

PERIPHYTON RESPONSE TO INCREASED LIGHT AND SALMON CARCASS
ENHANCEMENT IN SIX NORTHERN CALIFORNIA STREAMS

by

Heather E. Ambrose

A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

Of the Requirements for the Degree

Masters of Science

In Natural Resources: Fisheries Biology

May, 2003

ABSTRACT

Periphyton Response to Increased Light and Salmon Carcass Enhancement in Six Northern California Streams

Heather E. Ambrose

Concern that declining returns of Pacific salmon have resulted in a loss of nutrients that historically enriched nutrient-poor streams of the Pacific Northwest has prompted recent efforts to introduce salmon carcasses as a recovery technique. While some studies have reported increased periphyton response to nutrient enrichment from carcasses or other sources, other evidence suggests that light may serve as a primary limitation on stream productivity. This study examined periphyton response to simultaneous manipulations of light and salmon carcass enrichment. Chlorophyll *a*, biofilm ash-free dry mass (AFDM), gross primary production (GPP), and periphyton taxonomic structure were measured in 6 tributary streams in the Smith and Klamath River basins in northern California that received varying treatments of increased light and salmon carcass introductions. In each stream, red alder (*Alnus rubra*) and other hardwoods were felled from the riparian zone to increase light along a 100 m stretch of stream. In each stream another 100 m reach was established that had an intact riparian canopy. In 3 streams, salmon carcasses were introduced in both open and canopy-closed sections. Carcass enrichment provided a significant influx of phosphorus, but not nitrogen, into study streams. Results of an experiment using nutrient diffusing clay saucers to evaluate nutrient limitation, conducted in open and closed sections of a carcass-fertilized and a non-fertilized stream, implicated nitrogen as a limiting nutrient,

and established a strong canopy effect on periphyton accrual, measured as AFDM. Canopy and carcass treatments did not detectably affect biomass of periphyton on natural substrates. Taxonomic composition of the periphyton assemblage was dominated by diatoms in all stream reaches on all dates, but diatom coverage was significantly reduced in open stream sections in August 2002 with a concomitant increase in green algae. Gross primary production, which was estimated by measuring changes in oxygen concentration in light and dark respiration chambers in early summer, did not differ among treatments. Collectively, results suggest that stream productivity, as indexed by attributes of the periphyton assemblage, may be enhanced to a greater extent by opening of the riparian canopy than by salmon carcass enrichment.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the assistance of several people and agencies. The USGS-BRD Cooperative Research Units Program made this project possible by providing research funding which helped to cover my equipment and travel expenses. I would also like to extend a special thanks to Simpson Timber Company, first of all, for providing me with access to field sites. In addition, they were responsible for removal of the riparian canopy and proved to be a great help with carcass introductions and helping me to haul my equipment in and out with the use of their quads, which was invaluable.

I would like to thank Dr. Peggy Wilzbach and Dr. Ken Cummins for their guidance and knowledge in helping me with all aspects of my education and thesis and making this project come to life. I would also like to thank Dr. Bret Harvey, who continually found time to answer my many questions and provided much needed statistical help and Dr. Terry Roelofs and Dr. Walt Duffy, who also provided me with advice and guidance.

Without the help of the field crew and staff at the California Cooperative Fish Research Unit, this research would not have been possible. The field help provided by the stream crew at Redwood Science Lab with carcass introductions was also greatly appreciated. I thank everyone who helped me with my fieldwork and data collection.

And of course, I would not have made it without the support of my family who helped me in many ways over the past few years.

TABLE OF CONTENTS

	Page
ABSTRACT	iii
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS	vi
LIST OF TABLES	viii
LIST OF FIGURES	ix
INTRODUCTION	1
STUDY SITES	6
MATERIALS AND METHODS	10
<u>Experimental Design</u>	10
<u>Periphyton Sampling</u>	12
<u>Nutrient Limitation Experiment</u>	15
<u>Primary Production Measurement</u>	15
<u>Physical/Chemical Measurements</u>	19
<u>Data Analysis</u>	20
RESULTS	21
<u>Physical /Chemical Variables</u>	21
<u>Nutrient Limitation Experiment</u>	28
<u>Periphyton Biomass</u>	31
<u>Primary Production</u>	38

TABLE OF CONTENTS (CONTINUED)

	Page
DISCUSSION	41
LITERATURE CITED	47

LIST OF TABLES

Table	Page
1 General characteristics of open and closed reaches of Smith and Klamath River study sites. (C) denotes carcass introduction	8
2 Weights of salmon carcasses introduced into open and closed reaches of Klamath and Smith River study streams in January 2002.....	13
3 Summary of seasonal temperature regimes (°C) of open and closed reaches of Klamath and Smith River study streams after alder felling occurred in December 2001	22
4 Analyses of variance for the effects of carcass, canopy and the carcass x canopy interaction on periphyton biomass and GPP of Klamath and Smith River study streams in 2002. F denotes the F-value and (P) the p-value resulting from a split-plot ANOVA	32
5 Analyses of variance for the effects of carcass, canopy and the carcass x canopy interaction on percent benthic algal composition of Klamath and Smith River study streams in 2002. All data are log transformed. F denotes the F-value and (P) the p-value resulting from a split-plot ANOVA.....	35
6 Gross primary productivity and production/respiration (P/R) ratios of periphyton in open and closed reaches of Klamath and Smith River study streams in late June and early July 2002, estimated in clear and dark respiration chambers. A P/R < 1 indicates a heterotrophic system and a P/R > 1 indicates an autotrophic system. Carcass enriched streams are indicated with a (C).....	40

LIST OF FIGURES

Figure		Page
1	Klamath and Smith River study sites. All sites received a canopy treatment. South Fork Rowdy, Peacock and Tarup creeks received salmon carcasses	7
2	Experimental design of 6 study sites. Each stream had a 100 m reach in which the canopy was intact and a 100 m reach in which the canopy was removed. Three streams received salmon carcass introductions in both reaches.	11
3	Nutrient diffusing clay saucers staked into Tarup and Tectah creeks (Klamath River basin, California) to assess limitation of algal growth in August 2002. Each of 4 saucers were enriched with nitrogen, phosphorus, nitrogen + phosphorus and a control with no nutrients added	16
4	Clear respiration chamber with YSI Sonde used to measure gross primary production of benthic periphyton. Magnetic stirrer motor is positioned beneath chamber.	17
5	Mean TN concentration of stream water in closed and open reaches of Klamath and Smith River study sites from time of carcass introduction through June 2002 (n = 2). Dashed lines represent streams with carcass introductions and solid lines represent streams without carcass introductions	25
6	Mean TP concentration of stream water in closed and open reaches of Klamath and Smith River study sites from time of carcass introduction through June 2002 (n = 2). Dashed lines represent streams with carcass introductions and solid lines represent streams without carcass introductions	26
7	Mean TP concentration (\pm SE) of stream water in Klamath and Smith River study sites in May 2002 (n = 2), 4 months after carcass introductions. C = streams enriched with carcasses, N = streams not enriched with carcasses.	27

8	Mean chlorophyll <i>a</i> (\pm SE) content of periphyton scraped from nutrient diffusing clay saucers incubated in open and closed reaches of Tarup (carcass enriched) and Tectah (non-enriched) creeks in August 2002 (n = 2). C = control (no nutrient enrichment), N = nitrogen enrichment, P = phosphorus enrichment and N + P = enrichment with equal parts nitrogen and phosphorus.....	29
9	Mean AFDM (\pm SE) of periphyton scraped from nutrient diffusing clay saucers incubated in open and closed reaches of Tarup (carcass) and Tectah (non-enriched) creeks in August 2002 (n = 2). C = control (no nutrient enrichment), N = nitrogen enrichment, P = phosphorus enrichment and N + P = enrichment with equal parts nitrogen and phosphorus	30
10	Mean chlorophyll <i>a</i> content (\pm SE) of periphyton scraped from natural substrates in open and closed reaches of Klamath and Smith River study streams in 2002 (n = 3 samples, with each sample composited from scrapings of 3 rocks for each treatment combination on each date). C = streams enriched with carcasses, N = streams not enriched with carcasses.....	33
11	Mean AFDM (\pm SE) of periphyton scraped from natural substrates in open and closed reaches of Klamath and Smith River study streams in 2002 (n = 3 samples, with each sample composited from scrapings of 3 rocks for each treatment combination on each date). C = streams enriched with carcasses, N = streams not enriched with carcasses.	34
12	Mean green algal percentage (\pm SE) of benthic periphyton in open and closed reaches of Klamath and Smith River study streams in August 2002 (n = 3). C = streams enriched with carcasses, N = streams not enriched with carcasses.	37
13	Mean green algal thickness (\pm SE) of benthic periphyton in open and closed reaches of Klamath and Smith River study streams in August and October 2002 (n = 3). C = streams enriched with carcasses, N = streams not enriched with carcasses.	39

INTRODUCTION

Small streams of the Pacific Northwest are often oligotrophic (Rohm et al. 2002). Compared with streams in the eastern United States, for example, average concentrations of total nitrogen and phosphorus are often one-third as high. Low nutrient concentrations reflect both geological conditions and contemporary land uses in this largely forested, mountainous landscape. Steep terrain and underlying bedrock of sandstone and other sedimentary rock make the region unsuitable for agriculture (United States Soil Conservation Service 1967*a, b*), and land use is dominated by logging, recreation, grazing and mining. Elevated levels of nutrients in streams of the eastern USA are attributed largely to agricultural runoff and higher inputs from acid rain and other anthropogenic sources (Omernik 1977).

Low nutrient concentrations in streams of the Pacific Northwest may be further exacerbated by declines in numbers of Pacific salmon returning to natal streams to spawn. The spawning products and salmon carcasses delivered to streams are thought to have played an important role, historically, in nutrient enrichment. Pacific salmon do not eat once they leave their marine habitat and contain insignificant levels (<1%) of residual freshwater-derived constituents from the time when they were ocean-bound smolts (Kline et al. 1997). Therefore, the nutrients that they release in freshwater spawning streams are almost entirely of marine origin, termed marine derived nutrients (MDN). Although many Pacific Northwest streams support relatively high numbers of anadromous salmon which return to these fresh waters from the Pacific Ocean every year to spawn and die (Mathisen et al. 1988, Cederholm et al. 1999), Gresh (2000) estimated that declining

salmon runs in the region have potentially limited the amount of MDN available to these streams to only 6-7% of what they historically contained. Many, but not all, studies have demonstrated elevated nutrient levels in stream systems in response to decomposing salmon carcasses (Richey et al. 1975, Foggin and McClelland 1983, Schuldt and Hershey 1995, Schmidt et al. 1998, Minakawa and Gara 1999). Richey et al. (1975) found that levels of nitrate and phosphorus continued to stay high after the disappearance of carcasses due to the slow release of nutrients from periphyton in tributaries to Lake Tahoe. In contrast, Schuldt (1998) determined that carcasses raised nutrient levels in tributaries of Lake Superior during one year, yet the following year no effect was seen.

