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# Ecological Effects of Live Salmon Exceed Those of Carcasses During an Annual Spawning Migration

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## Abstract

We tested the hypothesis that the carcasses of anadromous Pacific salmon (*Oncorhynchus* spp.) constitute a significant source of nutrients in the nutrient-poor freshwaters where these fish migrate, spawn, senesce, and die. In a 110 m-long stream reach in Southeast Alaska, we retained nearly 3000 salmon carcasses and compared streamwater nitrogen (N), phosphorus (P), and the biomass of benthic biofilm in this reach with an upstream reference reach. The study spanned 5 months, bracketed the entire salmon run, and encompassed significant seasonal variation in abiotic stream conditions. Concentrations of dissolved and particulate N and P followed distinctly unimodal patterns through time, which tracked the abundance of live salmon, and we observed strong predictive relationships between live-salmon abundance and streamwater-nutrient concentrations. In contrast, we did not observe clear relationships between salmon carcasses and streamwater nutrients. Biofilm biomass within our study reaches seemed to more closely track the abundance of live salmon than the abundance of carcasses. The experimental retention of carcasses had a minor or undetectable influence on nutrient concentrations and biofilm within the study reach as compared to the reference reach. We conclude that physical factors such as temperature, discharge, nutrient limitation, and irradiance vary seasonally in ways that maximize the influence of nutrients provisioned by live salmon and minimize the influence of carcass-derived nutrients on the aspects of stream ecosystems that we examined. Overall, our results promote a new perspective on the ecological role of salmon in freshwaters, and contribute to a more mechanistic understanding of how migratory fishes can influence aquatic ecosystems.

**Key words:** fish migration; marine-derived nutrients; resource subsidy; salmon-derived nutrients; organic-matter retention.

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**Author Contributions:** S.D.T. analyzed the data and wrote the manuscript along with important contributions from all co-authors. In particular, S.D.T. overviewed the field study, and P.S.L. and J.R. played important roles in the execution of the field experiments. P.S.L. coordinated data collection involving water chemistry. J.R. coordinated data collection involving biofilm and nutrient limitation assays. D.T.C., J.L.T., and G.A.L. (lead) were investigators on the grant and conceived the original study design. S.D.T. implemented important modifications to the study design. All authors reviewed and commented on the content of the manuscript.

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## Introduction

Mobile organisms transport nutrients and energy across ecosystem boundaries, coupling spatially distinct ecosystems, and frequently providing limiting resources to recipient ecosystems (Polis and

others 2004). The impact of such resource subsidies can be pronounced. For example, seabirds amass marine-derived nutrients and fertilize the lush grasslands that typify islands of the Aleutian archipelago where these birds nest and roost; in the absence of this subsidy, plant communities convert to less-productive tundra dominated by low-lying forbs and dwarf shrubs (Maron and others 2006). Similarly, the spawning migrations of diverse anadromous fishes including salmon, herring, eel, alewife, eulachon, and shark transfer marine-derived nutrients into freshwater ecosystems (for example, Post and Walters 2009; MacAvoy and others 2009; Tiegs and others 2009; Flecker and others 2010). During migrations, these fish excrete compounds that contain nitrogen (N) and phosphorus (P), which are assimilated by microbial autotrophs and heterotrophs and are believed by researchers to have positive bottom-up effects on the productivity of aquatic and riparian food webs (for example, Gende and Quinn 2006). In addition, in the case of semelparous migratory species, such as most Pacific salmon (*Oncorhynchus* spp.), the particulate and dissolved nutrients provided by their carcasses after spawning and death are thought to be essential promoters of stream and riparian productivity (Cederholm and others 1999; Helfield and Naiman 2006; Gende and others 2002).

Declines in Pacific salmon populations due to human activities have been documented across the range of salmon around the Pacific Rim (Gresh and others 2000; Augerot 2005), especially in the southern extent of their range, raising concerns that, in the absence of salmon-derived nutrients, many freshwater ecosystems could be marked by reduced productivity and altered community structure (Schindler and others 2003). Such concerns have prompted widespread management activities intended to address what has been termed 'cultural oligotrophication' (Stockner and others 2000; Stockner 2003). For example, salmon carcasses are routinely added to lakes, streams, and rivers which suffer from reduced run sizes with the aim of augmenting whole-system productivity, increasing juvenile-salmon recruitment, and ultimately restoring marine-freshwater connectivity (Compton and others 2006; Shaff and Compton 2009).

Studies addressing the ecological effects of salmon carcasses in streams have varied in their spatial scale and degree of environmental realism, and have yielded diverse outcomes. The most common experimental approach has been to euthanize salmon that have not yet spawned (often obtained from hatcheries), and add their carcasses to natural and/or artificial stream channels. This approach usually elevates concentrations of dissolved nutrients (Mitchell and Lamberti 2005), increases algal biomass (Mitchell and Lamberti 2005), and positively influences the abundance and/or growth of stream organisms including invertebrates (Chaloner and Wipfli 2002; Claeson and others 2006) and juvenile salmonids (Wipfli and others 2003; but see Harvey and Wilzbach 2010). Interestingly, however, the magnitude of these experimental effects on stream biota tends to be much greater than that reported in field studies that examine natural salmon runs (that is, those that also include the effects of live salmon, not just carcasses) (for example, Chaloner and others 2002, 2007; Cak and others 2008; Lessard and others 2009). For example, in a meta-analysis, Janetski and others (2009) found that the average effect of carcass-addition experiments on invertebrates is 50 times greater than that documented in studies of natural runs. This effect and typically positive experimental effects on other organisms were attributed to several factors including artifacts associated with using stream mesocosms, lack of disturbance to stream sediments by migrating/spawning salmon activity (sensu Moore and Schindler 2008, 2010; Campbell and others 2011), and the sometimes unnaturally large quantities of carcasses that were added relative to stream size. Although carcass-addition studies have provided key insights, especially into the pathways via which salmon-derived nutrients enter steam food webs, these experiments did not explicitly explore the influence of the naturally senesced and naturally retained salmon carcasses in stream channels.

Naturally senesced salmon carcasses differ in their nutrient contents from the 'fresh' carcasses that have been used in carcass-addition experiments, and this and other discrepancies may have influenced experimental outcomes. Semelparous salmon, including highly abundant species such as pink (*O. gorbuscha*) and chum salmon (*O. keta*), generally do not feed during spawning runs but instead use energy reserves stored in their bodies in the form of fat and protein, replacing them with water as they gradually approach death in the weeks before and after spawning (Quinn 2005). During the course of a salmon run, naturally retained carcasses originating from salmon that experience a senescent death (hereafter ''senesced carcasses'') tend to constitute the majority of carcasses present in the stream channel, especially in larger streams where predation by bears is less efficient (Quinn 2005). Upon reaching senescent

death, female pink salmon have appreciably less carbon (C), N, and P in their bodies than they do at the start of their migration (Gende and others 2004). Thus, a substantial proportion of marine-derived nutrients that initially enters the stream channel early in the migration is released as gametes and excreted as metabolic wastes before the death of the salmon. These excreted nutrients are in a mineral form that is immediately available for uptake by members of the stream biofilm community whereas nutrients bound in carcasses must be mineralized before being readily assimilated. The idea that senesced carcasses have less of an impact on streamwater nutrients than fresh carcasses used in carcass experiments is further supported by field observations in which dissolved-nutrient concentrations were similar to pre-run concentrations despite the presence of abundant senesced carcasses (Levi and others unpublished data).

Naturally senesced carcasses, being of a similar density with respect to freshwater (Tiegs unpublished data), are readily transported downstream by stream flow unless retained by stream-channel structures such as accumulations of large wood, or slow-water areas of the stream channel such as pools that lack transport capacity. Human activities (for example, channelization) often reduce the prevalence of retentive features, and consequently limit the ability of stream channels to retain organic matter such as salmon carcasses (Bilby and Ward 1991), potentially increasing the export of nutrients from watersheds to downstream ecosystems such as lakes and estuaries (Levi and others unpublished data). Therefore, even when the influx of a resource subsidy is large, anthropogenic impacts may limit the capacity of ecosystems to retain and utilize the subsidy (Tiegs and others 2008a), an idea that has received little research attention despite the potentially adverse consequences for recipient ecosystems, such as salmon streams.

