Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A.

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Abstract: This study was conducted to determine if salmon carcasses (from spawning adults) increased stream biofilm ash-free dry mass (AFDM) and benthic macroinvertebrate abundance in southeastern Alaska, U.S.A. Thirty-six once-through artificial streams were situated along, and received water and drifting invertebrates from, a natural stream. Two treatments (salmon carcass, control) were sampled six times during a 3-month period in a randomized incomplete block design with a 2×6 factorial treatment structure. Additionally, two natural stream sites were sampled once for biofilm and macroinvertebrates, one site receiving 75 000 adult salmon migrants during 1996 and the other upstream of spawning salmon. While biofilm AFDM was 15 times higher in carcass-enriched reaches of Margaret Creek, there were no detectable treatment differences in the artificial streams. Total macroinvertebrate densities were up to eight and 25 times higher in carcass-enriched areas of artificial and natural streams, respectively; Chironomidae midges, *Baetis* and *Cinygmula* mayflies, and *Zapada* stoneflies were the most abundant taxa. The increased biofilm in Margaret Creek and macroinvertebrate abundance in both systems suggest that salmon carcasses elevated freshwater productivity. This marine-based positive feedback mechanism may be crucial for sustaining aquatic–riparian ecosystem productivity and long-term salmonid population levels.

Résumé : La présente étude visait à déterminer si les carcasses de saumon (géniteurs adultes) augmentaient la masse sèche exempte de cendres du film biologique d'un cours d'eau et l'abondance des macroinvertébrés benthiques dans le sud-est de l'Alaska (É.-U.). Trente-six cours d'eau artificiels à circulation ouverte ont été créés le long d'un cours d'eau naturel qui les alimentait en eau et en invertébrés à la dérive. Deux groupes de traitement (carcasse de saumon, témoin) ont été échantillonnés six fois pendant une période de trois mois dans le cadre d'un plan expérimental en blocs aléatoires incomplets avec une structure de traitement factorielle de 2×6. En outre, on a prélevé des échantillons de film biologique et de macroinvertébrés dans deux sites de cours d'eau naturels, un site recevant 75 000 saumons adultes migrants en 1996 et l'autre situé en amont de la frayère. Alors que le film biologique de masse sèche exempte de cendres était 15 fois plus élevé dans les tronçons du ruisseau Margaret enrichis par les carcasses, il n'y avait aucune différence de traitement décelable dans les cours d'eau artificiels. La densité totale de macroinvertébrés était respectivement jusqu'à huit et 25 fois supérieure dans les zones enrichies de carcasses des cours d'eau artificiels et naturels; les moucherons chironomidés, les éphémères *Baetis* et *Cinygmula* et les perles *Zapada* étaient les groupes les plus abondants. L'accroissement du film biologique dans le ruisseau Margaret et de l'abondance des macroinvertébrés dans les deux systèmes semblent indiquer que les carcasses de saumon font augmenter la productivité des eaux douces. Ce mécanisme de rétroaction positive provenant du milieu marin peut être critique pour le maintien de la productivité de l'écosystème aquatique et riverain et les niveaux de population de salmonidés à long terme.
[Traduit par la Rédaction]

Introduction

Aquatic productivity is often governed by dissolved organic carbon (DOC) and nutrient levels (Warren et al. 1964; Borchardt 1996; Stockner and MacIsaac 1996). Small increases in their concentrations can dramatically increase primary production (Stockner and Shortreed 1978; Peterson et al. 1993; Perrin et al. 1987), heterotrophic activity (Sobczak 1996), and secondary production (Peterson et al. 1993; Stockner and MacIsaac 1996). These "bottom-up" effects can reach upper trophic levels (Mundie et al. 1991; Lamberti 1996) including predatory fishes (Stockner and MacIsaac 1996; Kyle et al. 1997). DOC added as sucrose to a western Oregon stream increased bacterial growth, aquatic insect abundance, and predation by and subsequent production of coastal cutthroat trout (*Oncorhynchus clarki*) (Warren et al. 1964). Nitrogen and phosphorus additions to a small coastal stream increased periphyton standing crop and steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) fry size in British Columbia (Johnston et al. 1990). These nutrients, artificially added to lakes, also increased sockeye (*Oncorhynchus nerka*) and coho salmon production in Alaska (Kyle et al. 1997) and sockeye production in British Columbia (Stockner and MacIsaac 1996). Peterson et al. (1993) detected bottom-up effects up through several trophic levels including Arctic grayling (*Thymallus arcticus*) from phosphorus additions to a tundra stream in Alaska.

