Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids

Margaret A. Wilzbach, Bret C. Harvey, Jason L. White, and Rodney J. Nakamoto

Abstract: We studied the concurrent effects of riparian canopy opening and salmon carcass addition on salmonid biomass, density and growth rates in small streams over 2 years. In each of six streams in the Smith and Klamath River basins in northern California, red alder (*Alnus rubra*) and other hardwoods were removed along both banks of a 100-m reach to increase incident radiation. A second 100-m reach, with an intact canopy, was established in each stream as a light control. Salmon carcasses were added each year to both cut and uncut riparian sections in three of the six streams. Differences in total density and biomass of cutthroat trout (*Oncorhynchus clarki*) and rainbow trout (*Oncorhynchus mykiss*) from pretreatment levels responded positively to canopy removal but were not detectably affected by carcass addition. Differences in specific growth rates of the fish between open and closed canopy reaches were greater in sites without carcasses than in sites with carcasses. In light-limited settings where temperature gains associated with canopy opening are not problematic for aquatic resources, gains in salmonid production might be achieved by selective trimming of riparian hardwoods.

Résumé : Nous avons examiné sur une période de deux ans les effets concurrents de l'ouverture de la canopée du rivage et de l'addition de carcasses de saumons sur la biomasse, la densité et les taux de croissance des salmonidés dans de petits cours d'eau. Les aulnes rouges (*Alnus rubra*) et d'autres essences de bois francs ont été retirés sur les deux rives d'une section de 100 m dans six cours d'eau des bassins versants des rivières Smith et Klamath dans le nord de la Californie afin d'accroître la radiation incidente. Une autre section de 100 m à canopée intacte dans chaque cours d'eau a servi de témoin en ce qui a trait à la lumière. Des carcasses de saumons ont été ajoutées à chaque année dans des sections à rives déblayées et intactes dans trois des six cours d'eau. Il y a une augmentation de la densité totale (par comparaison aux valeurs initiales) de la truite fardée (*Oncorhynchus clarki*) et de la truite arc-en-ciel (*Oncorhynchus mykiss*) consécutive au retrait de la canopée, mais il n'y a pas d'effet décelable de l'addition de carcasses. Les taux de croissance spécifiques des poissons dans les sites à canopée ouverte et fermée diffèrent plus dans les sites sans addition de carcasses que dans ceux où il y a eu addition. Dans les situations où la lumière est un facteur limitant, une coupe sélective des bois francs sur les rives peut augmenter la production de salmonidés à la condition que l'accroissement de la température associée à l'ouverture de la canopée ne soit pas néfaste aux ressources aquatiques.

[Traduit par la Rédaction]

Introduction

Nutrient limitation may underlie the finding that, even in pristine settings, salmonid production in coastal streams of the Pacific Northwest often lags behind that achieved in other salmonid streams worldwide. When compared across broad spatial scales, salmonid production is correlated with ion and nutrient concentrations (Kwak and Waters 1997), often irrespective of stream physical features (Bisson and Bilby 1998). Coastal streams of the Pacific Northwest are typically oligotrophic and have relatively low acid-neutralizing capacity (Welch et al. 1998). The relationship between salmonid production and nutrient concentration does not appear to be direct but arises instead from the effect of nutrient concentrations on primary production, with cascading effects through the food web. When nutrients are in short supply, autochthonous production may be reduced, resulting in reduced availability of invertebrate prey and slower fish growth.

Nutrient limitation of Pacific Northwest streams may be exacerbated by a declining nutrient supply from carcasses of spawned adult salmon, as many regional salmon stocks have

Received 8 October 2003. Accepted 19 August 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 4 March 2005.
J17780

M.A. Wilzbach.[1] US Geological Survey, Biological Resources Division, California Cooperative Fish Research Unit, Humboldt State University, Arcata, CA 95521, USA.
B.C. Harvey, J.L. White, and R.J. Nakamoto. US Forest Service, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521, USA.

[1] Corresponding author (e-mail: paw7002@humboldt.edu).

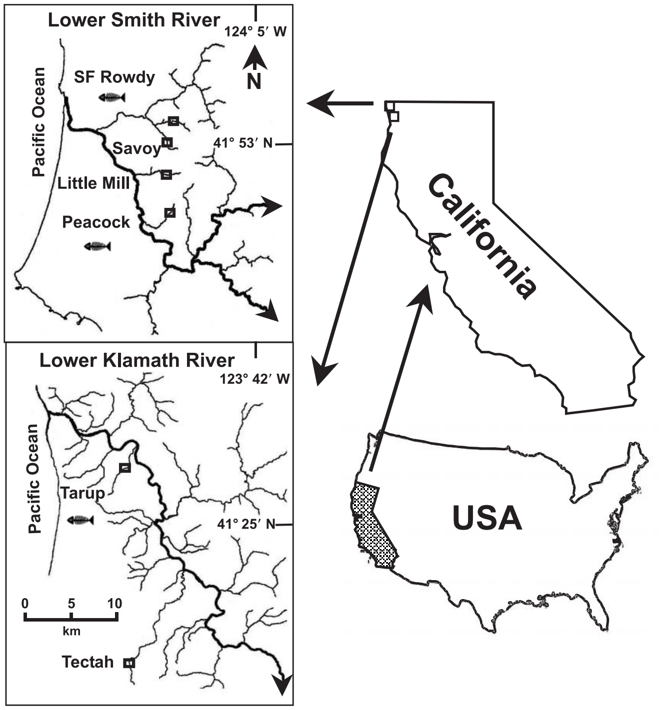
doi: 10.1139/F04-177

sharply declined (Nehlsen et al. 1991). Gresh et al. (2000) estimated that current salmon returns provide only 6–7% of the historical subsidy of marine-derived nitrogen and phosphorus once delivered to regional rivers. This subsidy results as the anadromous salmon migrate from their marine feeding grounds to spawn and die in their natal streams. Concern that the oligotrophic status of streams is limiting production of juvenile salmonids has prompted the increasing use of carcass introductions as a stream restoration technique (Lackey 2003).