Lack of nutrients often limits algal production in streams (Allan 1995). The specific nutrient(s) limiting algal production often varies and several studies have applied nitrate and phosphorus experimentally in stream systems to determine which nutrient is most limiting to algal growth (Stockner and Shortreed 1978, Gregory 1980, Triska et al. 1983, Pringle and Bowers 1984, Fairchild and Lowe 1984, Lowe et al. 1986, Perrin et al. 1987, Hill and Knight 1988, Tate 1990, Wellnitz et al. 1996, Kutka and Richards 1997, Mosisch et al. 2001). Within the Pacific Northwest, both Gregory (1980) and Triska et al. (1983) found that nitrogen was more limiting to periphyton growth in streams than phosphorus, yet Stockner and Shortreed (1978) reported that periphyton responded most dramatically to phosphate additions in a stream in British Columbia.

Evidence that the nutrients provided by salmon carcasses result in an increase in primary production is conflicting. Although based on measurement of algal standing crops rather than primary production per se, several studies have reported increased

primary production in association with the release of nutrients from decomposing salmon (Richey et al. 1975, Mathisen et al. 1988, Schuldt and Hershey 1995, Johnston et al. 1997, Kline et al. 1997, Kyle et al. 1997, Schuldt 1998, Wipfli et al. 1998, 1999, Wold and Hershey 1999, Chaloner et al. 2002). In contrast, Minshall et al. (1991) and Rand et al. (1992) found that salmonid carcasses did not increase stream primary productivity or periphyton growth. Differences in findings may reflect the operation of other factors that override or co-limit algal production.

Light is one such factor that frequently limits algal production, particularly in low-order forested streams (Vannote et al. 1980). The importance of light in affecting algal production and taxonomic structure of periphyton assemblages has been confirmed in a large number of studies that have examined periphyton response to removal of riparian vegetation (Kevern and Ball 1965, Hannsman and Phinney 1973, Lyford and Gregory 1975, Murphy and Hall 1981, Lowe et al. 1986, Hill and Knight 1988, Hetrick et al. 1998*a, b*, Quinn et al. 1997). Periphyton chlorophyll *a* and ash-free dry mass (AFDM) were found to be higher in open stream sections of the Pacific Northwest as opposed to those shaded by riparian canopy (Lyford and Gregory 1975, Murphy and Hall 1981, Johnson et al. 1986, Hill and Knight 1988, Hetrick et al. 1998*a, b*). Following clearcutting, filamentous green algae became more common where diatoms had once dominated (Hansmann and Phinney 1973, Shortreed and Stockner 1983, Lowe et al. 1986) and Quinn et al. (1997) observed green algal blooms in unshaded versus shaded channels. Taxonomic composition of periphyton assemblages varies in nutritional quality for stream invertebrate consumers. Filamentous algae and blue-green algae are

difficult for most invertebrates to ingest (Allan 1995), while diatoms appear to provide the most critical nutritional component of periphyton (Cummins and Klug 1979).

Considerable evidence supports a conclusion that light may override nutrients in limiting periphyton productivity in shaded streams (Lyford and Gregory 1975, Moore 1977, Gregory 1980, Triska et al. 1983, Lowe et al. 1986, Hill and Knight 1988, Rand et al. 1992, Hill et al. 2001). Gregory (1980) and Triska et al. (1983), for example, found that nitrogen enrichment of streams in northern California had little effect on increasing primary productivity unless the canopy was removed to increase light. In contrast, Shortreed and Stockner (1983) found that periphyton accumulation was similar before and after logging and that phosphorus, not light, was the major factor limiting primary productivity in a coastal rainforest stream in British Columbia. Apart from major nutrients and light, other factors that may also affect periphyton abundance include micronutrients, temperature, discharge, substrate and grazing (Allan 1995).

Energy for salmonid production has been shown to derive largely from autotrophic pathways. Many studies support the idea that increasing the light in a stream system increases primary production by increasing periphyton growth, which provides increased food to some macroinvertebrates and eventually results in an increased food supply for juvenile salmon (Murphy and Hall 1981, Johnson et al. 1986, Hetrick et al. 1998*a, b*, Thedinga 1989), particularly during the spring or summer period of major growth (Bilby and Bisson 1992). A similar “bottom-up effect” of carcass enrichment (Wipfli et al. 2003) and nutrient enrichment mimicking carcass additions (Kyle et al. 1997) on stream trophic structure has also been demonstrated. One goal of salmonid

management and recovery is to increase juvenile growth to increase overwinter survival in the marine environment following migration from freshwater spawning and rearing streams (Gende et al. 2002). Although the transfer of carcass-derived nutrients to higher trophic levels may occur by pathways other than via autotrophic uptake (Cederholm et al. 1999), failure to consider factors limiting algal production may limit the success of carcass introductions in enhancing salmonid growth.

The objectives of this study were to evaluate the relative effects of increased light together with salmon carcass introduction on biomass, production, and taxonomic composition of stream periphyton assemblages, and to evaluate periphyton response to *in situ* nutrient manipulations of nitrogen and phosphorus. The hypothesis that periphyton community structure, AFDM, chlorophyll *a* content and primary productivity will differ among light and nutrient treatments was tested with the following expectations: 1) periphyton growth will be greater in stream reaches where the riparian canopy is removed than in reaches with an intact canopy, and greater in streams with carcass enhancement than in non-fertilized streams 2) periphyton growth will be greatest in stream reaches that receive both light and nutrient enhancement and 3) periphyton composition will shift from a community dominated by single cell and small colony diatoms with interspersed blue-green and green algae to a community dominated by filamentous blue-green and green algae in streams that receive increased light, with the blue-green and green filamentous response greatest in stream reaches that receive both light and nutrient enhancement.

STUDY SITES

The study was conducted in 6 northwestern California streams (Figure 1). Little Mill, Peacock, Savoy and South Fork Rowdy creeks are tributaries of the Smith River in Del Norte County. Tarup and Tectah creeks are tributaries of the Klamath River in Humboldt County (Table. 1). Sites were all located on Simpson Timber Company lands in areas of second-growth coniferous stands. All study sites are 2nd and 3rd-order streams and lie on the western border of the Northern Coast Range. Study sites were chosen to be as similar as possible in watershed area, stream order, gradient, their potential for increasing solar radiation through removal of riparian canopy, and fish species composition dominated by resident salmonids rather than anadromous Pacific salmon (*Oncorhynchus* spp.). The selection of drainage basins was constrained by a need to have a fish hatchery located within the basin to provide a source of California Department of Fish and Game (CDFG) approved salmon carcasses.

The climate is predominantly maritime with warm, dry summers and cool, wet winters. The Smith River sites and Klamath River sites receive an average of 168 cm and 205 cm of rainfall per year, respectively. The bedrock of both the Klamath and Smith River study sites is of the Franciscan complex (California Division of Mines and Geology 1964) and the soil bodies are of the Hugo-Josephine association (United States Soil Conservation Service 1967a, b). Substrate composition of Little Mill, Savoy and South Fork Rowdy creeks consists mainly of large boulders and cobbles. Tectah, Tarup and Peacock creeks contain a cobble and pebble substrate. Channel morphology of all

Table 1. General characteristics of open and closed reaches of Klamath and Smith River study sites. (C) denotes carcass introduction.

Stream Site	Basin	Drainage Area (km ²)	Latitude/ Longitude	Mean Bankfull		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° 55' 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

sites consists of an alternating pool-riffle sequence. Little Mill, Savoy and South Fork Rowdy creeks have a higher gradient than Tectah, Tarup and Peacock creeks and contain several plunge pools. Large woody debris is present in all sites, yet not abundant. Little Mill, Savoy and South Fork Rowdy creeks have a few debris dams.

The study was conducted from November 2001 to November 2002, in a water year in which peak discharges, measured at downstream United States Geological Survey (USGS) gauging stations on the mainstem Smith and Klamath rivers, occurred with recurrence intervals of approximately 1 year. Based on 70 or more years of record, average monthly discharges in both basins were low, particularly during summer.

The dominant riparian vegetation at all study sites is red alder (*Alnus rubra*) mixed with occasional Douglas fir (*Pseudotsuga menziesii*), redwood (*Sequoia sempervirens*), bigleaf maple (*Acer macrophyllum*) and tan oak (*Lithocarpus densiflorus*). Understories are mixtures of salmonberry (*Rubus spectabilis*), elderberry (*Sambucus racemosa*), blackberry (*Rubus ursinus*), thimbleberry (*Rubus parviflorus*), stink currant (*Ribes bracteosum*), and ferns. Mosses and lichens are common on and around stream substrates. The most common vertebrates at all sites included coastal cutthroat trout (*Oncorhynchus clarki clarki*) and rainbow trout/steelhead (*Oncorhynchus mykiss*) with scattered coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*), Pacific giant salamander (*Dicamptodon tenebrosus*), tailed frog (*Ascaphus truei*) and northern red-legged frog (*Rana aurora aurora*).

MATERIALS AND METHODS

Experimental Design

A split-plot experimental design was employed to evaluate relative effects of increased light and salmon carcass enrichment on algal communities (Figure 2). Light manipulation involved falling alder and other hardwoods along a 20 m width on both sides of the stream reaches to increase the amount of solar radiation entering the stream. Alder felling was completed in December of 2001, after deciduous leaf fall. The few conifers within riparian zones were left intact. Fallen trees remained on the site. The study areas in each stream consisted of a 100 m reach in which the riparian vegetation was removed and a 100 m reach with an intact alder canopy used as a light control. Reaches to receive canopy removal within a stream were randomly chosen. Each open and closed reach was separated by a 150 to 200 m buffer stream section.

Nutrients were enhanced through the introduction of chinook salmon (*Oncorhynchus tshawytscha*) carcasses. Carcasses introduced into the Klamath River sites were procured from the CDFG Iron Gate Hatchery and carcasses introduced into the Smith River sites were obtained from the Rowdy Creek Hatchery and by hand-collection from within the basin. Peacock, South Fork Rowdy and Tarup creeks were randomly chosen to receive salmon carcasses in both the open and closed reaches. Carcasses were staked into study reaches with rebar in mid January 2002. Carcasses were anchored to the streambed to ensure that they wouldn't be immediately flushed out during high flows. Carcass introductions were standardized by mass rather than number because carcass size

Figure 2

differed considerably between the 2 basins. Approximately 3 kg of carcass (ranging from 2.63-3.07 kg) were introduced per meter of stream (Table 2).

Periphyton Sampling

Biomass of periphyton (attached algae plus associated detritus, microbes and microzoans) was measured using both chlorophyll *a* and AFDM, which was sampled from all study streams in November 2001 (pre-treatment) and in March, June, August and November 2002. Chlorophyll *a* and AFDM were measured from natural substrates within each study reach. At each sampling event, periphyton was scraped from a 4 cm² area from each of 3 cobbles in 3 randomly chosen riffles of each study reach. Periphyton was removed from the rocks with a copper bristled brush and rinsed off into a container using stream water. A 4 cm² rubber template was adpressed to each rock to ensure the same area was scraped each time. Samples from the 3 cobbles in each riffle were composited, and subsamples were withdrawn for measurement of chlorophyll *a* and AFDM. The sample was filtered through a 250 µm mesh net into a graduated cylinder to remove debris, mixed well, and filtered onto 2 separate 25 µm glass fiber filters for determination of chlorophyll *a* and AFDM, with sample volumes noted. Filters were kept frozen until time of analysis. Preliminary samples were kept frozen for 3 months, while all post-treatment samples were kept frozen for a maximum period of 3 weeks. Chlorophyll *a* was corrected for pheophytin and measured with a spectrophotometer (Model 335401, Spectronic Instruments, Rochester, New York) (Wetzel and Likens 1991). Filters were oven-dried at 60°C for 24 hours, weighed on an analytical balance to

Table 2. Weights of salmon carcass introduced into open and closed reaches of Klamath and Smith River study streams in January 2002

Stream Site	Carcass Weight (kg/m)	
	Open	Closed
Peacock	2.83	2.93
South Fork Rowdy	3.01	3.07
Tarup	2.64	2.63

the nearest 0.1 mg, ashed at 500°C for 2 hours and weighed again to determine AFDM.