Timber harvest is perhaps the most widespread human land use in the forested watersheds within the spawning range of Pacific salmon. Timber harvest can simplify stream habitats and reduce the prevalence of features such as debris jams (Reeves and others 1993) that are effective at retaining salmon carcasses (Cederholm and Peterson 1985). Although managers commonly add large wood to streams (Woolsey and others 2007), which can increase their retentive capacity (Entrekin and others 2008), information is lacking about how such management actions influence salmon-carcass retention. Furthermore, the increased abundance of naturally senesced salmon carcasses as a result of restoration has the potential to influence fundamental attributes of stream ecosystems such as streamwater-nutrient concentrations and primary production.

In this article, we present the results from a field manipulation in which we augmented the capacity of a stream channel to retain naturally senesced salmon carcasses. This experiment lacked the artifacts of previous carcass additions and allowed us to evaluate the effect of carcasses that were in an environmentally realistic condition and abundance. We performed the manipulation in a watershed with a history of timber harvest, and the stream channel lacked the retentive capacity of unimpacted streams in the region. Using a before–after control–intervention (BACI) experimental design, we evaluated the effects of live salmon and salmon carcasses by sampling streamwater-nutrient concentrations and benthic biofilms. Frequent sampling (for example, 39 dates for dissolved streamwater nutrients) enabled a higher-resolution characterization of nutrient and biofilm dynamics than what was previously available. Our results are contrary to previous findings relating to the ecological effects of salmon carcasses in streams, provide a more mechanistic understanding of how and when salmon resource subsidies can be delivered to stream ecosystems, and inform the management of salmon and the freshwater ecosystems where these fish spawn and die.

## Methods

### Study Site

We conducted this study in the Maybeso Creek Experimental Forest (USDA Forest Service), Prince of Wales Island, Southeast Alaska, USA. Like many watersheds in Southeast Alaska, the Maybeso Creek watershed has a history of timber harvest; from 1953 to 1960 approximately 22% of the 39 $km^2$ drainage area above our study site was logged, including much of the riparian zone. Consequently, the contemporary Maybeso Creek channel has less large wood, fewer pools and side channels, and more abundant riffle-type habitats than before logging (Bryant 1980). In our study reach (55°29′N 132°40′W), substrate in the stream channel is dominated by gravel with a mean particle size of 47 mm (SD = 32). The low-flow wetted channel has a mean width of 18.5 m (SD = 4.6) and base-flow discharge is approximately 450 L/s (Tiegs and others 2008a). The riparian forest is dominated by second-growth western hemlock

(*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and red alder (*Alnus rubra*). The volume of large wood present in the bankfull stream channel is 5.96 $m^3$/100 m of stream-channel length. Maybeso Creek has abundant runs of pink (*O. gorbuscha*) and chum (*O. keta*) salmon, which typically start in July. Other salmon species are relatively rare (*O. kisutch* and *O. mykiss*) or absent.

## Study Design

This study consisted of a manipulative field experiment and frequent field sampling from June to November 2007 that bracketed an entire annual salmon migration. This approach allowed us to evaluate the influence of live salmon and salmon carcasses on streamwater nutrients and benthic biofilm dynamics. The field manipulation consisted of retaining a large number of naturally senesced salmon carcasses in a reach of Maybeso Creek. Observations in this reach were made in parallel with those in an upstream reference reach on numerous dates before and after the time when carcasses began to accumulate in the stream channel. Observations made in the reference reach during the weeks before the start of the salmon migration allowed us to evaluate changes to stream variables that occurred with the onset of the salmon migration, but before carcasses were present in the stream channel. After spawning, when live fish were largely absent, observations made in the upstream reference reach allowed us to evaluate the influence of carcasses that were naturally retained in the stream channel.

## Carcass-Retention Experiment

In mid-June 2007, approximately 6 weeks before the start of the salmon migration, two 110-m-long reaches of Maybeso Creek were selected, which in previous studies were found to have similar channel morphology, sediment size, aspect, temperature, and use by migrating and spawning salmon (Tiegs and others 2008a, 2009). The reaches were separated by a 150 m-long buffer. The upper reach functioned as a reference. In the lower reach, 140 carcass-retention devices were installed (modified after Tiegs and others 2008b). The devices were intended to function like natural retention structures, such as debris dams, and capture salmon carcasses as they naturally drifted downstream (Minakawa and Gara 2005) without adding a source of organic C to the stream. Each retention device consisted of a 1.56 m-long piece of steel conduit pipe (~2 cm in diameter) that was affixed underwater to two rebars that were hammered into the stream bed. Each piece of rebar was fitted with a plastic safety cap. The devices were aligned perpendicularly to stream flow to maximize their efficiency in retaining drifting carcasses. Concentrations of nitrate ($NO_3^-$-N), ammonium ($NH_4^+$-N), and soluble reactive phosphorus (SRP) were nearly identical in the two reaches before, during, and after the salmon run across a broad range of stream discharges in 2006, as was biofilm biomass (Tiegs and others 2008a). During a period of low flow in 2006 and before the salmon run, the differences in concentrations of SRP, $NH_4^+$-N, and $NO_3^-$-N between the two reaches were less than 2 µg/L. Across four sampling dates that year that spanned the salmon run, the differences between the two reaches were less than 1 µg/L.

## Salmon and Salmon-Carcass Counts

Live salmon and senesced salmon carcasses were counted on approximately 15 dates in both the carcass-retention reach and the reference reach starting on the date that salmon first appeared in Maybeso Creek in July until carcasses were no longer present in November. At 10-m intervals along the stream channel, a 4 m-wide belt transect was visualized which ran perpendicular to the low-flow channel. All live fish and carcasses occurring within these transects were counted, thereby representing 40% of the channel area. Data were interpolated to estimate the total number of live fish and carcasses present on each date in the two reaches.

## Stream-Channel Retentiveness

The capacity of the stream channel to retain organic matter was quantified in the retention and reference reaches by releasing 100 strips of paper (4 cm × 14 cm, Weyerhaeuser 20 lb. 30% recycled white Xerocopy™) at the upstream end of each reach and counting the number of strips that passed through the entire reach (Webster and others 1994; Lamberti and Gregory 2006).

## Streamwater Chemistry

Three replicate water samples (60 ml) were collected from the bottom of the carcass-retention and reference reaches on 39 dates from June 21 to November 18. In the field, water was filtered through a Whatman® GF/F (0.7 µm) filter into polyethylene bottles for analysis of SRP, $NO_3^-$-N, and $NH_4^+$-N, and stored at −20°C before laboratory analysis. An additional volume of water, typically about 1.5 L, was passed through each filter, and

stored at −20°C for later determination of particulate concentrations of C, N, and P. N and P were analyzed on filters from alternating sampling dates because we could only sample one of these nutrients from each filter due to the limited total nutrient mass that was retained. $NO_3^-$ and $NH_4^+$ were combined to estimate total dissolved inorganic nitrogen (DIN). DIN and SRP were also converted to molar ratios to evaluate changes in nutrient stoichiometry through time, as were particulate C and N.

Upon return to the laboratory, a Lachat® QC8500 Flow Injection Autoanalyzer (Lachat Instruments, Loveland, CO, USA) was used to determine SRP concentration with the ascorbic-acid method, and was also used to determine particulate P following a hydrochloric acid digestion (Stainton and others 1977). $NO_3^-$ concentration was determined using the cadmium-reduction method (APHA 1999), and $NH_4^+$ concentration was run by hand on a Shimadzu® UV-1601 spectrophotometer (Shimadzu Corporation, Columbia, MD, USA) using the phenol-hypochlorite method (Solorzano 1969, APHA 1999). A Costech 4010 Analyzer (Costech Analytical, Valencia, CA, USA) was used to quantify particulate C and N. After determination of dissolved-nutrient concentrations, analytic replicates were pooled to obtain a mean for each reach on each sampling date.

