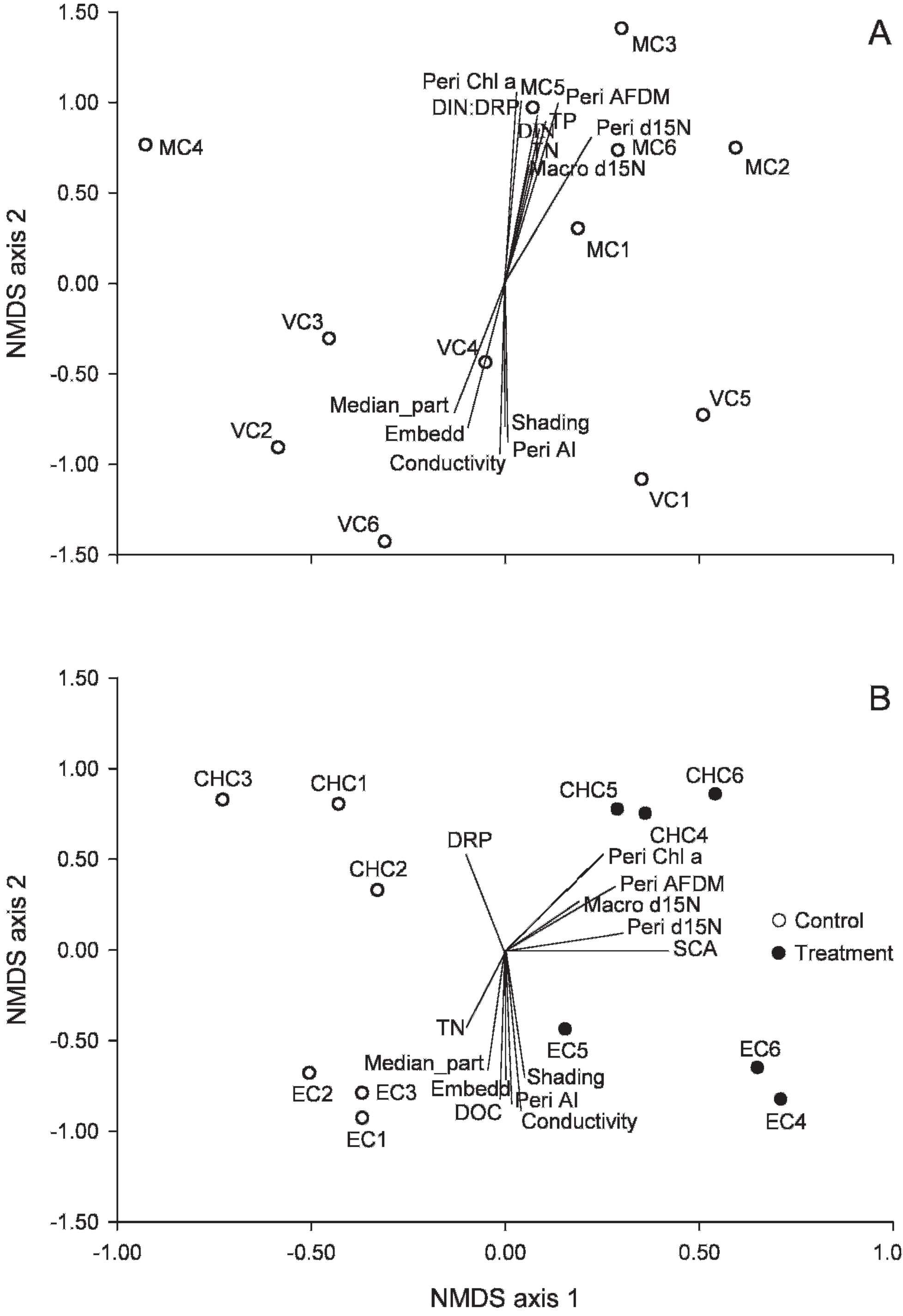

FIG. 6. Posttreatment nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate assemblages at control (Marsh Creek [MC] and Valley Creek [VC]) (A) and treatment (Cape Horn Creek [CHC] and Elk Creek [EC]) (B) streams. Samples were collected above and below the addition of a salmon carcass analogue (SCA) treatment in downstream (treatment) reaches. Significantly correlated stream foodweb and environmental variables are shown as axis vectors. Peri Chl *a* = periphyton chlorophyll *a*, Peri AFDM = periphyton ash-free dry mass, Peri AI = periphyton autotrophic index, Peri d15N = periphyton δ^{15}N stable isotope, Macro d15N = macroinvertebrate δ^{15}N stable isotope, TN = Total N, DIN = dissolved inorganic N, DRP = dissolved reactive P, DIN:DRP = ratio of DIN to DRP, DOC = dissolved organic C, Median_part = median particle size, Embedd = embeddedness, Shading = canopy shading. Sampling units are identified as in Fig. 3.

TABLE 3. Pearson correlation coefficients for the relationships between environmental and stream foodweb variables and nonmetric multidimensional scaling (NMDS) axis scores in control streams (Marsh Creek and Valley Creek; Fig. 6A) and treatment streams (Cape Horn Creek and Elk Creek; Fig. 6B). The sampling period followed salmon carcass analogue additions in treatment streams. Variables significantly correlated to NMDS axes 1 or 2 are shown in bold. AFDM = ash-free dry mass, DIN = dissolved inorganic N, DRP = dissolved reactive P, DOC = dissolved organic C.

