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Impacts of marine-derived nutrients on stream ecosystem functioning

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Energy and nutrient subsidies transported across ecosystem boundaries are increasingly appreciated as key drivers of consumer–resource dynamics. As purveyors of pulsed marine-derived nutrients (MDN), spawning salmon are one such cross-ecosystem subsidy to freshwaters connected to the north Pacific. We examined how salmon carcasses influenced detrital processing in an oligotrophic stream. Experimental manipulations of MDN inputs revealed that salmon carcasses indirectly reduced detrital processing in streams through temporarily decoupling the detrital resource–consumer relationship, in which detrital consumers shifted their diet to the high-nutrient resource, i.e. salmon carcasses. The average decomposition rate of alder leaves with salmon carcass addition was significantly lower than that without the carcass, which was associated with lower abundance and biomass of detritivorous Trichoptera on the carcass-treated leaves. There were generally larger in size Trichopteran detritivores on the carcasses than on leaves. These results imply that cross-boundary MDN subsidies indirectly retard the ecosystem processing of leaf litter within the short term, but may enhance those food-limited detritivorous consumers. Because unproductive freshwaters in the Pacific northwest are highly dependent upon the organic matter inputs from surrounding forests, this novel finding has implications for determining conservation and management strategies of salmon-related aquatic ecosystems, in terms of salmon habitat protection and fisheries exploitation.

Keywords: consumer-resource dynamics; salmon; red alder; detritivores; functional feeding groups; streams

1. INTRODUCTION

Understanding trophic fluxes of energy and nutrient resources across ecosystem boundaries differing in productivity status is a key theme in contemporary ecology (Vannote *et al.* 1980; Polis & Hurd 1995; Polis *et al.* 1997; Nakano & Murakami 2001). Many ecosystems are characterized by pulsed allochthonous resource subsidies with dramatically higher availability, such as marine-derived nutrients (MDN) to freshwater and terrestrial systems, and terrestrial organic matter to aquatic systems. Such cross-ecosystem trophic subsidies are especially important in coastal freshwaters of the Pacific northwest, where most coastal streams are oligotrophic and unproductive (Bisson & Bilby 1998).

Because secondary production within unproductive streams along the Pacific coast is not sufficient to support large salmonid populations, juvenile Pacific salmon enter the north Pacific Ocean, which is more productive than most high-latitude freshwaters, to access abundant food resources for growth (Gross *et al.* 1988). Maturing salmon return to their natal freshwaters to reproduce. After spawning the adults die and the flux of MDN, especially nitrogen (N) and phosphorus (P) from decomposing salmon carcasses, may result in whole ecosystem nutrient enrichment (Willson *et al.* 1998). The nutrient content supplied by salmon carcasses can be 3.04% N and 0.36% P of wet body weight (Larkin & Slaney 1997). As cross-ecosystem subsidies, these MDN fluxes can be crucial resources for sustaining productivity and influencing biodiversity of the recipient ecosystems (Naiman *et al.* 2002) by enhancing trophic pathways in oligotrophic freshwaters (Kline *et al.* 1997). MDN can stimulate autotrophic production in streams, and dissolved organic matter (DOM) released by decomposing carcasses fuels microbial metabolism, and thereby increases productivity and enhances trophic dynamics (Bilby *et al.* 1996; Wipfli *et al.* 1999). Salmon carcasses are also directly consumed by macroinvertebrates (Kline *et al.* 1997; Minakawa & Gara 1999). Although some studies have demonstrated that MDN from salmon carcasses increased stream productivity (Bilby *et al.* 1998; Wipfli *et al.* 1998), and salmon carcasses were often retained with organic debris (Cederholm & Peterson 1985; Cederholm *et al.* 1989), very little is known about the influence of salmon carcasses on the processing of organic matter, a critical ecosystem function. In theory, given the consensus that coastal freshwaters have generally low productivity, the release of dissolved carbon, N and P from decomposition of salmon carcasses increases nutrient levels in streams, which in turn should enhance leaf litter breakdown (Robinson & Gessner 2000; Rosemond *et al.* 2001). Determining how MDN impact stream ecosystem functioning through influencing organic matter processing is important for quantifying the relative contribution of the allochthonous resource fluxes from highly productive marine systems into low-productivity headwater ecosystems.