## Nutrient Flux

The flux of dissolved and particulate nutrients was calculated by multiplying nutrient concentrations by the mean daily discharge on each collection date. Flux was expressed as kg/d. Discharge was determined by relating multiple direct measurements of discharge with hourly recordings of river stage. Direct discharge measurements using a flow meter were taken in each of the two experimental reaches on multiple dates with contrasting discharge and found to be nearly identical in the two reaches. Stage was measured with a logger located near the downstream end of the reference reach. Because discharge did not differ between the two reaches the discharge estimates made with the stage logger in the reference reach were also used in the retention reach.

## Benthic Algae and Biofilm Biomass

Sampling of benthic biofilm was conducted on 12 dates from June 18 to October 29 in the retention reach and the reference reach. Five individual rocks were collected from each reach on each sampling date. Biofilm was sampled from each rock with a syringe–toothbrush sampler (Steinman and others 2006) and analyzed for chlorophyll *a* (chl*a*) content and ash-free dry mass (AFDM) according to techniques described by Tiegs and others (2008a). The following stratified-random design was used to determine the location from where each rock was taken. The longitudinal position of each sample was fixed such that rocks were gathered at 20 m intervals along each reach on each date. At each interval, the location of each sample within the cross section of the stream channel was determined at random, and a rock was chosen haphazardly from this location. If the rock was too small to be sampled (minimum diameter approximately 50 mm), then it was discarded and another was chosen from the same location. This approach resulted in a minor bias for particles that were larger than the average particle in the Maybeso Creek (mean medial diameters of 135 and 133 mm in the reference and retention reaches, respectively). Larger particles have been shown to be less susceptible than smaller particles to disturbance by spawning salmon (Tiegs and others 2008a, b; Janetski and others 2009; Holtgrieve and others 2010), and our sampling was not intended to characterize the response of the entire benthic community.

## N and P Limitation

Nutrient-diffusing substrata (NDS) (after Tank and Dodds 2003; Johnson and others 2009; Rüegg and others 2011) were used to test for nutrient limitation of the autotrophic (for example, algae) and heterotrophic (for example, bacteria, fungi) constituents of the benthic-biofilm community. NDS were deployed in the carcass-retention and reference reaches on dates before the salmon run (June 28–July 11), during the run when both live salmon and carcasses were present in the stream channel (August 25–September 13), and after the salmon run when only carcasses were present in the stream channel, and no live fish remained (October 3–October 20). NDS consisted of 30-ml polyethylene cups filled with a 2% agar solution amended with 0.5 M $NH_4Cl$ (N treatment), 0.5 M $KH_2PO_4$ (P treatment), both (N + P treatment), or no amendment as a control. Each treatment was replicated six times in each of the two reaches. NDS were capped with either inorganic fritted-glass disks or organic cellulose-sponge disks. Fritted glass was used as a porous inorganic substratum to test for nutrient limitation of algae, and cellulose sponge was used at an organic substratum to assess the nutrient limitation of heterotrophs (after Johnson

and others 2009). After incubation in the stream, the fritted-glass disks and cellulose sponges were placed in 50-ml plastic centrifuge tubes along with stream water, transported to the laboratory, and stored overnight at 4°C. Respiration of microbes on cellulose sponge was determined by measuring the consumption of dissolved oxygen from stream-water after 2 h of incubation at room temperature in the dark (see Rüegg and others 2011). Chl*a* was extracted from the fritted glass disks by submerging them individually in 10 ml of ethanol for 24 h at 4°C, and determining concentration fluorometrically (after Sartory and Grobbelaar 1984).

### Statistical Analysis

The influence of experimentally retained salmon carcasses was evaluated for each response variable by first calculating the difference between the carcass-retention reach and the reference reach on each sampling date, and then using one-way analysis of variance (ANOVA) on these differences to compare data gathered before carcasses were present in the stream channel with data gathered on dates when carcasses were present. This BACI approach has been used successfully in other unreplicated studies where the large scale of the manipulation prohibits replication of treatments (for example, Taylor and others 2006; Greenwood and others 2007). Using the differences between paired observations minimizes non-independence arising from data collected in a series (Stewart-Oaten 2003). Ordinary least-squares regression was used to test for relationships between the abundance of live salmon and salmon carcasses, and response variables related to nutrients and biofilm in each of the two reaches. Differences in the slopes of these regressions were evaluated using analysis of covariance (ANCOVA). Quadratic equations were applied to direct counts of live salmon and carcasses with the curve estimation procedure in SPSS 15.0 (SPSS Inc., Chicago, IL, USA) and used to estimate the abundance of salmon and carcasses. ANOVA was performed on data from the NDS assays to test for treatment effects of N, P, and N and P (after Tank and Dodds 2003). Unless otherwise specified, statistical analyses were performed in SYSTAT 12 (Systat Software, Point Richmond, CA, USA).

## Results

### Channel Retentiveness

Channel retentiveness increased after the installation of the carcass-retention devices, as evidenced by increased retention of experimentally released paper strips. Before the installation of the carcass-retention devices only 7% of the paper strips were retained in the retention stretch. After installation, 100% of the strips were retained in the stretch, with 70% of the strips being retained on the devices. In contrast, retentiveness of the upstream reference reach was consistent across the two sampling dates; 36 and 34% of the strips were retained, respectively, before and after the devices were installed downstream.

### Live Salmon and Carcass Dynamics

Live salmon were first observed in the two reaches on July 31, and live-salmon abundance then increased steadily until maximum values of 1462 and 1592 individuals were reached in the retention and reference reaches, respectively, during the third week of August (Figure 1A). Abundance declined steadily thereafter until the first week of October, after which live salmon were no longer observed in either of the reaches. This unimodal pattern of live salmon abundance through time was well described with quadratic equations that explained 89 and 83% of the variation in live salmon across sampling dates in the retention reach and reference reaches, respectively ($P < 0.001$). Before the start of the carcass-retention experiment (that is, the onset of carcass accumulation), the mean difference in the abundance of live salmon between the retention and reference reaches (mean difference = 132.6 individuals, SE = 73.0) was similar to that after the start of the carcass-retention experiment (mean difference = 32.4 individuals, SE = 58.3) (Figure 1B).

Salmon carcasses began to accumulate in the stream channel on August 20, a date that coincided with the decline in the abundance of live salmon, and delineated the periods ''before'' carcasses and ''after'' carcasses in our BACI experimental design. Carcass numbers then increased in both reaches, but at a greater rate in the retention reach (Figure 1C). Maximum values were observed on September 10, when 2782 and 485 carcasses were counted in the retention and reference reach, respectively. The number of carcasses declined after this date, and by early November, no carcasses were observed in either of the reaches. As with the number of live salmon surveyed, a unimodal pattern of carcass abundance through time was explained with quadratic equations that explained 86 and 62% of the variation in carcass abundance in the retention and reference reaches, respectively ($P < 0.036$). More carcasses were observed in the

