

AN ABSTRACT OF THE THESIS OF

Jennifer B.S. Walsh for the degree of Master of Science in Forest Science presented on February 2, 1996. Title: Effects of Streamside Riparian Forest Management on Ephemeroptera and Trichoptera Community Structure in Four Western Oregon Streams.

Abstract approved: _____

Michael Newton

In order to restore conifers in hardwood dominated riparian forests 25% of the experimental reach forests alongside four streams in western Oregon was clearcut. Clearcutting removed 400 m without residual buffers from a 1600-m streamside forest reach in patchcuts spanning 100 and 200 meters. To assess the cumulative and direct effects of the 25% removal on the biotic stream community, Ephemeroptera (mayflies) nymphs and Trichoptera (caddisflies) larvae were sampled on each stream under the buffered and exposed reaches. Samples were collected using a Surber sampler at four locations during the summers of 1993 and 1994, and identified by genus and functional feeding group. Absolute and relative abundance of genera and functional feeding groups and the Shannon-Wiener diversity index were calculated to compare community responses between sample sites. Insects from three untreated reference streams were also analyzed to compare natural versus treated community variability.

Spatially, genera generally increased in abundance midway through the 25% clearcut reach. Specific genera, including *Baetis*, *Glossosoma*, and *Micrasema*, increased in the exposed clearcut. Collector-gatherers and scrapers also increased in the exposed reach and collector-filterers peaked below the 200-m patchcut. Shredders and predators did not show significant differences either year. Temporally, more individual taxa as well as the diversity index increased the second year after treatments. However, reference stream data indicated that even on untreated streams there is background variability among congeners at different sampling points and in different sampling years. Yearly differences in diversity were likely within the range of normal community variability. The responses of treated stream genera, however, greatly exceeded the few changes in

population observed on the reference streams. Therefore, increases and/or decreases in abundance both years may be assumed to be a response to localized harvesting treatment effects. Treatment effects, however, occurred primarily in mid-reach. Genera increases spanned short longitudinal distances and most taxa and functional feeding groups had returned to reference levels at the bottom of the 1600-m reach. The total 25% harvest removal did not appear to influence the mayfly and caddisfly absolute and relative abundance, functional feeding groups, or diversity on these four western Oregon streams other than locally.

Master of Science thesis of Jennifer B.S. Walsh presented on February 2, 1996

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Effects of Streamside Riparian Forest Management on Ephemeroptera and Trichoptera
Community Structure in Four Western Oregon Streams

by

Jennifer B.S. Walsh

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This thesis is dedicated to the thousands of insects who gave their lives for its conclusions.

May your streams always run clear.

PREFACE

Forests and fish are intrinsically linked to the Pacific Northwest ecology, economy, culture, and spirit. The fish of greatest economic and cultural importance, the ocean-going or anadromous salmon, hatch in hundreds of the region's small forest streams, spend their adult life battling oceanic predators (including human), currents, and pollution, and then return to the stream of their birth, spawn and die. A myriad of challenges and hazards confront the salmon throughout its migration; however, the quality and certainty of the forested streams where they are born and die is crucial.

Historically, logging in the Pacific Northwest forest has used streams and adjacent lands as floodgates to transport timber to mills and as convenient thoroughfares for railroads and roads. Streams were biologically ignored as logging operations left them exposed to increased solar radiation, water temperature, biological oxygen demand from fallen slash, and siltation from poorly constructed logging roads and harvest practices. Stream protection became an Oregon state law in 1972. In the last thirty years, a steady decrease in the number of salmon returning to spawn has raised the alarm of biologists and foresters alike. Scientists realized that the vegetation bordering and shading streams is critical to healthy salmon habitat because it adds nutrients, modifies stream temperatures, filters sediment and debris from upslope sources, and contributes structure to form rearing pools and high flow refugia (Meehan et al. 1977). Foresters have attempted to protect streams from timber harvest and to improve salmon spawning and rearing habitat by leaving streamside buffer strips, restoring streamside vegetation, removing logging debris, and installing stream structure (Koski et al. 1984, Barton et al. 1985, House & Boehne 1987, Sullivan et al. 1987, Beschta et al. 1991, Bisson et al. 1992).

In any integrated study of riparian forest silviculture, consideration for fish and other stream biota must be given. Measurement of physical and/or chemical parameters alone do not directly reflect potential biological responses. As in the case of this study, a detailed survey of fish response to treatments was not possible. However, fish are predators and therefore should be affected by changes in the prey they depend upon

(Murphy & Meehan 1991). To form an educated guess as to how fish might respond to forest management operations, we stepped down the food chain to assess changes in one of fishes' primary food sources: aquatic insects. Fish intensively feed on aquatic invertebrates as both nymphs and adults. Of 67 families of freshwater fishes, 42 families feed on aquatic insects and of 180 Canadian fish species, 144 feed on aquatic invertebrates (Healey 1984). Immature benthic invertebrates live on stream substrates but actively and passively enter the water column and drift to downstream substrates, refugia, and food sources. During drift, insects are especially prone to predation by fish. Fish also consume insects found in pools, eddies, backwaters, and the downstream edges of riffles (Healey 1984, De Moor 1991). Food of the youngest salmon fry reflect the total composition of bottom insect fauna more accurately than older individuals, who are more selective (Bergersen 1989). Bergersen (1989) observed that only 2-4 species dominate the stomach contents of a fish at any one time. Therefore, although fish definitely consume insects, there is not a direct correlation between total benthic community structure and fish food supply.

However, while waiting to serve as fish food, aquatic insects also perform critical ecological functions within the stream's energy and nutrient processes (Benke 1984). Here, benthic community structure *is* important because individual species perform various functions at various times and in various habitats. In fact, it has been said that "the structure of the benthic macroinvertebrate community reflects the state of the entire [stream] ecosystem." (Reice & Wohlenberg 1993). Aquatic insects convert terrestrial detritus and energy stored in aquatic vegetation into forms accessible by secondary consumers and other insect processors. In the process, they release nutrients into the water column, helping to enrich nutrient-poor headwater creeks on their way downstream. Two common orders of aquatic insects, Trichoptera (caddisflies) and Ephemeroptera (mayflies), serve both as abundant sources of primary and secondary fish food and as critical consumers and processors of stream nutrients (Needham et al. 1935). By measuring changes within caddisfly and mayfly community structure, one may infer potential alterations to stream nutrient dynamics and consequences to the food supply of secondary consumers such as fish. Forest management strategies that significantly alter

the dynamics of the aquatic insect community have the potential to severely alter the quality of the stream for salmon habitat. Examining one of the connections that links salmon health to forest streams may provide insight into methods of maintaining and even improving salmon habitat and stream health through sound forest management.

Effects of Streamside Riparian Forest Management on Ephemeroptera and Trichoptera Community Structure in Four Western Oregon Streams

1. INTRODUCTION

Bountiful salmon and majestic forests have long defined the Pacific Northwest to others. The seemingly unending supply of these organisms made each a valuable resource to the rapidly growing human population. Through the years, timber harvesting and other pressures from increasing human population has stressed freshwater aquatic systems that salmon depend upon for rearing their young and reproducing the next generation. The primary silviculture technique in the Pacific Northwest has been clearcutting since the 1880's (Murphy & Meehan 1991). Only since the 1950's has the large-scale removal of trees also been accompanied by replanting with either conifer seeds or small seedlings. In the 1960's, the process of forest regeneration became a science in itself in an attempt to maintain the supply of high quality Douglas-fir. This science is now contributing to research on the restoration of vegetation necessary to healthy salmon habitat.

Along with the scientific and management advancements in forest regeneration, scientists began to observe that harvesting to the edge of streams and removing the canopy and vegetation shading them caused increased stream temperatures, increased sediment delivery, decreased bank stability, and increased autochthonous (produced within the system) production. In attempts to protect salmon habitat, scientists designed buffer strips to lie between upslope clearcuts and stream channels. The residual trees and understory vegetation shade the stream, prevent drastic micro-climate fluctuations, and continue to function as a source of allochthonous (produced outside the system) energy. The width of these streamside forests has varied with policy over the years. Most scientists and policy makers agree, however, that buffer vegetation includes at least a portion of the riparian area.

There is evidence that the buffer strips designed to protect streams combined with the effects of nearby logging are significantly changing the successional course of

streamside terrestrial vegetation. Soil disturbance from high flows and mass movements historically favored red alder (*Alnus rubra* Bong.) regeneration in small, localized pockets immediately next to stream channels. Today, however, the soil disturbance created by clearcutting also offers favorable sites for red alder colonization, allowing it to invade forests farther upslope. These hardwoods grow rapidly on well-scarified, moist, well-lit, deep alluvial soils and by age ten are prolific seed producers and dispersers (Carlton 1988, Froyd 1993). They have a short life span of approximately 50-80 years and, because of the wood's low concentrations of fungitoxic extractives, high nitrogen content, and low fiber content, decay rapidly.

The combination of a deciduous red alder overstory and greater edge area along narrow riparian buffer strips favors the growth of salmonberry (*Rubus spectabilis* Pursh.) dominated understories (Froyd 1993). Salmonberry is a tenacious competitor with asexual and sexual reproduction, long-lasting viable seed, and early season growth initiation which allows it to capture light before the red alder canopy has developed (Henderson 1970, Froyd 1993). The combined effects of a red alder overstory and salmonberry understory do not permit conifer establishment because of low light levels, heavy litter fall, and high salmonberry stem densities. As a result, red alder and salmonberry appear to form a stable community which precludes natural conifer regeneration within the riparian area (Newton et al. 1968, Henderson 1970, Andrus & Froehlich 1988).

During early forest stream research, scientists observed that tree tops and stems that fell or were deposited into streams during harvesting clogged stream channels. Along with physical and chemical changes in streams that may have been reducing salmon's ability to thrive, scientists incorrectly determined that these woody inputs were blocking upstream salmon migration and removed all wood (large, small, recent, old) from many stream channels. Woody debris provides structure in stream systems lacking large boulders or rocks. Structure helps determine substrate distribution, current velocity, and detrital deposition. It also provides refugia for young salmon fry. Today, scientists recognize the value of large woody structure and are experimenting with methods of

reintroducing this component into the stream system (Bilby 1984, Bisson et al. 1987, Robison & Beschta 1990, Van Sickle & Gregory 1990).

As a result of the combined effects of stream management, harvesting, and red alder and salmonberry biology, successful natural and planted conifer regeneration occurs farther and farther from the stream bank. Because of its rapid decay rate, red alder is unable to provide structural woody inputs to the stream that will persist for more than five to ten years. Without conifer regeneration, continued sources of long lasting, large woody debris are unavailable to the stream channel to form salmonid rearing pools or to provide stable structure, nutrient retention, and refugia for fish and invertebrates during high and low flows.

Concern about the future supply of large woody debris and conifers in the stream and riparian communities stimulated researchers at the Department of Forest Science at Oregon State University, working with the CRAFTS (Coordinated Research on Alternative Forestry Treatment and Systems) cooperative, to propose a riparian silviculture study that would assess the feasibility of restoring conifers to hardwood dominated riparian zones. Integration was enhanced by the cooperation and input of the Oregon State Department of Forest Engineering and the adaptive Coastal Oregon Productivity Enhancement Program (COPE). Forest engineers monitored and assessed riparian tree removal and stream debris placement with production and cost studies (see Kellog et al. 1993). COPE scientists recorded stream temperature and climate conditions and assessed the stability and movement of large-woody debris inputs. Forest scientists designed the conifer restoration study and planted and monitored conifer growth. The researchers determined that successful reintroduction of conifers would occur most rapidly in clearcut-like conditions. However, because large streamside openings in the riparian canopy have been shown to increase stream temperature, smaller patchcuts were installed to effectively remove 25% of the riparian forest over a 1600-m length of stream. The objectives of the riparian silviculture project were to:

- evaluate performance of Douglas-fir, western redcedar, and western hemlock between high-water lines and 30 m back from class-one streams in western Oregon, where soils are non-hydric.

- evaluate size of opening in hardwood cover and shrub removal in their effects on conifer establishment and growth.
- detect effects of removal of streamside cover on water quality with removals from zero to 25% of stream reach lengths, when in patches of less than 200-m of stream length, both sides of the stream.
- establish a long-term study available for interdisciplinary research on various parameters of riparian zone management and its effects.

Because feasibility of conifer restoration and stream protection for the small land owner was of primary interest to the researchers, the experiments were installed in conjunction with industrial harvest operations upslope. Three patchcuts ranging from 200 m to 100 m of stream length were planted with two sizes of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*) seedlings.

The aquatic macroinvertebrate study specifically addresses the third objective of the silviculture study and complements the managed riparian forest silviculture project by assessing the effects of the 25% removal of stream canopy on two orders of aquatic insects, Ephemeroptera (mayflies) and Trichoptera (caddisflies). In general, aquatic insects serve as primary links between the riparian forest system and secondary consumers in the stream by processing allochthonous and autochthonous inputs such as leaves, wood, periphyton, and algae, converting them into coarse organic particulate matter (CPOM) and fine organic particulate matter (FPOM) for nutrient use by other stream biota, and then serving as food for fish, crayfish, and other predators. Ephemeroptera and Trichoptera were specifically used to assess treatment effects because they are abundant in western Oregon, small, forested, lotic streams, have high generic diversity, occupy most stream micro-habitats, are significant sources of fish food, historically respond to harvesting disturbances, and have good, published identification keys. Other orders such as Plecoptera and Diptera which are also found in forested streams were not used because they are not as generically sensitive to the types of environmental change introduced by streamside harvesting and can be difficult to identify to genus. I also specifically wanted to avoid the commonly used PET index (Plecoptera-Ephemeroptera-Trichoptera) because

I wanted to focus on the biology and specific responses of genera rather than over-generalizations created by indices I had used in another study (see Walsh 1992). Indices are useful, however, in studies that must be completed in short timespans and focus on general trends. Mayflies and caddisflies were identified to the genus level and divided into functional feeding groups to gain an understanding of community structure, diversity, and function. Congeners inhabit fairly narrow ranges of stream substrates, vary slightly in their feeding strategies and nutrient sources, and may rapidly colonize areas exposed to increased light and primary productivity. Changes in the abundance, both relative and absolute, diversity, and functional feeding group composition of the genera within these two orders may indicate shifts in stream nutrient processing functions and in the content and composition of food sources for fish populations.

The broad objective of the aquatic insect study was to determine the effects of removing 25% of the riparian forest canopy and streamside vegetation on the Ephemeroptera and Trichoptera genera sampled under the residual buffer and out in cut-over areas. By focusing on both the cumulative (1600-m reach) and direct (exposed reach) disturbance effects of patchcut harvesting, I attempt to supplement the information gained from the stream temperature and silviculture analyses, and to aid in creating an integrated study of the riparian system. In order to accomplish these objectives, I formed specific objectives which would facilitate the analysis. They were to:

- evaluate changes in Ephemeroptera and Trichoptera abundance, functional feeding groups, and diversity as a result of two 100-m and one 200-m patchcuts in a 1600-m stream reach.
- evaluate changes in Ephemeroptera and Trichoptera abundance, functional feeding groups, and diversity as a result of two 100-m patchcuts within an 800-m stream reach.
- evaluate changes in Ephemeroptera and Trichoptera abundance, functional feeding groups, and diversity as a result of one 200-m patchcut within an 800-m stream reach.
- assess immediate changes in Ephemeroptera and Trichoptera caused by removal of the riparian canopy.

- compare the longitudinal downstream variability in Ephemeroptera and Trichoptera populations in our treated streams with unmanaged reference streams.

Many benthic researchers have explored the effects of clearcutting on aquatic insects, vegetation, and fish (Meehan et al. 1977, Newbold et al. 1980, Holtby 1988 to name a few). Few, however, have examined the effects of a partial removal of riparian canopy and adjacent forest along otherwise buffered and/or canopied streams. Few studies have also explored the spatial and temporal recovery of insect communities in a downstream direction over a period of two years after silvicultural disturbances. Because of potential increases in both stream temperature and solar radiation loading and, therefore, primary productivity caused by removal of the riparian canopy, I postulated that aquatic insect abundance would increase in the exposed reaches, diversity would decrease from upstream reference levels downstream through the 1600-m reach, and functional feeding group composition of the stream would shift to include fewer shredders and more scrapers, collector-gatherers, and collector-filterers below and within the harvest units. Predator abundance would remain unchanged. Research on the effects of forest harvesting is brought into perspective in terms of whether short-term increases or decreases in stream fauna are to be expected during management efforts at long-term improvement.

2. LITERATURE REVIEW

Freshwater aquatic macroinvertebrates inhabit a complex environment where nutrient delivery, habitat availability, and life history success depends on the physical, chemical, and vegetative conditions of both the stream and the terrestrial environment. Nutrient sources reach insect communities from three directions; vertically from the surrounding terrestrial vegetation, horizontally from upstream processing sources and overland flow, and locally from the production of periphyton (algae, diatoms, microscopic invertebrates, and bacteria attached to a substrate) and aquatic macrophytes. The delivery and residence time of nutrients depend on current velocity and substrate structure. Current velocity and substrate composition also determine the availability of suitable microhabitats for colonization, growth, and life history success. Nutrient quality and quantity depends on terrestrial and aquatic vegetation, water chemistry, water temperature, light intensity, local microfauna, and upstream processing. Streamside vegetation provides detrital inputs, moderates water temperature and light intensity, and contributes eventually to channel structure. Water temperature and light input also determine insect metabolic processes, such as respiration and growth, and behavior, such as drift or foraging habits.

2.1. Caddisfly and Mayfly Communities

Aquatic insects, including caddisflies (Trichoptera) and mayflies (Ephemeroptera), spend larval life stages in an environment that both buffers and facilitates micro-habitat changes. Habitat conditions such as food availability, stream temperature, and flow may remain relatively constant as a result of water's chemical properties and channel morphology or these conditions may alter rapidly. Caddis and mayflies exhibit a wide range of either constrained or flexible responses to changing environmental conditions,

are abundant in freshwater systems, encompass a wide range of habitats in forested streams, and are important players in the transfer of energy from the terrestrial and aquatic system to higher order consumers. Both orders exhibit close relationships with features of the aquatic environment, such as substrate, water temperature, flow, and terrestrial vegetation, so that responses of the community are fairly informative indicators of changes within the stream and riparian system. Close relationships with abiotic stream characteristics also, however, add to the variability observed within the insect community.

Variability. Variability observed within an insect community depends on the community boundaries defined by the researcher and the sampling variability created by the patchiness of the environment, the sample number, and the sampling method. Spatial and temporal scales vary among taxa so that no one boundary definition will capture all the variability present within the entire community. Yet, stream researchers are faced with spatial dimensions that vary by orders of magnitude and so, spatial constraints must be constructed (Minshall 1988). Choice of experimental sample unit size can alter resulting generalizations about insect community response and stream processes. Without measurements at a number of habitat levels or clear stratification of sample sites, expectations of community variance are unknown and detection of system changes is limited (Ralph et al. 1994). Natural variability can highly confound attempts to detect differences between communities as result of treatment (Norris & Georges 1993, Resh & McElvay 1993).

Environmental variability. Stream size has a significant effect on the diversity and density of the taxa collected (Brönmark et al. 1984). Small headwater streams experience low light intensity, variable flows, and heavy detrital inputs while large rivers, for example, experience high light levels, more constant flows, and higher quantities of suspended food. Taxa density also varies considerably over spatial scales smaller than stream order, including within riffles and pools (Lamberti & Resh 1979, Downes et al. 1993). The patchy nature of stream resources and diverse microhabitats creates clumped populations of insects that aggregate based on physical flow, substrate, temperature, and food availability. These environmental factors are, in turn, highly variable and dependent on each other (Reice 1985). For example, flow and food availability are directly affected

by substrate and substrate and food availability are directly affected by flow. Food availability is indirectly affected by stream temperature which is slightly affected by substrate and directly affected by flow and terrestrial/climatic conditions. Spatial sampling in such environments to determine treatment effects or change in a particular variable is an arduous task (Downes et al. 1993).

Substrate's effects on macroinvertebrates are substantial and have been extensively studied because of direct (habitat) and indirect (food sorting) effects on insect dispersal (Cummins 1962, Rabeni & Minshall 1977, Lamberti & Resh 1979). Many researchers recommend that benthic insect studies be organized around particular substratum in order to reduce population variability and, that accurate measurements of the substrate using core samplers or other such devices be taken (Gaufin et al. 1956, Cummins 1962, Chutter & Noble 1966, Lamberti & Resh 1979, Resh 1979, Clements 1987, Malmqvist & Otto 1987). Sampling only one type of substrate habitat, however, may bias the assessment of general stream biota (Kerans et al. 1992). Variability of flow and current velocities also increases with diverse substrate habitats. Current velocity should be measured as close to the substrate (within the boundary layer) as possible to adequately assess its influence on benthic biota. The variability of physical stream parameters such as temperature and solar radiation loading is usually far less than the variability within biotic parameters and is, therefore, not as great a concern for benthic researchers (Osenberg et al. 1994). Care should still be taken in acquiring accurate data.

