

Periphyton response to increased light and salmon carcass introduction in northern California streams

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Abstract. Periphyton response to riparian canopy opening and salmon carcass addition in coastal streams of northern California was evaluated in a manipulative field experiment. The experiment followed a split-plot design, with streams as whole plots and two 100-m reaches in each of 6 streams as subplots. At the subplot level, riparian hardwoods were removed from one reach in each stream. At the whole-plot level, carcasses were added to both open- and closed-canopy reaches of 3 of the streams. Thus, treatments consisted of reaches with open or closed canopies, in the presence and absence of carcasses. Nutrient limitation of the periphyton was assessed in 2 streams (1 with carcasses and 1 without carcasses) using nutrient-diffusing clay saucers (N-enriched, P-enriched, N+P-enriched, or unenriched control) incubated in open- and closed-canopy reaches in the streams. Canopy and carcass treatments did not affect gross primary productivity or periphyton biomass on natural substrates. The periphyton assemblage consisted primarily of diatoms in all reaches on all dates. N amendment of agar in nutrient-diffusing, clay saucers and canopy removal increased biofilm ash-free dry mass on the saucers, but carcass introduction did not. Failure of periphyton to respond to carcass addition may have reflected overriding light limitation, inadequate within-stream retention of carcass nutrients, and/or limitations of the study design.

Key words: periphyton, salmon carcasses, riparian canopy, nutrient enrichment, algae, primary productivity, light, streams.

Low nutrient concentrations that characterize forested streams of the Pacific Northwest (Welch et al. 1998) are probably a consequence of parent geology and declines in numbers of Pacific salmon returning to natal streams to spawn. Many Pacific Northwest streams support relatively high numbers of anadromous salmon, which return to these fresh waters every year to spawn and die (Mathisen et al. 1988, Cederholm et al. 1999). However, Gresh et al. (2000) estimated that declining salmon runs in the region potentially have limited the amount of carcass-derived nutrients available to these streams to only 6 to 7% of historical levels. Many studies have demonstrated elevated nutrient levels in association with decomposing salmon carcasses in streams. Minakawa and Gara (1999), for example, found greater concentrations of Kjeldahl N,

NH₄, and total soluble P in a stream reach with spawning salmon than in an upstream reach without salmon. Lack of macronutrients potentially limits primary productivity in Pacific Northwest streams (Gregory et al. 1987), with the specific limiting nutrient appearing to vary with geology in forested landscapes.

Evidence that resources provided by salmon carcasses cause an increase in primary productivity is sparse and conflicting, regardless of which macronutrient may limit primary productivity. Richey et al. (1975), Wipfli et al. (1998, 1999), Wold and Hershey (1999), and Johnston et al. (2004) reported greater primary productivity or increased biofilm standing crop in streams with spawning salmon runs or following artificial carcass introduction. By contrast, Rand et al. (1992) and Minshall et al. (1991) found no effect of salmonid carcasses on primary productivity or periphyton standing crop. Differences in response may reflect differences among streams in retentiveness, discharge, am-

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bient water chemistry, or riparian conditions (Gende et al. 2002, Chaloner et al. 2004).

In particular, riparian condition is likely to be critical to periphyton response to carcass addition because shading by streamside vegetation can override the potential stimulation of primary productivity by nutrient inputs (Gregory et al. 1987). Nutrient enrichment of streams in the Pacific Northwest has little effect on increasing primary productivity unless the canopy is opened to increase light (Gregory 1980, Triska et al. 1983, Hill and Knight 1988). Light also affects the taxonomic structure and physiognomic forms of periphyton assemblages (Lowe et al. 1986, Bothwell et al. 1993). Replacement of diatom communities with filamentous green algae following clearcutting has been observed in several studies (e.g., Hansmann and Phinney 1973, Shortreed and Stockner 1983, Lowe et al. 1986). The effect of light on assemblage structure of periphyton is likely to result in differences in overall stream trophic structure because diatoms and filamentous algae differ in palatability to invertebrate consumers (Cummins and Klug 1979, Lamberti et al. 1989).

A significant goal of many stream and watershed restoration programs is to enhance abundance and growth of juvenile salmonids in coastal streams of the Pacific Northwest that have experienced depleted salmon runs. Salmonid productivity appears to depend largely on autotrophic pathways, particularly during spring and summer (e.g., Bilby and Bisson 1992). Thus, understanding the relative importance of factors potentially limiting primary productivity is a critical underpinning for the development of restoration strategies. However, the increasing use of salmon carcass introductions or their analogs to enhance salmon runs by replacing missing marine-derived nutrients as a stream restoration tool (Lackey 2003) appears to be proceeding without this understanding. The transfer of carcass-derived nutrients to higher trophic levels may occur by pathways other than autotrophic uptake (Cederholm et al. 1999), but failure to consider factors limiting primary productivity may limit the success of carcass introductions in enhancing salmonid growth.