	Axis 1 Within stream differences		Axis 2 Between stream differences	
Environmental variable	Correlation	p	Correlation	p
Marsh Creek and Valley Creek				
Periphyton chlorophyll *a*	0.182	0.572	0.911	**<0.001**
Periphyton AFDM	0.284	0.371	0.892	**<0.001**
Periphyton Autotrophic Index	0.026	0.936	−0.880	**<0.001**
Periphyton δ^{15}N	0.386	0.215	0.823	**0.001**
Macroinvertebrate δ^{15}N	0.245	0.442	0.749	**0.005**
DIN	0.233	0.466	0.886	**<0.001**
Total N	0.250	0.433	0.851	**<0.001**
Total P	0.254	0.426	0.883	**<0.001**
DIN:DRP	0.187	0.561	0.910	**<0.001**
Conductivity	−0.185	0.565	−0.916	**<0.001**
Median particle size	−0.335	0.286	−0.781	**0.003**
Embeddedness	−0.279	0.380	−0.817	**0.001**
Shading	0.002	0.994	−0.799	**0.002**
Cape Horn Creek and Elk Creek				
Periphyton chlorophyll *a*	0.418	0.176	0.781	**0.003**
Periphyton AFDM	0.593	**0.042**	0.627	**0.029**
Periphyton Autotrophic Index	0.104	0.748	−0.940	**<0.001**
Periphyton δ^{15}N	0.842	**0.001**	0.176	0.584
Macroinvertebrate δ^{15}N	0.613	**0.034**	0.642	**0.024**
Salmon carcass analog	0.936	**<0.001**	0.102	0.751
Total N	−0.247	0.439	−0.780	**0.003**
DRP	−0.269	0.399	0.779	**0.003**
DOC	−0.007	0.982	−0.932	**<0.001**
Conductivity	0.148	0.646	−0.966	**<0.001**
Median particle size	−0.076	0.815	−0.861	**<0.001**
Embeddedness	<0.001	0.999	−0.921	**<0.001**
Shading	0.169	0.599	−0.931	**<0.001**

within-stream reach-level differences (Appendix 3). However, we found significant within-stream reach-level differences (MRPP, $p < 0.030$) in treatment stream macroinvertebrate assemblages (Fig. 8B). Percent Heptageniidae was negatively correlated and % Chironomidae was positively correlated with NMDS axis 1 and illustrated potential responses to SCA treatments (Table 5).

In control streams, % Hydropsychidae, % Perlodidae, % Philopotamidae, % Elmidae, % Hydroptilidae, % Leuctridae, % Simuliidae, % Taeniopterygidae, % Tipulidae, and % Nemouridae were significantly correlated with NMDS axis 2, indicating an association with between-stream differences (MRPP, $p < 0.001$; Table 5). In treatment streams, % Ephemerellidae, % Leptophlebiidae, % Lepidostomatidae, % Chloroperlidae, and % Taeniopterygidae were significantly correlated to NMDS axis 2, indicating between-stream differences (MRPP, $p < 0.001$; Table 5) in macroinvertebrate assemblages. Macroinvertebrate family % composition means, 95% confidence intervals, and ranges are presented in Appendix 3.

Discussion

Organic nutrient enrichment has been linked to poor biotic integrity in streams (Miltner and Rankin 1998). However, many freshwater habitats that historically supported abundant returns of anadromous salmon and steelhead suffer from a lack of marine-derived C, N, and P. The absence of spatially diverse, large spawning populations of anadromous fishes across the Pacific Northwest landscape has had dramatic consequences for stream nutrient subsidies and fluxes, aquatic and terrestrial food webs, and ecosystem-based management (Cederholm et al. 1999, Moore et al. 2007). Freshwater productivity and the growth and survival of juvenile salmonids have been diminished (Kline et al. 1990, Larkin and Slaney 1997). In this context, current Endangered Species Act