Among common deciduous riparian tree species in the Pacific northwest coast ecoregion, red alder (*Alnus rubra*) is an abundant riparian tree distributed along streams and

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rivers from California to Alaska (Naiman *et al.* 2002). Red alder is an N-fixing, fast-growing and early-successional species, which can influence nutrient cycling and long-term productivity in the forests by contributing large amounts of N to soils and streams (Naiman *et al.* 2002). As an allochthonous organic matter subsidy, red alder leaf litter can have a significant ecological impact on headwater streams (Piccolo & Wipfli 2002). In this study, we investigated effects of MDN on breakdown rate of red alder leaf litter in a forested, oligotrophic stream. We manipulated the flux of MDN (salmon carcasses) in experimental streams to examine the functional consequences of this cross-ecosystem subsidy on stream ecosystem functioning. We predicted that MDN addition should increase the breakdown rate of red alder leaf litter. Here, we present a striking and unexpected process linking the dynamics of MDN and its influence on the ecosystem function of organic matter processing.

2. METHODS

This study was conducted in experimental streams on the floodplain of Mayfly Creek (49°18′ N, 122°32′ W), which is located in the Coast Range Mountains 60 km east of Vancouver, British Columbia, Canada. The maritime climate of this area is characterized by high annual precipitation and moderate temperatures with dry, cool summers and wet, warm winters. Mayfly Creek is a second-order, oligotrophic headwater tributary of the North Allouette River, which drains an area of second-growth, coastal western hemlock forest. This stream had low concentrations of inorganic P (less than 5 $\mu g\,l^{-1}$ as orthophosphate) and inorganic N (less than 60 $\mu g\,l^{-1}$ as nitrate). The vegetation of the watershed is dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and Douglas fir (*Pseudotsuga menziesii*). The riparian vegetation is red alder, vine maple (*Acer circinatum*) and salmonberry (*Rubus spectabilis*). Among Pacific salmon species, chum salmon (*Oncorhynchus keta*) have the widest geographical distribution in the northern Pacific Ocean (Salo 1991). Spawning chum salmon enter headwater streams and rivers from August to February and carcasses can remain for several months in some headwater streams in the Pacific northwest (Cederholm *et al.* 2000).