The objectives of our study were to evaluate the effects of increased light resulting from canopy removal and increased nutrient input resulting from the introduction of Chinook salm-

on carcasses on periphyton in coastal California streams. Based on published findings that riparian shading can override stimulation of primary productivity by nutrient inputs (Gregory et al. 1987), our expectation was that increased light from canopy removal would stimulate periphyton growth more than increased nutrient input from introduction of salmon carcasses in the absence of canopy removal. We expected positive additive effects of treatments on periphyton growth in stream reaches where the riparian canopy was removed and salmon carcasses were added.

Methods

Study sites

The study was conducted in 6 coastal streams in northern California (Fig. 1). Little Mill, Peacock, Savoy, and South Fork Rowdy creeks are in the Smith River basin, and Tarup and Tectah creeks are tributaries of the lower Klamath River. Stream sites were similar in catchment area, stream size, and gradient (Table 1), and red alder (*Alnus rubra*) accounted for >80% of riparian cover. Fish assemblages were dominated by resident salmonids (cutthroat trout, *Oncorhynchus clarki*; rainbow trout/steelhead, *Oncorhynchus mykiss*). Sites were located in basins with 40- to 60-y-old conifers (coastal redwood, *Sequoia sempervirens*; Douglas-fir, *Pseudotsuga menziesii*; Sitka spruce, *Picea sitchensis*). Bedrock in the area belongs to the Franciscan complex, which is predominantly sandstone (Harden 2003). The regional climate is predominantly maritime with warm, dry summers and cool, wet winters and an average annual precipitation of 170 to 200 cm. The study was conducted from November 2001 to November 2002, in a water year in which recurrence intervals of peak discharges at US Geological Survey gauging stations on the mainstem Smith and Klamath rivers were ~1 y. Based on ≥70 y of record, average monthly discharges in both basins were low during the study, particularly during summer. For example, over the period of record, mean monthly flows in August on the mainstem Smith River were 9.57 m³/s. In August 2002, mean flows were 7.36 m³/s.

Experimental design

Both light and salmon carcasses were manipulated in a field experiment (Fig. 2). The exper-

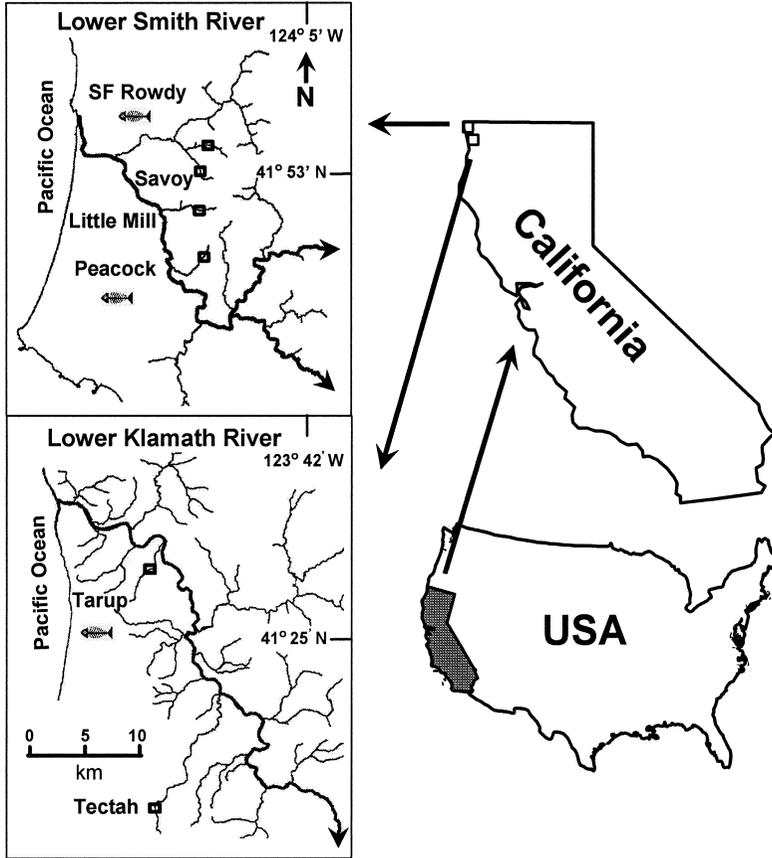


FIG. 1. Locations of study sites (open squares) in the Smith and Klamath River basins in coastal northern California. Fish symbol = sites with carcasses added. SF Rowdy = South Fork Rowdy Creek.

iment followed a split-plot design, in which streams served as whole plots, and two 100-m reaches within each stream served as subplots. Carcasses were added at the whole-plot level to avoid the potential for downstream reaches to be affected by carcass placement in upstream

reaches. Carcasses were added to both reaches of 3 randomly selected streams (Peacock, South Fork Rowdy, and Tarup creeks). Light was manipulated at the subplot level. Within each of the 6 study streams, light was increased by canopy removal in one randomly selected reach. The

TABLE 1. Characteristics of open- and closed-canopy reaches of the study sites. c = sites with carcasses added.