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Fig. 1. Proposed major trophic pathways influenced by anadromous salmonids in freshwater ecosystems. Bold text and arrows represent energy flow within freshwater food webs; lightface text and arrows show the major links with marine and terrestrial systems.
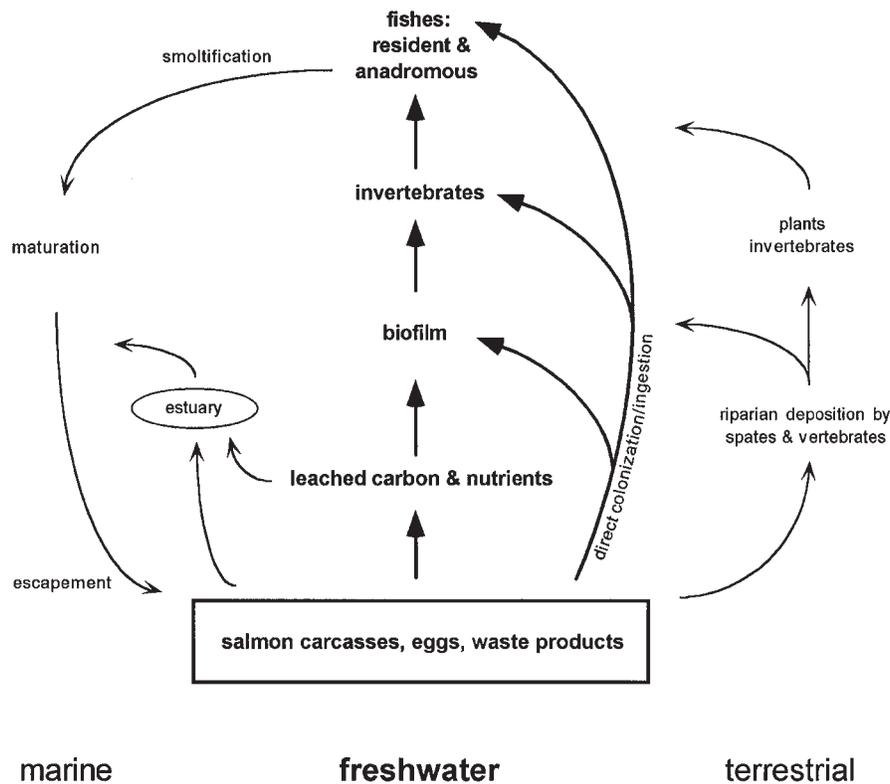
Returns of salmon and other anadromous species may be important for aquatic–riparian ecosystem productivity (Levy 1997), particularly in nutrient-poor systems characteristic of western North America (Stockner and MacIsaac 1996), including Alaska (Peterson et al. 1993; Kyle et al. 1997). Fish carcasses and eggs can contribute nutrients and DOC (Mathisen et al. 1988; Schuldt and Hershey 1995; Kyle et al. 1997) that stimulate primary production leading to possible elevated productivity of higher trophic levels. Additionally, fish and other animal carcasses may act as "slow-release" fertilizers providing nutrients through much of the year (Parmenter and Lamarra 1991). Although there is good evidence that marine-derived nutrients (e.g., nitrogen) are present in some aquatic food webs that receive annual returns of anadromous fishes (Bilby et al. 1996; Johnston et al. 1997; Kline et al. 1997), little information exists about whether marine-derived nutrients or carbon increase aquatic productivity.

Salmonid escapements appear to be at or near historic levels in southeastern Alaska and parts of western Canada (Baker et al. 1996; Slaney et al. 1996), unlike other regions of the world (Wheeler and Sutcliffe 1990; Nehlsen et al. 1991). Spawning adults deposit marine-based carbon and nutrients in freshwater via excretion, eggs, and adult carcasses (Mathisen et al. 1988; Kline et al. 1997) and may have important consequences for aquatic–riparian productivity. Increased carbon and nutrients should stimulate biofilm (i.e., mixed assemblage of autotrophic and heterotrophic microbes embedded in a glycoprotein polysaccharide matrix attached to stream substrates) production (Fig. 1). More biofilm means more food directly for invertebrate scrapers and collectors and indirectly for predatory

invertebrates. These bottom-up effects should continue passing through the food web reaching higher trophic levels including juvenile salmonids and other predatory fishes, leading to their increased production (Fig. 1). Determining all functions of salmonid escapements in freshwater–riparian ecosystems is crucial for understanding marine–freshwater–terrestrial linkages (Fig. 1) for fisheries and ecosystem management. This information is critical for managing fish escapements in the Pacific Northwest and globally, and may be particularly important in parts of the world for restoring suppressed salmon stocks.

The objectives of this study were to assess the influence of salmon carcasses on aquatic productivity through changes in biofilm ash-free dry mass (AFDM) and benthic macroinvertebrate abundance in artificial and natural streams in southeastern Alaska. We tested the hypothesis that material leached from salmon carcasses increase biofilm AFDM and benthic macroinvertebrate abundance in lotic ecosystems.

Methods

Study site
The study took place within the Margaret Creek watershed on Revillagigedo Island near Ketchikan, Alaska. The climate is maritime, cool, and moist; precipitation can exceed 500 cm·year^{-1} in some areas. The Margaret watershed is 38 km^2 and supports anadromous sockeye, pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and coho salmon, steelhead and cutthroat trout, and Dolly Varden (*Salvelinus malma*). A fish ladder installed in 1990 around a natural fish barrier (i.e., waterfalls that historically prevented upstream movement of fishes) about 1 km upstream of salt water has

provided anadromous fishes with access to upstream reaches of the watershed. Resident fishes included kokanee salmon (*O. nerka*), cutthroat trout, and rainbow trout (*O. mykiss*), Dolly Varden, prickly sculpin (*Cottus asper*), and threespine stickleback (*Gasterosteus aculeatus*). Juvenile sockeye salmon stocking has occurred in Margaret Lake within the watershed between 1988 and 1994 (McCurdy and Bryant 1997).

Experiments were conducted from 18 August through 12 November. Spawning salmon densities were greatest from July through October 1996. About 75 000 adult pink, chum, coho, and sockeye salmon returned to Margaret Creek during 1996, and 25 000 of those passed through the fish ladder into upper parts of the watershed (S. McCurdy, Pacific Northwest Research Station, USDA Forest Service, 2770 Sherwood Lane, Juneau, AK 99801, U.S.A., personal communication). Pink salmon were the most abundant anadromous species.