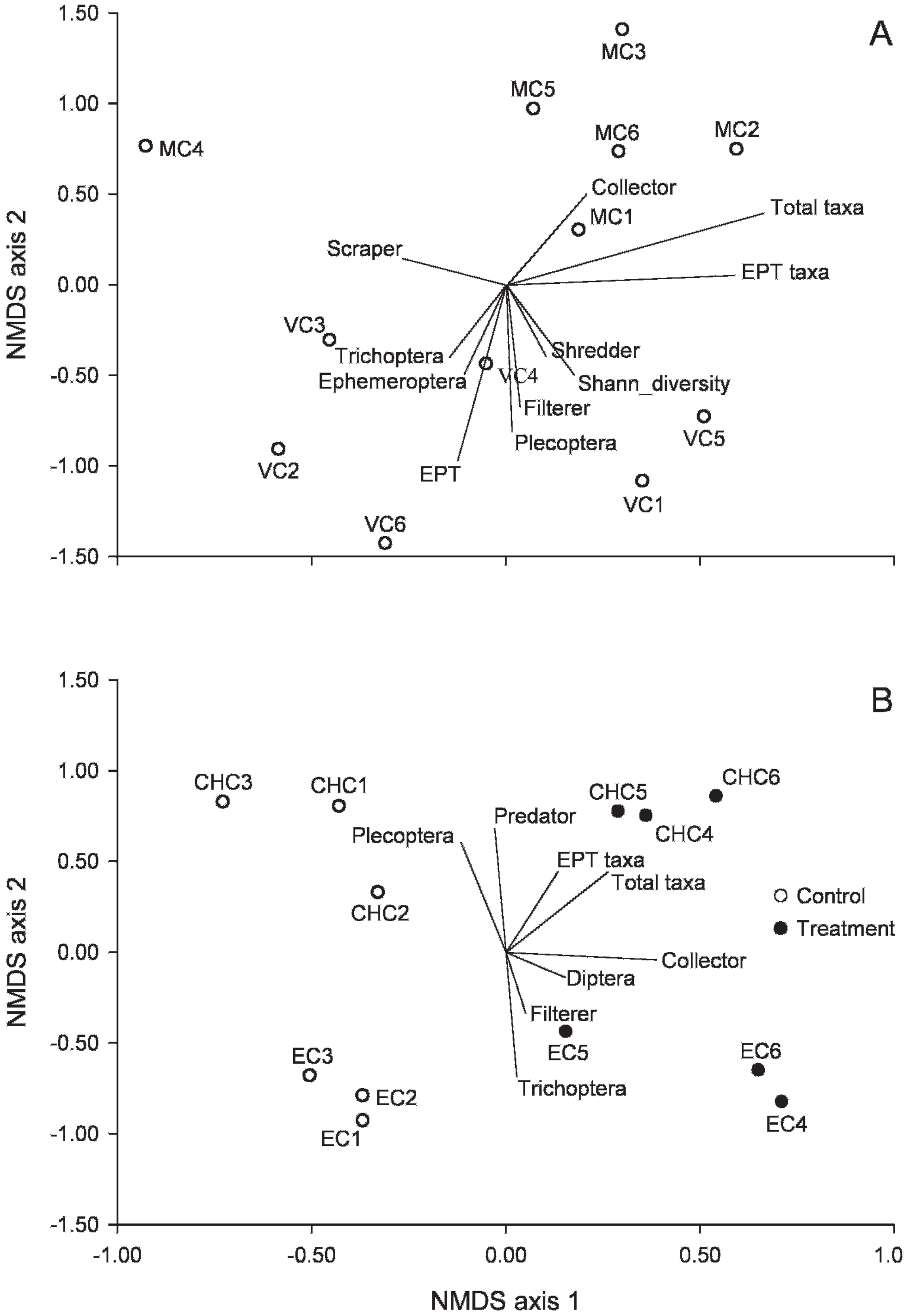

FIG. 7. Posttreatment nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate assemblages at control (Marsh Creek [MC] and Valley Creek [VC]) (A) and treatment (Cape Horn Creek [CHC] and Elk Creek [EC]) (B) streams. Samples were collected above and below the addition of a salmon carcass analogue treatment in downstream (treatment) reaches. Significantly correlated macroinvertebrate metric variables are shown as axis vectors. EPT taxa = Ephemeroptera, Plecoptera, and Trichoptera taxonomic richness, Total taxa = total taxonomic richness, EPT = % Ephemeroptera, Plecoptera, and Trichoptera, Shann_diversity = Shannon–Wiener diversity index. Sampling units are identified as in Fig. 3.

TABLE 4. Pearson correlation coefficients for relationships between macroinvertebrate metric variables and nonmetric multidimensional scaling (NMDS) axis scores in control streams (Marsh Creek and Valley Creek; Fig. 7A) and treatment streams (Cape Horn Creek and Elk Creek; Fig. 7B). The sampling period followed salmon carcass analogue (SCA) additions in treatment streams. Variables significantly correlated to NMDS axes 1 or 2 are shown in bold. EPT = Ephemeroptera, Plecoptera, Trichoptera.

	Axis 1 Within stream differences		Axis 2 Between stream differences	
Macroinvertebrate metric variable	Correlation	p	Correlation	p
Marsh Creek and Valley Creek				
Shannon–Wiener Diversity	0.306	0.333	−0.602	**0.039**
% Ephemeroptera	−0.342	0.277	−0.642	**0.024**
% Plecoptera	0.038	0.906	−0.813	**0.001**
% Trichoptera	−0.427	0.167	−0.604	**0.038**
% collector	0.580	**0.048**	0.426	0.167
% filterer	0.040	0.903	−0.704	**0.011**
% scraper	−0.670	**0.017**	0.095	0.769
% shredder	0.269	0.399	−0.551	**0.063**
% EPT	−0.348	0.267	−0.924	**<0.001**
EPT taxon richness	0.739	**0.006**	0.121	0.708
Total taxon richness	0.804	**0.002**	0.508	**0.092**
Cape Horn Creek and Elk Creek				
% Plecoptera	−0.323	0.305	0.857	**<0.001**
% Trichoptera	0.206	0.522	−0.851	**<0.001**
% Diptera	0.606	**0.037**	−0.370	0.237
% collector	0.816	**0.001**	−0.151	0.639
% filterer	0.159	0.623	−0.590	**0.043**
% predator	−0.225	0.482	0.877	**<0.001**
EPT taxon richness	0.304	0.336	0.467	0.126
Total taxon richness	0.485	0.110	0.428	0.165

listings of salmonid fishes in the Columbia River Basin have focused attention on artificial nutrient enhancement measures.

We evaluated macroinvertebrate community composition and structure in stream reaches experimentally treated with SCAs. Use of NMDS to ordinate macroinvertebrate communities allowed us to reduce the variation within the macroinvertebrate assemblage and to describe important relationships between streams, reaches within streams, and associated stream foodweb and environmental variables before and after SCA treatments. Our results show that biological assessment and multivariate ordination techniques were an effective method to identify SCA treatment response and to explore patterns of macroinvertebrate community composition and structure.

Macroinvertebrate community ordination and SCA treatment

Nutrient enrichment and environmental variables generally exert strong influences on macroinvertebrate assemblages (Hawkins et al. 1982, Wipfli et al. 1998). Rosario et al. (2002) found increased chironomid densities 4 wk after cow manure enrichment in California streams. Sylvestre and Bailey (2005) found distinctly different macroinvertebrate communities on leaf packs in high- and low-nutrient streams of the Fraser River Basin, British Columbia, Canada. Kohler et al. (2008) demonstrated an increase in macroinvertebrate density and biomass following SCA treatments. In our study, macroinvertebrate assemblages differed between streams during all sampling periods. Previous studies of streams in local geographic regions also found dissimilar macroinvertebrate assemblages (Reynoldson et al. 1997, Turak et al. 2000), presumably because of local-scale habitat and stream foodweb characteristics. Unique physicochemical conditions within stream habitats probably will produce variable stream foodweb responses to SCA.

Macroinvertebrate taxonomic response

An important research question addresses the macroinvertebrate community response to SCA treatment relative to alternative nutrient enrichment strategies (e.g., inorganic fertilizer) and more natural forms of marine-derived nutrients (i.e., naturally spawning and decomposing salmon and steelhead and direct carcass placements). Our analysis examined macroinvertebrate community response to SCA treatments and relationships to common bioassessment measures (stream foodweb and physicochemical) and macroinvertebrate community metrics (rela-

