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Retention of salmon-derived N and P by bryophytes and microbiota in mesocosm streams

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Abstract. Annual migrations of anadromous salmon are an important source of nutrients for many coastal streams. Much of the current research on salmon-derived nutrients has focused on nutrient retention via carcass consumption by mammals, birds, and macroinvertebrates, whereas retention and transfer of nutrients by microbiota has received less attention. Our research objective was to investigate nutrient movement from decomposing salmon tissue into periphyton, bryophytes, leaf-pack microbiota, and amphipods in laboratory mesocosm streams. We measured $\delta^{15}N$ of microbiota growing on unglazed tiles (periphyton), microbiota growing on leaf packs, bryophytes on partially submerged stones, and amphipods; C:N and C:P ratios of microbiota and bryophytes; and periphyton biomass (ash-free dry mass and chlorophyll *a*) in channels with and without decomposing salmon tissue. Periphyton, bryophytes, and leaf-pack microbiota had lower C:N ratios and leaf-pack microbiota had lower C:P ratios in salmon channels than in reference channels. These results indicate increased nutrient quality in salmon channels. Periphyton ash-free dry mass and chlorophyll *a* were greater in salmon channels than in reference channels. $\delta^{15}N$ values for periphyton, leaf-pack microbiota, and bryophytes were more enriched in salmon channels than in reference channels, a result that demonstrates that salmon-derived nutrients can be retained in streams through multiple mechanisms. Transfer of salmon-derived nutrients through leaf-pack microbiota to a higher trophic level was evidenced by higher $\delta^{15}N$ in amphipods from salmon channels than from reference channels. Last, higher P concentrations (as much as 90% higher) in biota from salmon channels than from reference channels indicate uptake of salmon-derived P in salmon channels. These results suggest that periphyton, leaf-pack microbiota, and bryophytes might play a critical role in capturing salmon-derived nutrients.

Key words: salmon-derived nutrients, artificial streams, bryophytes, periphyton, microbiota, $\delta^{15}N$, C:N ratios, C:P ratios.

Anadromous Pacific salmon (*Oncorhynchus* spp.) move nutrients from the northern Pacific Ocean to Pacific Rim coastal streams. Pacific salmon accumulate 99% of their biomass in the nutrient-rich marine environment and carry these marine nutrients as they migrate to relatively nutrient-poor freshwater streams to spawn and die (Naiman et al. 2002). Their carcasses provide the stream ecosystem with a subsidy of salmon-derived nutrients. Retention of these nutrients by stream and riparian communities might be important for sustaining stream processes, and declines in Pacific salmon runs might have ecosystem-wide effects on salmon-bearing streams (Larkin and Slaney 1997). Therefore, federal and state agencies are using nutrient enhancement and additions of salmon carcasses to increase the nutrient capital in some Pacific Northwest streams. The goal of this enrichment is to increase survivorship of juvenile salmon through bottom-up effects (Lackey 2003).

Two nutrient-retention processes link salmon carcasses to stream communities. Salmon-derived nutrients are transferred directly into the stream community when macroinvertebrates feed on salmon carcass tissue (Chaloner and Wipfli 2002, Chaloner et al. 2002). Salmon-derived nutrients move through indirect pathways when they enter stream water during decomposition and are captured by downstream periphyton (e.g., Wipfli et al. 1999, Chaloner et al. 2002, Mitchell and Lamberti 2005). However, evidence detailing mechanisms by which salmon-

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derived nutrients are captured from water and transferred to food webs is lacking.

