Stream food web response to a salmon carcass analogue addition in two central Idaho, U.S.A. streams

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SUMMARY

1. Pacific salmon and steelhead once contributed large amounts of marine-derived carbon, nitrogen and phosphorus to freshwater ecosystems in the Pacific Northwest of the United States of America (California, Oregon, Washington and Idaho). Declines in historically abundant anadromous salmonid populations represent a significant loss of returning nutrients across a large spatial scale. Recently, a manufactured salmon carcass analogue was developed and tested as a safe and effective method of delivering nutrients to freshwater and linked riparian ecosystems where marine-derived nutrients have been reduced or eliminated.

2. We compared four streams: two reference and two treatment streams using salmon carcass analogue(s) (SCA) as a treatment. Response variables measured included: surface streamwater chemistry; nutrient limitation status; carbon and nitrogen stable isotopes; periphyton chlorophyll $a$ and ash-free dry mass (AFDM); macroinvertebrate density and biomass; and leaf litter decomposition rates. Within each stream, upstream reference and downstream treatment reaches were sampled 1 year before, during, and 1 year after the addition of SCA.

3. Periphyton chlorophyll $a$ and AFDM and macroinvertebrate biomass were significantly higher in stream reaches treated with SCA. Enriched stable isotope ($\delta^{15}N$) signatures were observed in periphyton and macroinvertebrate samples collected from treatment reaches in both treatment streams, indicating trophic transfer from SCA to consumers. Densities of Ephemerebellidae, Elmidae and Brachycentridae were significantly higher in treatment reaches. Macroinvertebrate community composition and structure, as measured by taxonomic richness and diversity, did not appear to respond significantly to SCA treatment. Leaf breakdown rates were variable among treatment streams: significantly higher in one stream treatment reach but not the other. Salmon carcass analogue treatments had no detectable effect on measured water chemistry variables.

4. Our results suggest that SCA addition successfully increased periphyton and macroinvertebrate biomass with no detectable response in streamwater nutrient concentrations. Correspondingly, no change in nutrient limitation status was detected based on dissolved inorganic nitrogen to soluble reactive phosphorus ratios (DIN/SRP) and nutrient-diffusing substrata experiments. Salmon carcass analogues appear to increase freshwater productivity.

5. Salmon carcass analogues represent a pathogen-free nutrient enhancement tool that mimics natural trophic transfer pathways, can be manufactured using recycled fish bones.
products, and is easily transported; however, salmon carcass analogues should not be viewed as a replacement for naturally spawning salmon and the important ecological processes they provide.

Keywords: macroinvertebrate, nutrient enrichment, periphyton, salmon carcass analogue, stable isotope analysis

Introduction

Abundant populations of anadromous salmonids (Oncorhynchus spp.) historically contributed large amounts of marine-derived carbon (C), nitrogen (N) and phosphorus (P) to aquatic and terrestrial ecosystems in the Pacific Northwest (PNW) of the United States of America (California, Oregon, Washington and Idaho) (Kline et al., 1990; Larkin & Slaney, 1997; Cederholm et al., 1999; Gresh, Lichatowich & Schoonmaker, 2000; Bilby et al., 2003). Nutrients and carbon sequestered in the marine environment, where approximately 95% of the body mass of Pacific salmon accumulates, are subsequently delivered to inland catchments via upstream migrations (Groot & Margolis, 1991). Spawning salmon contribute an estimated 5–95% of the P and N loading in salmon-bearing catchments (Gresh et al., 2000), and even small input of nutrients and C may be important to the maintenance of trophic productivity (Larkin & Slaney, 1997). After reaching natal spawning habitat, Pacific salmon complete their life cycle and in turn deliver ecologically significant amounts of marine-derived nutrients (MDN) to freshwater ecosystems (Thomas et al., 2003). This process has been described as a positive feedback loop functioning to enhance freshwater productivity for future generations of anadromous and resident stream biota (Wipfli, Hudson & Caouette, 1998; Hicks et al., 2005).

Following periods of intense commercial harvest, hydrosystem development, hatchery production, and habitat loss, significant declines in Pacific salmon abundance have occurred throughout the region (Lichatowich, 1999). Healthy populations of salmon and steelhead that once provided annual nutrient subsidies to otherwise nutrient impoverished environments remain depressed or have been extirpated (Levy, 1997). Currently, Pacific salmon occupy approximately 40% of their historical range (Nehlsen, Williams & Lichatowich, 1991) and contribute just 6–7% of the MDN historically delivered to PNW rivers and streams (Gresh et al., 2000). Consequently, many forested streams of the region are now characterized as ultra-oligotrophic (Welsh, Jacoby & May, 1998), a condition of low nutrient concentrations suggested to result from a combination of parent geology and low numbers of returning salmon (Ambrose, Wilzbach & Cummins, 2004).

In the upper Salmon River basin of central Idaho, the paucity of returning adult salmon and catchment scale nutrient deficits may constrain freshwater productivity and effectively limit efforts to recover salmon and steelhead populations. Thomas et al. (2003) estimated that 25–50% of Idaho streams are nutrient limited and Achord, Levin & Zabel (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. In a recent analysis, Scheuerell et al. (2005) examined phosphorus-transport dynamics by spring/summer Chinook salmon (Oncorhynchus tshawytscha) in the Snake River basin and estimated that over the past 40 years <2% of historic marine-derived phosphorus reached natal streams. Moreover, observations of variable density-dependent mortality at low spawning densities could lead to a net nutrient export from freshwater ecosystems, as more nutrients leave as smolts than are returned as adults (Moore & Schindler, 2004). Given contemporary anadromous production, hydrosystem conditions, low smolt to adult returns (SAR), and ocean productivity trends, conservation efforts could be stymied by a lack of available nutrients to freshwater rearing habitat in the Salmon River basin (Achord et al., 2003; Thomas et al., 2003).