Populations and their environments exhibit large temporal variation from both time to time and from place to place (Lealand et al. 1986, Minshall 1988, Rosillon 1989, Underwood 1994). Concurrence of spatial and temporal variation is extremely common (Resh & Rosenberg 1989). Although variation from time to time may be accounted for through analysis, correcting for temporal variation between locations while attempting to assess for an environmental impact is exceedingly difficult. Differences in instar-specific patterns, life stage aggregations, and life history habitat preferences contribute to temporal variability (Resh 1979). However, this variation may be accounted for by choosing sampling sites that incorporate the characteristic range of environmental

conditions of the entire treatment area, replicating the treatment and the control, increasing control locations, and sampling over time (Underwood 1994).

Normal population variability caused by life history patterns or behavior must be known in order to recognize deviations in time and space (Towns 1985, Johnson et al. 1993). Between-year variation occurs in aquatic insect populations normally, but is especially critical when climate conditions differ between years (Lealand et al. 1986, McElravy & Resh 1987). Changes in water level through drought or heavy precipitation may affect year-to-year variation of insects, especially Trichoptera which build permanent cases near the water line (Rosillon 1989). Abiotic factors can be used to predict richness and density responses of certain taxa once responses have been observed (McElravy et al. 1989). Incorporating considerations of climatic factors in long-term studies may help reduce unexplained variability. Sampling, design, and statistical methods are also available to reduce the natural variation as much as possible in order for strong treatment effects to show through.

Sampling variability. Examination of population variability requires appropriate sampling in both size and number. Small samples may not have high within-sample variability but may have high between-sample variability. Samples taken from streams within a basin may have high within-sample variability but low between-sample variability (Allan 1975a). Collecting enough samples is critical to gaining an adequate representation of a population because of the patchy nature of benthic insect assemblages (Gaufin et al. 1956, Cummins 1962, Chutter 1972, Resh 1979, Allan 1984). Obviously, reducing the risk of Type I and Type II errors while adequately observing the responses of the insects is desirable. However, time, energy, and resources often place constraints on the number of samples that can be collected and processed in a short enough time so that the results are relevant.

The number of samples needed to capture the variability in biomass and abundance within a single riffle was explored by Needham and Usinger (1956). They determined that 194 and 73 Surber samples from one riffle were necessary to determine insect weight and abundance respectively within a 95% confidence level. Measurements based on frequency of occurrence were less variable and required only 2 or 3 samples to insure that at least

one member of the most common genera was sampled. Chutter and Noble (1966) also found that 3 Surber samples would capture at least one member of all the most common taxa. In their study, these most common taxa represented 97% of all the individual insects measured. Townsend et al. (1987) also found that 5 samples included 75% of the observed species and all taxa making up more than 0.7% of the total invertebrate population. Frequency of occurrence is akin to presence/absence data. The information offered by it must be judged accordingly and its use should depend on research objectives.

Sample number may not be as important as understanding the variability inherent in a particular stream system and how it will alter or affect the data's conclusions. Chutter (1972), reanalyzing Needham and Usinger's (1956) data, discovered errors in analysis that underestimated the actual variability within the riffle. He found that instead of 73 samples, 448 samples would be needed to estimate abundance's variance within a 95% confidence interval. Others have found that to accurately estimate a 100% difference in means, 11 to 9,591 samples are required, depending on the benthic measure used (Allan 1984). Because such intensive sampling is highly destructive if not logistically impossible, Chutter (1972) suggests instead to choose sample size based on acceptable variability. Therefore, in Needham and Usinger's (1956) riffle, irrespective of sampling depth, 3 samples would show 61% variability around the sample mean, 5 samples would show 47% and 10 samples would show 33%. Improvements may be made by sampling at optimal depths for the Surber sampler. Resh and McElvay (1993) found that six samples reflected $\pm 40\%$ of the mean total number of individuals.

Use of different samplers or biotic indices may also improve the estimated variability of single samples and require fewer samples to be collected (Stark 1993). Modified samplers may permit plotting of insect position on the substrate, allowing the separation and distinction of microhabitats (Rossiter 1988). However, for comparison among studies, consistent use of similar samplers, such as Surber and Hess, aids in the accumulation of a comparable information base (Kerans et al. 1992).

Limiting studies to one or two taxa may provide maximum information per sample unit effort, but limits depth in ecological scope in order to gain entomological detail (Cummins 1962, Resh 1979, Downes et al. 1993, Reice & Wohlenburg 1993, Osenberg

1994). Grouping insects into functional groups or guilds may either smooth variability or obscure informative spatial or life history variation (Hawkins & Sedell 1981, Brussock & Brown 1991, Downes et al. 1993). Kerans et al. (1992) observed that the biological conditions described by stonefly taxa richness, dominance (proportions of individuals in the two most dominant taxa), and proportions of chironomids, omnivores, filterers, and predators were not sensitive to structural differences between riffles and pools, thereby allowing sampling across these physical habitats using these population measures. Mayfly and caddisfly taxa richness and total abundance, which are used in this study, were two of six community structure attributes that varied by habitat between years and rivers.

Osenberg et al. (1994) observed, however, that population-based parameters have low probabilities of generating demonstrable results while individual parameters based on single species wield much higher predictive and analytical power. In general, replicated quantitative sampling of as specific population parameters as possible better determines differences among streams than unreplicated, qualitative sampling (Kerans et al. 1992).

Despite the desire to reduce variability to gain interpretability, insects are valuable indices of environmental change precisely because they incorporate the stream's environmental conditions into their metabolic and behavioral systems (Carlson 1981). Insect life histories and distribution are a product of the combined effects of complex and interrelated abiotic and biotic phenomena. Teasing out the response to changing or manipulated conditions from the observed and "natural" variability is often only partially successful. Mean values tend to "homogenize" the spatial and temporal variance of population parameters, but lose information about variability. Temporal replication is necessary because too few samples during a season or year may greatly under- or overestimate population responses (Towns 1985, Underwood 1994). However, sampling intensively on each date may reduce the percentage sampling error more effectively than sampling on more dates (Osenberg et al. 1994). Resh and Rosenberg (1989) suggest that it is the variability inherent in the system that often explains observed responses. A high degree of variability within an insect community, although frustrating to researchers eager to explain causality, may be a primary indication of the system's resiliency. Exploring the factors contributing to community resiliency will help determine what could compromise

its ability to survive disturbance. This therefore necessitates the study of, not the compensation for, community variability. Knowledge of the insect community's spatial and temporal aggregation as well as clearly stated research objectives help reduce "noisy," erroneous variability. Fluctuations and extremes, however, should be incorporated into the study design. Individual insect taxa, or even representative population parameters, offer greater opportunity for explanation of differences in populations subject to external influence.

Diversity. Ecological diversity may be subdivided into physical, species, genetic, and functional diversity components, each of which contributes to the biotic community at some scale to provide measures of biodiversity (Kimmins 1992). Species, physical, and functional diversity are each important in describing aquatic insects' interactions in the stream environment. Species diversity (richness and constancy) is a useful measure in ecological stream studies because, typically, stream insect communities are relatively more diverse than biotic stream communities, such as fish (Christensen 1996). Severe reductions in invertebrate diversity may indicate fundamental shifts in the physiological environment and in the biological processes that certain insects perform in the stream.

There are three types of diversity: alpha, beta, and gamma (Whittaker 1972, Kimmins 1991, McCune 1995). Alpha (α) diversity is a measure of local species richness, i.e., the number of species within a given sample unit. Beta (β) diversity is a measure of the degree of change in species diversity across a landscape and indicates the number of species spread out over or squeezed into a gradient of increasing or decreasing niche space (Whittaker 1972, Magurran 1988). Gamma (δ) diversity is landscape-level diversity or the diversity of a total sample. Diversity is composed of species richness, i.e., the number of species present, and species evenness, i.e., the consistency of relative abundance among species. When all species are equally represented and, therefore, evenness is maximized, diversity is assumed to be at its greatest (Magurran 1988). Indices are available that combine species richness and evenness into an expression of the relative concentration of species dominance (Whittaker 1972). Some of the most commonly used diversity indices in aquatic insect research are Simpson's index and the Shannon-Wiener index (H').

Simpson's index is based on the assumption that as communities become more diverse, the probability of randomly identifying the same species twice decreases. It emphasizes the first one to three common species over rare ones and, therefore, the degree of dominance in the community (Whittaker 1972, McCune 1995). Although Simpson's index is not dependent on the form of different taxa's frequency distributions, it is dependent on sample size. This makes comparisons with other like studies difficult (Norris & Georges 1993). It can be used on small samples, however, because once an insect has been sampled it is theoretically returned to the sample pool so that the probability of selecting it again on the next try does not change.

The widely used Shannon-Wiener index is based on information theory which states that the more uncertain one is of observing a species again after it has been observed once, the more information is contained within the population (Norris & Georges 1993, McCune 1995). Advantages are that it is moderately sensitive to rare species, moderate capacity to discriminate between samples, strongly affected by intermediately abundant species, and insensitive to sample size as long as samples are not too small (Whittaker 1972, Magurran 1988, Norris & Georges 1993, McCune 1995). Shannon-Wiener is affected primarily by the number of species and their proportional representation and will not vary between samples as long as species number and their relative proportion remain constant (Allan 1975b, Magurran 1988). Disadvantages are that the number of the index is not as meaningful as, say, species richness, the index value may be affected by species clumping and habitat, and values depend often on individual study designs (Allan 1975b, Norris & Georges 1993). However, this index is widely used in macroinvertebrate research (Resh & McElvay 1993). In using H' , one must remember, however, that it is simply the "best equitability measure for inferring relative diversity" rather than a direct measure of diversity itself (Whittaker 1972). Although the Shannon-Wiener index accounts for evenness, there are more directly informative methods of evaluating sample evenness. One such method, the Shannon evenness index (E), calculates the ratio of observed diversity (H') to maximum diversity ($\ln S$, where S is the total number of species) to measure evenness (Magurran 1988). Both Simpson's and the Shannon-Wiener indices are linearly related to species richness and evenness, although

the Shannon-Wiener index increases more rapidly with increasing species richness and Simpson's index is influenced more by species evenness (DeJong 1975).

Functional feeding groups. Together, Ephemeroptera and Trichoptera represent each of the major functional feeding groups described by Merritt and Cummins (1984). There has been criticism of accepting Merritt and Cummins' classifications and/or of using functional feeding group categories because generalizations may limit the potential information gained (Minshall 1988). Many insects function predominantly in one functional feeding group, but under different conditions may function in another. Some insects also shift functional feeding groups during development. The Hydropsychid caddisfly, *Parapsyche*, for example, is a collector-filterer at early instars but becomes a predator at later instars. Instars were not distinguished in this study, so some functional feeding group classifications may be incorrect for the particular insect sampled but correct for the genera in general. Without gut content analysis, species identification, and electron microscope analysis of mouth parts, however, a more complex and possibly accurate functional group classification system could not be developed.

The functional feeding groups represented by taxa in this study are shredders, scrapers, collector-gatherers, collector-filterers, and predators. Piercers from the Hydroptilidae caddisfly family were observed on one stream, but were not included in the analysis. Shredders process terrestrial detritus conditioned by bacteria and microfauna (Cummins & Klug 1979). Caddisfly genera within this functional feeding group found in our four streams were *Lepidostoma*, *Micrasema*, *Homophylax*, *Hydatophylax*, and *Onocosmoecus*. There were no mayfly shredders found in our streams. Scrapers scrape periphyton from substrate surfaces with morphological adaptations such as specialized mandibles. Scrapers found within our streams were *Glossosoma*, *Dicosmoecus* (which may also be a shredder), *Neothremma*, *Neophylax*, *Ironodes*, *Heptagenia*, *Drunella*, and *Cinygmula*. Collector-gatherers forage on CPOM deposited on the stream substrate and, in the process of utilizing its nutrients, reduce it into nutrient rich FPOM for use by insects downstream (Cummins & Klug 1979). Collector-gatherers found in our streams were *Ecclisomyia*, *Psychoglypha*, *Baetis*, *Epeorus*, *Caudatella*, *Eurylophella*, *Serratella*, *Timpanoga*, *Paraleptophlebia*, and *Rhithrogena*. Collector-filterers filter seston, the

inorganic and organic particulates suspended in the water column, using either morphological appendages or woven silk nets (Wallace & Merritt 1980). They are critical for local nutrient conservation because, by trapping suspended particles, they increase nutrient retention time within reaches (Wallace & Merritt 1980). The collector-filterers in our streams were all caddisflies and included the Hydropsychids, *Hydropsyche*, *Parapsyche*, and *Arctopsyche*, and Philopotamidae *Wormaldia*. Invertebrate predators prey on other insects and other small non-insects, including fish. Predators found in our streams were *Rhyacophila* and *Polycentropus*. *Polycentropus* can also function as a collector-filterer or a shredder.

Life histories and cycles. A basic understanding of the varied and diverse life histories of caddisflies and mayflies is necessary to interpret community responses to riparian timber harvest treatments (Resh 1979, Butler 1984, Towns 1985, Bowles & Allen 1992). An insect's life history reflects the overall patterns of growth, emergence, and reproduction of a population and may, depending on the particular species, exhibit flexibility to changes in environmental conditions (Towns 1985). Sampling logistics rendered growth and instar development measures unfeasible.

Life histories differ from life cycles in that life cycles link generations and life histories are the "qualitative and quantitative details of the variable events associated with life cycles" (Butler 1984, Johnson et al. 1993). Life cycles are not flexible although aspects of life cycles, such as voltinism, may differ among congeners. Life history aspects, such as rate and efficiency of larval growth and timing of emergence, also differ latitudinally and among species of congeners (Sweeney 1984, Newbold et al. 1994). Coupled with considerations for hatching and emergence periods are considerations of habitat and food preferences which also influence life-history patterns. Obtaining accurate, local life history information for the specific genera collected at our four streams in western Oregon, therefore, was difficult. Most Trichopteran life-history studies have been completed in eastern Appalachian forests. In the Mediterranean climate of northern coastal Californian, McElravy and Resh (1987) observed longer flight patterns in adult caddisflies than had been reported in temperate climates. Therefore, nymph and adult insect life histories from western Oregon which also has a Mediterranean climate may be

expected to differ from eastern reports. Generalizations from global species research will be presented, combined with knowledge gained from field observations for genera observed in our streams. Table 1 contains life history information collected from the literature for the dominant genera found in the four western Oregon streams.

Table 1. Summary of life history and ecological characteristics of dominant mayfly and caddisfly genera found in Ames, Mosby, Buttermilk, and Pancake Creeks. Voltinism has the potential to change depending on environmental conditions. C-G=Collector-gatherers, C-F=Collector-filterers, Pr=Predators, Sc=Scrapers, Sh=Shredders.

Genus	Voltinism	FFG ⁷	Habit or Case Type ⁷
<i>B. Baetis</i>	multi- ³	C-G, Sc	swimmers, clingers
<i>E. Drunella</i>	uni- ⁹	C-G, Sc	clingers, sprawlers
<i>H. Cinygmula</i>	uni- ^{4,5}	Sc, C-G	clingers
<i>H. Epeorus</i>	uni- ⁹	C-G, Sc	clingers
<i>H. Rhithrogena</i>	uni- ³	C-G, Sc	clingers
<i>L. Paraleptophlebia</i>	uni- ³	C-G, Sh	swimmers, clingers, sprawlers
<i>B. Micrasema</i>	uni- ²	Sh, C-G	mineral/vegetative curved, tapered case
<i>G. Glossosoma</i>	bi- ¹¹	Sc	mineral turtle-shell case
<i>H. Arctopsyche</i>	semi- ¹	C-F	net spinners, fixed retreats
<i>H. Hydropsyche</i>	uni- ¹⁰	C-F	net spinners, fixed retreat
<i>L. Lepidostoma</i>	uni- ⁶	Sh	square, bark "log-cabin" or cylindrical, sand/silk cases
<i>P. Wormaldia</i>	bi- ¹	C-F	saclike silk nets
<i>R. Rhyacophila</i>	uni- ¹	Pr	free ranging
<i>U. Neothremma</i>	semi- ⁸	Sc, C-G	mineral, tapered, curved case

¹Anderson 1976, ²Anderson, N., personal communication, ³Clifford 1982, ⁴Edmunds et al. 1976, ⁵Gilpin and Brusven 1970, ⁶Grafius and Anderson 1979, ⁷Merritt and Cummins 1984, ⁸Ogilvie and Clifford 1986, ⁹Rader and Ward 1987a, ¹⁰Wallace and Merritt 1980, ¹¹Wiggins 1977.

Trichoptera. Caddisflies are holometabolous insects that occupy diverse habitats because of their use of silk. Lotic freshwater habitats range from bedrock glides, cobbles, boulders, and woody debris in silt bottomed streams to pools, springs, seeps and rivers (Gordon & Wallace 1975, Merritt & Cummins 1984). Caddis use silk to construct fixed or mobile cases of rock, wood, plant material, and/or sand to weave filtering nets or to attach themselves to substrates. Cases increase the larvae's respirational efficiency by forcing water past primitive gills, provide some protection from predators, and offer ballast in flowing waters (Wiggins 1977). Caddis construct cases that vary greatly in form among taxa but are typically consistent at the generic level (Merritt & Cummins 1984).

Caddisflies in northern latitudes are typically univoltine, meaning they undergo one life cycle a year (Merritt & Cummins 1984, Bowles & Allen 1992). Life history characteristics, including voltinism, are listed in Table 1 for common caddisflies found in our four streams. Georgian and Wallace (1984) observed that univoltine species lack the life-history flexibility to respond rapidly to unexpected changes in resources, such as would be created by removing the riparian canopy. Some caddis do retain some life history flexibility depending on stream temperature conditions. *Hydropsyche*, for example, may be univoltine in cool streams but bivoltine in warmer reaches downstream (Wallace & Merritt 1980). Not all caddis are univoltine. Some, such as *Glossosoma*, are bivoltine with both a summer and winter cohort (Wiggins 1977, Georgian & Wallace 1984). *Glossosoma*, a dominant scraper, is therefore able to take advantage of increased summer periphyton. Others, such as *Neothremma*, are semivoltine, and require two years to grow from first to fifth instars and would take even longer to reveal responses to changes in the riparian environment (Ogilvie & Clifford 1986). After completing five to seven instars, larvae seal the ends of their cases and pupate. Pupation length varies widely with taxa. *Neophylax* may remain within its sealed case through the entire summer and emerge in early fall (Wiggins 1977). Egg and larval development and adult emergence vary depending on primary food sources and habitat conditions such as periods of drought, high flows, or temperature patterns (Merritt & Cummins 1984, Jamieson-Dixon & Wrona 1992).

Genera found in our western Oregon streams were composed of seven families (Appendix A). The filter-feeder, *Hydropsyche*, was found at most stations. Its family, Hydropsychidae, comprises approximately 80% of all caddis in North American streams, and this particular genera is widely distributed from headwaters to large rivers (Gordon & Wallace 1975, Wallace & Merritt 1980). Species ranges are segregated by stream temperature and dissolved oxygen content across basins. Within stream reaches, however, species may segregate based on feeding habitat and suspended particle size differences, velocity, and/or resource concentration (Gordon & Wallace 1975, Wallace & Merritt 1980, Alstad 1987). *Hydropsyche* uses drift as a primary form of movement (Kerans 1992). *Glossosoma* dominates scraper production and was observed at most of the stations, particularly those with cobbled riffled substrates. The free-living predator, *Rhyacophila*, was ubiquitous in our streams and can tolerate a wide variety of habitats within its natural range (Jamieson-Dixon & Wrona 1992). Many of the caddisflies collected in the streams were locally rare taxa, in that they did not occur in adequate populations to be included within the statistical analysis. The uncommon caddisflies in this study, such as *Dicosmoecus* and *Psychoglypha*, often made up a large portion of the collected biomass.

Ephemeroptera. Mayflies are free living, hemimetabolous insects abundant in small, temperate, forest streams. Nymphs, subimagos, and adults serve as important components of secondary stream production, specifically as fish food (Needham et al. 1935). This study focuses only on the nymphal phase of the life cycle. Mayflies utilize a variety of morphological and behavioral mechanisms for adapting to current, such as abdominal disks that facilitate adhesion to substrates, behavioral drift, and specialized gills that obtain oxygen from slow moving water. *Baetis* is well known for its propensity to drift, which makes it an important early colonizer of disturbed areas (Ciborowski 1983, Kohler 1985, Bergey & Ward 1989). Most mayflies, such as *Baetis*, *Epeorus*, *Rhithrogena*, and *Drunella* gather and/or scrape detritus and periphyton from the stream substrate. Life history characteristics, including functional feeding groups, are listed in Table 1 for common mayflies found in our four streams. Rader and Ward (1987b) observed that these four genera, along with the caddisfly, *Glossosoma*, comprised 79% of

the total number of collector-gatherers and scrapers within two montane study sites.

Baetis and *Drunella doddsi* consumed primarily diatoms while *Rhithrogena*, *Epeorus*, and *Drunella grandis* consumed primarily detritus.

Based on resource consumption, these genera and species separated into two groups with high within-group overlap but low between-group overlap. The first group preferred exposed rock surfaces while the second preferred rock undersides and crevices. Habitat preferences reflect food preferences. These four genera were observed in our four western Oregon streams. Although *Drunella* was not identified to species, the fairly distinct division between habitat and food preferences among genera within the same functional feeding groups and in similar substrates is worth noting. The level of sampling intensity in this study was insufficient to distinguish such differences. Some mayflies species filter-feed, although none were observed in our streams. Many mayflies are generalist feeders, especially as early instars. Some appear not to distinguish greatly among food sources. *Paraleptophlebia*, for example, a collector-gatherer/shredder, experiences increased growth rates when feeding on leaf material over FPOM, but grows well on many food types, including periphyton (Mattingly 1987).

