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Marine Subsidies in Freshwater Ecosystems: Salmon Carcasses Increase the Growth Rates of Stream-Resident Salmonids

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Abstract.—We tested the hypotheses that marine-derived resource subsidies (salmon carcasses) increase the growth rates of stream-resident salmonids in southeastern Alaska and that more carcasses translate into more growth. Five carcass treatments of pink salmon *Oncorhynchus gorbuscha* (0, 1, 2, 3, and 4 carcasses/m^2 or 0, 1.9, 3.7, 5.6, and 7.4 kg wet mass/m^2) were replicated six times in once-through artificial channels, then each channel was stocked with three live age-0 coho salmon *O. kisutch*. The experiment spanned more than 9 weeks: 16 August to 24 October 1998. The body mass and fork length of the young coho salmon significantly increased from carcass additions, but the incremental increases sharply diminished at carcass-loading levels above 1 carcass/m^2. Further, in a small stream in which we added salmon carcasses to a cumulative density of 0.54 carcasses/m^2, both cutthroat trout *O. clarki* and Dolly Varden *Salvelinus malma* grew significantly faster during the 2 months in which carcasses were added (September–October) compared with fish in control reaches. Fish maintained their assimilated body mass through winter into the following spring. This study illustrates that marine nutrients and energy from salmon spawners increase growth rates of resident and anadromous salmonids in streams. This elevated growth should translate into increased survival and reproduction, ultimately elevating freshwater and marine salmon production. Ecological relationships between salmon runs and aquatic community nutrition and productivity may be important considerations for salmon stock protection and restoration and for freshwater and marine ecosystem management.

Each year, tons of marine-produced biomass are spread throughout freshwater and riparian ecosystems in Alaska and other coastal regions when salmon migrate to their natal habitats to mate (Mathisen et al. 1988; Levy 1997; Cederholm et al. 1999). Pacific salmon sequester marine carbon and nutrients while maturing at sea and transfer this accumulated biomass to freshwater habitats where they spawn and die (Mathisen et al. 1988; Groot et al. 1995). The effects of this biomass influx include transfer of marine nutrients and energy to plants and animals in freshwater and riparian ecosystems, resulting in increased densities, biomass, and marine isotopic signatures of many species (Kline et al. 1997; Bilby et al. 1998; Wipfli et al. 1998). Although some evidence shows that more spawners equates to increased stream productivity (Wipfli et al. 1999), the broader ecological effects of this marine subsidy remain poorly understood (Gende et al. 2002; Naiman et al. 2002). These anadromy-driven linkages may be crucial for sustaining the trophic structure and productivity of freshwater food webs that ultimately support the populations responsible for this mass influx (Wipfli et al. 1998). A variety of populations are involved in that food web (Michael 1995), including invertebrates (Chaloner and Wipfli 2002) that are food for these fishes (Wipfli 1997).

The sharp declines of Pacific salmon stocks in many regions of North America (NRC 1996; Stouder et al. 1997) may create important losses of nutrient and energy inputs to many river systems (Gresh et al. 2000). In Alaska and parts of western Canada where historic salmon run sizes have been largely maintained (Baker et al. 1996; Slaney et al. 1996), millions of salmon return to streams, lakes, and other freshwater habitats providing nutrient- and energy-rich biomass to consumers (Levy 1997; Willson et al. 1998; Wipfli et al. 1998). In southeastern Alaska high rainfall and

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steep topography may facilitate the rapid flushing of nutrients from the forest soils (Stednick 1981). However, these forests are incised by 40,000 km of anadromous salmonid streams (Halupka et al. 2000) providing a vast network for marine nutrients to infiltrate freshwater and riparian food webs. Demonstrating the importance of marine-derived biomass to freshwater food webs in southeastern Alaska would illustrate a crucial mechanism through which salmon maintain freshwater productivity. This demonstration may justify the conclusion that salmon productivity in major rivers such as the Fraser, Columbia. and Snake rivers has been diminished, at least partially because of reductions in the numbers of salmon returning to these systems (NRC 1996; Stouder et al. 1997).

There are several pathways through which marine biomass can affect freshwater fishes. Adult salmon are energy and nutrient rich (Mathisen et al. 1988; Groot et al. 1995; Olsen 1998) and contain a stoichiometry (Sterner et al. 1992) that resembles the nutritional needs and biochemical makeup of potential consumers. Nutrients and carbon released during decay apparently increase the productivity of lower trophic levels (Wipfli et al. 1998; Minakawa and Gara 1999), which provides more prey for fishes (Wipfli et al. 1999). Fishes also ingest salmon tissue and eggs (Bilby et al. 1998). In Alaska, salmon return to spawn in the latter half of summer and fall. Their carcasses infuse streams with nutrients and energy as predation rates by rearing salmonids may be declining (Groot et al. 1995), which potentially helps to ensure the overwinter survival of freshwater fishes. Overwinter survival often depends on body size and lipid content at the end of the growing season (Groot et al. 1995; Adams 1998; Olsen 1998), although Bilby et al. (1998) have shown that freshwater-rearing salmonids do feed on salmon eggs during fall and winter. Therefore, not only do salmon runs essentially extend the growing season by providing more food late in the season, they may drive a positive feedback (Wipfli et al. 1998) that influences the fitness, survivorship, population density, and productivity of their deme. This possible feedback is probably most prominent in places where stocks are still strong (Baker et al. 1996; Slaney et al. 1996) and may explain why salmon recovery attempts along the eastern Pacific coast have fallen short (NRC 1996; Stouder et al. 1997).