Mesocosm experiment

The mesocosm consisted of 36 straight once-through artificial stream channels**,** each 250 cm long × 18 cm wide, constructed in the riparian forest along Spike Creek, a second-order tributary of Margaret Creek. Stream water containing naturally drifting invertebrates was gravity-fed through black polyethylene pipes from a nonanadromous portion of Spike Creek (immediately upstream of a waterfall) to a header tank. Water was then delivered from the header tank to each channel through T-valves, passed through the channels, and then into an outflow flume that collected and carried it back to the natural stream. Six channels were constructed per table, on six tables.

Each channel was divided into three experimental sections: a 60-cm pool for treatments (salmon carcass or no carcass), a 45-cm pool habitat, and a 85-cm riffle habitat, all containing mineral substrata (collectively 7 L of 4-cm-diameter gravel and 5 L of 4- to 20-cm-diameter gravel) from the natural stream. A 15.0 × 15.0 cm unglazed clay tile was placed at the downstream end of each riffle habitat for sampling biofilm. Invertebrates could freely drift in and out of channels throughout the experiment and immediately began colonizing substrata in channels via drift from the natural stream. The benthic macroinvertebrate community composition in these channels normally resembles the Spike Creek community within 1–2 weeks after stream water begins flowing through channels (M. Wipfli, Pacific Northwest Research Staion, Juneau, Alaska, unpublished data); some taxa with a low propensity to drift (e.g., cased Trichoptera) were less frequent in artificial streams versus the natural stream. Discharge through each channel was 0.52 ± 0.03 L·s^{-1} throughout the experiment. Water temperature in the mesocosm, logged at continuous 1-h intervals, averaged 7.5°C (range 1.6–13.3°C) during the experiment.

Two treatments were applied: single salmon carcass and control (no carcass). Twenty-one live female pink salmon containing eggs were collected from Margaret Creek on 18 August, killed, and weighed (range 1.4–1.8 kg wet mass). Stream water passed through the channels for 2 days, and then, one fish was placed in each of 18 channels, in three randomly selected channels per table, for all six tables. Carcasses were secured with monofilament line in the upstream pool. Discharge of 0.52 L·s^{-1} through the channels resulted in 3.2 kg carcass wet mass·L water^{-1}·s^{-1} (3.6–4.7 kg carcass wet mass·m^{-2}). Fiberglass screen was placed beneath each carcass to facilitate its removal for dry mass determinations. The three remaining fish were weighed wet and then oven-dried at 80°C and reweighed to calculate a mean dry mass to wet mass ratio. This value (0.28) was used to estimate dry mass loss for carcasses placed in channels. Pools of all channels were covered with Plexiglas® fastened to channel tops to protect carcasses from bears and other scavengers.

Biofilm and benthic macroinvertebrates were sampled six times during the 87-day experiment. Six randomly chosen channels (one carcass replicate and one control replicate from each of three tables) were destructively sampled during each of the six sampling events.

Biofilm

Biofilm was collected from a 56-cm^2 portion of the upper surface of the unglazed clay tiles for AFDM measurements. Tiles were removed from channels, scraped, brushed, and flushed with water into Nalgene® bottles. Individual samples were refrigerated while at the field site and then transported to the laboratory and filtered, oven-dried, weighed, ashed at 500°C, and reweighed for calculation of AFDM (see Steinman and Lamberti 1996).

Macroinvertebrates

Benthic macroinvertebrates were collected directly from carcasses and from mineral substrata in both pool and riffle habitats. They were also counted on the top surfaces of the clay tiles, without physically disturbing the tiles, every few days throughout the experiment.

Riffle- and pool-dwelling macroinvertebrates were collected on two consecutive days during each sampling period. Using our hands, we agitated riffle substrata three times for 4 min each per channel; dislodged invertebrates were collected in 250-µm Nitex® nets that were attached to channel outflows. Pool-dwelling macroinvertebrates were sampled similarly on the following day. After invertebrates were collected from the substrata, a subsample of macroinvertebrates representative of all visible taxa was collected from the surface of each carcass or from its associated microbial layer. Macroinvertebrates were sorted, identified to the lowest reliable taxon, and, for noncarcass taxa, counted. Finally, carcasses were removed, dried at 80°C, and weighed to determine their dry mass loss during the experiment. To do this, we estimated their initial dry mass by multiplying 0.28 (dry mass to wet mass ratio described above) by their starting wet mass and subtracting their final dry mass to give dry mass lost.

Natural stream experiment

Although this study centered around the mesocosm, we sampled a natural stream to determine whether patterns in biota abundance occurring in a natural system were similar to those in the more controlled and statistically rigorous artificial streams. Even though we carefully chose study sites that minimized natural between-site differences, some obvious differences existed. A 55-ha lake separated the two study reaches. While both sites contained predominantly gravel and cobble, the downstream habitat on average had larger substrate, was higher gradient, and was about twice as wide as the upstream site. Water temperature, logged at continuous 1-h intervals, averaged 8.8°C (range 4.4–12.9°C) and 10.6°C (range 6.3–16.5°C) in the upstream and downstream reaches, respectively, between 26 August and 23 October. We collected no additional physical or chemical data from Margaret Creek.

Baseflow stream discharge recorded on 14 August was 752 and 1539 L·s^{-1} in the upstream and downstream reaches, respectively. At these discharges and 75 000 salmon, the "carcass concentration" in upper and lower Margaret Creek was between 0 and 80 kg carcass wet mass·L water^{-1}·s^{-1}, respectively (relative to 3.2 kg carcass wet mass·L water^{-1}·s^{-1} in the artificial streams). Actual carcass concentration in lower Margaret Creek was probably much less than 80 kg carcass wet mass·L water^{-1}·s^{-1} because many fish are eaten by vertebrates (Willson and Halupka 1995) or get flushed downstream into the estuary (M.S. Wipfli, personal observation).