Mayflies have potentially extremely high rates of reproduction (Needham et al. 1935). Most temperate stream mayflies exhibit a univoltine life cycle with staggered emergence of congeneric species, such as *Rhithrogena*, *Drunella*, *Paraleptophlebia*, and *Epeorus* (Clifford 1982, Towns 1985, Rader & Ward 1987a) (Table 2). Emergence rates of these genera also differ with elevation and presumably water temperature (Rader & Ward 1987a). However, some mayflies, particularly *Baetis*, exhibit seasonal multivoltine or bivoltine life cycles (Clifford 1982, Rader & Ward 1987a). *Baetis* is a common, abundant genus that reproduces frequently throughout the summer depending on resource abundance and temperature (Merritt & Cummins 1984). Certain *Baetis* spp. have univoltine life cycles under specific winter temperature conditions (Illies & Masteller 1977). Although mayflies emerge throughout the summer, emergence for most univoltine genera usually is in late summer or early autumn (Rader & Ward 1987b). Seasonal synchrony, such as this, may result from direct control of larval development by temperature through periods of temperature-threshold induced quiescence (Newbold et al.

1994). Photoperiod plays a secondary role, but increases in importance in years of unusual temperatures.

2.2. Disturbance

Disturbance has been defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” whether the event is perceived as normal or not (Pickett & White 1985, Resh et al. 1988). The degree to which a disturbance affects a community depends on spatial and temporal dimensions such as habitat size, substratum, and organism life history as well as the magnitude, frequency, predictability, and duration of the disturbance (Minshall 1988). A community’s response to disturbance is related to its functional and taxonomic diversity in terms of the broader community’s adaptation to environmental change (Resh et al. 1988). Whether this response is rapid or slow is a measure of the system’s resiliency.

Resiliency is the speed of return to some measure of a predisturbance state (Connell & Sousa 1983). Benthic invertebrates have shown a high degree of resiliency to localized disturbances aided by recolonization from drift, upstream migration, and oviposition by aerial adults as well as local movement up from the hyporheic zone (Waters 1964, Williams & Hynes 1976, Wallace et al. 1986, Meffe & Minckley 1987, Anderson 1992, Boulton et al. 1992, Lamberti et al. 1992, Tikkanen et al. 1994). High resiliency may be an adaptation to a system that experiences frequent disturbances. The high frequency of disturbance within Pacific Northwest forested stream systems is the principal factor driving insect abundance (McAuliffe 1984, Anderson 1992). After moderate disturbances, insects may recover in a period of weeks because of efficient and rapid dispersal mechanisms (Williams & Hynes 1976, Busch 1978, Reice 1985, Fuller et al. 1986). Communities exposed to severe biological and environmental disturbances (i.e., major disruption of physical and chemical stream features) require more time to reset, and recover more quickly with patchier disturbances (Wilzbach et al. 1983).

Communities accustomed to frequent disturbances also may recover more rapidly because their structure may still be a function of the previous disturbance (Boulton et al. 1992). The stability and resiliency of aquatic insects has been attributed to the condition and stability of streamside vegetation (Triska et al. 1982, Cummins et al. 1989, Anderson 1992), but must also be considered with respect to seasonal disturbances triggered by hydrologic events.

Vannote et al. (1980) and others have proposed a river continuum concept for Pacific Northwest streams. This concept includes streamside vegetation, stream channel characteristics, and stream biota in a spatial and temporal progression from headwater reaches to large rivers (Minshall et al. 1985, Rader & Ward 1987b, Triska et al. 1982). As a stream moves from headwater reaches dominated by narrow channels, steep gradients, cool temperatures, and allochthonous inputs to larger streams and rivers characterized by wider channels, shallow gradients, warmer water, and autochthonous energy sources, insect communities shift from primarily detrital processors such as shredders to filter feeders and collectors that capture nutrients suspended within the water column or deposited on the river bottom. Within forested, third- to fifth-order streams, the transition from small, cool flowing, nutrient poor systems to warmer, nutrient rich systems occurs. It is in this transition area that the potential exists for rapid response and high resiliency to disturbance within the insect community. It is also in middle-ordered stream systems that disturbance may cause shifts in community structure. The proximity of certain functional groups or taxa prominent further downstream or in tributaries provides populations for recolonization (Pickett & White 1985, Lamberti et al. 1992). Refugia available within the stream substrate, channel, and basin is a strong determiner of community resilience and persistence (Sedell et al. 1990). Within a channel, substrate and structure supply much of this refugia. Substrate is especially critical in insect community response to flow disturbances.

Recovery after a disturbance, despite high resiliency, does not necessarily return the community to a predisturbance state. Wilzbach et al. (1983) suggest that non-catastrophic disturbances do not play a role in determining insect community structure on an ecological time scale. Richards and Minshall (1992), however, observed headwater

streams disturbed by fire to have lower species richness, higher year-to-year variation, and less similarity to reference streams over five years of observation. A community's persistence between years is highly dependent on the annual maximum and/or range of stream temperatures (Townsend et al. 1987). Communities experiencing lower maximum temperatures as well as low, stable pH and low discharge are more persistent between years. Fire disturbance can increase stream temperatures as well as change pH and flow conditions (Amaranthus et al. 1989). The long-term differences between Richards and Minshall's (1992) reference and treatment communities may reflect consequent changes in riparian and terrestrial vegetation which influence the productivity and nutrient cycling of a stream system.

Forest harvesting within the riparian zone is an anthropogenic, variable-scale, low-frequency, unpredictable disturbance that affects the composition of streamside vegetation without necessarily directly affecting the stream channel (Gurtz & Wallace 1984). Harvesting, depending on the applied silvicultural method, may or may not alter terrestrial components of the nutrient, chemical, and physical environment that are critical to aquatic insects' recovery. Comparative research conducted on clearcut, buffered and non-harvested streams has shown that aquatic insect diversity is highest in non-harvested streams and lowest in the completely clearcut reaches, despite increases in abundance of some taxa on the clearcut streams (Newbold et al. 1980, Anderson 1992). Ecosystem components which may change as a result of harvesting are streamside vegetation, dissolved nutrients, stream temperature, and solar radiation loading. Streamflow may also change slightly as a result of harvesting with the effect depending on the tree density remaining within reach of the stream. Generally, flows increase (Harr et al. 1979, Harr 1980). Because such a small proportion of the watershed in this study was harvested, potential changes in streamflow were probably minimal.

2.3. Stream Substrate

Substrate has been identified as a major driver of microdistributional benthic community structure and diversity in lotic streams (Pennak & Van Gerpen 1947, Minshall 1968, Cummins & Lauff 1969, Allan 1975a, Rabeni & Minshall 1977, Minshall 1984). Substrate is generally described by size classes ranging from large rock-face surfaces, boulders, and cobbles to sand and fine sediments (Cummins & Lauff 1969). Substrate heterogeneity, which is a strong determinant of local community diversity, is generally low at the large and fine ends of the scale and peaks in the boulder/cobble range (Figure 1) (Pennak & Van Gerpen 1947, Minshall 1968, Allan 1975a, Minshall & Minshall 1977, Rabeni & Minshall 1977, Reice 1980).

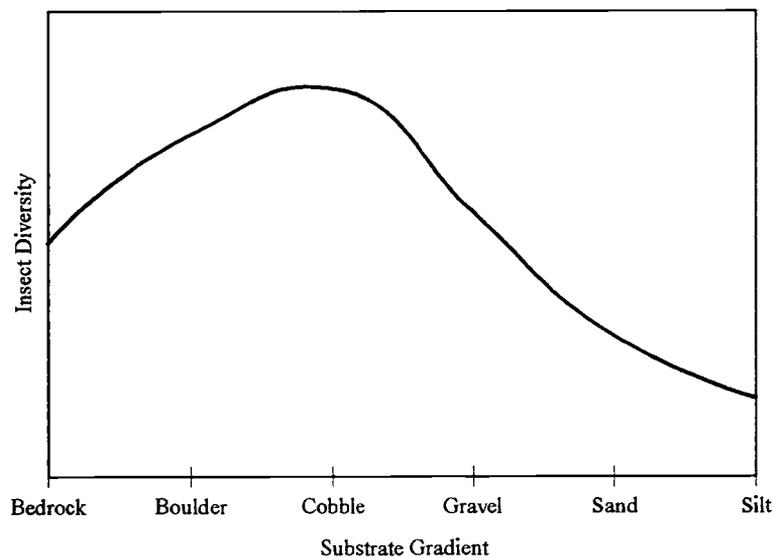


Figure 1. Insect community diversity or abundance as it varies across a gradient from large to fine substrates. Moderate sized substrates create greater heterogeneity which typically results in greater community diversity and/or abundance.

Gurtz and Wallace (1984) observed that the smaller the substrate size in a stream reach, the greater the negative effects associated with clearcutting disturbance. Murphy and Hall (1981) found that predator taxa concentrated in riffles (cobble/gravel, erosional areas) showed greater increases in population than did taxa in pools within clearcut reaches.

Substrate heterogeneity influences habitat availability and its capacity to retain detritus (Minshall 1984). Boulders and cobbles offer large surface area, temporal stability, and a variety of habitat and refugia that accommodates insects that prefer high current velocities and those that demand slower velocities (De March 1976, Minshall & Minshall 1977, Lancaster & Hildrew 1993). Clements (1987) observed that *Baetis* showed the strongest positive response to available surface area over seven dominant taxa, including the caddisfly, *Hydropsyche*, and the mayfly, *Epeorus*. He also demonstrated that substrate preference became insignificant after accounting for surface area. *Baetis* has been shown in other studies to prefer boulders and large cobbles which may be linked to its tendency to suffer rapid mortality at high population densities (Rabeni & Minshall 1977, Kohler 1992). Linduska (1942) observed that the mayfly, *Cinygmula*, was most common on cobbled substrates and avoided larger boulders or finer gravel substrates. *Rhithrogena* mayflies are also common on cobbled substrates (Saleem & Iftikhar 1987). Boulders and cobbles retain large leaf packs, CPOM, FPOM, and support periphyton assemblages. Shredders, such as *Lepidostoma*, and scrapers, such as *Glossosoma*, are often found in cobble riffles which have high nutrient retention capacities (Huryn & Wallace 1988). However, although pools also have high nutrient retention rates, Rabeni and Minshall (1977) never observed *Glossosoma* in pools. *Lepidostoma*, however, is frequently found in pools (Grafius & Anderson 1979). Current velocity may indirectly influence *Glossosoma*'s habitat choice because, at slower velocities, the deposition of fine particles increases and interferes with grazing. Gurtz and Wallace (1984) observed that scrapers and collector-gatherers increase and shredders decline as substrates increase in size from sand to cobbles to rock face.

Despite their lack of heterogeneity, rock-faces and bedrock support diverse communities because of large surface areas. Insect abundance and biomass increase when these substrates are associated with bryophytes (Edington 1968, Gordon & Wallace 1975,

Cummins & Klug 1979, Gurtz & Wallace 1984). Filter-feeders that inhabit areas of high velocity, such as Hydropsychidae, are often found on bedrock and rock faces (Hurn & Wallace 1988). Gravel retains large quantities of detritus, but has less surface area than larger substrates. However, when gravel occurs in pools that experience flow reversal, gravel adds substrate complexity. Flow reversal is a phenomenon where during high flows, erosional areas (riffles) become depositional areas and depositional areas (pools) become erosional areas. The presence of gravel in pools indicates habitat stability. Invertebrate abundance and diversity increases in these pools compared to pools without gravel substrate, i.e., those which experience substrate disturbance (Brown & Brussock 1991). Sand and silt are generally unstable substrates and support specialized communities adapted to low velocities, high deposition rates, and low respiratory demands (De March 1976, Strommer & Smock 1989). *Paraleptophlebia* is one of few mayfly genera that can persist in depositional areas (Minshall 1968). However, *Paraleptophlebia* populations increased in numbers when stony substratum was added to fine substrate areas (Minshall & Minshall 1977). Holomuzki et. al. (1990) observed higher *Paraleptophlebia* densities in riffles than in pools while Mattingly (1987) reports two species of *Paraleptophlebia* colonizing both riffles and pools. Substrate heterogeneity generally increases insect habitat.

2.4. Current Velocity

Current velocity is intrinsically related to substrate (Linduska 1942, Rabeni & Minshall 1977, Reice 1980, Saleem & Iftikhar 1987). The structure and size of substrate influences velocity, particularly at the boundary layer between substrate and the water column where insects exist. Velocity influences the distribution of smaller substrates such as gravel, sand, and silt. Statzner and Higler (1986) have proposed that stream hydraulics, or the physical characteristics of flow, are the primary determinants of benthic insect zonation. Physical flow characteristics incorporate substrate, structure, channel form, and current at the boundary layer into one concept. Primary emphasis, however, remains on flow rather than substrate (Statzner et al. 1988). Researchers have observed

that some insects may choose habitat based on velocity. Net-spinning caddisflies, such as Hydropsychidae, may weave net mesh in specialized dimensions to accommodate the force of the current and optimize the capture of seston (Edington 1968, Wallace 1975). *Baetis* and *Hydropsyche* spp. are often found on tops of boulders and rock faces where currents are at their greatest because the water column's depth is compressed across the rock surface (Linduska 1942, Edington 1968, Smith-Cuffney & Wallace 1987). This high, concentrated flow optimizes the delivery rate of food (Englund 1993). Although the two caddisflies, *Rhyacophila*, which is free-living, and *Wormaldia*, which constructs a fine mesh net, are not well adapted to high current velocities, they depend on the current to deliver sufficient oxygen across their body surfaces to meet metabolic needs (Philipson 1954). Despite some mayflies and caddisflies' apparent responses to velocity, most appear to respond more strongly to substrate. Studies have found that many insects exhibit substrate preferences after velocity differences were eliminated (Minshall & Minshall 1977, Reice 1980).

2.5. Streamside Vegetation

Freshwater lotic systems and their surrounding terrestrial vegetation are closely linked because of a high ratio of shoreline to stream bottom (Anderson & Sedell 1979, Gregory et al. 1991, Reice & Wohlenberg 1993). Haefner and Wallace (1981) observed that vegetation succession and sequential changes in macroinvertebrates are closely related so that recovery of stream communities disturbed by altering riparian vegetation is dependent on the simultaneous recovery of the vegetation. Hawkins (1988), however, observed that after disturbance encompassing entire watersheds (i.e., the eruption of Mt. St. Helens in southern Washington), insect composition and functional structure recovery were based on adaptations to stream substrate and physical habitat rather than vegetation. Obviously, both physical habitat and streamside vegetation contribute to insect community success. The potential contribution of each element is highly variable, thus limiting a specific definition of the primary features. Delineation of the principal

determinant may never be achieved. Considerations for potential insect response to both changes in physical habitat and stream vegetation should be given.

The vegetation bordering streams and extending to the upslope forest community boundary is the riparian zone. Site area, substrate type, flow or upslope disturbances, wetness, and light penetration determine the riparian plant community. Frequently disturbed areas often support only herbs and forbs. Deep, moderately disturbed soils support deciduous trees that grow more rapidly than conifer counterparts. Conifers grow in sunlit patches on less moist substrates with infrequent physical disturbance. Riparian vegetation describes the long- and short-term disturbance history of the channel (Swanson et al. 1982, Gecy & Wilson 1990).

In forested riparian systems, deciduous and coniferous trees differ somewhat in the ways they modify the stream microclimate, drop litter and leaves into streams, stabilize streambanks, and offer velocity slowing structure and areas of deposition during high flow events. Both eventually provide in-channel structure with stems and roots, although conifer debris is more persistent than hardwood debris. Herbs, forbs, and aquatic macrophytes shade stream edges, modify velocity, trap seston, and provide habitat for stream biota. These plants also decompose at rates at least five times faster than average leaf and woody debris decomposition rates (Anderson & Sedell 1979).

Aquatic insects are one of the important links connecting terrestrial and aquatic systems because insects consume and process terrestrial detritus, releasing nutrients to the stream system. Corkum (1989) observed distinct benthic invertebrate assemblages across drainage basins based on vegetation and land use types around and, even beyond the riparian zone. The composition of benthic invertebrate assemblages based on riparian plant communities is a major tenet of the River Continuum Concept (Vannote et al. 1980). Within a stream, Hawkins et al. (1982) found that presence or absence of a stream canopy and its type influenced benthic invertebrate abundance and guild structure more significantly than substrate. Guilds differ from functional feeding groups in that insects are grouped not only by how they eat, but also by what they eat.

Coniferous and deciduous inputs. Small, cold, forested streams are typically nutrient poor. Nutrient levels increase as terrestrial detritus enters the channel from

canopy litter or overland flow and water temperatures warm. However, the nutrients held within leaves, needles, cones, and twigs are not readily accessible for entry into the water column. Physical abrasion, leaching, microbial processing, and consumption by aquatic invertebrates help to transfer energy into the stream. Most tree leaves and needles, compared to herbs and forbs, provide less available nutrients because of abundant structural tissue and non-nutritive chemical compounds (Irons III et al. 1988). Fungi, bacteria, diatoms, and other microfauna "condition" the leaves by colonizing them, increasing their protein content, and making them attractive to aquatic insects (Merritt et al. 1984, Cummins et al. 1989).

Aquatic insects accelerate breakdown of litter. They shred, graze, scrape, gouge, and pierce the conditioned terrestrial litter, breaking it into smaller pieces for further processing by collector-gatherers. After digesting it and incorporating a relatively small portion of the nutrients into their bodies, the rest is eliminated as nutrient rich fecal material for further processing (Triska et al. 1982, Wallace et al. 1982, Cummins et al. 1989). Some filter-feeders are able to collect FPOM and in the process of digestion compact it into CPOM for use again by collector-gatherers, increasing nutrient retention time. In the absence of invertebrate fauna, detrital processing rates slow significantly and organic detritus accumulates. This build-up of nutrient sources reduces the steady downstream flow of nutrients and leads to nutrient delivery by high flow pulses which offer little time for nutrient capture and utilization (Wallace et al. 1982).

Different species of leaves condition at different rates. Conditioning rates also depend on stream temperature, water chemistry, and pH. Generally, deciduous terrestrial detritus conditions rather quickly and is readily consumed and broken down by aquatic insects (Triska et al. 1982). Some shredder aquatic insect populations surge in the fall to coincide with the autumn leaf drop while others surge in the spring when floods transport fallen terrestrial leaves to the streams (Merritt et al. 1984, Linklater & Winterbourn 1993). Coniferous needles take much longer to condition and because they remain within the stream channel longer are year-round sources of food. Because leaves condition at different rates and insects consume the detritus which conditions first, a continuous supply

of available food material is maintained as long as there is a diversity of tree species with a range of conditioning rates (Anderson & Sedell 1979).

Proportions of coniferous and deciduous material may affect insect functional feeding group biomass. Molles (1982) observed that shredder biomass was much higher in conifer dominated streams primarily because of increased nutrient retention in the conifer streams. Grazer biomass showed no difference between conifer or aspen streams. Aspen (*Populus tremuloides*) did not supply long-term sources of woody debris necessary for retention. Foliar biomass is greater in conifer-dominated riparian zones than in deciduous-dominated riparian zones, although only a fraction of the needles reach the stream channel each year (Gregory et al. 1991). Palatable and available tree detritus fluctuate considerably in deciduous canopied streams; conifer canopied streams show a more even distribution of detritus through the year (Anderson & Sedell 1979, Cummins et al. 1989, Duncan et al. 1989).

Large woody debris. Nutrient spiraling describes the process of breakdown and reutilization of nutrients within stream reaches (Anderson & Sedell 1979, Merritt et al. 1984, Gregory et al. 1991, Murphy & Meehan 1991). The rate and length of downstream spiraling depends on the retention capacity of a stream reach and the energy inputs and storage options available within the stream. Prolonged retention of nutrients increases the efficiency of nutrient uptake by consumers and the degree of processing presented to the communities further downstream. A stream's retention capacity depends partially on the structure within the stream channel. While substrate can supply important structure, most forested streams lack the large size boulders important for slowing flow and trapping large quantities of organic detritus, such as leaf packs and small wood. In forested streams, large woody debris is critical for supplying stream structure for both aquatic insects and salmonids. Structure aids in the formation of pools necessary for fish rearing (Sedell & Swanson 1982, Bisson et al. 1987, House & Boehne 1987).

Unlike boulders, woody substrates also provide long-term, slowly processed sources of food for invertebrate gougers (Anderson & Sedell 1979, Harmon et al. 1986). The debris dams that form behind velocity slowing structures are important habitat for invertebrate shredders, which are critical in processing leaves and CPOM into FPOM

(Anderson & Sedell 1979, Harmon et al. 1986, Roeding & Smock 1989, Linklater & Winterbourn 1992). In a small forested stream, Triska et al. (1982) found that 75% of the invertebrates sampled were classified as shredders. Fifty percent of the stream channel area was comprised of wood and the organic debris and sediments stored behind the wood. These percentages declined in third-order streams where only 12% of the insects were shredders and 25% of the substrate was created and maintained by wood (Anderson & Sedell 1979, Murphy 1979, Triska et al. 1982, Sedell & Swanson 1982). Although the percentage of mineral substrate in higher order streams increases, woody debris still plays a major role in riffle/pool distributions and nutrient retention (Evans et al. 1993, Triska et al. 1982, Trotter 1990).