The objectives of this study were to determine the effects of marine-derived biomass on salmonid growth in streams. Our hypotheses were that (1) salmon carcasses provide a resource subsidy that increases growth rates of freshwater-rearing coho salmon *Oncorhynchus kisutch*, cutthroat trout *O. clarki*, and Dolly Varden *Salvelinus malma*, and (2) the effects of this subsidy are larger at higher carcass-loading levels. It is essential to recognize that this marine-derived biomass contains a broad array of nutrients, minerals, proteins, lipids, and other biochemicals and macromolecules. Because of this, the focus of our research was on understanding the effects of these collective materials on stream fishes, not identifying which components produced the effects (e.g., nutrients, minerals, or macromolecules) or to decipher the pathways responsible for the effects (e.g., either directly through consumption of salmon tissue or indirectly through preying on invertebrates that fed on carcasses). This research should contribute to a better ecological understanding of marine–freshwater linkages and thereby aid fisheries and ecosystem management throughout the northern Pacific rim.

Methods

Study area.—This study was conducted on Revillagigedo Island, southeastern Alaska (Figure 1). Details of the study area are given in Wipfli et al. (1998). An artificial stream (mesocosm) experiment spanned 16 August to 24 October 1998, and a natural stream experiment extended from 4 September 1998 through 16 May 1999. We conducted the mesocosm experiment to add experimental and statistical rigor to the study. This level of rigor is difficult to achieve in studies limited to natural streams because of low replication and high natural variability.

Mesocosm experiment.—The mesocosm consisted of 36 once-through artificial stream channels, constructed six per platform on six platforms (Wipfli et al. 1998). Channels contained pool habitat (237 × 18 × 12.5 cm) filled with 16 L of mineral substrata collected from the natural streambed. A Vexar basket (20 × 18 × 5 cm, 6-mm-bar mesh) lined with fiberglass screen (1.6-mm mesh) and filled with mineral substrata collected from a natural stream was placed at the downstream end of each channel to sample invertebrates (see Wipfli et al. 1998). Pools were divided into four reaches of equal length by attaching three wood blocks (4 × 9 × 11 cm) to alternate sides of channel walls. Blocks protruded halfway across channels to add sinuosity to water flow and provide current-breaks for the age-0 coho salmon that were to be stocked in the channels. One flat stone (about 13 × 13 × 2 cm) placed on top of a few larger stones in each between-block reach pro-

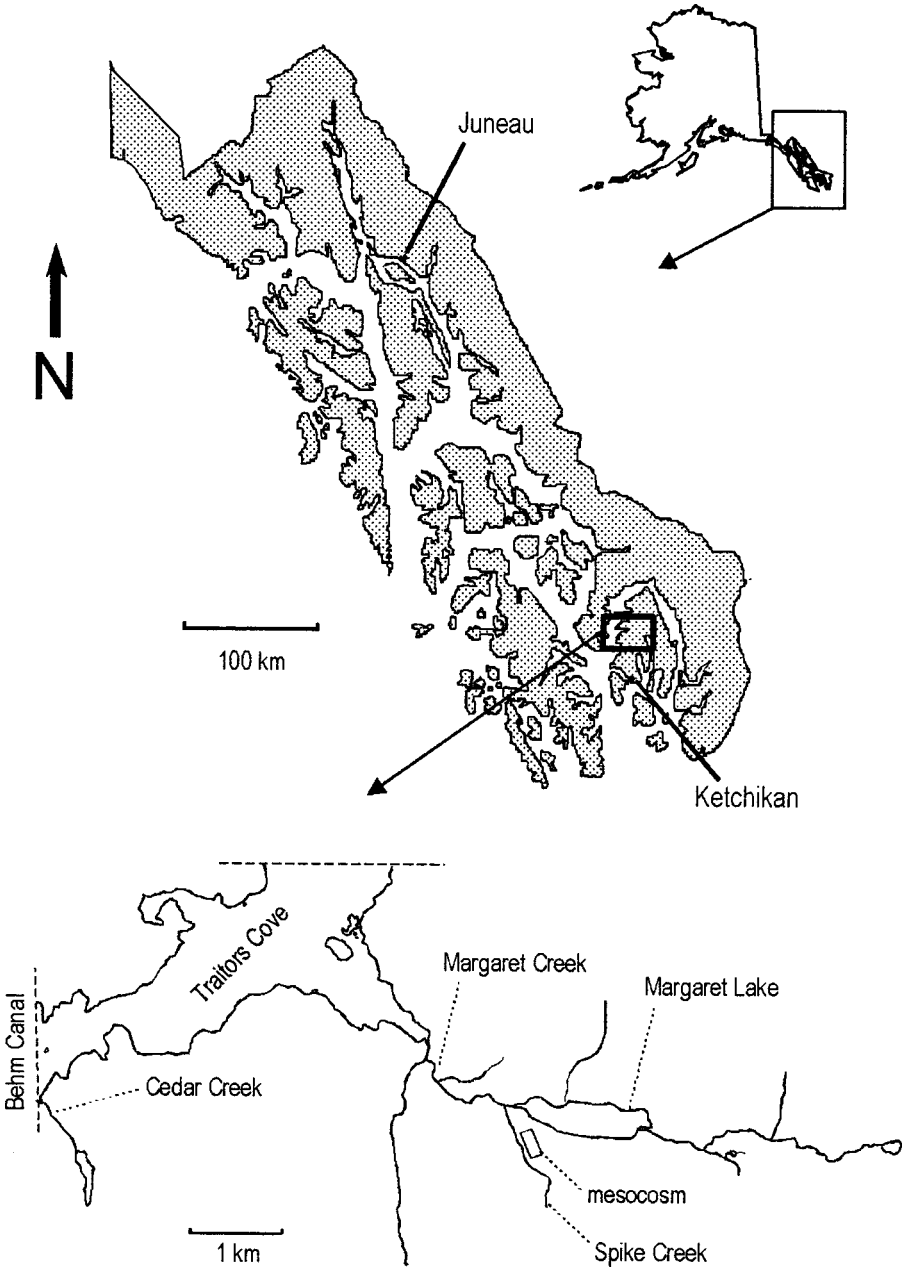


FIGURE 1.—Site north of Ketchikan in southeastern Alaska (55°41′N, 131°36′W) used in the study of salmon carcass effects on the growth of stream-rearing salmonids.