Although several studies have documented that marine-derived nutrients are incorporated into salmonid tissue in freshwater systems (e.g., Kline et al. 1990; Bilby et al. 1996; Chaloner et al. 2002), compelling evidence that salmon carcass introductions affect salmonid population parameters has not yet been established. Only two studies to date have evaluated effects of carcass addition on salmonid densities, biomass, condition factors, or growth. Bilby et al. (1998) compared two Washington streams in which hatchery carcasses were added in late fall to augment carcasses from naturally spawning salmon with paired streams with few spawning salmon. They found that densities and condition factors of age 0+ coho salmon (*Oncorhynchus kisutch*) and age 0+ and 1+ steelhead (*Oncorhynchus mykiss*) increased with carcass addition over the period of salmon spawning and decomposition, but these effects did not persist into spring. Wipfli et al. (2003) found that carcass additions increased growth of age-0 coho salmon in small artificial channels over a 2-month period. Wipfli et al. (2003) also observed that October–May growth of cutthroat trout (*Oncorhynchus clarki*) in a reach of an Alaskan stream where pink salmon (*Oncorhynchus gorbuscha*) carcasses were added in late summer – early fall exceeded the growth of fish in a control reach.

A variety of factors affect the ability of stream salmonids to utilize nutrients provided from salmon carcasses and may dictate the pathways by which carcass-derived nutrients are transferred to salmonids. Carcass-derived nutrients may be transferred to salmonids via (*i*) uptake by autotrophs, which is transferred to fish that feed on primary consumers, (*ii*) substrate sorption of dissolved organic matter and uptake by microfauna, and (*iii*) direct consumption by fish of carcasses, eggs, and fry (Cederholm et al. 1999). Factors affecting pathways of nutrient transfer and the ability of salmonids to benefit from salmon carcasses include stream retentiveness, discharge, consumption by aquatic consumers and terrestrial wildlife, riparian conditions, and ambient water chemistry (Gende et al. 2002). For example, based on laboratory experiments demonstrating uptake of nitrogen by gravel through abiotic processes and comparisons of stable isotope ratios among trophic categories in streams with spawning coho salmon, Bilby et al. (1996) concluded that direct consumption of spawning products by secondary consumers and substrate sorption of dissolved organic matter, but not autotrophic uptake, were important avenues of transfer. However, the streams that they studied were heavily shaded by riparian vegetation, and light limitation of primary production may have influenced their findings. Other studies in fresh water ecosystems have found or suggested that primary production is of primary importance as a pathway to the production of salmonid fishes (e.g., Richey et al. 1975; Mathisen et al. 1988; Kline et al. 1997).

Fig. 1. Location of study sites within the Smith River and Klamath River basins in northern California. The fish symbols identify the three creeks that received salmon carcasses.



Considerable evidence suggests that light limitation of primary production often overrides nutrient limitation in small, forested streams (e.g., Lowe et al. 1986; Rand et al. 1992; Hill et al. 2001). This may be particularly common in the Pacific Northwest, where both coniferous vegetation and an increasing dominance of alder (*Alnus* spp.) (Hu et al. 2001) can provide heavy riparian shade. In coastal settings, summer fog may also reduce light reaching streams.

Where light limits algal production, the ability of stream systems to respond to carcass enrichment may be affected and transfer pathways to salmonids restricted. Autotrophic pathways are particularly important in sustaining salmonid growth during spring and summer (Bilby and Bisson 1992) and are at the basis of the finding that logged streams often support higher salmonid production than their forested counterparts (e.g., Murphy and Hall 1981; Wilzbach et al. 1986). Restoration techniques using carcass introductions to increase growth of juvenile salmonids may fail to fully achieve desired results if factors limiting primary production are not also considered. Previous studies of salmonid response to carcass addition have not concurrently examined the effect of decreasing riparian canopy.

We designed this study to evaluate the response of growth and abundance of resident salmonids to simultaneous manipulations of canopy opening and salmon carcass enrichment, with the expectation that canopy opening and carcass enrichment would have additive positive effects on salmonid density and growth.

Table 1. Geographic coordinates, catchment area, and mean bankful width and channel gradient of open and closed canopy reaches of the study sites.

Stream	Geographic coordinates	Catchment area (km^2)	Mean bankful width (m) Open	Mean bankful width (m) Closed	Gradient (%) Open	Gradient (%) Closed
Tectah	41°15′47″N, 123°57′52″W	7.9	6	7.2	2.9	1.7
Tarup	41°27′45″N, 123°59′32″W	4.9	7.9	7.2	2.8	1.8
Peacock	41°50′11″N, 124°5′23″W	3.5	3.8	4.4	2.4	4.2
Little Mill	41°52′27″N, 124°6′47″W	3.4	6.5	5.9	7.7	9.5
South Fork Rowdy	41°55′16″N, 124°5′23″W	4.9	7.9	7.8	5.6	5.1
Savoy	41°54′14″N, 124°5′12″W	5	8	8.6	4.7	5.6

Materials and methods

Study sites

Six second- to third-order streams in coastal northern California were selected for study (Fig. 1): four tributaries of the Smith River (Little Mill, Peacock, Savoy, and South Fork Rowdy creeks) and two tributaries of the lower Klamath River (Tarup and Tectah creeks). Study sites on the six streams were located in stands of 30- to 60-year-old conifers (coastal redwood (*Sequouia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis*)). Channel morphology of the sites was similar and consisted of alternating riffle–pool sequences with some but not abundant accumulations of large woody debris. Sites were similar in catchment area, stream size, and gradient (Table 1), with riparian vegetation dominated by red alder (*Alnus rubra*) and fish assemblages dominated by resident salmonids (coastal cutthroat trout (*Oncorhynchus clarki clarki*) and rainbow trout/steelhead). In October 2001, salmonid biomass averaged 3.3 $g \cdot m^{-2}$ across all of the study sites (range 2.0–5.0 $g \cdot m^{-2}$, while salmonid density averaged 0.4 $fish \cdot m^{-2}$ (range 0.2–0.7 $fish \cdot m^{-2}$). Sites were selected to be above upstream limits of anadromy for Pacific salmon, as we wished to focus on fishes with extended fresh water residency as well as reduce confounding effects from naturally distributed salmon carcasses. However, we observed small numbers of juvenile coho salmon and chinook salmon (*Oncorhynchus tshawytscha*) in Savoy and South Fork Rowdy creeks in May–June 2002 following a winter with high regional escapement and stream discharge. Neither species was observed in any of the reaches during fall samplings. Other vertebrates present included the coastal (Pacific) giant salamander (*Dicamptodon tenebrosus*), tailed frog (*Ascaphus truei*), and adult foothill yellow-legged (*Rana boylei*) and red-legged (*Rana aurora*) frogs.