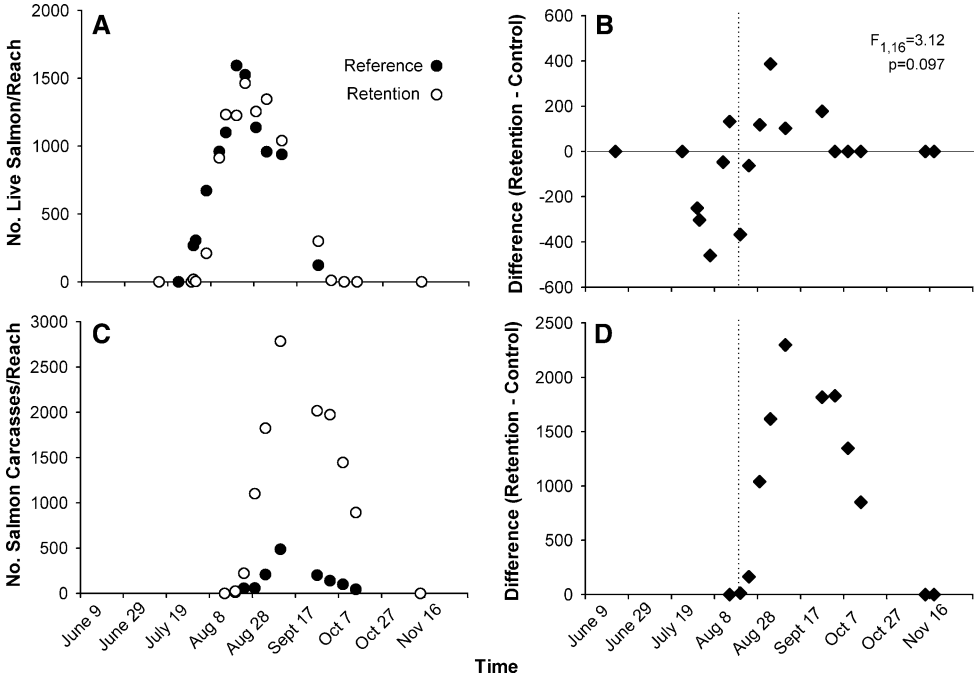


**Figure 1.** Abundance of live salmon (**A**) and salmon carcasses (**C**) in the upstream reference reach (*closed circles*), and the carcass-retention reach (*open circles*) through time. Differences in the abundance of live salmon between the two reaches (**B**) were similar before and after the onset of carcass accumulation in mid-August (*vertical dashed line* indicates onset of carcass accumulation). Differences in carcass abundance between the retention and reference reaches (**D**) were positive (that is, greater in the retention reach) on all the sampling dates.

carcass-retention reach relative to the reference reach on all sampling dates, with the carcass-retention reach having as many as 6X more salmon carcasses (Figure 1D), most of which were retained on carcass-retention devices. For example, on the September 10 sampling date, 74% of the carcasses in the retention reach were retained on carcass-retention devices.

## Discharge and Temperature Dynamics

At the start of our study in mid-June, mean daily streamwater temperature was 6.3°C and was influenced by snowmelt. Temperature then increased steadily until mid-August when it reached a maximum of 12.7°C (Figure 2A). Temperatures then tended to decline until reaching a minimum value of 3.7°C at the end of the study in mid-November. Mean daily discharge was variable among dates at the onset of the study, and decreased until a period of steady low flow from August 3 to August 23 (Figure 2B) that coincided with the time when live salmon (but few carcasses) were present in the stream channel. After this time, precipitation events became more frequent and discharge increased in both magnitude and variability until the end of the study period (Figure 2B).

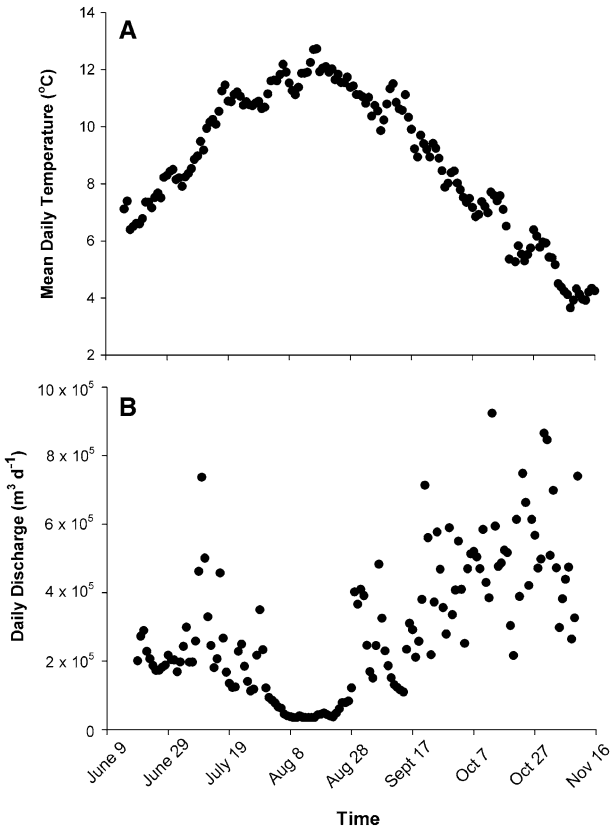


**Figure 2.** Mean daily temperature (**A**) and total daily discharge (**B**) of Maybeso Creek during the study period.

## Nutrient Dynamics

During the weeks before the salmon migration, concentrations of $NH_4^+$, $NO_3^-$, and SRP were at their lowest, were highly consistent among sampling dates, and were similar between the two reaches (Figure 3A–C). During the same period, concentrations of particulate C, N, and P were more variable among dates and between reaches (Figure 4A–C). Clear increases in dissolved and particulate nutrients coincided with the onset of salmon migration, and continued until the time when live-salmon abundance began to decline. The increase in $NH_4^+$ was more immediate relative to the other dissolved and particulate nutrients examined. Immediately after their peak, nutrient concentrations tended to be more variable among sampling dates and then steadily declined until early October when concentrations returned to approximately what they were before the salmon run, and were once again consistent among sampling dates and between reaches (Figures 3A–C, 4A–C).

## Nutrient Response to Carcass-Retention Experiment

Nutrient concentrations were similar between the two reaches before the presence of salmon carcasses; however, following the onset of carcass accumulation, dissolved nutrients tended to be slightly greater in the carcass-retention reach relative to the reference reach (Figure 3D–F). Differences in $NH_4^+$ between the carcass-retention and the reference reaches were minor before carcass accumulation (mean difference = 0.4 µg/L, SE = 1.5) and although concentrations tended to be slightly greater in the carcass-retention reach after carcass accumulation (mean difference = 4.2 µg/L, SE = 1.5), they were not statistically significant (Figure 3D). When the first two sampling dates after the onset of carcass accumulation were removed from analysis, dates on which few carcasses had accumulated in the stream, however, $NH_4^+$ concentrations were significantly greater in the carcass-retention reach. Before carcasses accumu-