vided overhead cover for the coho salmon. Channels were covered with a thin sheet of Plexiglas to deter carcass tampering by vertebrate scavengers. Water flowed through channels for 26 d before the experiment began, allowing benthic invertebrates to colonize substrata. Past mesocosm studies have shown that benthic communities similar to those in the natural stream will be achieved in channels within 2–3 weeks of initiating water flow (Wipfli et al. 1998). During the experiment, water temperature in the outflow flume, logged at 1-h intervals, averaged 9°C (range, 5–13°C); discharge through channels was 0.45 ± 0.03 L/s (mean ± SD).

The age-0 coho salmon were exposed to five

TABLE 1.—Salmon carcass treatments, mass, and corresponding concentrations and density used in the mesocosm experiment with age-0 coho salmon.

Variable	Treatment (carcasses/m^2)				
	0	1	2	3	4
Carcass wet mass/channel (kg)[a]	0	0.71	1.43	2.14	2.85
Estimated dry mass (kg)[b]	0	0.21	0.41	0.62	0.82
Mass per stream discharge (kg wet mass·L $water^{-1}·s^{-1}$)	0	1.58	3.17	4.75	6.34
Mass per stream bed area (kg wet mass/m^2)	0	1.86	3.72	5.58	7.44
Density per stream bed area (number of carcasses/m^2)[c]	0	1	2	3	4

[a] Egg mass = 16%.
[b] Egg mass = 22%.
[c] Based on average body mass (1.81 kg wet mass) of pink salmon caught in coastal waters of North America, 1962–1971 (Groot and Margolis 1991).

treatments (amounts) of pink salmon *O. gorbuscha* carcass flesh and eggs (Table 1). Fifty-three live female pink salmon collected in Margaret Creek on 16 August were euthanized, and their egg skeins were removed and divided into egg clusters (28 g wet mass). Carcass chunks (150 g wet mass) were also cut from each carcass between the pectoral girdle and anus. We initiated four carcass-loading treatments (4, 8, 12, 16 salmon carcass chunks and egg clusters) and a control treatment (no salmon tissue) to the six channels in each platform. Treatment levels were equivalent to whole-carcass loading rates of 0, 1, 2, 3, and 4 pink salmon carcasses/m^2 (Table 1) and were within the range of pink salmon densities observed in area steams and in other regions (Groot and Margolis 1991). Salmon carcass chunks and egg clusters were scattered along the length of each channel. To simulate natural fragmentation and physical breakdown of salmon carcasses that we observed in nearby streams, carcass chunks (25% of the original number) were partially macerated by hand on days 24, 38, and 52 of the experiment. Maceration left various-sized tissue fragments scattered among the substrata; egg clusters largely remained intact. Some suspended fragments were seen drifting from channels.

Age-0 coho salmon in nearby streams were captured in minnow traps baited with salmon eggs, and the fish were separated into three fork length-groups: 44–54 mm (small; mean, 50 mm), 50–58 mm (medium; mean, 55 mm), and 53–67 mm (large; mean, 60 mm). One individual from each size-group was selected, anesthetized (Finquil), measured (wet mass and fork length), and released into each channel, providing a total of three fish per channel. This density was within the range for age-0 coho salmon in nearby natural streams and elsewhere (Groot and Margolis 1991), and the three size-groups were similar across treatments. Large and medium coho salmon were given an upper and lower caudal fin-clip, respectively, to identify size-group throughout the experiment. Fish were released into channels 2 d (channels 19–36) and 3 d (channels 1–18) following treatment with salmon tissue. Approximately every 3 weeks, we captured, anesthetized, and remeasured wet mass and fork length of each fish, for a total of three capture dates throughout the experiment. Measurements were taken over a 2-d period: mesocosm channels 19–36 on the first day and channels 1–18 on the following day. Channels were inspected daily for dead fish. During the experiment 12 fish (4 large, 2 medium, and 6 small) died or were missing: one-third in the control treatment and one-third in the 1-carcass/m^2 treatment, and the remaining third was evenly distributed across the remaining three treatments. These losses were replaced with fish of similar size as soon as they was discovered (within 14 d). Live fish remaining in the channels may have experienced briefly greater growth rates, which could have added more variability to the treatments and replicates and led to a more conservative statistical test (i.e., increasing the chances of not detecting treatment differences). Relative growth was calculated for individual fish as the percentage change (per day and over the entire experiment) from initial wet mass and fork length.

Benthic invertebrate baskets were sampled 3 weeks into the experiment to assess treatment effects on invertebrate density. After removing baskets from channels, the invertebrates were washed from the substrata, and those retained by a 250-μm sieve were preserved in 70% ethyl alcohol. Invertebrates were sorted and counted with the aid of a dissecting scope.

Natural stream experiment.—We conducted an additional experiment to measure the effect of salmon carcasses on the growth of resident salmonids in a natural stream, Cedar Creek (name chosen for study purposes). Cedar Creek is a second-order stream containing cutthroat trout, Dolly Varden, occasional threespine stickleback *Gasterosteus aculeatus* and no salmon. The study site consisted of a control reach (length = 420 m) and, downstream of that, a carcass-enriched reach (length = 155 m). Mean base flow discharge was 9 L/s and channel wetted-width was 2.2 m. An Optic Stowaway logged water temperature at 1-h intervals during the experiment. Water temperature averaged 11°C from September through Oc-

TABLE 2.—Salmon carcass numbers, mass, and density added to Cedar Creek, Alaska, in September and October 1998 to study effects on stream-rearing salmonids.