Salmon carcass analogues developed by Pearsons et al. (2007b) contain similar complements of nutrients and carbon-based compounds (including rare earth elements) as naturally returning salmon; therefore, their effect on stream food webs is hypothesized to mimic natural enrichment pathways. Salmon carcass analogues are pasteurized to create a pathogen-free product that slowly releases nutrients and particulates similar to naturally decomposing salmon and are easy
to store, transport and distribute. Benefits include direct consumption by juvenile salmonids (Pearsons et al., 2007a). Other advantages include the ability to produce large amounts of SCA for dispersal into areas where hatchery carcass placement or inorganic nutrient application is unwarranted due to access (i.e. roadless areas), availability (lack of hatchery returns), or potential pathogen and contaminant issues (fish pathogens and heavy metals). Pearsons et al. (2007b) suggest that SCA could be produced using unused fish parts recycled from commercial fisheries. Large-scale production costs of SCA are not available at this time; however, the development and production details have been published and the benefits over alternative nutrient enhancement methods outlined. Readers are referred to Pearsons et al. (2007b) for a detailed discussion of the development, production and benefits of SCA.

We examined local-scale stream food web response to SCA addition in two central Idaho streams. Response variables were measured for 1 year prior to treatment applications, before and during treatment applications the following year, and 1 year post-treatment application (periphyton measures in treatment streams only). We selected streams that historically supported abundant salmon populations in the upper Salmon and Middle Fork Salmon River basins (Fulton, 1968). Currently, our study streams contain greatly diminished extant populations of wild/natural Chinook salmon. Salmon carcass analogue treatments were applied subsequent to natural spawning of spring Chinook salmon (Oncorhynchus tshawytscha) to mimic natural timing and delivery of marine-derived nutrients. Our study goals were to assess the stream food web response to a short-term SCA addition. 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 in central Idaho.

Methods

Study area

The study was conducted in the Middle Fork Salmon River (MFSR) and upper Salmon River (USR) basins, ID, U.S.A. (Fig. 1). Four streams: Cape Horn Creek and Marsh Creek in the MFSR; and Elk Creek and Valley Creek in the USR, were sampled from 2002 to 2004. Stream sites within the MFSR and the USR were similar in catchment area, valley form, gradient and stream size (Table 1). Parent geology in all 4 catchments is dominated by Cretaceous granite, quartz diorite and Idaho batholith (Omernik, 1987); vegetation is primarily upland lodgepole pine (Pinus contorta) with willow (Salix) dominated riparian areas. Typical of intermountain west streams, precipitation is largely a result of winter snowfall with high flows occurring during spring runoff and base flows occurring during the months of July to October.

Experimental design

Upstream-downstream, before-after comparisons and experimental introduction of SCA were used to investigate the response in stream food web variables to nutrient enrichment. Salmon carcass analogue treatments were randomly allocated to two of four study streams. Study sites within streams were divided into 1 km upstream (reference) and 1 km downstream (treatment) reaches. Stream reaches were stratified into upper, middle and lower stratum for sampling. Within each stratum, a riffle sample site was randomly chosen for sampling. Sample collection periods occurred after spring freshets in July (pre-spawn) and following spring Chinook salmon spawning activities from 15 September to 15 October (post-spawn). In 2002,
sampling events represented pre-treatment baseline conditions; in 2003, an SCA treatment occurred in Cape Horn Creek and Elk Creek; and in 2004, sampling in Cape Horn Creek and Elk Creek characterized conditions 1 year after nutrient enrichment. Marsh Creek and Valley Creek received no treatments in any year. In streams receiving SCA additions, longitudinal effects of elevated nutrient levels were evaluated by measuring periphyton biomass at two sites downstream of treatment reaches. Stream uptake length ($S_w$) estimates using the formula:

$$S_w = \frac{(v_{wat} \times z \times 1000)}{v_i}$$

described in Thomas et al. (2003) were used to establish the length of downstream reaches. This approach converts $S_w$ to an uptake velocity ($v_i$: mm s$^{-1}$) where $v_{wat}$ is mean water velocity (m s$^{-1}$) and $z$ equals mean stream depth (m). Published values of $v_i$ given in Thomas et al. (2003) ranged from 0.03 to 0.13 mm s$^{-1}$, 0.006 to 0.16 mm s$^{-1}$ and 0.007 to 0.18 mm s for NH$_3$, NO$_3$ and PO$_4$ respectively. Thomas et al. (2003) suggest using these values to estimate the approximate longitudinal distance over which elevated nutrient conditions may exist during a nutrient treatment. We used the lower and upper end of these ranges for nutrients expected to be limiting to establish downstream sampling sites (SW1 and SW2) in treatment streams. Physical habitat characteristics of the study streams are presented in Table 1.

### Table 1 Characteristics of the four study streams

| Stream       | Catchment area (km$^2$)* | Gradient (%) | Discharge (m$^3$ s$^{-1}$)$^1$ | Water temperature (°C)$^1$ | Median particle size (mm)$^1$ | Canopy cover (%)$^6$ |
|--------------|--------------------------|--------------|-------------------------------|----------------------------|-------------------------------|---------------------|
| Cape Horn Creek | 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     | 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)                 | 42.2 (25–60)        |

*Catchment area represents catchment drainage area upstream of study sites only.