Samples were held in a dessicator after drying and ashing to avoid any water absorption.

The field-based rapid periphyton survey approach of Stevenson and Bahls (1999) was used to make semi-quantitative assessments of algal composition. These were made in Savoy, South Fork Rowdy and Tarup creeks in mid August 2001, in Tectah Creek in mid September 2001 and in Little Mill and Peacock creeks in early November 2001, prior to experimental manipulations. All stream sites were assessed again in March, June, August and November 2002. Percentage algal composition and thickness on benthic substrates were estimated using a viewing bucket (0.3 m²) marked with a 50-dot grid. Algae were functionally classified as diatoms, blue-greens or greens and ranked according to thickness. Thickness ranks were as follows: 0 - substrate rough with no visual evidence of algae, 0.5 – substrate slimy, but no visual accumulation of algae evident, 1 – a thin algal layer visually evident, 2 – accumulation of algal layer from 0.5 mm to 1 mm thick, 3 – accumulation of algal layer from 1 mm to 5 mm thick, 4 – accumulation of algal layer from 5 mm to 2 cm thick and 5 – accumulation of algal layer greater than 2 cm thick. Assessments were taken from 3 randomly chosen riffles per study reach, with a measurement taken from the left, middle and right bank of each riffle. The mean density of each type of algae was calculated as the sum of the number of grid points over algae of different thickness ranks multiplied by the thickness rank and divided by the total number of grid points covering the algae. Averages were calculated for each riffle and for all riffles in each study reach.

Nutrient Limitation

Nutrient limitation of algal growth was evaluated in Tarup (with carcasses) and Tectah (without carcasses) creeks in August 2002. Nutrient limitation was assessed using nutrient-diffusing clay saucers incubated in the stream sites (Tate 1990). Each of four 10.2 cm diameter clay flowerpot saucers were glued to a 12 x 12 cm plexiglass plate (Figure 3). Each saucer was filled with 225 ml of a 2% agar solution: 1 saucer was enriched with nitrogen (N) using 0.5 mol/liter NaNO_3 , 1 with phosphorus (P) using 0.1 mol/liter KH_2PO_4 , 1 with N + P using 0.5 mol/liter NaNO_3 and 0.1 mol/liter KH_2PO_4 , and 1 was a control with no nutrients added. Plexiglass plates were attached to wooden frames constructed in a diamond shape with the control saucer placed upstream, the N and P saucers placed side by side and the N+P saucer placed downstream, to minimize cross contamination. Frames were secured into the stream bed of each study reach with rebar. Two frames were randomly placed in both the open and closed study reaches of both streams and allowed to incubate for approximately 3 weeks. Periphyton on each saucer was then sampled and analyzed for chlorophyll *a* and AFDM using the methods described under Periphyton Sampling above.

Primary Production Measurements

Oxygen production by periphytic algae was estimated in late June-early July at all study sites. Clear and dark respiration chambers (25.4 x 20.3 x 15.2 cm) constructed of plexiglass and fitted with an oxygen probe and data logger (Sonde 6600-0, YSI Environmental, Yellow Springs, Ohio) were used to measure oxygen changes (Figure 4).



Figure 3. Nutrient diffusing clay saucers staked into Tarup and Tectah creeks (Klamath River basin, California) to assess nutrient limitation of algal growth in August 2002. Each of 4 saucers were enriched with nitrogen, phosphorus, nitrogen + phosphorus and a control with no nutrients added.



Figure 4. Clear respiration chamber with YSI Sonde used to measure gross primary production of benthic periphyton. Magnetic stirrer motor is positioned beneath chamber.

In each study reach a cobble (averaging 350 cm²) was chosen from which to measure oxygen production of colonized periphyton in the clear box, which was placed on the streambank. Likewise, a cobble was chosen from which to measure oxygen depletion in the dark box. A magnetic stirrer was placed under each chamber to allow aeration in the chamber during production measurements. Chambers were completely filled and securely shut and kept air tight during oxygen measurements. Oxygen changes were logged for equal periods of time in both chambers. Gross primary production (gC cm⁻² d⁻¹) was estimated as the sum of the oxygen increase in the clear chamber (net primary production) + the oxygen depletion in the dark chamber (community respiration). The increase and decrease of oxygen in the chambers was standardized by multiplying the change in oxygen times the volume of the chamber divided by the surface area of the rock. After production estimation, periphyton on the cobbles was sampled for chlorophyll. Rock surface areas were measured by taking an aluminum foil mold of the area scraped and using the mass of the foil mold to determine area. Temperature inside the chambers was not allowed to rise more than 1° C by keeping ice on the tops of the chambers during production estimation. Data were expressed on a 24 hour basis by multiplying the time period over which oxygen was measured in the light and dark chambers times the number of time intervals occurring during 24 hours. Data were converted to carbon using a photosynthetic quotient (PQ, mol O₂ released during photosynthesis/mol CO₂ incorporated) of 1.2 and a respiratory quotient (RQ, mol CO₂ released/mol O₂ consumed) of 0.85 (Bott 1996).

Equations employed were:

1. For photosynthesis, $gC = gO_2 \times 1/PQ \times 12/32$,
where 12 = atomic weight of C and 32 = molecular weight of O_2 .
2. For respiration, $gC = gO_2 \times RQ \times 12/32$.

Physical/Chemical Measurements

The data collected in this study are part of a larger investigation of stream ecosystem response to enhanced light and introductions of salmon carcasses. Other measurements included temperature, light and nutrients. Water temperatures in both open and closed reaches of all sites were recorded hourly with temperature data loggers (Hobo Temperature Logger, Onset Computer Corporation, Bourne, Massachusetts). Potential available sunlight was measured using a solar pathfinder (Solar Pathfinder, Pleasantville, Tennessee) at all study reaches before the riparian canopy was removed. Instantaneous light readings were measured in both open and closed reaches of all study sites using a quantum sensor (LI-190SA with LI-1400 data logger, Li-Cor, Lincoln, Nebraska). Grab samples of water from all study reaches were analyzed for concentrations of nitrate (NO_3^-), ammonia (NH_3), total nitrogen (TN), phosphate (PO_4), total phosphorus (TP) and silica (SiO_2) at the University of Michigan Biological Station following the Standard Methods for the Examination of Water and Wastewater (American Public Health Association 1999). Laboratory controls were certified by Environmental Resource Associates, Arvada, Colorado. Two grab samples were taken at each study reach in late January, mid March, late April-early May, and late June 2002.

Data Analysis

Treatment effects on periphyton chlorophyll *a* and AFDM sampled from rocks, percentage algal composition and thickness, GPP and nutrient concentrations were analyzed using a split-plot ANOVA. Streams acted as the whole-plot factor, with the effects of carcasses as the experimental factor at this level. Reaches within the streams that received light manipulations acted as sub-plot factors. At the sub-plot level the effects of light manipulation were examined along with the effects of the interaction of light manipulation and carcass treatments. Algal composition percentages were arcsine transformed.

Treatment effects on periphyton chlorophyll *a* and AFDM from nutrient diffusing clay saucers were analyzed using a 4-way ANOVA, with stream, light manipulations, nitrogen levels and phosphorus levels acting as treatment effects. Data were log transformed. The effects of stream and light manipulations on cumulative degree-days were analyzed using a 2-way ANOVA. Statistical analyses were carried out using PROC GLM (SAS Institute, Inc. 1999-2001). Significance levels for all analyses were set at $P \leq 0.05$.

RESULTS

Physical/Chemical Variables

Removal of the riparian canopy did not significantly affect water temperature. Cumulative degree-days, summed from January 2002 through September 2002, did not differ among streams or light manipulations. Mean cumulative degree-days in open reaches were 2850.3 (SD = 81.8, n = 6) and 2783.2 (SD = 170.1, n = 6) in closed reaches. Mean seasonal water temperatures never varied more than 1°C between open and closed reaches of study streams (Table 3). The open reaches of Little Mill, Peacock and Savoy creeks were generally warmer than the closed reaches. The closed reach of South Fork Rowdy Creek was warmer than the open reach in every season except winter when the open reach was 0.01°C warmer. The closed reach was warmer than the open reach during every season in Tarup Creek. In Tectah Creek the closed reach was warmer than the open reach during the winter and fall. Fall temperatures for both Little Mill and Tectah creeks were only recorded through September, instead of October, because the recorders were lost during high flows.

The canopy removal was very effective in increasing light in the affected reaches. Potential available sunlight did not significantly differ among study reaches before the canopy was removed. Original attempts to measure integrated light energy using ozalid papers (Sullivan and Mix 1983) proved unsuccessful, and photosynthetically active radiation (PAR) was subsequently measured simultaneously in open and closed canopy reaches of a stream with instantaneous readings taken with a quantum sensor on selected

Table 3. Summary of seasonal temperature regimes (°C) of open and closed reaches of Klamath and Smith River study streams after alder felling occurred in December 2001.

Stream Site	Canopy	Winter (Jan 2002-Feb 2002)			Spring (Mar 2002-May 2002)			Summer (Jun 2002-Aug 2002)			Fall (Sep 2002-Oct 2002)		
		Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Little Mill	Open	8.82	6.91	10.77	9.23	6.44	12.32	12.08	9.38	14.8	11.84	7.73	14.64
	Closed	8.63	6.63	10.64	9.03	6.47	11.26	11.68	9.56	13.59	11.9 ^a	10.64 ^a	13.59 ^a
Peacock	Open	9.03	6.46	11.25	9.49	6.61	13.27	12.65	9.54	16.87	12.07	7.23	16.71
	Closed	8.97	6.43	11.07	9.35	6.43	12.31	12.21	9.67	14.47	11.82	7.98	14.47
South Fork Rowdy	Open	8.62	6.12	11.24	9.29	5.81	12.79	12.86	10.31	15.77	11.83	8.14	15.13
	Closed	8.61	5.97	11.23	9.32	5.81	13.09	12.94	10.31	15.27	11.87	7.99	14.8
Savoy	Open	8.47	6.13	10.8	9.11	5.97	12.82	12.61	9.86	16.28	11.93	8.47	16.12
	Closed	8.5	6.18	10.83	9.03	6.02	11.92	12.22	10.06	13.93	11.81	9.28	13.62
Tarup	Open	9.19	7.69	10.64	9.37	7.84	11.26	11.6	8.93	14.99	10.75	6.92	13.58
	Closed	9.25	7.69	10.63	9.52	7.69	12.18	11.99	8.92	14.66	10.96	5.82	14.04

Table 3. Summary of seasonal temperature regimes (°C) of open and closed reaches of Klamath and Smith River study streams after alder felling occurred in December 2001 (continued).