Variable	September				October	
	4	11	22	26	31	Cumulative
Number of carcasses[a]	27	49	45	24	21	166
Carcass wet mass (kg)	47.5	81.7	55.7	33.2	35.5	253.6
Estimated dry mass (kg)	13.3	23.1	8.8	5.3	6.7	57.1
Percent wet mass as eggs	10	12	0	0	12	
Mass per stream discharge[b] (kg wet mass·L water^{-1}·s^{-1})	5.3	9.1	6.2	3.7	3.9	28.1
Mass per streambed area[b] (kg wet mass/m^2)	0.15	0.27	0.18	0.11	0.12	0.82
Density per streambed area[b] (number carcasses/m^2)	0.09	0.16	0.15	0.08	0.07	0.54

[a] Includes flesh and eggs, except flesh only on 22 and 26 September.
[b] Streambed area and discharge measured at baseflow.

tober and 4°C from November through May. The temperature range was slightly higher than that of the mesocosm probably because the creek drained a small (6-ha) lake.

Cutthroat trout and Dolly Varden were captured with baited Gee minnow traps on 1–3 September and 6 September. After the fish had been anesthetized with Finquil, we recorded the fork length, wet mass, species, and capture location of each fish and implanted a passive integrated transponder (PIT) tag into its body cavity. Fish were given an adipose fin-clip, allowed to recover, and released at the site of capture. A total of 122 fish were tagged, 48 in the control reach and 74 in the treated reach. For the control and treated reaches, respectively, beginning mean fork lengths averaged 109 and 102 mm for cutthroat trout, and 84 and 91 mm for Dolly Varden.

Pink salmon carcasses and eggs were added to the treatment reach on 4, 11, 22, and 26 September and 31 October (Table 2) to simulate the timing and magnitude of natural pulses of spawners into streams in the area. Live male and female (containing eggs) pink salmon were collected from Margaret Creek on 4 and 11 September, and on 22 and 26 September recently dead and dying male and female pink salmon were collected from the same location. Carcasses were transported to Cedar Creek and weighed wet. Whole carcasses or pieces were submerged in pools, undercut banks, and debris jams to reduce scavenging by terrestrial vertebrates. Single eggs and egg clusters from the carcasses were weighed and scattered throughout the treatment reach as well. Frozen pink salmon carcasses (whole), carcass chunks, and eggs were added to the treatment reach on 31 October. Salmon carcass additions provided a cumulative carcass-loading rate of 0.54 carcasses/m^2 (0.83 kg wet mass/m^2; Table 2). Tagged fish were recaptured and measured during October 1998 and May 1999 to assess short- and longer-term effects of salmon carcass enrichment on fish growth. Relative growth rate, calculated by reach (control and treated), species, and period (September–October and October–May) for individually tagged fish, was the percent change in wet mass and fork length divided by number of days between tagging and recapture.

Experimental design and statistical analyses.—For the mesocosm experiment, we used a randomized block, split-plot design, replicating five treatments (0, 1, 2, 3, and 4 carcasses/m^2) and three subtreatments (small, medium, and large size-groups) across six blocks. Mesocosm platforms served as blocks ($N = 6$). Channels within a platform were the whole units to which treatments were applied. Individual coho salmon within a channel were subunits (split-plot) on which the subtreatment of size-group was applied. To minimize confounding between treatment and channel location, treatments were assigned to six channels across six platforms, which facilitated a 6×6 Latin square. Response variables were percent growth in mass and fork length measured for each fish. Data were analyzed using PROC GLM (SAS Institute 1989) at $\alpha = 0.05$. Hypothesis testing for coho growth (mass and fork length) included (1) a test for differences in growth due to the presence or absence of carcasses (i.e., control versus carcass-enriched), (2) a test for linear growth due to increases in carcass-loading levels (i.e., best linear fit with slope $\neq 0$), and (3) a test for lack of fit for the linear model used in the previous test. We also tested for significant interaction between fish size and treatment.

For the natural stream experiment, we tested for

TABLE 3.—Analysis of variance results for percentage change in wet mass and fork length of age-0 coho salmon exposed to none (control) versus four treatment amounts of pink salmon carcass tissue and eggs. SS stands for sum of squares.

		Mass change (%)		Length change (%)	
Source of variation	df	SS	*P*	SS	*P*
Platform	5	0.448		0.022	
Treatment	5	12.018	<0.001	0.647	<0.001
Control versus carcass	1	11.541	<0.001	0.594	<0.001
Linear fit (slope ≠ 0)	1	0.460	0.024	0.048	0.003
Lack of fit	3	0.014	0.916	0.004	0.672
Platform × treatment	25	1.993		0.110	
Size group	2	0.679	<0.001	0.029	0.003
Treatment × size class	10	0.254	0.596	0.017	0.647
Error	60	1.819		0.131	
Total	107				

differences in percentage change in fish mass and fork length between two reaches: the upstream control and the downstream carcass-enriched (*t*-test, $\alpha = 0.05$). Two species, cutthroat trout and Dolly Varden, were tested. The cutthroat trout were tested once in fall and again the following spring; Dolly Varden were tested in fall. There were no Dolly Varden recaptures from the control treatment in spring. We tested growth during three distinct periods (September–October, October–May, and September–May) to capture growth during the period of carcass addition, during the winter after carcass addition, and throughout the entire experiment, respectively.