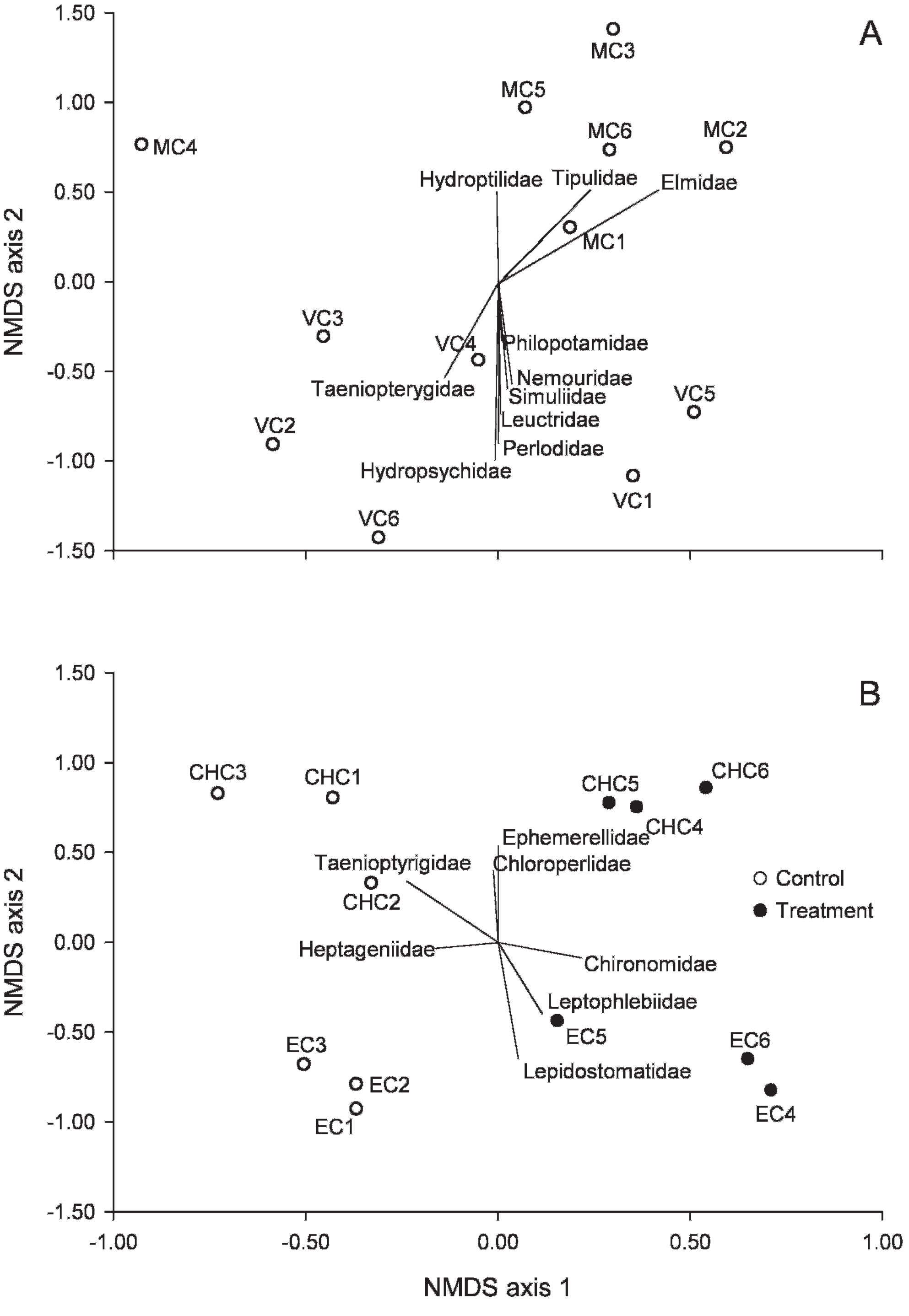

FIG. 8. Posttreatment nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate assemblages at control (Marsh Creek [MC] and Valley Creek [VC]) (A) and treatment (Cape Horn Creek [CHC] and Elk Creek [EC]) (B) streams. Samples were collected above and below the addition of a salmon carcass analogue treatment in downstream (treatment) reaches. Significantly correlated macroinvertebrate composition variables are shown as axis vectors. Sampling units are identified as in Fig. 3.

TABLE 5. Pearson correlation coefficients for relationships between macroinvertebrate % composition variables and nonmetric multidimensional scaling (NMDS) axis scores in control streams (Marsh Creek and Valley Creek; Fig. 8A) and treatment streams (Cape Horn Creek and Elk Creek; Fig. 8B). The sampling period followed salmon carcass analogue (SCA) additions in treatment streams. Variables significantly correlated to NMDS axes 1 or 2 are shown in bold.

	Axis 1 Within stream differences		Axis 2 Between stream differences	
Macroinvertebrate composition variable	Correlation	*p*	Correlation	*p*
Marsh Creek and Valley Creek				
% Hydropsychidae	−0.019	0.954	−0.920	**<0.001**
% Perlodidae	−0.080	0.806	−0.882	**<0.001**
% Philopotamidae	0.023	0.944	−0.631	**0.028**
% Elmidae	0.620	**0.032**	0.672	**0.017**
% Hydroptilidae	0.111	0.731	0.654	**0.021**
% Leuctridae	0.007	0.982	−0.823	**0.001**
% Simuliidae	0.162	0.616	−0.678	**0.015**
% Taeniopterygidae	−0.334	0.289	−0.662	**0.019**
% Tipulidae	0.471	0.122	0.654	**0.021**
% Nemouridae	0.199	0.535	−0.657	**0.020**
Cape Horn Creek and Elk Creek				
% Ephemerellidae	−0.006	0.985	0.683	**0.014**
% Heptageniidae	−0.660	**0.020**	−0.148	0.647
% Leptophlebiidae	0.230	0.473	−0.834	**<0.001**
% Lepidostomatidae	0.253	0.428	−0.938	**<0.001**
% Chloroperlidae	−0.055	0.864	0.637	**0.026**
% Taeniopterygidae	−0.463	0.130	0.665	**0.018**
% Chironomidae	0.734	**0.007**	−0.275	0.387

tive abundance, diversity, and FFG). FFG designations emphasize mouthpart morphology and means of consumption rather than food type or direct resource assimilation (Mihuc 1997). Many macroinvertebrates are polyphagous, and functional plasticity is an important aspect of invertebrate community structure (Dangles 2002). Therefore, we used FFG to classify macroinvertebrate taxa into groups performing different functions relative to broad resource classes but not to infer information regarding specific resource assimilation or the heterotrophic/autotrophic status of our study streams (Merritt and Cummins 1996).

