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MACROINVERTEBRATE COMMUNITY RESPONSE TO
EXPERIMENTAL MANIPULATION OF LIGHT AND
NUTRIENTS IN SECOND ORDER STREAMS OF
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MACRONVERTEBRATE COMMUNITY RESPONSE TO EXPERIMENTAL MANIPULATION OF LIGHT AND NUTRIENTS IN SECOND-ORDER STREAMS OF NORTHERN CALIFORNIA.

By

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ABSTRACT

MACROINVERTEBRATE COMMUNITY RESPONSE TO EXPERIMENTAL MANIPULATION OF LIGHT AND NUTRIENTS IN SECOND-ORDER STREAMS OF NORTHERN CALIFORNIA.

By

Osvaldo Hernandez

Benthic macroinvertebrate community response to increased light and nutrient augmentation, via riparian canopy removal and salmon carcass addition, was evaluated in second order coastal streams of northern California. The study followed a split-plot experimental design in a total of six streams within the Klamath and Smith River catchments. Each stream consisted of two study reaches (100m) separated by a 250m buffer. Three randomly selected streams received carcass addition (whole-plot factor) and within each stream a study reach randomly received riparian hardwood removal (subplot factor), resulting in four replicated treatments (C- control, N- nutrient augmented, L- light augmented, L+N- light and nutrient augmented). Stream reaches were sampled once pre-manipulation and four times post-manipulation. Main effect results show that while carcass addition had no effect on macroinvertebrate biomass, canopy removal led to moderately greater biomass (*F*(1,4)=5.33 *p*=0.0819), and all post-manipulation biomass were greater than pre-manipulation levels (*F*(4, 149)=5.14 *p*=0.0007). Pairwise comparisons of macroinvertebrate biomass treatment means, pre and post-manipulation, show no difference within C and N treatments, and greater macroinvertebrate biomass in L (*p*=0.09) and L+N augmented treatments (*p*=0.0025). Additionally, red alder (*Alnus rubra*) leaf pack

mass loss was evaluated among experimental treatments in both spring and fall 2002. During both seasons, 1) all experimental treatments (N, L, L+N) had greater mass loss relative to controls, and 2) control leaf packs had slowest decay coefficients (*k*), while light (L) treatments had fastest decay coefficients. Decay coefficients in the spring were significantly faster in streams with carcass additions than in streams with out carcass additions. Decay coefficients in the fall were significantly faster in the light (L) treatment than in the controls (C).

Results of this study revealed no significant main effect of carcass addition on benthic macroinvertebrate community structure and function in these low order coastal California streams. An ongoing study on nutrient (P) spiraling in the study streams (Harvey and Hill in prep) has shown streams are very non-retentive, i.e. they leak phosphorus rapidly. So the physical, chemical, and biological conditions to effectively take up phosphorus are absent with or without carcasses. Nonetheless, pairwise comparisons pre and post-treatment did reveal a significant effect of augmenting both light and nutrients on mean invertebrate biomass. These results suggest the importance of considering light availability as a component of studies investigating management options that aim to increase salmonid fish production through cascading food web pathways.

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INTRODUCTION

Northern California's economy is dependent on its natural resources. Much of the landscape has been designated for timber harvest. Del Norte, the most northwestern county has almost equal acreage designated for national forest (157,000) than it does for the forest industry (135,000), although timber production has steadily been decreasing from 60,105,000 board feet in 1996 to 22,691,000 board feet in 2001. Humboldt County located just south of Del Norte, has 262,000 acres designated as national forest and 608,000 acres in the forest industry. Similarly, timber production has been steadily declining in Humboldt County from 517,524,000 board feet in 1996 to 358,225,000 board feet in 2001 (California Department of Forestry Website).

As a result, previously harvested areas are now characterized by a dense red alder (*Alnus rubra*) riparian canopy. Red alder is an early successional species that quickly colonizes disturbed areas with exposed mineral soils. With rapid growth rates of one meter or more in the first year and maximum annual growth of more than three meters a year by two to five year old seedlings (Harrington and Curtis 1986), it quickly dominates riparian margins. However, red alder is a relatively short-lived species maturing at 60 to 70 years with a maximum age of about 100 years and has low commercial value. However, its ecological value to streams has been the focus of studies in the Pacific Northwest. Red alder is capable of fixing atmospheric nitrogen (N_2) that can result in increases in nitrogen availability both in the soil and in leaf litter that could potentially benefit the quality of allochthonous organic matter to adjacent streams. For example, in an effort to determine how the distribution of macroinvertebrates is affected by interstitial detritus quality and quantity, Culp and Davies (1985) found that total macroinvertebrate densities and biomass were greater in alder detritus than in no detritus and low hemlock detritus in the main channel of Carnation Creek, Vancouver Island, British Columbia. In addition, research on the effects of canopy type on benthic macroinvertebrate and detritus export from headwater streams in southeast Alaska, has shown streams with a red alder dominated young growth canopy exported significantly more macroinvertebrates than did streams with a conifer-dominated young growth canopy (Piccolo and Wipfli 2002).

In addition to the economic importance of timber in northern California, there are numerous streams that are economically important for salmonid fish production. The commercial value of samonids in California in 2001 was $4,692,093 (Department of Fish and Game website) primarily from Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*). Coho salmon (*Oncorhynchus kisutch*) present in some watersheds in California are currently listed as threatened, which reflects the decline in salmonid populations in the Pacific Northwest (Gresh et al. 2000). The importance of salmonid fish to California's economy has resulted a need for management options that will likely lead to their increased production.

One current management option being considered to stimulate fish production is removal of riparian red alder. Removal of riparian canopy has led to increases in periphyton production (Hansmann and Phinney 1973; Duncan and Brusven 1985a; Feminella et al. 1989; Hetrick et al. 1998a) that enhances benthic invertebrate production (Burns 1972; Newbold et al. 1980; Hawkins et al. 1982; Duncan and Brusven 1985b; Hetrick et al. 1998b). This enhanced invertebrate production may partly be due to the generally higher protein content and digestibility of algae and algal-based detritus than most incoming terrestrial plant matter (Triska et al. 1975). The change in the relative importance from allochthonous organic matter sources on which small order streams depend upon (Vannote et al. 1980) to autochthonous organic matter will result in changes to the invertebrate community composition from primarily shredders and detritivores to scrapers and gathering-collectors (Gregory et al. 1987). These changes in community composition and greater production of benthic invertebrates will result in greater food availability for fish by way of greater invertebrate abundances or possibly through behavioral differences such as invertebrate drift, ultimately leading to greater production of fish.

Another management option for increased fish production is fertilization of streams. Harvey et al. (1998) showed that experimental additions of phosphorus and nitrogen to an arctic tundra stream stimulated production at all trophic levels relative to an unfertilized reach. Declining nutrient supplies historically derived from carcasses of spawned salmon, known as marine derived nutrients, has likely led to increased nutrient limitation in streams of the Pacific Northwest

(Gresh et al. 2000). Fertilization of streams is believed to result in a positive feedback mechanism whereby nutrients from salmon carcasses are incorporated by stream autotrophs. The increased production of autotrophs would then result in greater food availability for organisms in higher trophic levels, up to top predators (salmonid fish). Greater production of fish would result in greater spawner returns and therefore a greater nutrient subsidy of marine derived nutrients.

In an effort to assess the efficacy of these management options we propose to experimentally manipulate light and nutrient levels in previously harvested second order streams with a red alder riparian canopy in northern California. Experimental manipulation is a logical approach to determining the relative effects of increased light, nutrients, or both by contrasting manipulated and controlled areas in natural streams. The objective of this study is to document the effects of increased light and nutrients on coastal cutthroat (*Salmo clarki*) fish production by the food web pathways that support them.

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CHAPTER 2

BENTHIC MACROINVERTEBRATE RESPONSE TO EXPERIMENTAL MANIPULATION OF LIGHT AND NUTRIENTS IN SECOND ORDER STREAMS OF NORTHERN CALIFORNIA

INTRODUCTION

Coastal waterbodies of the Pacific Northwest are characterized as oligotrophic (Bisson and Bilby 1998), particularly with respect to phosphorus (Welsh et al. 1998). It has been proposed that in general, this condition has been exacerbated due to declining salmonid stocks (Larkin and Slaney 1997) that historically provided an estimated 95% of the N and P in those systems to a marine derivation (Gresh et al. 2000), before nitrogen-fixing red alder became the dominant riparian tree. Fertilization has been proposed and used as a management technique with the goal of reversing or ameliorating this trend. The idea is that fertilization would lead to greater primary production and cascade up the food web, ultimately increasing the number of salmonid spawners that will return and perpetuate the cycle. There is evidence from southeast Alaska that stream biota, at multiple trophic levels, assimilate these marine derived nutrients (Chaloner et al. 2002), where the effects of enrichment have been evaluated. For example, salmon carcass and carcass analog (salmon cakes - dried salmon pellets) enrichment to stream tributaries in Alaska were shown to result in higher mean condition, production and lipid content of cutthroat trout (*Oncrhynchus clarki*) than in un-enriched stream sections (Wipfli et al. 2004). Although, these positive responses to enrichment have been documented, effects on stream chemistry and biota have been inconsistent and context dependent (Janetski et al. 2009; Wilzbach et al. 2005).

In addition to nutrient limitation, many of these coastal streams have undergone a history of timber harvest of their riparian vegetation, which has led to a change in their composition, to a dominance of hardwoods (particularly red alder *Alnus rubra*) with youngest stands having the highest levels of canopy cover (Russell 2009). This dense canopy cover, which limits primary production, may further be problematic to salmonid production, as autotrophic pathways are important to salmon growth in the spring and summer (Bilby and Bisson 1992; Wilzbach et al. 2005). Removal of riparian canopy has led to increases in periphyton production (Hansmann and Phinney1973; Duncan and Brusven1985a; Feminella et al. 1989; Hetrick et al. 1998a) that enhances benthic invertebrate abundances and biomass (Burns 1972; Newbold et al. 1980; Hawkins et al. 1982; Duncan and Brusven 1985b, Nislow and Lowe 2006). This enhanced invertebrate production may be due partly to the generally higher protein content and digestibility of algae and algal-based detritus than most incoming terrestrial plant matter (Triska et al. 1975). A change in the relative importance from allochthonous organic matter sources upon which small order streams depend (Vannote et al. 1980) to autochthonous organic matter, results in changes to the invertebrate community functional composition from dominance by shredders and gathering-collectors to scrapers (Gregory et al. 1987). These changes in community composition of benthic invertebrates likely result in greater food availability for fish by way of greater invertebrate abundances or possibly through behavioral differences such as increases in invertebrate drift.

In an effort to determine the relative effects of increased light, nutrients, or both, on macroinvertebrate communities, we augmented light (via canopy removal) and nutrient levels (via salmon carcass additions) in previously harvested second order forested streams with a predominantly red alder riparian canopy in northern California.

METHODS

Study Area

The study was conducted in coastal northern California (Del Norte and Humboldt counties) between October 2001 and October 2003. The area typically experiences warm dry summers and cool wet winters, with average yearly temperatures ranging from 5.5 - 16.5°C and average yearly rainfall ranging between 170 to 200cm. Study reaches were established upstream of anadromy on 2 tributaries of the Klamath (Tarup and Tectah) and 4 tributaries of the Smith River (South Fork Rowdy, Savoy, Little Mill and Peacock) basins (Figure 2.1). Study reaches on second to third order streams had similar catchment areas (Table 2.1). Riparian vegetation consisted primarily (>80%) of red alder (*Alnus rubra*); while surrounding vegetation included coastal redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), big leaf maple (*Acer macrophyllum*), tan oak (*Lithocarpus* *densiflorus*), and California bay laurel (*Umbellularia califomica*). Resident salmonids were cutthroat trout (*Oncorhynchus clarki*), and rainbow trout / steelhead (*Oncorhynchus mykiss*) and hybrids (Wilzbach et al. 2005).

Experimental Design

In an effort to augment nutrients and light to study reaches, salmon carcasses were added to streams, and riparian hardwoods were removed from the riparian margin. The first phase of the study followed a split-plot experimental design, with carcass treatment (carcass, no carcass) as the whole-plot factor and canopy treatment (open, closed) as the sub-plot factor. Each of the streams consisted of two 100m study reaches separated by a 150-200m buffer. Three of the six streams were randomly selected to receive carcass addition, and a study reach within each stream was randomly selected to undergo canopy removal (Table 2.1). The design resulted in three replicate study reaches of four treatments; control (C), augmented nutrients (N), augmented light (L), and augmented light and nutrients (L+N).

Carcass addition of Chinook salmon (*Oncorhynchus tsawytscha*) carcasses to the three streams was conducted in January of both 2002 and 2003. Salmon carcasses for Tarup creek were procured from California Department of Fish and Wildlife's Iron Gate Fish Hatchery on the Klamath River. Carcasses for Little Mill and Peacock creeks were collected from the privately owned Rowdy Creek Fish Hatchery and from spawned carcasses on the Smith

River. Carcasses were stored frozen until introduced at a level of approximately 1 $kg \bullet m^{-2}$. Carcasses were anchored throughout study reaches with rebar in areas of slack water and near debris dams. Grab samples of water were collected in 2002 from each study reach at 2, 6, 15 and 22 weeks after carcass addition and analyzed for multiple water chemistry parameters (Wilzbach et al. 2005).

The canopy treatment was carried out in December 2001 after leaf fall, and involved falling red alder and other hardwoods from a 20m wide band on each side of the stream for the 100m length of each randomly selected stream reach. A 2-man team with a chainsaw and a winch felled the trees to minimize disturbance and direct the cut trees away from the stream. Prior to canopy treatment, the potential available sunlight reaching streambeds was estimated at 20m intervals of all study reaches using a Solar Pathfinder™. Photosynthetically active radiation (PAR) was measured simultaneously in open and closed canopy reaches of a stream using a Li-Cor® quantum sensor model LI-190S after canopy removal. Stream temperatures were monitored using Stowaway® TidbiT™ submersible data loggers (Wilzbach et al. 2005).