Data were checked for normality, variance homogeneity, and additivity. Analysis of data showed these assumptions were satisfactory. Sample and treatment independence were assumed for all data based on experimental design used.

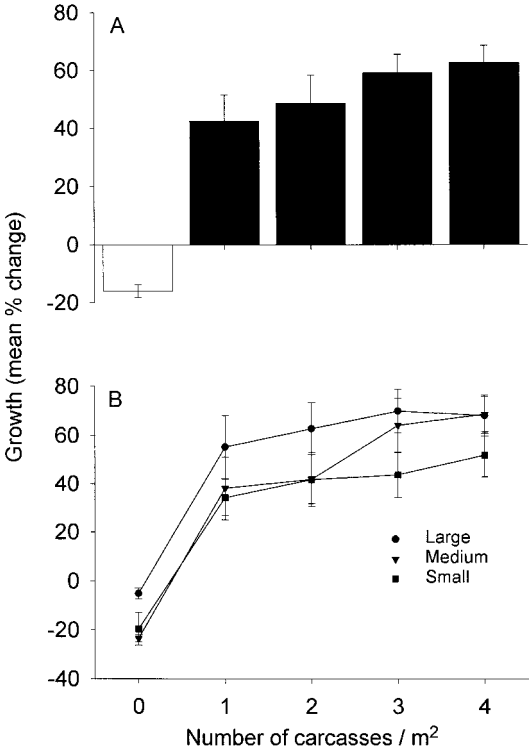


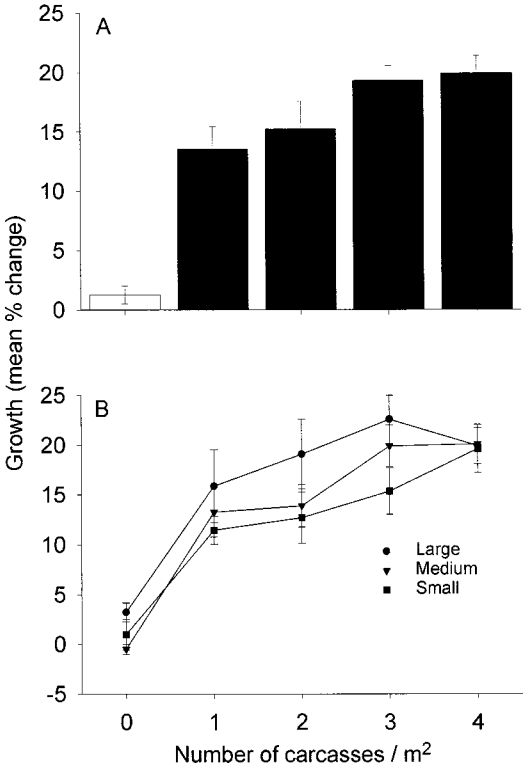
FIGURE 2.—Growth (mean percent change in wet mass over 66 d) of age-0 coho salmon exposed to five salmon carcass treatments in a mesocosm, as determined for **(A)** all size-groups combined and **(B)** each of three size-groups (error bars = 1 SE).

Results

Mesocosm Experiment

Growth (mass gain) of the age-0 coho salmon was significantly greater in the carcass-enriched channels than in the control channels ($P < 0.001$; Table 3). The salmon accumulated 43–63% mass across the carcass treatments (1–4 carcasses/m^2, respectively), whereas fish in the control treatments lost 16% body mass (Figure 2A). Fish growth increased significantly in response to carcass loading (slope = 7.2%, $P = 0.024$; Figure 2A). The interaction between size-group and treatment was not significant ($P = 0.596$; Figure 2B, Table 3). The most rapid growth occurred during the first 3 weeks of the experiment before carcasses were macerated and available as food for the coho salmon.

Change in fork length of the age-0 coho salmon was significantly greater in the carcass-enriched channels than in the control channels ($P < 0.001$; Table 3). The fork length increase ranged 14–20% for the carcass-enriched treatments versus 1% for the control (Figure 3A). As with body mass, fork length increased significantly in response to increases in carcass loading levels (slope = 2.3%,



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$P = 0.003$; Table 3). Interaction between size-group and treatment was not significant ($P = 0.647$; Figure 3B; Table 3).

Invertebrate densities were also significantly higher in the carcass-enriched treatments than in the control ($P = 0.024$). Community densities averaged 930 individuals/m^2 in the control channels versus 1,145 and 1,515 individuals/m^2 in the 1 and 4 carcasses/m^2 treatments, respectively.

Natural Stream Experiment

Twenty-six (14 cutthroat trout, 12 Dolly Varden) of 122 (21%) tagged fish were recaptured the following October and May, collectively. Growth of cutthroat trout in Cedar Creek was significantly greater in the salmon carcass-enriched reach than in the control reach in fall and spring ($P < 0.001$; Table 4). The average pretreatment mass was lower for tagged fish in the enriched reach, but they soon outgrew control fish after carcasses were added (Figure 4). Growth rate was 24 times higher in the enriched versus control reach from September through October, during the period salmon carcasses were added to the stream and 2.5 times higher from September through May. Conversely, growth rate for control fish was two times higher than that for fish in the enriched habitat during the winter, late October through May. Relative growth rates of Dolly Varden were significantly greater (by 5 times) in the carcass-enriched reach than in the control reach in fall ($P = 0.0045$). Wet mass of 17 fish in the treated reach increased 51–137% from September through October. No tagged Dolly Varden were recaptured in the control reach during the following spring and apparently either died or emigrated.