Stream site	Basin	Basin area (km ²)	Latitude/longitude	Mean bankfull width (m)		Gradient (%)	
				Open	Closed	Open	Closed
Savoy	Smith	5.0	41°54'14"N/124°5'12"W	8.0	8.6	4.7	5.6
South Fork Rowdy (c)	Smith	4.9	41°51'16"N/124°5'23"W	7.9	7.8	5.6	5.1
Peacock (c)	Smith	3.5	41°50'11"N/124°5'11"W	3.8	4.4	2.4	4.2
Little Mill	Smith	3.4	41°52'27"N/124°6'47"W	6.5	5.9	7.7	9.5
Tarup (c)	Klamath	4.9	41°27'45"N/123°59'32"W	7.9	7.2	2.8	1.8
Tectah	Klamath	7.9	41°15'47"N/123°57'52"W	6.0	7.2	2.9	1.7

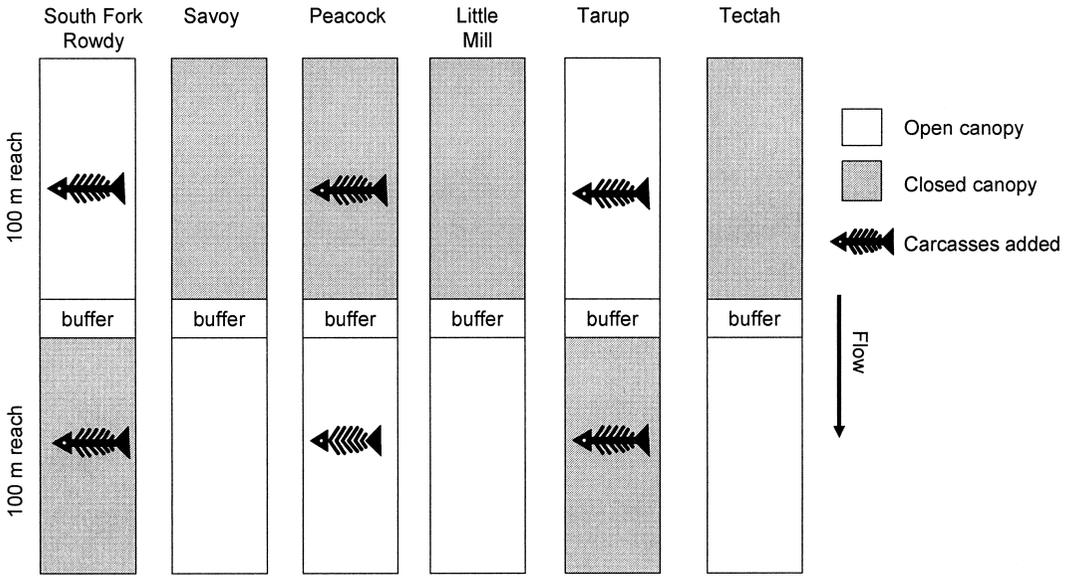


FIG. 2. Experimental design at 6 study sites. In each stream, the canopy was left intact on one 100-m reach, and it was removed in the other. A 150- to 200-m buffer separated the 2 reaches (not drawn to scale). Salmon carcasses were added to both open-canopy and closed-canopy reaches in 3 streams.

canopy in the other reach was left intact. Open- and closed-canopy reaches were separated by a 150- to 200-m buffer. A limitation of this experimental design was that the power of the tests for the canopy-removal effect and the interactive effect of canopy and carcass treatments exceeded the power of the test for a carcass effect.

Light was increased in open-canopy reaches by felling alder and other hardwoods within a 20-m-wide band on both sides of the stream. Felling was done in a way that minimized damage to the few conifers in the riparian zone. Cut trees were laid primarily upslope and left in place, except to drag them outside the active channel when necessary. Trees were cut in late December, after leaf-fall was finished. Thus, tree harvest did not affect the supply of litter and associated nutrients from autumnal leaf-fall to the stream reaches during the study year. Potential available sunlight was measured every 20 m midchannel in each section with a solar pathfinder (Solar Pathfinder, Pleasantville, Tennessee).