Macroinvertebrate Sampling

Macroinvertebrates were sampled once pre-treatment in October 2001 and 4 times post-treatment (March and July 2002, and July and October 2003). A total of three macroinvertebrate samples were collected from each study reach at each sampling event. Individual samples were collected from cobble habitats from randomly selected riffles within a study reach. Other habitats were sampled, but have not yet been analyzed. Individual samples were collected with a D-frame aquatic net placed immediately downstream of agitated habitat for 30 seconds. Samples were rinsed through a 250-μm sieve and transferred into Whirl-Paks®, preserved in 80% ethanol, and returned to the lab for sorting under a dissecting scope. Invertebrates were picked from samples, counted, measured to the nearest millimeter, and identified mostly to generic level for Insecta (except for Chironomidae) using Merritt & Cummins (1996; Merritt et al. 2008). Chironomidae were identified to subfamily and non-insect invertebrates were not identified beyond order level. A total of 180 samples were collected and analyzed.

Invertebrate biomass was calculated using INVERTCALC software (Merritt et al. 2002). Richness was measured as mean number of taxa present. Diversity was calculated based on invertebrate biomass using the Shannon-Weiner diversity index (Hauer and Resh 1996), and percent Chironomidae was also calculated based on invertebrate biomass. Macroinvertebrates were assigned a functional group status (shredders, scrapers, filtering-collectors, gathering-collectors, and predators) according to Merritt and Cummins (1996; Merritt et al. 2008). Percent functional group and functional feeding group ratios (P/R, CPOM/FPOM, Drift Food) were calculated based on biomass (Merritt et. al. 2002).

The response variables biomass, and functional feeding group ratios (CPOM/FPOM and Drift Food) were analyzed by a split-split-plot ANOVA, with carcass treatment (carcass, no carcass) as the whole-plot factor canopy treatment (open, closed) as the sub-plot factor and sampling event (Oct 2001, March 2002, July 2002, July 2003, and Oct 2003) as the sub-sub-plot factor. Richness, diversity, percent functional group, and P/R ratio were analyzed similarly, however, only Oct 2001 and Oct 2003 sampling events were evaluated, for comparison pre and post manipulation during the same time of year. Additionally, four pair-wise comparisons of macroinvertebrate biomass treatment means, pre and post-treatment, were conducted using Bonferroni adjusted alpha levels of 0.0125 per test (0.05/4). Response variable residuals were tested for normality, and results were transformed where necessary. Means were separated using Fishers LSD at $p = 0.05$. Although response variables were transformed, they have been presented in untransformed fashion in graphs and tables.

RESULTS

Carcass addition had no significant effect on the following water chemistry parameters tested, SiO_2, nitrogen (TN, NO_3^-, and $NH4^+$), or phosphorus (TP and PO_4^{3-}) (Wilzbach et al. 2005). Availability of potential sunlight did not differ among streams or study reaches prior to canopy removal, however, canopy removal often led to a tenfold increase in PAR, (Ambrose et al. 2004). Additionally, canopy removal resulted in higher NH_4^+ levels in open-canopy reaches, however, winter, summer and maximum weekly average temperatures did not differ between open and closed study reaches. Small temperature increases (1.5°C) were noted at the downstream end of open-canopy reaches (Wilzbach et al. 2005).

Macroinvertebrate Biomass

There were no differences in mean macroinvertebrate biomass among study reaches during pre-treatment sampling (all $p \geq 0.60$). Mean macroinvertebrate biomass did not differ between streams with and without carcasses ($p = 0.64$), or between open and closed-canopy reaches ($p = 0.08$). However, biomass did differ among sampling dates with lowest levels at pretreatment sampling (Figure 2.2a). Additionally, biomass was greater in streams with carcasses than in streams without carcasses during March 2002 (Figure 2.2b). Results of pair-wise comparisons of macroinvertebrate biomass treatment means, pre and post-treatment, show no difference within C, N, or L treatments, and greater post-treatment biomass in L+N augmented streams ($p = 0.0025$) (Figure 2.3).

Mean % Chironomidae did not differ among study reaches during pre-treatment sampling (all $p > 0.21$), or between streams with and without carcasses ($p = 0.07$). Canopy treatment ($p = 0.004$) and sampling event ($p < 0.0001$) did affect % Chironomidae, with closed-canopy and post-treatment samples having a greater percentage of Chironomidae biomass (Figure 2.4a). Additionally, the interaction of canopy and sampling event treatments also resulted in significantly greater (all $p < 0.0001$) % Chironomidae in closed-canopy reaches sampled in October 2003 (Figure 2.4b).

Richness and Diversity

A total of 83 insect genera and three chironomid subfamilies were collected from study reaches of the Smith and Klamath River basins of Northern California, in addition to eight non-insect taxa (Table 2.2). Mean taxa richness did not differ significantly among study reaches during pre-treatment sampling (all $p \geq 0.14$). Mean taxa richness did not differ between streams with and without carcasses ($p = 0.47$), or between open and closed-canopy reaches ($p = 0.50$). However, mean taxa richness was greater during the October 2001 (pre-treatment) sampling event, than during October 2003 ($p < 0.0001$)(Figure 2.5a). There were no significant interaction effects on taxa richness. Shannon-Weiner diversity did not differ significantly between streams with and without carcasses ($p = 0.12$), between open and closed-canopy reaches ($p = 0.91$), or among sampling events ($p = 0.32$) (Figure 2.5b). Additionally, there were no significant interaction effects on diversity (all $p > 0.06$).

Functional Analysis

Percent functional group composition for scrapers (Sc), filtering-collectors (Fc), gathering-collectors (Gc) and predators (Pr) did not differ between streams with and without carcasses (all $p > 0.19$), or between open and closed-canopy reaches (all $p > 0.14$). Additionally, there were no significant interactions on percent composition for these groups (all $p > 0.05$). However, there were significant differences on percent composition during pre and post-treatment October sampling effects on these groups (all $p < 0.05$)(Figure 2.6). The predators were the most dominant functional group present at both pre and post-treatment sampling events, comprising about 40% of the total biomass. *Calineuria* (Perlidae) and *Rhyacophila* (Rhyacophilidae) were the dominant (Pr) taxa; each had between 30-50% more biomass in the post-treatment samples. Scraper biomass was overall greater in post-treatment samples. The snail *Juga* (Pleuroceridae) was the dominant (Sc) taxon in both pre and post-treatment samplings with three times as much biomass in the post-treatment sampling. Similarly, filtering-collector biomass was greater in post-treatment samples. The (Fc) caddisfly *Hydropsyche* (Hydropsychidae) was the dominant taxa in both pre and post-treatment samples with ten times more biomass in post-treatment samples. Gathering-collector biomass was greater overall in pre-treatment samples, with Oligochaeta being the dominant taxon with similar levels of biomass in both pre and post-treatment samplings. There was greater biomass of both *Cinygmula* (Heptageniidae) and *Baetis* (Baetidae) in post-treatment samples. Percent shredder (Sh) composition did not differ between streams with and without carcasses ($p = 0.79$), or between open and closed-canopy reaches ($p = 0.71$), or between pre and post-treatment sampling events ($p = 0.46$) (Figure 2.6). However, there was a significant interaction between sampling event and canopy type ($p = 0.008$). There was a greater percentage of shredders in October 2003 than in October 2001 within closed-canopy reaches ($p = 0.03$), as a result of more *Pteronarcys* (Pteronarcyidae), *Amphinemoura* and *Malenka* (Nemouridae) biomass in closed-canopy reaches in post-treatment samples than in closed-canopy reaches in pre-treatment samples. There were also a greater percentage of shredders within closed-canopy reaches than in open-canopy reaches during October 2003 ($p = 0.02$) (Figure 2.7), as a result of more *Pteronarcys* and the Nemouridae stoneflies *Zapada*, *Malenka* and *Amphinemoura*, in post-treatment closed-canopy reaches than in post-treatment open-canopy reaches.

Analysis of mean P/R ratios resulted in no significant main effects of carcass ($p = 0.63$), canopy ($p = 0.30$), or sampling event ($p = 0.60$) treatments, in addition to no significant interactions (all $p > 0.16$)(Table 2.3). Similarly there was no main effect of carcass and canopy treatments on CPOM/FPOM ($p = 0.92$ and $p = 0.49$) or Drift Food ($p = 0.33$ and $p = 0.33$) ratios. Sampling event ($p = 0.0035$), and the interaction of sampling event and carcass treatment (all $p < 0.05$) led to significant differences in CPOM/FPOM ratios (Figure 2.8). Similarly, sampling event ($p = 0.0008$) (Figure 2.9), and the interaction of sampling event and carcass treatment ($p = 0.04$) led to significant differences in Drift Food ratios (Figure 2.10).

DISCUSSION

Macroinvertebrate Biomass

Overall study design limitations (lower degrees of freedom at the wholeplot level) led to greater significant findings at the subplot (primarily sampling event) and interaction levels of treatments in this study. Invertebrate biomass varied significantly among sampling events, potentially due to seasonal differences in standing stock biomass. However, biomass was significantly greater at all sampling dates post-treatment, including the final sampling event that occurred in the same month as the pre-treatment sampling event. Sampling events yielded similar results in taxonomic composition, according to Jaccard coefficients, no two sampling events were less than 76% similar. Additionally, the top five dominant taxa comprised between 40-55% of the total biomass across sampling dates (Table 2.4), suggesting all sampling dates were dominated similarly by these same taxa. The stonefly *Calineuria* (Perlidae) was present across all sampling dates as the most biomass dominant organism, comprising 11-17% of the total biomass. A positive response by perlid stoneflies to carcass additions and indirect uptake of nutrients occurring about two months after the addition also was recorded in Washington (Claeson et al. 2006). This evidence and the finding that the greatest percentage of salmon derived nutrients occurs in macroinvertebrates three months after additions (Honea and Gara 2009), lends support to our finding of greater invertebrate biomass in streams with carcass addition than in streams without carcass addition in March 2002.

Analysis of invertebrate biomass using Bonferroni adjusted pair-wise comparisons of treatment means pre versus post-manipulation reveals a gradual pattern of increased biomass from C to N, and L reaches. Previous studies have shown greater densities of Chironomidae and Ephemeroptera following nutrient additions to experimental stream channels (Perrin and Richardson 1997; Kiffney and Richardson 2001). This study, conducted in natural streams with a red alder riparian canopy failed to show a significant increase in invertebrate biomass subsequent to carcass additions. Carcass additions to streams with a red alder riparian canopy have been shown not to affect stream water chemistry or quality (Edmonds and Mikkelsen 2006; Wilzbach et al. 2005). Previous studies have documented greater abundances of invertebrates in streams with clearcut canopies (Hawkins et al. 1982), in addition to greater biomass of invertebrates in open versus closed canopies (Hetrick et al. 1998b). Our study resulted in greater amounts of invertebrate biomass in light-augmented treatment reaches, although the difference was not significant (*p* = 0.09). However, we did show positive additive effects on invertebrate biomass through the augmentation of both light and nutrients, suggesting the need to consider light as a limiting factor in marine or salmon derived nutrient study designs.

Chironomidae abundance and biomass have been shown to have a positive relationship with marine derived nutrients (Lessard and Merritt 2006). In addition, chironomid density has been shown to increase in nutrient enriched experimental streams (Kiffney and Richardson 2001). Our study showed no such relationship to carcass addition, again a potential limitation of the study design. Additionally, our study showed lower % Chironomidae biomass in open versus closed canopy stream reaches, opposite of what is commonly described. Chironomidae have been shown to increase three times after tree harvest (Garman and Moring 1993), and low canopy cover has been shown to result in increased numbers of Chironomidae larvae (Nislow and Lowe 2006). There was a greater percentage of Chironomidae, in terms of biomass, during the post-treatment sampling particularly in the closed canopy reaches.

Richness and Diversity

Invertebrate taxa richness and diversity did not respond significantly to experimental addition of salmon analogs (dried salmon pellets) in Idaho (Kohler et al. 2008). However, invertebrate diversity has been shown to decline during salmon spawning (Lessard and Merritt 2006), presumably the result of disturbance during salmon spawning. We did not assess invertebrate diversity during carcass addition. The difference in mean richness pre and post-treatment in this study resulted from some rare taxa that appeared in between 1-8 of the total number of samples (*Moselia, Polycentropus, Hydatophylax, Ceratopsyche, Rhantus*).

Functional Analysis

A dominance of predators in study reaches suggests a need for a food base with rapid turnover rates (Merritt et al. 2002), such as chironomid larvae, whose turnover rates have been shown to decrease when in the presence of nutrient enrichment (Ramirez and Pringle 2006). Greater scraper biomass in post-treatment sampling was presumed the result of increased periphyton growth expected after canopy removal (Hetrick et al. 1998a). The absence of significant differences in periphyton ash-free dry mass pre and post-manipulation in this study (Ambrose et al. 2005) may have resulted from increased scraper feeding pressure or scouring. Collectors have been implicated as important for the transfer of marine or salmon derived nutrients through food webs (Chaloner and Wipfli 2002) although in some cases Heptageniidae and Baetidae have been shown to have greater abundances and biomass in control reaches of marine derived nutrient studies (Lessard and Merritt 2006). The positive response by *Cinygmula* and *Baetis* in this study likely reflect a lack of disturbance by salmon migration, as our carcass introductions were experimental rather than natural. Shredder biomass only differed at the interaction level (sampling event*canopy treatment) of the study. Invertebrate samples from cobble habitats of closed-canopy stream reaches had greater shredder biomass than the same habitat in open-canopy reaches, likely because of the greater availability of food resource in the form of red alder riparian litter.

Due to sample variability, there were no significant differences in P/R functional group ratios as was expected between open and closed-canopy reaches. Mean P/R ratios by treatment and sampling event show heterotrophy dominated stream reaches, although autotrophy appeared to dominate during the October 2003 sampling event across all treatments during leaf drop (Table 2.3).

CPOM/FPOM functional group ratio varied by sampling event with March 2002 and July 2002 having the smallest ratios, as a result of low numbers of large individuals (ex. Ptronarcys). The March sampling event was marked by a small overall shredder biomass (75mg) versus >140mg at other sampling events, while collector biomass was large in July 2002 (3900mg) versus < 2300mg at other sampling events. Streams without carcass addition had more (ca. 100mg) shredder biomass than streams with carcass additions, particularly during pre and post-treatment October sampling events.