Discussion

The presence of salmon carcasses and eggs from spawning salmon dramatically increased the growth rates and body mass of the salmonids sampled in this study. Even at relatively low densities of carcasses, we detected significant effects for all species tested: coho salmon, cutthroat trout and Dolly Varden. Further, this dramatic increase in body mass in fish presented with salmon carcasses

TABLE 4.—Growth of cutthroat trout and Dolly Varden in carcass-enriched (treatment) and unenriched (control) reaches of Cedar Creek, Alaska, as measured for three periods between September 1998 and May 1999. Growth was calculated as percent change in wet mass per day (SEs in parentheses).

Species and treatment type	*N*	Sep–May	Sep–Oct	Oct–May
Cutthroat trout				
Carcass-enriched	9	0.59 (0.05)	2.60 (0.19)	0.13 (0.02)
Unenriched	5	0.24 (0.05)	0.11 (0.04)	0.25 (0.05)
t-test *P*-value		0.0008	<0.0001	0.0247
Dolly Varden				
Carcass-enriched	12	0.69 (0.05)	1.90 (0.23)	0.29 (0.02)
Unenriched	4		0.39 (0.25)	
t-test *P*-value			0.0045	

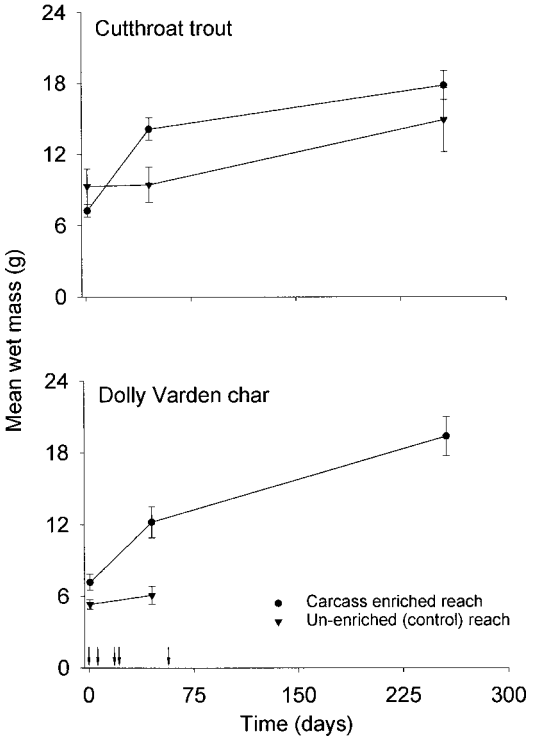

FIGURE 4.—Mean wet mass of cutthroat trout (top panel) and Dolly Varden (lower panel) in carcass-enriched and control reaches of Cedar Creek, Alaska, from September 1998 to May 1999. Arrows indicate timing of carcass additions; error bars = 1 SE.

and eggs occurred over a short period, 8–10 weeks, and in fall when stream temperatures are much lower than those of summer. Our results in Alaska with coho salmon, cutthroat trout, and Dolly Varden growth are consistent with that of Bilby et al. (1998), who reported elevated density and condition factor for steelhead *O. mykiss* and elevated rearing coho salmon density in two Washington streams where hatchery carcasses were added. Benthic invertebrate densities also increased in response to carcass addition in our study, which was consistent with that of previous work (Wipfli et al. 1998, 1999).

However, we detected significantly greater winter growth rates in the control cutthroat trout (2× higher) than in trout exposed to carcasses. One possible explanation is that after the initial boost from marine biomass (in fall), fish that did not have access to carcasses relied on other food sources that may have partially masked or compensated for the large, albeit short-lived, subsidy from the ocean. In other words, the enriched fish may not have fed as much as the control fish during the winter, possibly to sustain a predetermined yearlong growth rate. If so, this may have allowed the control fish to compensate for some of the mass that the enriched fish acquired from marine sources. This ''catch-up'' or ''compensatory'' growth occurs in fishes, especially if they have dropped below growth rates of conspecifics (Jobling 1994). Clearly, other sources of prey are available in streams: terrestrial invertebrates from streamside vegetation and invertebrates from headwater channels (Wipfli 1997; Wipfli and Gregovich 2002) and instream production. An alternative explanation is that smaller cutthroat trout of the control group would be expected to have higher growth rates (% mass gain/d) than the larger fish under the circumstance of both groups gaining about the same mass for a given period (i.e., October through May, as indicated by Figure 4). Thus, even though the smaller fish had higher growth rates (% mass gain per day), both groups of fish gained roughly the same amount of mass through the winter. Nonetheless, both factors appeared to be playing a role in the observed cutthroat trout growth responses in winter.

Although not statistically tested, there appeared to be size-specific differential growth rates for the coho salmon fry in the mesocosm experiment. Large fish appeared to grow more at first, small fish showing more growth later. A possible explanation is that size-related dominance hierarchy was occurring, whereby the larger fish sequestered food resources at higher rates and therefore grew faster than the small fish during the beginning of the experiment (Jobling 1994). After the large fish attained a more ideal growth rate, their ingestion rates and subsequent growth rates may have slowed, allowing the smaller fish to catch up (Jobling 1994), as seen later in the experiment. Perhaps fewer fish per channel or higher carcass densities would have changed this apparent response.

For both the natural and artificial streams in our study, we chose age-0 coho and pink salmon carcass densities that were within the typical range of densities noted in nearby streams. Age-0 coho salmon are often found in high densities immediately following swim-up stage, often emulating schooling (Groot and Margolis 1991). We believe that testing other densities (higher or lower) would probably have invoked different responses to treatments (e.g., higher densities of coho salmon leading to less individual and overall growth or higher mortality from interference competition), but we felt that 3 age-0 coho salmon per channel was about midway in the common range of age-0 coho

salmon densities during that stage of their life cycle, given the natural habitat simulated in the experimental channels. Pink salmon spawner densities often reach 1–2 spawners/m^2 or more in streams (Groot and Margolis 1991), and subsequent carcass densities can be even higher when they accumulate in localized areas (pools or eddies), where coho salmon and other fishes often rear (J. P. Hudson, personal observation). Added to that, other species such as chum salmon *O. keta* and coho salmon may spawn in the same reaches providing cumulative densities throughout and beyond the range tested in this study. In the watershed where we conducted this study, we have observed high spawner densities (>1–2 spawners/m^2) in places where adults congregate, such as below waterfalls that are barriers to adult upstream migration (Groot and Margolis 1991) or in mainstem reaches near saltwater.