Most studies targeting mechanisms for direct and indirect uptake of salmon-derived nutrients have relied heavily on $\delta^{15}N$ measurements because salmon nutrients can be traced through their isotopic signature (e.g., Mathieson et al. 1988, Kline et al. 1990, Chaloner et al. 2002). Fewer studies have investigated retention of salmon-derived P, possibly because of the lack of a natural P isotope tracer and the assumption that N isotopes are effective tracers for both salmon-derived N and P. The assumption is that the ratio of N, C, and P remains consistent as nutrients move directly from salmon to stream organisms via consumption (Gende et al. 2002). However, when nutrients from a decomposing carcass become mineralized, N and P might have different fates because N, P, and C released into the water are chemically decoupled and undergo different cycles within the stream (Gende et al. 2002). Organisms might incorporate more N or P relative to C, depending on nutrient limitation in a particular stream. Therefore, the effect of N and P must be studied separately in investigations of indirect uptake mechanisms of salmon-derived nutrients.

Salmon carcasses might affect the stream food web through bottom-up effects. Many studies have focused on responses of downstream periphyton biomass to salmon-derived nutrients (Ambrose et al. 2004, Claeson et al. 2006, Kiffney 2008). In nutrient-limited microbial communities, introduction of salmon nutrients via indirect pathways might increase microbial biomass and, therefore, food availability for higher trophic levels. However, nutrient limitation affects both biomass and *quality* of food available to higher trophic levels (Elser et al. 2001). Increasing nutrient availability can reduce microbial C:N and C:P and provide more nutritious food for consumers. Increased quality of food sources might link salmon carcasses to higher trophic levels regardless of changes in the biomass of lower trophic levels. Here, we refer to stream biota with lower C:N or C:P as more nutrient-rich and of higher quality.

Responses of periphyton on rocks to salmon-derived nutrients has received much attention (e.g., Wipfli et al. 1999, Chaloner et al. 2002). Grazers use periphyton on rocks as a food source in streams, but other invertebrates, such as amphipods, consume microbiota on leaf litter, a process that has received less attention. Microbiota on leaf litter can affect P spiraling length by capturing and using dissolved P (Newbold et al. 1981, Mulholland et al. 1985). In a forested stream, P spiraling length was shortest after autumn leaf fall, when the mass of coarse particulate organic matter was highest, and longest immediately before leaf fall (Mulholland et al. 1985). Thus, the presence of leaves as a substrate for microbiota might increase the ability of a stream to retain salmon-derived nutrients and, thus, increase the community-wide effects of the nutrients.

Responses of lotic bryophytes to salmon-derived nutrients also have received little attention. In-stream bryophytes use dissolved nutrients and can be limited by P availability (Steinman and Boston 1993, Stream Bryophyte Group 1999); thus, bryophytes might retain dissolved salmon-derived nutrients. Bryophytes provide important habitat for invertebrates, particularly larval stages of macroinvertebrates, and are a food source for some macroinvertebrates, including *Zapada* (Plecoptera) and Tardigrada (Stream Bryophyte Group 1999). Thus, the response of the bryophyte community to salmon carcasses could link salmon nutrients to stream consumers, even if the bryophytes are not directly consumed.

The breadth of salmon-derived nutrient impacts in stream and riparian communities can be significant; however, the indirect mechanisms by which salmon nutrients move in streams are not well understood. We designed stream mesocosm experiments to investigate the incorporation of salmon-derived N and P into the food web via microbiota and bryophytes. Our objectives were to: 1) compare water quality in streams with and without decomposing salmon tissue; 2) determine whether downstream periphyton, leaf-pack microbiota, and bryophytes could capture salmon-derived N and P; 3) determine whether incorporation of salmon-derived nutrients led to differences in periphyton biomass; 4) compare C:N and C:P ratios of organisms as indicators of nutrient richness; and 5) determine whether salmon-derived nutrients captured by microbial communities were transferred to macroinvertebrates.

Methods

Laboratory streams and experiment setup

We did our experiment in 12 laboratory mesocosm streams at the Western Washington University Hannegan Road research facility (Bellingham, Washington, USA). Streams were straight, 1-way, wooden channels (0.2 m × 1.2 m) sealed with epoxy paint and aquarium-grade sealant. Channels were supplied with dechlorinated, low-alkalinity, low-nutrient municipal tap water. Light was provided by overhanging full-spectrum fluorescent lights (15:9 h light:dark).