Drift Food functional group ratio was largest during the July 2002 sampling event. The biomass of the mayflies *Baetis* and *Acentrella* (Baetidae) was 2-5 times greater during this sampling event resulting in twice as much behavioral drifter biomass than other sampling events. In streams without carcass additions, primarily *Baetis* (Baetidae), and to a lesser part *Paraleptophlebia* (Leptophlebiidae), are responsible for the greater biomass of behavioral drifters during March 2002, July 2002 and October 2003 when compared to the pre-treatment sampling event. The difference in Drift Food functional ratio between streams with and without carcasses in March 2002 was attributable to accidental drifters such as *Pteronarcys* (Pteronarcyidae), *Calineuria* (Perlidae) and *Rhyacophila* (Rhyacophilidae), in streams with carcasses.

Conclusion

Results of this study revealed no significant main effect of carcass addition on benthic macroinvertebrate community structure and function in these low order coastal California streams. However, invertebrate biomass was significantly greater in streams reaches 2-3 months following carcass additions, suggesting a need to re-evaluate carcass addition effects on a more focused shorter timeframe and a larger spatial scale than in this study. A two year follow up study to WIlzback et al. 2005 was conducted by Harvey and Wilzbach (in prep) in which the design was to add no carcasses to the upper reaches (both canopy treatments) and carcasses to all the down stream reaches (both canopy treatments). Again, this two-year study showed the same fish results - no carcass effect on fish growth. The lack of carcass addition effects may likely reflect limitations of the study's experimental design, in which the subplot factors of canopy removal and sampling date have greater power. In 2-3 months, the effect would likely be largely downstream well out of the experimental area. An ongoing study on nutrient (P) spiraling in the study streams (Harvey and Hill in prep) has shown streams are very non-retentive, i.e. they leak phosphorus rapidly. So the physical, chemical, and biological conditions to effectively take up phosphorus are absent with or without carcasses.

Similarly, removal of riparian hardwoods did not lead to significant main effects in all but one response variable (% Chironomidae). Pairwise comparisons pre and post-treatment however did reveal a significant effect of augmenting both light and nutrients on mean invertebrate biomass. These results suggest the importance of considering light availability as a component of studies investigating management options that aim to increase salmonid fish production through cascading food web pathways.

Table 2.1. Study stream characteristics. * Denotes streams with carcass addition.

	Catchment Area	Latitude / Longitude	Open Canopy	Gradient (%)	
Stream	(km^2) / Basin		Reach	Open	Closed
Tectah	7.9 / Klamath	41°15'47"N / 123°57'52"W	Lower	2.9	1.7
Tarup *	4.9 / Klamath	41°27'45"N / 123°59'32"W	Upper	2.8	1.8
Little Mill	3.4 / Smith	41°52'27"N / 124°6'47"W	Lower	7.7	9.5
Peacock *	3.5 / Smith	41°50'11"N / 124°5'23"W	Lower	2.4	4.2
South Fork Rowdy *	4.9 / Smith	41°55'16"N / 124°5'23"W	Upper	5.6	5.1
Savoy	5.0 / Smith	41°54'14"N / 124°5'12"W	Lower	4.7	5.6

Table 2.2. Checklist of taxa collected from cobble habitats within study reaches of the Smith and Klamath River basins of Northern California. (a- premaipulation, b- postmanipulation, c- open canopy, d- closed canopy, e- control, f- nutrient, g- light, h- light+nutrient, Sc- scraper, Gc- gathering collector, Fc- filtering collector, Sh- shredder, Pi- Piercer, Pr- predator, Pa- parasite, A- Accidental Drifter, B- Behavioral drifter)

Family	Genus	Presence	FFG	Drift type
Ephemeroptera				
Ameletidae	*Ameletus*	a b c d e f g h	Gc	B
Baetidae	*Acentrella*	a b c d e f g h	Gc	B
	Baetis	a b c d e f g h	Gc	B
Ephemerellidae	*Attenella*	a b c d e g h	Gc	A
	Caudatella	a c d e	Gc	A
	Drunella	a b c d e f g h	Sc	A
	Ephemerella	a b d f	Gc	A
	Serratella	a b c d e f g h	Gc	A
	Timpanoga	b c g h	Gc	A
Heptageniidae	*Cinygma*	a b c d f g h	Sc	A
	Cinygmula	a b c d e f g h	Gc	A
	Epeorus	a b c d e f g h	Gc	A
	Heptagenia	a b c d f g	Sc	A
	Ironodes	a b c d e f g h	Sc	A
	Rhithrogena	a b c d e f g h	Gc	A
Leptophlebiidae	*Paraleptophlebia*	a b c d e f g h	Gc	B
Plecoptera				

Table 2.2 (cont.)

Capniidae		a	b	c	d	e	f	g	h	Sh	A
Chloroperlidae	*Kathroperla*	a	b	c	d	e			h	Gc	A
	Suwallia	a	b	c	d	e	f	g	h	Pr	A
	Sweltsa	a	b	c	d	e	f	g	h	Pr	A
Leuctridae	*Despaxia*	a	b	c	d	e	f			Sh	A
	Moselia	a		c	d	e				Sh	A
	Perlomyia	a	b	c					h	Sh	A
Nemouridae	*Amphinemura*	a	b	c	d	e	f	g	h	Sh	A
	Malenka	a	b	c	d	e	f		h	Sh	A
	Nemoura	a		c	d	e				Sh	A
	Zapada	a	b	c	d	e		g	h	Sh	A
Peltoperlidae	*Soliperla*	a	b	c	d	e	f	g		Sh	A
Perlidae	*Calineuria*	a	b	c	d	e	f	g	h	Pr	A
	Doroneuria	a	b	c	d	e	f	g		Pr	A
	Hesperoperla	a	b	c	d	e	f	g	h	Pr	A
Perlodidae	*Isoperla*	a	b	c				g		Pr	A
	Osobenus	a	b	c				g		Pr	A
Pteronarcyidae	*Pteronarcys*	a	b	c	d	e		g	h	Sh	A
Odonata											
Gomphidae		a	b	c	d	e	f	g	h	Pr	A
Megaloptera											
Corydalidae	*Orohermes*	a	b		d	e	f			Pr	A

Table 2.2 (cont.)

Sialidae	*Sialis*	a	b		d	e	f			Pr	A
Trichoptera											
Apatanidae	*Apatania*	a	b	c	d	e	f	g	h	Sc	A
Brachycentridae	*Brachycentrus*	a	b	c	d	e	f			Fc	A
	Micrasema	a	b	c	d	e	f	g	h	Sh	A
Calamoceratidae	*Heteroplectron*	a	b	c	d	e	f	g	h	Sh	A
Glossosomatidae	*Glossosoma*	a	b	c	d	e	f	g	h	Sc	A
Hydropsychidae	*Ceratopsyche*	a		c		e				Fc	A
	Hydropsyche	a	b	c	d	e	f	g	h	Fc	A
	Parapsyche	a	b	c	d	e	f		h	Fc	A
Hydroptilidae	*Ochrotrichia*		b	c					h	Gc	A
Lepidostomatidae	*Lepidostoma*	a	b	c	d	e		g	h	Sh	A
Leptoceridae			b		d	e				Sc	A
Limnephilidae	*Cryptochia*		b	c					h	Sh	A
	Ecclisomyia	a	b	c	d	e	f	g	h	Gc	A
	Hydatophylax	a		c	d	e				Sh	A
Philopotamidae	*Wormaldia*		b	c					h	Fc	B
Polycentropodidae	*Polycentropus*	a		c		e				Pr	A
Rhyacophilidae	*Rhyacophila*	a	b	c	d	e	f	g	h	Pr	A
Sericostomatidae	*Gumaga*	a	b	c	d	e	f	g	h	Sh	A
Uenoidae	*Neophylax*	a	b	c	d	e	f	g	h	Sc	A
	Neothremma	a	b	c	d	e	f		h	Sc	A

Table 2.2 (cont.)

Hymenoptera											
Scelionidae			b		d		f			Pa	A
Coleoptera											
Dytiscidae	*Laccophilus*		b	c				g		Pr	A
	Oreodytes		b	c	d		f		h	Pr	A
	Rhantus	a		c		e				Pr	A
Elmidae	*Ampumixis*	a	b	c	d	e	f	g	h	Gc	A
	Cleptelmis		b		d	e				Gc	A
	Dubiraphia		b	c				g		Gc	A
	Lara	a	b	c	d	e	f	g	h	Sh	A
	Narpus	a	b	c	d	e	f	g	h	Gc	A
	Optioservus	a	b	c	d	e	f			Sc	A
	Rhizelmis	a	b	c	d	e	f	g	h	Sc	A
	Zaitzevia	a	b	c	d	e	f	g		Sc	A
Hydrochidae	*Hydrochus*	a	b	c	d	e	f	g		Sh	A
Hydrophilidae	*Paracymus*		b	c				g		Gc	A
Psephenidae	*Acneus*	a	b	c	d	e	f	g	h	Sc	A
Diptera											
Ceratopogonidae		a	b	c	d	e	f	g	h	Pr	A
	Atrichopogon		b		d		f			Pr	A
Chironomidae	*Orthocladinae*	a	b	c	d	e	f	g	h	Gc	B
	Tanypodinae	a	b	c	d	e	f	g	h	Pr	A

Table 2.2 (cont.)

		Tanytarsini	a	b	c	d	e	f	g	h	Fc	B
	Dixidae	*Dixa*	a	b	c	d	e	f	g	h	Gc	B
	Empididae	*Chelifera*	a	b	c	d	e	f	g	h	Pr	A
		Clinocera	a	b	c	d	e	f	g	h	Pr	A
		Hemerodromia	a	b	c	d	e	f	g	h	Pr	A
	Pelecorhynchidae	*Glutops*	a	b	c	d	e	f		h	Pr	A
	Psychodidae		a	b	c	d	e	f	g		Gc	B
		Maurina		b		d		f			Sc	A
	Simuliidae	*Simulium*	a	b	c	d	e	f	g	h	Fc	B
	Stratiomyidae	*Nemotelus*		b		d	e				Gc	A
	Thaumaleidae		a	b	c	d	e		g		Sc	B
	Tipulidae	*Antocha*	a	b	c	d	e	f	g	h	Gc	A
		Dicranota	a	b	c	d	e	f	g	h	Pr	A
		Hexatoma	a	b	c	d	e	f		h	Pr	A
		Pedicia	a	b	c	d	e	f	g	h	Pr	A
		Non-Insect										
Collembola			a	b	c	d	e	f	g	h	Gc	A
Turbellaria			a	b	c	d	e	f	g	h	Pr	A
Oligochaeta			a	b	c	d	e	f	g	h	Gc	A
Hydracarina			a	b	c	d	e	f	g	h	Pr	A
Copepoda			a	b	c	d	e	f	g	h	Fc	B
Ostracoda			a	b	c	d	e	f	g	h	Gc	A

Table 2.2 (cont.)

Amphipoda											
Gammaridae		a	b	c	d	e	f	g	h	Sh	B
Gastropoda											
Pleuroceridae	*Juga*	a	b	c	d	e	f	g	h	Sc	A

Table 2.3. Mean P/R ratio analog, calculated from macroinvertebrate biomass by sampling event and treatment. Ratios (>0.75) are autotrophic, (<0.75) heterotrophic. No statistically significant differences.

	Sampling Event				
Treatment	(OCT01)	(MARCH02)	(JULY02)	(JULY03)	(OCT03)
C	0.27	0.46	0.36	0.24	0.76
N	0.41	0.52	0.58	0.61	0.70
L	0.50	0.46	0.56	0.37	0.83
L+N	0.24	0.32	0.33	8.33	1.64

Table 2.4. Percent of total biomass of top five taxa per sampling event

	FFG	(OCT01)	(MARCH02)	(JULY02)	(JULY03)	(OCT03)
Calineuria	Pr	14.88	17.08	17.40	11.26	13.41
Oligochaeta	Gc	8.54	6.27	7.41	6.24	
Rhyacophila	Pr	9.15	10.07	7.78		
Pteronarcys	Sh		14.00		11.62	
Turbellaria	Gc	7.35				5.79
Hesperoperla	Pr	6.89			6.42	
Juga	Sc				6.91	8.30
Ironodes	Sc		8.05			
Cinygmula	Gc					8.04
Drunella	Sc			6.12		
Hydropsyche	Fc					4.75
Narpus	Gc			5.70		
Percent Dominance		55.48	44.41	42.45	40.30	46.82

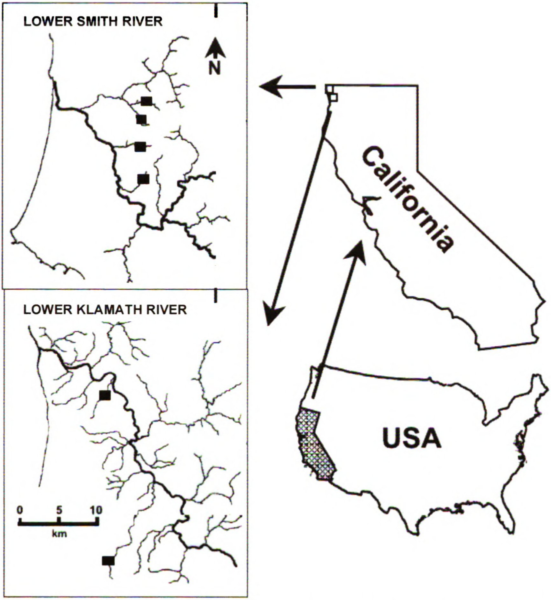

Figure 2.1. Study reaches within the lower Smith and Klamath River Basins of northern California (after Wilzbach et al. 2005).

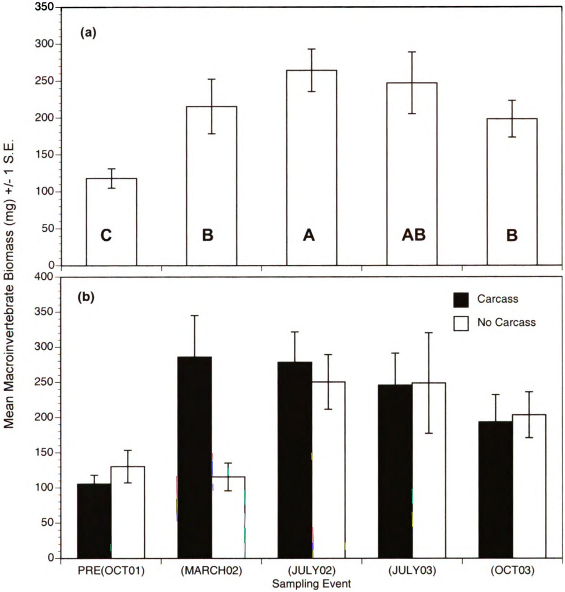

Figure 2.2. Mean macroinvertebrate biomass (± 1 S.E.) by (a) sampling event. Bars with same letters are not significantly different from each other, Fishers LSD (*p* = 0.05). And (b) sampling event by carcass interaction, March 2002 t = 2.19, df=9, p = 0.05.

