Influence of salmon spawner densities on stream productivity in Southeast Alaska

Mark S. Wipfli, John P. Hudson, Dominic T. Chaloner, and John P. Caouette

Abstract: We conducted this study to determine the relationship between salmon spawner abundance and stream biofilm and benthic macroinvertebrate abundance in Southeast Alaska. Experiments took place in outdoor artificial and natural streams. Six pink salmon (*Oncorhynchus gorbuscha*) carcass treatments (0.00, 1.45, 2.90, 4.35, 5.80, and 7.25 kg wet mass) placed in artificial channels were subsampled repeatedly for biofilm ash-free dry mass (AFDM), chlorophyll *a*, and macroinvertebrates. In a small (nonanadromous) forest stream, we sampled benthos throughout a 66-m reach 17 days after distributing 60 carcasses along the lower half of that reach. All response variables significantly increased in response to carcass additions in both artificial and natural streams. Chlorophyll *a* continued to increase across all loading rates, while AFDM and total macroinvertebrate densities showed no further response to loading beyond the first treatment (1.45 kg) in artificial streams. In the natural stream, AFDM and chironomid densities continued increasing across loading levels. These results indicated that increased spawner densities increased lower trophic level abundance until a trophic capacity was reached. Salmon escapement goals should consider food web effects, especially on trophic levels that support juvenile salmonids, that ultimately affect freshwater salmon production.

Résumé : Nous avons entrepris cette étude pour déterminer la relation entre, d’une part, l’abondance des saumons reproducteurs et, d’autre part, l’abondance des films biologiques fluviaux et des macroinvertébrés dans le sud-est de l’Alaska. Les expériences ont été effectuées à l’extérieur dans des canaux artificiels et un cours d’eau naturel. On a procédé à cinq traitements consistant en l’introduction de carcasses de saumon rose (*Oncorhynchus gorbuscha*) (1,45, 2,90, 4,35, 5,80, et 7,25 kg poids humide) avec témoin (0,00 kg) dans des canaux artificiels; on y a prélevé à plusiers reprises des sous-échantillons pour mesurer la masse à sec sans cendre des films biologiques ainsi que la chlorophylle *a* et les macroinvertébrés. Dans un petit cours d’eau forestier non fréquenté par des saumons anadromes, nous avons échantillonné le benthos d’un tronçon de 66 m 17 jours après avoir distribué 60 carcasses dans la moitié inférieure de ce tronçon. Toutes les variables mesurées se sont significativement accrues en réponse aux introductions de carcasses tant dans les canaux artificiels que dans le cours d’eau naturel. La quantité de chlorophylle *a* n’a pas cessé de s’accroître d’un traitement à l’autre, tandis que la masse à sec sans cendre des films biologiques et les densités de macroinvertébrés ont plafonné dès le premier traitement (1,45 kg) dans les canaux artificiels. Dans le cours d’eau naturel, la masse à sec sans cendre des films biologiques et les densités des chironomides n’ont cessé de s’accroître d’un traitement à l’autre. Ces résultats ont indiqué que l’accroissement des densités de reproducteurs a eu pour effet d’accroître l’abondance des organismes des niveaux trophiques inférieurs jusqu’à atteinte d’une capacité trophique donnée. Dans l’établissement des objectifs concernant l’échappée des saumons, on devrait considérer les phénomènes intervenant dans le réseau alimentaire, particulièrement ceux qui touchent les niveaux trophiques dont dépendent les salmonidés juvéniles, lesquels déterminent ultimement la production de saumons dans les eaux douces.

[Traduit par la Rédaction]

Introduction

Movements of nutrients, detritus, and prey among habitats can influence populations and community dynamics, increasing consumer resources and subsidizing food webs (Polis et al. 1997). Subsidies across habitats are common in stream ecosystems where they often elevate productivity. For instance, nutrients received from groundwater can stimulate stream primary production (Coleman and Dahm 1990), allochthonous litter from riparian forests comprises the trophic base for detritivores in small forested streams (Cummins et al. 1983), and terrestrial invertebrates falling from riparian vegetation form a large fraction of some salmonid diets (Wipfli 1997).

Contrary to the conventional view that material flows from land to freshwater and then to the sea (Vannote et al. 1980; Maser and Sedell 1994), a massive movement of organic material and nutrients occurs annually from marine to freshwater and terrestrial ecosystems via the migration of anadromous fishes (Levy 1997). This “upstream” marine subsidy to freshwater and land is poorly understood and the ecological effects likely underestimated (Willson et al. 1998). These linkages may be critical for sustaining freshwater and terrestrial productivity, especially at land–water interfaces (Polis et al. 1997; Wipfli et al. 1998).

Alaska and parts of western Canada represent the few re-

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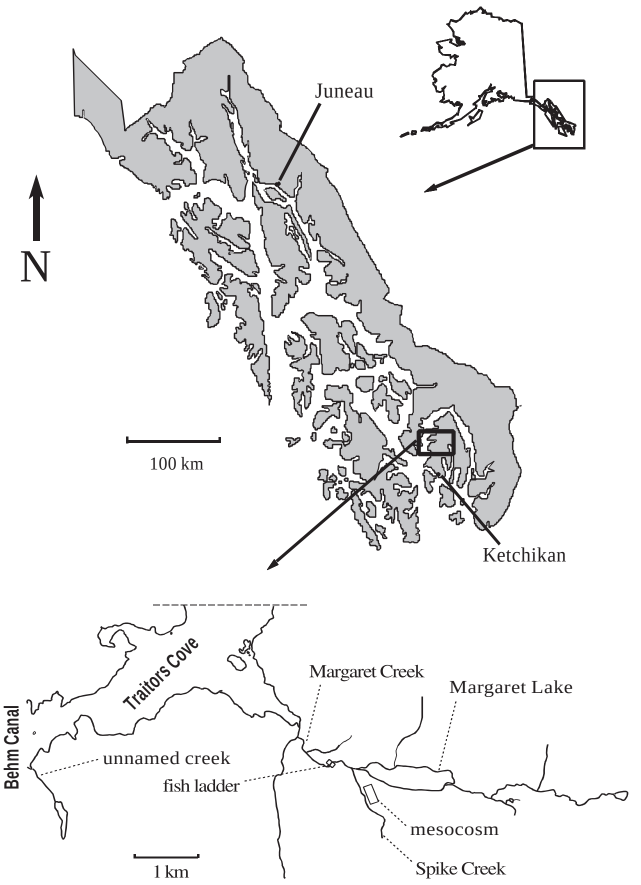
Fig. 1. Study site on Revillagigedo Island, Southeast Alaska.



maining areas of North America that still support historic runs of salmon (Baker et al. 1996; Slaney et al. 1996). Here, millions of salmon return to their natal habitats every year to spawn and die (Wertheimer 1997), bringing with them thousands of tons of marine-derived nutrients (MDN) to freshwater (Mathisen et al. 1988). Southeast Alaska is a major Pacific salmon producer (Wertheimer 1997) and contains over 5200 anadromous salmon streams totaling 40 000 km in length (Halupka et al. 1999). Salmon have great potential to subsidize multiple trophic levels in these systems because (*i*) they are nutrient rich (Mathisen et al. 1988), (*ii*) they contain desirable stoichiometry (Hesson 1997), (*iii*) their runs often span much of the year and achieve high numbers (Groot and Margolis 1991), (*iv*) they can decompose slowly (from weeks to months) (Kline et al. 1997; Wipfli et al. 1998) metering nutrient release over time (Parmenter and Lamarra 1991), and (*v*) they are consumed by many invertebrates and vertebrates in both freshwater and riparian food webs (Cederholm et al. 1989; Bilby et al. 1996; Wipfli et al. 1998).