To examine the effects of chum salmon carcasses on the breakdown of red alder leaf litter, we established three treatments in experimental streams, each with three replicate streams (nine stream channels): chum carcass plus alder leaves—a high nutrient level; alder leaves only—an intermediate nutrient level; and artificial leaves—a low nutrient level. The experiment ran from 22 December 2000 to 11 April 2001. Although alder leaf litter fall peaked in autumn, the amount of leaf litter directly entering streams was relatively small. A large part of the alder litter remained along stream banks. Leaf litter from banks entering streams was a continual process driven by wind blowing, storm run-off and large animal movement. Experimental, flow-through stream channels (15 m long and 0.3 m wide) located on the floodplain of Mayfly Creek contained rounded gravel substratum with a 4 cm maximum diameter that created a riffle habitat. Experimental streams were fed by stream water with naturally drifting invertebrates, which was diverted from Mayfly Creek 100 m upstream of the channels, and passed through a holding tank to reduce mineral sediments before entering the experimental streams. Because natural spawning runs of chum salmon did not reach Mayfly Creek owing to impassable barriers, we collected chum salmon carcasses from the North Allouette River, where chum salmon were a predominant salmon species spawning from October to December. Chum carcasses that had been in the river for about one week were collected 1 day before starting the experiment and preserved in snow overnight. We added a 1.3 kg piece of carcass trunk for each of the salmon carcass treatment channels, or a stone of similar size for the controls, in a 25 cm pool in the experimental stream. We placed 10.00 ± 0.25 g air-dried alder leaves or 22.50 ± 0.25 g artificial polyester leaves (standardized for surface area to match the real leaves) into 15 cm × 15 cm plastic mesh bags (1 cm mesh size). Artificial leaves were used to simulate microhabitats created by leaves. Three alder leaf packs or artificial leaf packs were set 30 cm downstream of the pool with a carcass or a stone in each channel. Average discharge in each experimental stream was 1.27 $l\,s^{-1}$ and mean water temperature logged at 1 h intervals was 3.1 °C (range of 0.2–5.4 °C) during the study period. Experimental streams were covered with 2 m-wide aluminium mesh (mesh spacing 2 cm) above those treatments for protection. We retrieved leaf packs on days 62, 85 and 111 of the experiment. Leaf litter remaining at each sampling date was carefully removed from the plastic mesh pack, washed, dried for at least 24 h and reweighed in the laboratory. Organic matter and benthic invertebrates were rinsed from leaf surfaces and washed through 1 mm and 64 μm sieves. Invertebrates were picked under a stereomicroscope (15× magnification) from organic matter for the sieve fraction greater than 500 μm and stored in 70% ethanol. Fine organic matter (FOM) (0.63 $\mu m < \text{FOM} < 1$ mm) was dried, weighed, ashed for 2 h at 500 °C and reweighed to obtain ash-free dry mass (AFDM). We also picked some invertebrates from carcasses in the experimental streams, because those carcasses were deeply decomposed by day 111 and we could not sample all invertebrates. Benthic invertebrates were identified to species following keys (Merritt & Cummins 1996) or to the lowest level we could reach. We used body length–mass regressions (Benke *et al.* 1999) to calculate invertebrate biomass.

The percentages of remaining dry weight of alder leaf packs in the streams with and without carcass addition were analysed using repeated-measures (sampling date) analyses of variance (ANOVA) with treatments as the main effect. Because repeated-measures ANOVA can only determine the overall effect of three sampling dates, we subsequently used one-way ANOVAs to test the treatment effect on the amounts of alder leaf remaining on each sampling date. We used a series of one-way multivariate analyses of variance (MANOVAs) to test effects of three treatments (i.e. artificial leaves, alder leaves with and without carcass addition) on species richness, abundance and biomass of benthic invertebrates and different functional groups on each sapling datum. Univariate ANOVAs were used to examine treatment effects on each response variable. The normality of all raw data was examined using a Shapiro–Wilks *W*-test, and non-normal data were log-transformed.

3. RESULTS AND DISCUSSION

The salmon carcass treatment had a significant effect on the alder litter remaining (percentage) in leaf packs (one-way, repeated measures ANOVA: $F_{1,3} = 19.03$, $p = 0.02$; figure 1). Salmon carcass addition reduced alder litter breakdown in the experimental streams during the overall period. The within-subject effect of sampling date was significant on the amount of litter remaining