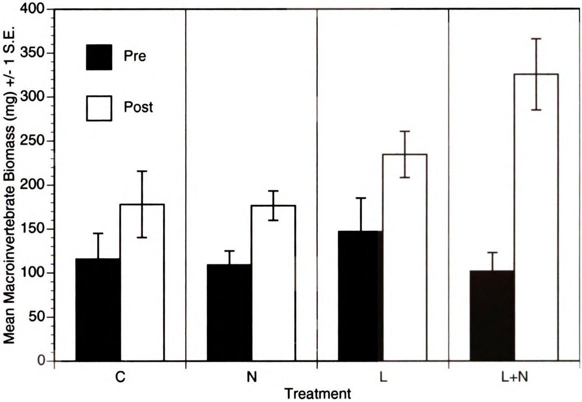

Figure 2.3. Pairwise comparison of pre and post-treatment macroinvertebrate biomass treatment means (± 1 S.E.). L+N significant t = 3.08, df=150, p =0.0025.

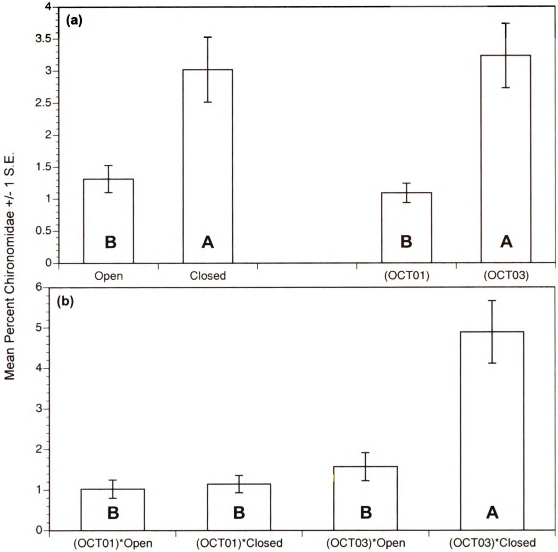

Figure 2.4. Mean percent Chironomidae by (a) the main effects of canopy type, and sampling event, and by (b) interaction between canopy and sampling event treatments. Bars with same letters are not significantly different from each other, Fishers LSD (p = 0.05).

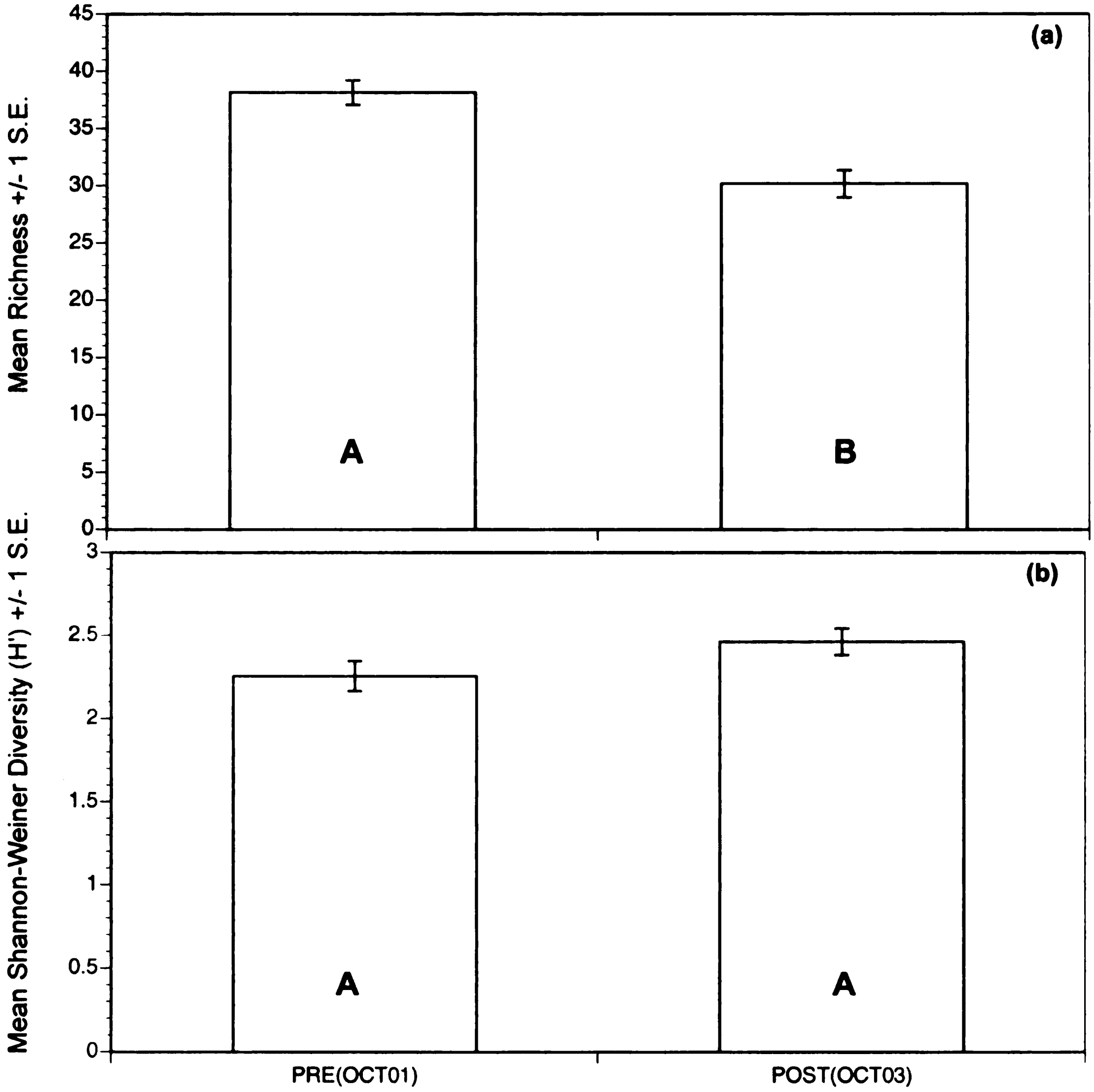

Figure 2.5. (a) Mean Richness and (c) Mean Shannon-Weiner Diversity pre and post-treatment (± 1 S.E.). Bars with same letters are not significantly different from each other ($p < 0.05$).

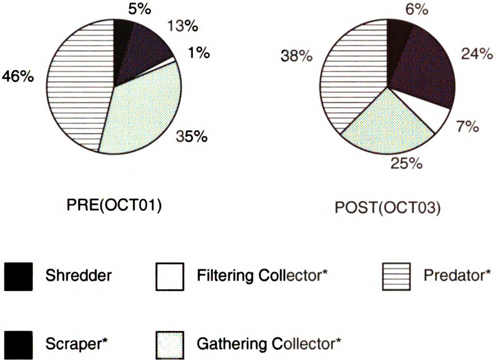

Figure 2.6. Functional feeding group composition pre (October 2001) and pos-treatment (October 2003) across all treatments. * Indicates significantly different pre and post-treatment (ANOVA, $p < 0.05$).

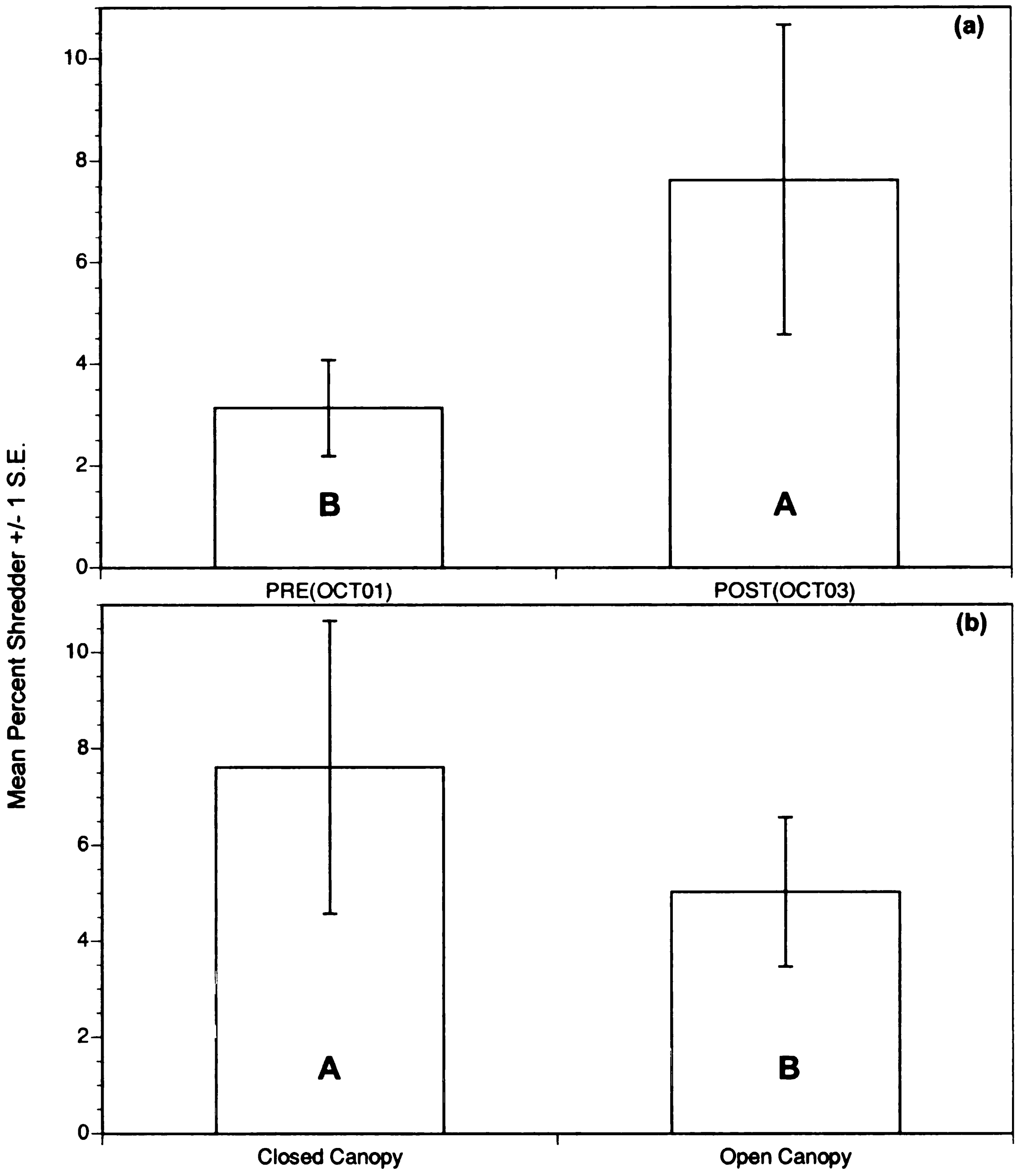

Figure 2.7. Interaction effect on percent Shredder (a) pre (October 2001) and post-treatment (October 2003) within closed-canopy reaches, and (b) post-treatment open versus closed-canopy reaches (± 1 S.E.). Bars with same letters are not significantly different from each other, Fishers LSD (*p* = 0.05).

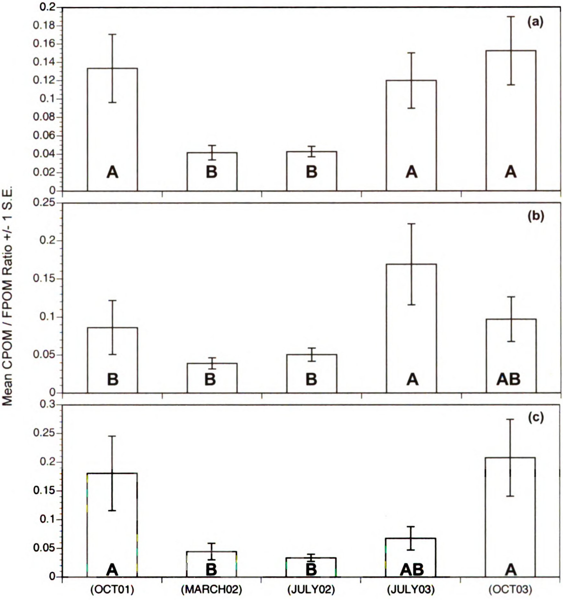

Figure 2.8. Mean CPOM / FPOM ratio (± 1 S.E.) calculated from macroinvertebrate biomass by (a) sampling event, (b) sampling event by carcass streams, and (c) sampling event by no carcass streams. Bars with same letters are not significantly different from each other, Fishers LSD (p = 0.05).

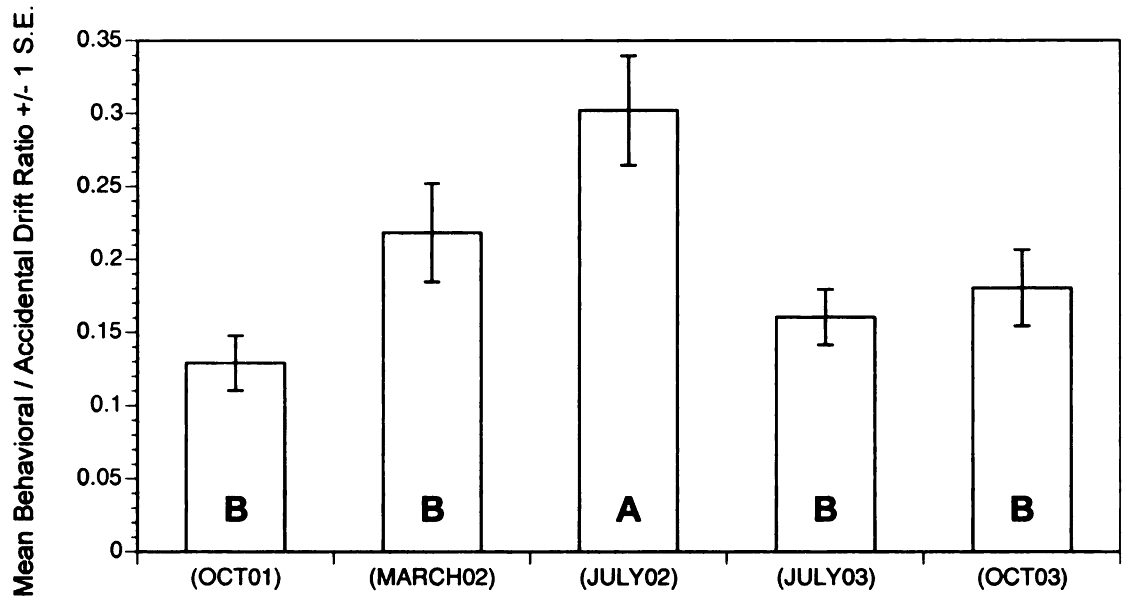

Figure 2.9. Sampling event effect on mean behavioral / accidental drift ratio (± 1 S.E.). Bars with same letters are not significantly different from each other, Fishers LSD (*p* = 0.05).