†Average (range); values from period June to October 2003.

‡Median (range); values from pebble counts ($n = 100$) at sampling sites ($n = 6$).

§Average (range); values estimated from October 2003 using a spherical densitometer.

Salmon carcass analogue treatment

Salmon carcass analogues used as nutrient treatments were produced using fall Chinook salmon carcasses and marine fish bone meal (Bio-Oregon Inc., Warrenton, OR, U.S.A.). The 11 g, 2.5 cm diameter pellets contained approximately 54.5% crude protein, 13.5% crude fat, 8.7% N and 3.9% P by mass. Salmon carcass analogues were stocked at densities of 30 g analogue material m$^{-2}$ of bankfull channel width. Stocking densities were based on target carcass levels developed from Wipfli et al. (2003). Target levels were then converted into specific nutrient goals based on SCA composition. A desired level of 0.0063 kg P m$^{-2}$ of stream surface area was used to estimate SCA stocking densities. Analogue pellets were pasteurized and tested for common fish pathogens prior to application. Refer to Pearsons et al. (2007b) for details regarding the development of SCA.

Surface water chemistry

Water samples were collected and analysed from upper, middle and lower stratum in each reach from all study streams in 2002 and 2003. In 2002, we collected water samples during two sample periods: pre- and post-spawn; and in 2003, we collected water samples during four sample periods: pre-spawn, pre-treatment, 2 weeks post-treatment and 4 weeks post-treatment. Dissolved nutrient concentrations were determined for nitrate (NO$_3$), nitrite (NO$_2$), ammonium (NH$_4^+$), soluble reactive phosphorus (SRP; PO$_4$), silicate (Si(OH)$_4$), total nitrogen (TN) and total phosphorus (TP) using a Technicon Autoanalyzer II segmented flow analyzer (Valderrama, 1981; UNESCO, 1994). Dissolved inorganic nitrogen (DIN) was calculated by summing inorganic nitrogen species. Dissolved organic carbon (DOC) was determined using a Shimadzu model TOC5000$^®$ high temperature combustion carbon analyzer and analysed using the high temperature catalytic oxidation method (Sharp et al., 2002).
In-situ nutrient limitation experiments

Differential algal response to in situ, point source nutrient manipulations was used to determine nutrients limiting periphyton biomass in each study stream. Macro-nutrient limitation was evaluated using nutrient-diffusing substrata (NDS) amended with N, P and a combination of N and P. Nutrient-diffusing substrata were constructed using wooden frames that held 35 mL polystyrene vials capped with porous porcelain crucibles (Gibeau & Miller, 1989; Davis et al., 2001). Vials were filled with 2% agar amended with: a 0.5 M solution of NaNO₃ (N treatment); a 0.2 M solution of KH₂PO₄ (P treatment); a combination of N and P; and a non-amended agar (control). Six replicates of each treatment (control, N, P and N + P in an upstream to downstream order) were secured to wooden racks and incubated in riffle habitat units for 30 (±2) days. Samples were then analysed for chlorophyll a and ash-free dry mass (AFDM) using methods described below.

Periphyton sampling

Periphyton biomass, measured as chlorophyll a (mg m⁻²) and AFDM (g m⁻²) was measured on samples collected from unglazed ceramic tiles (c. 112 cm²). Six to 12 randomly placed tiles were incubated in situ for 30 (±2) days before sampling. Samples were collected from all streams in 2002 and 2003 and from Cape Horn Creek and Elk Creek in 2004. A measured area from each tile was scraped, brushed, rinsed and filtered onto glass fibre filters (0.45 μm). Filters were frozen and subsequently analysed for chlorophyll a and AFDM using standard laboratory methods (APHA, 1995). The trophic nature of stream periphyton communities was evaluated using the autotrophic index and was calculated using the following equation: \[ AI = \frac{[AFDM \text{ (mg m}^{-2})]}{[\text{Chlorophyll a (mg m}^{-2})]} \] (Steinman & Lamberti, 1996). Soft bodied algae and diatom community composition was evaluated by EcoAnalysts, Inc., Moscow, ID, U.S.A. from samples collected at riffle habitat units. Algal samples were counted and identified to the lowest practical taxon using the strip method until at least 300 counting units were encountered. Counting and identification was made at 400× magnification using a light microscope. Algal cell density was calculated by dividing the total number of cells by the substrate area. For detailed methods please refer to Charles, Knowles & Davis (2002).

Macroinvertebrate sampling

Macroinvertebrates were sampled from riffle habitat units using a modified Hess sampler (363 μm). Samples were collected from all study streams in October of 2002 and 2003. Three randomly placed samples were collected at each riffle sampling unit. Substrate within the sampler was disturbed for 3 minutes to a depth of approximately 10 cm to standardize sampling effort. Macroinvertebrates were then rinsed and stored in 70% ethanol. Preserved samples were sorted, identified to the lowest feasible taxonomic level (usually genus), dried at 50 °C for 48 h, and weighed to estimate whole sample biomass.