Carcasses of chinook salmon (*Oncorhynchus tshawytscha*) were introduced to the stream channels in January. Carcasses used in the Klamath River sites were procured from the California Department of Fish and Game Iron Gate Hatchery. Carcasses used in the Smith Riv-

er tributaries were procured from the private Rowdy Creek Hatchery and by hand-collection from within the basin. Approximately 1 kg/m² of carcass (range: 0.7–1.5 kg/m²) was added to the study reaches. This loading was slightly greater than that used in studies examining salmonid response to carcass addition in natural systems (0.56 kg/m² and 0.62 kg/m² in Bilby et al. 1998; 0.83 kg/m² in Wipfli et al. 2003). The higher loading was chosen to maximize the potential response of the biotic community. Carcasses were anchored to the streambed with rebar in areas of slack water to ensure that they would not be flushed out during high flows.

Periphyton sampling

Chlorophyll *a* (µg/cm²) and ash-free dry mass (AFDM) (mg/cm²) were measured on samples from natural substrates in each study reach in November 2001 (pretreatment) and in March, June, August, and November 2002 (post-treatment). Periphyton was scraped from a 4-cm² area on each of 3 cobbles in 3 randomly chosen riffles in each study reach. A rubber template was used to ensure that the surface area sampled was consistent among rocks. Samples from the 3 cobbles in each riffle were combined, and 2 subsamples were withdrawn for mea-

surement of chlorophyll *a* and AFDM. Subsamples were filtered and mixed thoroughly, with sample volumes noted (Steinman and Lambert 1996). Subsamples were not ground because the periphyton assemblage consisted mostly of single-celled rather than filamentous forms. Chlorophyll *a* was corrected for pheophytin and measured with a spectrophotometer (Model 335401, Spectronic Instruments, Rochester, New York) following the monochromatic method described by Wetzel and Likens (1979). Filters analyzed for AFDM were dried at 60°C for 24 h, weighed (± 0.1 mg), ashed at 500°C for 2 h, and reweighed. Samples were held in a desiccator after drying and ashing to minimize water absorption.

Semiquantitative assessments of % coverage by diatoms, green algae, and cyanobacteria were made using a field-based, rapid periphyton survey approach, modified from Stevenson and Bahls (1999) in November 2001 (pretreatment) and in March, June, August, and November 2002 (post-treatment). Percent coverage of diatoms, green algae, and cyanobacteria were estimated using a 0.3-m² viewing bucket marked with a 50-dot grid. Transects were established in 3 randomly chosen riffles per study section, and surveys were made on both ends and in the middle of each transect. At each location, the number of dots occurring over each algal form was counted. Averages were calculated for each riffle and for all riffles in each study reach, and these values were used to estimate the % coverage of diatoms, green algae, and cyanobacteria in a reach.

Nutrient-limitation experiment

Nutrient limitation of algal growth was evaluated in the 2 Klamath basin sites, Tarup (with carcasses) and Tectah (without carcasses) creeks in August 2002. Logistic constraints made it impossible to conduct this experiment at all sites, and these sites were chosen for pragmatic reasons (closer proximity to the laboratory). Nutrient limitation was assessed using nutrient-diffusing clay saucers incubated at the stream sites (Tate 1990). Clay flowerpot saucers (10.2-cm diameter) were filled with 225 mL of 2% agar that had been enriched with either 0.5 mol/L NaNO₃ (N), 0.1 mol/L KH₂PO₄ (P), 0.5 mol/L NaNO₃ and 0.1 mol/L KH₂PO₄ (N+P), or nothing (control). Four saucers (1 of each nutrient-enrichment

treatment) were glued to each of eight 12 × 12-cm Plexiglas plates attached to wooden frames constructed in a diamond shape. Frames were secured into the streambed of each study reach with rebar. The plates were oriented in the stream so that the control saucers were upstream, the N and P saucers were side-by-side, and the N+P saucers were downstream to minimize cross contamination. Two frames were randomly placed in the open- and closed-canopy reaches of both streams and allowed to incubate for ~3 wk. Periphyton on each saucer was sampled and analyzed for chlorophyll *a* and AFDM using the methods described above.