Biofilm

A biofilm sample was collected from each of four stones from each of two Margaret Creek sites (= treatments) within riffle habitats on 20 October. One site was in a lower reach that contained the highest concentration of salmon carcasses (carcass-enriched treatment), and the other was upstream of spawning anadromous salmonids (control treatment). Stones were selected based on location (midchannel within a riffle), size (as large as possible, yet small enough for one person to carry from the stream), and shape (slightly flattened to facilitate sampling). A 56-cm^2 patch on the upper surfaces of each stone was scraped with a razor blade, brushed with a toothbrush, and

Fig. 2. Mean salmon carcass dry mass remaining in artificial channels throughout the 87-day mesocosm experiment. Error bars represent 1 SEM.
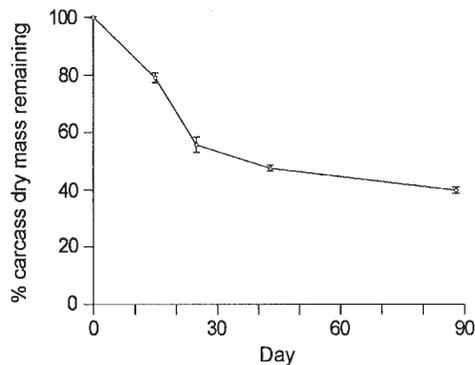
then flushed with water into individual plastic bags and refrigerated. Samples were processed for AFDM as described earlier.

Macroinvertebrates

Benthic macroinvertebrates were collected on 23 October from seven stones in a similar fashion as biofilm samples. Invertebrates within a $100\text{-}cm^2$ area were brushed from the top surface of each stone, flushed with water through a 250-µm sieve, placed in 95% ethanol, identified, and counted.

Experimental design and statistical analyses

Response variables for analyses were biofilm AFDM and benthic macroinvertebrate abundance in both natural stream and mesocosm experiments. Macroinvertebrates were identified to the lowest reliable taxa and analyzed at two general taxonomic resolutions: total invertebrates (all taxa combined) and either family or genus.

An incomplete block design was used with a 2×6 factorial treatment structure in the mesocosm and data analyzed with PROC GLM (SAS Institute Inc. 1989). Power analyses indicated that this design would provide the most information, while optimizing statistical power, to test hypotheses. We performed *t*-tests on Margaret Creek data. All count data (benthic macroinvertebrates) were transformed via natural logarithm to meet ANOVA assumptions (e.g., nonhomogeneous variance).

We caution that an upstream–downstream comparison within one stream (Margaret Creek) is pseudoreplication (Hurlbert 1984) and does not provide a means of separating treatment factors (carcasses, no carcasses) from other variables (e.g., gradient, substrate, discharge, lake effects). Nonetheless, this approach did provide the opportunity to determine if differences in invertebrate abundance and biofilm AFDM in the natural stream corresponded to the responses measured in the artificial channels.

Results

Mesocosm experiment

Salmon carcasses lost 60% of their original dry mass by the end of the 3-month experiment; mass loss was most rapid within the first 25 days (Fig. 2). They apparently lost mass through several processes, including microbial and invertebrate processing and dissolution and leaching. They became covered with invertebrates and a thick, fuzzy-looking microbial layer and slowly deflated through time; a cream-colored amorphous suspension was seen leaking from the carcasses. Macroinvertebrates were also seen burrowing into carcasses.

Fig. 3. Mean biofilm AFDM and benthic macroinvertebrate densities that colonized clay tiles in artificial channels, contrasting carcass-enriched (solid circles) and control (open circles) treatments, throughout the 87-day mesocosm experiment. Error bars represent 1 SEM.
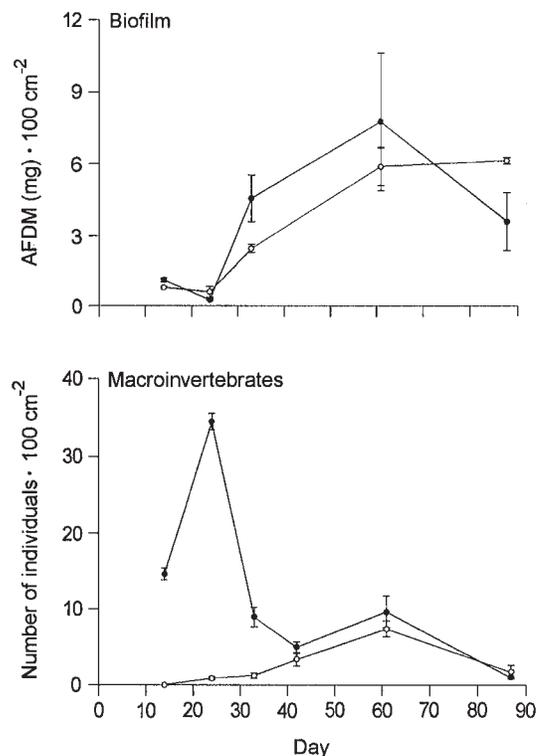
As a result of carcasses being placed in pools, we observed no physical breakdown (e.g., abrasion by water or sediments).

Biofilm

Although we observed a thicker mat of biofilm on carcass-treatment tiles during the experiment, no significant differences in AFDM were found between treatments (Fig. 3, $p > 0.05$). While the lack of AFDM differences could have been due to absence of treatment effects, it appeared that grazers and physical sloughing removed much of the biofilm layer as it developed, potentially masking treatment effects. Significantly more macroinvertebrates were counted on the tiles in channels containing carcasses, especially during the first 30 days (Fig. 3, $p < 0.001$), demonstrating that they were probably responding to an elevated food resource (i.e., biofilm) absent in the control channels.