The climate in the region is characterized as marine west coast with an annual average precipitation of 170–200 cm, approximately 75% of which falls as rain between November and March. Bedrock of both the Klamath and Smith River study sites is of the Franciscan complex (California Division of Mines and Geology 1964), and soils are of the Hugo-Josephine association (United States Soil Conservation Service 1967).

The experiment was conducted from October 2001 to October 2003. In both water years, US Geological Survey gauging stations on the mainstem Smith and Klamath rivers recorded peak discharges with recurrence intervals of approximately 1 year. Based on ≥70 years of record, discharges during March–June 2003 exceeded mean monthly stream flows but were below them during March–June 2002. Discharges in both basins were below mean monthly stream flows during summer months in 2002 and 2003.

Experimental design

In the field experiment, we supplemented stream nutrients with the addition of salmon carcasses and increased incident light through the removal of riparian hardwoods. The experiment followed a split-plot experimental design, with streams as whole plots and two 100-m reaches within each stream as subplots. The two 100-m reaches were separated by 150–200 m of stream channel. To eliminate the possibility that carcass addition would influence "no-carcass" treatments while retaining the ability to randomly assign treatments, we manipulated carcasses at the whole-stream (whole-plot) scale. Thus, we randomly selected three of the six study streams for carcass addition (Tarup, Peacock, and South Fork Rowdy creeks), and each of the two study reaches in these three streams received carcasses. Within each study stream, we randomly assigned the canopy removal treatment to one of the two study reaches. Stream sections were not blocked during this study. One consequence of this experimental design was that the power of the tests of the canopy removal effect and the interaction of canopy and carcass treatments exceeded the power of the test for a carcass effect.

Carcasses of chinook salmon were introduced into both study reaches in the three selected streams in January of 2002 and 2003. Carcasses were obtained from the California Department of Fish and Game Iron Gate Hatchery for placement in the Klamath River sites and from the private Rowdy

Table 2. ANOVA model used for analyzing fish response to canopy and carcass treatments.

Source of variation	df	Error term
Among streams		
Carcass effect	1	Streams (carcass)
Streams (carcass)	4	
Within streams		
Riparian effect	1	Riparian × streams (carcass)
Carcass × riparian	1	Riparian × streams (carcass)
Riparian × streams (carcass)	4	
Date effect	1	Date × streams (carcass)
Carcass × date	1	Date × streams (carcass)
Date × streams (carcass)	4	
Riparian × date	1	Riparian × date × streams (carcass)
Carcass × riparian × date	1	Riparian × date × streams (carcass)
Riparian × date × streams (carcass)	4	

Creek Hatchery and by hand collection for placement in the Smith River tributaries. The carcasses added to the streams were from salmon that had returned from the sea. They had been spawned prior to placement in the stream, but small quantities of eggs remained in the body cavities of some females. Because mean carcass size differed considerably between the two basins (8.6 kg, Smith River; 5.4 kg, Klamath River), we standardized introductions by mass rather than number to approximately 3 kg·m^{-1} (SD = 0.18) or on an areal basis at 0.94 kg·m^{-2} (SD = 0.33). This exceeds the carcass loading used in other studies of salmonid response to carcass addition (0.56 and 0.62 kg·m^{-2} in Bilby et al. (1998) and 0.83 kg·m^{-2} in the natural stream studied by Wipfli et al. (2003)). Natural carcass densities in streams of coastal northern California are typically less than 100 fish·km^{-1} (Bell 2001; J.B. Waldvogel, University of California Cooperative Extension 586 G Street, Crescent City, CA 95531, USA, personal communication). Carcasses were distributed throughout stream sections in areas of slack water and anchored to the streambed with rebar to ensure that they would not be rapidly flushed from the sections. In the first year of the study, we attached radiotransmitters to an additional six unanchored carcasses within each stream to track their movement.

Riparian hardwood removal involved falling alder and other hardwoods from a 20-m-wide band on each side of the channel. Falling was conducted to minimize damage to the few conifers within the riparian zone. Cut trees were left in place but dragged when necessary out of the active channel. Trees were cut in late December 2001, after leaf drop had occurred, so that we would not affect the supply of litter inputs to the streams from autumnal leaf drop. The canopy manipulation was not repeated in 2002, as little riparian regrowth occurred. Canopy removal was effective in increasing incident radiation. Potential available sunlight received by the streams, estimated using a solar pathfinder (Solar Pathfinder, Pleasantville, Tennessee), did not differ among study reaches prior to canopy removal. After canopy removal, photosynthetically active radiation was measured simultaneously in open and closed canopy reaches with a quantum sensor (LI-190S, LI-COR, Lincoln, Nebraska) on selected dates. Photosynthetically active radiation was generally less than 50 µmol·s^{-2}·m^{-2} in closed sections and often greater than 500 µmol·s^{-2}·m^{-2} in open sections during daylight hours.

Fish sampling

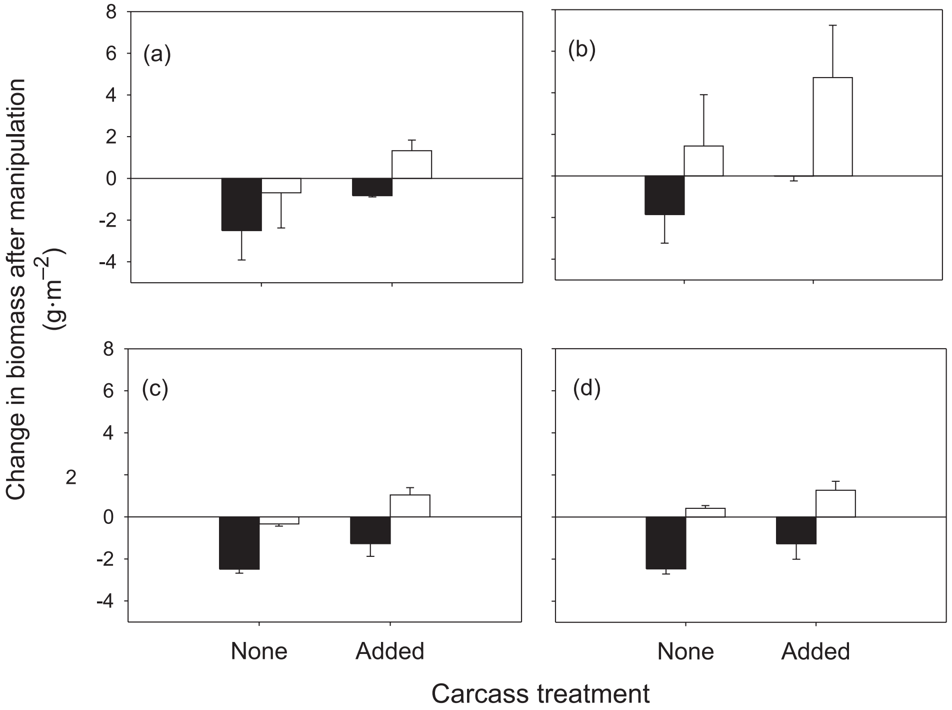
Fish were sampled in all sections by multiple-pass electroshocking in October 2001 (prior to treatment) and in June and October of 2002 and 2003. Each sampling included three passes and, if necessary, additional passes until the number of trout removed was less than 25% of those removed during the previous pass. Captured fish were anesthetized with Alka-Seltzer® tablets before measuring fork length to the nearest millimetre and wet mass to the nearest 0.01 g. Salmonids that could not be identified to species were designated “trout”. Individuals greater than or equal to 70 mm fork length were implanted with passive integrated transponder tags on all sampling occasions except in June 2003 and scanned for the presence of tags in June and October of 2002 and 2003.