Primary productivity measurements

Primary productivity was estimated in all study reaches during late June and early July 2002 by measuring change in O₂ concentration in paired light and dark respiration chambers. The 25.4 × 20.3 × 15.2 cm chambers were fitted with a temperature–oxygen probe and data logger (Sonde 6600-0, YSI Environmental, Yellow Springs, Ohio). Streamside incubations were run between 1030 and 1330 h, with water circulation maintained by magnetic stirrers placed underneath the chambers. Water temperature was maintained within 1°C of the starting temperature by adding ice as needed to the outside of the top surface of the chamber. Light levels during incubation were similar to those in the stream channel. One cobble (averaging 350 cm²) that was representative of ambient stream conditions was placed inside each chamber. O₂ concentrations were logged for equal periods of time in both chambers, and incubations lasted 1 to 2 h, depending upon the rate of O₂ production. Area-specific gross primary productivity (GPP) (mg C cm⁻² d⁻¹) was estimated as the sum of the O₂ increase in the light chamber (net primary productivity) and the O₂ depletion in the dark chamber (community respiration). Values were adjusted for substrate surface area and chamber volume and expressed on a 24-h basis. Changes in O₂ concentration were converted to amounts of C fixed using a photosynthetic quotient of 1.2 and a respiratory quotient of 0.85 (Bott 1996). After productivity measurements were made, periphyton on the cobbles was sampled for chlorophyll *a* (chl *a*), and chl *a*-specific GPP was expressed as mg C (mg chl *a*)⁻¹ h⁻¹. Chlorophyll *a* on cobbles used in incubations

TABLE 2. Analysis of variance (ANOVA) model for effects of carcass treatment (with and without carcasses), riparian canopy (open and closed), dates, and interactions on periphyton chlorophyll *a* and ash-free dry mass (AFDM) from natural substrates. See text for explanation of statistical details. "Streams (carcass)" refers to variation attributable to streams within the carcass treatment.

Source of variation	df	Error term
Among streams		
Carcass	1	Streams (carcass)
Streams (carcass)	4	
Within streams		
Riparian canopy	1	Riparian canopy \times streams (carcass)
Riparian canopy \times carcass	1	Riparian canopy \times streams (carcass)
Riparian canopy \times streams (carcass)	4	
Date	3	Date \times streams (carcass)
Date \times carcass	3	Date \times streams (carcass)
Date \times streams (carcass)	12	
Date \times riparian canopy	3	Date \times riparian canopy \times streams (carcass)
Date \times carcass \times riparian canopy	3	Date \times riparian canopy \times streams (carcass)

did not differ from mean chl *a* sampled from natural substrates in June (paired *t*-test: $p = 0.02$, $df = 11$).

Data analysis

The effects of treatments on periphyton biomass (chl *a* and AFDM) and composition (% coverage by diatoms, green algae, and cyanobacteria) were evaluated by comparing pretreatment (November 2001) reach means and post-treatment reach means (March, June, August, and November 2002). Periphyton composition percentages were arcsine-square-root transformed. Response variables were analyzed by 3-factor analysis of variance (ANOVA), with carcass treatment (with and without carcasses), riparian canopy (open and closed), and date (March, June, August, and November) as factors. Canopy and date were subplot factors, and the carcass treatment was analyzed as a whole-plot factor (Winer et al. 1991). The structure of the model used in these analyses is given in Table 2. A similar model structure was used to evaluate the effect of carcass treatment, riparian canopy, and their interaction on GPP, but date was omitted as a factor as GPP was estimated only once in each reach. The effects of treatments on periphyton chl *a* and AFDM from nutrient-diffusing, clay saucers were analyzed using 3-factor ANOVA, with stream, riparian canopy, and nutrient amendment (control, N, P, and N+P) acting as factors. These data were log

transformed to meet assumptions of homogeneity of variance. Post hoc multiple comparisons of main effects were done with Tukey's studentized range (HSD) tests. Statistical analyses were carried out using PROC ANOVA (version 8.0, SAS Institute, Cary, North Carolina). Significance levels for all analyses were set at $\alpha = 0.05$.

Results

Potential available sunlight did not differ among streams or between sections prior to canopy removal (2-way ANOVA, $p = 0.69$ and $p = 0.67$, respectively). Canopy removal was effective in increasing light in treated sections of the streams. Simultaneous measurement of photosynthetically active radiation (PAR) with a quantum sensor (LI-190SA, Li-Cor, Lincoln, Nebraska) in open- and closed-canopy reaches of a stream on selected dates showed that PAR was generally $<50 \mu\text{mol m}^{-2} \text{s}^{-1}$ in closed-canopy reaches and often $>500 \mu\text{mol m}^{-2} \text{s}^{-1}$ in open-canopy reaches during daylight hours on clear days. Canopy removal did not affect stream temperature. Mean monthly temperatures and degree-day accumulation did not differ between open- and closed-canopy reaches (Ambrose 2003).