Stream Site	Canopy	Winter (Jan 2002-Feb 2002)			Spring (Mar 2002-May 2002)			Summer (Jun 2002-Aug 2002)			Fall (Sep 2002-Oct 2002)		
		Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Tectah	Open	7.7	5.59	9.92	8.18	5.74	12.86	12.52	6.99	17.56	10.13	3.73	17.24
	Closed	7.72	5.79	9.98	8.1	5.79	11.99	11.84	7.04	15.42	10.92 ^a	8.12 ^a	14.0 ^a

^aFall temperatures are only through September 2002 due to loss of temperature recorders.

dates. PAR in the open reach of a site was usually 5-7 times or more greater than in the closed reach. For example, at 0900-1000h on November 1, 2002, mean PAR in the open reach of Tectah Creek was $588 \mu\text{mol s}^{-1} \text{m}^{-2}$ (SD = 384, n = 5) and $6.47 \mu\text{mol s}^{-1} \text{m}^{-2}$ (SD = 1.18, n = 3) in the closed reach.

Mean NO_3^- concentrations were consistently, but not significantly, higher in both open and closed reaches of carcass enriched streams during all 4 post-treatment sampling dates and higher in the open versus closed reach of enriched streams. Differences in June between both open and closed reaches and carcass enriched and non-enriched streams were quite small, however, within only 0.011 mg/l of each other. Mean NO_3^- was highest in January (0.45 mg/l), 2 weeks after carcass introductions, in both open (SE = 0.1) and closed (SE = 0.07) reaches. Mean NH_3 concentrations were more erratic, although higher in the open versus closed reach of all streams except in January in non-enriched streams. Mean NH_3 was highest in all study reaches in March and peaked at 8.7×10^{-3} mg/l (SE = 0.00) in the open reach of enriched streams. Treatment effects on NH_3 were not significant. Total nitrogen mean values were not consistent throughout the study (Figure 5). Mean concentrations were highest in both open and closed reaches, 0.53 (SE = 0.09) and 0.50 mg/l (SE = 0.09) respectively, of enriched streams in January.

Mean TP concentrations were consistently higher in both open and closed reaches of enriched versus non-enriched streams (Figure 6). There was a significant carcass effect on TP concentrations in May (Figure 7). Mean TP was highest in the closed reach of enriched streams in June at 10.98 $\mu\text{g/l}$ (SE = 1.22). PO_4 mean concentrations followed

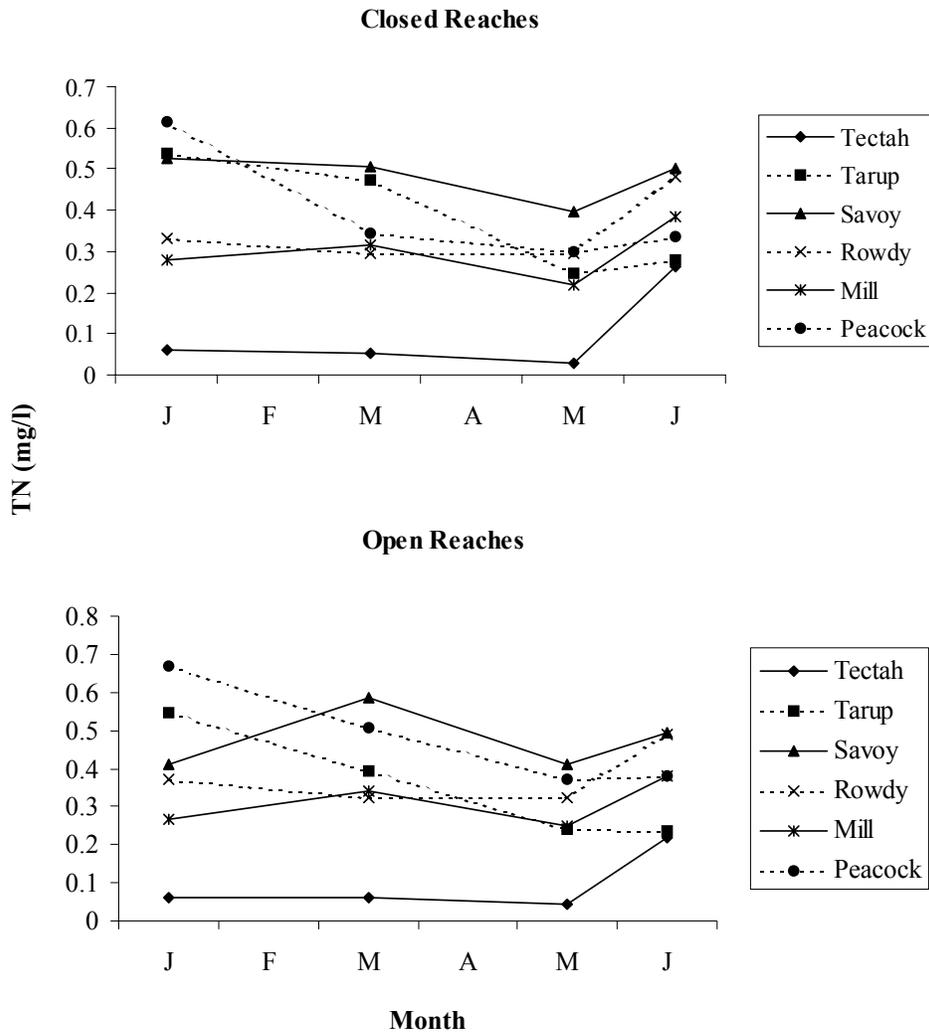


Figure 5. Mean TN concentration of stream water in closed and open reaches of Klamath and Smith River study sites from time of carcass introduction through June 2002 (n = 2). Dashed lines represent streams with carcass introductions and solid lines represent streams without carcass introductions.

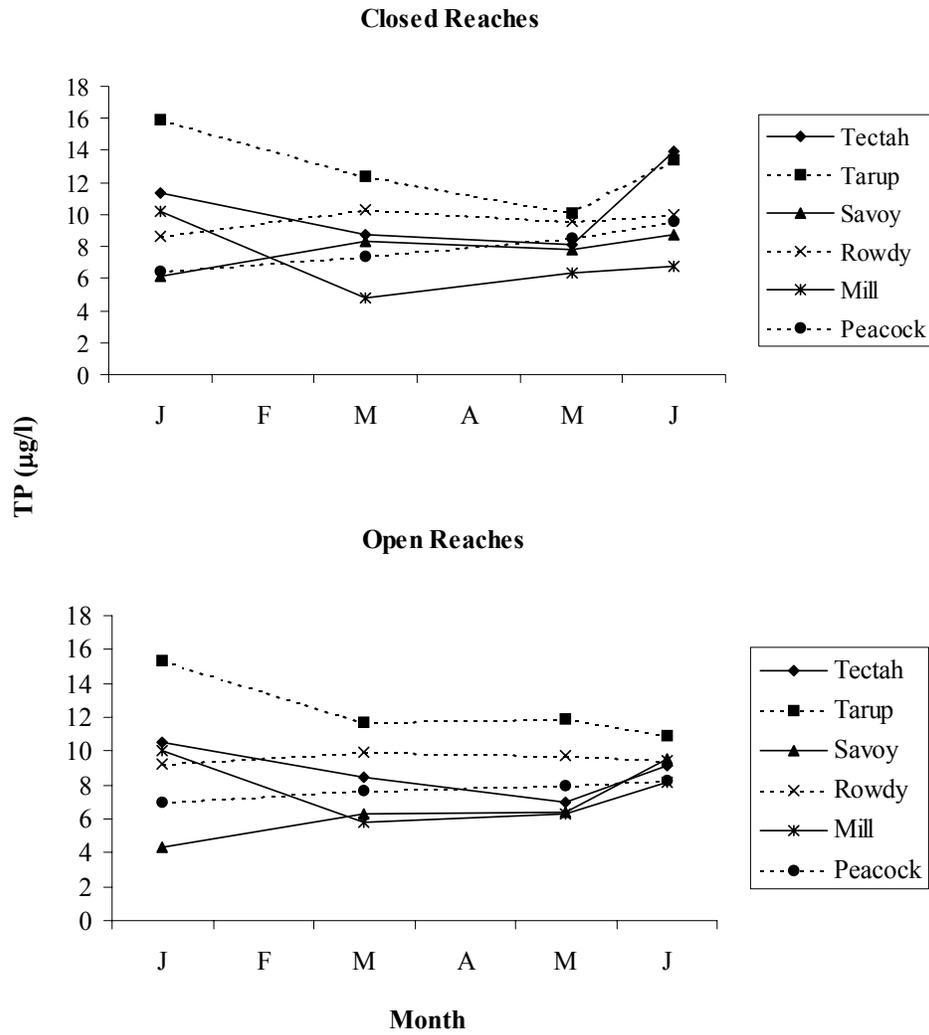


Figure 6. Mean TP concentration of stream water in closed and open reaches of Klamath and Smith River study sites from time of carcass introduction through June 2002 (n = 2). Dashed lines represent streams with carcass introductions and solid lines represent streams without carcass introductions.

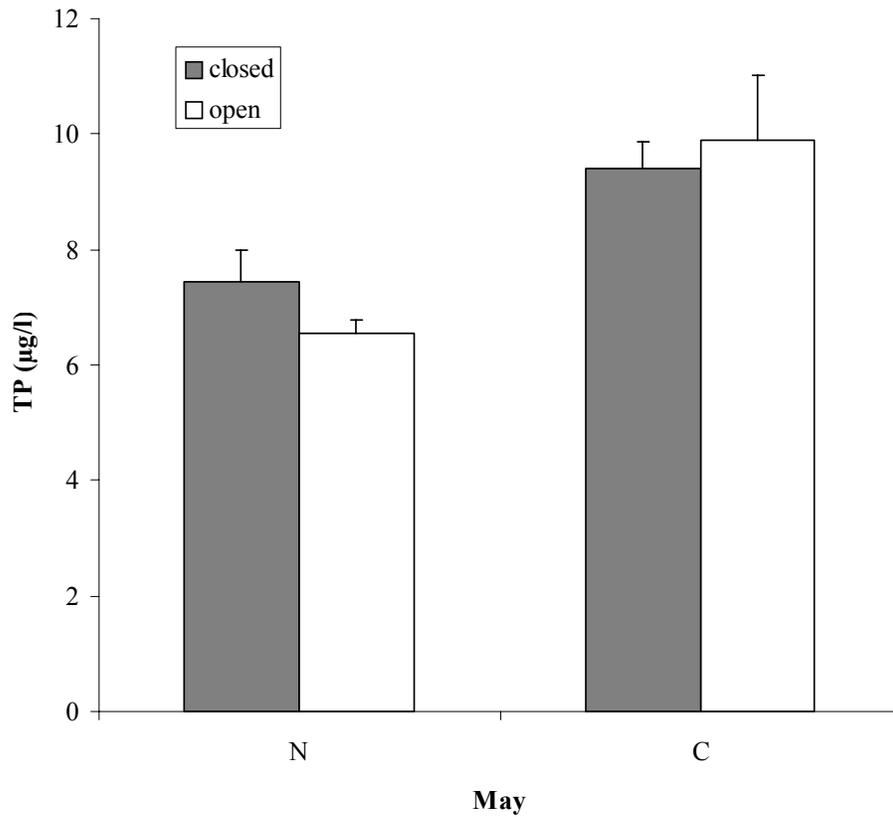


Figure 7. Mean TP concentration (\pm SE) of stream water in Klamath and Smith River study sites in May 2002 ($n=2$), 4 months after carcass introductions. C = streams enriched with carcasses, N = streams not enriched with carcasses.

a pattern similar to that of TP, with concentrations consistently higher in both open and closed reaches of enriched than non-enriched streams. Mean concentrations peaked in the open reach of enriched streams at 10.45 $\mu\text{g/l}$ (SE = 1.27) in May. Carcass effects on PO_4 concentrations in May were also significant. Significant effects on SiO_2 concentrations due to treatment effects were not seen. The trend was for SiO_2 to be higher in both open and closed stream reaches enriched with carcasses.