Leaf decomposition rates

Leaf litter decomposition rates \( (k) \) were estimated in Cape Horn Creek and Elk Creek following SCA treatment. Willow leaves collected from riparian areas prior to abscission were placed in plastic mesh leaf packs with 5 mm openings. Ten leaf packs were placed at each riffle sampling unit and removed at days 15 \((n = 5)\) and 30 \((n = 5)\) in upstream reference and downstream treatment reaches. Collection, deployment, processing, and analytic techniques followed methods described by Benfield (2006). Leaf decomposition \( k \)-values were computed using an exponential decay model that assumed the rate of loss from leaf packs was a constant proportion over time. Cumulative temperature degree days were used in place of days as a measure representing incubation periods.

Stable isotope analyses

Stable isotopes of C and N \( (\delta^{15}N \text{ and } \delta^{13}C) \) were measured for periphyton samples collected from unglazed ceramic tiles. A measured area \((cm^2)\) was scraped, brushed, rinsed and filtered onto glass fibre filters \( (0.45 \mu m) \) and subsequently frozen. Macroinvertebrate samples were collected using a modified Hess sampler \((363 \mu m)\), sorted for scraper/grazer taxa, held in freshwater for 24 h to allow for gut evacuation and frozen. A Costech elemental analyzer
and a Finnigan MAT conflo III interface with a Delta + XL mass spectrometer was used to analyse all periphyton and macroinvertebrate samples. Stable isotope samples were analysed at the University of Alaska, Fairbanks, AK, U.S.A. Alaska Stable Isotope Facility. Sample values were calculated using the following formula:

$$\delta^{15}N/\delta^{13}C = \left[\frac{(R_{\text{sample}} - R_{\text{standard}})}{R_{\text{standard}}}\right] \times 1000$$

where $R_{\text{sample}}$ = the stable isotope ratio in the sample and $R_{\text{standard}}$ = the stable isotope ratio in the standard.

**Statistical analysis**

Samples collected within riffles were considered subsamples and used to calculate mean values for each stream reach. Mean reach values for streamwater nutrient concentrations, periphyton biomass, macroinvertebrate measures and stable isotope values were analysed using a multilevel model (MIXED) analysis of variance (ANOVA) to facilitate comparisons between treatment and reference streams (PROC MIXED; SAS Institute Inc.; 2003; (Table 2). This approach allowed for correct estimation of standard errors and resulted in improved estimation of fixed and random effects (Wagner, Hayes & Bremigan, 2006). Streams were considered replicates and a treatment by reach interaction effect was analysed for statistically significant differences using a probability of alpha 0.10 (Table 2). The effect of nutrient amendments on chlorophyll a values from NDS was determined using a one-way ANOVA to test for differences among treatment groups. Leaf litter decomposition rates in Cape Horn Creek and Elk Creek were analysed using a paired t-test to determine potential differences between reaches. Data that violated the assumptions of ANOVA were natural log transformed prior to analysis.

**Results**

**Surface water chemistry response to salmon carcass analogue treatment**

Water chemistry variables did not exhibit longitudinal trends in any stream prior to or during SCA additions. Salmon carcass analogue treatments had no detectable effect on water chemistry variables ($P > 0.29$; Fig. 2; Table 2).

**In-situ nutrient limitation experiments**

Chlorophyll a concentrations of periphyton sampled from NDS differed ($P < 0.01$) among treatments

| Dependent variable | Effect | d.f. | F-value | P-value |
|--------------------|--------|------|---------|---------|
|                    |        | Numerator | Denominator |         |         |
| Total N            | Treatment | 1 | 2       | 1.80    | 0.3122  |
|                    | Reach | 1 | 2       | 1.02    | 0.4188  |
|                    | Treatment × reach | 1 | 2       | 2.00    | 0.2931  |
| Total P            | Treatment | 1 | 2       | 0.01    | 0.9439  |
|                    | Reach | 1 | 2       | 0.09    | 0.7951  |
|                    | Treatment × reach | 1 | 2       | 0.11    | 0.7756  |
| Dissolved inorganic N | Treatment | 1 | 2       | 0.07    | 0.8208  |
|                    | Reach | 1 | 2       | 0.65    | 0.5035  |
|                    | Treatment × reach | 1 | 2       | 0.06    | 0.8237  |
| Soluble reactive P | Treatment | 1 | 2       | 4.97    | 0.1556  |
|                    | Reach | 1 | 2       | 6.47    | 0.1260  |
|                    | Treatment × reach | 1 | 2       | 0.37    | 0.6070  |
| Dissolved organic C | Treatment | 1 | 2       | 0.00    | 0.9516  |
|                    | Reach | 1 | 2       | 0.86    | 0.4518  |
|                    | Treatment × reach | 1 | 2       | 0.07    | 0.8192  |
| Silicate           | Treatment | 1 | 2       | 0.33    | 0.6233  |
|                    | Reach | 1 | 2       | 0.03    | 0.8694  |
|                    | Treatment × reach | 1 | 2       | 0.60    | 0.5206  |

See text for explanation of experimental design and statistical details.

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within streams (data not shown). Results suggest that Cape Horn Creek, Elk Creek and Valley Creek were nitrogen limited; Marsh Creek was phosphorus limited. No change in nutrient limiting status was observed within streams between reaches following SCA additions. Redfield ratios (DIN/SRP) calculated from water chemistry data collected prior to and during SCA additions generally supported results from nutrient limiting assessments made from NDS experiments in all study streams (CHC, EC, VC: DIN/SRP values 0.09–3.60; MC: DIN/SRP values 21.31–48.76). Phosphorus limitation was assumed when the DIN to SRP ratio was greater than 20 and nitrogen limitation was assumed when the ratio was less than 16; intermediate values indicated co-limitation (Allan, 1995).