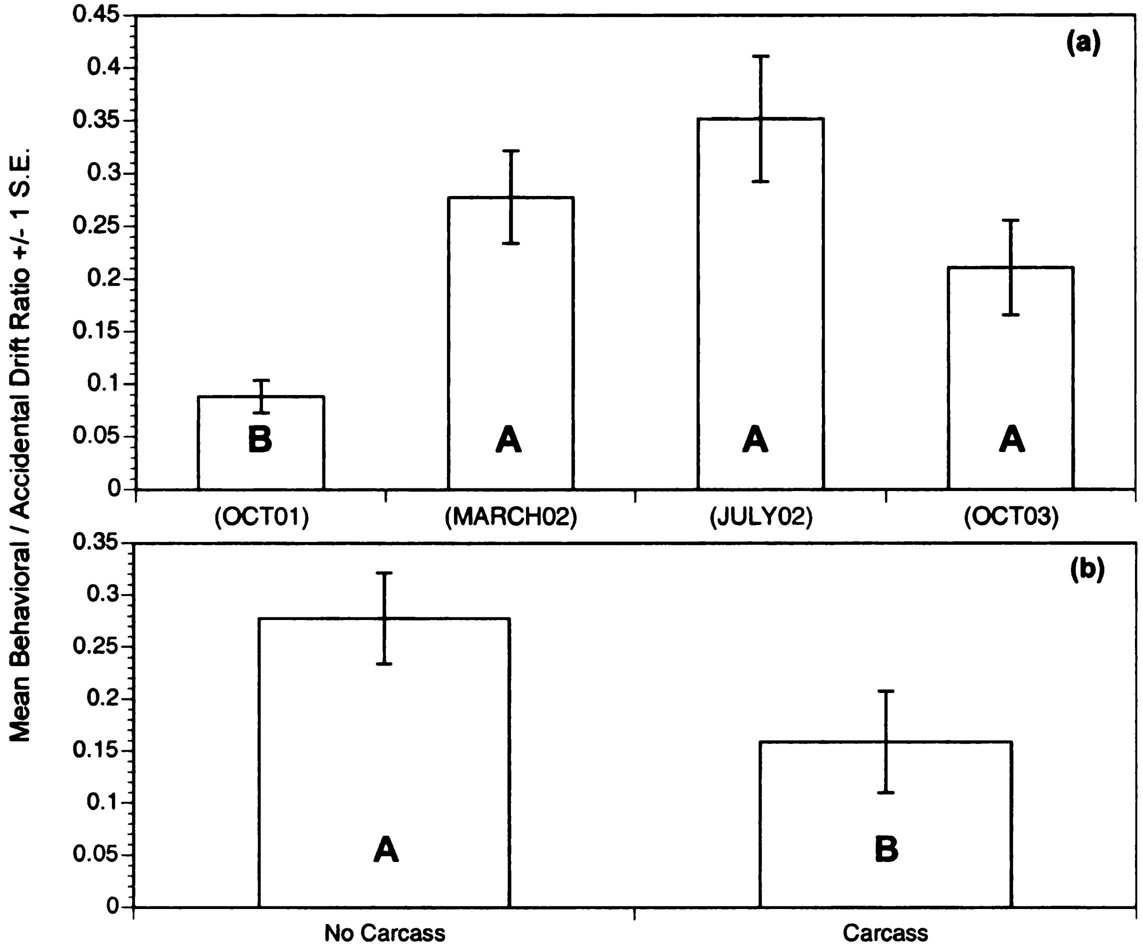

Figure 2.10. Interaction effect (sampling event by carcass treatment) on mean behavioral / accidental drift ratios (± 1 S.E.) in (a) no carcass streams, and (b) in March 2002 between carcass and no carcass streams. Bars with same letters are not significantly different from each other, Fishers LSD (*p* = 0.05).

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CHAPTER 3

RED ALDER (*Alnus rubra*) LEAF PACK MASS LOSS AND MACROINVERTEBRATE RESPONSE TO EXPERIMENTAL MANIPULATION OF LIGHT AND NUTRIENTS IN SECOND ORDER STREAMS OF NORTHERN CALIFORNIA.

INTRODUCTION

Leaf litter is a primary energy source for streams and rivers, particularly temperate headwater streams with a deciduous riparian canopy (Peterson and Cummins 1974). Low order and headwater streams heavily shaded by a riparian canopy are dependent upon these allochthonous sources of energy, as a heavily shaded canopy serves to limit available sunlight to the streambed and therefore limits primary production. Macroinvertebrate shredders are adapted to take advantage of the litter resource, and convert it from coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) that is used by filtering and gathering collectors downstream (Merritt and Cummins 1996; Merritt et al. 2008; Vannote et al. 1980). This breakdown of leaf litter is an important process in streams (Benfield 1996), because it involves the conversion of plant biomass to the animal biomass of higher trophic levels.

Leaf litter mass loss rates have been shown to vary depending on microbial conditioning (Crowl et al. 2006), leaf species (Peterson and Cummins 1974), leaf species assemblages (Kominoski and Pringle et al. 2007), nutrient enrichment, and riparian condition. Nutrient enrichment has resulted in mixed effects on leaf litter mass loss, depending on the amount of nutrient enrichment

(Knorr et al. 2005). Studies have reported no effect on leaf mass loss (Ferreira et al. 2007), as well as no effect on leaf pack invertebrate richness or abundance (Ferreira et al 2006). Conversely, some studies have shown a positive effect on leaf mass loss from nutrient enrichment (Yanai 2005; Paul 2006), and yet others have reported suppression of leaf mass loss as a result of nutrient enrichment (Zhang 2003). Riparian condition (light intensity) has similarly yielded mixed results with respect to litter mass loss. For example, Ishikowa et al. (2007) reported effects of clear-cutting on leaf mass loss to be species specific, while Franken et al. (2005) reported no effect of light intensity on leaf mass loss, and Bates et al. (2007) reported 37% greater leaf mass loss in streams with cut riparian vegetation when compared to those with uncut riparian vegetation. It is therefore important to determine and document the effects of natural stream manipulations on organic matter processing dynamics. Two manipulations proposed to stimulate stream productivity and ultimately salmonid growth and abundance are stream fertilization by way of carcass addition and increasing light by way of canopy removal.

METHODS

Study Area

This study was conducted in coastal northern California (Del Norte and Humboldt counties) between October 2001 and October 2002. The area typically experiences warm dry summers and cool wet winters, with average yearly air temperatures ranging from 5.5 - 16.5°C and average yearly rainfall ranging between 170 to 200cm. Study reaches were established upstream of anadromy on 2 tributaries of the Klamath (Tarup and Tectah) and 4 tributaries of the Smith River (South Fork Rowdy, Savoy, Little Mill and Peacock) basins (Figure 3.1). Study reaches on second to third order streams had similar catchment areas (Table 3.1). Riparian vegetation consisted primarily (>80%) of red alder (*Alnus rubra*); while surrounding vegetation included coastal redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), big leaf maple (*Acer macrophyllum*), tan oak (*Lithocarpus densiflorus*), and California bay laurel (*Umbellularia californica*). Resident salmonids were cutthroat trout (*Oncorhynchus clarki*), and rainbow trout / steelhead (*Oncorhynchus mykiss*) and hybrids (Wilzbach et al. 2005).

Experimental Design

In an effort to augment nutrients and light reaching study reaches, salmon carcasses were added to streams, and riparian hardwoods were removed from the riparian margin. The study followed a split-plot experimental design, with carcass treatment (carcass, no carcass) as the whole-plot factor and canopy treatment (open, closed) as the sub-plot factor. Each of the streams consisted of two 100m study reaches separated by a 150-200m buffer. Three of the six streams were randomly selected to receive carcass addition, and a study reach within each stream was randomly selected to undergo canopy removal (Table 3.1). The design resulted in three replicate study reaches of four treatments; control (C), augmented nutrients (N), augmented light (L), and augmented light and nutrients (L+N).

Addition of Chinook salmon (*Oncorhynchus tsawytscha*) carcasses to the three streams was conducted in January 2002. Salmon carcasses for Tarup creek were procured from California Department of Fish and Wildlife's Iron Gate Fish Hatchery on the Klamath River. Carcasses for Little Mill and Peacock creeks were collected from the privately owned Rowdy Creek Fish Hatchery and from spawned carcasses on the Smith River. Carcasses were stored frozen until introduced at approximately 1 $kg \bullet m^{-2}$. Carcasses were anchored throughout study reaches with rebar in areas of slack water and near wood debris dams. Grab samples of water were collected in 2002 from each study reach at 2, 6, 15 and 22 weeks after carcass addition and analyzed for multiple water chemistry parameters (Wilzbach et al. 2005).

The canopy treatment was carried out in December 2001 after leaf fall, and involved falling red alder and other hardwoods from a 20m wide band on each side of the stream for the 100m length of each randomly selected stream reach. A 2-man team with a chainsaw and a winch felled the trees to minimize disturbance and direct the cut trees away from the stream. Prior to canopy treatment, the potential available sunlight reaching streambeds was estimated at 20m intervals along all study reaches using a Solar Pathfinder^{TM}. Photosynthetically active radiation (PAR) was measured simultaneously in open and closed canopy reaches of a stream using a Li-Cor® quantum sensor model LI-190S after canopy removal. Stream temperatures were monitored using Stowaway® TidbiT™ submersible data loggers (Wilzbach et al. 2005).

Leaf Packs

Individual leaf litter packs were constructed using red alder leaves at abscission. Leaves were air-dried, weighed to 5-g packs, rewetted, loosely fastened together with a quilting gun and tethered two to a brick for introduction into streams. A total of 720 leaf packs (60 per stream reach) were constructed and deployed 60 per stream reach in both late spring (May-June) and early fall (August-September) 2002. Leaf packs were collected at day-2 (10 leaching packs), day-15 (5 packs), day-23 (5 packs), and day-30 (10 packs), in addition to 30 initial packs to account for handling loss. Handling loss packs were subjected to all conditions, however, time in the water was approximately 5 seconds. Individual packs were removed from bricks, placed in a zip-lock™ bag, and transported to the lab in an ice chest. In the lab, leaf packs were rinsed with de-ionized water and air-dried to a constant mass. After weighing, a sub-sample of each leaf pack was collected for ash-free dry mass (AFDM) determination. Percent AFDM leaf pack remaining and decay coefficients (*k*) were computed following Benfield (1996). Leaf pack-associated macroinvertebrates were collected from day-15, day-23 and day-30 samples and preserved in 70% ethanol for later identification and enumeration. Invertebrate biomass was calculated using INVERTCALC software (Merritt et al. 2002), and richness was measured as number of taxa present. Invertebrate diversity was calculated based on invertebrate biomass using the Shannon-Weiner diversity index (Hauer and Resh 1996, Hauer and Resh 2007). Invertebrates were assigned to a shredder, scraper, filtering-collector, gathering-collector or predator functional group status (Merritt and Cummins 1996; Merritt et al. 2008). Percent of each functional group, shredder biomass and shredder diversity were also calculated based on biomass (Merritt et al. 2002). Shredder richness was measured as number of taxa present.

Differences in decay coefficients (*k*) among experimental treatments (C, N, L, L+N) as well as invertebrate response variables were assessed by analysis of covariance (ANCOVA) with time (days) as the covariate (Barlocher 2005). Initial values at day_0 were excluded from analysis. Response variable residuals were tested for normality, and results were transformed where necessary. Means were separated using Fishers LSD at $p = 0.05$. Although response variables were transformed, they are presented in untransformed fashion in figures and tables.

RESULTS

Water Chemstry / PAR / Temperature

Carcass addition had no significant effect on the following water chemistry parameters tested, SiO_2, nitrogen (TN, NO_3^-, and $NH4^+$), or phosphorus (TP and PO_4^{3-}) (Wilzbach et al. 2005). Availability of potential sunlight did not differ among streams or study reaches prior to canopy removal, however, canopy removal often led to a tenfold increase in PAR, (Ambrose et al. 2004). Additionally, canopy removal resulted in higher NH_4^+ levels in open-canopy reaches, however, winter, summer and maximum weekly average temperatures did not differ between open and closed study reaches. Small temperature increases (1.5°C) were noted at the downstream end of open-canopy reaches (Wilzbach et al. 2005).

% AFDM remaining / Decay coefficients (*k*)

Leaf mass loss was faster in fall the than in the spring 2002. Leaf packs in the control stream reaches had the greatest % AFDM remaining at the end of both spring (55% +/-1.7) and fall (29% +/-1.9) experiments. Leaf packs in the (L) treatment reaches had the least percent remaining in both spring (38.7% +/- 3.5) and fall (11.8% +/-1.9) experiments (Figure 3.2). In the spring, carcass addition had a significant effect ($F_{1,317}=22.31$ $p <0.0001$), resulting in greater experimental leaf pack mass loss than in streams without carcass addition (Table 3.2). Invertebrate biomass in streams with carcass additions was dominated primarily by the scraper *Juga* (Pleuroceridae) and the Trichoptera shredder *Heteroplectron* (Table 3.3).

In the fall, the interaction of carcass and canopy treatments had a significant effect ($F_{1,304}=8.36$ $p =0.004$) on decay rates, with faster breakdown of leaf packs in the (L) treatment than in the (C) treatment (Table 3.2). Fall invertebrate biomass was dominated by *Juga sp.*, and was approximately 2-5 times greater in (L) than in (C) treatments (Table 3.4).