In the Pacific Northwest, red alder does not supply long-term, large woody debris because it lacks both the size and decay resistance (Andrus & Froehlich 1988, Carlson et al. 1990). Meanwhile, the presence of conifers along streams is increasingly rare because of lack of natural regeneration and past and present logging and stream management practices (Murphy 1979, Bisson et al. 1987, House & Boehne 1987, Murphy et al. 1987, Sullivan et al. 1987, Murphy & Koski 1989, Robison & Beschta 1990, Bilby & Ward 1991, Ralph et al. 1994). Large wood pieces are necessary because wood length is directly related to its stability within the stream channel (Swanson et al. 1982). Pieces longer than stream channel width have greater stability in high flows and improve reach retention by trapping smaller pieces in debris jams behind them (Bisson et al. 1987, Lienkaemper & Swanson 1987). Decay resistant wood, such as western redcedar and Douglas-fir, do not break down rapidly, remain in the channel longer, and aid in the development of stable salmonid rearing pools.

Primary production. Autotrophs are important components of stream energy and nutrient dynamics in many non-forested and higher order forested streams (Minshall 1978). Within forested streams, there may be a longitudinal trend from heterotrophic systems in heavily canopied streams to autotrophic systems in wider, low gradient streams (Towns 1979). Removing-stream shading tree canopy by clearcutting increases light amounts which may shift autotrophic systems upstream (Cummins & Klug 1979). Diatoms and bryophytes are the dominant sources of primary productivity in heavily

shaded streams (Hansmann & Phinney 1973, Anderson & Sedell 1979, Noel et al. 1986). Mosses are not usually consumed as food, but rather slow velocity, act as a substrate, and trap detritus (Cummins & Klug 1979, Gregory 1983). With greater light, the aquatic plant community responds by increasing the quantity and diversity of algae, including periphyton and filamentous and macro-algae (Lyford & Gregory 1975, Towns 1979, Murphy et al. 1981, Noel et al. 1986, Steinman & McIntire 1986, Holopainen & Huttunen 1992).

Periphyton is an important source of autotrophic energy in streams, and its presence is linked to higher densities of insects (Perry et al. 1986). Per unit biomass, periphyton is capable of supporting far greater standing crops of consumers than allochthonous detritus because of rapid turnover rates (Gregory 1983, Lamberti & Moore 1984). When clearcutting, clearing by beavers, windfall, bank erosion or changing landforms opens the canopy of small, shaded streams, one source of stream energy, terrestrial detritus, is replaced by another, light energy (Murphy 1984). This occurs especially in the case of clearcutting, because loggers are required to remove most tree litter that falls into streams. Elevated primary production increases the quantity and, especially, the quality of available food. As a result, increases in algae have a far greater impact on consumers than biomass may alone indicate (Gregory 1983). Newly exposed forested reaches exhibit high immediate increases in net primary production because the insect community, low in grazers and gatherers, cannot process the surplus (Murphy 1984). However, as the community adapts and increases processing rates, net primary production may decline. Faunal biomass, however, increases and production:biomass ratios are higher than previously observed under forested cover. Increases in periphyton abundance are inversely related to stream size, so that larger streams that are already less shaded do not experience proportional increases in primary production (Murphy 1979).

Changes occur within the insect community over time as allochthonous consumers, such as shredders, experience a reduced food base and those which respond quickly to increases in autochthonous energy, such as scrapers and collectors, gain food resources. Rounick et al. (1982) used stable carbon isotopes to determine ingestion percentages of allochthonous and autochthonous material in insects from recently

harvested catchments. They found that insects in the earliest logged catchments (5 years old) showed the greatest dependency on autochthonous sources while those in the most recently logged catchments (2 years) showed no difference from forested controls. Although benthic primary productivity had increased in the two years since logging, forest-derived organic materials had not yet been flushed from the recently logged stream reaches.

Rounick et al. (1982) also noted that in New Zealand streams there was little change in species diversity or relative abundance between unlogged and logged catchments. Many aquatic insects feed on both autochthonous and allochthonous food sources so that dramatic shifts in community structure may not result after opening the canopy (Dudgeon 1989). However, Hawkins et al. (1982) found that, in the Pacific Northwest, the effect of canopy removal dominated the effect of substrate in determining insect guild abundance in harvested areas. Differences in growth rates and life history patterns between forested and non-forested members of the same species may also occur. In many studies, increases in absolute abundance of specific taxa, particularly *Baetis* mayflies, have been observed in harvest-exposed reaches (Murphy et al. 1981, Fuller et al. 1986, Gurtz & Wallace 1984, Noel et al. 1986, Richards & Minshall 1988, Robinson et al. 1990, Kohler 1992). *Baetis*' short, multivoltine, fecund life history aids in rapid colonization of exposed reaches. High population densities are usually short-lived, however, because primary production levels decline quickly as shade from herbs, forbs, and eventually trees increases (Murphy 1979).

Newbold et al. (1980) observed depressed insect community diversity on streams without buffer strips as a result of higher densities of *Baetis*, a common stonefly, and Chironomidae related to increases in primary productivity. Some caddisflies, such as *Micrasema*, also show preferences for periphyton and algae, although Becker (1994) observed the addition of moss increased *Micrasema*'s preference for moss/periphyton substrates over periphyton alone. Because moss occurs most often under shade, *Micrasema*'s response to canopy openings may be difficult to distinguish. Towns (1981) found filter-feeders in higher numbers beneath an artificial canopy while collector-gatherers and herbivore-piercers predominated in unshaded reaches. Interestingly,

scrapers were more abundant than collector-gatherers underneath the canopy and less abundant in the exposed stream sections. Predator abundance may increase in open-canopied riffles because of corresponding increases in collector (i.e., prey) populations (Murphy & Hall 1981). Dudgeon (1989) found predator populations to be strongly related to densities of collectors and filter-feeders.

Salmon also respond to removal of stream shading with increases in population (Hawkins et al. 1983, Koski et al. 1984). Thedinga et al. (1989) observed weight and length increases that were directly proportional to periphyton biomass and benthos density. Although increases in periphyton and insects may correlate with short-term increases in salmon fry and parr, these increases may only be seasonal. Johnson et al. (1986) observed parr density in Alaskan clearcuts decreased by 91% in the winter from summer densities while densities in buffered and old-growth reaches increased by 400% and 100% respectively compared to summer densities. Alaskan streams flowing through clearcuts freeze over more rapidly during the winter which may have contributed to the 91% decline. The greater increase in buffered reaches as compared to old-growth may be a result of more easily processed deciduous and herb detritus under the buffered reach which increased insect abundance and production compared to old-growth communities (Duncan et al. 1989).

Forest road building and harvesting directly adjacent to the stream also may increase sedimentation and the delivery of suspended food sources in the form of seston (Gurtz et al. 1980, Ahtiainen 1990). This may affect filter-feeding insects by either increasing food sources or clogging nets. However, initial increases in productivity and collector/scrapper abundance resulting from opening the stream canopy may overshadow any detrimental effects of sedimentation (Murphy et al. 1981). Short-term effects of opening the stream canopy result in initial increases in primary productivity and potential increases in direct solar radiation at the stream's surface. This may increase stream temperature (Brown & Krygier 1970, Beschta et al. 1987).

2.6. Stream Temperature

Stream temperature is a critical component of the stream's physical, chemical, and biological nature. Physically it affects the rate of litter decomposition. It also is affected in turn by streamflow and substrate character. Higher temperatures increase leaf litter processing (Noel et al. 1986), lower streamflows facilitate more rapid heating, and substrates like bedrock may provide resident heat storage (Brown 1970). Chemically, temperature affects dissolved oxygen concentrations, nutrient solubility and concentrations, water density, and insect food quality. Dissolved oxygen and other chemical concentration levels are inversely related to stream temperature while nutrient solubility and the productivity of aquatic plants are directly related to water temperature. Food quantity and quality are positively affected by stream temperature. Therefore, streams with higher temperatures experience both decreases in dissolved oxygen as well as increases in biological oxygen demand (BOD). BOD is also triggered by increases in any organic debris. Biologically, stream temperature affects insect growth, food ingestion and assimilation, reproduction, diapause, quiescence, pupation, metabolism, and respiration (Sweeney 1984, Hogue & Hawkins 1991, Bowles & Allen 1992, Newbold et al. 1994). It is often difficult to separate the indirect effects of temperature on food quality from its direct effects on insect metabolism (Cummins & Klug 1979). Low temperatures slow developmental processes while temperature increases up to threshold levels speed development rates. Increases past temperature thresholds cause decreases in development. Moderate increases in stream temperatures may also increase salmon smolt numbers, stimulate earlier fry emergence, lengthen fry's summer growing season, and cause earlier seaward migrations (Holtby 1988, Thedinga et al. 1989).

Aquatic insects tolerate a wide range of stream temperatures, from cold extremes of 0°C to temperatures as high as 50°C. Insects are thought to have evolved from cold water habitats, so most tolerate low extremes more readily than maxima (Ward & Stanford 1982). Shredders especially appear to be adapted to low temperatures which coincide with peaks in populations after the autumn leaf drop (Lamberti & Morre 1984). However, some species of insects can tolerate quite high temperatures, such as the fly,

Scatella thermarum, which has been collected from hot springs at 47.7°C (Merritt & Cummins 1984). The thermal death point of caddisflies and mayflies is typically around 30°C (Merritt & Cummins 1984). Fuller and Fry (1991) observed that at 5°C growth of *Hydropsyche* was slower than at 14°C. At 20°C, the growth response was mixed, with negative growth rates on low quality food and positive growth rates on high quality food. Hogue and Hawkins (1991), however, observed greater body size achievement in three species of caddisflies growing at low temperatures because low temperatures extended each development phase and therefore the time for structural growth. Fecundity, or egg production, improves with body size, so larger body sizes are desirable. Ward and Stanford (1982) also remarked that egg hatching success is optimum at moderately low temperatures, although higher temperatures provide for more rapid egg development. According to the thermal equilibrium hypothesis, body size and fecundity are maximized at optimum temperature ranges within geographic areas and latitudes (Rader & Ward 1990). Life history and morphological characteristics decline as temperatures become warmer or colder outside the insects' latitudinal range.

Threshold temperatures determine the timing of different life history stages, such as emergence, quiescence, pupation, voltinism, and diapause (Ward & Stanford 1982, Jamieson-Dixon & Wrona 1992, Newbold et al. 1994). In the case of *Rhyacophila vao*, early instar growth may be temperature dependent while final instar development and pupation may be controlled by predetermined life-cycle stages (Jamieson-Dixon & Wrona 1992). *Rhyacophila evoluta*'s life cycle varies from 1 to 3 years depending on temperature (Ward & Stanford 1982). Some mayflies, specifically Baetidae, produce an extra generation under warm summer conditions. *Baetis vernus*, a European species, however, exhibits a univoltine life cycle under above-average winter temperatures and a bivoltine or multivoltine cycle under colder winter conditions (Illies & Masteller 1977). Higher water temperatures may also cause greater separation between the emergence of males and females resulting in mating difficulties (Ward & Stanford 1982). Lehmkuhl (1972) observed that because a reservoir elevated water temperatures in the winter and cooled them in the summer, mayfly abundance was reduced 40% downstream. Although water temperatures did not reach lethal levels, the reversal of natural temperature regimes

caused by the dam confused mayfly life histories and prevented hatching, growth, and emergence. Perry et al. (1986) found that, by lowering summer river temperatures, deep release reservoirs caused a 2 to 4 week delay in peak emergence times for *Drunella* and *Hydropsyche*.

Clearcutting and other disturbances, such as fire, which remove stream canopy cause localized increases in summer stream temperatures and decreases in winter stream temperatures, depending on the shade provided by dead or residual vegetation and topography (Lee & Samuel 1976, Amaranthus et al. 1989, Nakamura & Dokai 1989, Ahtiainen 1992). Increases in stream temperatures are undesirable because of their direct metabolic and indirect oxygen concentration effects on resident and anadromous fish populations. Water temperature rises primarily as a result of direct solar radiation loading (Brown 1969, Beschta et al. 1987, Brown 1991). Advection from incoming and outgoing water, convection from the surrounding air, evaporation, and conduction from the surrounding soil and substrate are more minor components of a stream's heat budget (Brown 1969, Brown 1970, Beschta et al. 1987). In the absence of increases in solar radiation, these factors may contribute to an individual stream's temperature equilibrium. Rates of increase are also affected by flow where streams with slow velocities and large surface area absorb more heat than those with rapid currents and narrow channels. However, although flow and stream temperature are highly correlated, no consistent relationship between the two exists (Statzner & Higler 1986). There is increasing evidence that after returning beneath the riparian canopy, water heated through the clearcut or other opening cools to a baseline stream temperature "signature" (Newton et al. 1995). A stream's temperature signature is created by the unique geomorphic, channel, and climatic conditions found at that stream. Cooling may be a function of convective loss to the surrounding air, conduction from surrounding soil and substrate, and advection from incoming groundwater.

The Alsea Watershed Study conducted on three stream basins in western Oregon in the late 1960's, was one of the first attempts to piece together stream energy budgets and the effects of forest harvesting. Despite its limitations which include lack of replication, confounding of channel morphology with treatment, and no attention to

stream cooling outside of clearcut areas, it has offered a starting point for other stream temperature, biology, and harvest research. Brown and Krygier (1970) observed that the minimum stream temperatures recorded on the clearcut and burned Alsea watershed were similar to the maximum stream temperatures found in the control watershed. Maximum stream temperatures in the clearcut watershed increased by 7.8°C the first year after harvesting. A third Alsea stream basin was partially cut and strips of vegetation were left alongside the stream. These streamside strips of residual vegetation proved effective in shading the stream and preventing increases in stream temperature. Because of the strong positive effects of solar radiation loading on stream temperature, riparian vegetation shading the stream has the largest effect in preventing local temperature increases during summer low flows and ameliorating rapid and large fluctuations in stream temperatures (Brown & Krygier 1970, Rishel et al. 1982, Barton et al. 1985). Streamside cover also insulates streams in winter, helping to keep them warmer (Beschta et al. 1987, Weatherly & Ormerod 1990). The degree to which stream temperature responds to buffer strips depends on stream velocity, stream depth, and ground water inflow.

Currently there is debate over the longevity of stream temperature increases. Streams typically warm as they travel from headwaters to low elevation rivers as a result of air temperature increases, proportional decreases in groundwater inflow compared to streamflow, and natural widening of rivers (Minshall 1968, Beschta et al. 1987, Sullivan et al. 1990). In natural systems, once stream temperature has increased as a result of increased solar energy, it does not continue to do so indefinitely. Rather, there is evidence that after increasing through an exposed reach, stream temperatures may cool as a result of groundwater inflow and shading through forested areas (Levno & Rothacher 1967, Newton et al. 1995). After passing through a 200-m clearcut, cooling from between 0.5° and 1.5°C was observed downstream under a buffered riparian canopy (Dent 1995). Newton et al. (1995) observed that cooling after exposure to solar radiation as a result of clearcutting or beaver dams occurs within a relatively short distance downstream. Figure 2 of the seven day running mean temperatures on the hottest day in July 1995 for one creek from headwaters to seventh-order stream in the Oregon Coast Range shows both a downstream warming trend as the stream travels farther from its

origin and rapid cooling after exposure to solar radiation. Point A illustrates that under undisturbed riparian vegetation, peaks observed within a clearcut bordering both sides of the stream quickly dissipate to levels characteristic of a moderate longitudinal downstream increase. Studies have also shown that streams exposed in small patches do not show significant increases in temperature (Levno & Rothacher 1967).

Clearcutting affects diurnal temperature fluctuations as well as raising average maximum and mean stream temperatures. Within 100 to 200-m clearcut reaches, diurnal stream temperature fluctuations rose 1.5° to 4.3°C higher than in forested reaches (Dent 1995). Small, exposed streams may fluctuate 3°C per hour which is more than the daily fluctuation in some rivers (Ward & Stanford 1982). Diurnal fluctuations are greatest in the spring and/or early summer depending on the hydrologic regime (Edington 1965, Rishel et al. 1982, Beschta et al. 1987). Rishel et al. (1982) observed spring fluctuations 3°C greater in a clearcut watershed with 30-m buffer strips than a control watershed. Newton et al. (1995) observed increases in diurnal fluctuations below a 100-m sized clearcut. However, 330 m downstream, diurnal fluctuations were of similar magnitude and range as pre-clearcut diurnal fluctuations. Rishel et al. (1992) observed that a clearcut watershed with negligible cover exhibited an 11°C increase in diurnal fluctuations compared to the control watershed. Vegetation obviously ameliorates diurnal fluctuations as well as long-term maxima and means. Aquatic insects respond to diurnal fluctuations with changes in drift, movement, and feeding activity (Ward & Stanford 1982). The magnitude of diel fluctuations also affects egg development speed and success (Sweeney 1984). High or prolonged peaks may accelerate growth processes, increase drift, and alter feeding habits.

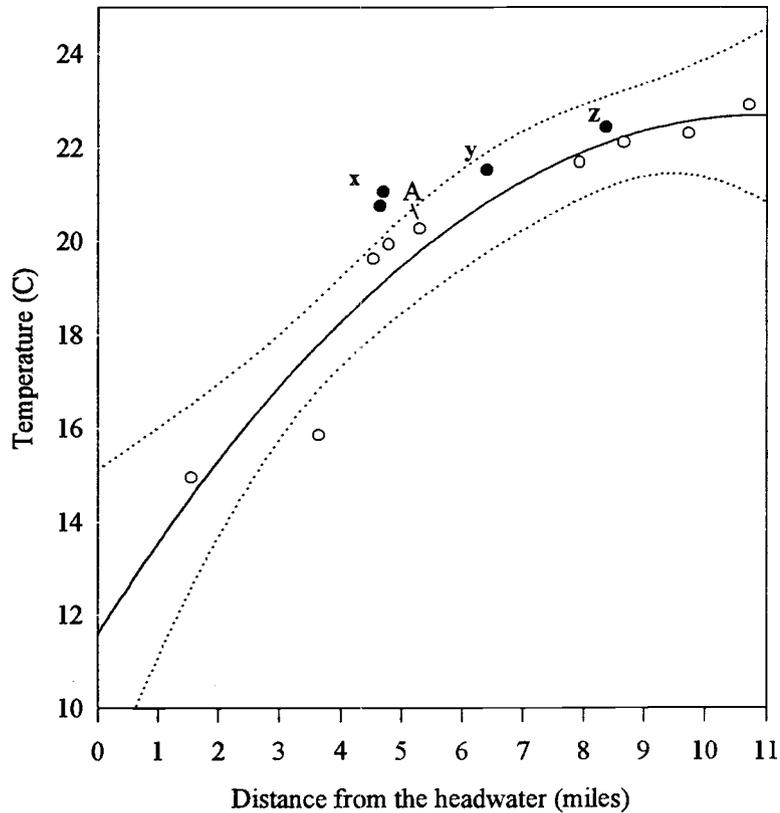


Figure 2. Seven day running mean maximum temperatures ($^{\circ}\text{C}$) of Brush Creek, central Coast Range, Oregon for the hottest July day (07/18/95) from headwaters to confluence. Point A shows that peaks observed within a clearcut exposed reach quickly dissipate under riparian buffer. \circ =undisturbed riparian vegetation buffer. \bullet =disturbed riparian vegetation: x =clearcut, y =beaver complex, z =clearcut under new Oregon Department of Forestry rules. — = regression line based only on temperature readings underneath undisturbed riparian vegetation. = 95% confidence interval. Reproduced from Newton et al. 1995.

3. METHODS AND PROCEDURES

3.1. Site Descriptions

Silvicultural treatments were installed on four creeks in western Oregon in the early winter of 1993. Two creeks, Ames and Mosby, are located in the low elevation western Cascades. Ames Creek is a third-order stream located five miles southwest of Sweet Home, Oregon (44° 22' lat. 122° 41' long.) and is primarily a gravel, cobble stream with interspersed bedrock reaches and mild gradient (Table 1). Mosby Creek is a fourth-order stream located approximately 16 miles southwest of Cottage Grove, Oregon (43° 33' lat. 122° 50' 30" long.) and is a boulder, cobble, higher gradient stream with no bedrock and little velocity slowing structure, including channel meandering. Buttermilk and Pancake Creeks are in the central Oregon Coast Range approximately 19 miles east of Newport, Oregon (44° 40' lat. 123° 42' 30" long.). Buttermilk Creek is a third-order stream and Pancake Creek is a second-order tributary of Buttermilk. Both Buttermilk and Pancake have large colonies of beaver (*Castor canadensis* (Kuhl.)) with frequent gradient-breaking steps created by their dams. General locations of beaver colonies are identified in Figure 3b. Ames and Mosby did not have resident beaver colonies during the two sampling seasons. The Coast Range streams tended to have more small and fine substrates, less bedrock, and more channel sinuosity than the Cascade Range streams. Stream width, gradient, and mean summer flow are given in Table 2. All streams except for Pancake Creek flow in a northwest direction. Pancake Creek flows northeastward. Streams are located on private forest land that has been harvested under pre-1994 Oregon Forest Practice Rules prior to treatment harvests. Oregon Forest Practice Rules, at that time, enforced the use of stream buffer strips between the harvest area and stream channel based primarily on a minimum standard of leave-tree basal area.