In light of the nutrient-poor nature of freshwater ecosystems along much of the North Pacific coast (Ashley and Slaney 1997; Gresh et al. 2000), the nutrients that adult salmon provide to some freshwater habitats every year may be crucial for sustaining an elevated level of productivity. Wipfli et al. (1998) reported large effects from salmon carcasses on stream food webs. Schmidt et al. (1998) discussed the importance of marine-derived nutrients from salmon spawners on lake productivity and emphasized using this information for establishing salmon escapement goals (i.e., spawner densities). Other organic materials (Mundie et al. 1983) or artificial nutrients (Ashley and Slaney 1997) have also been shown to produce effects in nutrient-poor systems. Although speculative, the nutrient-poor nature of these systems may make them candidates for responding to nutrient additions, artificial or natural. And because the food webs in these systems have evolved with high influxes of marine nutrients from large salmon runs, they may have developed a dependence on this annual and predictable (in time but not in magnitude) influx of biomass. Although red alder *Alnus rubra*, through fixation, may supply nitrogen to these ecosystems, especially in timber-harvested watersheds where red alder is often abundant (Hibbs et al. 1994), phosphorus may actually be production-limiting (Mundie et al. 1983; Perrin et al. 1987).

Certain species (e.g., pink and chum salmon) may be supporting populations of others (e.g., coho, chinook *O. tshawytscha*, sockeye *O. nerka*, and steelhead; Michael 1995). In southeastern Alaska, many watersheds typically receive large returns of pink and chum salmon (Halupka et al. 2000), and those large returns may supply the bulk of the marine biomass that enters these food webs. However, pink and chum salmon progeny rear little in freshwater (Groot et al. 1995), whereas the other salmon species, which spend a year or more feeding and rearing in freshwater, may be the primary beneficiaries of the marine subsidy from pink and chum salmon returns. Salmon spawners other than pink and chum salmon probably also have the same subsidy effect on their own and other species. If so, this phenomenon may have important implications for salmon management. Perhaps multispecies management may replace single-species management, such that all anadromous salmonids are managed concurrently (Michael 1995).

Now that salmon runs have been shown to deliver nutrients and energy to coastal Pacific freshwater ecosystems (Kline et al. 1997; Cederholm et al. 1999; Gresh et al. 2000)—apparently elevating their productivity (Bilby et al. 1998; Wipfli et al. 1998; Minakawa and Gara 1999; Chaloner and Wipfli 2002)—one of the next steps is to accurately determine the number of spawners necessary to sustain a certain level of enrichment that will subsequently achieve a given level of productivity. Several regional-specific or watershed-specific factors will dictate the amount of nutrients and carbon needed for a given system (Wipfli et al. 1999). Although some watersheds could require high spawner densities to sustain their productivity, others that have higher inherent nutrient levels, alkalinity, or carrying capacity, may require fewer spawners. Further, some systems may have a low capacity for utilizing nutrients, and therefore, large runs would be inconsequential. Additionally, some may be nitrogen limited and others phosphorus limited (Perrin et al. 1987), and the presence of red alder will probably influence nitrogen levels and nutrient limitation (Hibbs et al. 1994). Wipfli et al. (1999) illustrated that lower trophic levels in streams continued to positively respond to incremental increases in salmon carcasses. Small amounts of tissue provided a large increase in biofilm and invertebrate abundance, additional increments of salmon tissue providing smaller incremental responses. In our study we showed that growth of age-0 coho salmon increased across the full range of carcass densities tested. Bilby et al. (2001) suggested optimal escapements to be well below 1 carcass/m^2 for Washington streams.

Stoichiometry probably plays a key role in the eventual outcome of enrichment, whether it is from salmon carcasses, commercial fertilizers, agricul-

tural or urban runoff, or other sources. Not only is the ratio of nutrients, minerals, and biochemicals probably important to these food webs, but their chemical form may be equally critical (Elser and Urabe 1999). In addition to elemental nutrients, salmon contain minerals, amino acids, proteins, fats, carbohydrates, and other biochemicals essential for living organisms (Olsen 1998) that are not contained in commercial fertilizers or other inorganic nutrient sources. The significance of these biochemicals and their availability to the food web may be more important to consumers than nitrogen, phosphorus, or other nutrients. What component(s) in the salmon tissue the food web is responding to (nutrients, minerals, or biochemicals) is unverified, as are the various pathways (direct feeding on salmon tissue or via ingesting consumers that are feeding on salmon tissue) through which the effects are manifested. Although certain nutrients (nitrogen or phosphorus) often appear to be limiting production in freshwater food webs (Perrin et al. 1987), the role of minerals, biochemicals, or micronutrients may ultimately play a key role in the overall health of certain species and the entire food web. If so, survivorship, fecundity, competitive ability, behavior, and other key demographics of fishes and other consumers may be greatly influenced by the presence of these biochemicals, ultimately affecting salmon production in both marine and freshwater ecosystems. However, this is speculative and needs to be tested.