Other measurements

Stream temperature was monitored to evaluate its response to canopy opening. We deployed submersible temperature data loggers (Stowaway TidbiT) (Onset Computer Corporation, Bourne, Massachusetts) in each stream section prior to manipulation and collected data throughout the experiment. Over a 2- to 3-week period in September 2002, we evaluated the longitudinal extent of temperature effects by deploying additional temperature recorders at the top and bottom of upper stream reaches, 150 m below upper reaches, the bottom of lower reaches, and 130–150 and 350 m below lower reaches.

Grab samples of water from all study reaches were analyzed for concentrations of nitrate (NO_3^-), ammonium (NH_4^+), total nitrogen (TN), soluble reactive phosphorus (PO_4^{3-}), total phosphorus (TP), and silica (SiO_2) in 2002 following carcass addition. Two grab samples were taken at each study reach in late January, mid-March, late April to early May, and late June 2002, corresponding to 2, 6, 15, and 22 weeks following carcass addition. Samples were run using an AutoAnalyzer II (Technicon Industrial Systems/Tarrytown, New York) system following the standard methods (American Public Health Association 1999).

Fig. 2. Change in biomass of all salmonids (coastal cutthroat trout and rainbow trout, age classes combined) in (*a*) June 2002, (*b*) October 2002, (*c*) June 2003, and (*d*) October 2003 from the October 2001 (pretreatment) sample (solid bars, uncut riparian; open bars, cut riparian). Vertical lines above or below bars represent standard error; $n = 3$ stream reaches for each treatment combination on each date.



Data analysis

Salmonid response variables included total and age-specific abundance expressed as biomass and density as well as specific growth rates of post-age-0 fish. Abundance was expressed as the difference in biomass (grams per square metre) or density (fish per square metre) of all salmonids between pretreatment samples (October 2001) and subsequent posttreatment samples (June and October in 2002 and 2003). Specific growth rate (G) of passive integrated transponder tagged individuals was measured as $G = ((\ln W_t - \ln W_0)/t) \times 100$, where W_t is the final mass (grams), W_0 is the initial mass (grams), and t is the growth period (days). Growth was estimated for the overwinter (October 2001 – June 2002) and oversummer (June 2002 – October 2002) periods of 2002 and the overwinter period (October 2002 – June 2003) of 2003. Response variables were analyzed by three-factor ANOVA, with carcass treatment (with and without introduced carcasses), riparian cover (open and closed riparian cover), and date (June 2002, October 2002, June 2003, and October 2003) as factors, with repeated measures on riparian cover and date (Table 2) (Winer et al. 1991). Analyses of specific growth rates included only three levels of date (June 2002, October 2002, and June 2003).

Differences between cut and uncut riparian sections of streams in mean winter (mid-December through mid-March) and summer (mid-June through mid-September) temperature and maximum weekly average temperatures were tested with two-tailed paired t tests on postmanipulation data from the first year of the study. Treatment effects on water chemistry variables (NO_3^-, NH_4^+, TN, PO_4^{3-}, TP, and SiO_2) were analyzed by three-factor ANOVA as described for salmonid response variables. Levels of date for these analyses were late January, mid-March, late April to early May, and late June 2002.

Results

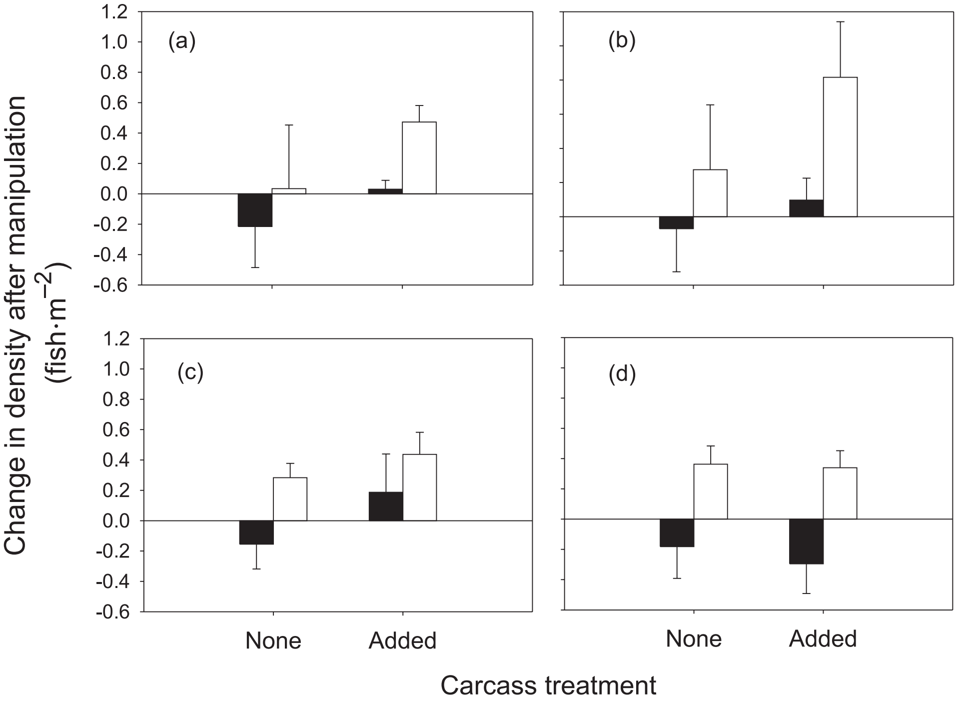
Fate and decomposition of salmon carcasses

A majority (14 of 18) of unanchored, radiotagged salmon carcasses remained within the study reaches and exhibited little displacement from the point of introduction. Ten (56%) of these carcasses were scavenged, and the remainder decomposed within the stream. Only three of 243 anchored carcasses in the first year of the study, however, showed evidence of vertebrate scavenging over a 10-week period of carcass inventory. Both anchored and unanchored salmon carcasses largely decomposed within 1 month after introduction.