Table 2. Descriptive stream characteristics by treated stream. Ames creek basin area encompasses the watershed area extending down to the lower end of the experiment site; all other creeks are for the entire basin. * includes both Buttermilk and Pancake Creek within the same basin.

Stream	Basin Area (hectares)	Average Stream Width (m)	Gradient	Average flow (cms)	
				1993	1994
Ames	1441	3.6	3%	0.282	0.138
Buttermilk	702*	3	3%	0.204	0.113
Mosby	26022	7	5%	1.065	0.275
Pancake	148	1.4	6%	0.085	0.031

Western Oregon has a Mediterranean summer-dry climate where approximately 87% of the annual precipitation falls from October to May with little appreciable precipitation from July to September. Total precipitation varies locally with estimated totals being 240 cm for Buttermilk and Pancake Creeks, 120 cm for Ames Creek, and 160 cm for Mosby Creek (Newton, M., personal communication). The summer of 1993 was an exception to this pattern with rain and cool weather persisting into August. Average maximum air temperature in Corvallis, Oregon reached 24.6°C for the first sample season after harvesting and cloud cover was heavy during June and July (U.S. Weather Bureau 1993). Cloud cover may slow development of periphyton and macro-algae densities. The summer of 1994, however, was warmer with air temperatures in Corvallis, Oregon reaching an average maximum of 26.7°C and no effective rainfall from July to September (U.S. Weather Bureau 1994). The effects of stream temperature and solar radiation on mayflies and caddisflies were expected to be more visible in 1994, despite moderation from a year of vegetation growth and possible adaptation from multivoltine insects.

In all streams, upslope forests are of the Douglas-fir/western hemlock climax forest type (Franklin & Dyrness 1973). Riparian overstory vegetation is predominantly deciduous and consists of red alder, bigleaf maple (*Acer macrophyllum* Pursh.),

cottonwood (*Populus trichocarpa* Torr. and Gray) and hazel (*Corylus cornuta* var. *californica* Sharp.). Conifers include Douglas-fir (*Psuedotsuga menziesii* (Mirb.) Franco.), western redcedar (*Thuja plicata* Donn ex D.Don.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and grand fir (*Abies grandis* (Dougl.) Lindl.). Understory vegetation was primarily salmonberry, Himalayan blackberry (*Rubus procera*), nettle (*Urtica gracilis*), thimbleberry (*Rubus parviflorus* Nutt.), swordfern (*Polystichum munitum* (Kaulf.) Presl.), bracken fern (*Pteridium aquilinum* (L.) Kuhn.), and some salal (*Gaultheria shallon* Pursh.) and mountain Oregon grape (*Berberis nervosa* Pursh.). Red alder stands were widely spaced and mature on most streams although the salmonberry and Himalayan blackberry understories could be quite dense.

Treatment harvests were installed using cable yarding with full suspension or “shovels” to remove timber from alongside the streams. Three clearcuts of two different sizes were installed along a 1600-meter reach in the same order on each stream. Streamside clearcuts were extensions of upslope harvest operations so the total area harvested varied on each creek. The length of clearcut alongside the creeks, however, did not vary. Both sides of a stream were harvested to within 3 m of the channel and all major and/or marketable overstory species were removed. There were no recognizable tree buffers along the streams although bankside shrubs often remained.

On Ames and Mosby Creeks a 200-m clearcut was installed in the upper 800 m of the treatment reach and two 100-m clearcuts were installed within the lower 800 m (Figure 3a). At Buttermilk Creek, the landowner’s property line was within 300 m of the upper 100-m patchcut, leaving no room for the 200-m patchcut. The 200-m patchcut was therefore installed up Pancake Creek (Figure 3b). Because Pancake Creek contributes approximately 25% of the total flow to the section of Buttermilk Creek downstream of the tributary junction, the 100-m patchcuts do not receive the full effect of the 200-m clearcut.

3.2. Experimental Methods

Insect sampling. Four sampling stations were installed on each stream (Figure 3). Sampling was designed to maximize the area monitored on each creek while keeping the number of samples in the overall study to a workable maximum. Station sites were located arbitrarily without preconceived bias by determining the general area where assessment was required and then randomizing the exact location of the station somewhere within 200 m of that area in uncut, buffered reaches and within a 60-m reach in the clearcut. This was done to avoid a bias toward particular stream environments and to approximate a stream's general habitat among the four stations.

The four stations are generally located: a) upstream from the treatment reach (station 1) (Figure 3), b) downstream of the 200-m clearcut but above the upper 100-m clearcut (station 2), c) within the upper 100-m clearcut (station 3), and d) below the entire 1600-m treatment reach (station 4). Station 1 serves as a reference and is located anywhere between 70 m and 190 m upstream of the 200-m clearcut. Station 2 is designed to capture the influence of half of the treatment removal of stream canopy and is located between 25 m and 50 m upstream of the middle 100-m clearcut. Station 3 reflects the direct influences of the silviculture treatment, including exposure to radiation and any streamside disturbance and is located at least 20 m from either edge of the upper 100-m clearcut. Station 4 is a sensor of the cumulative effects of all upstream events including the local removal of the riparian canopy along the 1600-m reach, and is located between 30 m and 100 m downstream of the lower 100-m clearcut. Stations 1, 2, and 4 remain under riparian canopy to minimize the direct influences of canopy removal while station 3 tests these direct effects. Because of the differences in study design at Buttermilk and Pancake Creeks, Pancake Creek contains only stations 1 and 2. Buttermilk Creek has four stations. However, station 1 is located upstream of the confluence of Pancake Creek and station 2 does not reflect the full effect of the 200-m clearcut (Figure 3a). The mayfly and caddisfly responses on Buttermilk were included in the analysis although each station received a slightly different treatment effect than the corresponding stations on the other

three streams. Even the reference station (1) on Buttermilk differs from other reference stations in that it is directly downstream of an established beaver dam. All four treatment reaches were 3-6 miles from their respective headwaters.

Macroinvertebrates were sampled on four equally spaced collection dates beginning in June and ending in September during the summers of 1993 and 1994. Samples were collected using a Surber sampler with a 0.09m^2 sampling area and a 500μ mesh net. Each sampling station is 5-m long. Width varies with fluctuating stream flows, but is divided into right, left, and center sections. Length-wise, the station is divided into 15 0.33-m sections (Figure 4). This provided approximately 45 potential sample areas in which to randomize sample collection. Six samples were collected; two from the left, center, and right sides of the creek. After sampling each month, those six areas on the 5-m grid which had been sampled were removed from the pool of potential sample sites for the following month. Because insects have been shown to recover from sampling disturbance within two to four weeks (Williams & Hynes 1976, Reice 1985), and I allowed eight weeks between potentially repeating sample sites, the chance of including repeated sampling effects was minimized.

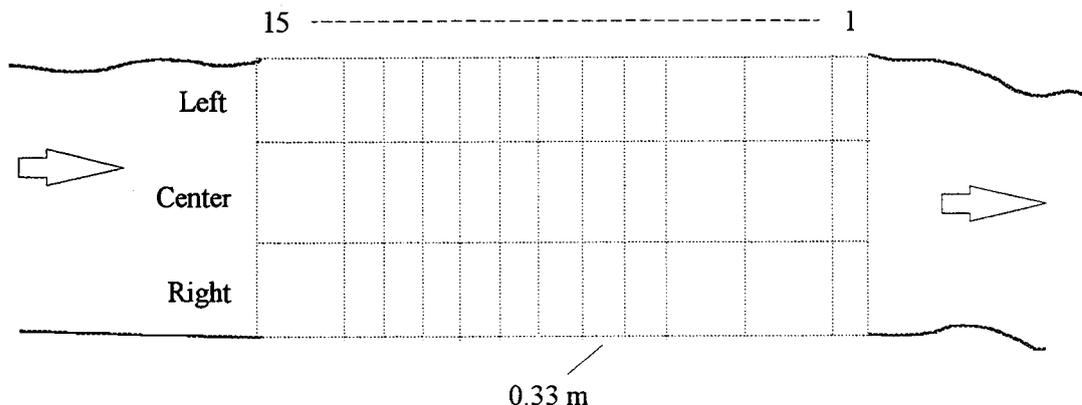


Figure 4. Schematic design of sample location grid used to randomize samples at each station.

Samples were preserved in 95% ethyl alcohol and returned to the lab for cleaning, picking, and identification. Macroinvertebrates were separated from debris larger and smaller than 500 μm by wet-sieving through a series of stacked sieves (4mm, 2mm, 500 μm). Cleaned samples were stored in 95% ethyl alcohol. The cleaned six samples from each stream, station and date were pooled into a single sample unit and subsampled to 50% of the original sample size. Subsample size was determined by calculating initial sample variance with 20 of 112 sample units to determine what percentage of the pooled sample provides an accurate representation of the entire sample. Subsampling was necessary to speed the picking and counting process and is commonly used in macroinvertebrate studies (Resh & McElvay 1993). Subsampling was completed by evenly distributing the six samples in a tray, placing a 3X4 grid over the tray and then randomly selecting six of the twelve grids. Grid samples were placed under a microscope and all insects were picked and separated into Ephemeroptera, Trichoptera, and "Other" vials. The contents of the mayfly and caddisfly vials were then placed under the microscope, identified to genus because of the paucity of species level identification keys, and counted. The mayfly and caddisfly counts are based on the subsampled population and represent approximately half of the original sample.

Mayflies and caddisflies were assigned to functional feeding groups based on classifications in Merritt and Cummins (1984). Because some mayflies and caddisflies function in more than one functional feeding group, I chose the two primary functional feeding groups for taxa with more than one and then arbitrarily weighted the second functional feeding group half of the first. So, for example, *Baetis* are generally thought to be collector-gatherers. However, they have also been observed, based on mouthparts and behavior, as scrapers. Because I could not distinguish between their two functions in our streams, I included *Baetis* populations in the scraper functional feeding group, but weighted its count by 0.5. Diversity at each station was calculated using the Shannon-Wiener index ($H' = -\sum p_i \log p_i$, where p_i represents the proportion of individuals in a sample unit belonging to species i .) and the Shannon evenness index ($E = H' / \ln S$). I chose Shannon-Wiener's index because it is widely used in other macroinvertebrate studies,

emphasizes proportions of the number of genera collected, and increases rapidly with increasing species richness while still being linearly related to species evenness. In addition, index values from a number of samples are normally distributed which allows the comparison of diversity between stations using analysis of variance (Taylor 1978, as cited in Magurran 1988).

Absolute abundance and relative abundance were used as abundance measures because we were interested in the actual increase in invertebrate numbers as potential sources of fish food and in the relative increase in certain genera in response to either treatment effects or longitudinal differences within streams. Resh and McElvay (1993) report that a large percentage of benthic macroinvertebrate studies use either total or relative abundance. Relative abundance differs from absolute abundance in that it transforms absolute counts into percentages of the total population; a "piece of the pie" transformation where, as a result of treatment, some insects are cut a larger slice while others are served less. When analyzing absolute abundance, one can only determine whether actual counts of a particular insect change with time or between locations. By incorporating relative abundance, one can determine if this increase was a real increase in a genus's population or if the entire community increased relatively as well. If there were no significant increases/decreases in absolute number, relative abundance would allow one to determine if, as a result of treatment, an insect's relative proportion in the community increased/decreased. Sample density was not calculated because the habitat within the 5 m sampling point was quite diverse and patchy. After pooling the six samples and combining habitats, I was uncertain if the calculated density accurately reflected the actual invertebrate density within the station. Had I not pooled the station samples, density would have been a useful and informative abundance measure. Biomass was also not calculated because of time and budget constraints.

Environmental parameters. Stream flow was recorded at each sample date using a Marsh-McBurney flow meter to measure stream velocity. Velocity and discharge were measured at the downstream edge of the station at every sample date. These locations were often not ideal for discharge calculations because of irregular channel bottoms. Discharge readings frequently varied more than ten percent between stations on

the same stream and date. However, measuring velocity close to where the insects experienced it was critical to assessing local habitat conditions. Unfortunately, equipment constraints did not allow velocity readings near or at the boundary layer. Substrate composition was measured ocularly at each sample date to estimate the percentages of boulders, cobbles, gravel, sand, silt, and bedrock at each station. Estimations did not vary by more than 10% each month and by not more than 5% between years accounting for changes in channel width from decreasing flow. Substrate composition was fairly stable within the streams throughout the experiment.

Stream temperature was monitored continuously by Adaptive COPE throughout each summer with Hobo™ thermistors and Omni Datapods. Unfortunately, communication within integrated research projects is often lacking and/or misunderstood. As a result of miscommunication, stream temperatures were not recorded within the clearcut reaches corresponding with station 3. Therefore, maximum and mean temperatures experienced by insects in exposed reaches are not known precisely for this study. They, however, can be estimated with reasonable precision. Other studies have reported increases in stream temperatures through clearcuts of 100 to 200-m between 1° and 10°C. Average temperature increases vary between 3°-5°C (Beschta et al. 1987, Holtby 1988, Amaranthus et al. 1989, Sullivan et al. 1990, Brown 1991, Holopainen & Huttunen 1992, Lorensen et al. 1993) although recent data from Newton et al. (1995) suggests a more moderate 1.5°C temperature increase. To fill the missing data points in the temperature data, I added 3°C to the temperatures recorded nearby upstream at station 2. These constructed temperatures, however, are not used for graphical or means separation analysis. Thermistors, such as the HOBO, measure temperature continuously at small time intervals throughout the sampling period. In order to obtain a discrete data point to represent the temperature conditions insects experienced 30 days prior to sampling, mean and maximum temperatures were averaged over the period prior to sampling.

Radiation was measured near each station in the center of the stream channel using a Solar Pathfinder™ in August of 1993 by Adaptive COPE. Solar Pathfinders estimate the absolute energy striking the stream's surface by incorporating vegetative

shading, cloud cover, and topographic shading with the sun's latitudinal path to produce the amount of unobstructed energy striking a surface. Energy is measured in BTU's/foot²/day. In 1994, radiation was measured within the clearcut stream portions only and so the dataset was inadequate for assessing effects between the three stations under the riparian buffer. However, despite less cloud cover in 1994 which may have increased incident solar radiation, streamside vegetation recovered the second summer after harvesting and may have provided more shade along the exposed reaches. Therefore, solar radiation levels may have likely been either similar or less than 1993 levels beside the stream edges. A lack of solar radiation effect in 1993 may also be assumed in 1994. Although there was a significant correlation between stream temperature and solar radiation in our four streams in 1993, solar radiation was not used to determine stream temperature because other studies had observed a low correlation between stream temperature and solar radiation (Tait et al. 1994).

Reference stream data. Reference stream data were obtained from a macroinvertebrate sampling study being conducted jointly by the Oregon State University Department of Fisheries and Wildlife and the Environmental Protection Agency. Samples used as reference streams in this study were collected from three second- to third-order streams in the western Cascades along randomized systematic sampling stations. Reference streams were similar in order, gradient, and aspect to the treated streams but differed in the downstream length of sampled stream reach. The creeks are Ennis Creek located southeast of Nimrod, Oregon (44° 06' lat. 122° 22' long.), Southfork of Crabtree Creek located northeast of Lebanon, Oregon (44° 42' lat., 122° 37' long.), and Mack Creek located in the H.J. Andrews Experimental Forest (44° 10' lat. 122° 05' long.). Mayflies and caddisflies were sampled once each summer in 1992 and 1993 in mid-July or August using a Surber sampler with a 500 μ mesh net.

For the purposes of this study, reference stream Surber samples were pooled to include the same stream bottom area (three Surber samples) as the treated subsampled dataset. The pooled samples were taken from samples collected at the upper, middle, and lower end of the reference stream sample reach. In this way, "stations" were created that could be tested for natural sampling variability of samples collected in a downstream

direction. Only stations 1, 2, and 4 are represented because each is underneath riparian canopy cover. The lengths of the stream reaches were between 150 and 200 m and the maximum distance between "stations" 1 and 4 is 116 m. Stream reach length does not approximate the 1600 meters between stations 1 and 4 on the treated streams. Therefore, along with treatment differences the stations on the reference streams differ from treatment streams in longitudinal population variation. It is impossible to discern between these two sources of variation. Reference stream mayflies and caddisflies at "stations" 1 and 4 may have a higher likelihood of shared populations through aerial oviposition and upstream migration by adults than stations 1 and 4 on the treated streams. Although nymph habitat areas are relatively small, drift effects lengthen population influences by 10-20 times the stream width downstream (Gregory, S.V., personal communication). However, the reference streams may still offer a picture of untreated sampling variation which offers a comparison to the variation observed on the treated streams. The reference streams do not, however, provide a direct comparison between untreated and treated mayfly and caddisfly communities.

Species representation among the treated and reference creeks was very similar with a few minor differences (Appendix B). The orders Ephemeroptera and Trichoptera were analyzed at the genus level and the same genera used in the treated streams were used in the reference stream analysis for absolute abundance. All mayflies and caddisflies sampled in the reference streams were used to calculate relative abundance, functional feeding groups, and diversity calculations. Comparable environmental parameters were not measured on the reference streams that had been measured on the treated streams. Therefore, the statistical analysis of the reference streams differs. However, reference streams were used solely to compare untreated streams with treated, and this was accomplished to the extent possible with the data available.

3.3. Statistical Analysis

Not all mayfly and caddisfly genera were found each year in each stream. Many, particularly of the Limnephilidae family, were sampled only once or twice a summer. Because of the resulting large number of zeros within the dataset, many of the rare mayfly and caddisfly genera exhibited nonconstant variance, skewed distributions, and non-normality. Those mayflies and caddisflies which exhibited these conditions based on plotting residuals by expected values and reviewing boxplot diagrams, normal probability plots, and stem-leaf diagrams as well as the Shapiro and Wilk W -test for normal residuals (Stafford & Sabin 1995), were removed from the mayfly and caddisfly absolute count dataset. These taxa were used, however, to calculate relative abundance, functional feeding groups, and diversity. The remaining insects used for the absolute count analysis consist of the most numerous and typically common stream caddisflies and mayflies in western Oregon (Appendix A). Mayfly and caddisfly counts, functional feeding groups, and average stream velocity (cm/sec) were expressed as transformed natural logs (insects, $\log[x+0.25]$; velocity, $\log[x+0.05]$). Relative abundance of mayflies and caddisflies and substrate percentages were analyzed as transformed arcsine square-roots. Reference stream mayfly and caddisfly counts and functional feeding group data were expressed as log transformed data ($\log[x+0.25]$) and relative abundance data as arcsine square root transformed data.

Transformations were necessary because the assumptions of the analysis of variance require that, in order to test for significance, experimental errors must be independently and normally distributed with a common variance and that the scale of variable measurement must be linear (Steel & Torrie 1960). Stafford and Sabin (1994) recommend that if the ratio of largest to smallest count is greater than ten, a log transformation may be needed. *Baetis* counts, for example, ranged between 3-529 per subsampled sample and *Neothremma* counts ranged between 0-156 per subsampled sample. These orders-of-magnitude differences caused increasing variance above the treatment mean and nonlinear scales of measurement (Allan 1984, Norris & Georges 1993). Log-transformations equalized the variances in genera with a wide range of

population counts. Arcsine square-root transformations are appropriate for percentages that cover a wide range of values (i.e., from 0.20-0.80 or greater) because as a proportion approaches 1 or 0, its variance approaches 0 (Steel & Torrie 1960, Stafford & Sabin 1994).

After dividing data into individual months for each year, the absolute and relative abundance of each mayfly and caddisfly genus, functional feeding group, and diversity index were correlated with maximum stream temperature ($^{\circ}\text{C}$), log-transformed average stream velocity, radiation ($\text{BTU} \cdot \text{s}/\text{ft}^2/\text{dy}$), and the boulder, cobble, gravel, sand, silt, and bedrock arcsine square-root transformed percentages at each station. Pearson correlation coefficients were used to determine the intensity of the simple linear association between an environmental variable and mayfly and caddisfly abundance, functional feeding group or diversity (Steel & Torrie 1960, Stafford & Sabin 1994). Both high negative and positive correlations were used. Based on the Pearson correlation coefficients and graphical analysis, environmental variables with the greatest consistent significant correlation with individual dependent variables across months and years were then regressed against the absolute and relative abundance of *each* mayfly and caddisfly genus, each functional feeding group, and the diversity index to explain the proportion of the data's variance contributed by environmental conditions (Appendix D).

Residuals from the separate month regressions were merged into a single dataset and then analyzed in a repeated measures analysis of variance to determine the effects of the silvicultural treatment over the course of each summer. Repeated measures analysis is necessary for samples that do not meet the assumption of independence through time. Our samples were collected from the same location four times a summer and one month's sample could not be assumed to be independent of previously collected samples. Testing for repeated measures is a rather subjective statistical operation in that there are a number of criteria that may be assessed in order to determine if compound symmetry is approximated. Compound symmetry is the condition where all variances are equal and all covariances are equal to the product of a constant and the variance (Stafford & Sabin 1995). Compound symmetry is often difficult to meet and no one method for determining repeated measures alone can adequately indicate if it has been met. As a result,

conservative tests (Greenhouse-Geisser coefficient) and less rigorous tests (Mauchly's Test for Sphericity, Huynh-Feldt coefficient) have been developed to determine if the assumption of independence through time is met. Based on 1) correlation matrices for the polynomial contrasts of each mayfly and caddisfly count (functional feeding group, etc.), 2) Mauchly's Test for Sphericity, 3) the Greenhouse-Geisser epsilon coefficient, and 4) the Huynh-Feldt epsilon coefficient, I decided whether there was enough evidence to say that repeated measures existed. If a genus demonstrated repeated measures, then repeated measures analysis of variance was used to determine if stations differed from each other.