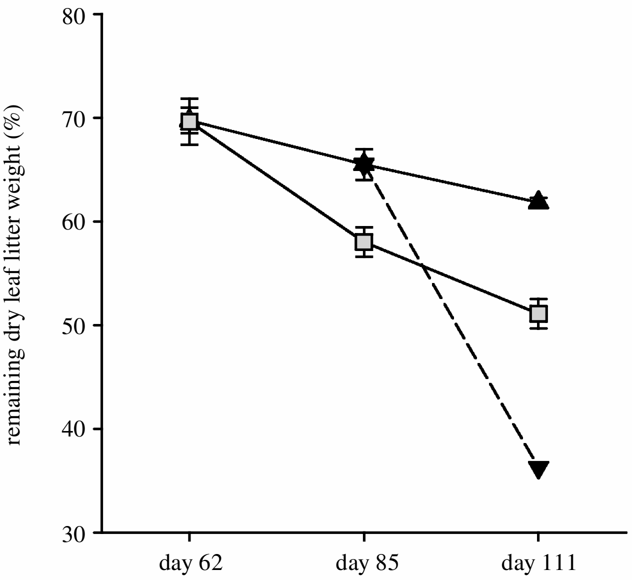

Figure 1. Effects of MDN on dry mass remaining of red alder leaves. Mean percentage (± s.e.) of alder leaf dry weight remaining in the litter packs in the experiment streams ($n = 3$ streams, except leaf plus salmon on day 111 with $n = 2$, and leaf plus salmon removed with $n = 1$). Upright triangles, leaf plus salmon; squares, leaf; inverted triangles, leaf plus salmon removed. The artificial leaf weights remained at 100% (not shown).

($F_{2,6} = 31.64$, $p < 0.001$). There was a significant interaction between sampling date and treatment ($F_{2,6} = 7.41$, $p = 0.02$), which was because the slopes of the regressions of litter remaining data with and without carcasses were different (figure 1). ANOVAs on amount of alder litter remaining (percentage) revealed no difference between treatments on day 62. However, by day 85, the litter weight remaining (percentage) in alder leaf packs in the streams with the carcass treatment was significantly higher than that without carcass addition ($F_{1,4} = 13.03$, $p = 0.02$), and this difference was further increased by day 111 ($F_{1,3} = 32.41$, $p = 0.01$). After day 85, the carcass from one experimental stream was removed by a small mammal, and the rate of leaf breakdown in this pack before day 111 sharply increased (data from this litter pack were not used in any ANOVA). By day 111, only 36% of the original litter weight remained in the stream from which the salmon carcass had been removed, in contrast to 62% for streams with carcasses and 51% without carcasses (figure 1).

Why does salmon carcass enrichment retard the detrital-processing ecosystem function, contrary to our prediction? The cause is related to detritivorous consumers that switched food resources during the experimental period. Among 36 common benthic taxa found in leaf packs, 13 detritivore species constituted 54%, 51% and 67% of the total benthic macroinvertebrate biomass on the three sampling occasions. Within the detritivore group, five species of larval caddisflies (Trichoptera) made up 22%, 69% and 69% of the detritivore biomass by days 62, 85 and 111, respectively. Detritivorous caddisfly biomass in the litter packs without carcass addition was significantly higher than in the carcass-treated litter packs and the artificial leaves on day 85 ($F_{2,6} = 12.56$, $p = 0.007$; table 1, figure 2*a*) and day 111 ($F_{2,5} = 9.71$, $p = 0.019$). The key detritivore species among these consumers was *Ecclisomyia conspersa* (Trichoptera, Limnephilidae), whose biomass made up 66.3% of total detritivore biomass across all treatments on day 85, and 63.6% on day 111 (table 1). There was no *E. conspersa* in artificial leaf packs. The average total biomass of *E. conspersa* in the litter packs without carcasses was 10 times greater than that in carcass-treated packs on day 85 (figure 2*b*). On day 111, *E. conspersa* was not found in the carcass-treated litter packs, but only in the litter packs without carcasses. The large amount of litter remaining with carcass addition was related to the absence of this key detritivore on the leaf litter. Because nutritional constraints generally determine the energy balance and growth rate or fitness of consumers (Tilman 1982), high-quality food supports rapid growth of consumers. P is often limited in oligotrophic headwaters of the northwest Pacific coast (Willson *et al.* 1998). Mature salmon may contain 3.04% N and 0.36% P of average body weight (Larkin & Slaney 1997). The carcasses enriched with N and P were a high-quality resource for the growth of detritivorous Trichoptera (Chaloner & Wipfli 2002). An organism's growth and reproduction depend on its physiological state and its condition, such as habitat quality, foraging strategy and energy reserves (McNamara & Houston 1996). Apparently using a state-dependent foraging decision, those detritivores shifted from their low-quality detrital diet to exploit the resource patches with high nutritional value, i.e. salmon carcasses. In a laboratory growth experiment, *E. conspersa* did show faster growth on coho salmon carcasses than on red alder leaves (Minakawa *et al.* 2002). By day 111 we found 11 detritivorous species on carcasses in the experimental streams, with four species of Trichopteran detritivores including *E. conspersa*. The average total biomass of detritivorous Trichoptera on the carcasses was 4.5-fold more than that in the carcass-treated leaf packs. The average individual biomass of *E. conspersa* on the carcasses was 19% greater than that on the leaves without carcass addition by day 111.