Salmonid responses to treatments

The change in total salmonid biomass from pretreatment levels differed between cut and uncut riparian canopies ($P = 0.02$) and among sampling dates ($P = 0.01$) but did not detectably differ between carcass-enriched and unfertilized streams ($P = 0.32$). None of the interaction terms in this analysis achieved statistical significance (all $P > 0.43$). Irrespective of carcass treatment or date, reaches with cut riparian canopies were always associated with a more positive change in biomass compared with uncut reaches (Fig. 2). In cut reaches, biomass increased in all treatment combinations except for streams without carcass additions during the

Fig. 3. Change in density of all salmonids (coastal cutthroat trout and rainbow trout, age classes combined) in (*a*) June 2002, (*b*) October 2002, (*c*) June 2003, and (*d*) October 2003 from the October 2001 (pretreatment) sample (solid bars, uncut riparian; open bars, cut riparian). Vertical lines above or below bars represent standard error; n = 3 stream reaches for each treatment combination on each date.



overwinter period (June 2002 and June 2003 samples). In uncut reaches, biomass always decreased.

Age-specific analyses of salmonid biomass revealed that neither young-of-the-year (P = 0.61) nor post-young-of-the-year (yearling and older) (P = 0.20) responded detectably to carcass addition, but these age groups differed in their responses to the other factors. The biomass of young-of-the-year fish was not strongly affected by canopy opening (P = 0.07), but biomass differed among dates (P < 0.01). Predictably, the biomass of young-of-the-year fish was higher in October than in June in both years. Conversely, biomass of post-young-of-the-year salmonids was higher in reaches where riparian canopies were cut (P = 0.01) but did not differ over the four posttreatment sampling dates (P = 0.11). Age-specific analyses of salmonid biomass did not yield any significant interaction terms.

As with total salmonid biomass, the change in total salmonid density from pretreatment densities differed between cut and uncut riparian canopies (P = 0.05) but not between carcass-enriched and unfertilized streams (P = 0.53). The change in total density was not affected by sampling date or interaction terms (all P > 0.15). Regardless of carcass treatment or date, reaches with cut riparian canopies supported greater increases in salmonid density than reaches with intact canopies (Fig. 3). The effect of riparian canopy on change in density was greater for yearling and older individuals (P = 0.01) than it was for young-of-the-year fish (P = *0.07).* Carcass treatment, date, and interaction terms did not detectably affect the density of either age group (all P > 0.08).

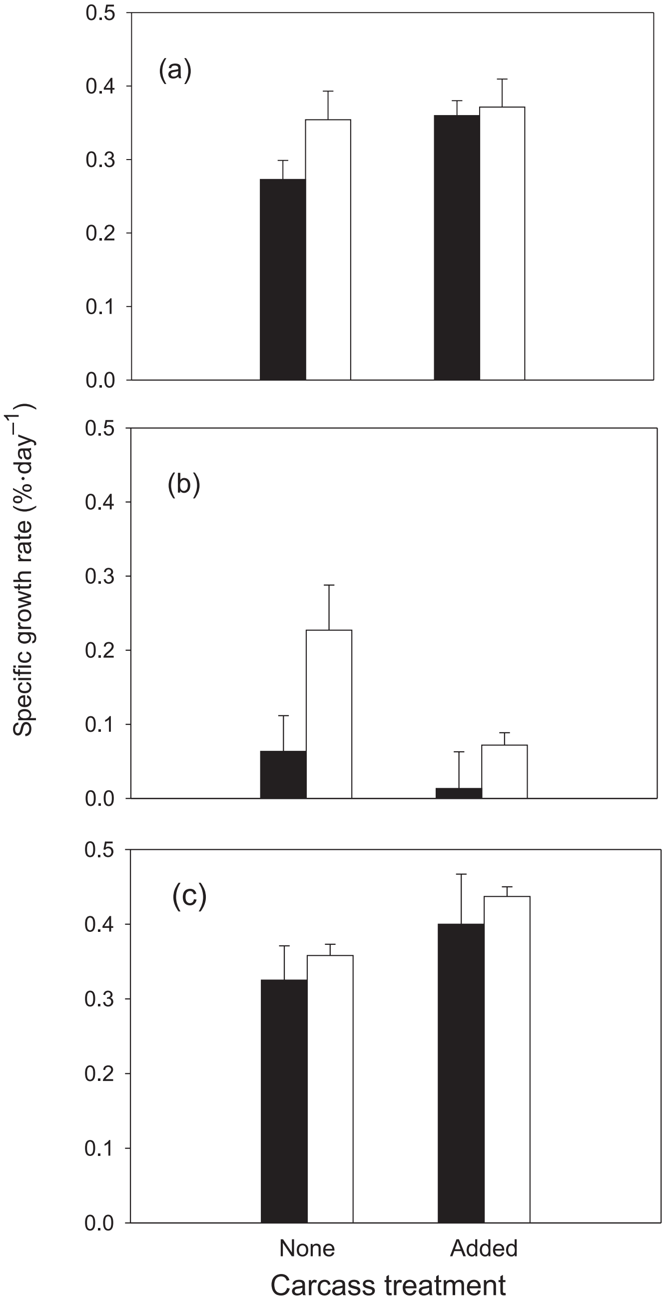
Mean specific growth rates of marked individuals varied among dates (P < 0.01) and by treatment combination (carcass × riparian interaction) (P = 0.02) (Fig. 4). Fish achieved higher growth in open than in closed canopy reaches (Fig. 4). Differences in growth between open and closed canopy reaches were greater in sites without carcasses (open canopy: mean = $0.31\%\cdot\text{day}^{-1}$, SD = 0.09, n = 3 reaches; closed canopy: mean = $0.22\ \%\cdot\text{day}^{-1}$, SD = 0.13, n = 3 reaches) than in sites with carcasses (open canopy: mean = $0.29\%\cdot\text{day}^{-1}$, SD = 0.17, n = 3 reaches; closed canopy: mean = $0.26\%\cdot\text{day}^{-1}$, SD = 0.20, n = 3 reaches). Growth was at least threefold greater for individuals recaptured at the end of overwinter periods (June 2002 and June 2003 samples) than it was for individuals recaptured at the end of the oversummer period (October 2002).