Those mayflies and caddisflies which met the conditions for independence through time and did not exhibit repeated measures effects were analyzed in a strip plot analysis with station as the whole unit treatment and month as the sub-unit treatment. Stations which represent the location of the measured mayfly and caddisfly community within each 1600-m experimental reach were the closest concrete measure of treatment effect given the large scale and limited repetition of the harvest areas. Because the study's objective is to determine the cumulative effect of a 25% removal of riparian canopy on mayflies and caddisflies, the insects' responses in a downstream direction to increasing harvest exposure provided the closest insight into possible treatment effects. A Fisher's Protected Least Significant Differences (FPLSD) multiple comparisons test was applied to the analyses to determine significant differences between adjusted means of dependent variables at each station ($p < 0.05$). The adjusted least significant means from this comparison test were used for graphing results.

Reference stream data did not have corresponding environmental variables and therefore, could not be analyzed similarly to account for variation induced by environment conditions. However, because I was not analyzing this dataset for the effects of treatment, but rather for general, "natural" variability in a downstream direction, there was little need to separate out the sources of "natural" and treated variation. Instead, a simple analysis of variance using a randomized block design was run using absolute counts, relative abundance, functional feeding groups, and the Shannon-Wiener index of diversity to test the difference between "stations." FPLSD multiple comparison tests

tested for differences between mayfly and caddisfly adjusted means at each stations ($p < 0.05$).

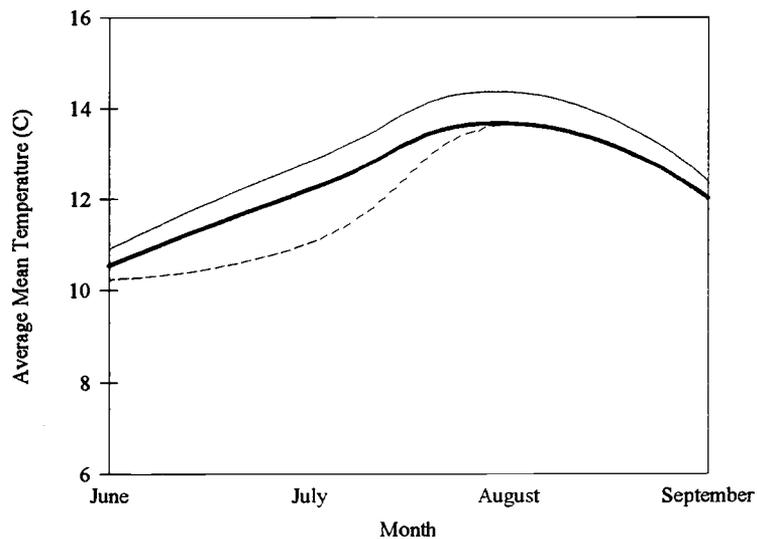
The ANOVAs involved up to 120 multiple comparisons (20 population measures against 6 treatment comparisons). Therefore, 6 correlations with a probability of less than 5% would be expected even in the absence of real treatment effects. No more than 6 should be expected, however, because FPLSD controls for Type I Errors (experiment-wise errors) at the 0.05 probability level. This multiple comparison procedure adds the restriction that the F-test for equal means must be significant at the 0.05 level before those treatments' means may be compared (Stafford & Sabin 1995). Despite the large number of comparisons, spurious correlation where the experiment-wise error rate increases as multiple comparisons increase is corrected for within the analysis.

4. RESULTS

4.1. Physical Stream Characteristics

Temperature. Mean stream temperature increased in a downstream direction in both 1993 and 1994 (Figures 5a & 5b). In 1993, station 4 consistently had higher mean temperatures than stations 2 and 1 (p-values=0.02). Station 2's mean temperatures were higher than station 1's in June and July when solar radiation loading is greater, although differences were not significant. In 1994, station 4's mean temperatures were significantly higher than those at station 1 (p-value=0.0003) but did not differ from station 2. Station 2 exhibited higher mean temperatures than station 1 in 1994 (p-value=0.002). In 1994, most downstream warming appears to have occurred by station 2 (below the 200-m clearcut), though in 1993 significant warming differences occurred between stations 2 and 4. In 1994, temperatures did not increase significantly below station 2 through the two 100-m clearcuts. Station 3's temperatures, which would reflect the actual increase of stream temperature in an exposed reach, were not included in this analysis because the data were not based on actual stream measurements. Mean stream temperatures differed significantly by month in both 1993 and 1994 (93: p-value=0.003; 94: p-value=0.001). In both years, mean temperatures increased through June and July, peaked in August and declined in September at all stations (Figures 5a & 5b). Average mean temperatures at stations 1, 2, and 4 were higher in 1994 than 1993 (p-values=0.0001), likely as a result of less cloud cover, lower flow levels, and higher air temperatures (Table 3).

a)



b)

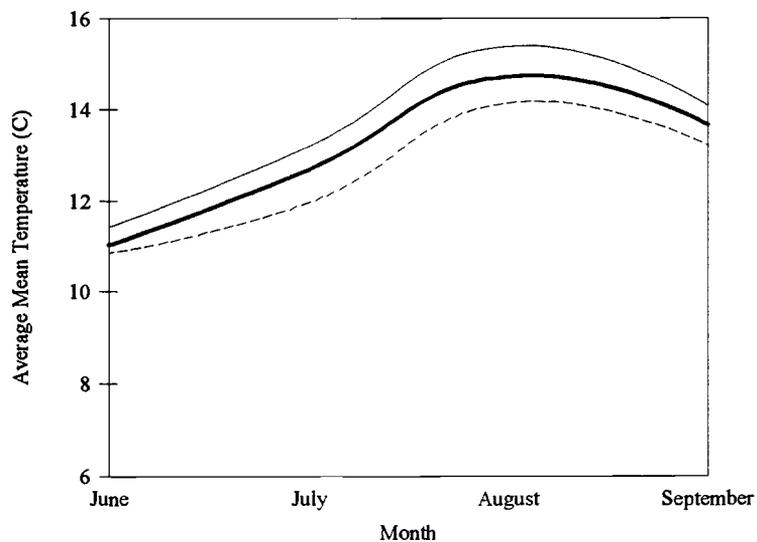


Figure 5a and 5b. Mean stream temperature ($^{\circ}\text{C}$) by month for stations 1, 2, and 4 averaged over the four streams for 1993 (a) and 1994 (b). ----- = Station 1, — = Station 2, — = Station 4.

Maximum stream temperature increased in a downstream direction in both 1993 and 1994 (Figures 6a & 6b). In 1993 and 1994, station 4 had higher maximum

temperatures than station 1 (1993, p-values=0.001; 1994 p-values=0.006) but did not differ from station 2. Station 2's maximum temperatures were consistently higher than station 1's in both 1993 and 1994 (1993: p-value=0.01; 1994: p-value=0.01).

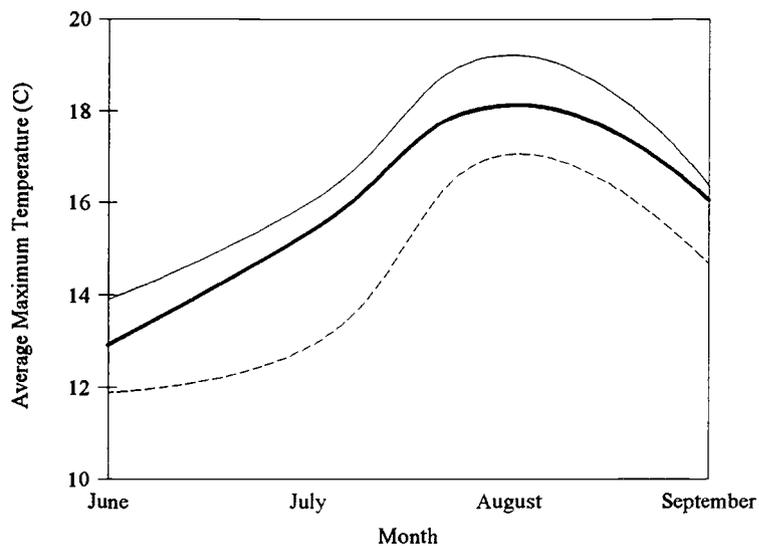
Table 3. Mean and maximum stream temperature (°C) at stations 1, 2, and 4 averaged for the months prior to sampling dates in 1993 and 1994. Standard errors are in parentheses.

Station	Mean		Maximum	
	1993	1994	1993	1994
1	11.9 (0.50)	12.5 (0.46)	14.4 (0.70)	15.4 (0.65)
2	12.1 (0.42)	13.0 (0.44)	15.6 (0.57)	17.0 (0.52)
4	12.6 (0.55)	13.5 (0.51)	16.4 (0.75)	17.8 (0.67)

In both years, maximum downstream warming had occurred by station 2 below the 200-m clearcut and did not significantly increase further through the two lower 100-m clearcuts.

Maximum stream temperatures differed significantly by month in both 1993 and 1994 (1993: p-value=0.001; 1994: p-value=0.002). In both years, maximum temperatures increased through June and July, peaked in August and declined in September at stations 1, 2, and 4. In 1993 there was a large increase in maximum temperature between July and August (Figure 6a). Air temperatures had remained cool and cloud cover heavy into the end of July in 1993. This weather pattern changed in August. Average maximum temperatures did not differ significantly at the reference station between years, but temperatures at stations 2 and 4 were higher in 1994 than 1993 (p-values<0.03) (Table 3).

a)



b)

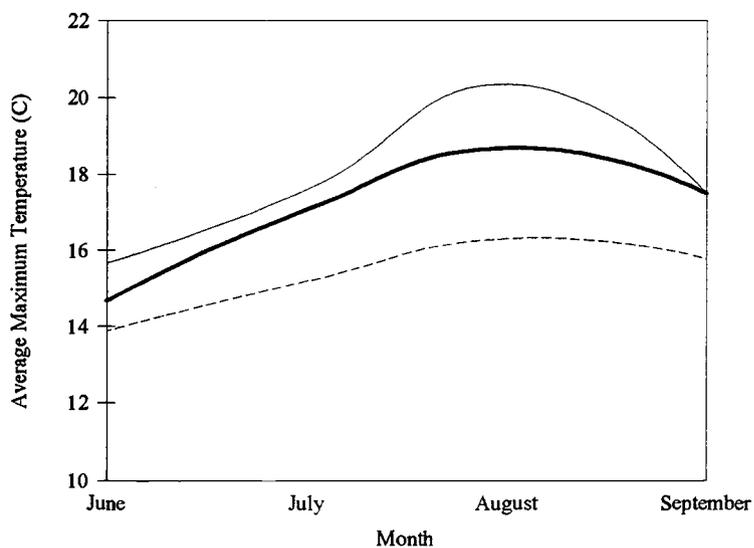


Figure 6a and 6b. Maximum stream temperature ($^{\circ}\text{C}$) by month for stations 1, 2, and 4 averaged over the four streams for 1993 (a) and 1994 (b). ----- = Station 1, — = Station 2, — = Station 4.

Solar radiation. In 1993, radiation loading differed significantly between stations and months (station, $p\text{-value}=0.001$; month, $p\text{-value}=0.004$). Station 3 received the greatest degree of solar radiation energy at the stream surface and showed significantly

higher radiation levels than stations 1, 2, and 4 (p -values <0.0001) (Figure 7, Table 4). Radiation loading patterns, even at station 3, did not strictly follow a seasonal solar path curve in Figure 7 because of the incorporation of topographic and stream shading into calculations of the energy levels striking the stream surface.

Table 4. Mean, maximum, and minimum 1993 solar radiation loading (BTU's/ft²/dy) at stations 1, 2, 3, and 4. Standard errors for the mean are in parentheses.

Station	Mean	Maximum	Minimum
1	333 (64.44)	825	57
2	230 (32.29)	433	62
3	1398 (78.67)	1781	917
4	520 (47.35)	771	302

Station 2 received the least incident solar radiation of all stations (p -values <0.0001). Solar radiation loading at stations 1 and 4 did not differ significantly. Energy levels reaching the stream surface appear to follow similar patterns as stream temperatures though there is no actual data for stream temperatures at the exposed station 3. There was a high degree of correlation between solar radiation and mean and maximum stream temperatures throughout the summer (average Pearson $r_{\text{MEANTMP}}=0.71$, p -value=0.004; average Pearson $r_{\text{MAXIMUMTMP}}=0.75$, p -value=0.003).

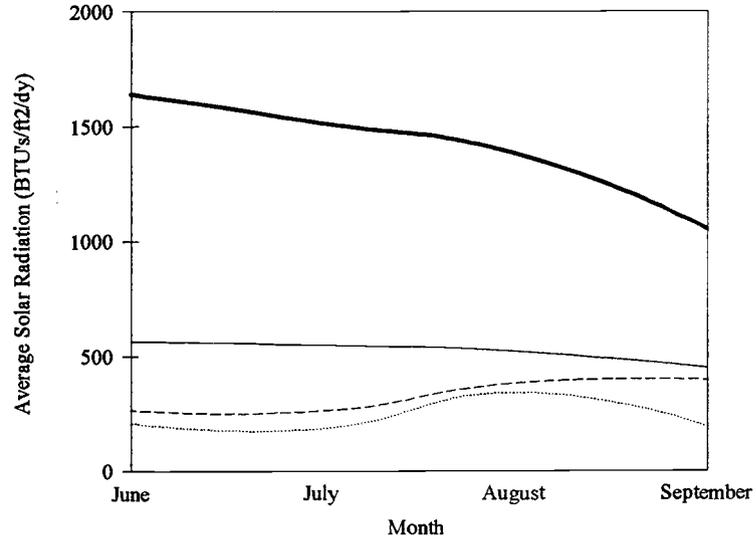


Figure 7. Solar radiation (BTU's/ft²/dy) by month for stations 1, 2, 3, and 4 averaged over the four streams in 1993. ---- = Station 1, = Station 2, ——— = Station 3, — = Station 4.

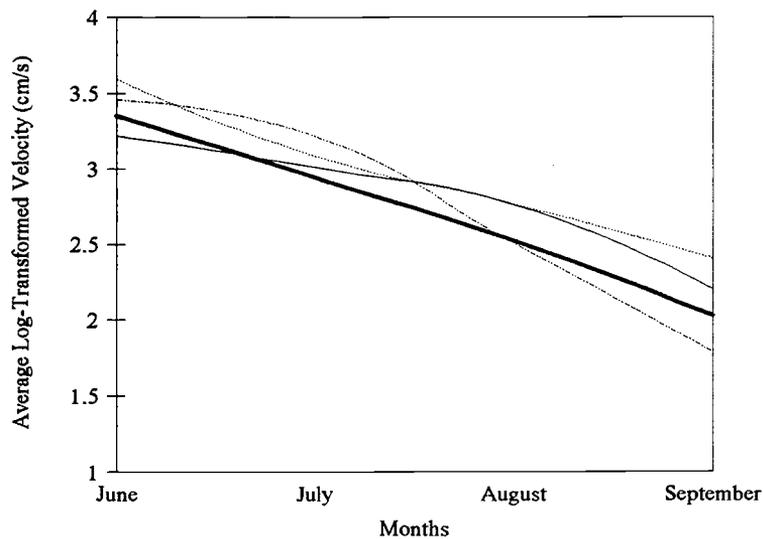
Substrate and current velocity. In 1993, station 2 had significantly higher velocity than stations 1, 3, and 4 (p-values=0.03, 0.001, and 0.01 respectively). Station 2 has the highest average percentage of bedrock substrate, which provides more laminar flow conditions than more complex substrate, which generally causes turbulence and, thus currents to vary and slow (Table 5).

Table 5. Mean, maximum, and minimum current velocities (cm/s) at stations 1, 2, 3, and 4. Standard errors for the mean are in parentheses.

Station	Mean		Maximum		Minimum	
	1993	1994	1993	1994	1993	1994
1	18 (2.97)	12 (1.54)	36	23	2	4
2	29 (6.19)	14 (2.82)	88	45	2	3
3	17 (3.54)	12 (1.78)	35	23	3	3
4	19 (3.36)	15 (2.62)	44	38	6	8

Velocity at stations 1, 3, and 4 did not differ in 1993. In 1994, velocity at stations 2, 3 and 4 did not differ. In 1994, station 1 had significantly lower current velocities than station 4 (p-value=0.01).

a)



b)

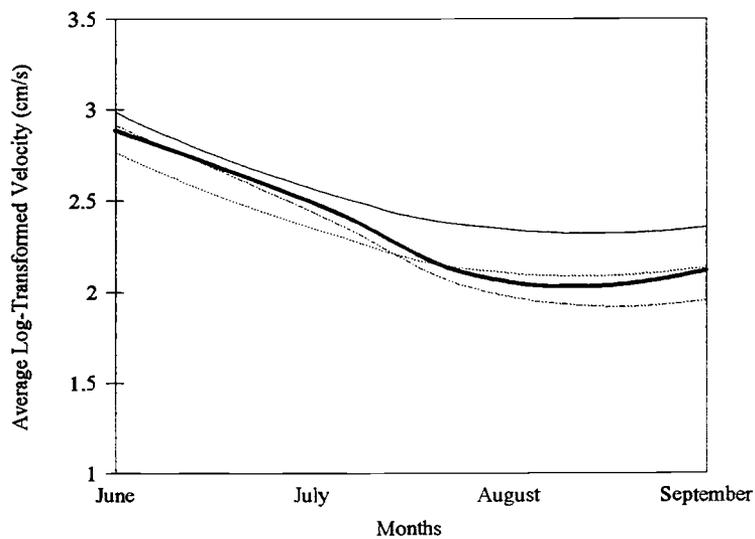


Figure 8a and 8b. Velocity (cm/s) by month for stations 1, 2, 3, and 4 averaged over the four streams for 1993 (a) and 1994 (b). ----- = Station 1, - - - - - = Station 2, ——— = Station 3, — = Station 4.

There was a significant difference between current velocities in 1993 and in 1994 with higher velocities in 1993 (p-value=0.02). Velocity differed over months in both 1993 and 1994 (93, p-value=0.001; 94, p-value=0.0002). Current velocities declined consistently from June through September in 1993 while in 1994, they reached low levels in August and plateaued through September (Figures 8a & 8b).

Cobble and gravel comprise the highest percentages of substrate found at all stations (Table 6). Bedrock was observed in large percentages at stations 2 and 3 but did not exist at station 1 on any stream and was observed at low average concentrations at station 4. Boulders, sand, and silt were observed in similar concentrations at all stations, except for silt at station 2, which was quite low. The high percentage of bedrock and high current velocities at station 2 probably accounted for the low silt concentrations. Substrate percentage of any type did not vary between months or years. However, substrate type did vary significantly between stations.

Table 6. Average substrate concentration percentages at stations 1, 2, 3, and 4 for all streams.

Station	Bedrock	Boulder	Cobble	Gravel	Sand	Silt
1	0%	11.5%	30.5%	32%	14.5%	12%
2	20%	11.5%	29.5%	26%	9.5%	3%
3	19%	11.5%	22.5%	27%	11%	9.5%
4	12%	15.5%	29%	23.5%	11.5%	7%

4.2. Treatment Streams

Environmental effects. Substrate composition at the stations explained the most variance within absolute and relative abundance of genera and functional feeding groups. The actual amount of variance explained by substrate differed from genus to genus and

for substrate type (Appendix D). Proportionally, however, substrate was significantly correlated with taxa more often than velocity, radiation, or temperature. Diversity was explained by both maximum stream temperature and substrate. Based on the correlation and regression coefficients of the substrate types, the presence of cobbles had the most positive influence on mayfly and caddisfly abundance and diversity. Of those mayflies and caddisflies that preferred cobbles, most also had a significant negative association with the presence of silt and/or bedrock substrates (Table 7). Scrapers and predators were positively associated with cobble substrates. Scrapers and collector-gathers were negatively associated with silt, and predators were negatively associated with bedrock. The presence of gravel contributed to the variance of only a few mayflies and caddisflies, though those that favored the larger substrates such as boulders and cobbles had a negative association with gravel. The shredder functional feeding group was positively associated with gravel.

Table 7. Positive and negative genera associations with substrate type.

Genus	Bedrock	Boulder	Cobble	Gravel	Sand	Silt
<i>Baetis</i>			+	-		-
<i>Micrasema</i>				-	-	
<i>Drunella</i>		+	+			-
<i>Glossosoma</i>			+			
<i>Cinygmula</i>			+			
<i>Epeorus</i>		+				
<i>Rhithrogena</i>			+			
<i>Arctopsyche</i>	+					
<i>Hydropsyche</i>	+					
<i>Lepidostoma</i>		-				+
<i>Paraleptophlebia</i>						+
<i>Wormaldia</i>				+	+	
<i>Rhyacophila</i>	+		+			
<i>Neothremma</i>			-		+	

Of the remaining environmental variables, average stream velocity explained the second largest proportion of variance. Stream velocity is affected by and affects stream substrate distributions. This interaction may explain its statistical significance and the accompanying autocorrelation where particular substrates are also highly influential. Mayflies and caddisflies that were positively associated with bedrock, such as the Hydropsychids, tended also to be positively correlated with average velocity. Highest average velocities at Ames and Buttermilk Creeks were associated with bedrock glides which appeared to support greater abundance of these mayflies and caddisflies (personal observation). Mayflies and caddisflies that were negatively associated with average velocity were positively associated with silt. Silt deposits are most common in areas of the stream channel with low average velocities. Collector-filterers were positively correlated with velocity and negatively correlated with silt which may reflect food acquisition requirements.