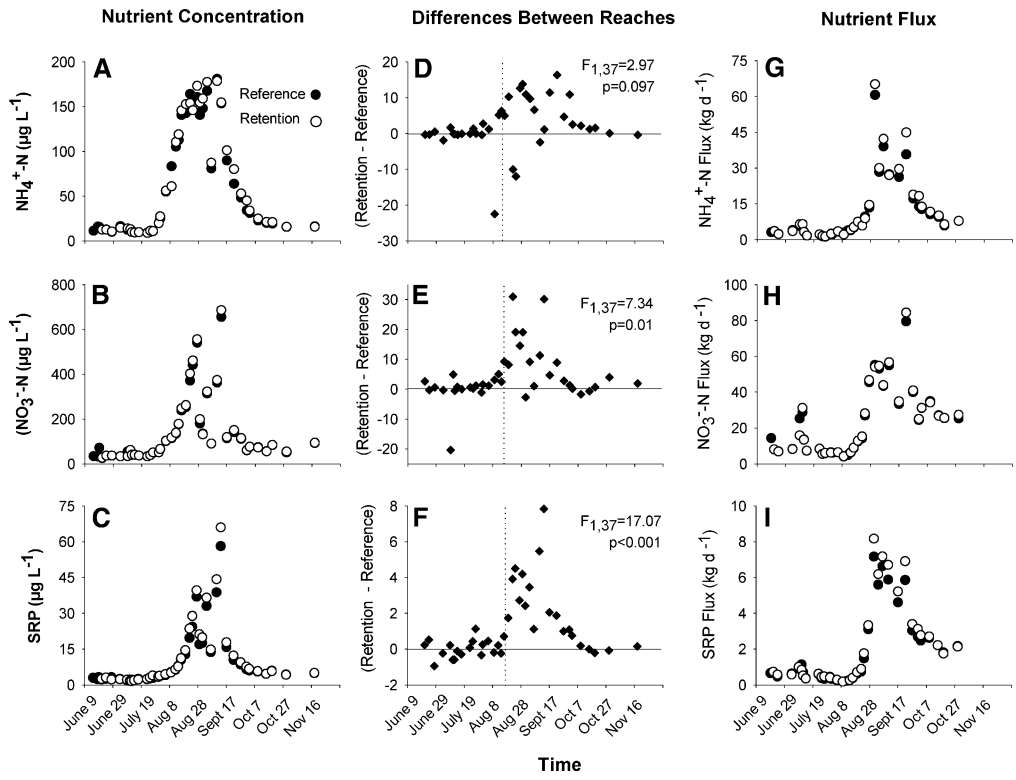


**Figure 3.** Concentrations of dissolved nutrients through time (**A–C**) in the reference (*closed circles*) and retention reaches (*open circles*). Differences in nutrient concentrations between the retention and the reference reaches before and after the onset of carcass accumulation (*vertical dashed line*) (**D–F**). *F*-ratios and *P*-values shown are for tests of mean differences between the dates before and dates after the onset of carcass accumulation. Flux of nutrients through time from each of the two reaches (**G–I**). Discharge did not differ between the two reaches, and differences between the two reaches are due to differences in nutrient concentration.

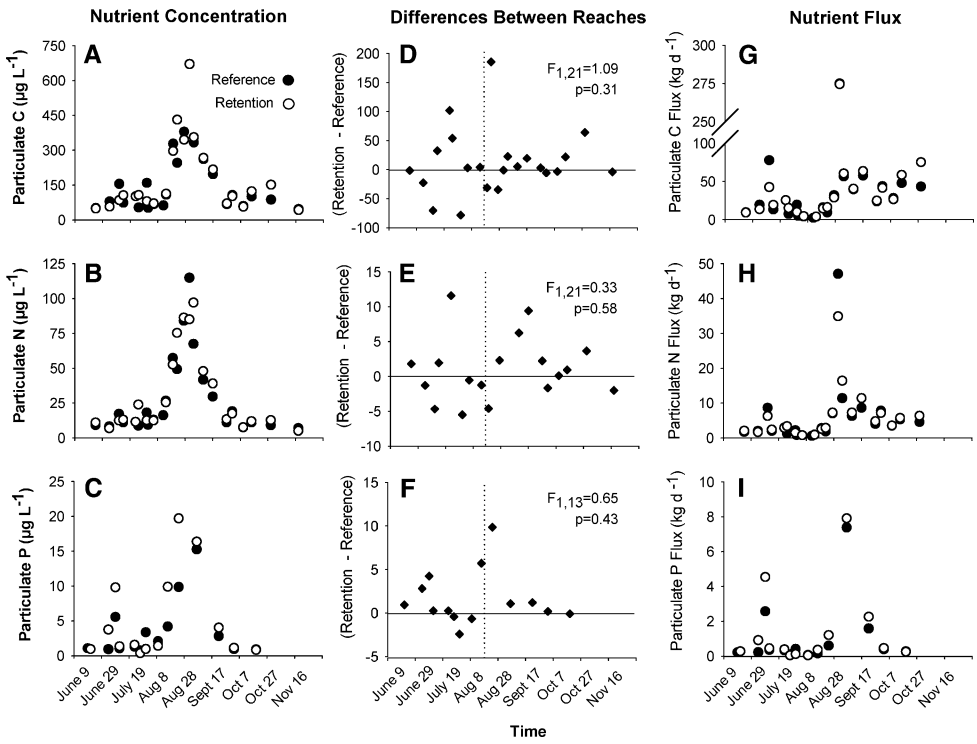


**Figure 4.** Concentrations of particulate nutrients through time (**A–C**) in the reference reach (*closed circles*) and retention reaches (*open circles*). Differences in nutrient concentrations between the retention reaches and the reference reaches before and after the onset of carcass accumulation (*vertical dashed line*) (**D–F**). *F*-ratios and *P*-values shown are for tests of mean differences between the dates before and dates after the onset of carcass accumulation. Flux of nutrients through time from each of the two reaches (**G–I**). Discharge did not differ between the two reaches, and differences between the two reaches are due to differences in nutrient concentration.

lated in the stream channel, differences in $NO_3^-$ were similar in the two reaches (mean difference = 1.0 µg/L, SE = 1.8), whereas $NO_3^-$ was slightly greater in the retention reach on dates after the accumulation of carcasses (mean difference = 8.1 µg/L, SE = 1.9) (Figure 3E). Similarly, differences in SRP between the two reaches were minor before carcass accumulation (mean difference = 0.1 µg/L, SE = 0.4), but increased slightly when carcasses were present (mean difference = 2.2 µg/L, SE = 0.4) (Figure 3F).

Before carcass accumulation, differences in concentrations of particulate C between the two reaches varied among dates, and the mean difference between reaches among dates before carcass accumulation was minor and not significant (mean difference = 0.8 µg/L, SE = 16.4) (Figure 4D). After the accumulation of carcasses, differences in particulate C between reaches tended to be less variable among dates, and greater in the carcass-retention reach on most sampling dates, although the overall difference between reaches was not significant (mean difference = 22.9 µg/L, SE = 15.7). Trends in particulate N were very similar to those of particulate C, and the mean difference in N concentration among the two reaches before the accumulation of carcasses (mean difference = 1.2 µg/L, SE = 3.5) was not significantly different from the mean difference after the accumulation of carcasses (mean difference = 3.9 µg/L, SE = 3.5) (Figure 4E). Similarly, no treatment effects were observed for particulate P, which had mean differences in concentration of 1.09 µg/L (SE = 0.9) before the accumulation of carcasses compared with 2.45 µg/L (SE = 1.4) after the accumulation of carcasses (Figure 4F).

## Nutrient-Flux Dynamics

Before the start of salmon migration, the daily flux of dissolved and particulate nutrients was low, and consistent among the sampling dates (Figures 3G–I, 4G–I). An exception to this general pattern occurred in early–mid-July when a minor and brief increase in flux corresponded to an episode of precipitation (Figure 2B). With the onset of the salmon migration, fluxes increased for all the dissolved and particulate nutrients examined, despite

low discharge (Figure 2B). Nutrient fluxes peaked at the end of August, near the date of maximum live-salmon abundance. Fluxes then decreased through September and stabilized at values that were greater than those observed before the start of the salmon run. The decrease through September was interrupted by a sharp increase in nutrient flux on September 22 that coincided with an episode of precipitation.

## Relationships Between Nutrient Concentrations, Live Salmon, and Senesced Carcasses

Concentrations of dissolved and particulate nutrients were all positively related to the abundance of live salmon (Figure 5A–F). The slopes of these relationships did not differ between reaches (ANCOVA, $P > 0.22$), except for $NH_4^+$, where the reference reach had a marginally greater slope than the retention reach (Figure 5A) (ANCOVA, $P = 0.049$).

Relationships between nutrient concentrations and the abundance of carcasses in the stream channel were less clear than the relationships observed with live salmon. Scatter plots of nutrient concentrations versus carcass abundance tended to illustrate hysteresis loops that reiterated the influence of live salmon on nutrient concentrations through time rather than indicate a relationship with carcasses (Figure 5G–L). This phenomenon is most clearly illustrated by concentrations of $NH_4^+$ in the carcass retention reach (Figure 5G), but is also apparent for relationships between carcasses and other nutrients. During the period when salmon carcasses were initially accumulating in the retention reach, live-salmon abundance and nutrient concentrations were at their maximum. Carcass abundance then increased with each consecutive sampling date, but without corresponding increases in $NH_4^+$. Concentrations decreased with each consecutive sampling date, corresponding to decreases in the number of live salmon, whereas carcass abundance remained relatively constant. By early October, few live salmon were present in the stream channel, and whereas carcass abundance declined steadily after this date, nutrient concentrations changed little.