There are several pathways by which MDN can influence freshwater and riparian food webs. The death and decomposition of salmon after spawning increases freshwater nutrient levels (Mathisen et al. 1988; Schuldt and Hershey 1995); increased productivity associated with this enhanced nutrient supply can influence food webs (Kline et al. 1990; Wipfli et al. 1998). Also, direct material transfer occurs through ingestion of salmon tissue and eggs by invertebrates and fishes including juvenile salmon (Kline et al. 1997; Bilby et al. 1998). This subsidy may be particularly important to juvenile salmon whose overwinter survivorship is largely dependent on body size (Quinn and Peterson 1996), a function of food intake during the growing season (Groot and Margolis 1991). As a consequence of these mechanisms, anadromous salmon runs may not only affect other taxa, but they may also be driving a positive feedback that controls their own productivity and population density.

Stable isotope analyses (carbon and nitrogen) have shown that MDN occur in selected components of freshwater and terrestrial food webs in the Pacific Northwest (Kline et al. 1990; Bilby et al. 1996). It is unclear if MDN are an obligate component of watersheds with salmon runs, truly subsidizing their productivity, or a facultative component where local nutrient supply could otherwise substitute for MDN. In view of the inherent nutrient-limited state of Pacific Northwest freshwater ecosystems (Gregory et al. 1987; Kyle et al. 1997), ecological effects of MDN enrichment could be immense. Further, the ramifications of suppressed or lost salmon runs, and consequent reduced nutrient supply, could be severe. Placing spawned-out hatchery salmon in streams has been considered to help facilitate salmon stock restoration in Washington and Oregon (Levy 1997). Slow-release “salmon bricks” (processed and compressed salmon byproducts designed to meter nutrients into surface waters) as well as artificial fertilizers are also being used as salmon stock restoration tools in Pacific Northwest systems (Ashley and Slaney 1997; P. Kiffney, NMFS, Seattle, Wash., personal communication) where stocks have sharply declined (Gregory and Bisson 1997).

The objectives of this study were to determine the effects of carcass loading (range of salmon carcass densities) on aquatic productivity, in terms of biofilm, chlorophyll *a*, and macroinvertebrate abundance, in artificial and natural streams in Southeast Alaska. Our hypotheses were that (*i*) salmon provide a nutrient subsidy that stimulates freshwater productivity, measured as increased standing stock of lower trophic levels (microbes, invertebrates), and (*ii*) increasing spawner density (i.e., nutrient loading) supports increased lower trophic level standing stock until a trophic capacity is reached beyond which more nutrients provide no additional subsidy. In addition to evaluating an emerging paradigm in ecosystem ecology, marine subsidy of freshwater food webs, these results should aid in developing more complete guidelines for fisheries and ecosystem management, including salmon stock protection and restoration, throughout the North Pacific Rim.

Methods

Study site

This study was conducted on Revillagigedo Island, Southeast Alaska (Fig. 1). Details of the study area, including species of anadromous and resident fishes, are given in Wipfli et al. (1998). Artificial stream experiments spanned from 1 September through 31 October 1997 and a natural stream experiment from 18 August through 4 September 1997.

Mesocosm experiment

The mesocosm experiment was conducted in 30 straight once-through artificial stream channels described by Wipfli et al. (1998), each 250 cm long × 18 cm wide and constructed next to Spike

Table 1. Salmon carcass treatments and mass and corresponding carcass concentrations and densities used in the mesocosm and natural stream experiments.

	Treatment (mesocosm) or Pool No. (natural stream)					
	1	2	3	4	5	6
Mesocosm						
Number of carcasses[a]	0	1	2	3	4	5
Wet mass (kg)	0	1.45	2.90	4.35	5.80	7.25
Estimated dry mass (kg)	0	0.54	1.07	1.61	2.15	2.68
Carcass concentration per volume of water (kg wet mass·L water^{-1}·s^{-1})	0	3.02	6.04	9.06	12.08	15.10
Carcass mass per streambed area (kg wet mass·m^{-2})	0	3.22	6.44	9.67	12.89	16.11
Natural stream						
Number of carcasses	0	0	0	20	40	60
Cumulative wet mass (kg)	0	0	0	35	73	112
Estimated cumulative dry mass (kg)	0	0	0	13	27	41
Cumulative carcass concentration (kg wet mass·L water^{-1}·s^{-1}) during baseflow (9 L·s^{-1})	0	0	0	4.2	8.7	13.3
Cumulative carcass concentration (kg wet mass·L water^{-1}·s^{-1}) during typical flow (53 L·s^{-1})	0	0	0	0.7	1.4	2.1
Progressive carcass mass per streambed area (kg wet mass·m^{-2}) calculated at baseflow	0	0	0	2.1	1.7	1.9

[a] Minus the tail section from each fish.

Creek, a second-order tributary of Margaret Creek. Stream water from a nonanadromous portion of Spike Creek was gravity-fed with plastic pipes through 170-L sediment traps and then into a header tank. Water flowed from the header tank into each channel through flow-control valves and was then directed back to Spike Creek. The mesocosm was designed to provide unrestricted invertebrate drift with stream flow into and out of channels.

Each channel was divided into three areas: a 60-cm pool for carcass treatments, a 20-cm turbulence reduction area, and a 160-cm riffle. The riffle was subdivided into substrate baskets for sampling invertebrates and tiles for sampling biofilm. Six Vexar® substrate baskets (20 × 18 × 5 cm, 6 × 6 mm opening mesh) were used, each lined with fiberglass mesh (1.6-mm openings) and filled with sand and gravel collected from a natural stream. Eighteen unglazed clay tiles (5 × 5 cm), in a 6 × 3 matrix and level with the substrate baskets, were placed at the downstream end of each riffle. Invertebrates immediately began colonizing substrata in channels via drift from the natural stream. Stream water passed through the channels for 4 days before the experiment began. During the experiment, discharge through channels was 0.48 ± 0.02 L·s^{-1}, and water temperature, continuously logged at 1-h intervals, averaged 8.8°C (range 2.3–12.9°C).