We used clay tiles, cobbles with bryophytes, and leaf packs as substrata. We soaked porous clay tiles (5 cm × 5 cm) in a local stream for 3 d and then placed them in the channels to provide the microbial inoculums and

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to add surface roughness in the channels. We collected bryophyte-covered stream cobbles (10–15 cm in longest axis) and placed them in the channels. We collected cobbles and soaked tiles in a stream reach that was above structures that we assumed were barriers to anadromous salmonids. Thus, we assumed that bryophytes and microbiota were free of salmon-derived nutrients at the start of the experiment. We collected senescing bigleaf maple (*Acer macrophyllum*) leaves from a single tree in Sehome Hill Arboretum (Bellingham, Washington) that was not adjacent to any stream, and that we assumed was not influenced by salmon-derived nutrients. We shook tree branches gently to dislodge leaves, which we collected on a large tarp and dried at room temperature for 5 d.

We placed substrata in the streams 3 to 4 d before adding salmon carcasses. We placed 2 bryophyte-covered rocks on opposite sides of each channel and arranged 28 presoaked tiles in rows of 2, beginning 2 cm downstream from the net fence and extending to the end of the channel. We added 1 leaf pack (38.0–41.0 g) at the middle of each stream channel.

We added salmon tissue (2.1 kg/m^2) to the upstream end of 6 randomly assigned channels; the remaining 6 channels served as references (0 kg/m^2). Salmon concentration was comparable with lower end salmon concentrations used in previous mesocosm studies (Wipfli et al. 1999, Chaloner et al. 2002, Mitchell and Lamberti 2005). We used thawed salmon muscle tissue cut from adult Chinook carcasses obtained from a local fish hatchery (Samish River, Washington) because hatcheries are the main source of salmon carcasses for carcass enhancement management practices. We placed a 500-μm-mesh Nitex fence immediately downstream of the salmon tissue to prevent large pieces of salmon from moving downstream and to prevent amphipods from consuming salmon tissue. After 7 wk, we added 20 amphipods (*Gammarus* spp.; Carolina Biological Supply, Burlington, North Carolina).

Response variables

We measured all response variables in each channel before adding salmon and after decomposition of salmon tissue was complete (84 d). We collected water from the outlet of each channel to measure total P, soluble reactive P (SRP), NO_3^- (= NO_2^- + NO_3^-), NH_4^+, and total N concentrations (APHA 2005).

We sampled periphyton growing on the sides and bottom of each channel with a spatula and volumetric pipette and homogenized it in a blender. We partitioned aliquots of the blended material with a volumetric pipette. We filtered each aliquot through Whatman 25-mm glass-fiber filters (GF/F; 0.7-μm pore; Whatman Inc., Florham Park, New Jersey). We dried the filters for analysis of N isotopes; C, N, and P concentrations; and ash-free dry mass.

We clipped bryophyte leaflets growing at water level to avoid portions of bryophytes that were dry and portions that were deeply submerged and might have been inhabited by periphyton. We dried the leaflets and analyzed N isotopes and C, N, and P concentrations.

We used a cork borer to collect 10 circular, 1-cm-diameter leaf samples from 6 randomly selected leaves in each leaf pack. We dried leaf samples at 60°C for 24 h and stored them in a desiccator. We used scissors to shred dried subsamples of leaf packs into small, uniform fragments and analyzed the subsamples for N isotopes and C, N, and P concentrations.

We collected amphipods at the end of the experiment, and froze and then dried them for analysis. We analyzed only C:N and $\delta^{15}N$ of amphipods because of biomass limitations.