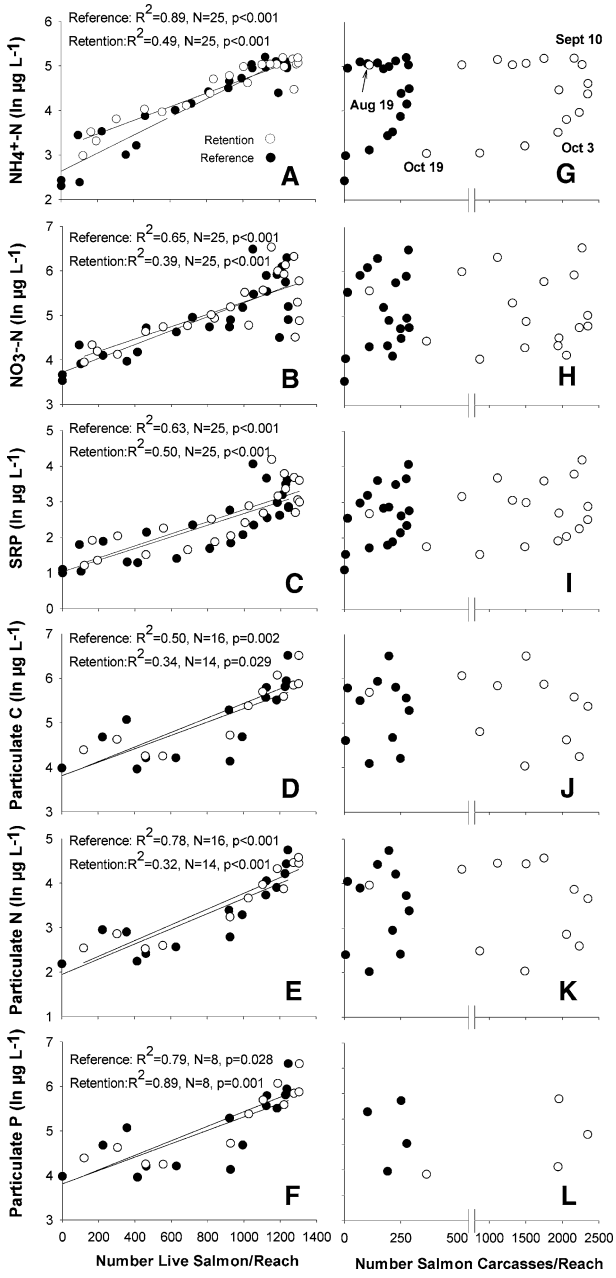


**Figure 5.** Relationships between live-salmon abundance and nutrient concentrations in the reference reach (*closed circles*), and the retention reach (*open circles*) (**A–F**), and nutrient concentrations and carcass abundance (**G–L**). Hysteresis loops were apparent in scatter plots of carcass abundance and nutrient concentrations that further implicate live salmon as sources of in-stream nutrients, a pattern that is most evident in the plot of $NH_4^+$ and carcasses (**G**).

## Nutrient Stoichiometry

Ratios of DIN:SRP and particulate C:N followed similar patterns through time. Before the salmon run, DIN:SRP ratios and particulate C:N varied sporadically among sampling dates (tending to fall between 30 and 60), and DIN:SRP ratios experienced a brief increase that corresponded to elevated $NO_3^-$ concentrations following a high-discharge event in early July. DIN:SRP and particulate C:N

increased after the arrival of salmon in late July (Appendix 1 in Supplementary material). DIN:SRP reached a maximum in mid-August, whereas maximum values of particulate C:N occurred approximately 2 weeks later. Both ratios declined steadily after their respective peaks, with the decline coinciding with that of live salmon abundance and increasing carcass abundance.

## Nutrient Limitation of Benthic Biofilms

Before the salmon run, autotrophs and heterotrophs of NDS were co-limited by N and P in both reaches, as evidenced by significant increases in chl*a* and respiration when N and P were amended together. Responses to treatments with N or P alone were of a relatively minor magnitude, but statistically significant (Appendices 2 and 3 in Supplementary material). During the salmon run when both live salmon and carcasses were present, autotrophs were no longer nutrient limited. Heterotrophs were weakly P-limited in the reference reach and weakly co-limited in the retention reach during and after the salmon run, suggesting that nutrient limitation was not alleviated for these members of the microbial community. Lack of nutrient limitation in the autrotrophs persisted in both reaches until after the salmon run. Overall, our experimental retention of carcasses had no influence of the nutrient limitation status of autotrophs and heterotrophs, and live salmon seemed to influence autotrophs more than heterotrophs.

## Biofilm Dynamics and Biofilm Response to Carcass Retention

Biofilm chl*a* and AFDM were both low during the weeks before the salmon run, very consistent among sampling dates, and nearly identical between reaches (Figure 6A–B). Biofilm biomass increased with the onset of the salmon run on the relatively large rocks that we sampled. Chlorophyll *a* and AFDM both reached a maximum on August 14, before declining to approximately pre-salmon run values by late September. Significant relationships were not observed between the abundance of live salmon and the two biofilm biomass metrics that we measured ($P > 0.29$), nor were relationships observed between biofilm metrics and carcass abundance ($P > 0.23$). Mean differences in biofilm biomass between the retention and reference reaches before the accumulation of carcasses were 10.8 mg/m$^2$ for chl*a* (SE = 6.9) and 99.8 mg/m$^2$ for AFDM (SE = 66.5) on the rocks that we sampled. The mean differences in the abundance of biofilm after the accumulation of carcasses was 0.5 mg/m$^2$ for chl*a* (SE = 5.9) and 667.2 mg/m$^2$ for AFDM (SE = 562.6). These values did not significantly differ between dates before and after the accumulation of salmon carcasses (Figure 6C–D).

# Discussion

The large amount of economic, cultural, and recreational interest in salmon has helped generate a

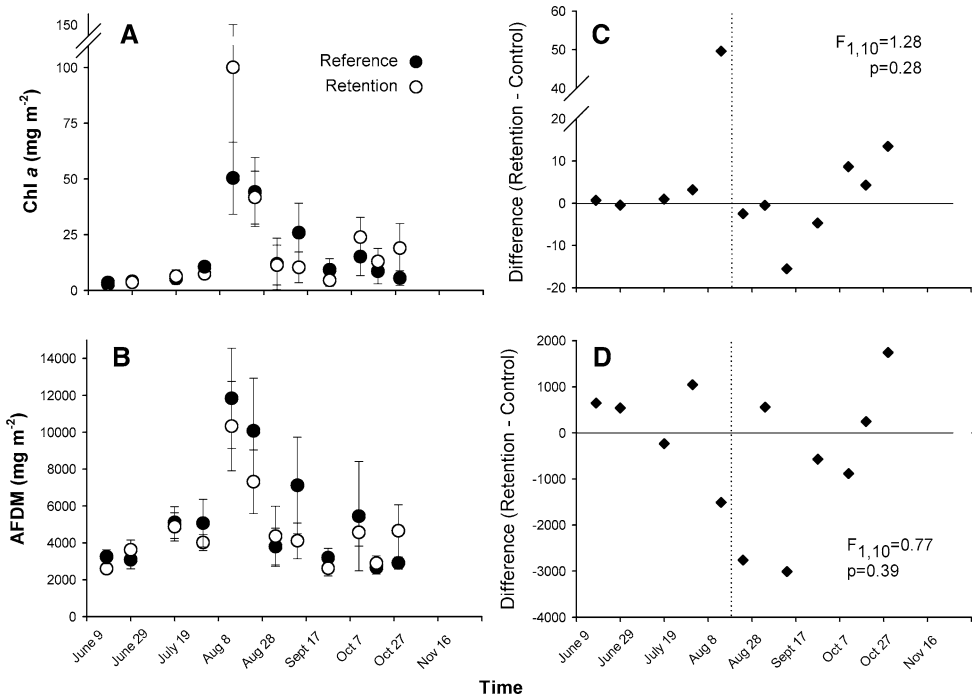


**Figure 6.** Mean abundance of benthic algae (chlorophyll *a* ± standard deviation) (**A**) and biofilm biomass [mean ash-free dry mass (AFDM) ± standard deviation] (**B**) in the upstream reference reach (*closed circles*), and the carcass-retention reach (*open circles*) through time. Differences in the abundance of benthic algae and biomass between the two reaches (**C**, **D**) were similar before and after the onset of carcass accumulation in mid-August (*vertical dashed line* indicates onset of carcass accumulation).