Percent collector and % Chironomidae were significantly and positively correlated with NMDS axis 1. These correlations and reach-level spatial separation of macroinvertebrate communities indicate a strong SCA treatment response. Unfortunately, this rapid response was measured over a relatively short temporal period. Collectors are presumed to derive energy from detrital food sources, both autochthonous and allochthonous (Cummins 1973) and might have benefited directly from increased fine particulate organic material resulting from the breakdown of SCA. Chironomidae, a taxonomically diverse group, probably incorporated marine-derived nutrients via multiple pathways. Our results are comparable to the chironomid responses observed by Rosario et al. (2002) in coastal and Sierra Nevada (California) streams and Wipfli et al. (1998) and Chaloner et al. (2004) in southeast Alaska streams. Rosario et al. (2002) documented a >5× increase in chironomid densities 4 wk after experimental organic (cow manure) enrichment. Wipfli et al. (1998) found dramatic increases in chironomid and total taxon densities 20 to 30 d after salmon carcass treatments in experimental stream channels. Chaloner et al. (2004) observed significantly higher chironomid biomass in stream reaches after salmon spawning than before. A similar increase in the density of Chironomidae and Heptageniidae 2 mo after salmon carcass addition occurred in western Washington streams (Claeson et al. 2006).

In our study, % Heptageniidae was negatively correlated with NMDS axis 1, indicating an inverse relationship with SCA treatment-reach macroinvertebrate assemblages. This result was unexpected. It seems logical that increased periphyton accrual following SCA additions should provide an important indirect food pathway for scrapers, such as Heptageniidae. Densities of scrapers increased in Alaskan streams with salmon carcasses, presumably because of changes in the quantity and quality of biofilm (Wipfli et al. 1998, 1999). Wipfli et al. (1999) suggested that a change in biofilm composition could negatively affect specialized grazers. The reduced relative abundance of Heptageniidae in the Elk Creek treatment reach was unique, and we have no clear explanation for this finding.

Our results compliment, but are not directly comparable to, changes in macroinvertebrate densities previously reported in Kohler et al. (2008). Macroinvertebrate taxa that respond to altered food-base conditions (i.e., increased autotrophic production) have short generation times and can respond rapidly at the population level (Newbold et al. 1980). The rapid increase in % Chironomidae and % collector FFG following SCA treatment supports earlier findings. Contrasting results reported in Moore and Schindler (2008) and Honea and Gara (2009) are logically explained by the profound impact of bioturbation (disturbance) on benthic communities during high-density salmon spawning events. Studies comparing natural spawning events, carcass placements, and SCA additions will help to explore the similarities and differences between these forms of nutrient delivery.

One important finding from our study is the absence of observed taxonomic sinks, representing loss of high-quality food sources and poorer-quality forage for endangered salmonids, following SCA treatments. Our results suggest that, in the short term, SCA additions did not alter macroinvertebrate assemblages in ways that raise concerns regarding the ecological integrity of our study streams.

Physicochemical and stream foodweb response

Periphyton AFDM, periphyton and macroinvertebrate δ^{15}N values, and the presence of SCA all were significantly correlated with reach-level differences in treatment stream macroinvertebrate assemblages along NMDS axis 1. Spatial separation of macroinvertebrate communities appeared to be related to increased autotrophic production and consumption. N stable isotopes indicated trophic transfer of marine-derived nutrients from SCA to periphyton and macroinvertebrate biota (Kohler et al. 2008). Treatment-reach periphyton and macroinvertebrate δ^{15}N values ranged from 5.41 to 6.16‰ and 5.75 to 7.03‰ in CHC and EC, respectively. These results are comparable to values observed by Bilby et al. (1996) in western Washington streams where spawning coho salmon (*Oncorhynchus kisutch*) were present.

We found significant correlations between macroinvertebrate assemblages and % canopy shading, embeddedness, median particle size, conductivity, DOC, TN, and periphyton autotrophic index in EC. Increased shading and higher periphyton autotrophic index values illustrate the heterotrophic nature of the EC periphyton community and might help to explain variable SCA treatment responses observed by Kohler et al. (2008). SCA additions significantly increased periphyton production in both treatment streams, and the periphyton response was stronger in CHC than in EC (Kohler et al. 2008). In CHC, SCA treatment was applied to a low-gradient, open-canopy reach with high channel connectivity to the floodplain, whereas in EC, SCA treatment was applied in a higher-gradient, more-confined reach with denser riparian shading. Thus, the stronger periphyton response in CHC appears to have been a consequence of physicochemical variables. Our results are consistent with those of previous researchers who found variable autotrophic response to carcass enrichment among study streams (Chaloner et al. 2004) and who identified strong canopy effects on light availability and autotrophic production in streams receiving nutrient enrichments (Hill and Knight 1988).

Measures of physical habitat complexity and estimates of N uptake length indicated shorter uptake lengths and increased retention of limiting nutrients in CHC relative to EC (Kohler et al. 2008). Interactions between nutrient dynamics and high-quality physical habitat decrease nutrient export via physical retention and increase biological uptake (Cederholm et al. 1999, Peterson et al. 2001). In Wisconsin streams, macroinvertebrate assemblage metrics were strongly correlated with physical variables and nutrient concentrations (Wang et al. 2007).

Our study and that of Kohler et al. (2008) provide evidence that physical habitat, stream food webs, and nutrient dynamics interact to influence short-term, reach-scale responses of macroinvertebrate assemblages to SCA. However, additional research is needed to document how resident and anadromous fishes will respond to SCA nutrient enrichment at broader spatial and temporal scales. Future studies are needed that will investigate whole-stream SCA nutrient enrichment across multiple years of treatment.

Naturally spawning salmon as habitat modifiers and SCA

The rationale behind SCA addition as a large-scale tool for ecosystem management has not been clearly articulated. Objectives could be to enhance salmon and steelhead runs constrained by limiting factors (e.g., hydroelectric development), to enhance productivity of stream ecosystems in general, or both. However, nutrient enrichment strategies, such as SCA, cannot be viewed as a substitute for the delivery of marine-derived nutrients from naturally spawning and decomposing salmon and steelhead because important ecological differences exist between these modes of nutrient delivery. Moreover, effective recycling of nutrients between marine and inland freshwater and terrestrial ecosystems depends upon viable and sustainable wild anadromous salmonid populations. Moore et al. (2007) described associations between spawning salmon and stream fluxes of nutrients and matter. Salmon replenished upstream habitats by transporting materials in their bodies while simultaneously redistributing nutrients and sediments downstream by digging redds (bioturbation). Moore and Schindler (2004) found that sockeye salmon were consistent net importers of nutrients to freshwater ecosystems, but that out-migrating smolts often exported a substantial fraction of those nutrient imports. Thus, anadromous salmon and associated spawning activities represent important components of freshwater nutrient and matter cycling and affect both import and export components of nutrient and matter budgets.