Six treatments were applied: five incremental increases of salmon carcass tissue (1.45, 2.90, 4.35, 5.80, and 7.25 kg wet mass) and a control (no carcass) (Table 1) that fell within the range of spawner densities observed in nearby streams. Live female pink salmon (*Oncorhynchus gorbuscha*) (48–52 cm fork length) with eggs were collected from Margaret Creek on 31 August and 1 September and were given a sharp blow to the head. A portion of the tail and caudal peduncle was removed, such that each fish weighed 1.45 kg (wet mass). Using one gender helped reduce among-channel variability. Although either gender could have been used, we chose females because of the visual abundance of eggs scattered on streambeds during and after spawning, which we postulated might also influence benthic communities. The eggs comprised 15% of fish wet mass. Fish were then randomly selected, and one to five were placed in the pools of channels to produce six treatment levels (Table 1). To determine the mean ratio of dry to wet mass, six fish were weighed wet and then oven dried at 80°C and reweighed. The ratio (0.37) was used to estimate the initial mass of carcass material placed into each channel. Each table was covered with Plexiglas® that was anchored with a wooden frame to protect carcasses from bears and other scavengers. Benthic invertebrates were sampled six times and biofilm was sampled five times during the 60-day experiment. All 30 channels were subsampled during each sampling event.

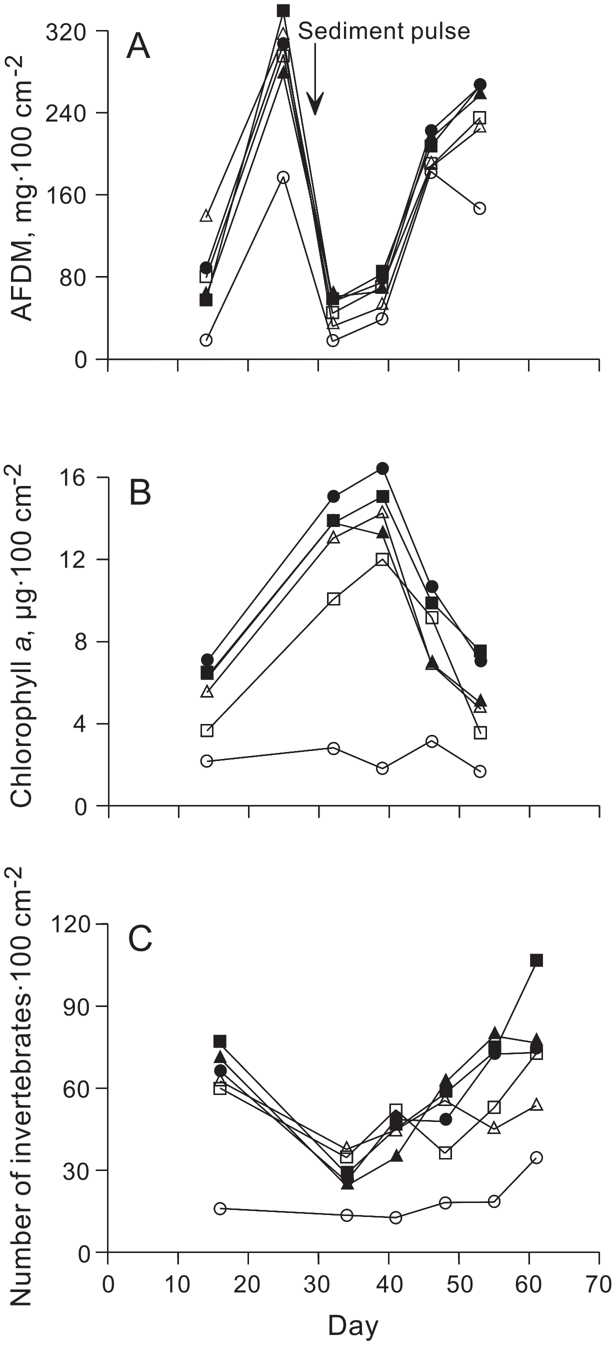
Benthic macroinvertebrates were sampled from sand–gravel substrata in baskets. Sampling of individual tables was completed each day, but sampling of all tables was spread over 2 days, two tables on the first day and three on the subsequent day. Individual baskets were removed with a 250-µm net placed downstream to collect any dislodged invertebrates. Removed baskets were immediately replaced with another substrate basket. Although this net mesh size may have allowed some small invertebrates to pass through, no treatments or channels were biased; they all received the same collection technique. Macroinvertebrates were washed from substrata, sorted live, identified to the lowest reliable taxon, and counted on-site. Unusual taxa were collected and examined more closely under magnification in the laboratory. Representative specimens are held in the invertebrate collection at the Pacific Northwest Research Station, Juneau, Alaska.

Biofilm was collected from the upper surface of tiles for ash-free dry mass (AFDM) and chlorophyll *a* measurements. Three tiles were removed from each channel and immediately replaced with three new tiles. An estimate was made of surface biofilm area coverage intact after sloughing; biofilm was scraped, brushed, and flushed from each tile with distilled water into a graduated cylinder. The sample was vigorously stirred, split between two cylinders, the total volume noted, and then filtered onto two separate glassfiber filters (Whatman® GF/F); filters used for AFDM were all preashed, prewashed, and preweighed. Samples were kept frozen until they were processed and transported to the laboratory in coolers. Filters for chlorophyll *a* analysis (see Steinman and Lamberti 1996) were stored with dry ice for the shipping to University of Notre Dame. Those for AFDM were oven dried, weighed, ashed at 500°C, and reweighed to determine AFDM (see Steinman and Lamberti 1996).

Natural stream experiment

As in Wipfli et al. (1998), this study focused around a controllable and statistically rigorous mesocosm experiment in conjunction with a natural stream experiment to see whether similar patterns in biota abundance were found in natural and artificial systems. We

Fig. 2. Mean (A) AFDM, (B) chlorophyll *a* density, and (C) benthic macroinvertebrate density in the mesocosm experiment in response to salmon carcass treatments: 0.00 (○), 1.45 (△), 2.90 (□), 4.35 (●), 5.80 (▲), and 7.25 kg wet mass (■). The arrow represents the timing of a large freshet that caused a sediment pulse to pass through the channels.



used six pool–riffle sequences over a 66-m reach within a nonanadromous portion of a small (2-m-wide) unnamed stream near Margaret Creek. In the riffle below each pool, we placed two 15 × 15 cm unglazed clay tiles and four baskets (25 cm wide × 25 cm long × 10 cm high) filled with natural substrate from Margaret Creek. Tiles were placed on the streambed surface and baskets buried flush with the surface of the rest of the substrata within the riffle. Water temperature in the natural stream, continuously logged at 1-h intervals, averaged 16.7°C (range 14.6–19.6°C) during the experiment. The temperature range was higher than that of the mesocosm, probably because this experiment was conducted during the warmer part of the season and because the creek drained the relatively warm surface water from a small (6 ha) lake.