Macroinvertebrates

A total of 74 insect genera and three chironomid subfamilies, and 8 non-insect taxa were collected from red alder leaf packs in study (Table 3.5). The caddisflies (Trichoptera), with representatives from 11 families and 21 genera had 9 shredder taxa. Stoneflies (Plecoptera) also had 9 representative shredder taxa.

Spring 2002

Leaf pack invertebrate biomass did not differ significantly between streams with and without carcass additions, between stream reaches with open or closed canopies, or among experimental treatments (C, N, L and L+N). However, an interaction with the covariate (time*carcass; $F_{1,94}=5.28$, $p=0.0238$) revealed a pattern of decreasing invertebrate biomass in streams with carcass additions, and increasing invertebrate biomass in streams without carcass additions (Figure 3.3a). Neither main nor interactive effects of the study significantly affected invertebrate richness (all $p>0.05$). Invertebrate diversity was significantly greater in streams without carcass additions than in streams with carcass additions ($F_{1,50}=5.34$, $p=0.025$). Additionally, an interaction with the covariate (time*carcass; $F_{1,94}$=4.79, p=0.031) revealed a pattern of increasing invertebrate diversity in streams with carcass additions (Figure 3.3b).

Neither main nor interactive effects of the study significantly (all p>0.05) affected percent functional group (shredder, scraper, gathering collector, filtering collector or predator) or shredder (biomass, richness or diversity).

Fall 2002

Leaf pack invertebrate biomass did not differ significantly between streams with and without carcass additions, between stream reaches with open or closed canopies, or among experimental treatments (C, N, L and L+N). There were interactions with the covariate. Leaf pack invertebrate biomass decreased through time in streams with carcass additions, and increased through time in streams without carcass additions (time*carcass; $F_{1,153}$=4.0, p=0.0472) (Figure 3.4a). Furthermore, leaf pack invertebrate biomass decreased through time in stream reaches with a closed canopy (time*canopy; $F_{1,150}$=6.67, p=0.01) (Figure 3.4b). Neither main nor interactive effects of the study significantly affected invertebrate richness (all p>0.05). Invertebrate diversity did not differ between streams with and without carcass additions, between stream reaches with open or closed canopies, or among experimental treatments (C, N, L, L+N). However, there were interactions with the covariate. Invertebrate diversity decreased through time in streams without carcass additions and increased through time in streams with carcass additions (time*carcass; $F_{1,158}$=4.71, p=0.03) (Figure 3.5a).

Furthermore, invertebrate diversity increased through time in all but the (L) treatment (time*carcass*canopy; $F_{1,157}$=7.19, p=0.008) (Figure 3.5b).

Although not significantly different ($F_{1,47}$=3.82, p=0.0565), mean shredder biomass was smallest in the (C) treatment and largest in the (L) treatment (Figure 3.6). Shredder richness was not significantly different between streams with and without carcass additions, between open and closed canopies, or among experimental treatments (C, N, L, L+N). Additionally, shredder diversity was significantly greater ($F_{1,159}$=5.77, p=0.0174) in closed than in open canopy reaches.

DISCUSSION

Although red alder leaf litter pack mass loss occurred faster in fall than in the spring within our experimental study reaches, lack of seasonal replicates prevents formal statistical comparison. There was a larger amount of invertebrate biomass in fall leaf litter packs relative to spring, but the opposite was true of shredder biomass. Perhaps, the greater mass loss in the fall was due to physical abrasion by scrapers, such as *Juga* which dominated the invertebrate biomass, feeding on surface biofilm, as has been reported for some marine gastropods (Proffitt and Devlin 2005). Furthermore, leaf litter pack mass loss is likely the result of greater shredder biomass. Although not statistically significant, faster leaf litter pack mass loss in the spring is due to the dominance of the shredder *Heteroplectron* in streams with carcass additions as well as in the fall in the open canopy no carcass (L) treatment. Shredder biomass and taxa richness is important to leaf litter mass loss rates (Jonsson et al. 2001). The greater shredder biomass on leaf packs in open canopy reaches may have been the result of lack of available natural leaf litter and therefore a concentration of shredder individuals on the leaf packs in the vicinity. An important aspect to note is that leaf mass loss rates were increased in all experimental treatments relative to control stream reaches, which may affect overall stream food web dynamics.

Leaf pack invertebrate richness was not affected by experimental treatments in this study, as has been previously reported in studies investigating logging effects on leaf processing (Kreutzweiser et al. 2008), perhaps a result of our low-impact approach to canopy removal. However, leaf pack invertebrate diversity was affected during both seasons of study, being overall lower in streams with carcass additions or changing through time. Invertebrate diversity on experimental leaf packs was primarily affected by the overwhelming presence of *Juga*.

CONCLUSIONS

Experimental augmentation of light, nutrients, and both light and nutrients reaching the stream of the study reaches resulted in greater red alder leaf pack mass loss in both late spring and early fall 2002. Although canopy removal in addition to carcass additions had a positive effect on benthic invertebrate biomass of cobble habitats, it's effects on red alder leaf litter mass loss and invertebrate community structure should also be taken into consideration. Further investigation of this data is needed.

Table 3.1. Study stream characteristics. * Denotes streams with carcass addition.

Stream	Catchment Area (km^2) / Basin	Latitude / Longitude	Open Canopy Reach	Gradient (%)	
				Open	Closed
Tectah	7.9 / Klamath	41°15'47"N / 123°57'52"W	Lower	2.9	1.7
Tarup *	4.9 / Klamath	41°27'45"N / 123°59'32"W	Upper	2.8	1.8
Little Mill	3.4 / Smith	41°52'27"N / 124°6'47"W	Lower	7.7	9.5
Peacock *	3.5 / Smith	41°50'11"N / 124°5'23"W	Lower	2.4	4.2
South Fork Rowdy *	4.9 / Smith	41°55'16"N / 124°5'23"W	Upper	5.6	5.1
Savoy	5.0 / Smith	41°54'14"N / 124°5'12"W	Lower	4.7	5.6

Table 3.2. Daily decay rates (k) of red alder leaf packs from experimental study reaches of the Smith and Klamath River basins, northern California. (C= controls, N= augmented nutrients, L= augmented light, L+N= augmented light and nutrients). *k* values with same letters are not significantly different from each other, Fishers LSD (*p* =0.05).

	Spring			Fall		
	k		R^2	k		R^2
Controls (C)	0.0195		0.81	0.0443	b	0.75
Nutrient (N)	0.0308		0.63	0.0595	ab	0.74
Light (L)	0.0326		0.64	0.0818	a	0.79
Light and Nutrient (L+N)	0.0303		0.70	0.0520	ab	0.61
Carcass	0.0302	a	0.61			
No Carcass	0.0245	b	0.53			

Table 3.3. Biomass (mg) and percent dominance of the most abundant taxa: nutrient treatment (carcass, no carcass) by time (Day 15, Day 23, Day 30), from Spring experimental red alder (*Alnus rubra*) leaf packs.

	Carcass			No Carcass		
	Day 15	Day 23	Day 30	Day 15	Day 23	Day 30
Biomass (mg)						
Juga	4038	1479	980	1357	1313	1286
Calineuria	671				846	876
Heteroplectron	564	2431	1169	476		694
Paraleptophlebia		936	498	434		
Hydatophylax					775	
% Dominance						
Juga	62	21	23	35	26	25
Calineuria	10				17	17
Heteroplectron	9	35	27	12		14
Paraleptophlebia		13	12	11		
Hydatophylax					15	

Table 3.4. Biomass (mg) and percent dominance of the most abundant taxa in (C) and (L) treatments by time (Day 15, Day 23, Day 30) from fall experimental red alder (*Alnus rubra*) leaf packs.

	Control			Light		
	Day 15	Day 23	Day 30	Day 15	Day 23	Day 30
Biomass (mg)						
Juga		1669	1818	1538	2935	10055
Paraleptophlebia	141		310	270		219
Heteroplectron	139	163	301	605	915	323
Calineuria	150					
Psychoglypha		640				
Hydatophylax					140	
% Dominance						
Juga		56	54	50	64	90
Paraleptophlebia	19		9	9		2
Heteroplectron	19	5	9	20	20	3
Calineuria	21					
Psychoglypha		22				
Hydatophylax					3	

Table 3.5 Checklist of taxa collected from experimental red alder (Alnus rubra) leaf packs from study reaches of the Smith and Klamath River basins of northern California. (a- Spring, b- Fall, Sc- scraper, Gc- gathering collector, Fc- filtering collector, Sh- shredder, Pi- piercer, Pr- predator)

Order	Family	Genus			FFG
Ephemeroptera					
	Ameletidae	*Ameletus*	a	b	Gc
	Baetidae	*Baetis*	a	b	Gc
	Ephemerellidae	*Attenella*	a	b	Gc
		Caudatella		b	Gc
		Drunella	a	b	Sc
		Ephemerella	a		Gc
		Serratella	a	b	Gc
		Timpanoga		b	Gc
	Heptageniidae	*Cinygma*	a	b	Sc
		Cinygmula	a	b	Gc
		Epeorus		b	Gc
		Ironodes	a	b	Sc
		Nixe		b	Sc
		Rhithrogena		b	Gc
	Leptophlebiidae	*Paraleptophlebia*	a	b	Gc
Plecoptera					
	Capniidae			b	Sh
	Chloroperlidae	*Kathroperla*	a	b	Gc
		Suwallia	a	b	Pr

Table 5 (cont.)

		Sweltsa	a	b	Pr
	Leuctridae	*Despaxia*	a	b	Sh
		Moselia		b	Sh
		Perlomyia	a	b	Sh
	Nemouridae	*Malenka*	a	b	Sh
		Zapada	a	b	Sh
	Peltoperlidae	*Sierraperla*	a		Sh
		Soliperla	a	b	Sh
	Perlidae	*Calineuria*	a	b	Pr
		Claassenia		b	Pr
		Hesperoperla	a	b	Pr
		Isoperla	a	b	Pr
		Osobenus	a	b	Pr
	Pteronarcyidae	*Pteronarcys*	a	b	Sh
Odonata					
	Gomphidae		a		Pr
Megaloptera					
	Sialidae	*Sialis*	a		Pr
Trichoptera					
	Apatanidae	*Apatania*		b	Sc
	Brachycentridae	*Brachycentrus*	a		Fc
		Micrasema	a	b	Sh

Table 5 (cont.)

	Calamoceratidae	*Heteroplectron*	a	b	Sh
	Hydropsychidae	*Hydropsyche*	a	b	Fc
	Hydroptilidae	*Hydroptila*		b	Pi
	Lepidostomatidae	*Lepidostoma*	a	b	Sh
	Limnephilidae	*Allocosmoecus*	a		Sc
		Chyranda	a		Sh
		Cryptochia		b	Sh
		Dicosmoecus	a	b	Sc
		Ecclisomyia	a	b	Gc
		Homophylax	a	b	Sh
		Hydatophylax	a	b	Sh
		Philocasca	a	b	Sh
		Psychoglypha	a	b	Gc
	Polycentropodidae	*Polycentropus*	a	b	Pr
	Rhyacophilidae	*Rhyacophila*	a	b	Pr
	Sericostomatidae	*Gumaga*	a	b	Sh
	Uenoidae	*Neophylax*	a	b	Sc
		Neothremma	a		Sc
Coleoptera					
	Dytiscidae	*Hydaticus*		b	Pr
		Hydrovatus		b	Pr
		Oreodytes	a	b	Pr

Table 5 (cont.)

	Elmidae	*Ampumixis*	a	b	Gc
		Lara	a	b	Sh
		Narpus	a	b	Gc
		Optioservus	a	b	Sc
		Rhizelmis		b	Sc
	Hydrochidae	*Hydrochus*	a		Sh
	Psephenidae	*Acneus*	a	b	Sc
Diptera					
	Ceratopogonidae		a	b	Pr
	Chironomidae	*Orthocladinae*	a	b	Gc
		Tanypodinae	a	b	Pr
		Tanytarsini	a	b	Fc
	Dixidae	*Dixa*	a	b	Gc
	Empididae	*Chelifera*	a	b	Pr
		Clinocera	a		Pr
		Hemerodromia	a	b	Pr
		Oreogeton	a		Pr
	Pelecorhynchidae	*Glutops*	a		Pr
	Psychodidae	*Pericoma*	a	b	Gc
	Simuliidae	*Simulium*	a	b	Fc
	Tipulidae	*Dicranota*	a	b	Pr
		Hexatoma	a	b	Pr

Table 5 (cont.)

		Pedicia	a	b	Pr
	Non-Insects				
Collembola			a		Gc
Turbellaria			a	b	Pr
Oligochaeta			a	b	Gc
Hydracarina			a	b	Pr
Copepoda			a	b	Fc
Ostracoda			a	b	Gc
Amphipoda			a	b	Sh
	Gammaridae				
Gastropodae					
	Pleuroceridae	*Juga*	a	b	Sc

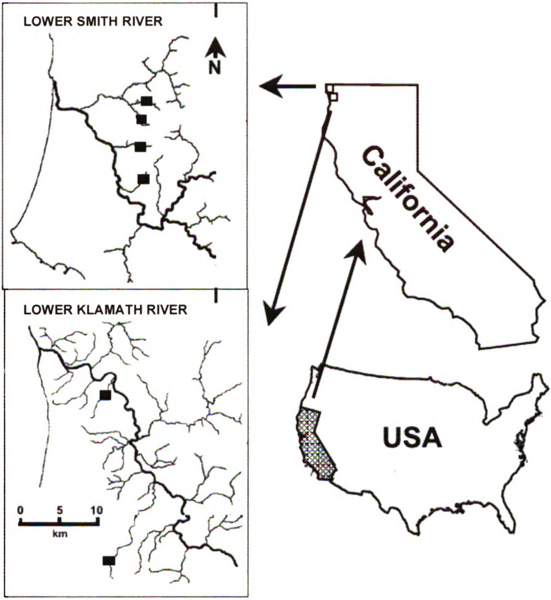

Figure 3.1. Study reaches within the lower Smith and Klamath River Basins of northern California (after Wilzbach et al. 2005).