N isotope analysis and C:N ratios

We measured naturally occurring N isotopes with an elemental analyzer coupled with an isotopic ratio mass spectrometer (EA-IRMS; Thermo Fisher Scientific, Walthow, Massachusetts) at the University of Washington, School of Oceanography Isotope Laboratory (Seattle, Washington, USA) to determine $\delta^{15}N$ values and C:N ratios for biotic samples from each stream channel. The isotope laboratory used a nicotinic working standard (58.5% C, 11.4% N), which has a known $\delta^{15}N$ relative to a recognized standard (atmospheric N_2). $\delta^{15}N$ values are expressed as the per mil (1/1000) deviation relative to the isotopic standard. Therefore, negative values are not uncommon, particularly in non-marine-influenced terrestrial and freshwater ecosystems (Lajtha and Michener 1994).

P concentrations and C:P ratios

We analyzed total P concentrations of leaf-pack subsamples and periphyton on filters with persulfate digestion followed by the ascorbic acid method (APHA 2005) as described by Elser et al. (2001). We soaked bryophyte clippings and salmon tissue in 1 mL hot 1N HCl for 30 min and diluted the mixture with 100 mL of deionized water before persulfate digestion and analysis of total P (method modified from Mulholland and Rosemond 1992, Stelzer and Lamberti 2001, 2002). We calculated P content as μg P/mg dry mass.

We determined chlorophyll *a* concentration of the periphyton with the direct extraction method (APHA

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TABLE 1. Median final water-column values for total P (TP), total N (TN), NH_4^+ NO_3^-, soluble reactive P (SRP), periphyton chlorophyll *a* (Chl *a*), and periphyton ash-free dry mass (AFDM) for salmon and reference channels. Kruskal–Wallis test statistics (χ^2) and *p* values are included for each response variable. Values below the detection limit are indicated as < value of the detection limit.

Response variable	Treatment	Median	χ^2	*p*
TP (μg P/L)	Salmon	6.3	3.692	0.055
	Reference	<3.9		
TN (μg N/L)	Salmon	563.5	8.308	0.004
	Reference	443.6		
NH_4^+ (μg N/L)	Salmon	51.7	8.308	0.004
	Reference	<5.4		
NO_3^- (μg N/L)	Salmon	385.2	0.410	0.522
	Reference	387.8		
SRP (μg P/L)	Salmon	4.3	5.026	0.025
	Reference	2.5		
Chl *a* ($\mu g/m^2$)	Salmon	1299.0	8.308	0.004
	Reference	4.7		
Periphyton AFDM ($\mu g/m^2$)	Salmon	1.5	8.308	0.004
	Reference	0.2		

2005). We measured periphyton and leaf-pack ash-free dry mass by combusting samples at 550°C for 1 h to remove organic material and subtracting postcombustion mass from precombustion dry mass (APHA 2005).

Statistical analyses

Most response variables did not meet assumptions of normality and homogeneous variances for parametric statistics; therefore, we tested for differences in response variables between treatments with nonparametric statistical tests. We used Kruskal–Wallis tests by ranks to identify significant differences between treatment medians and Kendall's τ to test for correlations among variables (Kendall 1938, as described by Zar 1999; Kruskal and Wallis 1952, as described by Zar 1999). The purpose of the correlation analysis was to provide evidence that the salmon introduction rather than environmental factors were responsible for the results of the exp eriments. With the exceptions of leaf-pack $\delta^{15}N$, leaf-pack C:N, and amphipod C:N, sample size for all tests was 6 samples/treatment. We collected duplicates for ≥10% of all experimental samples and ran the duplicates separately as quality-control samples.

Results

Water quality

Discharge rates in the channels ranged from 0.01 to 0.03 L/s and did not differ significantly between treatments (Kruskal–Wallis, $\chi^2 = 0.412$, $p = 0.521$). None of the response variables were significantly correlated with stream discharge (Kendall's τ, $p > 0.05$). Final stream water concentrations of SRP, total N, and NH_4^+ were significantly higher in salmon than in reference channels; median NH_4^+ was 10× higher in salmon than in reference channels (Table 1). NO_3^- (Kruskal–Wallis, $\chi^2 = 0.410$, $p = 0.522$) and total P (Kruskal–Wallis, $\chi^2 = 3.692$, $p = 0.055$) did not differ significantly between salmon and reference channels (Table 1).