Macroinvertebrates

Benthic macroinvertebrate densities were significantly higher in both pool (Fig. 4; Table 1, $p < 0.001$) and riffle (Fig. 5; Table 1, $p < 0.001$) habitats in the carcass-enriched channels. Total macroinvertebrate number was eight times higher 25 days into the experiment in both habitats (Figs. 4 and 5). By the end of the study, densities were still higher in the carcass-enriched channels. Chironomid midges (Diptera: Chironomidae) were the most abundant taxon in both pool and riffle habitats, comprising 85 and 35% (averaged for both carcass and control channels) of the total number, respectively. This

family comprised numerous genera (Table 1). *Paraleptophlebia* (Ephemeroptera: Leptophlebiidae) (4%) and *Zapada* (Plecoptera: Nemouridae) (3%) were the next most abundant taxa in pool habitats (Fig. 4), while *Baetis* (Ephemeroptera: Baetidae) (22%) and *Zapada* (17%) were the next most common insects in riffle habitats (Fig. 5), followed by *Cinygmula* (Ephemeroptera: Heptageniidae) (9%), Capniidae/Leuctridae (Plecoptera) complex (5%), and black flies (Diptera: Simuliidae) (4%). Capniidae/Leuctridae and Simuliidae were the only relatively common taxa (>3% abundance) that did not show a density increase in the presence of salmon carcasses (Fig. 5; Table 1, $p > 0.05$). The densities of remaining less common taxa in both pool and riffle habitats also generally increased with carcass enrichment (Table 1).

Additionally, the temporal colonization patterns were different among taxa. Chironomidae and *Baetis* were the earliest colonizers of the carcass-enriched habitat, followed by *Zapada*, then *Cinygmula* and *Paraleptophlebia*, and finally capniid and leuctrid stoneflies (Figs. 4 and 5). These patterns were not apparent in the control treatment.

Several taxa were observed on carcasses, including *Brillia*, *Corynoneura*, *Polypedilum*, and *Pseudodiamesa* (Diptera: Chironomidae), *Zapada*, *Ameletus* (Ephemeroptera: Ameletidae), and *Onocosmoecus* and *Ecclisomyia* (Trichoptera: Limnephilidae). Chironomidae were observed burrowing into carcasses and were abundant within the salmon tissue after 30 days.

Natural stream experiment

Biofilm and macroinvertebrates

Biofilm AFDM collected from stone surfaces was significantly higher in the carcass-enriched portion of Margaret Creek, about 15 times greater than in the upstream "control" reach (Fig. 6, $p < 0.001$). Benthic macroinvertebrate densities were also significantly higher in the carcass-enriched stream reaches than in the control reaches (Fig. 6, $p < 0.001$). As with the mesocosm experiment, Chironomidae, composed of *Cricotopus*, *Eukiefferella*, *Paratrissocladius*, and *Pseudosmittia*, were the most abundant taxa. *Baetis* was the second most abundant.

Discussion

This study generally supports the hypotheses that salmon carcasses increase freshwater biofilm and benthic macroinvertebrate abundance, suggesting that carcass-derived nutrients or carbon elevate stream productivity. Our results agree with previous freshwater nutrient-enrichment studies conducted in western North America in which artificially added inorganic nutrients, particularly nitrogen and phosphorus, and organic matter elevated biological activity at several trophic levels (Warren et al. 1964; Peterson et al. 1993; Lamberti 1996; Stockner and MacIsaac 1996).

Although treatment differences were not detected with biofilm AFDM in the artificial channels, we believe that the biofilm may have responded to carcass enrichment, as seen in the natural stream. We observed more sloughing in the artificial versus natural streams, possibly due to different microlayer conditions (e.g., turbulence, velocity, sediment load) that would affect sloughing rates. Also possible was a more rapid

Fig. 4. Mean benthic macroinvertebrate densities in the pool habitat within artificial channels, contrasting carcass-enriched (solid circles) and control (open circles) treatments, throughout the 87-day mesocosm experiment. These taxa represent the three most abundant groups in the pool habitat. Error bars represent 1 SEM.
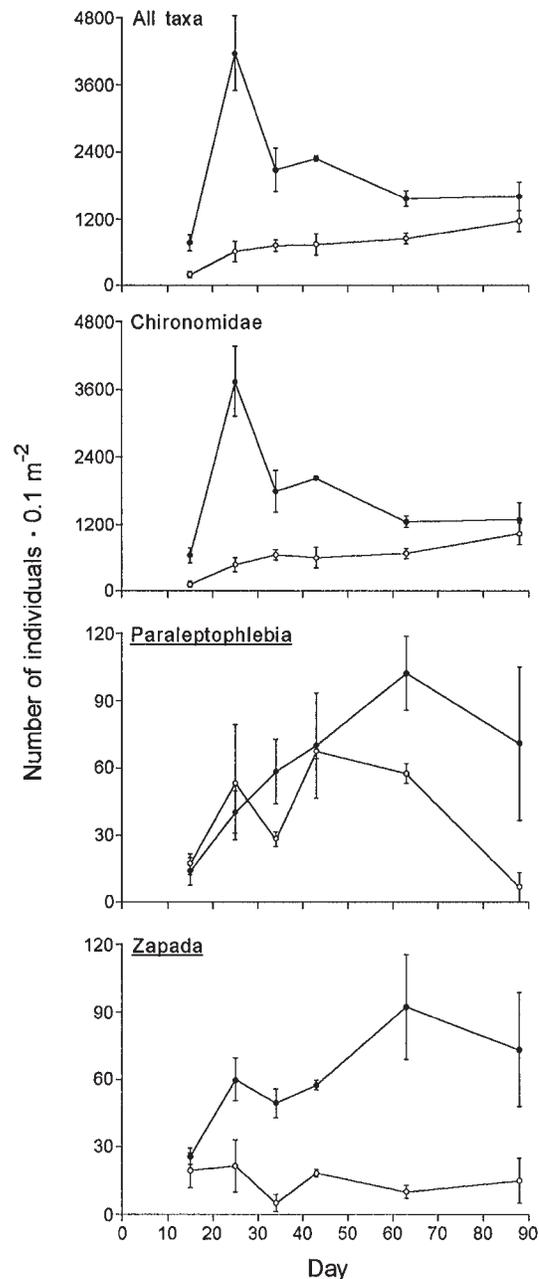
biofilm recolonization following sloughing in the natural stream from higher carcass concentrations there (i.e., more stream nutrients) (with about 80 versus 3.2 kg carcass wet mass·L water^{-1}·s^{-1} in the natural and artificial streams, respectively). On the other hand, the differences between treatments in Margaret Creek may have been a function of confounding variables including background nutrient levels (likely influenced by Margaret Lake), stream temperature, and light levels (due to different channel widths and riparian shading) between the upstream and downstream sites.