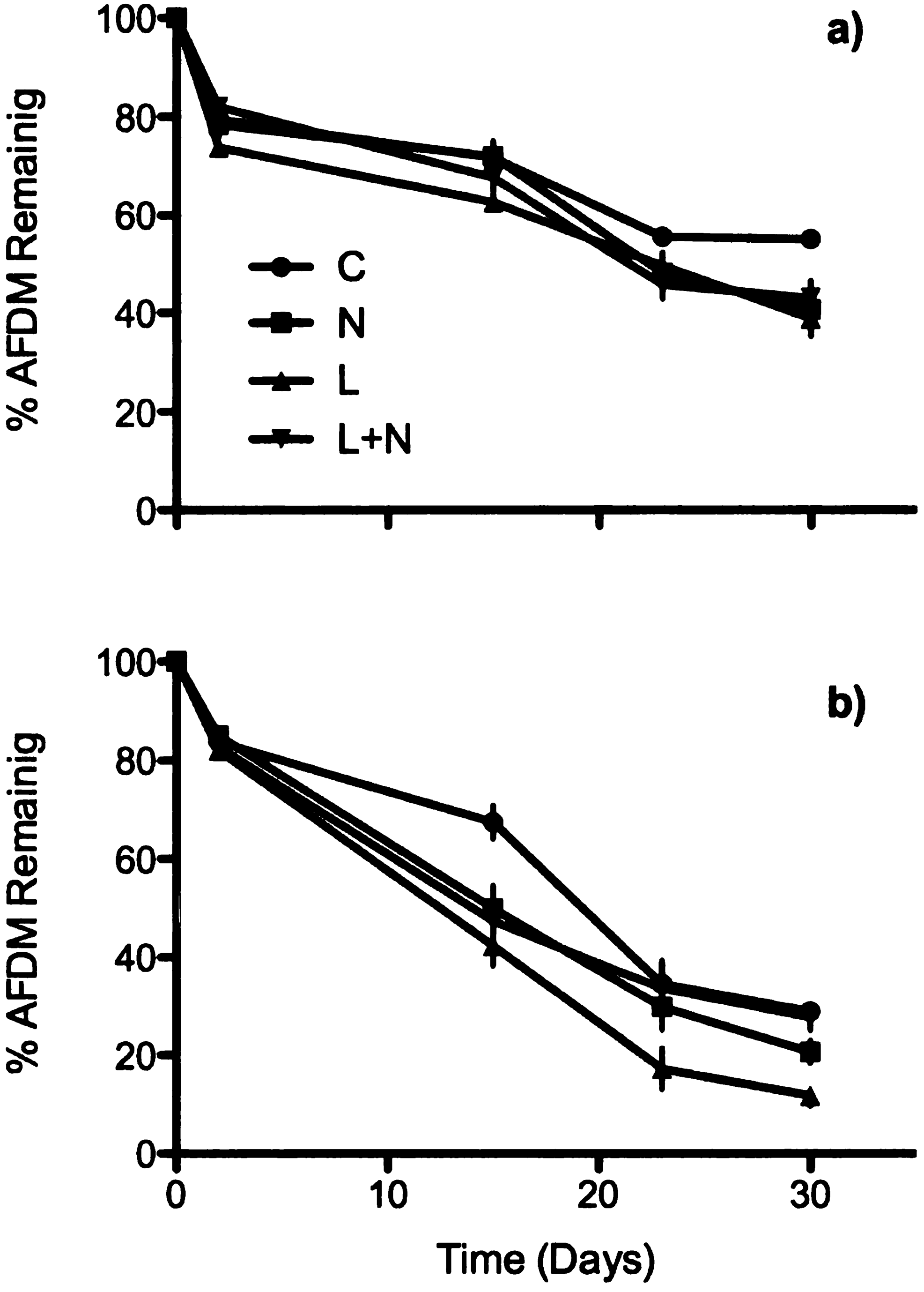

Figure 3.2. Percent AFDM experimental red alder leaf pack remaining (+/- 1 S.E.) at day (2, 15, 23, and 30) in study reaches of the Smith and Klamath River basins during a) spring and b) fall.

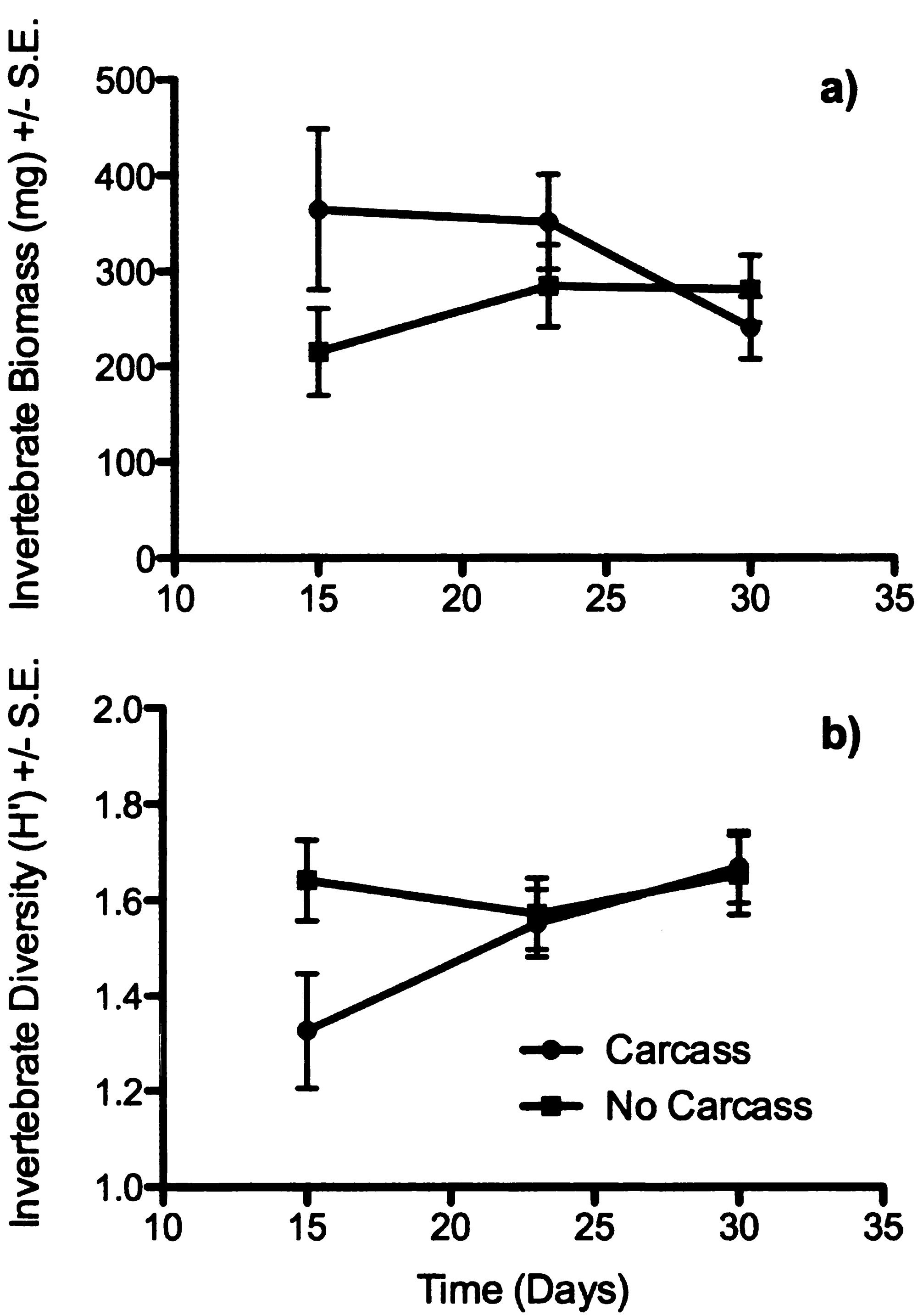

Figure 3.3. Spring a) dry mass and b) Shannon-Weiner diversity (H') (+/- 1 S.E.) of macroinvertebrates on experimental red alder leaf packs at days (15, 23 and 30) from streams of the Smith and Klamath River basins.

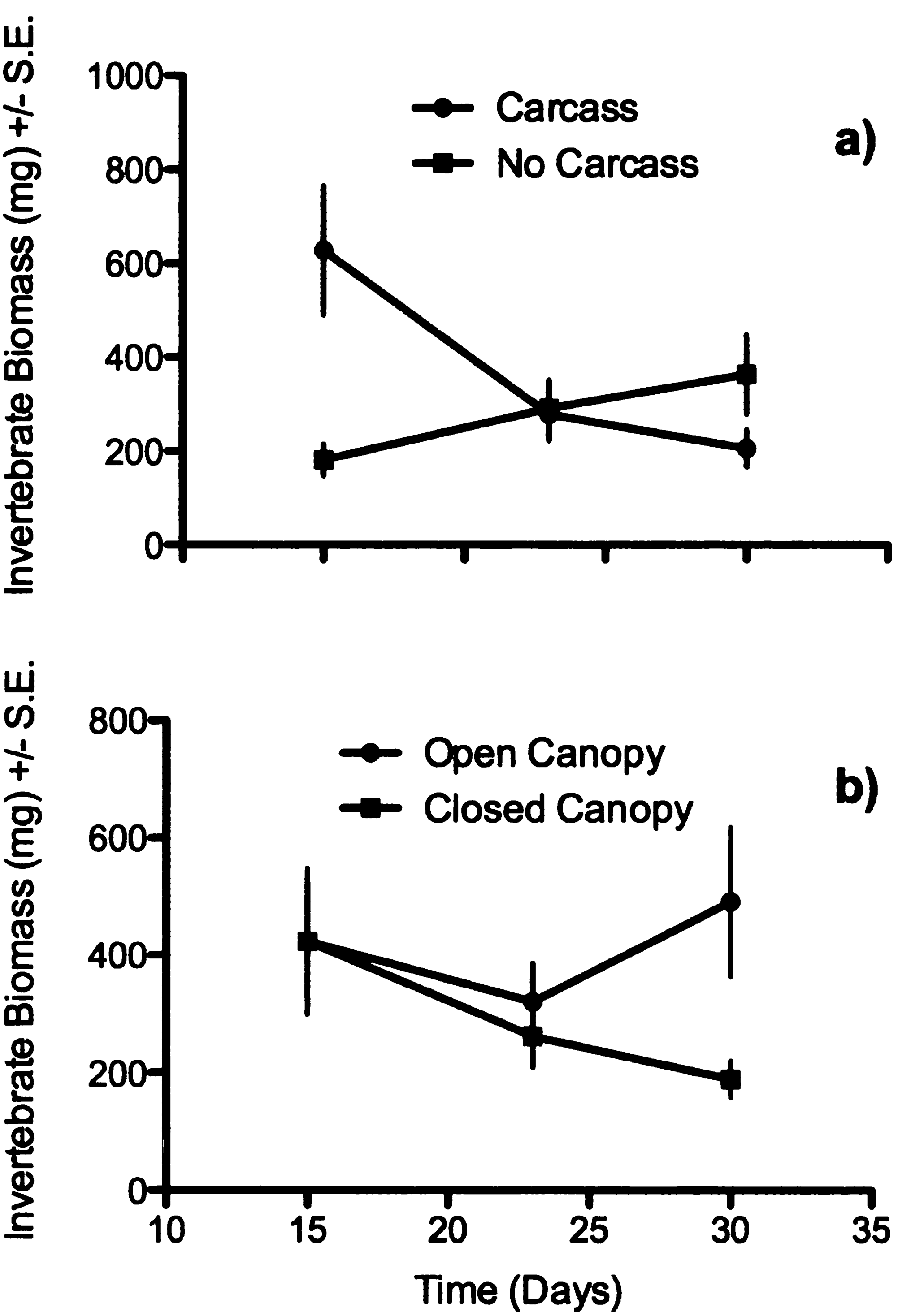

Figure 3.4. Fall dry mass (+/- 1 S.E.) of invertebrates on experimental red alder leaf packs at days (15, 23 and 30) from a) streams and b) study reaches of the Smith and Klamath River basins.

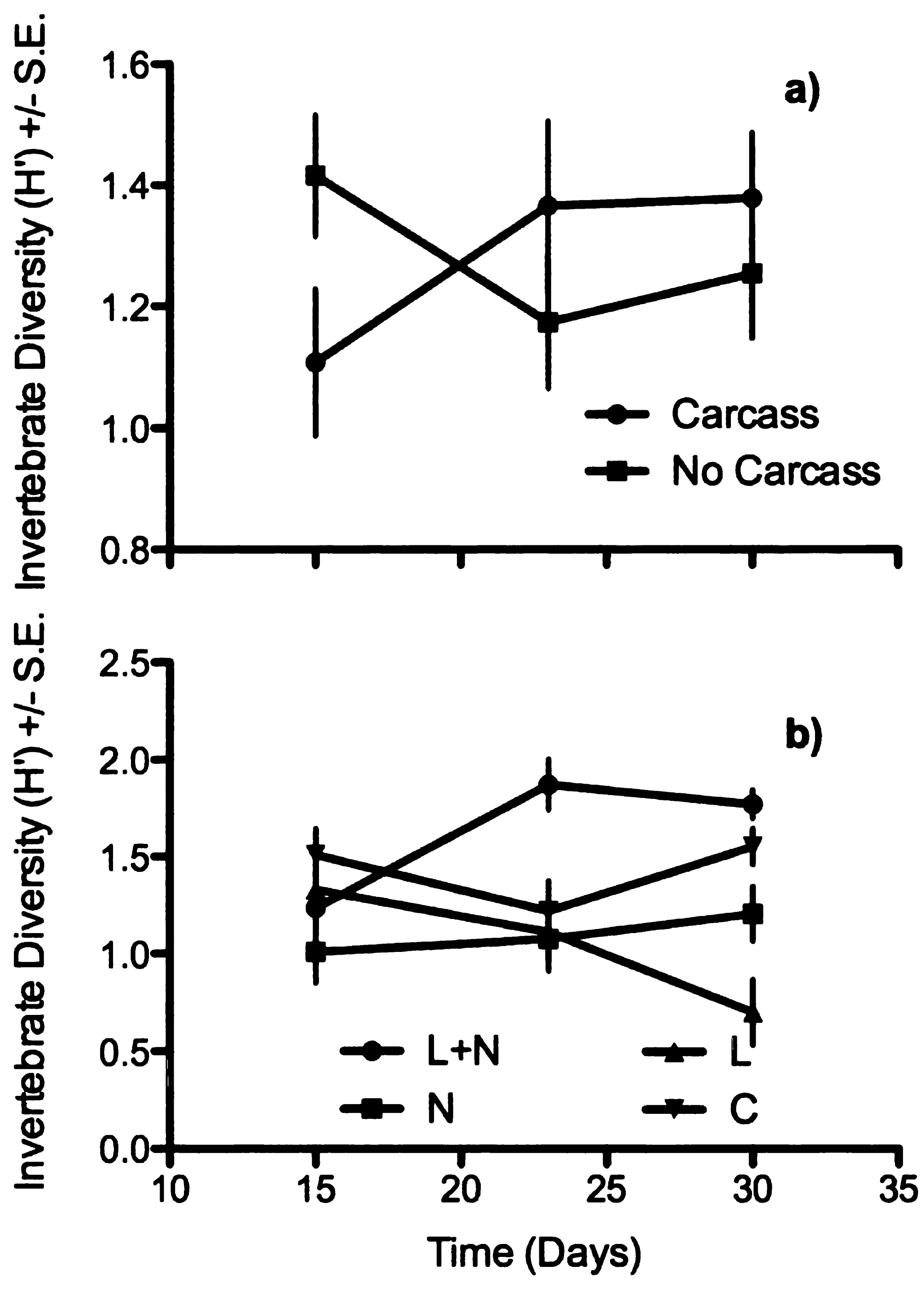

Figure 3.5. Fall Shannon-Weiner diversity (H') (+/- 1 S.E.) of macroinvertebrates on experimental red alder leaf packs at days (15, 23 and 30) from a) streams and b) treatment study reaches of the Smith and Klamath River basins.