Radiation load did not significantly explain the variance of any mayfly and caddisfly or functional feeding group. Maximum stream temperature was negatively correlated with total diversity in both 1993 and 1994, but did not significantly explain the variation of individual mayfly and caddisfly genera. The range of maximum stream temperatures was approximately 8°C for both 1993 and 1994 at all stations which may have been large enough to possibly have an effect on mayfly and caddisfly diversity by increasing stress levels. Maximum temperatures did not exceed biologically lethal limits however and so most mayflies and caddisflies may have adapted, migrated, and/or thrived within this range. There were no significant positive correlations with maximum stream temperature.

Treatment effects. Mayfly and caddisfly communities differ from year to year within and between streams primarily in response to disturbance (McElravy et al. 1989, Rosillon 1989, Richards & Minshall 1992). Undisturbed stream communities maintain relatively stable densities and community composition (Richards & Minshall 1992). However, even in untreated streams the background "noise" created by differences in substrate, velocity, and other unmeasured parameters such as food resources, competition, and local disturbance can be enough to create statistically significant

differences between sampled populations. To see beneath this “natural” variance to the possible treatment effects, abundance measures for each mayfly and caddisfly, functional feeding group, and the diversity index were normalized by using regression to account for the contributions of substrate and velocity to the population variance (see Methods and Procedures 3.3). Each mayfly and caddisfly and each functional feeding group has a unique polynomial value which includes those measured factors which significantly explained its variance within the stream system (Appendix C). The residuals from these regressions show the remaining “unexplained” distance from the expected mean response to the actual observation. This deviation is a measure of the treatment effect. Therefore, the residuals used to illustrate differences in absolute and relative abundance and diversity between stations and years in the following discussion are normalized for differences in local stream habitat. They theoretically represent abundance and diversity differences caused by treatment alone and can be viewed as such. Untransformed, subsampled taxa counts are available in Appendix E for comparison with other studies.

Between year variation in caddis and mayfly populations occurred at our four western Oregon streams. More mayfly and caddis genera differed at treated stations 2, 3, and 4 than differed at the reference station between 1993 and 1994 (Table 8).

Table 8. Significant differences in mayfly and caddisfly abundance between 1993 and 1994 for each station. The year listed has the higher abundance. P-values<0.01.

Genus	Station 1	Station 2	Station 3	Station 4
<i>Micrasema</i>			1994	
<i>Cinygmula</i>		1994	1994	
<i>Epeorus</i>				1994
<i>Hydropsyche</i>		1994	1994	
<i>Lepidostoma</i>		1994	1994	1994
<i>Paraleptophlebia</i>	1994	1994	1994	1994
<i>Rhyacophila</i>		1994		
<i>Neophylax</i>				1994

The mayfly, *Paraleptophlebia*, was significantly more abundant at all stations in 1994 which may reflect elevated populations across a large area that year. The caddisflies *Micrasema* and *Hydropsyche* were both more abundant at station 3 in 1994 than in 1993. *Micrasema* consumes periphyton which likely increased in biomass at the exposed station. *Hydropsyche*, a filter-feeder, may have responded to increases in both suspended food material and temperature, which encouraged more rapid growth. *Lepidostoma*, a shredder caddisfly, was significantly more abundant at stations 2, 3, and 4 in 1994 and may have either shown a delayed response to increased detrital input because of a univoltine life history or a recovery from decreases during the treatment season. Without pre-treatment data, however, it is uncertain whether the 1994 response was a return to or an increase above pre-treatment levels. *Rhyacophila* was significantly more abundant at station 2 in 1994 than in 1993. Increases may be an indirect function of increases in other insects that serve as its prey, including Chironomidae which were not measured in this study.

At the treated stations, more mayflies and caddisflies increased in abundance in 1994 than decreased. Again, however, without knowledge of pretreatment abundance levels, it is uncertain if these increases were above pretreatment levels or if they reflected a recovery from the first year after harvesting. Also, water temperatures were warmer and flows were lower in 1994, which may have increased population levels. However, there was moderate significant evidence that *Baetis* abundance decreased from 1993 to 1994 ($p=0.07$). *Baetis* is an initial colonizer of disturbed streamsites and its populations tend to peak quickly and then decline as other insects return to the site (Allan 1975a, Wallace & Gurtz 1986). The slight decrease between years when other mayflies and caddisflies increased in abundance suggests that the community may have been recovering from a disturbance. All other mayfly and caddis genera that were significantly different between years showed higher average abundance in 1994. Increases were greatest at stations 2 and 3.

Absolute counts. Only *Rhithrogena* (Mauchly's Criterion=0.03, $p=0.006$; Huynh-Feldt=0.98) in 1993 and *Arctopsyche* (Mauchly's Criterion=0.15, $p=0.05$; Huynh-Feldt=1.29) and *Lepidostoma* (Mauchly's Criterion=0.16, $p=0.07$; Huynh-Feldt=1.16) in

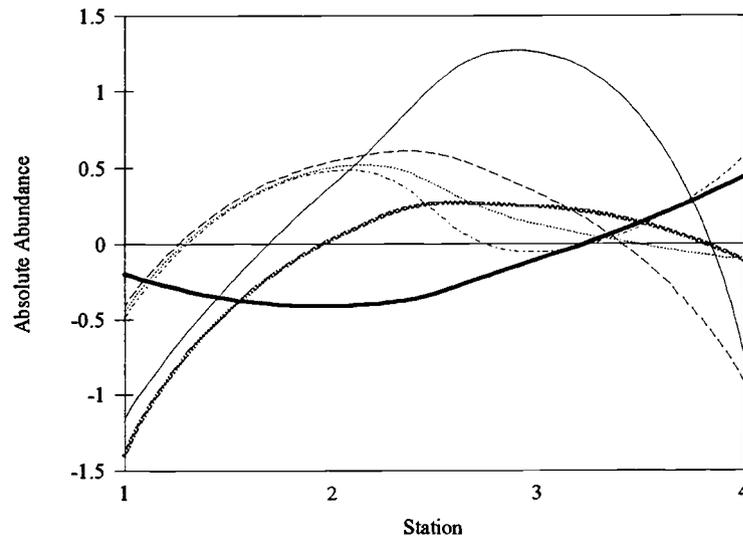
1994 exhibited evidence of repeated measures. The remaining mayflies and caddisflies were analyzed using a strip plot analysis of variance (Appendix C). Significant treatment effects were evaluated by comparing the differences between stations using Fisher's Protected Least Significant Differences (FPLSD) on the adjusted means of each genus's absolute abundance.

Table 9. Significant differences in mayfly and caddisfly absolute abundance between stations for 1993 and 1994. The station with the greater abundance is listed. **=p-value<0.01, *=p-value<0.05.

Genus	1 vs. 4		1 vs. 3		1 vs. 2		2 vs. 3		2 vs. 4		3 vs. 4	
	93	94	93	94	93	94	93	94	93	94	93	94
<i>Baetis</i>			3**	3**	2**		3**	2**	2*	3**	3**	
<i>Micrasema</i>				3*	2*	2**						3*
<i>Drunella</i>				3*		1*	3**	4*	4*			
<i>Glossosoma</i>				3**	2*	2**		2**	2*			3**
<i>Cinygmula</i>	4**	4*	3**	3**	2**	2**						
<i>Rhithrogena</i>		4**		3**		2**						
<i>Arctopsyche</i>												
<i>Hydropsyche</i>				3**		2**			2*			3*
<i>Paraleptophl.</i>						2*		2**	2*	3*		
<i>Neothremma</i>		1*				2*	3**	2*				

Station 2 differed with station 1 for more mayfly and caddisfly genera than any other reference station comparison, including 1 vs. 3 even though station 3 was positioned in the clearcut (Table 9). Station 2 also differed more from the shaded station 4 at the bottom of the experimental reach than from station 3. In almost every case, station 2 had higher abundance than either stations 1 or 4 (Figures 9a, 9b, 12a, & 12b). Figures 9a, 9b, 12a, and 12b provide a pictorial representation of adjusted mean residual responses of absolute genera abundance at each station. The curves connecting points on these and following graphs do not indicate relationships between points and do not illustrate or originate from a regression.

a)



b)

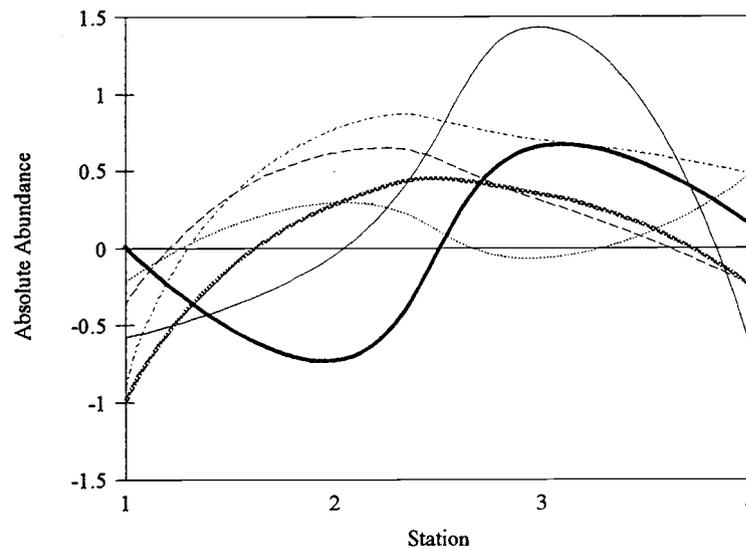


Figure 9a and 9b. Deviations of mayfly absolute abundance from the expected mean response at each station for 1993 (a) and 1994 (b). The center zero line represents the expected mean response given habitat characteristics, such as stream substrate, that correlated with each genus. Increases above or below the zero line signify population variance not explained by environmental parameters and, therefore, potentially introduced by treatment effects. —=*Baetis*; —=*Drunella*;=*Cinygmula*; -·-·-·=*Epeorus*; -·-·-·=*Rhithrogena*; - - - -=*Paraleptophlebia*.

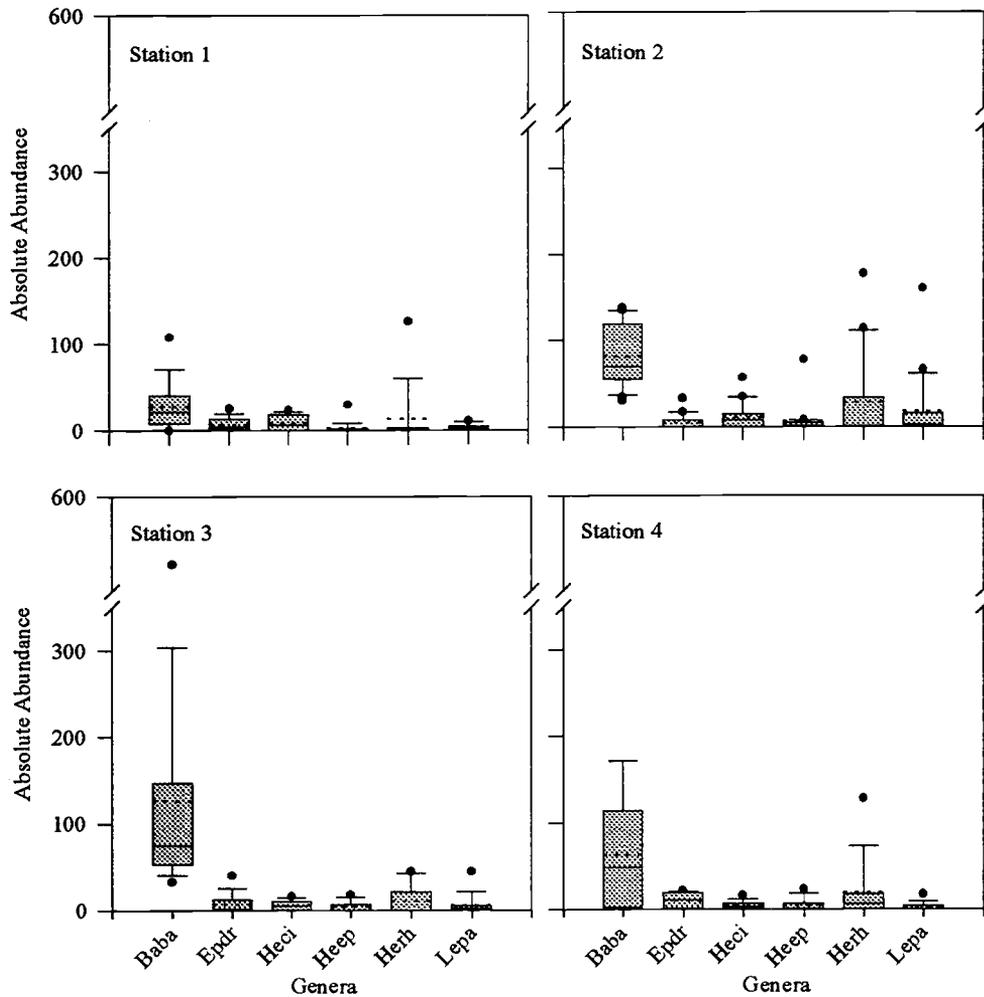


Figure 10. Population distributions for mayfly absolute abundance by station for 1993. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (●) represents data points greater than the 10th and 90th percentiles. Baba=*Baetis*, Epdr=*Drunella*, Heci=*Cinygmula*, Heep=*Epeorus*, Herh=*Rhithrogena*, and Lepa=*Paraleptophlebia*.

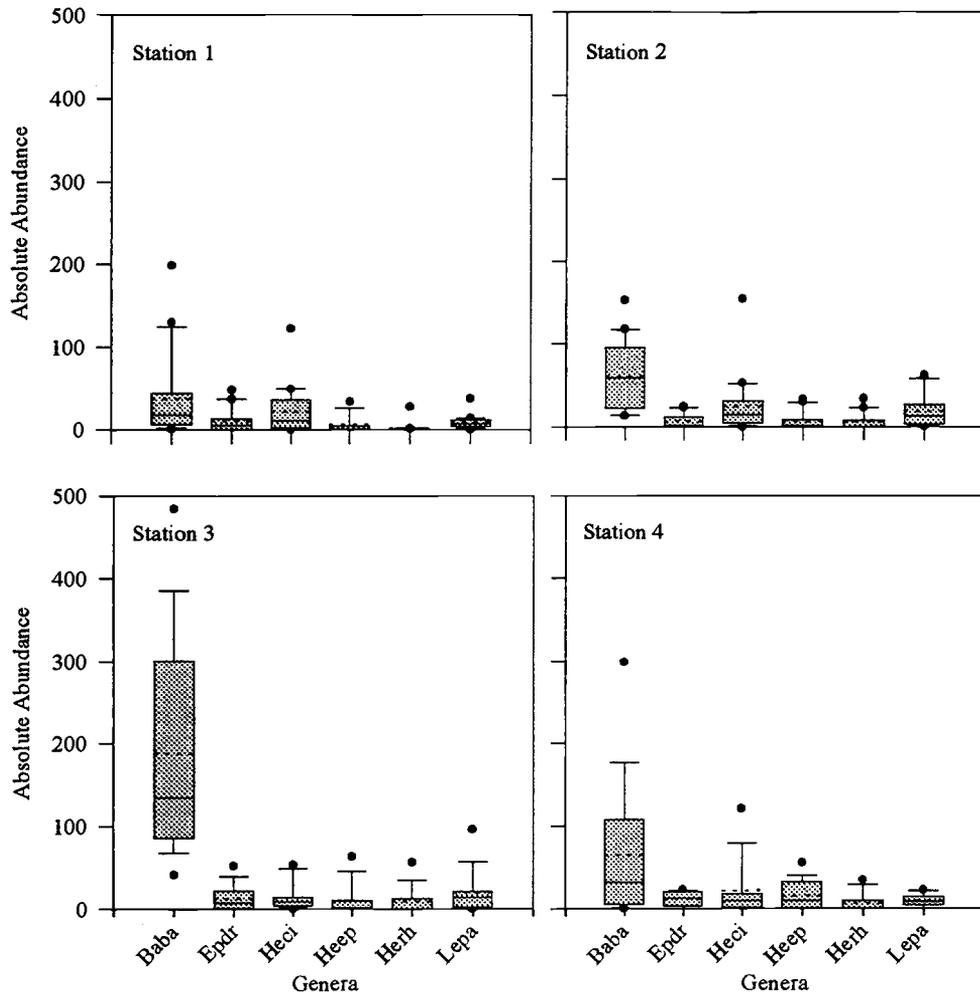


Figure 11. Population distributions for mayfly absolute abundance by station for 1994. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (•) represents data points greater than the 10th and 90th percentiles. Baba=*Baetis*, Epdr=*Drunella*, Heci=*Cinygmula*, Heep=*Epeorus*, Herh=*Rhithrogena*, and Lepa=*Paraleptophlebia*.

Each genus has its own unique polynomial related to the zero mean response line and mayfly and caddisfly data at each station are discrete and not necessarily dependent on levels at other stations. The curves serve to illustrate normalized trends in abundance pertaining to the comparative effects of the harvest treatment at each station. However,

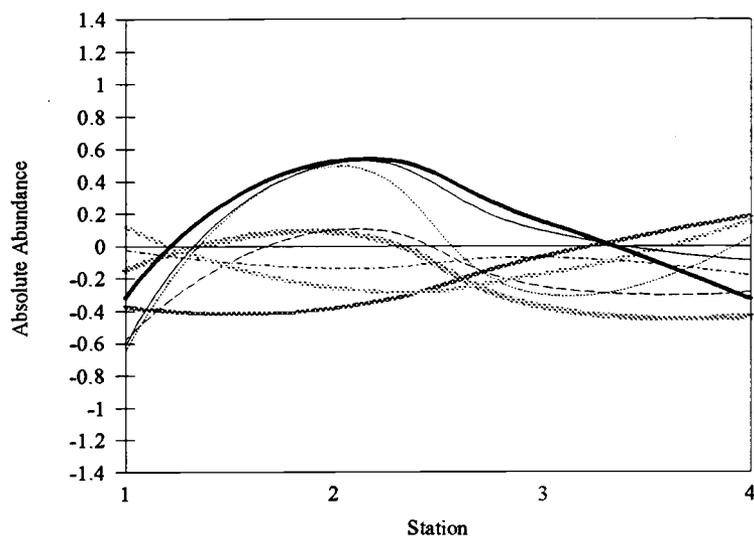
because these trend graphs do not provide a picture of actual populations, Figures 10 and 11 and Figures 13 and 14 are included to illustrate the range of population distributions at each station for the mayfly and caddisfly genera absolute abundance respectively. Actual population data is available in Appendix E.

General trends in absolute abundance show that for mayflies, *Baetis* consistently peaked at station 3 but maintained levels below the mean at stations 1 and 4; *Drunella* showed increasing abundance in a downstream direction except for a decline at station 2; *Cinygmula* was lowest in abundance at the reference station and achieved moderate abundance above the mean at stations 2 and 3; *Rhithrogena* was highest in abundance at station 4 with a slight increase at station 2; and *Paraleptophlebia* populations peaked at stations 2 and 3. In general, mayflies increased at stations 2 and 3 and were either similar to or higher in abundance at station 4 than at the reference station (Figures 9a & 9b).

The caddisflies *Glossosoma* and *Micrasema* had highest abundance at station 3 and low abundance at the reference station, and *Hydropsyche* and *Neothremma* populations peaked at station 2 (Figures 12a & 12b). *Arctopsyche*, *Lepidostoma*, and *Rhyacophila* maintained relatively level population abundance near the mean throughout both years across stations. Caddisflies, in general, showed an increase above the mean at station 2. In 1993, any increases in abundance occurred only at station 2. In 1994, genera responses were greater with more increases and decreases at station 3. Stations 1 and 4 did not differ dramatically either year as a result of treatment.