Table 1. Percent relative abundance, mean natural logarithm transformed abundance (no.· m^{-2}), and ANOVA results of benthic macroinvertebrates collected from pool and riffle habitats in artificial streams from carcass and control treatments.

Taxon	Functional feeding group[a]	% relative abundance[b]	Treatment means[c]		ANOVA	
			Carcass	Control	MS$_{error}$[d]	p
Pool						
Arthropoda						
Insecta						
Ephemeroptera						
Leptophlebiidae						
Paraleptophlebia	c-g	3.5	6.11	5.14	1.37	0.0218
Heptageniidae[e]	c-g, sc	0.2	2.70	0.14	1.31	<0.0001
Cinygmula	c-g, sc	0.6	4.36	1.47	2.81	<0.0001
Baetidae						
Baetis[f]	c-g, sc	0.5	3.37	1.82	3.30	0.0187
Ameletidae						
Ameletus validus	c-g, sc	0.3	3.02	0.65	2.83	0.0005
Plecoptera						
Nemouridae						
Zapada[g]	sh	2.7	6.28	4.53	0.88	<0.0001
Capniidae/Leuctridae	sh	1.2	4.95	4.32	1.09	0.0854
Chloroperlidae						
Sweltsa	pr	0.4	2.27	3.31	3.80	0.1257
Trichoptera[h, i]	Several	0.8	4.07	3.22	2.61	0.1334
Diptera[j]	Several	0.7	4.39	4.05	0.81	0.2800
Chironomidae (l)[k]	Several	85.1	9.62	8.43	0.13	<0.0001
Chironomidae (p)[l]	Several	2.3	4.24	2.75	1.01	0.0003
Arachnida						
Acari	om	0.2	2.98	1.92	2.96	0.0804
Annelida						
Oligochaeta	c-g	1.3	4.32	4.25	1.14	0.8363
All taxa		100.0	9.79	8.70	0.07	<0.000 1
Riffle						
Ephemeroptera						
Baetidae						
Baetis[f]	c-g, sc	21.8	7.05	5.32	0.42	<0.0001
Heptageniidae[e]	c-g, sc	1.9	4.72	3.34	0.39	<0.0001
Cinygmula	c-g, sc	9.0	6.07	4.89	0.15	<0.0001
Epeorus[m]	c-g, sc	0.2	2.06	0.89	1.40	0.0079
Ameletidae						
Ameletus validus	c-g, sc	1.2	3.35	2.15	0.89	0.0011

Soluble material from the salmon carcasses was rapidly released into stream water, apparently microbial and invertebrate mediated, as evidenced by the carcass mass loss (in the absence of apparent physical breakdown). Similar to other animal flesh, salmon contain proteins, fats, and other biochemicals (Mathisen et al. 1988), comprising potential productivity-limiting carbon, nitrogen, and phosphorus (Borchardt 1996; Stockner and MacIsaac 1996). Some combination of these stream-leached compounds appeared to influence biofilm and subsequently had a rapid and dramatic effect on benthic macroinvertebrate abundance in this study.

Although results from Margaret Creek need to be interpreted with caution (due to possible confounding variables as discussed earlier), we did observe the same general pattern in the biota — higher abundance in carcass-enriched stream reaches — in the natural and artificial streams (except for the artificial stream tile-colonized biofilm). This suggests that carcass-leached material may have had a similar effect on Margaret Creek benthos as it did in the mesocosm.

In addition to chemical processing through dissolution of tissue, biological processing of carcasses was apparent and may be ecologically important. Carcasses, with their associated microbial community, were colonized by macroinvertebrates in this study and may be an important food source for these scavengers. Macroinvertebrates (most commonly chironomid midge larvae) were seen on and penetrating into carcasses and were collected from carcasses after the experiment began; they became more abundant on carcasses through time. Kline et al. (1997) found several benthic macroinvertebrate taxa associated with salmon carcasses in interior Alaska streams, commonly several species of limnephilid caddisflies; these larvae were enriched with marine-derived nutrients. Minakawa (1997) also observed insects feeding on salmon tissue, and exhibiting higher growth rates, in Washington. In

Table 1 (*concluded*).