Redd construction and use of salmon-derived nutrients by macroinvertebrates might be critical to the process of nutrient transfer (Honea and Gara 2009). Spawning salmon are important habitat modifiers (Moore et al. 2004). Spawning salmon (*Oncorhynchus* spp.) affected macroinvertebrates negatively (decreased community biomass) through redd construction and positively (increased salmon-derived biomass) through direct and indirect nutrient pathways associated with carcass decomposition (Honea and Gara 2009). Moore and Schindler (2008) investigated biotic disturbance from spawning salmon and benthic community dynamics in southwest Alaska streams. Benthic algal and insect biomass decreased substantially during high-density salmon spawning events and aquatic insect biomass did not return to prespawning levels within the same season (Moore and Schindler 2008).

The presence of salmon organic matter and suspended silt and clay particulates increases the formation of organic–inorganic aggregates called salmon-derived flocs (Rex and Petticrew 2008). These flocs appear to play a role in nutrient cycling and might enhance delivery of marine-derived nutrients to benthic food webs. We observed substantial bacterial and fungal growth on SCA 2 to 4 wk after treatments (AEK, personal observation). We suggest that this growth might have been a type of floc formation, but we did not investigate the importance of this process or its subsequent effects on nutrient delivery. However, the association between salmon organic matter and suspended silt and clay, presumably resuspended during redd construction, and the subsequent delivery of marine-derived nutrients to stream beds is unlikely to be directly comparable to the floc observed on SCA.

Conclusions

Macroinvertebrate community structure is a function of processes that occur along multiple biotic and abiotic gradients from landscape to local scales (Wright and Li 2002). Better understanding of biotic responses to experimental SCA treatment at various scales is needed as managers explore options to increase stream productivity in freshwater ecosystems that have lost their historical levels of marine-derived nutrients. SCAs appear to be an effective way to increase short-term autotrophic and secondary production. Knowing how macroinvertebrate community structure changes following SCA additions will help managers predict SCA effects on higher trophic levels, such as endangered anadromous fishes. Further research is needed to investigate stream foodweb response to SCA enrichment across broader spatial and temporal scales, and evaluations of SCA treatment at lower trophic levels should be coupled with studies measuring fish responses. Large-scale studies across diverse landscapes are needed before managers adopt SCA nutrient enrichment as a mitigation measure. In the final analysis, the only sustainable nutrient enrichment strategy is to recover naturally spawning anadromous fishes. For this reason, we recommend viewing any nutrient enhancement activities, including SCA addition, as an interim strategy to be phased out when sufficient amounts of marine-derived nutrients are returned to freshwater ecosystems via anadromous spawners.

Acknowledgements

We thank Kenneth Ariwite and Robert Trahant for invaluable assistance in all aspects of field data collection. Heather Bechtold, Robert Griswold, Michael Haddix, Christopher Robinson, Pamela Silver, and anonymous referees provided comments that considerably improved our manuscript. This research was funded by the Bonneville Power Administration under an Innovative Project 2001-055-00 with contracting support from Peter Lofy.

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Received: 17 July 2009
Accepted: 19 February 2010

Appendix 1. Mean, 95% confidence interval, and range for stream foodweb and environmental variables significantly correlated to NMDS axes 1 or 2 in control streams (Marsh Creek, Valley Creek) and treatment streams (Cape Horn Creek, Elk Creek). Upstream reaches in all streams were control reaches. Downstream reaches were either untreated (control streams) or treated (treatment streams). Data represents samples collected from stream reaches following a salmon carcass analogue treatment. Peri = periphyton, AI = autotrophic index, Macro = macroinvertebrate, Med_particle size = median particle size, AFDM = ash-free dry mass, DIN = dissolved inorganic N, DRP = dissolved reactive P.