Three upstream pools within the experimental reach served as the control. Twenty pink salmon carcasses were tethered in each of the three downstream pools, providing a total wet mass of 35, 38, and 39 kg·pool^{-1}, respectively (1:1 gender ratio). The resultant cumulative carcass concentrations and densities are given in Table 1.

Biofilm was sampled from all tiles on 3 September using the whole tile and AFDM determined as described earlier. Because the natural stream study was intended as a less rigorous counterpart of the artificial stream experiment, we decided to measure one biofilm response and chose AFDM as a more robust indicator of the microbial community. Benthic macroinvertebrates were sampled from baskets on 4 September. Baskets were removed from the riffle with a kick net held downstream to capture escapees. The contents of the net and substrate were then washed from substrate with stream water. Although baskets were filled with the same volume of substrate, some lost or gained a small amount of substrate during the experiment. For this reason, the final volume of gravel within each basket was measured and used to make a correction to invertebrate abundance. The correction averaged 21% among baskets. The substrate was washed on a 250-µm sieve; material washed from substrate and retained on the sieve was preserved in a 5% formaldehyde solution. Samples were later washed with water through 1-mm and 250-µm sieves in the laboratory. All invertebrates retained by the 1-mm sieve and a quarter of those retained by the 250-µm sieve were processed as described earlier. Representative specimens were placed in the invertebrate collection of the Pacific Northwest Research Station, Juneau, Alaska.

Experimental design and statistical analyses

Response variables for analyses were biofilm AFDM and chlorophyll *a* and benthic macroinvertebrate abundance in the mesocosm experiment and biofilm AFDM and benthic macroinvertebrate abundance in the natural stream experiment. Macroinvertebrates were identified to the lowest reliable taxon and analyzed at two general taxonomic resolutions: total taxa and family or genus.

We used a randomized split-plot design replicating six treatments and six subtreatments across five blocks for the mesocosm experiment. Treatments (one control and five amounts of salmon carcass mass) were randomly assigned to one of six channels within a table (block). Channels were whole units that each contained six equal-sized substrate baskets (subunits) for macroinvertebrate sampling. To minimize confounding effects between basket location and time, basket selection was determined using a 6 × 6 Latin square. Experimental design and data structure were similar for AFDM and chlorophyll *a* responses. All data were natural logarithm transformed to meet ANOVA assumptions and were analyzed with PROC GLM (SAS Institute Inc. 1989) at $\alpha = 0.05$. Hypothesis testing included an *F* test for carcass effect (control versus average of all carcass treatments) and regression analyses (slope $\neq 0$) to test for significant responses to incremental carcass mass increases. Time effect and its interaction with carcass treatments were also tested. Data (AFDM and macroinvertebrate abundance) from the natural stream were analyzed similarly to mesocosm data: *F* tests for carcass effect and regression analyses testing for responses to carcass mass increases.

In the case of the natural stream experiment, we caution that comparing stream reaches (with multiple samples taken from each reach) within one stream is pseudoreplication and does not provide a means of separating treatment effects from other variables. Even if significant differences are detected

Table 2. Macroinvertebrate taxa and their corresponding functional feeding group and mean natural logarithm transformed abundance from the mesocosm and natural stream experiments and subsequent statistical output: treatment means and ANOVA and regression results.

Taxon	Functional feeding group[a]	% relative abundance[b]	Treatment mean[c]		ANOVA[c]		Linear regression test for slope ≠ 0, *p*
			Carcass	Control	MS_{error}	*p*	
Mesocosm							
Arthropoda							
Insecta							
Ephemeroptera							
Leptophlebiidae							
Paraleptophlebia	c-g	0.9	nt	nt			
Heptageniidae							
Cinygmula	c-g, sc	2.3	1.30	1.62	0.37	0.012	<0.001
Baetidae							
Baetis[d]	c-g, sc	7.4	1.87	1.14	0.48	<0.001	0.008
Ameletidae							
Ameletus	c-g, sc	0.2	nt	nt			
Plecoptera[e]		0.4	nt	nt			
Nemouridae							
Zapada[f]	sh	11.2	2.97	2.18	0.36	<0.001	0.360
Capniidae	sh	4.6	1.79	1.65	0.27	0.123	0.068
Leuctridae	sh	0.8	nt	nt			
Chloroperlidae							
Sweltsa	p	0.5	nt	nt			
Trichoptera[g]	Several	0.5	nt	nt			
Limnephilidae							
Onocosmoecus	sh	0.4	nt	nt			
Diptera[h]	Several	0.5	nt	nt			
Chironomidae	Several	69.3	4.73	3.32	0.25	<0.001	<0.001
Arachnida							
Acari	om	0.1	nt	nt			
Copepoda		0.4	nt	nt			
Annelida							
Oligochaeta	c-g	0.5	nt	nt			
All taxa		100.0	5.15	4.13	0.23	<0.001	0.091
Natural stream							
Arthropoda							
Insecta							
Ephemeroptera							
Leptophlebiidae							
Paraleptophlebia	c-g	14.2	5.52	5.05	0.12	0.009	0.519
Heptageniidae[i]		0.2	nt	nt			
Cinygmula	c-g, sc	0.9	nt	nt			
Ironodes	c-g, sc	0.6	nt	nt			
Baetidae[j]	c-g, sc	7.3	5.31	3.29	0.29	<0.001	0.159
Plecoptera							
Leuctridae	sh	0.1	nt	nt			
Nemouridae							
Zapada[k]	sh	4.3	4.44	3.94	0.10	0.003	0.514
Chloroperlidae							
Sweltsa	p	10.2	5.02	5.00	0.08	0.871	0.079
Trichoptera[l]	Several	0.5	nt	nt			
Rhyacophilidae							
Rhyacophila	p	1.1	nt	nt			
Hydropsychidae							
Hydropsyche	c-f	0.5	nt	nt			
Diptera							
Tipulidae							
Dicranota	p	0.1	nt	nt			
Ceratopogonidae	p, c-g	1.5	nt	nt			

Table 2 (*concluded*).