Taxon	Functional feeding group[a]	% relative abundance[b]	Treatment means[c] Carcass	Treatment means[c] Control	ANOVA MS_{error}[d]	ANOVA p
Leptophlebiidae						
Paraleptophlebia	c-g	0.5	1.44	3.30	1.64	0.0003
Ephemerellidae						
Drunella[n]	sc	0.2	2.29	0.45	1.65	0.0004
Plecoptera						
Nemouridae						
Zapada[g]	sh	16.5	7.05	5.49	0.07	<0.0001
Capniidae/Leuctridae	sh	5.1	4.96	4.38	0.85	0.0768
Chloroperlidae						
Sweltsa	pr	0.2	1.80	1.02	1.22	0.0496
Trichoptera[o, i]	Several	0.6	2.60	2.21	2.56	0.4662
Diptera[j]	Several	0.5	3.07	2.44	0.92	0.0547
Chironomidae (l)[p]	Several	35.4	7.41	5.78	0.13	<0.0001
Chironomidae (p)	Several	2.5	3.65	2.75	0.55	<0.0001
Simuliidae[q]	c-f	4.2	5.32	5.12	0.17	0.1494
All taxa		100.0	8.86	7.36	0.03	<0.0001

[a]c-g, collector–gatherer; sc, scraper; sh, shredder; pr, predator; om, omnivore; c-f, collector–filterer (Merritt and Cummins 1996).

[b]Relative abundance as a percentage of all macroinvertebrates pooled across both treatments.

[c]$n = 18$.

[d]df = 19.

[e]*Epeorus* and *Cinygmula* $\leq$2 mm long.

[f]*Baetis bicaudatus*, *B. tricaudatus*.

[g]*Zapada cinctepes*, *Z. columbiana*.

[h]*Ecclisomyia*, *Onocosmoecus unicolor*, *Micrasema*, *Glossosoma*.

[i]*Rhyacophila*, *Polycentropus*, *Wormaldia*, *Psychoglypha*.

[j]Empididae (*Clinocera*, *Oreogeton*), Tipulidae (believed to be *Raphidolabina*, *Dicranota*), Ceratopogonidae.

[k]*Corynoneura*, *Stilocladius*, *Brillia*, *Heterotrissocladius*, *Psuedodiamesa*, *Polypedilum*, *Macropelopia*, *Parametriocnemus*, *Micropsectra*, *Paramerina*, *Zavrelimyia*, *Eukiefferiella*, *Rheocricotopus*, *Heterotanytarsus*, *Paraphaenocladius*, *Chironomus*, *Phaenopsectra*; l, larvae.

[l]p, pupae.

[m]*Epeorus* spp. (believed to be *deceptivus*), *E. longimanus*, *E. grandis*.

[n]*Drunella doddsi*, *Drunella* spp. (believed to be *grandis*).

[o]*Glossosoma*, *Parapsychae elsis*, *Ecclisomyia*, *Onocosmoecus unicolor*.

[p]*Eukiefferiella*, *Corynoneura*, *Stilocladius*, *Brillia*, *Rheocricotopus*, *Psuedodiamesa*, Thienemannimyia group, *Macropelopia*, *Parametriocnemus*, *Micropsectra*, *Paramerina*, *Tvetenia*, *Heterotrissocladius*, *Paraphaenocladius*, *Polypedilum*.

[q]*Simulium pugetense*, *S. nebulosum*, *Stegopterna* sp.

Minnesota where salmon are not endemic, scavenging invertebrates were uncommon on salmon carcasses, with a shredding stonefly the most apparent (Schuldt and Hershey 1995).

This elevated invertebrate abundance from salmon carcass derived carbon or nutrients likely means more energy (via greater prey abundance) reaching upper trophic levels, including juvenile salmonids and other predators in both the aquatic and riparian systems (Fig. 1). Increased fish production is likely if these bottom-up forces transfer through the food web to upper (predator) levels. Food often appears to limit salmonid production in streams in western North America (Chapman 1966). Bilby et al. (1996) recorded increased juvenile coho salmon growth rates in a Washington stream after salmon began to spawn. Michael (1995) also noted higher juvenile coho salmon growth rates in a stream with spawning pink salmon than in one without.

These results have important implications for fisheries management. If freshwater ecosystems rely on this annual salmon-derived nutrient pulse for sustaining productivity, then managing salmon escapements at or above a certain threshold may be crucial. These marine-derived nutrients may be especially important for the naturally oligotrophic freshwater systems characteristic of the Pacific Northwest (Perrin et al. 1987; Stockner and MacIsaac 1996), providing a positive feedback mechanism that helps sustain regionally productive salmonid fisheries.

Another important fishery management implication concerns fish pass or "ladder" construction, a tool intended to "enhance" selected anadromous species. These artificial fish passes built at natural barriers (e.g., waterfalls) provide anadromous fishes access to previously unavailable upstream habitats. Concerns exist about possible negative effects of introduced anadromous species on native resident fishes (i.e., through competition or predation) in southeastern Alaska