In conclusion, because biomass provided by spawning salmon appears to increase productivity of multiple trophic levels in streams (Bilby et al. 1998; Wipfli et al. 1998; Minakawa and Gara 1999; Chaloner and Wipfli 2002; this study), maintaining this subsidy in freshwater appears to be important for sustaining fish production. More complete information on the effects of this marine subsidy for sustaining freshwater food webs should help improve overall salmon protection and restoration efforts. Restoring and protecting salmon stocks may have as much to do with restoring nutrients, food abundance, and nutrition through generous escapements, as restoring habitat, fish passage, and genetic diversity.

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References

Adams, S. M. 1998. Ecological role of lipids in the health and success of fish populations. Pages 132–160 *in* M. T. Arts and B. C. Wainman, editors. Lipids in freshwater ecosystems. Springer-Verlag, New York.

Ashley, K. I., and P. A. Slaney. 1997. Accelerating recovery of stream, river and pond productivity by low-level nutrient enrichment. Pages 13–1 and 13–24 *in* P. A. Slaney and D. Zaldokas, editors. Fish habitat rehabilitation procedures. British Columbia Ministry of Environment, Lands and Parks and Ministry of Forests, Watershed Restoration Technical Circular 9, Vancouver.

Baker, T. T., A. C. Wertheimer, R. D. Burkett, R. Dunlap, D. M. Eggers, E. I. Fritts, A. J. Gharrett, R. A. Holmes, and R. L. Wilmot. 1996. Status of Pacific salmon and steelhead escapements in southeastern Alaska. Fisheries 21(10):6–18.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Bilby, R. E., B. R. Fransen, J. K. Walter, C. J. Cederholm, and W. J. Scarlett. 2001. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. Fisheries 26(1):6–14.

Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific salmon carcasses: essential contribution of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries 24(10):6–15.

Chaloner, D. T., and M. S. Wipfli. 2002. Influence of decomposing Pacific salmon carcasses on macroinvertebrate growth and standing stock in southeastern Alaska streams. Journal of the North American Benthological Society 21:430–442.

Elser, J. J., and J. Urabe. 1999. The stoichiometry of

consumer-driven nutrient cycling: theory, observations, and consequences. Ecology 80:735–751.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. The ecological role of Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917–928.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25(1):15–21.

Groot, C., and L. Margolis, editors. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Groot, C., L. Margolis, and W. C. Clarke, editors. 1995. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver.

Halupka, K. C., M. D. Bryant, M. F. Willson, and F. H. Everest. 2000. Biological characteristics and population status of anadromous salmon in southeast Alaska. U.S. Forest Service General Technical Report PNW-GTR-468.

Hibbs, D. E., D. S. DeBell, and R. F. Tarrant, editors. 1994. The biology and management of red alder. Oregon State University Press, Corvallis.

Jobling, M. 1994. Fish bioenergetics. Chapman and Hall, London.

Kline, T. C., J. J. Goering, and R. J. Piorkowski. 1997. The effect of salmon carcasses on Alaskan freshwaters. Pages 179–204 *in* A. M. Milner and M. W. Oswood, editors. Freshwaters of Alaska: ecological syntheses. Springer-Verlag, New York.

Levy, S. 1997. Pacific salmon bring it all back home. BioScience 47:657–660.

Mathisen, O. A., P. L. Parker, J. J. Goering, T. C. Kline, P. H. Poe, and R. S. Scalan. 1988. Recycling of marine elements transported into freshwater systems by anadromous salmon. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 23:2249–2258.

Michael, J. H. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: managing one resource to benefit another. Northwest Science 69:228–233.

Minakawa, N., and R. I. Gara. 1999. Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. Journal of Freshwater Ecology 14:327–335.

Mundie, J. H., S. M. McKinnell, and R. E. Traber. 1983. Responses of stream zoobenthos to enrichment of gravel substrates with cereal grain. Canadian Journal of Fisheries and Aquatic Sciences 40:1702–1712.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater ecosystems. Ecosystems 5: 399–417.

NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Olsen, Y. 1998. Lipids and essential fatty acids in aquatic food webs: what can freshwater ecologists learn from mariculture? Pages 161–202 *in* M. T. Arts and B. C. Wainman, editors. Lipids in freshwater ecosystems. Springer-Verlag, New York.

Perrin, C. J., M. L. Bothwell, and P. A. Slaney. 1987. Experimental enrichment of a coastal stream in British Columbia: effects of organic and inorganic additions on autotrophic periphyton production. Canadian Journal of Fisheries and Aquatic Sciences 44:1247–1256.

SAS Institute. 1989. SAS/STAT user's guide, version 6, edition 4, volume 2. SAS Institute, Cary, North Carolina.

Schmidt, D. C., S. R. Carlson, G. B. Kyle, and B. P. Finney. 1998. Influence of carcass-derived nutrients on sockeye salmon productivity in Karluk Lake, Alaska: importance in the assessment of an escapement goal. North American Journal of Fisheries Management 18:743–763.

Slaney, T. L., K. D. Hyatt, T. G. Northcote, and R. J. Fielden. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21(10):20–35.

Stednick, J. D. 1981. Precipitation and stream water chemistry in an undisturbed watershed in southeast Alaska. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-291, Portland, Oregon.

Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. Biogeochemistry 17:49–67.

Stouder, D. J., P. A. Bisson, and R. J. Naiman, editors. 1997. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Willson, M. F., S. M. Gende, and B. Marston. 1998. Fishes and the forest: expanding perspectives on fish-wildlife interactions. BioScience 48:455–462.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. Canadian Journal of Fisheries and Aquatic Sciences 54:1259–1269.

Wipfli, M. S., and D. P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47:957–969.

Wipfli, M. S., J. P. Hudson, and J. P. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. Canadian Journal of Fisheries and Aquatic Sciences 55:1503–1511.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.