Taxon	Functional feeding group[a]	% relative abundance[b]	Treatment mean[c]		ANOVA[c]		Linear regression test for slope ≠ 0, *p*
			Carcass	Control	MS_{error}	*p*	
Chironomidae	Several	53.4	7.24	5.91	0.05	<0.001	<0.001
Simuliidae							
Simulium	c-f	1.6	nt	nt			
Arachnida							
Acari	om	0.1	nt	nt			
Crustacea[m]		0.1	nt	nt			
Annelida							
Oligochaeta	c-g	1.8	nt	nt			
All taxa		100.0	7.79	6.76	0.04	<0.001	0.002

[a] c-g, collector–gatherer; c-f, collector–filterer; sc, scraper; sh, shredder; p, predator; om, omnivore (based on Merritt and Cummins 1996).
[b] Relative abundance as a percentage of all macroinvertebrates pooled across both treatments.
[c] Mesocosm, $n = 5$, df = 20; natural stream, $n = 3$, df = 16; nt, not tested (when <2% of the total abundance).
[d] *B. bicaudatus*, *B. tricaudatus*.
[e] Too small to identify.
[f] *Z. cinctepes*, *Z. columbiana*.
[g] *Micrasema*, *Ecclisomyia*, *Rhyacophila*.
[h] Simuliidae, Certatopogonidae, Tipulidae.
[i] Too small to identify.
[j] *Baetis tricaudatus*, *Diphetor hageni*.
[k] *Z. cinctipes*, *Z. oregonensis*.
[l] *Lepidostoma*, *Wormaldia*, *Polycentropus*, Brachycentridae.
[m] Amphipoda, Ostracoda.

between treated and untreated reaches, pseudoreplication does not provide grounds for making conclusive statements about treatments. Nonetheless, this approach allowed us to compare patterns detected with biota in the natural stream with those in the statistically rigorous mesocosm experiment.

Results and discussion

Mesocosm experiment

Biofilm standing stock and benthic macroinvertebrate density were significantly higher in channels that contained salmon tissue (Fig. 2). Biofilm AFDM and chlorophyll *a* ranged up to two and eight times higher, respectively, than the control treatment ($p < 0.001$); differences were more pronounced with chlorophyll *a* than with AFDM, particularly during the intermediate sampling periods (Figs. 2A and 2B). Benthic macroinvertebrate densities ranged up to five times higher in the carcass treatments versus the control (Fig. 2C; Table 2). For clarity on data structure and analyses, ANOVA output for one response variable (mean logarithm-transformed macroinvertebrate abundance) is presented in Table 3.

There was also a significant time effect on AFDM, chlorophyll *a*, and benthic macroinvertebrates ($p < 0.001$) (Fig. 2). This in part appeared to be related to treatments but also to a sudden sediment pulse that passed through the channels during a spate 30 days into the experiment. Following the spate, we gently agitated by hand the surface substrate to facilitate flushing out some of the fine sediment that settled in the channels. We believe that the sediment and agitation contributed to the decline of AFDM (loosely attached) and invertebrate levels at about day 30 (Figs. 2A and 2C); however, their levels soon rebounded. Chlorophyll *a* did not appear to be negatively affected by the sediment pulse (Fig. 2B), and neither did the carcass loadings (i.e., treatments).

As was the case in a previous study (Wipfli et al. 1998), sloughing was apparent and grazing invertebrates were seen on clay tiles apparently removing biofilm as it developed, which probably reduced biofilm standing stock throughout the experiment. There appeared to be an emerging pattern of higher benthic macroinvertebrate density through time as a function of carcass loading (most apparent at the end of the study): higher densities at higher loading (Fig. 2C). If this pattern was real, it suggests that more nutrients may support more invertebrates in the longer term (>1.5 months), at least at these tested loading rates. Unfortunately, scavenging of salmon by bears forced us to start the experiment later than we intended and we therefore could not explore the loading effect beyond 60 days.

While there were large increases in AFDM, chlorophyll *a*, and macroinvertebrate abundance with carcass treatment at the lowest loading (1.45 kg), less dramatic responses were seen at subsequent higher loading levels (Fig. 3). The regression slope of 0.42 for chlorophyll *a* ($p = 0.015$) was significant across the 1.45–7.25 kg carcass loading; slopes were not significant for AFDM and benthic macroinvertebrate abundance ($p > 0.05$). These data suggest that a trophic capacity was generally reached somewhere between 0.00 and 1.45 kg carcass mass. These loading levels represent a common range of combined salmon spawner densities in Southeast Alaska and encompass the upper range of loading observed in many medium-sized rivers close to salt water where pink and chum salmon (*Oncorhynchus keta*) generally spawn at their highest densities (Groot and Margolis 1991). However, these data represent a two-month time frame. Although highly speculative, longer term effects (>two months) could be different depending on the system's storage capacity (Bilby et al. 1996; Kline et al. 1997). Some nutrients may be stored initially and released through time. In other words,

Table 3. ANOVA results for carcass and time effect and carcass treatment × time interaction from benthic macroinvertebrate mean natural logarithm transformed abundance data from the mesocosm experiment.

	df	Type III SS	MS	*F*	*p*
Table	4	2.48	0.62		
Treatment	5	27.36	5.47	24.26	<0.001
Orthogonal contrasts					
Carcass treatments versus control	1	26.92	26.92	119.37	<0.001
Regression slope ≠ 0	1	0.71	0.71	3.15	0.094
Lack of fit	3	0.41	0.14	0.61	0.618
Error (table × treatment)	20	4.51	0.23		
Time	5	19.95	3.99	21.36	<0.001
Treatment × time	25	7.05	0.28	1.51	0.071
Error (table × treatment × time)	116	21.67	0.19		
Total	175	83.02			

Note: Orthogonal contrast SS do not add up to treatment SS due to some missing data from one channel.

higher carcass loads may appear “excessive” beyond what the biota can immediately utilize in a given system in the short term (e.g., in autumn); however, the higher loads may provide nutrients that are stored (Bilby et al. 1996) and then released over time and utilized by biota over the longer term. This warrants further study.

Within the benthic macroinvertebrate community, taxa responded differently to carcass loading (Fig. 4). Three of the five common taxa (each comprising >2% of the total abundance) responded positively to carcass addition (control versus all loading treatments): Chironomidae (comprising a mixture of functional feeding groups), *Zapada* (shredders), and *Baetis* (collector–gatherers and scrapers) (Table 2). But over the five carcass loading rates, these three taxa responded differently. Chironomidae densities continued to increase over increased loading ($p < 0.001$), *Baetis* significantly decreased ($p = 0.008$), and *Zapada* showed no change to loading ($p = 0.36$). In addition, the shredder Capniidae did not respond to treatments ($p > 0.05$), while *Cinygmula* significantly decreased with increased loading ($p < 0.001$). These taxon-specific responses may have been due to food quality changes in the biofilm layer; we did observe a color succession from green to brown and gray of the biofilm across treatments throughout the experiment. Differences could also have been a reflection of food acquisition differences among instars or life history differences among taxa.