When a carcass piece was removed by a small mammal part way through the experiment, detritivorous consumers left the carcass. This escape response of leaving a disturbed food patch is common to stream detritivores (Y. Zhang, personal observation). Those detritivores required food resources for completion of their larval stage and the only other available resource was alder leaf litter in the experimental stream. These consumers moved to the litter pack and shifted their diet back to the lower-quality resource. In the carcass-removed stream, the average biomass of detritivorous caddisflies in the leaf pack was markedly higher on day 111 (figure 2*a*). The biomass of *E. conspersa* increased abruptly in the leaf pack in the carcass-removed stream (figure 2*b*), and the total dry mass of *E. conspersa* in this leaf pack was about 3.5-fold greater than that in the packs without carcasses on day 111. These large caddisfly larvae in the carcass-removed leaf pack must have come from the removed carcass, because *E. conspersa* was absent from leaf packs in channels where carcasses were not removed, but was present on those carcasses in the experimental streams. Diet switching may be a common phenomenon for detritivores, especially in Trichoptera (Anderson 1976). By feeding on a large amount of the low-quality resource, these big food-limited

Table 1. *F*-values of MANOVAs and ANOVAs for the effects of artificial leaves, alder leaves and alder leaves with carcass addition on species richness, abundance and biomass of benthic invertebrates and different functional groups on three sampling dates.

(Values in parentheses are average values of dependent variables under different treatments pooled on days 62, 85 and 111, respectively. S, alder leaf plus salmon carcass; L, alder leaf; A, artificial leaf; S*, alder leaf plus salmon carcass removed; rich., species richness; abun., abundance (individual number); biom., biomass (dry mass, mg). Probability levels are: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.)

			all invertebrates			detritivores			Trichoptera			*Ecclisomyia*	
source	d.f.	Wilks' lambda	rich.	abun.	biom.	rich.	abun.	biom.	rich.	abun.	biom.	abun.	biom.
day 62													
MANOVA	2, 12	24.19*											
ANOVAs	2		8.80*	32.4**	0.68	2.89	3.37	1.53	0.71	0.59	0.56	0.78	0.78
error	6												
S			(11.5)	(92.0)	(11.4)	(3.0)	(5.5)	(4.6)	(1.0)	(1.0)	(1.0)	(0)	(0)
L			(10.7)	(74.5)	(12.5)	(3.6)	(9.3)	(8.6)	(0.6)	(1.3)	(2.5)	(0.7)	(1.0)
A			(6.3)	(19.0)	(7.4)	(1.7)	(4.3)	(3.1)	(0)	(0)	(0)	(0)	(0)
day 85													
MANOVA	2, 12	11.28											
ANOVAs	2		25.03**	27.2***	9.72*	12.64**	8.32*	5.20*	4.70	6.48*	12.56**	7.24*	13.17**
error	6												
S			(18.7)	(173)	(20.9)	(6.3)	(16.7)	(10.9)	(3.0)	(4.3)	(3.6)	(1.3)	(2.4)
L			(15.3)	(142.3)	(44.3)	(5.3)	(19.3)	(27.2)	(1.7)	(6.0)	(23.4)	(5.0)	(23.3)
A			(8.3)	(40.7)	(10.5)	(2.0)	(3.7)	(0.7)	(0)	(0)	(0)	(0)	(0)
day 111													
MANOVA	2, 10	1.55											
ANOVAs	2		3.49	49.2***	11.19*	5.64	11.93*	15.4**	8.0*	8.95*	9.71*	25.30***	123.68***
error	5												
S			(12.5)	(158.5)	(39.2)	(4.5)	(18.5)	(19.9)	(1.5)	(4.0)	(5.4)	(0)	(0)
L			(11.7)	(79)	(27.8)	(4.3)	(12.7)	(23.9)	(1.3)	(5.3)	(19.5)	(4.7)	(19.4)
A			(7.7)	(20.3)	(8.9)	(1.3)	(3)	(0.8)	(0)	(0.0)	(0)	(0)	(0)
S*			(19)	(235)	(107.7)	(6)	(46)	(83.5)	(2)	(12)	(67.4)	(10)	(67.4)