Periphyton response to salmon carcass analogue treatment

Periphyton chlorophyll a and AFDM values were significantly higher ($P = 0.08$ and $0.04$, respectively; Figs 3, 5 & 9; Table 3) in stream reaches containing SCA. Autotrophic index values were not significantly different ($P > 0.20$; Fig. 3; Table 3). The periphyton community at all sites in Cape Horn Creek was dominated by Chrysophytes; Elk Creek sites were dominated by Chlorophytes, Cyanophytes and Bacillariophytes. Periphyton samples collected 1 year after SCA addition resembled baseline chlorophyll a and AFDM conditions in both treatment streams.

Macroinvertebrate response to salmon carcass analogue treatment

Macroinvertebrate biomass was significantly higher ($P = 0.05$; Figs 4, 6 & 9; Table 3) in stream reaches containing SCA. Total density measures were not significantly different ($P = 0.12$; Figs 4 & 6; Table 3); however, densities of Ephemereellidae, Elminidae and Brachycentridae were significantly higher ($P = 0.09$, 0.06 and 0.02, respectively; Table 3) in stream reaches following SCA treatment. Richness [Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa and total taxa] and diversity (Shannon-Wiener index) measures were not significantly different ($P > 0.13$; Table 3) in stream reaches containing SCA.

Leaf decomposition rate response to salmon carcass analogue treatment

Leaf breakdown rates in Cape Horn Creek ranged from 0.0045 $k$ degree day$^{-1}$ in the reference reach to 0.0046 $k$ degree day$^{-1}$ in the treatment reach; Elk Creek rates were 0.0039 and 0.0048 in the reference and treatment reaches respectively. No difference (paired t-test; $P = 0.79$; Figs 7 & 9) in decay rate was observed in the Cape Horn Creek treatment reach; however, breakdown rates of willow leaves were significantly higher (paired t-test; $P = 0.03$; Figs 7 & 9) in the Elk Creek treatment reach. Although within stream reach-level comparisons for $k$ using paired t-tests constitutes pseudoreplication (Hurlbert, 1984),
we believe our inference is meaningful using two treatment streams to evaluate k response to SCA additions.

**Stable isotope response to salmon carcass analogue treatment**

Enriched stable isotope signatures were observed in periphyton and macroinvertebrate samples collected from reaches receiving SCA additions (Figs 3, 4, 8 & 9; Table 3). Periphyton and macroinvertebrate \( \delta^{15}N \) were significantly higher \((P = 0.02 \text{ and } 0.06 \text{ respectively})\) in treatment reaches; periphyton and macroinvertebrate \( \delta^{13}C \) were not significantly different \((P = 0.8 \text{ and } 0.4 \text{ respectively})\).

**Discussion**

 Numerous studies have investigated freshwater food web response to nutrient enrichment from inorganic...
fertilizers and salmon carcasses (Stockner & Shortreed, 1978; Ashley & Slaney, 1997; Chaloner et al., 2004; Lang et al., 2006); however, very few have examined the efficacy and response of stream food web variables to a manufactured, pasteurized, SCA treatment (Wipfli, Hudson & Caouette, 2004; Pearsons et al., 2007a). We demonstrate that a single experimental addition of SCA in two central Idaho streams significantly stimulated periphyton and macroinvertebrate food web variables, with no apparent response in dissolved nutrient concentrations, no changes in nutrient limitation status, and no obvious shifts in macroinvertebrate community composition. Stable isotope analysis confirmed trophic transfer from SCA to the periphyton and macroinvertebrate community. A variable response was observed in leaf litter decay rates.

Surface water chemistry response

Contrary to results in Chaloner et al. (2004) where concentrations of dissolved ammonium and SRP were higher in the presence of salmon spawners, the addition of SCA did not significantly change reach-level nutrient concentrations. Salmon carcass analogues represent an inanimate nutrient treatment while spawning salmon represent an ecologically important source of bioturbation, physically disrupting the streambed and providing direct sources of metabolic waste products through excretion (Chaloner et al., 2004; Moore, Schindler & Scheuerell, 2004). The absence of bioturbation and excretory products in our SCA treatment reaches may help to explain observed differences and reinforce the concept that SCA should not be viewed as a substitute for spawning salmon. Similar to our findings, Pearsons et al. (2007a) documented no significant change in dissolved nutrient concentrations following SCA additions in central Washington streams. Rapid biological uptake and retention of dissolved nutrients and/or the inability of our sampling protocol to adequately capture elevated nutrient levels following SCA treatment may explain the absence of an observed response.
Periphyton response

Salmon carcass analogue treatment significantly increased periphyton biomass in two central Idaho streams. Cape Horn Creek – treated in a low gradient, open canopy stream reach with high channel connectivity to the adjacent floodplain – exhibited a stronger response in periphyton biomass relative to Elk Creek – treated in a relatively higher gradient, more confined reach with increased riparian shading. These results appear consistent with previous studies that found variable periphyton response to carcass enrichment among study streams (Chaloner et al., 2004) and identified strong canopy effects on light availability and periphyton accrual in streams receiving nutrient enrichments (Gregory, 1980; Hill & Knight, 1988).