Natural stream experiment

Similar patterns were observed with biota in the natural stream as recorded in the mesocosm (Fig. 5). Both biofilm AFDM and benthic macroinvertebrate densities significantly increased following carcass addition; AFDM was about five times greater at the highest loading level versus control reaches ($p < 0.001$) and benthic macroinvertebrate densities about three times greater ($p < 0.001$). Densities of the five most common benthic macroinvertebrate taxa increased significantly ($p < 0.001$ to $p = 0.009$) with carcass addition (Fig. 6), except *Sweltsa*, a predatory stonefly, which showed no change ($p = 0.87$). Further, the combined benthic macroinvertebrate community level increase with carcass loading was statistically significant ($p = 0.002$). Chironomidae were responsible for the observed benthic macroinvertebrate community level response (Fig. 6); they were the most abundant taxa (Table 2) and were the only taxa that showed a significant response to loading ($p < 0.001$). Even though the highest loading rate was a low carcass density (2 spawners· m^{-2}) relative to the natural range of spawner densities in the vicinity (0–20 spawners·m^{-2}) (Wipfli et al. 1998; S. Heinl, Alaska Department of Fish and Game, personal communication), it had a large effect on both trophic categories, biofilm and invertebrates. AFDM and benthic macroinvertebrate densities were still increasing at the highest carcass load ($p = 0.024$ and $p = 0.002$, respectively) and not reaching a trophic capacity as seen in the mesocosm. We believe that this was a function of the low loading rates in the natural stream versus the wide load range tested in the artificial streams (Table 1).

Ecological considerations and management implications

These results illustrate important concepts, MDN subsidy of stream food webs and trophic capacities, with implications for fisheries and ecosystem management and demonstrate the need for a better understanding of the ecological role of MDN in freshwater and riparian systems. This and other studies suggest that spawners may elevate stream productivity through stimulating lower trophic levels that support juvenile salmon and other fishes (Bilby et al. 1996; Wipfli et al. 1998). More spawners translate into higher nutrient loads and more energy-rich detritus (Mathisen et al. 1988) for scavengers and detritivores, in turn potentially providing more prey for fish. The large and rapid increase in biofilm and invertebrate abundance in this study shows that additional nutrients supported more benthos. In a parallel study, growth rates of *Psychoglypha* (Trichoptera: Limnephilidae) larvae were higher in carcass-enriched habitats (D.T. Chaloner, unpublished data), also reflecting increased productivity. More freshwater prey should support faster growing and more and larger juvenile salmonids (Groot and Margolis 1991), in turn reducing their time to smoltification and increasing overwinter survival. Any combination of these processes should elevate smolt production. Trophic capacities, as demonstrated in this study and present at some level in all natural systems, should ultimately control the amount of prey that a given system can produce. In these nutrient-limited systems of the Pacific Northwest, British Columbia, and Alaska (Gregory et al. 1987; Kyle et al.

Fig. 3. Mean (A) AFDM, (B) chlorophyll *a* density, and (C) benthic macroinvertebrate density in the mesocosm experiment averaged over time across six salmon carcass loading levels. Error bars represent ±1 SEM.

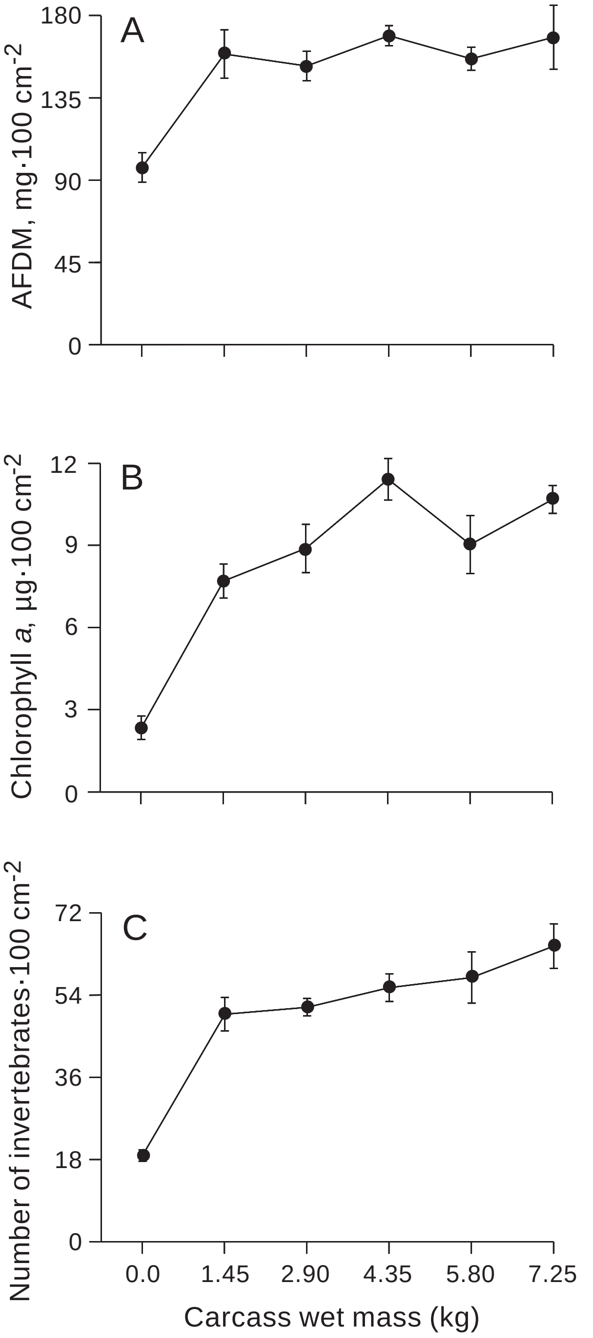
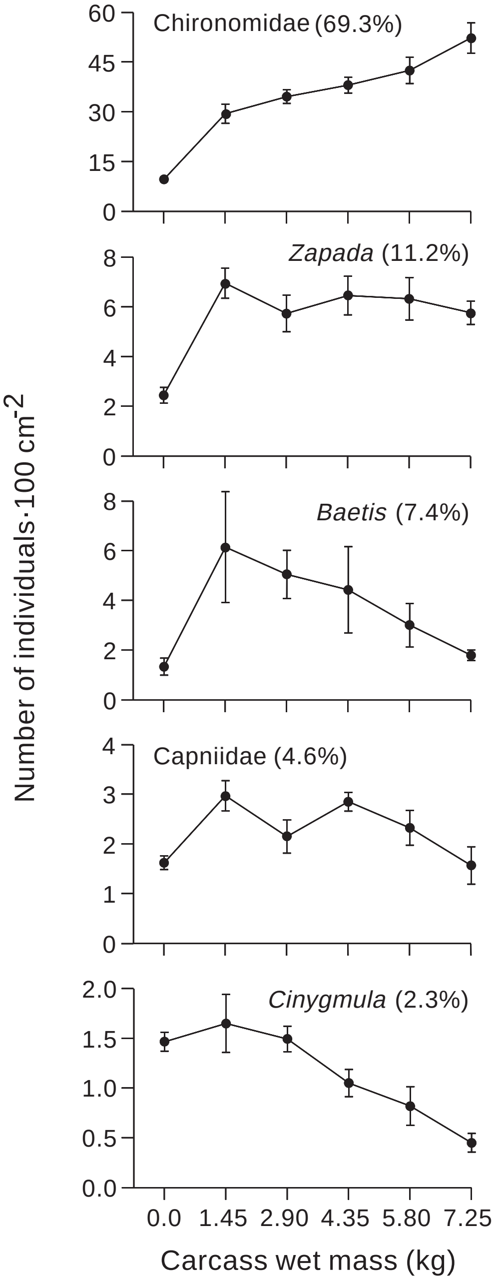


Fig. 4. Mean densities of the most common (by percentage) benthic macroinvertebrates in the mesocosm experiment averaged over time across six salmon carcass loading levels. Error bars represent ±1 SEM.