Nutrient Limitation Experiment

Nitrogen enrichment, as well as the interaction between carcass and canopy treatments, significantly affected chlorophyll *a* concentrations from algae that developed on the nutrient diffusing clay saucers. Mean concentrations of chlorophyll *a* were considerably greater (2.5-25x) in open than in closed reaches, with the greatest concentrations seen in the carcass enriched site. Chlorophyll *a* concentrations were greatest on N enriched saucers in both a carcass-fertilized (Tarup) and non-fertilized stream (Tectah) (Figure 8). In the fertilized stream, chlorophyll *a* concentrations were greater on N+P enriched saucers, followed by P enriched saucers, with the least concentration seen on control saucers. In the non-fertilized stream, concentrations were greater on P enriched saucers, followed by N+P saucers and then control saucers. AFDM on agar substrates was significantly affected by the canopy treatment, with mean mass 2.4-34 times greater in open than closed reaches of both streams (Figure 9). In the carcass treated streams, mean AFDM was greatest (and identical) on N and N+P enriched saucers, followed by P enriched saucers with the smallest biomass seen on the control saucers. In the stream without carcasses, AFDM was highest on N enriched saucers,

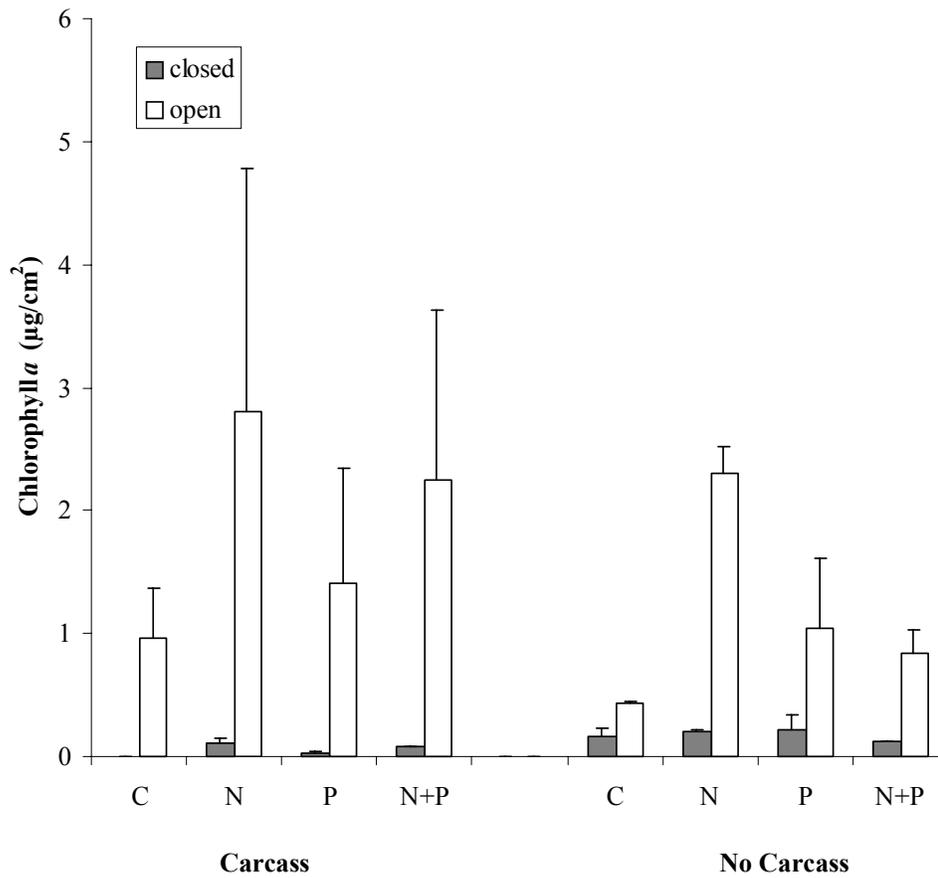


Figure 8. Mean chlorophyll *a* (\pm SE) content of periphyton scraped from nutrient diffusing clay saucers incubated in open and closed reaches of Tarup (carcass enriched) and Tectah (non-enriched) creeks in August 2002 ($n = 2$). C = control (no nutrient enrichment), N = nitrogen enrichment, P = phosphorus enrichment and N + P = enrichment with equal parts nitrogen and phosphorus.

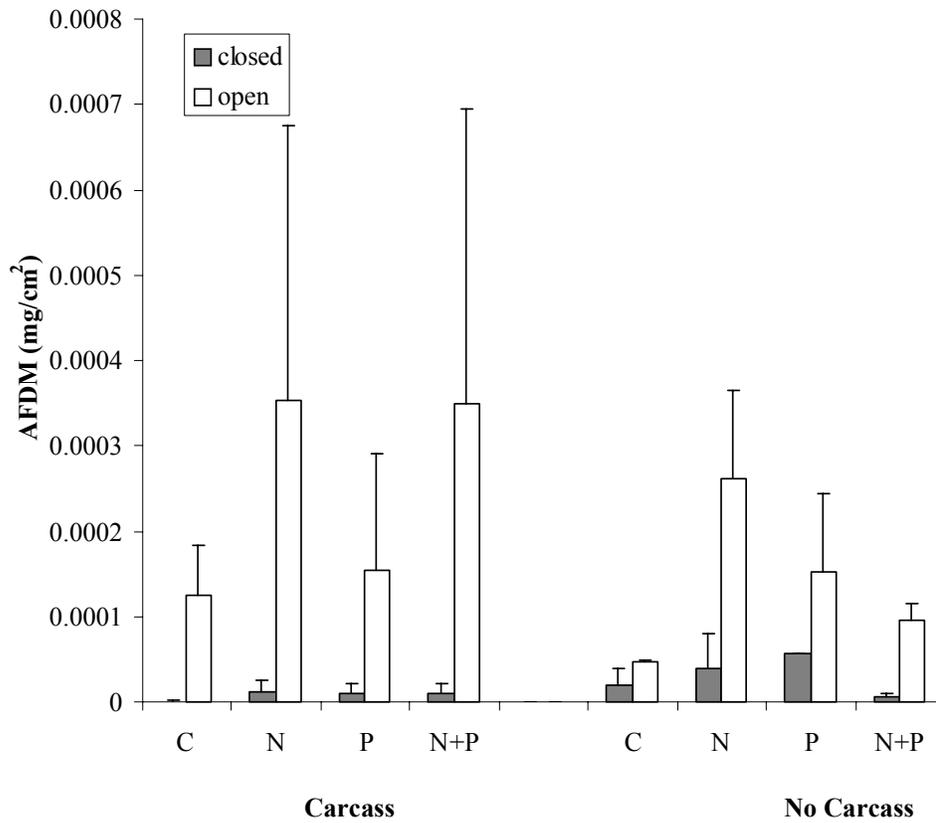


Figure 9. Mean AFDM (\pm SE) of periphyton scraped from nutrient diffusing clay saucers incubated in open and closed reaches of Tarup (carcass enriched) and Tectah (non-enriched) creeks in August 2002 ($n = 2$). C = control (no nutrient enrichment), N = nitrogen enrichment, P = phosphorus enrichment and N + P = enrichment with equal parts nitrogen and phosphorus.

followed next by P enriched and then N+P enriched saucers, with the smallest biomass seen on control saucers.

Periphyton Biomass

Canopy and carcass treatments did not significantly affect biomass of periphyton on natural substrates, measured as chlorophyll *a* or AFDM (Table 4). Chlorophyll *a* concentration and AFDM measured from natural substrates were also not significantly different among study reaches before treatments occurred. However, it was clear in August and October that open reaches of fertilized streams supported higher levels of chlorophyll *a* and AFDM (Figures 10 and 11). On each sampling date, both chlorophyll *a* concentrations and AFDM were always greater in the open reaches of carcass-enriched streams than in the open reaches of non-fertilized streams. Mean biofilm AFDM was also consistently greater in the open than in the closed reaches of all streams.

Differences in percentage algal composition of diatoms, blue-green and green algae among study sites before treatments occurred were not significant. Diatoms dominated all study sites throughout all post-treatment sampling dates, covering at least 85% of the substrate. In August, percentage diatom cover was significantly lower in open than in closed reaches (Table 5). Blue-green algae never covered more than 10% of the sampled substrate of any site before or after treatments occurred. Mean percentages were higher in open and closed reaches of carcass treated streams than non-fertilized streams in every post-treatment sampling date except March. During March percentages in enriched streams were 94% and 12% less than those in both open and closed reaches of non-enriched streams, respectively. Mean percentage coverage of blue-green algae was

Table 4. Analyses of variance for the effects of carcass, canopy and the carcass x canopy interaction on periphyton biomass and GPP of Klamath and Smith River study streams in 2002. F denotes the F-value and (P) the p-value resulting from a split-plot ANOVA.