Periphyton samples collected 1 year after treatments in Cape Horn Creek and Elk Creek resembled baseline

Fig. 6 Macroinvertebrate density (a) and biomass (b) box and whisker plots (median and 10th, 25th, 75th and 90th percentiles) 30 days after a salmon carcass analogue addition in Cape Horn Creek and Elk Creek. Marsh Creek and Valley Creek were not treated and serve as reference streams. Site codes are: CHC, Cape Horn Creek; MC, Marsh Creek; EC, Elk Creek; VC, Valley Creek.

Fig. 7 Leaf litter decay rate mean values (±1SD) for Cape Horn Creek and Elk Creek in reference and treatment reaches.

Fig. 8 Periphyton (a) and macroinvertebrate (b) dual isotope plots of $\delta^{15}$N and $\delta^{13}$C mean values (±1SD) for reference streams: Marsh Creek (MC) and Valley Creek (VC); and treatment streams: Cape Horn Creek (CHC) and Elk Creek (EC). Open symbols are upstream or reference reaches and closed symbols are downstream or treatment reaches.

Salmon carcass analogue treatment significantly increased periphyton biomass in two central Idaho streams. Cape Horn Creek – treated in a low gradient, open canopy stream reach with high channel connectivity to the adjacent floodplain – exhibited a stronger response in periphyton biomass relative to Elk Creek – treated in a relatively higher gradient, more confined reach with increased riparian shading. These results appear consistent with previous studies that found variable periphyton response to carcass enrichment among study streams (Chaloner et al., 2004) and identified strong canopy effects on light availability and periphyton accrual in streams receiving nutrient enrichments (Gregory, 1980; Hill & Knight, 1988). Periphyton samples collected 1 year after treatments in Cape Horn Creek and Elk Creek resembled baseline.
measures, suggesting a relatively short temporal response to SCA treatment.

**Nutrient dynamics and longitudinal periphyton response**

Nutrient-diffusing substrata and Redfield ratios identified N as a limiting nutrient to periphyton biomass in both treatment streams. Similar to Pearsons et al. (2007a), we found no change in nutrient limiting status following SCA treatment; streams remained N-limited. To further characterize nutrient dynamics and potential response to SCA treatment we measured periphyton biomass downstream of treatment reaches. We estimated stream nutrient uptake lengths ($S_w$) using a formula described in Thomas et al. (2003) to approximate the longitudinal distance over which our SCA treatment would elevate stream nutrient concentrations; thus, $S_w$ served as a measured proxy to examine nutrient spiralling and potential longitudinal periphyton response. Uptake length estimates using nitrogen forms were consistently shorter in Cape Horn Creek relative to Elk Creek, indicating tighter nutrient spirals and increased retention of limiting nutrients. Periphyton biomass measured downstream of treatment reaches was similarly variable: remaining elevated in Elk Creek but not in Cape Horn Creek. Nutrient uptake by stream autotrophs and microbes has been shown to reduce $S_w$ through the incorporation of nutrients into benthic biomass (Allan, 1995) and may help to explain differential periphyton response in treatment streams. Future research should include direct measurements of $S_w$ and incorporate nutrient spiralling concepts to better understand variable response to nutrient enrichment between stream environments.

**Macroinvertebrate response**

Similar to Wipfli et al. (1998, 1999) who found increased densities of macroinvertebrates in the presence of salmon carcasses in southeastern Alaskan streams, we demonstrated a significant increase in macroinvertebrate density and biomass following SCA treatment. Specifically: Ephemeroptera; Elmidae; and Brachycentridae densities were higher in the presence of SCA. These families are dominated by taxa associated with the grazer functional feeding group and illustrate a clear response to higher primary production. Other studies have demonstrated individual taxonomic response to carcass enrichments; few have investigated shifts in community composition and structure (Wipfli et al., 1998; Chaloner, Wipfli & Caouette, 2002b). We found no significant difference in basic richness and diversity measures as a response to SCA treatment. The apparent lack of a measurable response in community metrics may be germane to comments by Francoeur (2001), who noted that the low replication and high variability typical of ecological studies means that real and potentially biologically important responses occur, yet remain undetected. The low statistical power of our study design, and inherently variable data, only revealed large differences and may obfuscate more subtle shifts in macroinvertebrate community composition and structure.

**Leaf litter decay rates**

Differences in leaf litter decay rates were detected in Elk Creek following SCA addition; however, no differences were found in Cape Horn Creek. Other studies have found increased decomposition rates
with the addition of in-stream nutrients (Robinson & Gessner, 2000; Grattan & Suberkropp, 2001), few have addressed how marine-derived nutrients affect in-stream leaf decay rates (Ito, 2003). The observed difference in decay rates is likely due to warmer streamwater temperatures in Elk Creek stimulating microbial activity. We found increased percent organic matter associated with leaves in the Elk Creek treatment reach compared to the reference reach; Cape Horn Creek had no detectable differences in percent organic matter following SCA treatment. Similarly, Ito (2003) found that microbial activity associated with leaves in the presence of salmon carcasses was higher than those without. We propose that low streamwater temperatures in Cape Horn Creek reduced microbial activity, and that our leaf incubation periods of 15 and 30 days were too short to detect differences in decay rates. This finding is consistent with Royer & Minshall (2001) who documented similar results in a southeastern Idaho stream.