Biological responses

$\delta^{15}N$ values of periphyton (Kruskal–Wallis, $\chi^2 = 8.308$, $p = 0.004$), bryophytes (Kruskal–Wallis, $\chi^2 = 7.410$, $p = 0.006$), leaf packs (Kruskal–Wallis, $\chi^2 = 7.500$, $p = 0.006$), and amphipods (Kruskal–Wallis, $\chi^2 = 7.500$, $p = 0.006$) were higher in salmon channels than in reference channels (Fig. 1). P content of periphyton (Kruskal–Wallis, $\chi^2 = 4.333$, $p = 0.037$), bryophytes (Kruskal–Wallis, $\chi^2 = 4.333$, $p = 0.037$), and leaf packs (Kruskal–Wallis, $\chi^2 = 4.333$, $p = 0.037$) were ≥40% greater in salmon channels than in reference channels (Fig. 2).

Median C:N of periphyton (Kruskal–Wallis, $\chi^2 = 8.308$, $p = 0.004$), bryophytes (Kruskal–Wallis, $\chi^2 = 5.026$, $p = 0.025$), and leaf packs (Kruskal–Wallis, $\chi^2 = 6.000$, $p = 0.014$) were ≥20% lower in salmon channels than in reference channels (Fig. 3). C:N of amphipods did not differ significantly between salmon and reference channels (Kruskal–Wallis, $\chi^2 = 2.133$, $p = 0.144$). C:P of leaf packs was significantly lower in salmon than in reference channels (Kruskal–Wallis, $\chi^2 = 4.860$, $p = 0.027$), but C:P of bryophytes (Kruskal–Wallis, $\chi^2 = 3.692$, $p = 0.055$) and periphyton (Kruskal–

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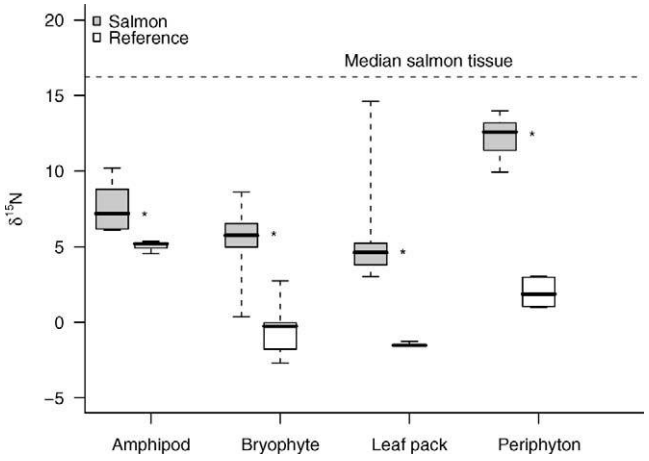

FIG. 1. Box-and-whisker plot for final $\delta^{15}N$ values for periphyton, bryophyte, leaf packs, and amphipods from salmon and reference channels ($n = 6$ for periphyton, bryophytes, and amphipods; $n = 5$ for leaf packs). Boxes show quartiles, heavy lines show medians, dashed lines show ranges. Asterisk indicates statistically significant differences ($p < 0.05$).