	Upstream control reach			Downstream treatment reach		
Environmental variable	Mean	95% CI	Range	Mean	95% CI	Range
Marsh Creek						
Peri chlorophyll *a*	2.67	1.60	1.23–4.06	3.94	1.55	2.94–5.50
Peri AFDM	1.13	0.39	0.78–1.46	1.10	0.26	0.84–1.26
Peri AI	470.98	164.46	360.91–635.72	294.27	109.19	229.24–405.13
Peri $\delta^{15}N$	5.27	0.25	5.07–5.50	5.32	0.92	4.40–5.61
Macro $\delta^{15}N$	5.64	1.20	4.67–7.02	5.54	0.97	4.40–6.26
DIN	35.80	1.30	34.84–37.08	37.61	1.98	35.75–39.22
Total N	107.06	12.74	96.82–119.12	111.19	7.85	106.24–119.12
Total P	19.07	0.58	18.51–19.50	18.85	0.58	18.27–19.21
DIN:DRP	31.07	5.79	26.19–36.40	44.62	4.57	40.69–48.76
Conductivity	66.17	0.50	65.67–66.50	65.89	0.76	65.50–66.67
Med_particle size	37.55	7.62	32.23–45.12	39.66	5.39	35.66–44.93
Embeddedness	9.44	0.87	9.00–10.33	10.81	2.18	8.86–12.71
Shading	0.00	0.00	0.00–0.00	0.67	1.31	0.00–2.00
Valley Creek						
Peri chlorophyll *a*	0.35	0.10	0.27–0.44	0.22	0.07	0.15–0.27
Peri AFDM	0.35	0.07	0.30–0.41	0.21	0.07	0.14–0.25
Peri AI	1011.25	178.91	907.30–1193.19	933.72	108.09	841.88–1032.53
Peri $\delta^{15}N$	3.24	0.49	2.82–3.68	3.06	0.77	2.52–3.82
Macro $\delta^{15}N$	2.68	1.00	1.64–3.68	2.59	1.35	1.11–3.82
DIN	1.56	0.97	0.67–2.39	0.92	0.20	0.73–1.09
Total N	62.43	2.75	59.67–64.26	58.01	3.43	54.71–60.66
Total P	14.76	0.17	14.59–14.86	14.43	0.09	14.35–14.51
DIN:DRP	1.43	0.51	0.95–1.83	1.18	0.33	1.00–1.52
Conductivity	102.22	0.11	102.17–102.33	102.67	0.68	102.17–103.33
Med_particle size	59.89	1.90	58.74–61.82	64.58	1.47	63.64–66.06
Embeddedness	27.89	5.19	23.33–32.50	31.94	4.37	27.50–34.50
Shading	16.00	7.42	10.00–23.00	14.00	11.92	4.00–25.00
Cape Horn Creek						
Peri chlorophyll *a*	1.98	1.30	0.97–3.23	38.15	23.02	26.66–61.64
Peri AFDM	0.50	0.25	0.25–0.64	9.25	6.38	5.08–15.66
Peri AI	271.46	101.39	191.07–368.06	237.31	46.29	190.68–267.13
Peri $\delta^{15}N$	2.32	0.70	1.42–3.51	5.41	0.53	4.85–6.34
Macro $\delta^{15}N$	5.37	0.54	4.80–5.90	7.03	0.78	6.18–7.74
SCA	[a]	[a]	[a]	[a]	[a]	[a]
Total N	70.24	25.80	47.78–93.36	52.23	9.02	45.79–61.15
Total P	3.28	0.73	2.54–3.71	2.30	0.27	2.06–2.53
DOC	252.32	29.81	236.41–282.73	250.66	56.01	218.60–307.37
Conductivity	54.39	0.54	53.83–54.67	55.06	1.36	53.67–55.83
Med_particle size	39.00	2.99	37.00–42.00	38.00	2.26	36.00–40.00
Embeddedness	12.39	4.37	8.83–16.50	11.72	2.68	9.17–13.83
Shading	0.00	0.00	0.00–0.00	0.00	0.00	0.00–0.00
Elk Creek						
Peri chlorophyll *a*	0.11	0.06	0.08–0.18	0.80	0.48	0.32–1.14
Peri AFDM	0.14	0.04	0.10–0.17	0.91	0.27	0.65–1.12
Peri AI	1341.67	518.54	946.30–1843.88	1346.92	684.35	987.26–2045.13
Peri $\delta^{15}N$	1.67	0.41	1.12–2.35	6.16	0.18	5.85–6.39
Macro $\delta^{15}N$	3.02	0.77	2.44–3.91	5.75	0.18	5.57–5.94
SCA	[a]	[a]	[a]	[a]	[a]	[a]
Total N	141.58	52.73	87.91–171.64	94.68	5.62	89.89–99.80
DRP	1.43	0.28	1.23–1.70	1.42	0.16	1.34–1.58

APPENDIX 1. Continued.

	Upstream control reach			Downstream treatment reach		
Environmental variable	Mean	95% CI	Range	Mean	95% CI	Range
DOC	656.11	95.07	584.85–748.74	609.32	115.55	522.15–721.66
Conductivity	63.11	0.39	62.83–63.50	62.94	0.22	62.83–63.17
Med_particle size	61.33	15.36	47.00–74.00	54.67	6.63	48.00–59.00
Embeddedness	30.06	2.89	27.17–32.00	27.39	3.43	24.00–29.83
Shading	33.67	24.69	10.00–53.00	53.33	17.29	40.00–70.00

[a] A salmon carcass analogue treatment occurred in the downstream reach of Cape Horn Creek and Elk Creek

APPENDIX 2. Mean, 95% confidence interval, and range for macroinvertebrate metric variables significantly correlated to NMDS axes 1 or 2 in control streams (Marsh Creek, Valley Creek) and treatment streams (Cape Horn Creek, Elk Creek). Upstream reaches in all streams were control reaches. Downstream reaches were either untreated (control streams) or treated (treatment streams). Data represents samples collected from stream reaches following a salmon carcass analogue treatment. EPT = Ephemeroptera, Plecoptera, Trichoptera.

	Upstream control reach			Downstream treatment reach		
Macroinvertebrate metric variable	Mean	95% CI	Range	Mean	95% CI	Range
Marsh Creek						
Shannon–Wiener diversity[a]	1.09	0.06	1.04–1.14	1.08	0.06	1.03–1.14
Ephemeroptera	35.56	8.44	31.15–44.16	35.80	11.00	28.92–46.92
Plecoptera	6.31	2.53	3.75–7.91	7.56	2.35	5.50–9.65
Trichoptera	12.92	4.47	8.41–15.79	16.56	3.68	14.47–20.30
Collector	48.24	5.08	39.57–54.60	40.69	2.10	37.62–44.04
Filterer	5.81	0.62	4.75–6.58	7.02	1.72	5.05–10.00
Scraper	30.87	7.36	23.74–43.85	37.20	4.89	28.62–42.44
Shredder	4.28	1.13	2.28–5.29	4.08	1.16	2.29–5.85
EPT	54.78	6.26	49.44–60.48	59.92	6.84	56.11–66.89
EPT taxon richness	18.67	1.64	17.67–20.33	17.67	2.95	14.67–19.33
Total taxon richness	25.89	1.90	24.33–27.67	24.78	4.07	20.67–27.33
Valley Creek						
Shannon–Wiener diversity[a]	1.15	0.02	1.14–1.17	1.21	0.05	1.16–1.23
Ephemeroptera	48.59	2.66	47.17–51.30	38.36	1.40	37.33–38.04
Plecoptera	12.39	1.44	10.98–13.44	14.35	5.01	9.96–18.82
Trichoptera	20.92	4.43	17.09–24.92	17.84	1.62	16.41–19.28
Collector	40.12	6.33	33.06–51.17	42.47	0.82	41.28–43.78
Filterer	9.99	1.05	8.40–11.61	11.31	1.64	8.53–13.39
Scraper	32.97	6.34	21.76–38.58	24.84	3.18	19.34–28.59
Shredder	6.62	1.02	5.33–8.36	7.67	1.50	5.04–9.26
EPT	81.90	3.66	79.38–85.54	70.55	4.77	66.57–74.96
EPT taxon richness	17.22	1.78	16.00–19.00	19.00	1.96	18.00–21.00
Total taxon richness	22.11	2.86	20.33–25.00	24.33	1.73	23.00–26.00
Cape Horn Creek						
Plecoptera	19.01	6.58	12.38–23.21	15.90	3.40	13.04–19.03
Trichoptera	5.83	3.92	3.72–9.83	5.47	3.34	2.27–8.08
Diptera	14.49	2.78	9.59–17.25	21.92	3.25	18.02–27.53
Collector	45.83	3.72	39.71–50.95	49.77	0.55	49.16–50.73
Filterer	4.79	2.06	1.17–6.96	5.45	2.46	1.40–8.86
Predator	17.20	1.42	14.69–18.50	17.20	2.90	13.80–22.22
EPT taxon richness	18.22	3.25	15.67–21.33	19.78	1.52	18.33–21.00
Total taxon richness	24.78	4.72	20.67–29.00	28.33	1.89	26.67–30.00
Elk Creek						
Plecoptera	6.31	2.53	3.75–7.91	7.56	2.35	5.50–9.65
Trichoptera	12.92	4.47	8.41–15.79	16.56	3.68	14.47–20.30