**Stable isotope values**

Trophic transfer of N from SCA was evident in treatment streams by enriched N stable isotope signatures measured in stream periphyton and macroinvertebrate samples. Analysis of N isotopes found that periphyton and macroinvertebrate $\delta^{15}N$ values were higher in treatment reaches, suggesting assimilation of N from SCA into the stream food web. This finding is similar to Pearsons et al. (2007a) who documented elevated $\delta^{15}N$ values with no change in $\delta^{13}C$ following SCA treatment in the Yakima River Basin, WA. The increase in $\delta^{15}N$ values from reference to treatment reaches is similar to what Kline et al. (1990) and Chaloner et al. (2002a) found in salmon-free and salmon-bearing reaches, where an enrichment of 5–6‰ relative to salmon-free reaches was observed. In our study we found an average enrichment of 3‰, slightly lower than Kline et al. (1990) and Chaloner et al. (2002a).

**Management considerations**

Different response magnitudes seen in the present study and variable results from other published work highlight the need to perform specific evaluations before embarking on large-scale nutrient enhancement efforts. Reach-level nutrient manipulations should be verified at broader spatial scales (catchment) using methods that mimic the delivery and timing of nutrients from naturally spawning salmon. Our study has important implications for resource managers seeking to increase the growth and survival of salmon and steelhead in food-limited freshwater rearing habitats. Pearsons et al. (2007a) documented direct consumption of SCA material by rainbow/steelhead trout (Oncorhynchus mykiss), cutthroat trout (Oncorhynchus clarkii) and juvenile Chinook salmon and increased growth rates of rainbow trout in the Yakima River basin, WA, U.S.A.; and Wipfli et al. (2004) documented an increase in stream-resident salmonid condition, lipid level measures and production in the presence of SCA in southeast Alaska, U.S.A. artificial stream channels. We reason that similar benefits to juvenile salmonids would occur in central Idaho streams following nutrient enrichment with SCA. However, although nutrient enhancement using SCA appears effective and ecologically innocuous at the scale of recent studies, analogues should not be viewed as a substitute for naturally spawning salmon. Moore et al. (2004) identified spawning salmon as important habitat modifiers in aquatic systems used by sockeye salmon. This bioturbation was shown to affect the structure and function of aquatic ecosystems and may play important roles not obvious to stream ecologists and natural resource managers. Managers adopting enrichment strategies that attempt to stimulate diminished stream productivity using SCA should understand the benefits and limitations of such an approach. Furthermore, SCA have only been applied in a research-oriented framework and no cost estimates are available for large-scale production and application at this time. However, benefits including trophic transfer pathways that include direct consumption of SCA particulates by stream-dwelling consumers (i.e. macroinvertebrates and salmonids), a pasteurized product that reduces the risk of disease transfer, and the ability to recycle fish products into a usable and widely applicable nutrient amendment tool hold great potential utility (Pearsons et al., 2007a).

**Marine-derived nutrients and threatened stocks of Pacific salmon**

Recent analyses by Achord et al. (2003), Thomas et al. (2003), and Scheuerell et al. (2005) in the Snake River...
basin highlight the importance of marine-derived nutrients to freshwater productivity and the survival of threatened stocks of Pacific salmon. Decreased freshwater productivity, and correspondingly diminished carrying capacities, may represent important limiting factors in what often appears to be otherwise near-pristine habitat. In the absence of abundant anadromous salmon and steelhead populations, nutrient enhancement may help to restore freshwater productivity affected by a severe lack of marine-derived nutrients and help promote restoration efforts aimed at increasing naturally spawning populations of salmon and steelhead. Thomas et al. (2003) suggest that historical primary and secondary productivity rates are substantially different from those observed today, and that reduced levels of N and P delivered by salmon and steelhead are not being replaced. Our results strongly indicate that supplemental nutrient additions are required to increase freshwater productivity in nutrient-limited streams of central Idaho. Novel approaches to nutrient enrichment, such as pathogen-free SCA, may better mimic the delivery of nutrients to freshwater ecosystems from anadromous salmon and steelhead than other artificial methods (i.e. inorganic soluble fertilizer). Recycled fish products used to manufacture SCA should be derived from sustainable sources. A cautious approach using SCA as an interim tool to restore freshwater productivity may be warranted.

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References

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

Allan D.J. (1995) Stream Ecology Structure and Function of Running Waters. Chapman and Hall, London.

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

APHA (1995) Standard Methods for the Examination of Water and Wastewater, 19th edn. American Public Health Association, Washington, DC.

Ashley K.I. & Slaney P.A. (1997) Accelerating recovery of stream and pond productivity by low-level nutrient enrichment. In: Fish Habitat Rehabilitation Procedures (Eds P.A. Slaney & D. Zaldokas), pp. 239–262. Catchment Restoration Tech. Circ. No. 9. British Columbia Ministry of Environment, Lands and Parks and Ministry of Forests, Vancouver, BC.

Benfield E.F. (2006) Decomposition of leaf material. In: Methods in Stream Ecology. (Eds F.R. Hauer & G.A. Lamberti), pp. 711–720. Academic Press, San Diego, CA.

Bilby R.E., Beach E.W., Fransen B.R., Walter J.K. & Bisson P.A. (2003) Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Transactions of the American Fisheries Society, 132, 733–745.

Cederholm C.J., Kunze M.D., Murota T. & Sibatani A. (1999) Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries, 24, 6–15.

Chalonier D.T., Wipfli M.S. & Caouette J.P. (2002b) Mass loss and macroinvertebrate colonization of Pacific salmon carcasses in south-eastern Alaskan streams. Freshwater Biology, 47, 263–273.