1997), even small nutrient pulses can be expected to have a large effect on food web productivity.

The amount of nutrients and their ratio necessary to sustain productivity may depend on preexisting physical, chemical, and biological system-specific conditions and their interactions (Fig. 7). The effects of nutrient loading on productivity, whether it be naturally by anadromous fishes or artificially by placing spawned-out hatchery carcasses (Levy 1997) or artificial nutrient additions (Ashley and Slaney 1997; Kyle et al. 1997), will likely depend on existing geology-based nutrient concentrations (Coleman and Dahm 1990), light levels and water temperature (Allan 1995), nutrient storage capacity (Bilby et al. 1996), among several other processes, specific to a given reach, subbasin, or watershed. Productivity of a system that is not nutrient limited will probably respond less to nutrient loading, as observed by Rand et al. (1992) in Lake Ontario tributaries. Nutrient–light interactions (Borchardt 1996) will also likely affect productivity, especially in small- to medium-sized forested streams (Vannote et al. 1980) common throughout the Pacific Northwest. More light for photosynthesis at a given nutrient level should increase primary production and, in

Fig. 5. Mean (A) AFDM and (B) benthic macroinvertebrate densities in riffle habitats in the natural stream, contrasting upstream control (○) and downstream carcass-enriched (●) reaches. Error bars represent ±1 SEM.

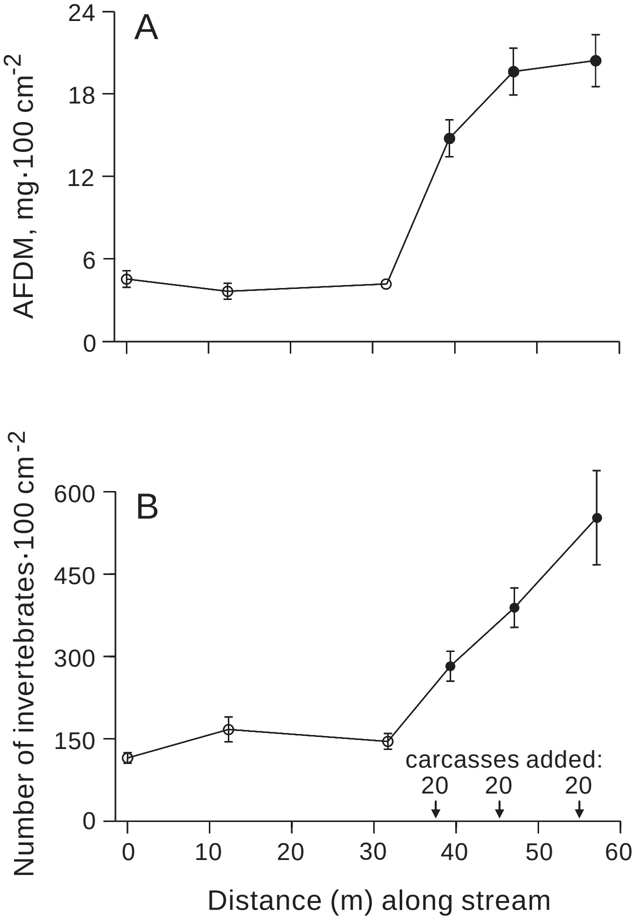
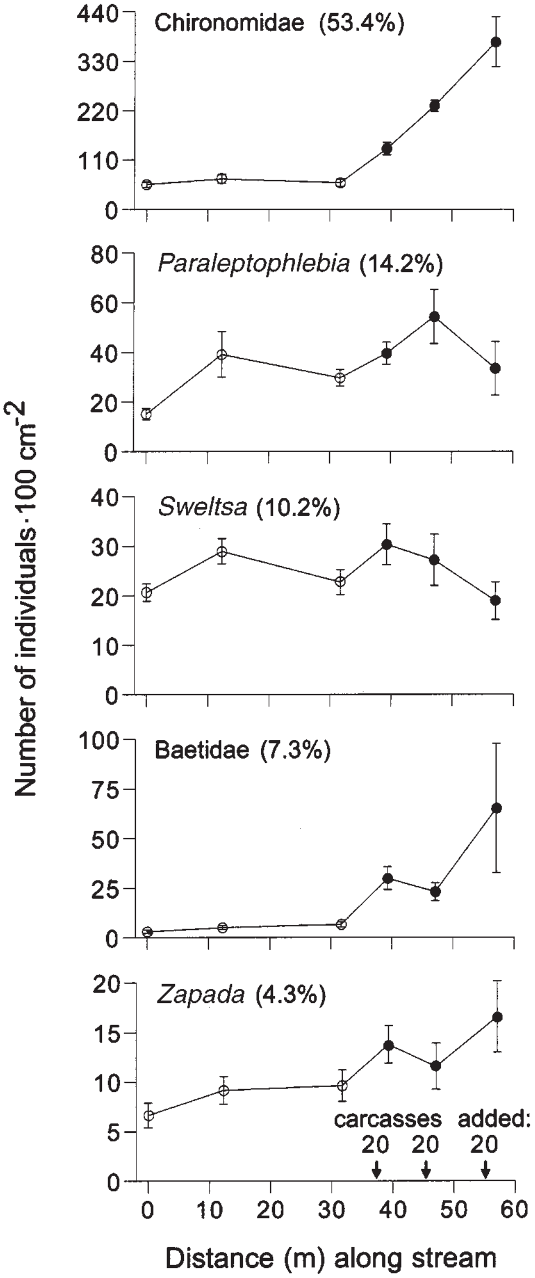


Fig. 6. Mean densities of the most common (by percentage) benthic macroinvertebrates in the natural stream, contrasting upstream control (○) and downstream carcass-enriched (●) reaches. Error bars represent ±1 SEM.

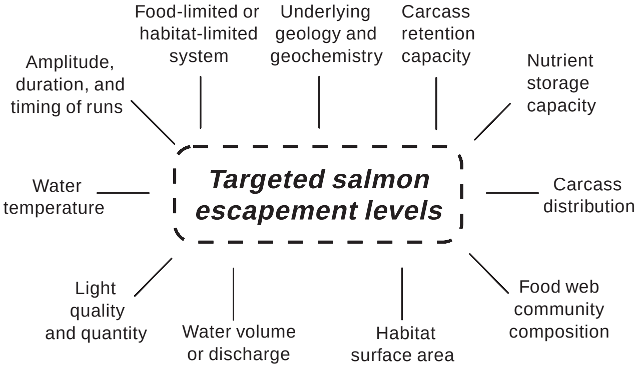


turn, grazer abundance. Additionally, higher water temperature, to a limit, may also increase metabolic and developmental rates of biofilm and invertebrates (Allan 1995), ultimately affecting their production.