Growth results do not appear to have been strongly affected by fish movement, as only one of 572 recaptured individuals was located in a reach different from the reach where it was originally tagged. However, seasonal retention of tagged individuals within study reaches was low, particularly overwinter. Site retention of tagged individuals did not differ between levels of carcass or riparian canopy treatments or their interaction (arcsine square-root transformed data, all P > 0.29) but were affected by date (P < 0.01). In October 2002, 51% of tagged individuals were recaptured (SD = 15, n = 12 reaches). In June 2002 and June 2003, retention was 18% (SD = 8, n = 12 reaches) and 12% (SD = 9, n = 12 reaches), respectively.

Temperature effects of canopy opening

Cut and uncut riparian reaches did not differ in winter or summer mean temperatures or maximum weekly average temperature (two-tailed paired t tests, df = 5, P = 0.30, 0.23, and 0.27, respectively). The difference in maximum weekly average temperature between cut and uncut reaches never exceeded 1 °C (Table 3). Examination of downstream pat-

Fig. 4. Mean specific growth rates of yearling and older PIT-tagged coastal cutthroat trout and rainbow trout recaptured in (*a*) June 2002, (*b*) October 2002, and (*c*) June 2003 (solid bars, uncut riparian; open bars, cut riparian). Vertical lines above bars represent standard error; $n = 3$ for each date and reach-specific mean, which together incorporate 572 separate observations.



terns in temperature during the late summer period in the first year of the study did, however, reveal the persistence of slight temperature increases below reaches with cut riparian canopies. For example, compared with the temperature at the upstream boundary of the cut reach in Tarup Creek, temperature measured 1.5 °C higher at the bottom of the reach (100 m downstream), 1 °C higher 300 m downstream, and 0.5 °C higher 430 m downstream.

Water chemistry response to carcass addition and canopy opening

Experimental manipulations and their interactions had little detectable effect on water chemistry. Carcass addition did not affect concentrations of SiO_2 or species of nitrogen (TN, NO_3^-, and NH_4^+) or phosphorus (TP and PO_4^{3-}) on the dates sampled (all $P > 0.10$). Canopy opening affected only NH_4^+ ($P = 0.01$), with concentrations greater in reaches with open canopies (mean = 0.006 mg·L^{-1}, SD = 0.001, $n = 6$ reaches) than with closed canopies (mean = 0.005 mg·L^{-1}, SD = 0.001, $n = 6$ reaches). Concentrations of SRP and SiO_2 varied with date (both $P < 0.01$) but in an inconsistent fashion. Concentrations of SRP increased steadily from January (mean = 6.18 µg·L^{-1}, SD = 2.53, $n = 12$) to June (mean = 8.6 µg·L^{-1}, SD = 1.90, $n = 12$). SiO_2 concentration was lower in March (mean = 5.85 mg·L^{-1}, SD = 1.99, $n = 12$) than in January (mean = 8.18 mg·L^{-1}, SD = 2.549, $n = 12$), May (mean = 8.33 mg·L^{-1}, SD = 1.97, $n = 12$), or June (mean = 8.87 mg·L^{-1}, SD = 2.27, $n = 12$). Across all dates and treatments, mean concentrations of NO_3^-, TN, and TP were 0.27 mg·L^{-1} (SE = 0.02, $n = 48$), 0.35 mg·L^{-1} (SE = 0.02, $n = 48$), and 9.05 µg·L^{-1} (SE = 0.36, $n = 48$), respectively.

Discussion

In our experiment, the addition of salmon carcasses did not detectably affect total or age-specific salmonid biomass, density, or growth. In contrast, with the exception of the biomass and density of young-of-the-year fish, removal of riparian canopy consistently enhanced salmonid biomass, density, and growth. The strong growth response to canopy opening is particularly salient because it occurred in reaches where fish densities were also greatest. The lack of a strong response to canopy opening by young-of-the-year fish is perhaps not surprising given the clear response of yearling and older fish, which can affect the availability of resources for younger fish. The only significant interaction between carcass and canopy treatments that we detected was that carcass addition reduced the difference in specific growth rates of salmonids between open and closed canopy reaches. Nonetheless, the greatest growth was achieved in open canopy reaches without carcasses.

The finding of a strong canopy effect is consistent with a large number of studies reporting increases in summer biomass and production of headwater salmonid populations after riparian logging (e.g., Hawkins et al. 1983; Johnson et al. 1986; Thedinga et al. 1989). In an experiment in which riparian alder were removed from small Alaskan streams, Keith et al. (1998) observed a reduction in summer abundance of age-0 coho salmon in both open and closed canopy sections, but abundance decreased at a higher rate in closed canopy sections. The general explanation in all of these studies is that canopy opening increased primary production, which appears to be the most important trophic pathway for increasing the availability of aquatic macroinvertebrates preferred by salmonids during spring and summer (Bilby and Bisson 1992). Increased light from canopy opening may also increase foraging efficiency of the fish (Wilzbach et al. 1986).

Table 3. Mean winter and summer temperatures and maximum weekly average temperature in the stream reaches.