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

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

Charles D.F., Knowles C. & Davis R.S. (2002) Protocols for the Analysis of Algal Samples Collected as Part of the U.S. Geological Survey National Water-Quality Assessment Program. Report No. 02–06, The Academy of Natural Sciences, Philadelphia, PA.

Davis J.C., Minshall G.W., Robinson C.T. & Landres P. (2001) Monitoring Wilderness Stream Ecosystems. General Technical Report RMRS-GTR-70, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
Francoeur S.F. (2001) Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. *Journal of the North American Benthological Society, 20*, 358–368.

Fulton L.A. (1968) Spawning areas and abundance of Chinook salmon, *Oncorhynchus tshawytscha*, in the Columbia River basin, past and present. U.S. Fish and Wildlife Service Scientific Report, Fish. 571.

Gibeau G.G. & Miller M.C. (1989) A micro-bioassy for epilithon using nutrient diffusing substrata. *Journal of Freshwater Biology, 5*, 171–176.

Grattan R.M. & Suberkropp K. (2001) Effects of nutrient enrichment on yellow poplar leaf decomposition and fungal activity in streams. *Journal of the North American Benthological Society, 20*, 33–43.

Gregory S.V. (1980) Effects of Light, Nutrients, and Grazers on Periphyton Communities in Streams. PhD Dissertation, Oregon State University, Corvallis, OR.

Gresh T., Lichatowich J. & Schoonmaker P. (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*, 15–21.

Groot C. & Margolis L. (Eds) (1991) *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, BC.

Hicks B.J., Wipfli M.S., Lang D.W. & Lang M.E. (2005) Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, south-central Alaska. *Oecologia, 144*, 558–569.

Hill W.R. & Knight A.W. (1988) Nutrient and light limitation of algae in two northern California streams. *Journal of Phycology, 24*, 125–132.

Hurlbert S.H. (1984) Psuedoreplication and the design of ecological field experiments. *Ecological Monographs, 54*, 187–211.

Ito T. (2003) Indirect effect of salmon carcasses on growth of a freshwater amphipod, *Jesogammarus jesoensis* (Gammaridea): an experimental study. *Ecological Research, 18*, 81–89.

Kline T.C., Goering J.J., Mathisen O.A., Poe P.H. & Parker P.L. (1990) Recycling of elements transported upstream by runs of Pacific salmon: I. \(\delta^{15}N\) and \(\delta^{13}C\) evidence in Sashin Creek, southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences, 47*, 136–144.

Lang D.W., Reeves G.H., Hall J.D. & Wipfli M.S. (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. & Slaney P.A. (1997) Implications of trends in marine-derived nutrient flux to south coastal British Columbia salmonid production. *Fisheries, 22*, 16–24.

Levy S. (1997) Pacific salmon bring it all back home. *Bioscience, 47*, 657–660.

Lichatowich J.A. (1999) *Salmon Without Rivers: A History of the Pacific Salmon Crisis*. Island Press, Washington, DC.

Moore J.W. & Schindler D.E. (2004) Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences, 61*, 1582–1589.

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

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

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

Pearsons T.N., Roley D.D. & Johnson C.L. (2007b) Development of a carcass analogue for nutrient restoration in streams. *Fisheries, 32*, 114–124.

Pearsons T.N., Johnson C.L., Schmuck M.R., Webster D.D. & Bilby R.E. (2007a) Do salmon carcass analogues reproduce food pathways provided by salmon carcasses and impact the growth and abundance of salmonids? *North American Journal of Fisheries Management*, in press.

Robinson C.T. & Gessner M.O. (2000) Nutrient addition accelerates leaf breakdown in an alpine springbrook. *Oecologia, 122*, 258–263.

Royer T.V. & Minshall G.W. (2001) Effects of nutrient enrichment and leaf quality on the breakdown of leaves in a hardwater stream. *Freshwater Biology, 46*, 603–610.

Scheuerell M.D., Levin P.S., Zabel R.W., Williams J.G. & Sanderson B.L. (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.

Sharp J.H., Carlson C.A., Feltzer E.T., Castle-Ward D.M., Savidge K.B. & Rinker K.R. (2002) Final dissolved organic carbon broad community intercalibration and preliminary use of DOC reference materials. *Marine Chemistry, 77*, 234–253.

Steinman A.D. & Lamberti G.A. (1996) *Biomass and Pigments of Benthic Algae. Methods in Stream Ecology*. Academic Press, London.
Stockner J.G. & Shortreed K.R.S. (1978) Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. *Journal of the Fisheries Research Board of Canada*, 35, 28–34.

Thomas S.A., Royer T.V., Minshall G.W. & Synder E. (2003) Assessing the historic contributions of marine-derived nutrients to Idaho streams. *Fisheries*, 34, 41–55.

UNESCO (1994) *Protocols for the Joint Global Ocean Flux Study (JGOFS). Core Measurements*. IOC Manual and Guides, 29, UNESCO, Paris, France.

Valderrama J.C. (1981) The simultaneous analysis of total nitrogen and total phosphorus on natural waters. *Marine Chemistry*, 10, 109–122.

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

Welsh E.B., Jacoby J.M. & May C.W. (1998) *Stream Quality. River Ecology and Management: Lessons From the Pacific Coastal Ecoregion*. Springer-Verlag, New York.

Wipfli M.S., Hudson J.P. & Caouette J.P. (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*, 56, 1600–1611.

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

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

Wipfli M.S., Hudson J.P., Caouette J.P. & Chaloner D.T. (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.

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