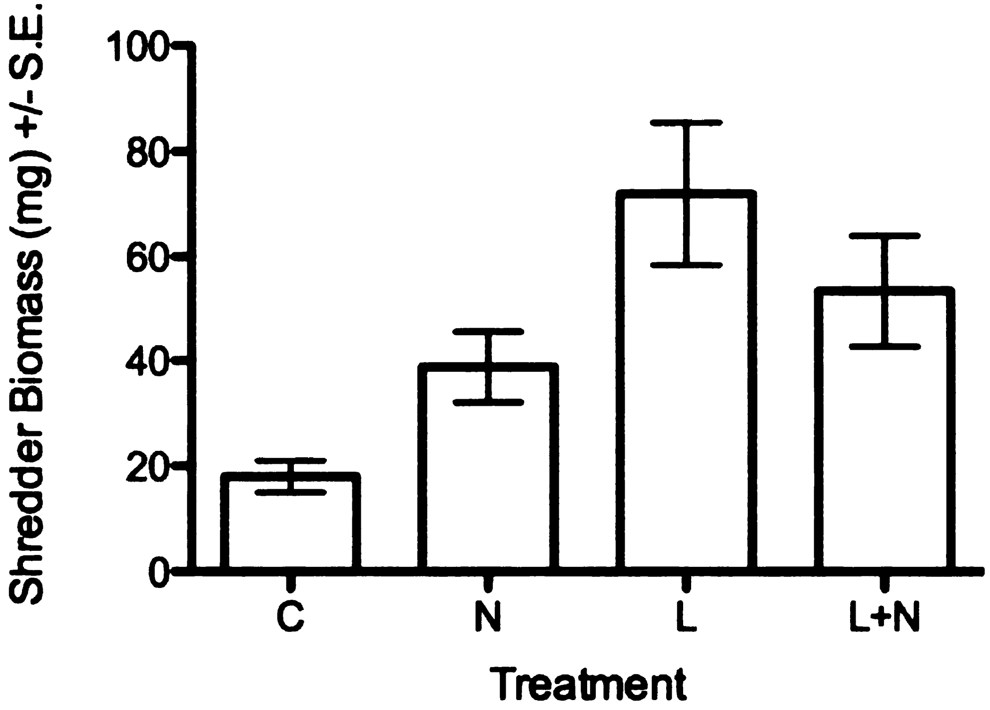

Figure 3.6. Fall shredder biomass (+/- 1 S.E.) on experimental red alder leaf packs among study treatments in the Smith and Klamath River basins.

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Literature Cited

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APPENDIX

Appendix 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2009-01

Title of thesis or dissertation (or other research projects):

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name(s) (typed)
Osvaldo Hernandez

Date 30. April 2009

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:
Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

Appendix 1.1

Voucher Specimen Data

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		Number of:							
Species or other taxon	Label data for specimens collected or used and deposited	Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
EPHEMEROPTERA									
Ameletidae									
Ameletus *sp.*	Smith River X 2001		1						MSU
Baetidae									
Acentrella *sp.*	Smith River III 2002		1						MSU
Baetis *sp.*	Smith River X 2001		1						MSU
Ephemerellidae									
Attenella *sp.*	Smith River X 2003		1						MSU
Caudatella *sp.*	Smith River X 2001		1						MSU
Drunella *sp.*	Smith River X 2001		1						MSU
Ephemerella *sp.*	Smith River V 2002		1						MSU
Serratella *sp.*	Smith River V 2002		1						MSU
Timpanoga *sp.*	Smith River X 2001		1						MSU
Heptageniidae									
Cinygma *sp.*	Klamath River V 2002		1						MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)
Osvaldo Hernandez

Date 30, April 2009

Voucher No. 2009-01

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Curator   Date 12 AUG 2009

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Voucher Specimen Data

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Species or other taxon		Label data for specimens collected or used and deposited		Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
		USA, CA, Del Norte & Humboldt Co.									
Cinygmula	sp.	Smith River	X 2001		1						MSU
Epeorus	sp.	Smith River	X 2001		1						MSU
Heptagenia	sp.	Smith River	X 2003		1						MSU
Ironodes	sp.	Smith River	X 2001		1						MSU
Nixe	sp.	Smith River	VIII 2002		1						MSU
Rithrogena	sp.	Smith River	X 2001		1						MSU
Leptophlebiidae											
Paraleptophlebia	sp.	Smith River	X 2001		1						MSU
PLECOPTERA											
Capniidae		Smith River	X 2001		1						MSU
Chloroperlidae											
Kathroperla	sp.	Klamath River	V 2002		1						MSU
Plumiperla	sp.	Smith River	X 2001		1						MSU
Suwallia	sp.	Smith River	V 2002		1						MSU
Sweltza	sp.	Smith River	X 2001		1						MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Osvaldo Hernandez

Date 30, April 2009

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Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
Leuctridae									
Despaxia sp.	Smith River VIII 2002		1						MSU
Moselia sp.	Klamath River X 2001		1						MSU
Perlomyia sp.	Smith River X 2001		1						MSU
Nemouridae									
Amphinemoura sp.	Smith River X 2003		1						MSU
Malenka sp.	Smith River X 2001		1						MSU
Nemoura sp.	Smith River X 2001		1						MSU
Zapada sp.	Smith River X 2001		1						MSU
Peltoperlidae									
Sierraperla sp.	Smith River V 2002		1						MSU
Soliperla sp.	Smith River VIII 2002		1						MSU
Perlidae									
Calineuria sp.	Smith River VII 2002		1						MSU
Claassenia sp.	Smith River X 2001		1						MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
Doroneuria *sp.*	Smith River X 2001		1						MSU
Hesperoperla *sp.*	Smith River VIII 2002		1						MSU
Perlodidae									
Isoperla *sp.*	Smith River V 2002		1						MSU
Osobenus *sp.*	Klamath River III 2002		1						MSU
Pteronarcyidae									
Pteronarcys *sp.*	Smith River VII 2002		1						MSU
ODONATA									
Gomphidae	Klamath River X 2003		1						MSU
MEGALOPTERA									
Corydalidae									
Orohermes *sp.*	Smith River X 2001		1						MSU
Sialidae									
Sialis *sp.*	Klamath River V 2002		1						MSU
TRICHOPTERA									

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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		Number of:							
Species or other taxon	Label data for specimens collected or used and deposited	Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
Apatanidae									
Apatania *sp.*	Klamath River X 2003		1						MSU
Brachycentridae									
Brachycentrus *sp.*	Smith River X 2001		1						MSU
Micrasema *sp.*	Smith River VIII 2002		1						MSU
Calamoceratidae									
Heteroplectron *sp.*	Klamath River VII 2002		1						MSU
Glossosomatidae									
Glossosoma *sp.*	Smith River X 2001		1						MSU
Hydropsychidae									
Ceratopsyche *sp.*	Smith River X 2001		1						MSU
Hydropsyche *sp.*	Smith River X 2001		1						MSU
Parapsyche *sp.*	Smith River VII 2002		1						MSU
Hydroptilidae	Smith River X 2001								
Hydroptila *sp.*	Smith River VIII 2002		1						MSU

(Use additional sheets if necessary)

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		Number of:							
Species or other taxon	Label data for specimens collected or used and deposited	Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
Ochrotrichia *sp.*	Smith River VII 2003		1						MSU
Lepidostomatidae									
Lepidostoma *sp.*	Smith River X 2001		1						MSU
Leptoceridae	Smith River X 2003		1						MSU
Limnephilidae									
Allocosmoecus *sp.*	Klamath River V 2002		1						MSU
Chyranda *sp.*	Smith River V 2002		1						MSU
Cryptochia *sp.*	Smith River X 2003		1						MSU
Dicosmoecus *sp.*	Smith River V 2002		1						MSU
Ecclisomyia *sp.*	Smith River V 2002		1						MSU
Homophylax *sp.*	Klamath River VIII 2002		1						MSU
Hydatophylax *sp.*	Smith River V 2002		1						MSU
Philocasca *sp.*	Smith River VIII 2002		1						MSU
Psychoglypha *sp.*	Smith River VIII 2002		1						MSU
Philopotamidae									

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Investigator's Name(s) (typed)

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Species or other taxon	Label data for specimens collected or used and deposited		Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.									
Wormaldia *sp.*	Smith River	X 2003		1						MSU
Polycentropodidae										
Polycentropus *sp.*	Smith River	VIII 2002		1						MSU
Rhyacophilidae										
Rhyacophila *sp.*	Smith River	X 2001		1						MSU
Sericostomatidae										
Gumaga sp.	Smith River	V 2002		1						MSU
Uenoidae										
Neophylax *sp.*	Klamath River	VII 2002		1						MSU
Neothremma *sp.*	Smith River	III 2002		1						MSU
HYMENOPTERA										
Scelionidae	Smith River	X 2003		1						MSU
COLEOPTERA										
Dytiscidae										
Hydaticus *sp.*	Smith River	VIII 2002		1						MSU

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Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
Hydrovatus sp.	Smith River VIII 2002		1			1			MSU
Laccophilus sp.	Smith River X 2003		1						MSU
Oreodytes sp.	Smith River VIII 2002		1						MSU
Rhantus sp.	Smith River X 2001		1						MSU
Elmidae									
Ampumixis sp.	Smith River X 2001		1						MSU
Cleptelmis sp.	Klamath River X 2003		1						MSU
Dubiraphia sp.	Klamath River X 2003		1						MSU
Lara sp.	Smith River VIII 2002		1						MSU
Narpus sp.	Smith River VII 2002		1			2			MSU
Optioservus sp.	Smith River VIII 2002		1						MSU
Rhizelmis sp.	Smith River VII 2002		1			1			MSU
Zaitzeviavia sp.	Smith River X 2003		1			1			MSU

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		Number of:							
Species or other taxon	Label data for specimens collected or used and deposited	Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
Hydrochidae									
Hydrochus *sp.*	Smith River X 2003					1			MSU
Hydrophilidae									
Paracymus *sp.*	Smith River VII 2003					1			MSU
Psephenidae									
Acneus *sp.*	Smith River X 2001		1						MSU
DIPTERA									
Ceratopogonidae	Smith River X 2001		1						
Atrichopogon *sp.*	Smith River VIII 2003		1						MSU
Forcipomyinae	Smith River VII 2002		1						MSU
Chironomidae									
Orthocladinae	Smith River X 2001		1						MSU
Tanypodinae	Smith River V 2002		1						MSU
Tanytarsini	Smith River X 2001		1						MSU
Dixidae									

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Species or other taxon	Label data for specimens collected or used and deposited	Number of:							
		Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
Dixa sp.	Smith River VIII 2002		1						MSU
Empididae	Smith River V 2002		1						
Chelifera sp.	Smith River VIII 2002		1						MSU
Clinocera sp.	Klamath River V 2002		1						MSU
Hemerodromia sp.	Smith River VIII 2002		1						MSU
Oreogeton sp.	Klamath River V 2002		1						MSU
Pelecorhynchidae									
Glutops sp.	Smith River VII 2002		1						MSU
Psychodidae									
Maurina sp.	Smith River X 2003		1						MSU
Pericoma sp.	Smith River VIII 2002		1						MSU
Simuliidae									
Simulium sp.	Klamath River V 2002		1						MSU
Stratiomyidae									
Nemotelus sp.	Klamath River VII 2002		1						MSU

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Species or other taxon	Label data for specimens collected or used and deposited	Number of:							
		Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
Thaumaleidae	Smith River VII 2002		1						MSU
Tipulidae									
Antocha sp.	Smith River X 2003		1						MSU
Dicranota sp.	Klamath River X 2003		1						MSU
Hexatoma sp.	Klamath River X 2003		1						MSU
Pedicia sp.	Klamath River X 2003		1						MSU
COLLEMBOLA									
Entomobyriidae	Smith River X 2001		1						MSU
Sminthuridae	Smith River X 2001		1						MSU
NON-INSECTA									
HIRUNDINEA									
Glossiphoniidae	Smith River X 2001		1						MSU
TURBELLARIA	Smith River X 2003		1						MSU
OLIGOCHAETA	Smith River X 2003		1						MSU

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Investigator's Name(s) (typed)

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		Number of:							
Species or other taxon	Label data for specimens collected or used and deposited	Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, CA, Del Norte & Humboldt Co.								
HYDRACARINA	Klamath River X 2003		1						
COPEPODA									
Cyclopoida	Smith River X 2001		1						MSU
OSTRACODA	Smith River X 2001		1						MSU
AMPHIPODA									
Gammaridae	Smith River V 2002		1						MSU
GASTROPODA									
Pleuroceridae									
Juga sp.	Klamath River X 2003		1						MSU

(Use additional sheets if necessary)

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