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Fig. 5. Mean benthic macroinvertebrate densities in the riffle habitat within artificial channels, contrasting carcass-enriched (solid circles) and control (open circles) treatments, throughout the 87-day mesocosm experiment. These taxa represent the six most abundant groups in the riffle habitat. Error bars represent 1 SEM.
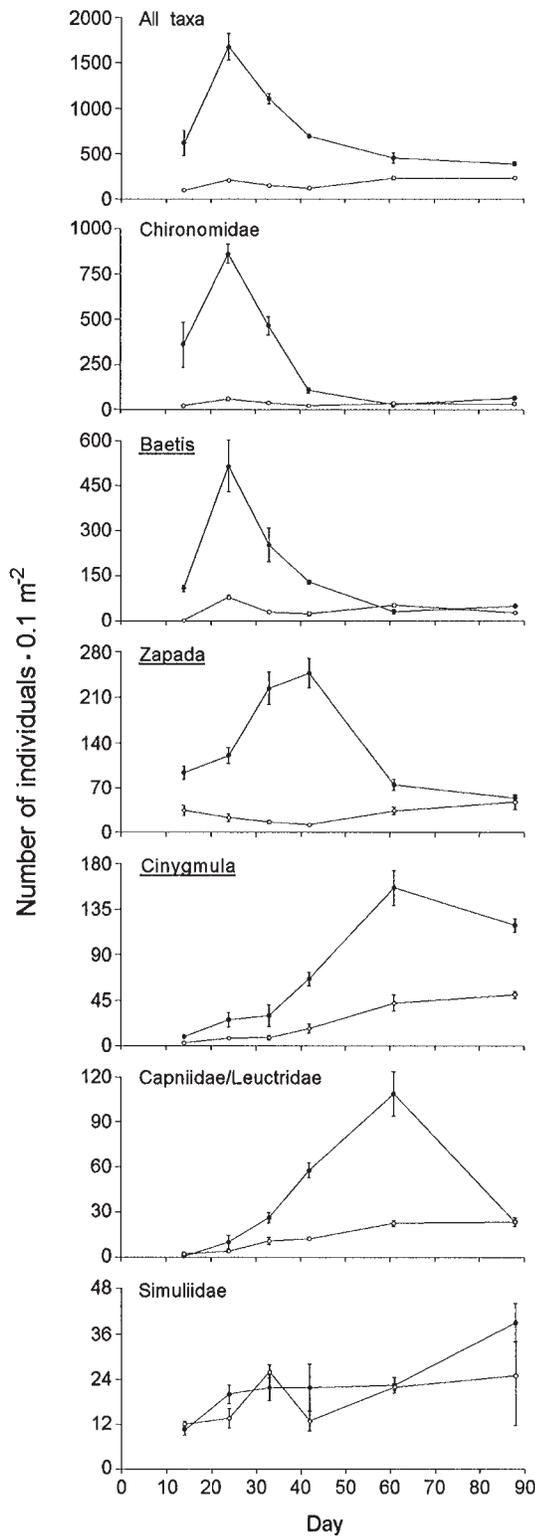
Fig. 6. Mean biofilm AFDM and benthic macroinvertebrate densities on stone surfaces within Margaret Creek, contrasting downstream carcass-enriched (shaded bars) and upstream control (open bars) riffle habitats. Error bars represent 1 SEM.
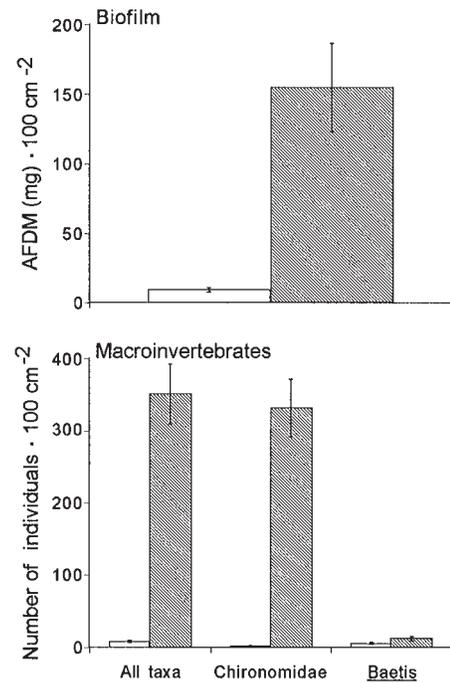
on resident fishes by elevating aquatic production, thereby providing more prey and less competition. Therefore, elevated freshwater food web productivity through anadromous species introductions may serve to increase both anadromous and resident fish production. Introduced anadromous salmon have not had a noticeable negative effect on resident fishes in the Margaret system (McCurdy and Bryant 1997), where this study was conducted. Theoretically, positive effects from enrichment could negate effects from competition or predation.

These results may also have important implications for restoring impoverished stocks in regions of the world where freshwater habitat destruction or overfishing has depleted runs. If freshwater ecosystems have historically depended on this annual influx of marine-derived material, they may first require elevated carbon or nutrient levels to boost trophic productivity before they can successfully recruit and sustain desired levels of fish production. Restoring suppressed stocks may initially require artificially elevating nutrients concurrently with other restoration strategies (i.e., juvenile stocking) until spawning salmon reach numbers that are sufficient for self-fertilization of the system. This strategy appeared successful in some Alaskan lakes where nutrient enrichment (nitrogen and phosphorus), together with juvenile salmon stocking, increased salmon production in systems that were experiencing depressed adult returns (Kyle et al. 1997). However, long-term effects (e.g., over decades) remain to be seen. Alternatively, even low returning adult numbers (of depleted stocks) may progressively fertilize a system through time, possibly enabling impaired systems to achieve naturally their trophic capacity.

A more advanced understanding of the role that anadromous salmonids play in freshwaters and associated terrestrial

(McCurdy and Bryant 1997). Alternatively, this annual nutrient influx via anadromous fishes may have beneficial effects

ecosystems is crucial for a more holistic approach to fisheries and ecosystem management. This annual nutrient influx via anadromous species may be critically important for sustaining productivity and biodiversity, both regionally and globally. Long-term sustainability may hinge on managing escapements to sustain trophic productivity of freshwater habitat. Understanding the significance of this nutrient influx should help the management of both healthy and impoverished stocks throughout the world.

Acknowledgments

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