	Carcass		Canopy		Carcass x Canopy	
	F	(P)	F	(P)	F	(P)
Chlorophyll <i>a</i> ($\mu\text{g}/\text{cm}^2$) (scraped from rocks)						
March	0.30	0.61	2.20	0.21	2.60	0.18
June	0.12	0.75	0.21	0.67	0.17	0.70
August	2.88	0.16	0.47	0.53	1.46	0.29
October	2.73	0.17	3.97	0.12	3.68	0.13
AFDM (mg/cm^2) (scraped from rocks)						
March	0.00	0.99	0.72	0.44	0.47	0.53
June	0.94	0.39	3.93	0.12	0.07	0.81
August	1.89	0.24	3.54	0.13	1.43	0.30
October	1.54	0.28	5.98	0.07	1.43	0.30
Chlorophyll <i>a</i> ($\mu\text{g}/\text{cm}^2$) (scraped from production estimation rocks)						
	0.00	0.98	0.16	0.71	3.87	0.12
GPP ($\text{mgC cm}^{-2} \text{d}^{-1}$)						
	0.24	0.65	1.26	0.32	0.03	0.88

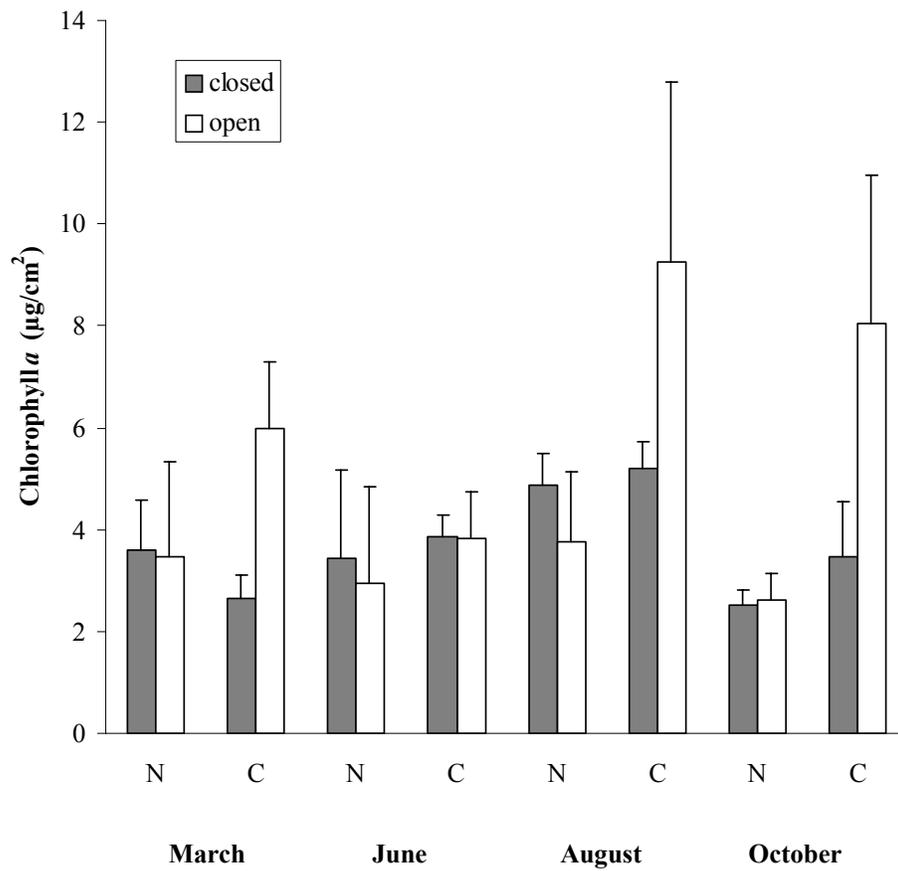


Figure 10. Mean chlorophyll *a* (\pm SE) content of periphyton scraped from natural substrates in open and closed reaches of Klamath and Smith River study streams in 2002 ($n = 3$ samples, with each sample composited from scrapings of 3 rocks for each treatment combination on each date). C = streams enriched with carcasses, N = streams not enriched with carcasses.

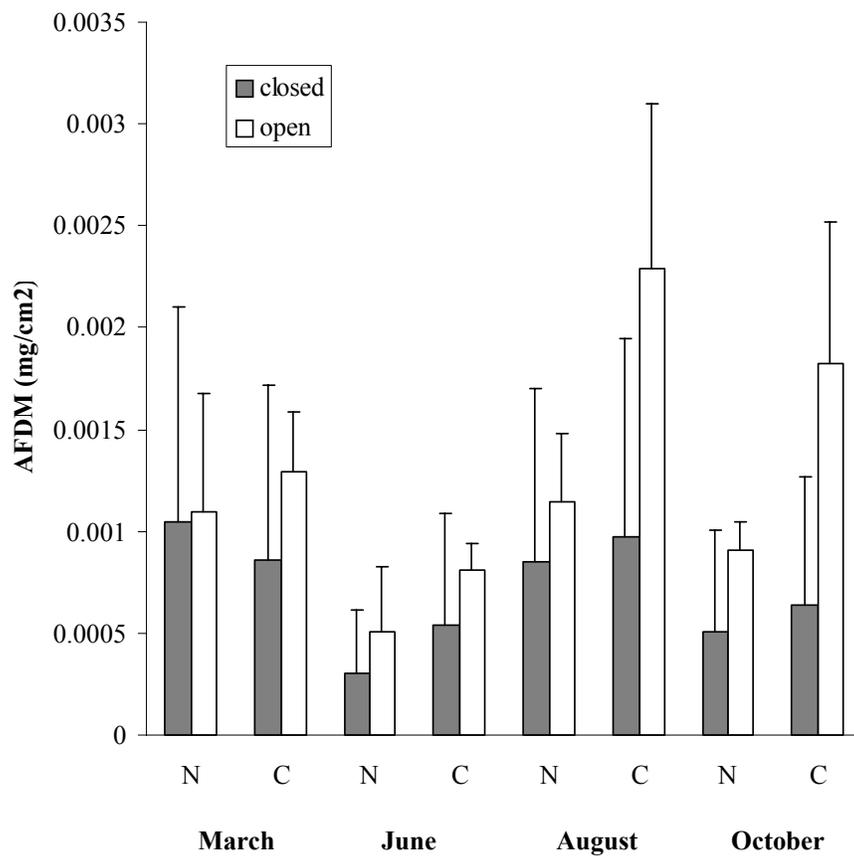


Figure 11. Mean AFDM (\pm SE) of periphyton scraped from natural substrates in open and closed reaches of Klamath and Smith River study streams in 2002 ($n = 3$ samples, with each sample composited from scrapings of 3 rocks for each treatment combination on each date). C = streams enriched with carcasses, N = streams not enriched with carcasses.

Table 5. Analysis of variance for the effects of carcass, canopy and the carcass x canopy interaction on percent benthic algal composition of Klamath and Smith River study streams in 2002. All data are log transformed. F denotes the F-value and (P) the p-value resulting from a split-plot ANOVA.

	Carcass		Canopy		Carcass x Canopy	
	F	(P)	F	(P)	F	(P)
Green algal composition (%)						
March	na	na	na	na	na	na
June	0.33	0.60	2.61	0.18	0.42	0.55
August	0.06	0.81	34.93	0.00	0.06	0.82
October	0.98	0.38	1.03	0.37	0.31	0.61
Blue-green algal composition (%)						
March	1.17	0.34	0.11	0.75	5.90	0.07
June	0.36	0.58	1.24	0.33	0.40	0.56
August	0.54	0.50	2.43	0.19	0.12	0.75
October	2.86	0.17	0.49	0.52	0.03	0.87
Diatom composition (%)						
March	0.95	0.38	0.36	0.58	3.91	0.12
June	0.69	0.45	0.40	0.56	0.59	0.48
August	0.64	0.47	13.63	0.02	0.00	0.99
October	6.86	0.06	1.49	0.29	0.38	0.57

highest in the open reach of enriched streams in August. Blue-greens were completely absent in closed reaches of non-enriched streams in August and October. Treatment effects on blue-green algal composition were not significant. Green algae was completely absent from all sites in March and covered less than 1% of all substrate in all sites in June. In August green algae covered 5% of the substrate in the open reach of both fertilized and non-fertilized streams and a canopy effect was significant (Figure 12). In October green algae had completely disappeared from the closed reach of non-fertilized streams, yet still covered 3% of the substrate in the open reach.

The thickness of diatom, blue-green or green algal communities did not differ significantly among study sites before treatments took place. Mean diatom thickness was higher in both open and closed reaches of enriched streams than it was in non-enriched streams in every post-treatment sampling month except March. During March, thickness of diatoms in enriched streams were 5% and 18% less than those in open and closed reaches of non-enriched streams, respectively. Diatom coatings were thicker in the open than closed reach of all streams that were fertilized. Mean diatom thickness (1.73 mm, SE = 0.82) was highest in open reaches of carcass treated streams in August. There were no significant effects of treatments on diatom thickness. Consistent patterns were not seen in mean blue-green algal thickness, and treatment effects were not significant. Mean blue-green algal thickness was highest (2.85 mm, SE = 1.09) in the open reach of non-fertilized streams in August. Mean green algal thickness was 2 times greater in the open reach of non-enriched streams than enriched streams in August, yet in October was 4 times thicker in the open reaches of enriched streams than non-enriched ones, where

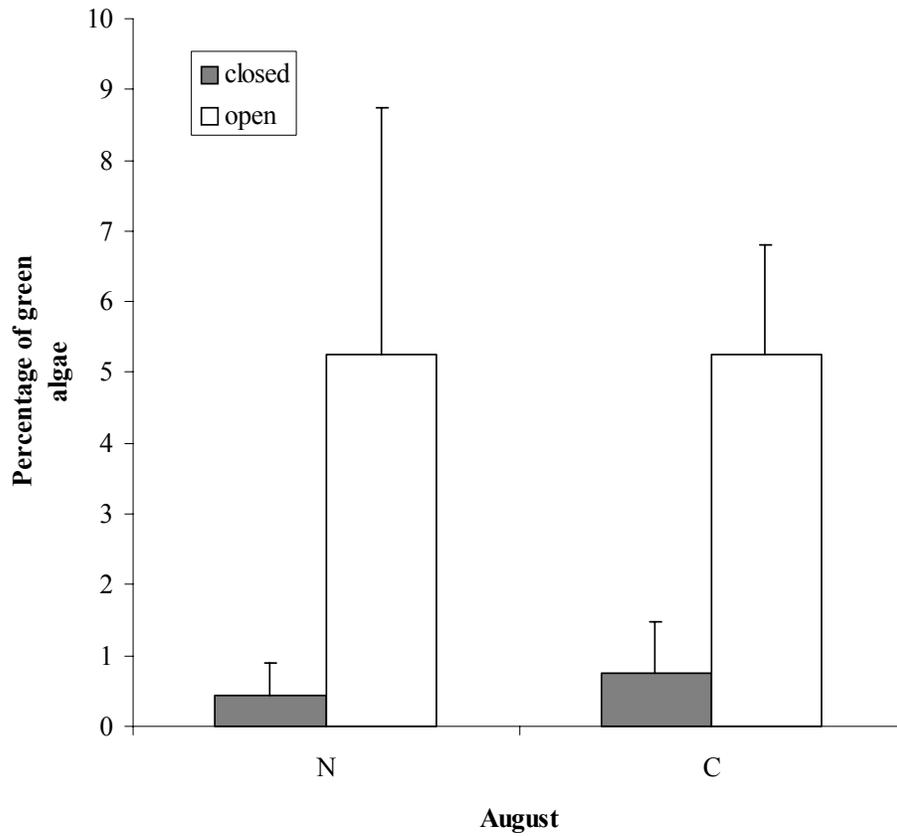


Figure 12. Mean green algal percentage (\pm SE) of benthic periphyton in open and closed reaches of Klamath and Smith River study streams in August 2002 ($n = 3$). C = streams enriched with carcasses, N = streams not enriched with carcasses.

mean thickness was highest at 2.3 mm (SE = 0.87). A significant canopy effect was seen on green algae thickness in August and a significant carcass effect was seen in October (Figure 13).