Periphyton biomass and composition

The change in chl *a* from pretreatment levels did not differ between streams with and with-

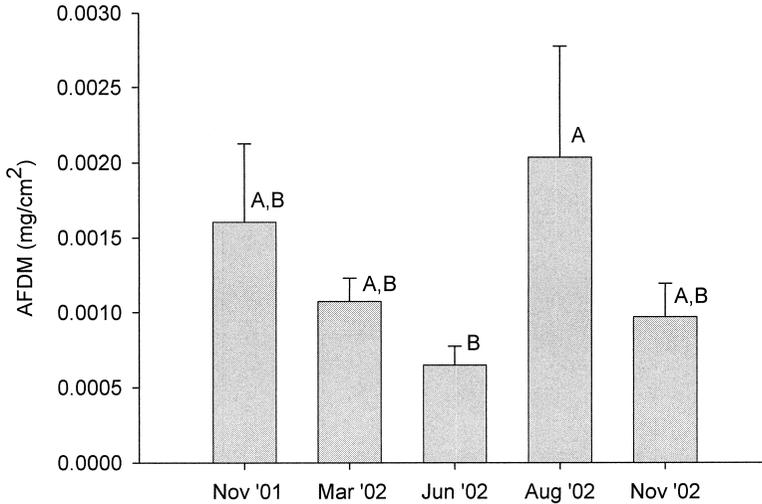


FIG. 3. Ash-free dry mass AFDM (+1 SE) of periphyton scraped from natural substrates in study streams on pre- (November 2001) and post-treatment sampling dates (March–November 2002). Carcass and canopy treatment effects were not significant, so data were combined across reaches and streams ($n = 36$ samples on each date). See text for sampling details. Bars with the same letter were not significantly different.

out carcasses ($p = 0.07$), between open- and closed-canopy reaches ($p = 0.52$), or among sampling dates ($p = 0.20$). No interaction effects were statistically significant (all $p \geq 0.30$). Mean concentration of chl *a* on natural substrates across all dates and sites was $3.92 \mu\text{g}/\text{cm}^2$ (SE = 0.36 , $n = 60$). The change in AFDM from pretreatment levels did not differ between streams with and without carcasses ($p = 0.44$) or between open- and closed-canopy reaches ($p = 0.43$), but it did differ among dates ($p = 0.05$). No interaction effects were statistically significant (all $p \geq 0.47$). Accumulation of periphyton AFDM was greater in August 2002 than in June 2002 ($p = 0.05$), but did not differ among other months (Fig. 3). The autotrophic index (AFDM/chl *a*, both measured as mg/cm^2) was <50 in all reaches on all dates, suggesting that relatively little of the periphyton community was bound up in nonliving organic material (APHA 1999).

Periphyton composition was dominated by diatoms at all study sites on all sampling dates. The change in % coverage of natural substrates by diatoms from pretreatment levels did not differ between streams with and without carcasses ($p = 0.59$), between open- and closed-canopy reaches ($p = 0.94$), or among sampling dates ($p = 0.39$). No interaction effects were statistically

significant (all $p \geq 0.46$). Mean % coverage of natural substrates by diatoms across all dates and sites was 96% (SE = 0.79 , $n = 60$). The change in % cover of green algae from pretreatment levels also was not affected by treatment factors or interactions among factors (all $p \geq 0.33$). The change in % cover of cyanobacteria from pretreatment levels was affected by date ($p = 0.01$), but not by other treatment factors or interactions among factors (all $p \geq 0.17$). Percent cover of cyanobacteria was greater in August 2002 than in March or June 2002 ($p = 0.05$), but differences between August and November 2002 were not statistically significant.

Nutrient-limitation experiment

Chlorophyll *a* concentrations of periphyton sampled from nutrient-diffusing clay saucers differed between open- and closed-canopy reaches ($p < 0.01$) and among nutrient amendments ($p = 0.02$). The interactive effect of carcass \times canopy treatments was statistically significant ($p = 0.03$) (Fig. 4A). Chlorophyll *a* concentrations were higher in open-canopy reaches than in closed-canopy reaches, and chl *a* concentrations were higher in the open-canopy reach of the stream with carcasses than in the open-canopy reach of the stream without car-