			Temperature (°C)		
Stream	Reach	Canopy	Winter mean	Summer mean	Maximum weekly average
Little Mill	Upper	Uncut	8.6	11.9	12.7
	Lower	Cut	8.8	12.2	13.2
Peacock	Upper	Uncut	8.9	12.4	13.3
	Lower	Cut	9	12.8	13.7
Savoy	Upper	Uncut	8.4	12.4	12.9
	Lower	Cut	8.4	12.8	13.5
SF Rowdy	Upper	Cut	8.6	13	13.8
	Lower	Uncut	8.5	13.1	13.8
Tarup	Upper	Cut	9.2	11.7	12.4
	Lower	Uncut	9.3	12.1	13.1
Tectah	Upper	Uncut	7.7	12.1	13.9
	Lower	Cut	7.7	12.9	14.9

Large variation among streams within carcass treatments influenced our ability to detect a carcass effect in this study, and a retrospective power analysis indicated that the ability of our experimental design to detect a significant carcass effect was low. For example, for overall density of fish, the experiment had approximately a 20% probability of rejecting a false null hypothesis of no difference among carcass treatments, assuming one wished to detect a difference of 0.5 fish·m^{-2} between treatments. That increases in mean age-specific and total salmonid biomass and density were always greatest in open stream reaches that also received salmon carcasses suggests that a larger sample size or different experimental design might have detected a significant response of salmonid abundance to carcass addition and that salmonid abundance may respond additively to canopy opening and carcass addition. Our future project plans include an amended design in which carcasses will be added to the lower ends of all six streams to further resolve the extent of any carcass effect. However, the failure of any effect of substantial carcass addition to overcome among-stream variation in salmonid abundance indicates that it may not be a powerful management tool in our study region.

Another potential limitation of this study concerns the spatial scale of investigation. The low overwinter retention of tagged fish within reach boundaries raises the possibility that extensive seasonal movement may have affected the results. This raises questions about the appropriate scale for addressing questions about the effects of carcass and riparian manipulations. Chaloner et al. (2004) emphasized the need to verify previous studies of carcass effects, all of which have been conducted at the reach scale, with studies at broader spatial scales. Because the ability of salmonids to respond to carcass enhancement depends on interactions between physicochemical conditions and biological communities that may be site specific, they believe that variability in salmonid responses to carcass enhancement may extend throughout the Pacific Northwest.

Among the differences that likely contribute to the potential for salmonids to respond to carcass addition are the specific loading of salmon carcasses coupled with the timing of carcass addition relative to stream discharge. The loadings that we used (0.7–1.5 kg·m^{-2}) approached those (1.9 kg·m^{-2}) at which Wipfli et al. (2003) found that increased salmonid growth from carcass additions began to diminish. However, we added carcasses during the wet season in northern California to correspond to the timing of spawning by anadromous salmonids in the study streams. During this time period, flows are generally high and fluctuating, and nutrients provided by carcasses may be flushed from the system before they can be sequestered. This may explain our inability to detect a response in nutrient concentrations to carcass treatments and the failure of Ambrose et al. (2004) to detect a periphyton response in the same stream reaches. A similar carcass loading would likely have a greater effect during low flow. The timing and extent of carcass deposition in the streams that we studied contrast sharply with streams that receive runs of mass-spawning salmon at the end of the dry season such as those represented in experiments by Wipfli et al. (2003) and may contribute to the differences in results between their study and ours. This suggestion corresponds to the recent observation by Bilby et al. (2003) that a nutrient subsidy from anadromous salmon was detectable in riparian vegetation along a Washington stream where dense aggregations of chum salmon (*Oncorhynchus keta*) spawn but not in a nearby stream where coho salmon spawn at lower densities.

Results of this study have important management implications in addition to suggesting avenues of future research. For example, gains in salmonid production might be achieved by selective trimming of riparian alder or other hardwoods if other habitat requirements are met. Selective trimming could reduce light limitation of primary production, resulting in increased availability of invertebrates to support salmonid growth. The importance of light in affecting food supply for fish has been generally undervalued by management agencies, and riparian vegetation that provides as much shade as possible is usually ranked as “better” in habitat evaluations than vegetation that provides less shade. This assumption is likely based on temperature increases that often accompany vegetation removal and the overhead cover that it provides fish. However, temperature increases are not problematic until they approach a level at which they become stressful for the organisms one is hoping to maintain. The magnitude of temperature increase from canopy removal varies by site and harvest treatment (Johnson and Jones 2000) and is affected by both external drivers that influence heat and water delivery to a system and internal hydrological characteristics that determine heat flux within the system (Poole and Berman 2001). The effect of a given temperature increase on salmonid production depends on interactions among growth, food consumption, temperature, and other factors (Railsback and Rose 1999); modest temperature increases need not reduce production. The spatial scale and extent of canopy opening are relevant inasmuch as multiple canopy openings within a watershed have the potential to cumulate thermal loadings downstream (Murphy and Meehan 1991). Additional research could establish the amount and spatial pattern of light gain necessary to optimize local food supplies without sacrificing the beneficial functions that riparian vegetation provides stream and terrestrial ecosystems or reducing salmonid production downstream. Carcass introductions, on the other hand, may fail to enhance salmonid production in settings where light limits primary production or when other factors operate that prevent successful use of carcasses by salmonids. The effectiveness of salmon carcass additions in sustaining salmonid production over at least an annual cycle, or on spatial scales larger than the reach level, has yet to be established. However, salmon carcasses and spawning products provide nutrient subsidies to terrestrial ecosystems, including riparian vegetation (Helfield and Naiman 2001; but see Bilby et al. 2003), as well as to aquatic consumers. The value of carcass introductions in enhancing system productivity becomes more evident at a larger, landscape level (Gende et al. 2002, 2004) than it may be at the level of individual populations.

Acknowledgements

Research was supported by the US Geological Survey, Biological Resources Division, Cooperative Research Units Program. The Green Diamond Resource Company provided access to their lands, staff, and logistical support and conducted the canopy removal. Michael Grant, analytical chemist with the University of Michigan Biological Station, conducted water chemistry analyses. We gratefully acknowledge the assistance of Lowell Diller, Chris Howard, Brian Michaels, and Matt House in site selection and carcass procural and introduction. Susan Corum, Donnie Ratcliff, and Travis Ayers assisted in fish sampling efforts. Osvaldo Hernandez and students and technicians of the US Geological Survey California Cooperative Fish Research Unit assisted with carcass introductions.

References

Ambrose, H.E., Wilzbach, M.A., and Cummins, K.W. 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. J. N. Am. Benthol. Soc. **23**: 701–712.

American Public Health Association. 1999. Standard methods for the examination of water and wastewater. 20th ed. American Public Health Association, Washington, DC.

Bell, E. 2001. Survival, growth, and movement of juvenile coho salmon (*Oncorhynchus kisutch*) over-wintering in alcoves, backwaters, and main channel pools in Prairie Creek, California. M.S. thesis, Humboldt State University, Arcata, Calif.

Bilby, R.E., and Bisson, P.A. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Can. J. Fish. Aquat. Sci. **49**: 540–551.

Bilby, R.E., Fransen, B.R., and Bisson, P.A. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can. J. Fish. Aquat. Sci. **53**: 164–173.