large body of scientific literature and makes salmon a potentially useful model for understanding the resource subsidies provided by fish migrations in general. Previous studies have tended to focus on semelparous salmon species and given particular attention to carcasses (reviewed by Janetski and others 2009). Studies focusing exclusively on the ecological effects of carcasses, however, are of potentially limited relevance for understanding nutrient delivery by other migratory fishes given that most species are iteroparous and experience less mortality during migrations than semelparous species. In this study, we found that concentrations of dissolved and particulate nutrients were positively related to live salmon abundance and that salmon carcasses had an undetectable or weak influence on these stream attributes. Our results were likely influenced by seasonal changes in stream discharge and temperature that promoted the ecological effects of live salmon and inhibited those of salmon carcasses. These findings contrast with those of previous salmon-carcass-addition experiments that showed strong positive responses to carcass treatments (for example, Chaloner and Wipfli 2002; Wipfli and others 2003; Peterson and Matthews 2009), and challenge the assertion that for semelparous species, the nutrients provided by carcasses and gametes are of greater ecological importance than nutrients excreted by live fish (Naiman and others 2002). In this light, salmon may be a suitable model for understanding nutrient secretion by other iteroparous migratory fish species.

## Influence of Experimental Artifacts

Artifacts associated with carcass-addition experiments may have resulted in overestimates of the effects carcasses have on nutrient concentrations and biofilm biomass in streams, and fostered the perception that nutrients provided by live salmon are necessarily of secondary ecological influence. Among experiments, variation in the strength of responses to carcass additions has been explained by the quantity of carcass material added (Janetski and others 2009), which commonly exceeds that observed in nature. For example, 20-fold increases in $NH_4^+$ concentration were observed in a mesocosm experiment in which fresh carcasses were applied at a density of 13.6 kg wet mass/$m^2$ (Mitchell and Lamberti 2005). In comparison, the maximum carcass density during our experiment was 1.5 kg wet mass/$m^2$ (maximum density of 1.22 carcasses/$m^2$) with an estimated mean initial individual carcass mass of 1.23 kg. The carcass density in our field experiment is appreciably less than that applied in many carcass-addition experiments (see Appendix 1 in Janetski and others 2009), but is greater than that typically observed in other streams in the region. For example, a field survey of Indian Creek on Prince of Wales Island revealed a maximum carcass density of 0.93 kg wet mass/$m^2$ (Tiegs unpublished data). Indian Creek is similar to Maybeso Creek in many ways (for example, drainage area, and valley slope), except that its watershed experienced relatively little timber harvest and the stream channel had abundant structures that effectively retain carcasses (Cederholm and Peterson 1985). Even in this highly retentive stream with large runs of pink salmon, carcass densities were less than those of previous carcass-addition experiments. Localized accumulations of carcasses are commonly observed in the field, often at very high density (for example, hundreds of carcasses may be retained within a debris jam), but at the reach scale, densities of carcasses tend to be much less.

In addition to quantity, the quality of the carcasses retained in our experiment differs from that of the fresh carcasses that have been used in previous experiments and may have resulted in overestimations of the effects carcasses have on streamwater-nutrient concentrations and biofilm biomass. Previous experimenters have used fresh-carcass density as a proxy for the quantity of salmon-derived nutrients that they were applying. The naturally senesced carcasses used in our experiment, however, had less C, N, and P on a per-carcass basis, differed in the relative abundance of these nutrients, and were colonized by microbes. These factors may have been responsible for the negligible or undetectable effect carcasses had on streamwater-nutrient concentrations. When corrected for losses that are known to occur during senescence (see Gende and others 2004), naturally senesced carcasses contain only 44% of the N found in the fresh carcass material that was used in most carcass-addition experiments (corresponding to a carcass density of 0.94 kg wet mass/$m^2$ in terms of N content), and only 75% of the P. These data suggest that not only is the total quantity of nutrients in naturally senesced carcasses appreciably less than that of fresh carcasses, but that the process of senescence influences the stoichiometry of the nutrients found in senesced carcasses by retaining disproportionately greater amounts of P.

A poorly understood but potentially important aspect of salmon-carcass ecology relates to the fact that senescing salmon are normally well colonized by aquatic fungi of the genus *Saprolegnia* by the time

they are fully senesced. The extent to which *Saprolegnia* immobilizes nutrients that would otherwise leach from carcasses or facilitates nutrient release is not understood. The differences in quality between senesced and fresh carcasses are apparently relevant to stream insects, however, that have been observed to feed preferentially on fresh carcasses (Winder and others 2005), suggesting that the process of senescence may influence the entry of salmon-derived nutrients into stream food webs. Overall, differences in nutrient quantity, stoichiometry, and colonization by *Saprolegnia* are distinctions between our experiment and other studies that used carcasses of fish that did not senesce.

## Effects of Seasonal Variation in the Abiotic Environment

The duration of fish migrations is often sufficient to encompass significant seasonal variation in abiotic conditions and this variation may influence the effects of nutrient provisions. Changes in discharge and temperature commonly function as migratory cues for fishes (Lytle and Poff 2004), further suggesting that such changes commonly coincide with migrations and regulate the effects that fish have on ecosystems. This regulation would seem to be particularly important at higher latitudes where seasonality tends to be pronounced and anadromy is most common.

During our 2007 study, low discharge and high water temperatures predominated early in the salmon run (July–August), whereas high discharge and lower water temperatures typified conditions later in the run (September–October). These patterns are consistent with longer-term data in the region (for example, see USGS, Staney Creek, gauge #15081497). Such seasonality in temperature and discharge should promote the uptake of nutrients in the late summer and diminish the effects of nutrients in the autumn, regardless of whether the nutrients originate from live salmon or carcasses. Similar changes to the abiotic environment likely accompany the migrations of other species of anadromous fishes (for example, spring alewife migrations) with as-of-yet unexplored consequences for recipient ecosystems.

Nutrient-excretion rates of fish increase with temperature, and like microbial-biofilm growth, tend to follow $Q_{10}$ rules (Schindler and Eby 1997; Vanni 2002). In our study, per-capita excretion rates by live salmon can be expected to have been reduced late in the run when temperatures were lower. In addition, the decreasingly hyperosmotic condition of migrating and spawning salmon that occur as they lose nutrients and energy stores and replace them with fresh water (Quinn 2005) may result in lower nutrient-excretion rates later in the run. The greater concentrations of mineral dissolved nutrients that accompany live salmon (versus the nutrients bound in carcasses) should promote biofilm growth in nutrient-limited systems such as Maybeso Creek, as should the higher water temperatures that are typical early in the run.