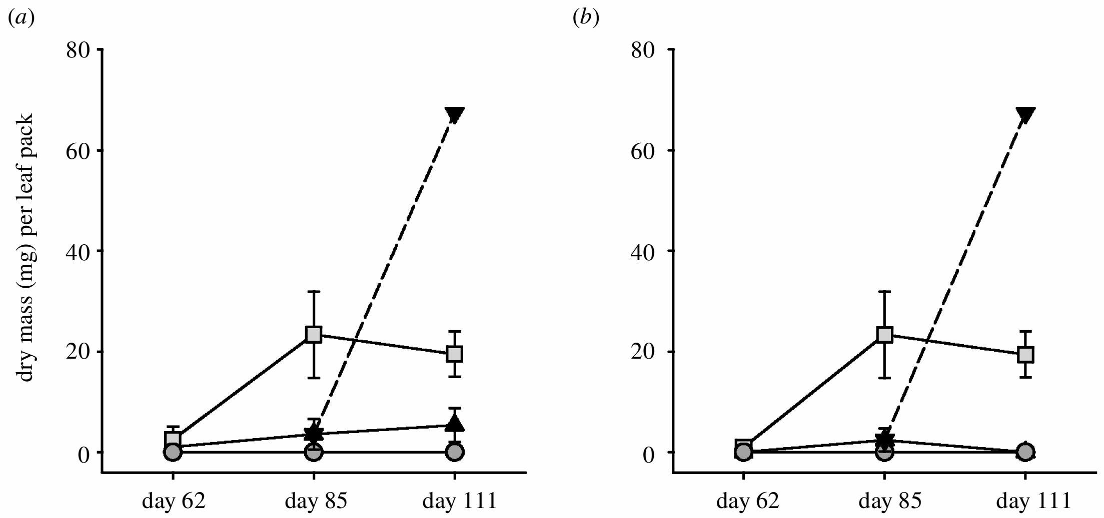

Figure 2. Effects of MDN on mean values (± s.e.) of detritivorous caddisfly biomasses: (*a*) biomasses of detritivorous larval caddisflies (Trichoptera); and (*b*) biomasses of a key caddisfly detritivore, *Ecclisomyia conspersa*, in the leaf litter packs with different treatments. Upright triangles, leaf plus salmon; squares, leaf; circles, artificial leaf; inverted triangles, leaf plus salmon removed.