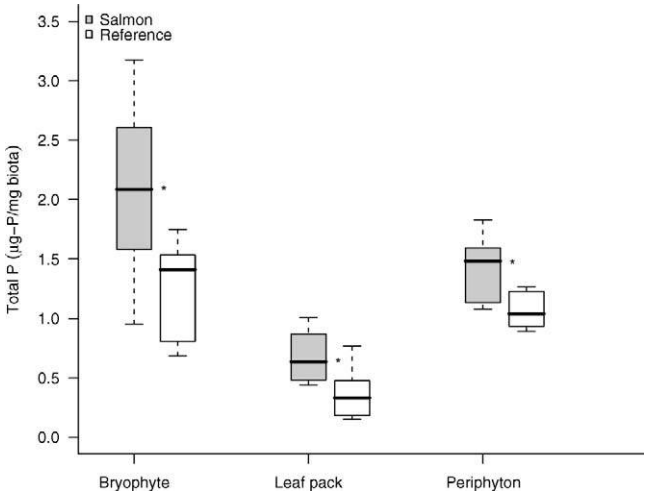

FIG. 2. Box-and-whisker plot for final total P content of periphyton, bryophyte, and leaf packs from salmon and reference stream channels ($n = 6$). Boxes show quartiles, heavy lines show medians, dashed lines show ranges. Asterisk indicates statistically significant differences ($p < 0.05$).

Wallis, $\chi^2 = 0.641$, $p = 0.423$; Fig. 4) did not differ between salmon and reference channels.

Median periphyton ash-free dry mass was 7× higher in salmon than in reference channels, and median chlorophyll *a* concentration was >250× higher in salmon than in reference channels (Table 1). Leaf-pack ash-free dry mass did not differ significantly between salmon and reference channels (Kruskal–Wallis, $\chi^2 = 2.564$, $p = 0.109$).

Discussion

Water quality

Our channels did not differ significantly with respect to stream discharge or initial nutrient concentrations, and lighting, substrate, and temperature conditions were consistent and similar in all stream channels. Thus, the differences in dissolved nutrient concentrations between salmon and reference streams were caused by the presence of decomposing salmon tissue. We measured higher NH_4^+, total N, and SRP concentrations in salmon channels than in reference channels, results consistent with those of other studies in natural and artificial streams (Richey et al. 1975, Wipfli et al. 1999, Mitchell and Lamberti 2005).

Biological responses

Three main questions arise during investigations of potential pathways for movement of nutrients from salmon carcass to stream water to stream organisms. 1) Can stream autotrophs and heterotrophs effectively capture and retain dissolved salmon-derived N and P that would otherwise be lost downstream? 2) If organisms do capture and retain salmon-derived nutrients, then is this enrichment reflected by an increase in biomass? 3) Does capture and retention of salmon-derived nutrients alter N or P content of organisms relative to C content or biomass? Salmon-derived nutrients might increase the nutrient content of microbiota without increasing biomass, or might increase microbial biomass without altering C:N or C:P of the biomass. These 2 scenarios might have different implications for stream organisms.

Consumption of nutrient-rich microbiota could lead to increases in biomass of macroinvertebrates or fish by providing more limiting nutrients per mass of food consumed. Thus, effects of salmon carcasses on food quality could be an important mechanism linking salmon carcasses and stream organisms. Our measures of $\delta^{15}N$ values, P concentrations, C:N, C:P, and biomass (ash-free dry mass and chlorophyll *a*) indicated that stream organisms obtained N and P from decomposing salmon tissue through at least 3 pathways: periphyton, bryophytes, and leaf-pack communities.

Higher leaf-pack $\delta^{15}N$ and P concentrations in salmon than in reference channels indicate movement of N and P from salmon tissue to stream water to the microbial community on the leaf packs. Thus, leaf-litter communities can affect nutrient movement in streams. In studies of nutrient spiraling through

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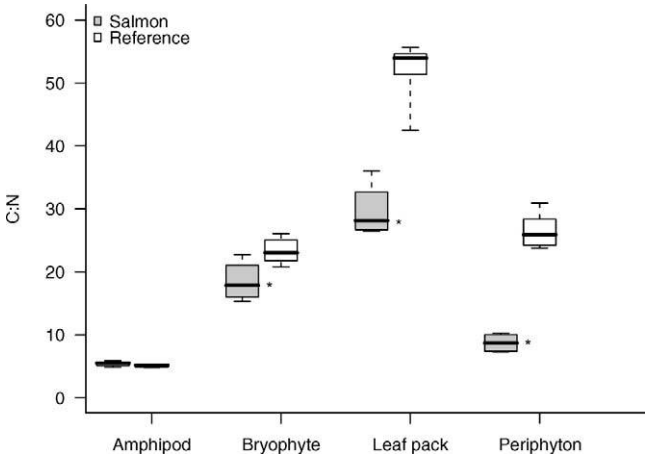