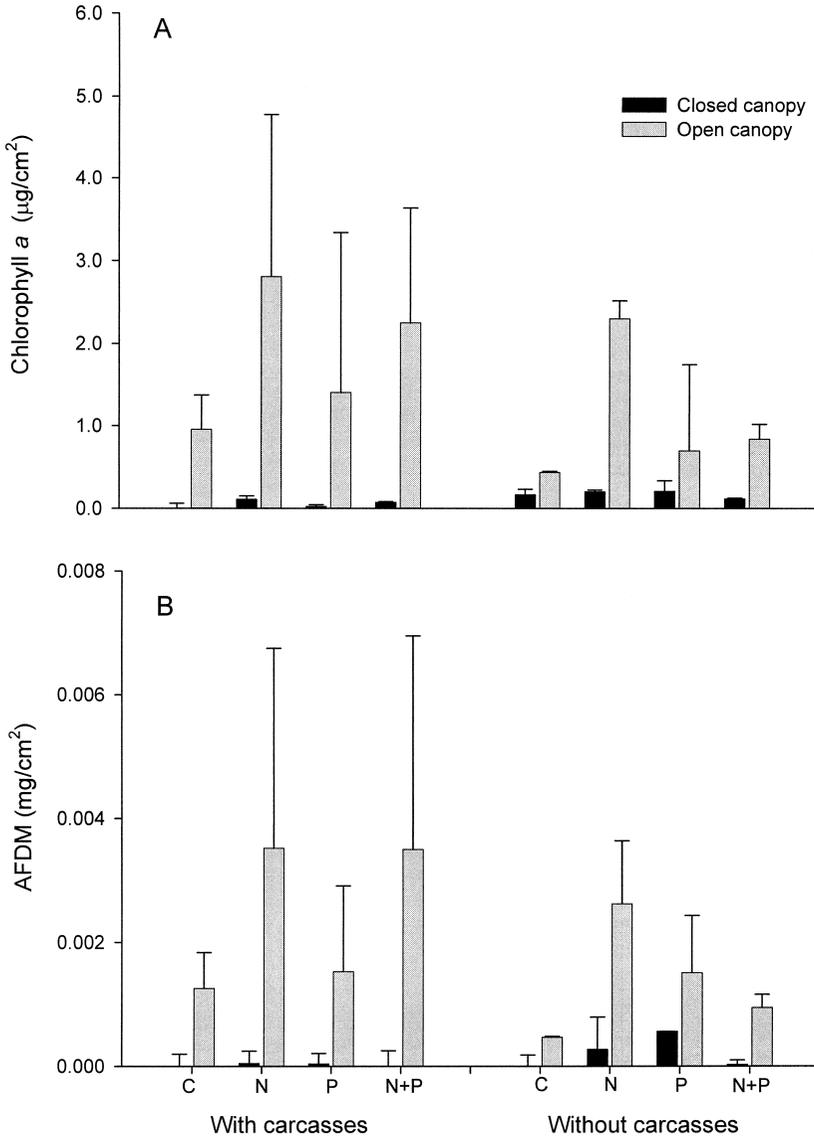


FIG. 4. Mean (+1 SE) chlorophyll *a* content (A) and ash-free dry mass (AFDM) (B) of periphyton scraped from nutrient-diffusing clay saucers incubated in open- and closed-canopy reaches of Tarup (with carcasses) and Tectah (without carcasses) creeks in August 2002 ($n = 2$). C = control (no nutrient enrichment), N = N enrichment, P = P enrichment, N+P = enrichment with N and P.

casses ($p = 0.05$). However, chl *a* concentrations were higher in the closed-canopy reach of the stream without carcasses than in the closed-canopy reach of the stream with carcasses. Chlorophyll *a* concentrations were higher on N-enriched saucers than on control saucers ($p = 0.05$), but chl *a* concentrations did not differ among N-enriched, P-enriched, or N+P-enriched saucers.

AFDM of periphyton sampled from the nutrient-diffusing clay saucers was higher in open- than in closed-canopy reaches of both streams ($p < 0.01$) (Fig. 4B). AFDM of periphyton sampled from the nutrient-diffusing clay saucers did not differ between the stream with carcasses and the stream without carcasses, nor did it differ among nutrient amendments. No interaction effects were statistically significant (all $p > 0.20$).

TABLE 3. Area- and chlorophyll *a* (chl *a*)-specific gross primary productivity (GPP) in open- and closed-canopy reaches of Klamath and Smith River study streams in late June and early July 2002. GPP was estimated using light and dark respiration chambers, with 1 light and 1 dark incubation conducted in each of the 12 stream reaches. c = with carcasses.

Stream site	GPP			
	Area-specific (mg C cm ⁻² d ⁻¹)		Chl <i>a</i> -specific (mg C [mg chl <i>a</i>] ⁻¹ h ⁻¹)	
	Open	Closed	Open	Closed
Little Mill	0.06	0.03	2.50	1.11
Peacock (c)	0.07	0.04	3.97	0.43
South Fork Rowdy (c)	0.02	0.03	0.36	0.28
Savoy	0.04	0.05	0.21	0.89
Tarup (c)	0.02	0.01	2.87	0.24
Tectah	0.03	0.02	4.24	1.09
Mean ± 1 SD	0.04 ± 0.02	0.03 ± 0.01	2.36 ± 1.73	0.67 ± 0.41

Primary productivity

GPP, expressed per unit area, did not differ between streams with carcasses and streams without carcasses ($p = 0.65$) or between open- or closed-canopy reaches ($p = 0.32$) (Table 3). The interaction effect was not statistically significant ($p = 0.88$). GPP, expressed per mg chl *a*, did not differ between streams with carcasses and streams without carcasses ($p = 0.72$). GPP, expressed per mg chl *a*, was higher in open-canopy than in closed-canopy reaches, but the difference was not statistically significant ($p = 0.08$) (Table 3). The interaction effect was not statistically significant ($p = 0.62$).