Bilby, R.E., Fransen, B.R., Bisson, P.A., and Walter, J.K. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Can. J. Fish. Aquat. Sci. **55**: 1909–1918.

Bilby, R.E., Beach, E.W., Fransen, B.R., and Walter, J.K. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Trans. Am. Fish. Soc. **132**: 733–745.

Bisson, P.A., and Bilby, R.E. 1998. Organic matter and trophic dynamics. *In* River ecology and management: lessons from the Pacific coastal ecoregion. *Edited by* R. Naiman and R. Bilby. Springer, New York. pp. 373–398.

California Division of Mines and Geology. 1964. California geology. California Division of Mines and Geology, Sacramento, Calif.

Cederholm, C.J., Kunze, M.D., Murota, T., and Sibatani, A. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries, **24**(10): 6–16.

Chaloner, D.T., Martin, K.M., Wipfli, M.S., Ostrom, P.H., and Lamberti, G.A. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. Can. J. Fish. Aquat. Sci. **59**: 1257–1265.

Chaloner, D.T., Lamberti, G.A., Merritt, R.W., Mitchell, N.L., Ostrom, P.H., and Wipfli, M.S. 2004. Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. Freshw. Biol. **49**: 587–599.

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

Gende, S.M., Quinn, T.P., Willson, M.F., Heitz, R., and Scott, T.M. 2004. Magnitude and fate of salmon-derived nutrients and energy in a coastal stream ecosystem. J. Freshw. Ecol. **19**: 149–160.

Gresh, T., Lichatowich, J.,and Schoonmaker, P. 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.

Hawkins, C.P., Murphy, M.L., Anderson, N.H., and Wilzbach, M.A. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Can. J. Fish. Aquat. Sci. **40**: 1173–1185.

Helfield, J.M., and Naiman, R.J. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology, **82**: 2403–2409.

Hill, W.R., Mulholland, P.J., and Marzolf, E.R. 2001. Stream ecosystem responses to forest leaf emergence in spring. Ecology, **82**: 2306–2319.

Hu, F., Finney, B.P., and Brubaker, L.B. 2001. Effects of Holocene *Alnus* expansion on aquatic productivity, nitrogen cycling, and soil development in southwestern Alaska. Ecosystems, **4**: 358–368.

Johnson, S.L., and Jones, J.A. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Can. J. Fish. Aquat. Sci. **57**(Suppl. 2): 30–39.

Johnson, S.W., Heifetz, J., and Koski, K.V. 1986. Effects of logging on the abundance and seasonal distribution of juvenile steelhead in some southeastern Alaska streams. N. Am. J. Fish. Manag. **6**: 532–537.

Keith, R.M., Bjornn, T.C., Meehan, W.R., Hetrick, N.J., and Brusven, M.A. 1998. Response of juvenile salmonids to riparian and instream cover modifications in small streams flowing though second-growth forests of southeast Alaska. Trans. Am. Fish. Soc. **127**: 889–907.

Kline, T.C., Goering, J.J., Mathisen, O.A., Poe, P.H., and Parker, P.L. 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. $\delta^{15}N$ and $\delta^{13}C$ evidence in Sashin Creek, southeastern Alaska. Can. J. Fish. Aquat. Sci. **47**: 146–144.

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

Kwak, T.J., and Waters, T.F. 1997. Trout production dynamics and water quality in Minnesota streams. Trans. Am. Fish. Soc. **126**: 35–48.

Lackey, R.T. 2003. Adding nutrients to enhance salmon runs: developing a coherent public policy. Fisheries, **28**(8): 34–35.

Lowe, R.L., Golladay, S.W., and Webster, J.R. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. J. North Am. Benthol. Soc. **5**: 221–229.

Mathisen, O.A., Parker, P.L., Goering, J.J., Kline, T.C., Poe, P.H., and Scalan, R.S. 1988. Recycling of marine elements transported into freshwater systems by anadromous salmon. Verh. Int. Ver. Limnol. **23**: 2249–2258.

Murphy, M.L., and Hall, J.D. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquat. Sci. **38**: 137–145.

Murphy, M.L., and Meehan, W.R. 1991. Stream ecosystems. *In* Influences of forest and rangeland management on salmonid fishes and their habitats. *Edited by* W.R. Meehan. Am. Fish. Soc. Spec. Publ. 19. American Fisheries Society, Bethesda, Md. pp. 17–46.

Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho and Washington. Fisheries, **16**(2): 4–21.

Poole, G.C., and Berman, C.H. 2001. An ecological perspective on instream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environ. Manag. **27**: 787–802.

Railsback, S.F., and Rose, K.A. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Trans. Am. Fish. Soc. **128**: 241–256.

Rand, P.S., Hall, C.A.S., McDowell, W.H., Ringler, N.H., and Kennen, J.G. 1992. Factors limiting primary productivity in Lake Ontario tributaries receiving salmon migrations. Can. J. Fish. Aquat. Sci. **49**: 2377–2385.

Richey, J.E., Perkins, M.A., and Goldman, C.R. 1975. Effects of kokanee salmon (*Oncorhynchus nerka*) decomposition on the ecology of a subalpine stream. J. Fish. Res. Board Can. **32**: 817–820.

Thedinga, J.F., Murphy, M.L., Heifetz, J., Koski, K.V., and Johnson, S.W. 1989. Effects of logging on size and age composition of juvenile coho salmon (*Oncorhynchus kisutch*) and density of presmolts in southeast Alaska streams. Can. J. Fish. Aquat. Sci. **46**: 1383–1391.

United States Soil Conservation Service. 1967. Report and general soil map, Del Norte County and Humboldt County, California. Soil Conservation Service, US Department of Agriculture, Ukiah, Calif.

Welch, E.B., Jacoby, J.M., and May, C.W. 1998. Stream quality. *In* River ecology and management: lessons from the Pacific coastal ecoregion. *Edited by* R. Naiman and R. Bilby. Springer, New York. pp. 69–94.

Wilzbach, M.A., Cummins, K.W., and Hall, J.D. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology, **67**: 898–911.

Winer, B.J., Brown, D.R., and Michels, K.M. 1991. Statistical principles in experimental design. 3rd ed. McGraw-Hill, New York.

Wipfli, M.S., Hudson, J.P., Caouette, J.P., and Chaloner, D.T. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Trans. Am. Fish. Soc. **132**: 371–381.