## Nutrient Dynamics

The increases in dissolved and particulate nutrients that we observed in association with live salmon can be traced to different origins. The increases in $NH_4^+$ and SRP concentrations can be directly attributed to salmon excretion, or in the case of $NO_3^-$, excretion of $NH_4^+$ followed by nitrification (Levi and others unpublished data). Increases in concentrations of particulate nutrients observed in our study can be best explained by benthic biofilm and associated particulates that become dislodged and entrained during salmon migration and nest construction. Increases in particulate nutrients with the onset of the salmon run have been reported previously (for example, Moore and others 2007; Levi and others unpublished data), as have reductions in the abundance of benthic biofilm caused by salmon migration and nest construction in Maybeso Creek (Tiegs and others 2009). A period of time on the order of many days to weeks usually separates the time when salmon enter freshwater and when they begin redd construction. This lag period may explain why dissolved nutrient concentrations increased earlier in the salmon run than did concentrations of particulates.

We are unaware of previously reported N:P ratios for the excreta of migrating salmon, but because pink salmon do not feed or feed only minimally while migrating, this value can be estimated with a mass-balance approach using published values of the N and P content of fresh and senesced salmon, and correcting for the N and P released as gametes in the stream during spawning. Based on Gende and others (2004), this approach indicates that from the time a typical male pink salmon begins upstream migration to the time of senescent death it excretes 13.6 g of N and 1.5 g of P. These salmon excreta have an N:P ratio of 9.1 (11.9 for females), which is within the range of excreta N:P reported for other fish species (for example, Schindler and Eby 1997; McIntyre and others 2007) and is comparable to that reported for anadromous alewives during their spawning migration (N:P of 12:1, Post and Walters

2009). Despite the seemingly P-rich excreta provided by migrating salmon, DIN:SRP ratios increased with the onset of the salmon run (Appendix 1 in Supplementary material), with perhaps the most parsimonious explanation for this discrepancy being greater uptake and sorption by the stream channel of dissolved P relative to N. This idea is supported by our observation of P-limitation in heterotrophs during the salmon run when N-limitation was not observed. The discrepancy between the increases in DIN:SRP ratio of streamwater that accompanied the salmon run and the relatively low DIN:SRP ratio of salmon excreta suggests that streams exert influence on salmon-derived nutrients with as-of-yet unknown consequences for downstream ecosystems.

Long spiraling lengths in Maybeso Creek may have contributed to the low nutrient retention within the carcass-retention reach. Water chemistry and NDS results during the salmon run suggest nutrient saturation, and reduced biofilm biomass stemming from salmon disturbance and high discharge should also limit uptake. Taken together, these results suggest that when both live salmon and carcasses were present in the stream, conditions promoted long spiraling lengths and low uptake of nutrients from experimentally retained carcasses.

## Factors that Influence Salmon Effects and Extrapolating to Other Systems

A key limitation of results generated by unreplicated field experiments such as the one presented here is that they cannot be extrapolated to other systems with measurable confidence. Maybeso Creek is similar to many streams in Southeast Alaska, however, in that its watershed has a history of timber harvest, and the attributes of this stream and watershed (for example, timber harvest intensity, large wood abundance, channel complexity, sediment size) are within the range of other streams sampled in the region (Tiegs and others 2008a), suggesting that our results are relevant to other systems. For example, the timing of pink salmon runs in Maybeso Creek relative to seasonal variation in streamwater temperatures and discharge is similar to that of other species in other regions, such as the sockeye salmon rivers of British Columbia, Canada. These sockeye salmon runs start in early summer when temperatures are at their maximum and discharge is at its minimum, with carcasses appearing and accumulating in the autumn when cooler conditions and higher discharges predominate (Verspoor and others 2010).

The method we used to sample benthic biofilm required us to sample rocks that were larger than the average rock found on the streambed of Maybeso Creek. Previous studies (Tiegs and others 2008a; Janetski and others 2009; Holtgrieve and others 2010) have shown that substrate size can influence the degree of disturbance that salmon impart on biofilm biomass during their migration and nest construction. Although our biofilm results from early-on in the salmon run suggest a positive effect of salmon on the benthic community, this effect may be an artifact of the larger-than-average rocks that we sampled; the net salmon effect on the Maybeso Creek benthos may have been negative.

Our results point to several variables that are relevant for understanding the effects of nutrient subsidies provided by migrations of other fish species. In our nutrient-limited stream, increases in nutrients from live salmon were associated with increased biofilm biomass on the relatively large rocks that we sampled from Maybeso Creek. Rates of nutrient excretion should thus be important for the effects that live salmon and other fishes have on stream habitats, especially those that are not disturbed by nest construction (for example, larger rocks, backwater pools, channel margins) and are most likely to be positively influenced by salmon runs. Although we are not aware of any published nutrient-excretion rates for live salmon, values can be estimated from differences in the nutrient contents of fish as they enter freshwater and of their carcasses immediately after they die, after correcting for nutrient losses that occur as gamete release. Assuming a residence time in the stream of 3 weeks (Quinn 2005), and using the nutrient content of salmon and carcasses presented in Gende and others (2004), male pink salmon excrete N at a rate of 16.87 μg/g fish wet mass/h and P at a rate of 1.86 μg/g fish wet mass/h. These rates are very similar to the only published values of excretion rates of anadromous fishes (alewife) of which we are aware (approximately 15.0 and 2.0 μg/g fish wet mass/h for N and P respectively; Figure 2 in Post and Walters 2009) and are within the range of values presented for freshwater fishes (Schindler and Eby 1997). When combined with fundamental data about the ecosystem of interest (for example, stream discharge, lake volume, nutrient status), data related to salmon abundance and nutrient excretion rates begin to provide a level of prediction of how ecosystem attributes, such as nutrient limitation, cycling rates, and primary productivity, will respond to fish migrations.

Although we observed a negligible overall effect of carcasses on streamwater nutrients and benthic

biofilm, other carcass-related mechanisms of nutrient delivery that we did not explicitly consider may exert their respective effects. For example, carcasses deposited on riparian soils during high discharge can provide nutrients to streams following the completion of the salmon run (Fellman and others 2008), and may have carry-over effects into subsequent summers (Verspoor and others 2010). Salmon nutrients, in the form of carcasses and dissolved nutrients, can also spiral into the estuaries of salmon streams and enrich those ecosystems (Cak and others 2008). Finally, numerous terrestrial and aquatic vertebrate and invertebrate species feed on carcasses, which can constitute a large fraction of their caloric intake (Cederholm and others 1999; Adams and others 2010). For these and other aspects of freshwater and terrestrial ecosystems, the nutrients provisioned in the form of carcasses are of ecological significance.

### Relevance for River Restoration

Salmon carcasses are added to freshwaters as a means of fertilizing systems with anthropogenically reduced salmon populations (Compton and others 2006). These carcasses are typically in the form used in previous carcass-addition experiments (that is, fresh) and in many instances have been shown to have positive bottom-up effects (for example, Stockner 2003; Compton and others 2006). Another common restoration measure is the reintroduction of large wood into streams that have suffered from adverse effects associated with timber harvest. Large wood in streams has diverse functions including the retention of organic matter such as salmon carcasses, and therefore has the potential to function like carcass additions. Results from our experiment indicate that the retention of naturally senesced carcasses may not have a strong effect on streamwater chemistry and biofilm biomass. However, restorative wood additions can be performed at scales much larger than our 110 m-long manipulation, and therefore have the potential to impact the stream ecosystem attributes that we examined. In such instances, monitoring activities that accompany large-wood additions (or other restoration activities) will be needed if their effects on salmon carcasses and stream ecosystems in general are to be fully understood (Woolsey and others 2007).

## Conclusions

We conclude that the influence of salmon carcasses can play a secondary role to that of live salmon. In our system, the timing of nutrient excretion by live salmon coincides with conditions in the stream (that is, low discharge, elevated water temperature, high light, and so on) that should promote nutrient enrichment of streamwater and biofilm. Conversely, the release of nutrients from carcasses coincides with stream conditions (that is, increasing discharge, declining temperature and light) that do not promote such effects. Given that most migratory fishes do not die after spawning, these results highlight nutrient excretion by live fish as a potentially dominant means of N and P delivery by migratory fishes in general.

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