Discussion

We were unable to detect any effects of carcasses on periphyton, and we found only partial support for a positive effect of canopy removal on periphyton. These results were contrary to our expectation that adding salmon carcasses and removing the riparian canopy would have positive, additive effects on periphyton growth and primary productivity. Our failure to find significant treatment effects on many of the response variables may have reflected inadequate within-reach sampling, limitations of our experimental design, or the influence of other factors that overrode or interacted with the manipulated factors.

Canopy effects on periphyton

A strong canopy effect was not expected on all sampling dates because differences in inci-

dent light between open- and closed-canopy reaches were small in November after leaffall and in March before leafout. However, in August, when temperature and irradiance were highest, periphyton chl *a* and AFDM on nutrient-diffusing substrates were much higher in open-canopy reaches than in closed-canopy reaches. Periphyton AFDM was highest on natural substrates in August, but canopy removal did not affect periphyton sampled from natural substrates. Differences in responses of periphyton on natural substrates and the nutrient-diffusing saucers may have reflected the naturally patchy distribution of stream periphyton. Random sampling of stream substrate may fail to select patches supporting high periphyton biomass, particularly when sample sizes are small (Marker 1976). Primary productivity of periphyton on natural substrate was higher in open-canopy than in closed-canopy reaches, particularly when expressed on a chl *a*-specific basis, but the difference was not significant. However, primary productivity was estimated from incubations of single rocks over short periods, and extrapolation of metabolic rates from small areas to whole reaches is problematic (Marzolf et al. 1994).

The response of periphyton to riparian canopy removal may have been less than expected because the algae were shade-adapted or because of grazing by snails and insects (Steinman 1996). The periphyton assemblages in all of our study reaches were dominated by diatoms, many of which have adaptations to low light (Boston and Hill 1991). Periphyton standing

crops are commonly greater in streams in clearcuts than in mature forest (e.g., Murphy et al. 1981, Hill and Knight 1988, Hetrick et al. 1998), but heavy grazing by aquatic herbivores may obscure increased primary productivity (e.g., Hill et al. 1992, Steinman 1992).

Carcass effects on periphyton

Our data gave no evidence that periphyton responded to addition of salmon carcasses. Positive responses of periphyton to N amendment on nutrient-diffusing substrates suggested that N may limit periphyton growth in these streams when sufficient light is available, but that carcasses were not effective sources of N to the periphyton. Periphyton responses to carcasses probably were affected by the timing of carcass addition. Salmon spawning runs and subsequent deposition of carcasses occur during or at the end of the dry season in many of the streams in which nutrients from carcasses influence periphyton (e.g., the Alaskan stream studied by Wipfli et al. 1998, 1999, or the British Columbia basins studied by Johnston et al. 2004). However, in our study, carcasses were added during the wet season to correspond with the timing of spawning by anadromous salmonids in streams in northern California. Flows during this period are generally high and fluctuating, and carcass nutrients may not be retained in the stream long enough to be effectively sequestered. Nutrient analyses from other work in these streams (Ambrose 2003) support this suggestion. Concentrations of NO_3 , NH_4 , and soluble reactive P did not differ between streams with and without added carcasses in grab samples collected 2, 6, 14, and 22 wk after carcass addition. Carcass nutrients may have been assimilated rapidly and stored in biota, but periphyton did not respond to carcasses in a manner consistent with this hypothesis.

Management strategies for salmonid restoration

Management agencies and local watershed groups are using introductions of salmon carcasses to enhance productivity of streams in the Pacific Northwest with increasing frequency (Lackey 2003). Carcasses are a direct source of food resources, including lipids and micronutrients, for both aquatic and terrestrial consumers (e.g., Cederholm et al. 1989, Gende et al. 2002),

and carcasses may fertilize riparian vegetation under conditions of high salmon spawning densities (Bilby et al. 2003). However, our study indicated that carcass introductions may fail to increase the transfer of salmon-derived nutrients to higher trophic levels via autotrophic pathways if limitation by other factors such as light overrides nutrient limitation of primary productivity or if carcasses are added when high flows prevent stream biota from using the nutrients effectively. Our study demonstrated that, despite the subtle benefits to periphyton associated with removing the riparian canopy on the scale of 100-m reaches, addition of salmon carcasses did not enhance the nutrient supply available to the periphyton base of the food chains in our study streams. This result suggests that the logistically difficult addition of salmon carcasses may not be an effective strategy for enhancing GPP in all streams.

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