FIG. 3. Box-and-whisker plot for final C:N of periphyton, bryophyte, leaf pack, and amphipods from salmon and reference stream channels ($n = 6$ for periphyton and bryophytes from salmon and reference channels, $n = 5$ for leaf packs from salmon and reference channels, $n = 6$ for amphipods from salmon channels, and $n = 5$ for amphipods from reference channels). Boxes show quartiles, heavy lines show medians, dashed lines show ranges. Asterisk indicates statistically significant differences ($p < 0.05$).

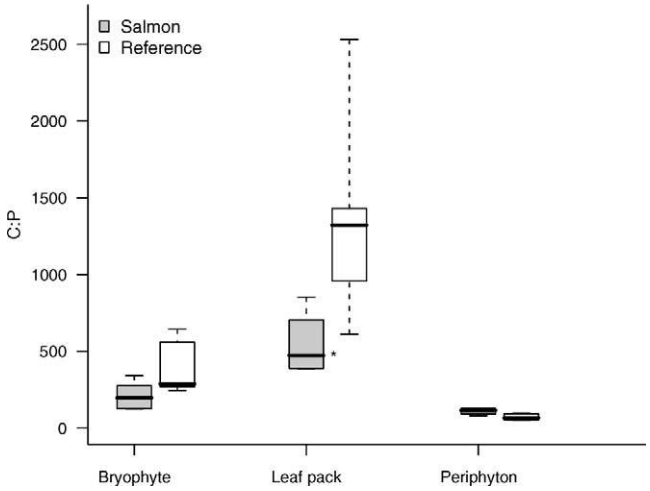

FIG. 4. Box-and-whisker plot for final C:P of periphyton, bryophytes, and leaf packs from salmon and reference channels ($n = 6$). Boxes show quartiles, heavy lines show medians, dashed lines show ranges. Asterisk indicates statistically significant differences ($p < 0.05$).

autotrophic and heterotrophic pathways in artificial and natural streams (Newbold et al. 1981, 1982, 1983, Mulholland et al. 1985), leaf packs decreased P spiraling length, and therefore, increased the amount of P used by stream biota. Our study indicates that leaf-pack microbiota can capture both salmon-derived N and P.

We were unable to detect differences in leaf-pack biomass between salmon and reference channels, so we lack evidence for the connection between nutrient capture and biomass. However, the biomass of the leaf-pack microbial communities probably was small compared with biomass of the leaf substrate, and changes in the biomass of the microbiota might have been too small to detect with our methods. Leaf packs in salmon channels had greater P concentrations, lower C:P, and lower C:N than did leaf packs in reference channels. These results suggest that leaf-pack microbiota became enriched in N and P when exposed to salmon-derived nutrients. Thus, even in the absence of a biomass response, lower C:N, C:P, and higher P concentration of leaf packs in response to salmon-derived nutrients might be ecologically important to stream communities.

Macroinvertebrates that consume leaf litter have the potential to benefit from salmon-derived nutrients. For example, increases in N and P content of the microbiota on leaves might increase the quality of the leaves as a food source for shredders. In our study, significant $\delta^{15}N$ enrichment of amphipods in salmon channels but not in reference channels indicated that nutrients captured from the water column by microbiota appeared to be passed to upper trophic levels. We cannot be certain that amphipods consumed leaf-pack microbiota, rather than periphyton growing in the stream channel, but we are certain that the amphipods did not consume salmon material directly because 500-μm netting separated the decomposing salmon tissue from the amphipods.