Primary Production

Gross primary production, which was estimated from respiration chamber measurements made approximately 5 months after carcass introductions, did not differ among treatments. Mean GPP was higher in open than in closed reaches of 4 streams, while no pattern was observed in comparison of carcass-enriched versus non-fertilized streams (Table 6). Chamber-based estimates of the ratio of 24 hr GPP to community respiration (P/R) indicated that the majority of sites were autotrophic and that Tectah Creek, the open reach of South Fork Rowdy Creek and the closed reach of Little Mill Creek were slightly heterotrophic. Treatment effects on chlorophyll *a* content of periphyton scraped from rocks following the production estimation were not significant. Chlorophyll *a* in the closed reaches of the enriched streams was 3 times higher than the open reaches of the enriched streams. In non-fertilized streams, open reaches were 2.5 times higher than the closed reaches.

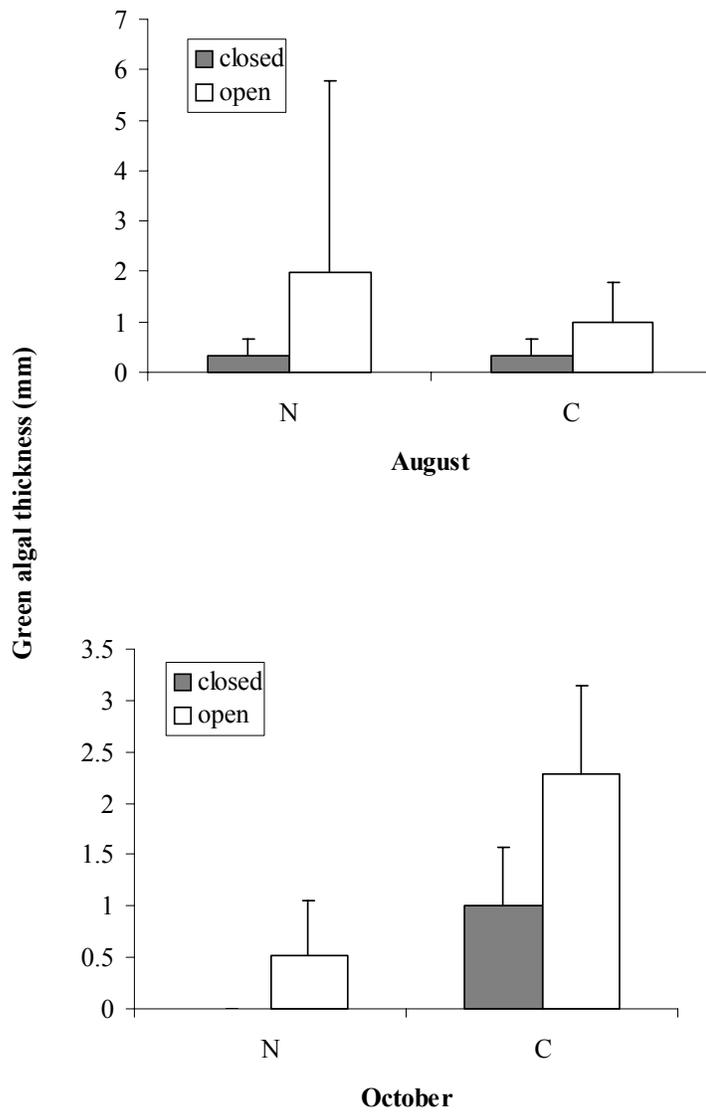


Figure 13. Mean green algal thickness (\pm SE) of benthic periphyton in open and closed reaches of Klamath and Smith River study streams in August and October 2002 ($n = 3$). C = streams enriched with carcasses, N = streams not enriched with carcasses.

Table 6. Gross primary productivity and production/respiration (P/R) ratios of periphyton in open and closed reaches of Klamath and Smith River study streams in late June and early July 2002, estimated in clear and dark respiration chambers. A P/R < 1 indicates a heterotrophic system and a P/R > 1 indicates an autotrophic system. Carcass enriched streams are indicated with a (C).

Stream Site	GPP (mgC cm ⁻² d ⁻¹)		P/R	
	Open	Closed	Open	Closed
Little Mill	0.06	0.028	1.598	0.934
Peacock (C)	0.073	0.039	2.715	3.014
South Fork Rowdy (C)	0.018	0.027	0.922	1.415
Savoy	0.036	0.051	1.170	1.941
Tarup (C)	0.018	0.008	1.643	1.062
Tectah	0.029	0.021	0.786	0.967

DISCUSSION

Lack of significance of treatment effects for many of the response variables make it difficult to draw strong conclusions about the relative importance of increased light, carcass introductions, or their interaction in affecting periphyton production.

Considerable variability in the data makes it clear that greater within reach replication would be required to demonstrate statistical significance. Nonetheless, results suggest that stream productivity, as demonstrated by attributes of the periphyton assemblage, may be enhanced to a greater extent by opening of the riparian canopy than by salmon carcass enrichment.

I hypothesized that periphyton biomass would be greater in open than in closed stream sections. This expectation was based on numerous studies documenting increased primary production in logged versus forested streams and on findings of Gregory (1980) and Triska et al. (1983) that periphyton communities in northern California and Oregon streams responded to nutrient enhancement only when light was not limiting. Large increases in periphyton biomass, measured both by chlorophyll *a* and AFDM, were observed on agar substrates placed in open as opposed to closed stream reaches in the *in situ* nutrient enrichment experiment, which was conducted in late summer. In addition, mean AFDM sampled from natural substrates was greater in open than in closed reaches of both fertilized and non-fertilized streams on all post-treatment sampling dates. Biomass measurements based on chlorophyll *a* were not totally consistent with AFDM measurements, yet the greatest values of both chlorophyll *a* and AFDM were seen in open reaches of fertilized streams in August and October. In March, differences in light

between open and closed reaches were slight because the deciduous canopy had not yet leafed out, and in June an accumulation of algal biomass may not have been seen because of the dominance of small, largely single celled diatoms. The appearance of a response to carcass enrichment and canopy opening in August and October is coincident with an increased abundance of filamentous green algae, and it may be that the green algae, rather than diatoms, are responding to nutrient enrichment where light limitation is reduced. Both AFDM and chlorophyll *a* are commonly used measures of algal standing crops (Steinman and Lamberti 1996), but AFDM does not allow for distinction of algal material from other organic material within the biofilm, or account for the physiological state of the organic material. At least in late summer and fall sampling dates, when flows were low and stream temperatures relatively high, open stream reaches supported greater concentrations of chlorophyll *a* than did closed reaches. In addition, primary production measurements, made in late June and early July, partially support a hypothesis of a greater periphyton response in open than in closed reaches. In 4 of 6 sites, GPP was greater in open than in closed reaches of streams. In 1 of the 2 exceptions (Savoy Creek, Table 6), as well as in Tarup Creek, oxygen production in the clear respiration chamber decreased during daylight when measurements were made. This could only have occurred if microbial respiration within the thick biofilm layer consumed oxygen at a greater rate than was being replenished by photosynthesis. The finding that study sites were autotrophic (i.e., $P/R > 1$) may have been affected by the short period of time over which production estimates were made. Apart from variability resulting from small sample sizes and swamping of photosynthesis by heterotrophic microbial respiration,

other factors could potentially contribute to the lack of a stronger canopy response.

Photoinhibition of shade-adapted algae (Boston and Hill 1991), reduction of light gain from canopy opening by topographic shading and top-down control of periphyton biomass by snails and other grazers (Bourassa and Cattaneo 1998, Rosemond et al. 2000 and Hill et al. 2001) are examples of such factors.

I also hypothesized a significant effect from salmon carcass introductions, and expected that periphyton biomass would be greatest in open reaches of carcass-enriched streams. Periphyton growth appears to have responded to carcass enrichment, but the evidence is more equivocal. Chlorophyll *a* measured from natural substrates was greater in open reaches of fertilized streams than in open reaches of non-fertilized streams during every post-treatment sampling date. AFDM measured from natural substrates was greater in both open and closed reaches of fertilized than non-fertilized streams every post-treatment sampling date. Gross primary production measurements, however, did not support the finding of a carcass effect. This is the first study to look at the response of stream primary productivity as a direct result of salmon nutrient inputs and more studies would greatly add to the understanding of the effects of such additions. Collectively, results suggest that removal of the riparian canopy had a greater relative effect on periphyton growth than did carcass enrichment, but that fertilization enhanced periphyton growth. Chlorophyll *a* and AFDM of periphyton scraped from natural substrates were often enhanced by fertilization alone, yet effects were greatest when light was not limited.

This experiment also identified nitrogen as more likely limiting periphyton growth than phosphorus in these streams. The findings that algal growth was nitrogen-limited but that the salmon carcasses were not providing a significant influx of nitrogen also argues against the significance of a carcass effect. Apart from carcasses, another potential source of nitrogen to streams in disturbed landscapes derives from inputs provided by nitrogen-fixing riparian alder, either through heterotrophic input from leaf litter or subsurface seepage into ground and stream water by root nodules. At least in these streams, however, alder does not appear to be providing enough nitrogen to stimulate periphyton growth. Although an algal response to nitrogen fertilization in open reaches of non-fertilized streams was seen, response to N + P additions was depressed. Microbial populations may have been stimulated by the phosphorus enrichment to the extent that they outcompeted or depressed the response of primary producers. Nitrate was added to the agar substrate in the clay saucers, which algae take up preferentially but which microbes are unable to use. Microbes require NH_3 or organic nitrogen sources. They are, however, able to use the inorganic phosphorus provided in the saucers, resulting in increased microbial growth. The greater turnover of bacterial than algal cells may allow them to outcompete algae.

In addition, I hypothesized a shift in periphyton assemblage from diatom dominance to dominance by filamentous blue-green and green algae in open and carcass-enriched stream reaches. This expectation was based on taxonomic shifts observed by Hansmann and Phinney (1973), Shortreed and Stockner (1983), and Lowe et al. (1986) in response to clearcut logging. Although diatoms were found to dominate periphyton

assemblages throughout this study, green algal coverage of the stream bottom increased with a decrease in diatom coverage in late summer in response to canopy opening. In addition, filamentous green algae were much more abundant on nutrient-diffusing clay saucers across all nutrient treatments in the open reaches. In the shaded reaches, algal assemblages consisted almost entirely of diatoms. Domination of periphyton assemblages by diatoms suggests that increases in light and nutrient enrichment were insufficient to override other controls on community composition in these reaches. Greater representations of green algae and cyanobacteria in summer months that have been described by others are likely partly attributable to warmer temperatures (Whitton 1975). In this study, temperature changes accompanying canopy opening were very slight. In several instances temperatures were greater in closed than in open stream reaches. This likely resulted from reduced evaporative cooling under canopy closure.