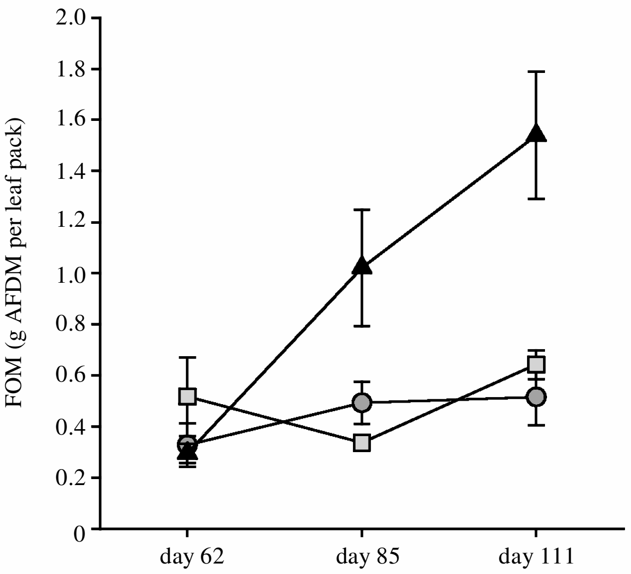

Figure 3. AFDM of FOM accumulated in the leaf packs with different treatments in the experimental streams. Upright triangles, leaf plus salmon; circles, artificial leaf; squares, leaf.

consumers sharply reduced litter remaining in this pack (figure 1).

AFDM of FOM that accumulated on leaf surfaces differed significantly among the three treatments (day 85, ANOVA $F_{2,5} = 6.49$, $p = 0.03$; day 111, $F_{2,5} = 16.47$, $p = 0.006$; figure 3). There was more FOM mass in the carcass-treated leaf packs by days 85 and 111. This difference of FOM mass among treatments increased with experimental duration. In carcass-treated leaf packs, the slope of the relationship between FOM mass and experimental duration was 0.62, which was considerably steeper than those for the leaf bags in the other two treatments (both less than 0.1). The FOM mass in the carcass-treated leaf packs on day 111 was threefold greater than in the artificial leaf packs, and 2.4-fold greater than in the alder leaf packs without carcasses upstream. There were no significant differences in FOM amount between the artificial leaf packs and the alder leaf packs without carcasses. Salmon carcass additions significantly increased FOM accumulation on leaf surfaces. Fine-particle collectors showed significantly higher abundance and biomass in the leaf packs in response to salmon nutrient enrichment (day 111, $F_{2,5} = 34.8$, $p = 0.0012$ for abundance, $F_{2,5} = 42.28$, $p = 0.0007$ for biomass; table 2). On day 111, collectors in carcass-treated leaf packs had twice as many individuals and 2.7-fold more biomass than in the alder leaf packs, and 10-fold more individuals and 7.6-fold more biomass than in the artificial leaf packs, which had a very low FOM level. High abundance and biomass of collector invertebrates in the carcass-treated leaf packs suggest that there was a significant nutrient contribution from salmon carcasses to the collector invertebrate community. It is not clear if this large amount of FOM in the carcass-treated leaf packs was related to the foraging process of detritivores on the carcasses, converting coarse particulate organic matter into finer particles that can be used by collectors. Organisms that modulate the availability of resources to other species are regarded as ecosystem engineers (Jones *et al.* 1997). The possible functional role of detritivores as ecosystem engineers for processing carcasses needs further investigation by manipulating detritivore densities and biomass, in terms of body size, on salmon carcasses. We speculate that the detritivores may function as ecosystem engineers that indirectly enhance the energy flow by processing salmon carcasses to produce FOM, which presumably are of higher quality than typical FOM and benefit the collectors. Given that such complementary resource use increases total resource capture and thus increases net ecosystem production (Hooper 1998), facilitation between these functional feeding groups through increasing community performance beyond that of single functional groups may be one of the important mechanisms influencing ecosystem processes (Heard & Richardson 1995; Loreau & Hector 2001; Cardinale *et al.* 2002).