Previous studies of the effects of salmon-derived nutrients on microbial communities focused primarily on the movement of $\delta^{15}N$ from salmon tissue to periphyton to grazers (Kline et al. 1990, Wipfli et al. 1999, Johnston et al. 2004, Claeson et al. 2006). Our study showed retention of N and P by the periphyton community, incorporation of $\delta^{15}N$ by microbiota inhabiting leaf packs, and movement of salmon-derived nutrients into amphipods. These results led us to ask whether the movement of salmon nutrients from salmon tissue to leaf-pack microbiota to shredders is as important as (or more important than) the periphyton–grazer pathway. If leaf-pack microbiota can capture salmon-derived nutrients at a rate equal to that of periphyton, then measures of periphyton biomass alone might not be effective estimates of overall effects of dissolved salmon-derived nutrients and stream retention capabilities.

Mechanisms by which salmon-derived nutrients are retained might be seasonal, particularly with regard to retention of nutrients in leaf packs. In the Pacific Northwest, salmon runs occur from July through

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November and December, depending on species and locations. Autumn leaf fall occurs between the late summer and the late autumn salmon runs; consequently, retention pathways for nutrients derived from late summer salmon runs might differ from those for nutrients derived from late autumn salmon runs. By late summer, leaf litter from the previous autumn often has been washed downstream by winter storms and high flows, whereas in late autumn, leaf litter is fresh from autumn leaf fall. Our study suggests that leaf litter might enhance the ability of a stream reach to retain dissolved salmon-derived nutrients because $\delta^{15}N$ and P concentrations and C:N and C:P were elevated in salmon channels. If fresh leaf litter can increase nutrient retention, then salmon streams might derive more benefit from the combination of dissolved salmon nutrients and leaves than from only dissolved nutrients.

We were unable to locate any published research that describes the effect of salmon carcass decomposition on lotic bryophytes. In our study, bryophyte $\delta^{15}N$ values and P concentrations differed between salmon channels and reference channels, a result that suggests that bryophytes can capture and retain dissolved salmon-derived nutrients and that bryophytes might increase the total retention of salmon-derived N and P in streams. Lower C:N and higher P concentrations in bryophytes from salmon than from reference channels suggests that salmon-derived N and P recaptured from the stream water increased nutrient richness of bryophytes.

Our study did not address the effect of salmon carcasses on bryophyte biomass, but long-term P fertilization of a section of the Kuparuk River, Alaska (USA), resulted in nearly a 10-fold increase in bryophyte coverage in riffles of the fertilized reach, with the consequence that bryophyte coverage was $>50\%$ in the enriched reach and $<5\%$ in a reference reach (Slavik et al. 2004). Thus, increases in salmon-derived dissolved P concentrations could lead to increased bryophyte biomass. Bryophytes are important habitat for stream macroinvertebrates and often act as refugia (Stream Bryophyte Group 1999). A bryophyte salmon-derived nutrient pathway might differ in important ways from a periphyton or microbial pathway. Increased bryophyte biomass or bryophyte resilience could affect macroinvertebrate communities through enhanced habitat rather than through consumption-related mechanisms, such as increased food availability. Bryophyte-covered rocks support higher densities of macroinvertebrates than do periphyton-covered rocks (Stream Bryophyte Group 1999, Korsu 2004). Further, the presence of bryophytes in newly restored stream reaches in Finland led to a more rapid recovery of stream macroinvertebrates (Muotka and Laasonen 2002, Korsu 2004).

Overall, our laboratory streams were used successfully to investigate effects of decomposing salmon carcasses on stream organisms. Mesocosm streams do not account for certain effects of natural salmon runs, such as the displacement of substantial nutrients and sediment through bioturbation during nest construction (Tiegs et al. 2008), but our choice of experimental setup fit our objective to investigate specific mechanisms of salmon-nutrient uptake. By focusing only on indirect uptake mechanisms, we were able to trace the movement of nutrients from salmon tissue to a macroinvertebrate species through downstream microbiota, and to demonstrate the ability of periphyton, bryophytes, and leaf-pack microbiota to capture and retain salmon-derived N and P.

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