APPENDIX 2. Continued.

Macroinvertebrate metric variable	Upstream control reach			Downstream treatment reach		
	Mean	95% CI	Range	Mean	95% CI	Range
Diptera	20.71	4.10	13.50–24.85	24.28	4.28	17.73–30.83
Collector	43.98	1.23	42.71–46.14	55.50	1.46	53.57–57.95
Filterer	8.25	1.23	6.11–9.60	10.17	0.24	9.83–10.56
Predator	9.27	1.72	7.42–12.29	8.66	1.36	6.37–10.42
EPT taxon richness	18.67	1.64	17.67–20.33	17.67	2.95	14.67–19.33
Total taxon richness	25.89	1.90	24.33–27.67	24.78	4.07	20.67–27.33

[a] $\mathrm{Log}_{10}(x)$–transformed

APPENDIX 3. Mean, 95% confidence interval, and range for macroinvertebrate composition variables significantly correlated to NMDS axes 1 or 2 in control streams (Marsh Creek, Valley Creek) and treatment streams (Cape Horn Creek, Elk Creek). Upstream reaches in all streams were control reaches. Downstream reaches were either untreated (control streams) or treated (treatment streams). Data represents samples collected from stream reaches following a salmon carcass analogue treatment.

Macroinvertebrate composition variable	Upstream control reach			Downstream treatment reach		
	Mean	95% CI	Range	Mean	95% CI	Range
Marsh Creek						
Hydropsychidae	0.18	0.12	0.00–0.36	0.24	0.14	0.00–0.43
Perlodidae	0.19	0.12	0.00–0.38	0.14	0.10	0.00–0.31
Philopotamidae	0.00	0.00	0.00–0.00	0.00	0.00	0.00–0.00
Elmidae	12.76	4.08	6.12–18.51	9.02	3.18	3.73–13.30
Hydroptilidae	0.43	0.12	0.28–0.64	0.33	0.10	0.16–0.43
Leuctridae	0.12	0.14	0.00–0.36	0.03	0.04	0.00–0.10
Simuliidae	0.16	0.03	0.11–0.19	0.12	0.07	0.00–0.22
Taeniopterygidae	0.03	0.03	0.00–0.09	0.00	0.00	0.00–0.00
Tipulidae	2.94	1.02	1.26–4.36	2.77	0.72	1.86–4.00
Nemouridae	0.78	0.46	0.11–1.51	0.83	0.39	0.16–1.27
Valley Creek						
Hydropsychidae	4.11	0.13	3.89–4.27	3.86	1.02	2.23–5.35
Perlodidae	1.26	0.40	0.56–1.71	1.08	0.06	0.97–1.14
Philopotamidae	0.76	0.43	0.00–1.14	0.00	0.00	0.00–0.00
Elmidae	5.97	1.82	3.79–9.12	5.09	0.15	4.84–5.31
Hydroptilidae	0.09	0.10	0.00–0.28	0.28	0.19	0.00–0.57
Leuctridae	1.82	0.51	1.11–2.65	2.64	0.58	1.68–3.41
Simuliidae	0.57	0.37	0.00–1.14	0.51	0.26	0.28–0.97
Taeniopterygidae	0.91	0.28	0.57–1.39	0.38	0.43	0.00–1.14
Tipulidae	1.23	0.60	0.56–2.27	1.31	0.59	0.28–1.95
Nemouridae	2.13	0.62	1.14–3.03	1.96	1.13	0.56–3.89
Cape Horn Creek						
Ephemerellidae	5.41	0.77	4.59–6.77	6.01	0.52	5.18–6.77
Heptageniidae	9.38	0.95	8.37–11.06	9.05	0.27	8.59–9.39
Leptophlebiidae	0.36	0.03	0.32–0.41	0.62	0.24	0.27–1.00
Lepidostomatidae	0.03	0.03	0.00–0.08	1.87	0.42	1.14–2.36
Chloroperlidae	3.88	0.83	2.43–4.78	4.75	0.76	3.88–6.07
Taeniopterygidae	2.35	0.91	0.82–3.55	0.56	0.21	0.19–0.80
Chironomidae	4.18	1.30	1.90–5.47	7.73	1.24	6.40–9.91
Elk Creek						
Ephemerellidae	3.99	0.82	3.04–5.41	3.80	0.62	2.79–4.66
Heptageniidae	10.85	0.33	10.29–11.29	5.87	1.05	4.45–7.62
Leptophlebiidae	3.19	1.24	1.78–5.34	3.15	1.05	1.34–4.44
Lepidostomatidae	1.87	0.42	1.14–2.36	2.35	0.32	1.78–2.64
Chloroperlidae	2.49	0.07	2.38–2.58	2.68	0.41	1.95–3.08
Taeniopterygidae	0.00	0.00	0.00–0.00	0.00	0.00	0.00–0.00
Chironomidae	6.17	0.97	4.47–7.12	8.30	1.78	5.63–11.07