Redistribution of salmon from streams onto land through flooding and vertebrate scavenging (Cederholm et al. 1989; Ben-David et al. 1998) may influence community responses to spawner loading. Nutrients that would otherwise leach directly into streams are often instead spread throughout the terrestrial environment via whole or fragmented carcasses or carnivore feces at various distances from the stream (Cederholm et al. 1989; Ben-David et al. 1998; Willson et al. 1998). In instances where carnivores remove all or nearly all of the spawners from a stream (M.S. Wipfli, personal observation), the stream biota may receive little nutrients directly. However, the nutrients should reach the stream system over time as they leach through the soil and hyporheos or after they are taken up by streamside vegetation and then enter the stream as plant litter (Vannote et al. 1980) and terrestrial invertebrates (Wipfli 1997).

Amplitude (salmon abundance), duration, and timing of the salmon runs and the salmon species present may also influence the ecological response to loading within watersheds. More salmon mean more nutrients. Runs spanning more time (e.g., six versus two months) will meter out nutrient additions over a greater portion of the year. Additionally, earlier runs will have an earlier effect on biota, potentially providing more prey for fishes through the growing season (before winter). Later runs (e.g., fall and winter) may have less immediate effects on stream biota because of prevailing low light levels (i.e., decreased photosynthesis of periphyton), colder water (i.e., reduced growth and developmental rates of microbes and macroinvertebrates and reduced feeding by fishes), or freezing. Thus, effects of late runs may be felt more during the following growing season pro-

Fig. 7. Conceptual model showing major system-specific physical, chemical, and biological features that may influence aquatic community responses to MDN from salmon runs.



vided some nutrients are stored through winter. Also, species-dependent spatial effects could be prominent. Coho (*Oncorhynchus kisutch*), chinook (*Oncorhynchus tshawytscha*), and sockeye salmon (*Oncorhynchus nerka*) generally spawn farther up watersheds than do pink and chum salmon (Groot and Margolis 1991); systems receiving mostly the latter will receive fewer nutrients farther into the watershed than systems receiving coho, chinook, or sockeye salmon. The species mix of spawners within a system could also play a role. A system receiving one or few species of salmon will likely get a much shorter nutrient pulse than one supporting early (sockeye and chinook salmon), midseason (chum and pink salmon), and late (coho salmon) spawners (Groot and Margolis 1991). Further, physical disturbance of the streambed by spawners during redd construction (Montgomery et al. 1996) may locally reduce biofilm and invertebrate densities. However, because redd construction is usually limited to certain areas within the stream and watershed, depending on spawner species and their densities, effects will be spatially limited. In addition, because spawning activities are limited to only a fraction of the year, with peak spawning activities generally occurring over several weeks, temporal effects of redd construction on benthos should be short-lived. The bulk of the nutrients probably leach into stream water, becoming available to benthos or going into storage, after redd construction when most of the salmon are dead or dying.

Physical characteristics of streams could also influence nutrient effects. High versus low discharges will dramatically affect carcass and nutrient concentrations in stream water (see Table 1, Natural stream). Stream gradient will likely affect carcass and nutrient retention; low-gradient systems may have a smaller flushing effect than high-gradient ones. Cederholm and Peterson (1985) and Cederholm et al. (1989) found that woody debris in streams functions to retain carcasses; more debris means more carcass and nutrient retention and may be particularly important during high flows. Boulders, pools, side channels, and lakes may also be important carcass storage areas. Carcasses buried in the hyporheic zone from spates (frequent during that time of year in Southeast Alaska) may also serve as longer term nutrient sources. Shallow hyporheic layers will have less retentive capacity than deep ones. The amount of wetted streambed and hyporheic area available for biofilm and macroinvertebrate colonization is also a factor that may influence nutrient effects in streams. More habitat surface area (e.g., streambed, woody debris, and interstitial spaces) will provide more space for colonists. Systems with extensive hyporheic zones extending well into the riparian flood plain could have large storage capacities. Additionally, fine-textured sediments contain more surface area for physical sorption (Bilby et al. 1996) than coarse-textured substrates, a function of the surface area to volume ratio.

A key biological factor is food web community structure, a function of stream size and energy pathways (Vannote et al. 1980). Grazers will utilize the microbial layer that develops following nutrient influx, as seen in this study. Sloughed microbial cells and organic particles will be available to collector–gatherers and collector–filterers. Predatory macroinvertebrates should respond to increased prey abundance, depending on their prey preference and on which taxa respond the most to nutrients and organic inputs. Wallace et al. (1997) documented negative effects of removing a large organic food base (allochthonous leaf litter) on multiple trophic levels in a forest stream, with effects felt from detritivores up through predators. Shredders, characteristic of small forested streams (Vannote et al. 1980), may respond the least if they are not utilizing the biofilm layered on their organic food base (e.g., leaves). On the other hand, they may respond dramatically if they consume energy-rich salmon tissue, particularly if they are food limited. Bilby et al. (1996) found 0% marine carbon uptake by shredders in two anadromous streams in Washington. River continuum theory (Vannote et al. 1980) predicts abundant shredders and few grazers in canopied streams, common habitats for spawning salmon in Southeast Alaska, and the reverse in larger streams. Communities in small forested streams dominated by shredders should respond less to MDN than grazer-dominated communities unless the species possess omnivorous habits.

Clearly, we need a better understanding of the role that MDN from salmon and other anadromous fishes play in freshwater and terrestrial ecosystems, including energy flow, nutrition, food web interactions and complexity, productivity, and biodiversity. Watersheds likely all respond to marine nutrient loading but probably do so differently; system-specific chemical, physical, and biological processes operating within a watershed will likely interact to regulate nutrient loading effects. More salmon may mean more nutrients but not necessarily greater availability; high loading may saturate the ability of a system to sequester and efficiently use nutrients, as demonstrated in this study. A given escapement level, e.g., 100 000 spawners, may not saturate the productive capacity of a system that has a large storage capacity (i.e., large hyporheic zone), that is autotrophically driven (i.e., sparse riparian canopy that provides much sunlight penetration and warmer water), and that is strongly nutrient limited. On the other hand, the productive capacity of a system characterized by bedrock (i.e., minimal storage capacity) and dense riparian canopy, and is not nutrient limited, will probably saturate more quickly at the same escapement level or spawner density. Depending on their preexisting character (Fig. 7), systems may need to be managed differently at various scales: subbasin, watershed, or regionally (based on ecology or underlying geology). Nonetheless, a more holistic fisheries and ecosystem management approach requires better information on the dependence on and consequences of marine-derived subsidies in freshwater and terrestrial ecosystems.

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