Results from this study, despite the tentative nature of the conclusions, are of significance and should be considered in stream and salmonid enhancement programs. Restoration strategies aimed at enhancing salmonid production in freshwater environments are increasingly focused on nutrient enhancement via carcass introductions or on attempts to increase the population of spawners. These strategies should not be discounted because salmon carcasses provide important food resources, including lipid and micronutrient supplies, to both invertebrate and fish consumers and terrestrial consumers (Cederholm et al. 1989, Bilby et al. 1996, Wipfli et al. 1998, Chaloner et al. 2002, Gende et al. 2002). However, these results suggest that a more effective strategy would be to supplement carcass enrichment with opening of the canopy to increase the

Comment: Date missing

transfer of salmon derived nutrients via autotrophic pathways. Bilby and Bisson (1992) found that salmonid production derived largely from autotrophic pathways, particularly during the period of major growth. Canopy opening should not involve complete removal of riparian vegetation as was done here, as riparian vegetation affords many beneficial functions to stream and terrestrial ecosystems (Gregory et al. 1991). Selective trimming, however, particularly of red alder, which now dominates our disturbed landscapes, could reduce light limitation of primary production. The importance of light has been generally undervalued by management agencies. Riparian vegetation that provides as much shade as possible is usually evaluated as 'better' than vegetation that provides less shade. This assumption is probably based largely on the corresponding temperature increases that accompany vegetation removal and the overhead cover it provides fish. But temperature increases are not problematic until they approach a level at which they become stressful for the organisms one is hoping to maintain. This is highly context-specific, and clearly was not an issue for the coastal headwater streams in this study. Future research is needed to identify ranges of light gain necessary to enhance primary production where light is limiting, and to develop pruning strategies that accomplish this without sacrificing the benefits that riparian vegetation provides. A next useful step would be an experimental design in which levels of salmon carcass introductions were varied, as well as amounts of pruning.

LITERATURE CITED

- Allan, J. D. 1995. Stream Ecology: Structure and function of running waters. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- American Public Health Association. 1999. Standard methods for the examination of water and wastewater. Twentieth Edition. American Public Health Association, Washington, D. C.
- Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested watersheds. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 540-551.
- Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 64-173.
- Boston, H. L. and W. R. Hill. 1991. Photosynthesis-light relations of stream periphyton communities. *Limnology and Oceanography* 36: 644-656.
- Bott, T. L. 1996. Primary productivity and community respiration. Pages 533-557 in F. R. Hauer and G. A. Lamberti, editors. *Methods in stream ecology*. Academic Press, San Diego, California.
- Bourassa, N., and A. Cattaneo. 1998. Control of periphyton biomass in Laurentian streams (Quebec). *Journal of the North American Benthological Society* 17: 420-429.
- California Division of Mines and Geology. 1964. *California Geology*. California Division of Mines and Geology, Sacramento, California.
- Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1347-1355.
- Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* 24(10): 6-15.

- Chaloner, D. T., K. M. Martin, M. S. Wipfli, P. H. Ostrom, and G. A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1257-1265.
- Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10: 147-172.
- Fairchild, G. W., and R. L. Lowe. 1984. Artificial substrates which release nutrients: effects on periphyton and invertebrate succession. *Hydrobiologia* 114: 29-37.
- Foggin, G. T., and B. R. McClelland. 1983. Influence of kokanee salmon and man on the water quality of lower McDonald Creek, Glacier National Park, Montana. Research Project Technical Completion Report, Montana Water Resources Research Center, Montana State University, Bozeman, Montana.
- Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *BioScience* 52: 917-928.
- Gregory, S. V. 1980. Effects of light, nutrients, and grazers on periphyton communities in streams. Doctoral dissertation. Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon.
- Gregory, S.V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* 41: 540-551.
- 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.
- Hansmann, E. W., and H. K. Phinney. 1973. Effects of logging on periphyton in coastal streams of Oregon. *Ecology* 54: 194-199.
- Hetrick, N. J., M. A. Brusven, W. R. Meehan, and T. C. Bjornn. 1998a. Changes in solar input, water temperature, periphyton accumulation, and allochthonous input and storage after canopy removal along two small salmon streams in southeast Alaska. *Transactions of the American Fisheries Society* 127: 859-875.
- Hetrick, N. J., M. A. Brusven, T. C. Bjornn, R. M. Keith, and W. R. Meehan. 1998b. Effects of canopy removal on invertebrates and diet of juvenile coho salmon in a small stream in southeast Alaska. *Transactions of the American Fisheries Society* 127: 876-888.

- Hill, W. R., and A. W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams. *Journal of Phycology* 24: 125-132.
- Hill, W. R., P. J. Mulholland, and E. R. Marzolf. 2001. Stream ecosystem responses to forest leaf emergence in spring. *Ecology* 82: 2306-2319.
- Johnson, S. W., J. Heifetz, and K. V. Koski. 1986. Effects of logging on the abundance and seasonal distribution of juvenile steelhead in some southeastern Alaska streams. *North American Journal of Fisheries Management* 6: 532-537.
- Johnston, N. T., J. S. Macdonald, K. J. Hall, and P. J. Tschaplinski. 1997. A preliminary study of the role of sockeye salmon (*Oncorhynchus nerka*) carcasses as carbon and nitrogen sources for benthic insects and fishes in the "Early Stuart" stock spawning streams, 1050 km from the ocean. British Columbia Ministry of Environment, Lands and Parks, Fisheries Project Report No. RD55, Victoria, British Columbia.
- Kevern, N. R., and R. C. Ball. 1965. Primary productivity and energy relationships in artificial streams. *Limnology and Oceanography* 10(1): 74-87.
- Kutka, F. J., and C. Richards. 1997. Short-term nutrient influences on algal assemblages in three rivers of the Minnesota River basin. *Journal of Freshwater Ecology* 12(3): 411-419.
- Kline, T. C., Jr., 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.
- Kyle, G. B., J. P. Koenings, and J. A. Edmundson. 1997. An overview of Alaska lake-rearing salmon enhancement strategy: nutrient enrichment and juvenile stocking. Pages 205-227 in A. M. Milner and M. W. Oswood, editors. *Freshwaters of Alaska: ecological syntheses*. Springer-Verlag, New York, New York.
- Lowe, R. L., S. W. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. *Journal of the North American Benthological Society* 5: 221-229.
- Lyford, J. H., Jr., and S. V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade Mountain streams. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 19: 1610-1616.

- 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. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 23: 2249-2258.
- 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.
- Minshall, G. W., E. Hitchcock, and J. R. Barnes. 1991. Decomposition of rainbow trout (*Oncorhynchus mykiss*) carcasses in a forest stream ecosystem inhabited only by nonanadromous fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 191-195.
- Moore, J. W. 1977. Some factors effecting algal densities in a eutrophic farmland stream. *Oecologia* 29: 257-267.
- Mosisch, T. D., S. E. Bunn, and P. M. Davies. 2001. The relative importance of shading and nutrients on algal production in subtropical streams. *Freshwater Biology* 46: 1269-1278.
- Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 137-145.
- Omernik, J. M., A. R. Abernathy, and L. M. Male. 1977. Nonpoint source-stream nutrient level relationships: A nationwide study. Environmental Protection Agency (EPA), Report 600/3-77-105, Washington D.C.
- 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.
- Pringle, C. M., and J. A. Bowers. 1984. An *in situ* substratum fertilization technique: diatom colonization on nutrient-enriched, sand substrata. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1247-1251.
- Quinn, J. M., A. B. Cooper, M. J. Stroud, and G. P. Burrell. 1997. Shade effects on stream periphyton and invertebrates: an experiment in streamside channels. *New Zealand Journal of Marine and Freshwater Research* 31: 665-683.

- Rand, P. S., C. A. S. Hall, W. H. McDowell, N. H. Ringler, and J. G. Kennen. 1992. Factors limiting primary productivity in Lake Ontario tributaries receiving salmon migrations. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2377-2385.
- Richey, J. E., M. A. Perkins, and C. R. Goldman. 1975. Effects of kokanee salmon (*Oncorhynchus nerka*) decomposition on the ecology of a subalpine stream. *Journal of the Fisheries Research Board of Canada* 32: 817-820.
- Rohm, C. M., J. M. Omernik, A. J. Woods, and J. L. Stoddard. 2002. Regional characteristics of nutrient concentrations in streams and their application to nutrient criteria development. *Journal of the American Water Resources Association* 38: 213-239.
- Rosemond, A. D., P. J. Mulholland, and S. H. Brawley. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 66-75.
- SAS Institute Inc. 1999-2001. Version 8. SAS Institute Inc., 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 of Karluk Lake, Alaska: importance in the assessment of an escapement goal. *North American Journal of Fisheries Management* 18: 743-763.
- Schuldt, J. A. 1998. Impact of chinook salmon spawning migrations on stream ecosystems. Doctoral dissertation. Department of Forest Resources, University of Minnesota, St. Paul, Minnesota.
- Schuldt, J. A., and A. E. Hershey. 1995. Effect of salmon carcass decomposition on Lake Superior tributary streams. *Journal of the North American Benthological Society* 14: 259-268.
- Shortreed, K. S., and J. G. Stockner. 1983. Periphyton biomass and species composition in a coastal rainforest stream in British Columbia: effects of environmental changes caused by logging. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1887-1895.
- Steinman, A. D., and G. A. Lamberti. 1996. Biomass and pigments of benthic algae. Pages 295-313 in F. R. Hauer and G. A. Lamberti, editors. *Methods in stream ecology*. Academic Press, San Diego, California.

- Stevenson, R. J., and L. L. Bahls. 1999. Periphyton protocols. Pages 6-1 – 6-21 in Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling, editors. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, 2nd edition. Environmental Protection Agency (EPA), Office of Water, Report 841-B-99-002, Washington, D. C.
- Stockner, J. G., and K. S. Shortreed. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. *Journal of the Fisheries Research Board of Canada* 35: 28-34.
- Sullivan, T. J., and M. C. Mix. 1983. A Simple and inexpensive method for measuring integrated light energy. *Environmental Science and Technology* 17: 127-128.
- Tate, C. M. 1990. Patterns and controls of nitrogen in tallgrass prairie streams. *Ecology* 71: 2007-2018.
- Thedinga, J. F., M. L. Murphy, J. Heifetz, K. V. Koski, and S. W. Johnson. 1989. Effects of logging on size and age composition of juvenile coho salmon (*Oncorhynchus kisutch*) and density of presmolts in southeast Alaska streams. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1383-1391.
- Triska, F. J., V. C. Kennedy, R. J. Avanzino, and B. N. Reilly. 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. Pages 129-159 in T. D. Fontaine and S. M. Bartell, editors. *Dynamics of lotic ecosystems*. Ann Arbor Science Publishers, Ann Arbor, Michigan.
- United States Soil Conservation Service. 1967a. Report and general soil map, Del Norte County, California. United States Department of Agriculture, Soil Conservation Service, Ukiah, California.
- United States Soil Conservation Service. 1967b. Report and General Soil Map, Humboldt County, California. United States Department of Agriculture, Soil Conservation Service, Ukiah, California.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.
- Wellnitz, T. A., R. B. Rader, and J. V. Ward. 1996. Importance of light and nutrients in structuring an algal community in a Rocky Mountain stream. *Journal of Freshwater Ecology* 11: 399-413.
- Wetzel, R. G., and G. E. Likens. 1991. *Limnological analyses*. 2nd edition. Springer-Verlag, New York, New York.

- Whitton, B. A. 1975. Algae. Pages 81-105 in B. A. Whitton, editor. River ecology. University of California Press, Berkeley, California.
- Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U. S. A. *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.
- Wipfli, M.S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society* 132: 371-381.
- Wold, A. P., and A. E. Hershey. 1999. Spatial and temporal variability of nutrient limitation in 6 north shore tributaries to Lake Superior. *Journal of the North American Benthological Society* 18: 2-14.