Table 2. ANOVA probabilities for the effects of the treatments (S, alder leaf plus salmon carcass; L, alder leaf; A, artificial leaf) on species richness, abundance and biomass (dry mass, mg) of four functional feeding groups per leaf pack on three sampling dates. (S, L and A in parentheses represent values of the dependent variables under each column title, i.e. species number, or individual number, or dry body mass. Four functional feeding groups in all leaf packs consisted of 13 species of detritivores, eight species of collectors, seven species of scrapers and eight species of predators. Probability levels are: n.s., no significant difference among treatments, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.)

functional feeding group	sampling date	species richness	abundance	biomass (mg)
detritivore	day 62	n.s.	n.s.	n.s.
	day 85	**(S > L > A)	*(L > S > A)	*(L > S > A)
	day 111	n.s.	*(S > L > A)	**(L > S > A)
collector	day 62	*(L > S > A)	***(S > L > A)	**(S > L > A)
	day 85	**(S = L > A)	**(S > L > A)	**(S > L > A)
	day 111	n.s.	**(S > L > A)	***(S > L > A)
scraper	day 62	n.s.	n.s.	n.s.
	day 85	*(S > L > A)	n.s.	n.s.
	day 111	n.s.	n.s.	n.s.
predator	day 62	n.s.	n.s.	n.s.
	day 85	n.s.	n.s.	***(A > L > S)
	day 111	n.s.	n.s.	n.s.

Our results show unexpected significant effects of MDN on the detrital-processing ecosystem function in a freshwater system, but contrary to our original predictions. Reciprocal exchanges of trophic flows across ecosystem boundaries have profound influences on ecosystem functioning. Alder leaf litter from the riparian ecosystem was processed by organisms in the stream ecosystem, and this ecosystem function was influenced dynamically by salmon-derived nutrients from the marine ecosystem. Our results indicate that one resource–consumer relationship (detritus processing) is temporarily decoupled through shifts in the foraging strategy of a key group of exploiters when an alternative, high-nutrient resource is supplied. We speculate that after the pulse of additional nutrients disappears, the resource–consumer relationship could be recoupled as the exploiters shift their diet back to their original resource. This delay in detrital processing could result in a nonlinear response of the ecosystem function to cross-ecosystem nutrient enrichment. Our results imply that cross-boundary MDN subsidies indirectly retard the ecosystem processing of leaf litter in the freshwater system within the short term, but may enhance these food-limited detritivorous consumers (Richardson 1991) that could have positive long-term effects on ecosystem function. Abundant evidence from stable isotopes and comparative studies indicates that salmon spawning streams are generally more productive and retain some MDN compared with non-salmon streams (reviewed by Gende *et al.* 2002; Naiman *et al.* 2002; Schindler *et al.* 2003). Our study suggests that salmon carcasses can influence stream ecosystem functioning by affecting detrital resource–consumer relationships, and enhance stream secondary production by increasing food-limited invertebrate growth (Wipfli *et al.* 1998, 1999; Chaloner & Wipfli 2002). The short-term foraging switches demonstrated in this study might relate to the long-term build-up effect of salmon carcasses in streams. Invertebrate foraging switches may facilitate carcass decomposition and subsequent DOM release. Through chemical uptake of DOM by streambed substrate, the DOM from carcasses can be sorbed onto the epilithic organic matter layer (Bilby *et al.* 1996). Furthermore, carcass use by invertebrates may produce fine organic debris that can directly cumulate on the streambed. These potential mechanisms may contribute the MDN retention and long-term storage in salmon-bearing streams.

The dynamic pattern of MDN impacts on stream ecosystem functioning found in this study could be important to the Pacific coastal ecoregion, because small streams in this region have extensive forest cover with a low light regime, and unproductive freshwaters with limited nutrient supplies are highly dependent upon the organic matter inputs from the forest. Moreover, small headwater streams are sensitive and vulnerable to disturbance by a variety of land uses, which alter stream hydrographs and riparian ecosystems. Reduced salmon populations in headwaters owing to human disturbance may inhibit the productivity of these aquatic ecosystems and decrease further from stream oligotrophication, in a negative feedback. Understanding MDN effects on ecosystem functioning in terms of terrestrial–aquatic linkages in organic matter processing dynamics is important for determining conservation and management strategies of salmon-related aquatic and riparian ecosystems, in terms of salmon habitat protection and restoration, and fisheries exploitation, in the Pacific northwest.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.