Genera at stations 2 and 3 did not differ significantly from each other in 1993 and differed for only three genera (*Baetis*, *Drunella*, and *Neothremma*) in 1994. Stations 2 and 3 are the nearest to each other spatially and differ primarily in their exposure to radiation and potential local increases in stream temperature. In 1994, the two mayflies, *Baetis* and *Drunella*, both had higher abundance at station 3 than at 2. *Baetis*, however, peaked at station 3 after rising from slightly below the mean at 2 while *Drunella* was farthest below the mean at station 2 and increased to "normal" levels at 3 (Figure 9b). This same pattern was apparent in 1993 though the differences were not statistically significant (Figure 9a).

a)



b)

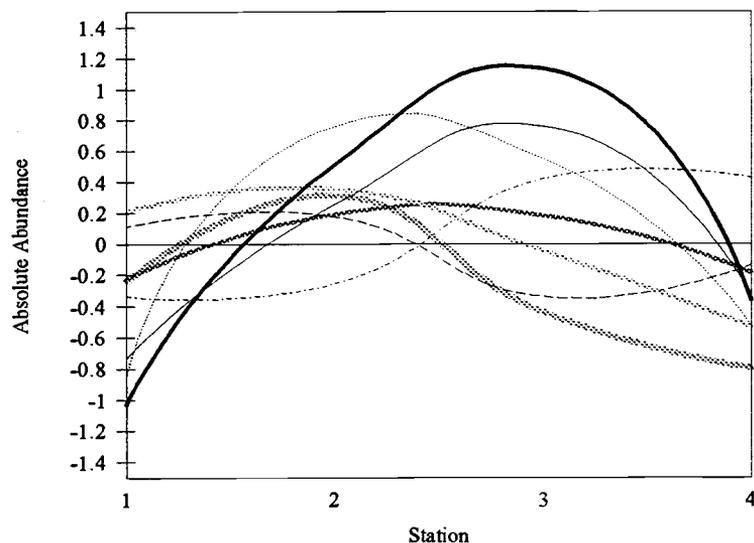


Figure 12a and 12b. Deviations of caddisfly absolute abundance from the expected mean response at each station for 1993 (a) and 1994 (b). The center zero line represents the expected mean response given habitat characteristics, such as stream substrate, that correlated with each genus. Increases above or below the zero line signify population variance not explained by environmental parameters and, therefore, potentially introduced by treatment effects. —=*Micrasema*; —=*Glossosoma*;=*Arctopsyche*;=*Hydropsyche*;=*Lepidostoma*;=*Wormaldia*;=*Rhyacophila*;=*Neothremma*.

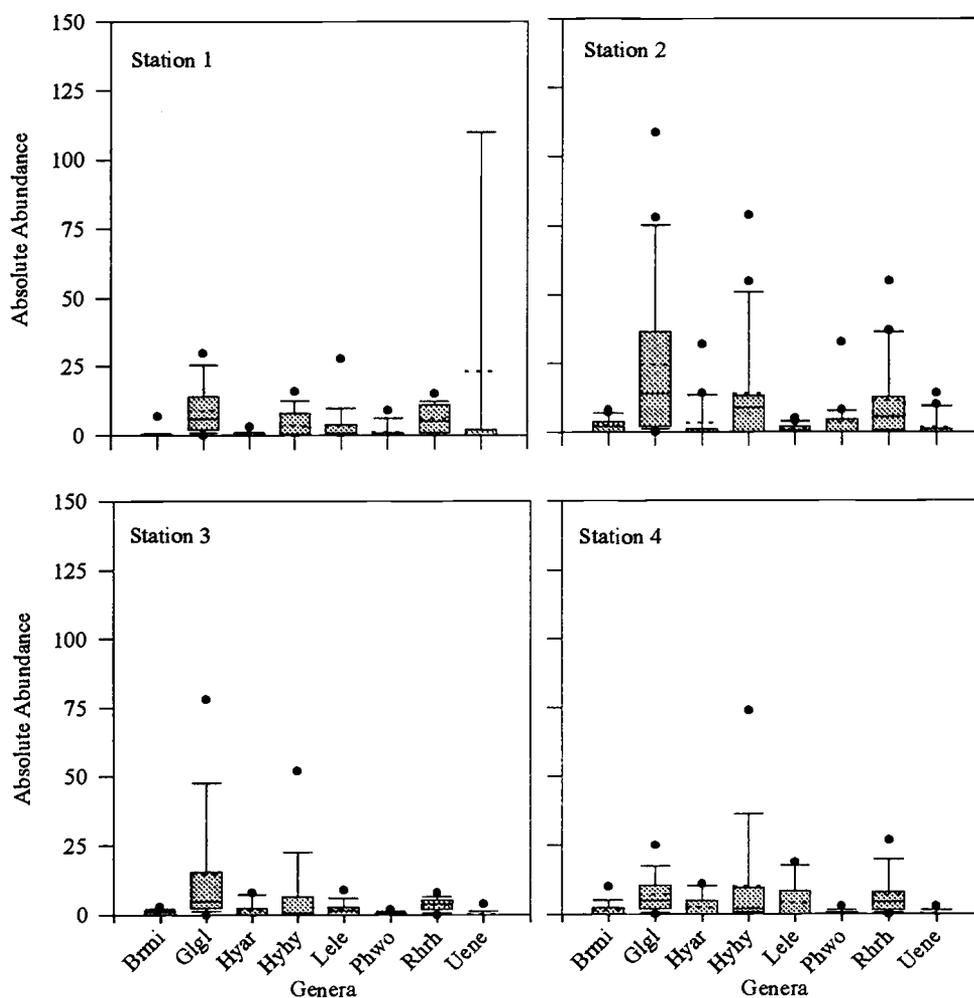


Figure 13. Population distributions for caddisfly absolute abundance by station for 1993. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (●) represents data points greater than the 10th and 90th percentiles. Birmi=*Micrasema*, Glg1=*Glossosoma*, Hyar=*Arctopsyche*, Hyhy=*Hydropsyche*, Lele=*Lepidostoma*, Phwo=*Wormaldia*, Rhrh=*Rhyacophila*, and Uene=*Neothremma*.

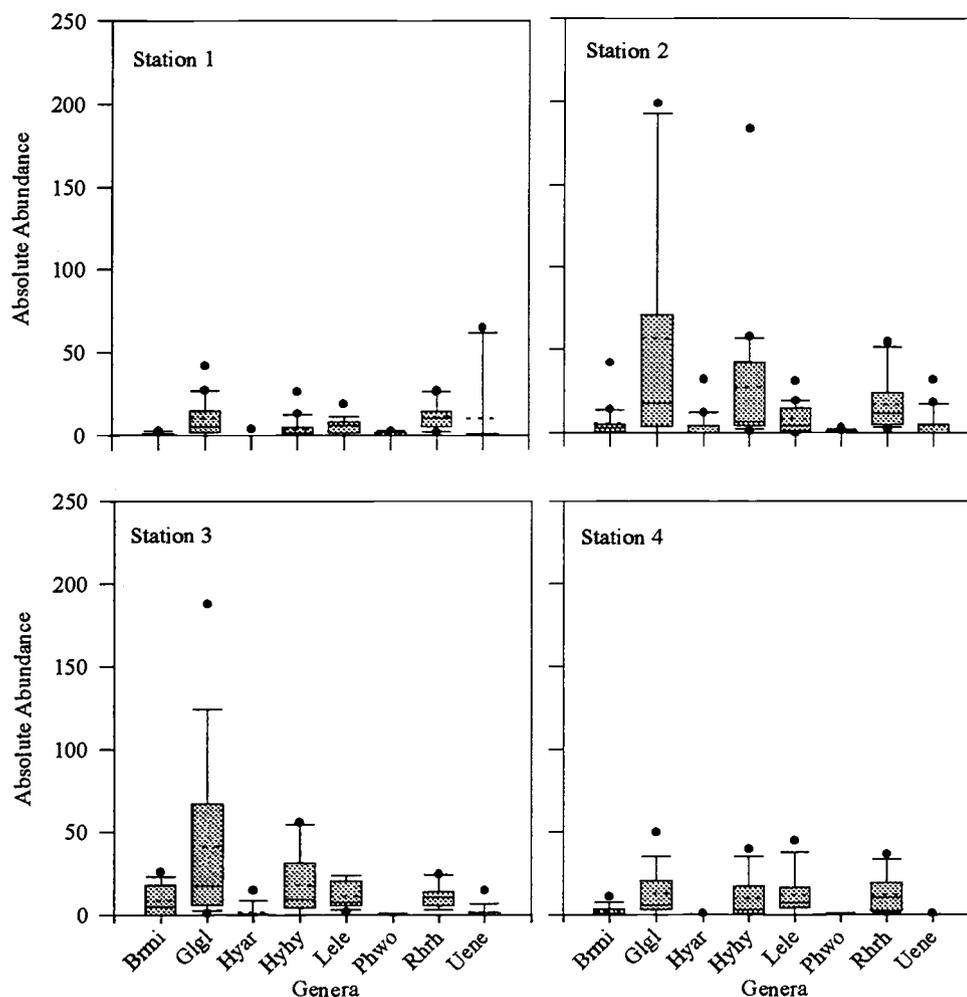


Figure 14. Population distributions for caddisfly absolute abundance by station for 1994. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (•) represents data points greater than the 10th and 90th percentiles. Birmi=*Micrasema*, Ggl=*Glossosoma*, Hyar=*Arctopsyche*, Hyhy=*Hydropsyche*, Lele=*Lepidostoma*, Phwo=*Wormaldia*, Rhrh=*Rhyacophila*, and Uene=*Neothremma*.

At station 2, *Baetis* comprises 43% in 1993 and 22% in 1994 of the total mayfly and caddisfly population. At station 3, *Baetis* comprised 57% in 1993 and 47% in 1994 of all the taxa. The caddisfly, *Neothremma*, declined below the mean from station 2 to station 3

(Figure 12b). The caddisfly, *Micrasema* showed abundance increases above the mean at stations 2 and 3 compared to stations 1 and 4. *Micrasema* prefers periphyton and algae over detritus and prefers periphyton/moss combinations over periphyton alone (Becker 1994). It showed no difference between stations 2 and 3. Station 2 on all four streams tended to have higher moss abundance than the other stations (personal observation) and therefore, the combination of increased periphyton at 3 and mossy substrates at 2 may have maintained similar abundance between these two stations. Mayfly and caddisfly responses between stations 2 and 3 differed only in the second year of the study, indicating that immediately following harvesting, mayfly and caddisfly absolute abundance did not respond to the direct effects of clearcutting.

Differences in absolute abundance between stations 2 and 4 indicate that abundance was generally lower at station 4, except for the mayfly, *Drunella*, which had higher abundance at station 4. Those taxa that decreased in abundance from station 2 to station 4 do not significantly differ between stations 4 and the reference station (1), indicating that the decline from station 2 to 4 returned taxa to abundance levels similar to the reference station. *Neothremma* abundance, however, peaked at station 2 and then fell below reference station levels, which were similar to the expected mean, at station 4. Fewer mayflies and caddisflies differed significantly between stations 2 and 4 as differed between stations 1 and 2, which may indicate greater treatment effects from the single, larger 200-m clearcut than from the two smaller 100-m clearcuts. Stations 1 and 4 differed for few genera in either 1993 or 1994, showing little response of absolute mayfly and caddisfly abundance to the entire 25% canopy removal (Figures 9a, 9b, 12a, & 12b). Of those that did differ, such as the mayflies *Rhithrogena* and *Cinygmula*, station 4 had higher abundance. Again however, the caddisfly, *Neothremma*, maintained higher abundance at the lesser treated station, in this case, station 1, the reference station. Differences in absolute abundance between stations were more numerous and more pronounced in 1994 than in 1993, with additional mayflies and caddisflies showing significant differences the second year after harvesting (Table 9). Increases in measured treatment effects may be a result of more extreme climate conditions in 1994 and/or adjustment caused by population increase/decrease lags in life history responses.

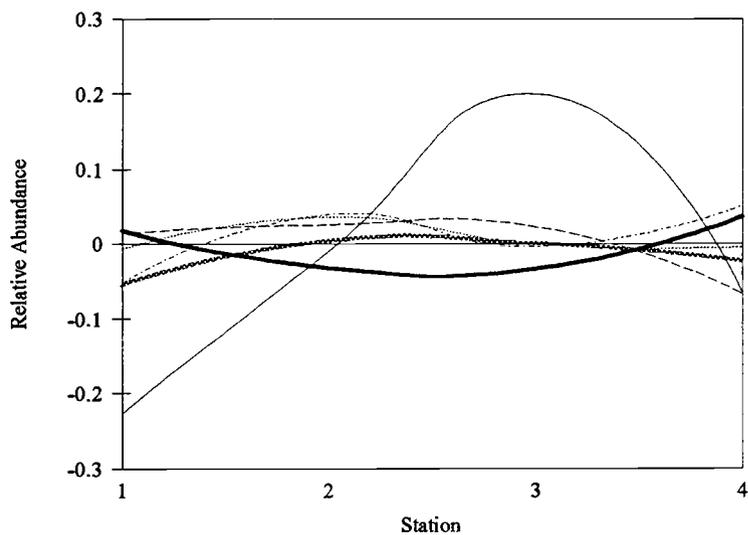
Relative abundance. Removing the absolute differences in mayfly and caddisfly abundance between stations and analyzing differences based on generic relative abundance allows relative changes in mayfly and caddisfly community composition to emerge. Figures 15a and 15b show that *Baetis* relative abundance increased dramatically above the mean at station 3. Figure 15b shows that *Drunella* relative abundance decreased at station 2 and was similar at the other three stations. The remaining mayflies' abundance were similar to the mean across all stations with minor deviations in both years, indicating that treatment explained little of the remaining variance for the relative abundance of these mayflies and caddisflies. Figures 16 and 17 show population distributions for mayfly relative abundance in both sampling seasons. Figures 18a and 18b show that *Glossosoma* relative abundance decreased at station 3 from stations 1 and 2 in 1993 and from station 2 in 1994. *Glossosoma*'s absolute abundance was higher at 3 than at either 1 or 2 in those years. *Hydropsyche* relative abundance also decreased to below the mean at station 3 from above the mean at station 2. *Lepidostoma* and *Rhyacophila* relative abundances were higher at stations 1 and 4. *Lepidostoma* prefers red alder leaves above other food sources and because 75% of the alder canopy remained on the stream reach, this food supply may not have significantly altered (Grafius & Anderson 1979). *Neothremma* and *Glossosoma* relative abundance trends closely followed each other's each year at each station. Both insects are members of the scraper functional feeding group. *Micrasema*, *Arctopsyche*, and *Wormaldia* relative abundance showed moderate changes through the stations clustered around the expected mean. Figures 19 and 20 show actual rather than residual caddisfly relative abundance distributions at the four stations. Treatment differences between stations 1 and 2 and 2 and 4 significantly affected relative genera abundance, though not for as many taxa as the absolute count analysis (Table 10). For mayflies and caddisflies that differed significantly at station 2 in both years, as many insects declined as increased. This is in contrast to absolute count results which show that most caddis and mayflies with significant differences between stations 1 and 2 and 2 and 4 increased in absolute abundance at station 2.

Table 10. Significant differences for mayfly and caddisfly relative abundance between stations. The station with the greater abundance is listed. **=p-values<0.01, *=p-values<0.05.

Genus	1 vs. 4		1 vs. 3		1 vs. 2		2 vs. 3		2 vs. 4		3 vs. 4	
	93	94	93	94	93	94	93	94	93	94	93	94
<i>Baetis</i>			3**	3**	2*		3**	3**			3**	3**
<i>Drunella</i>									4*		4*	
<i>Glossosoma</i>	1*								2*			
<i>Epeorus</i>												4**
<i>Rhithrogena</i>				3*								
<i>Hydropsy.</i>						2*				2*		
<i>Lepidost.</i>		4**				1*				4**		4**
<i>Wormaldia</i>				1**				2*				
<i>Rhyacoph.</i>		1*	1*	1**	1*	1**		2*				4**
<i>Neothrem.</i>								2*		2*		

Station 3's effect on relative abundance was not as clear as with absolute abundance comparisons. Of the mayflies and caddisflies showing differences between stations 1 and 3, as many decreased in relative abundance at station 3 as increased. However, although *Micrasema*, *Drunella*, *Glossosoma*, *Cinygmula*, and *Hydropsyche* all increased in absolute abundance at station 3 compared to 1, none exhibited proportional differences from the reference station. Apparently, their proportion in the community remained the same despite numerical increases. *Baetis* showed a significant positive response to removal of the riparian canopy with consistent increases at station 3 compared to the other stations (Figures 15a & 15b). Stations 1 and 4 did not differ significantly for a large number of genera. Of taxa that did differ, station 1 has higher relative abundance slightly more often than station 4. In 1994, *Wormaldia* exhibited a preference for shaded stations with higher relative abundance at stations 1 and 2 than at 3. *Rhyacophila* were more relatively abundant at the reference station than at stations 2, 3, and 4. In 1994, station 2 supported higher relative *Rhyacophila* abundance than station 3.

a)



b)

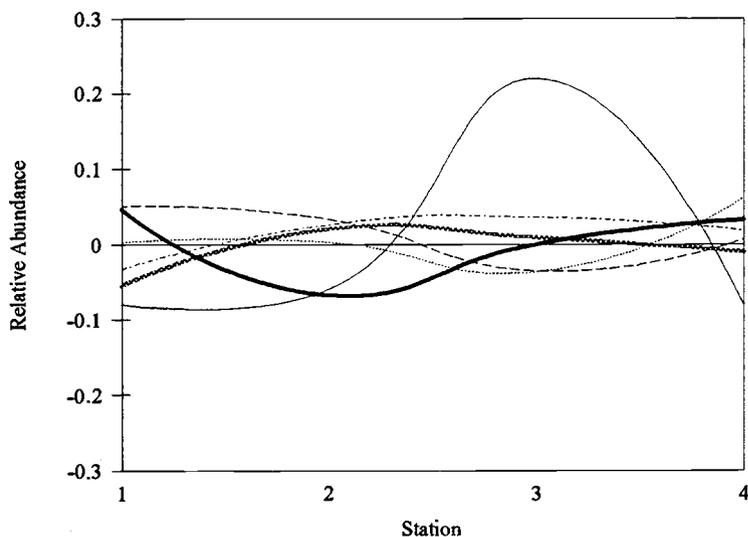


Figure 15a and 15b. Deviations of mayfly relative abundance from the expected mean response at each station for 1993 (a) and 1994 (b). The center zero line represents the expected mean response given habitat characteristics, such as stream substrate, that correlated with each genus. Increases above or below the zero line signify population variance not explained by environmental parameters and, therefore, potentially introduced by treatment effects. —=*Baetis*; —=*Drunella*;=*Cinygmula*;=*Epeorus*;=*Rhithrogena*;=*Paraleptophlebia*.

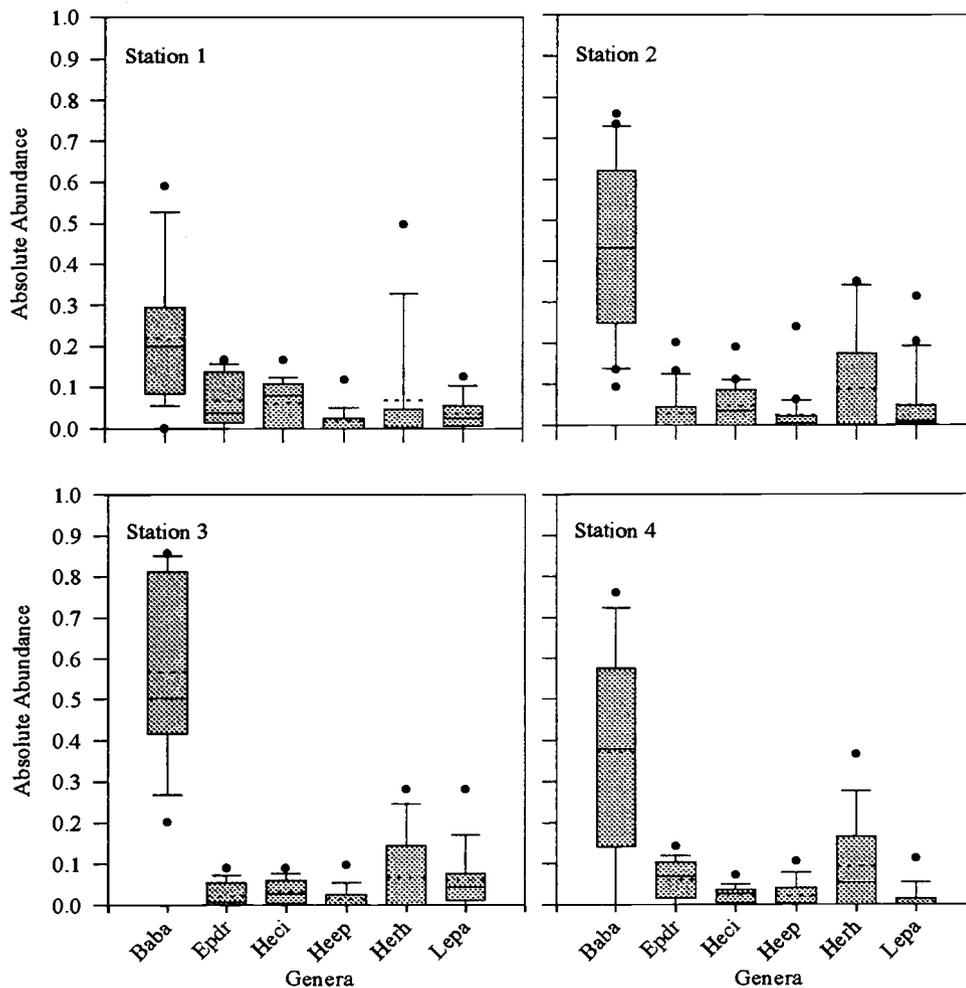


Figure 16. Population distributions for mayfly relative abundance by station in 1993. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (●) represents data points greater than the 10th and 90th percentiles. Baba=*Baetis*, Epdr=*Drunella*, Heci=*Cinygmula*, Heep=*Epeorus*, Herh=*Rhithrogena*, and Lepa=*Paraleptophlebia*.

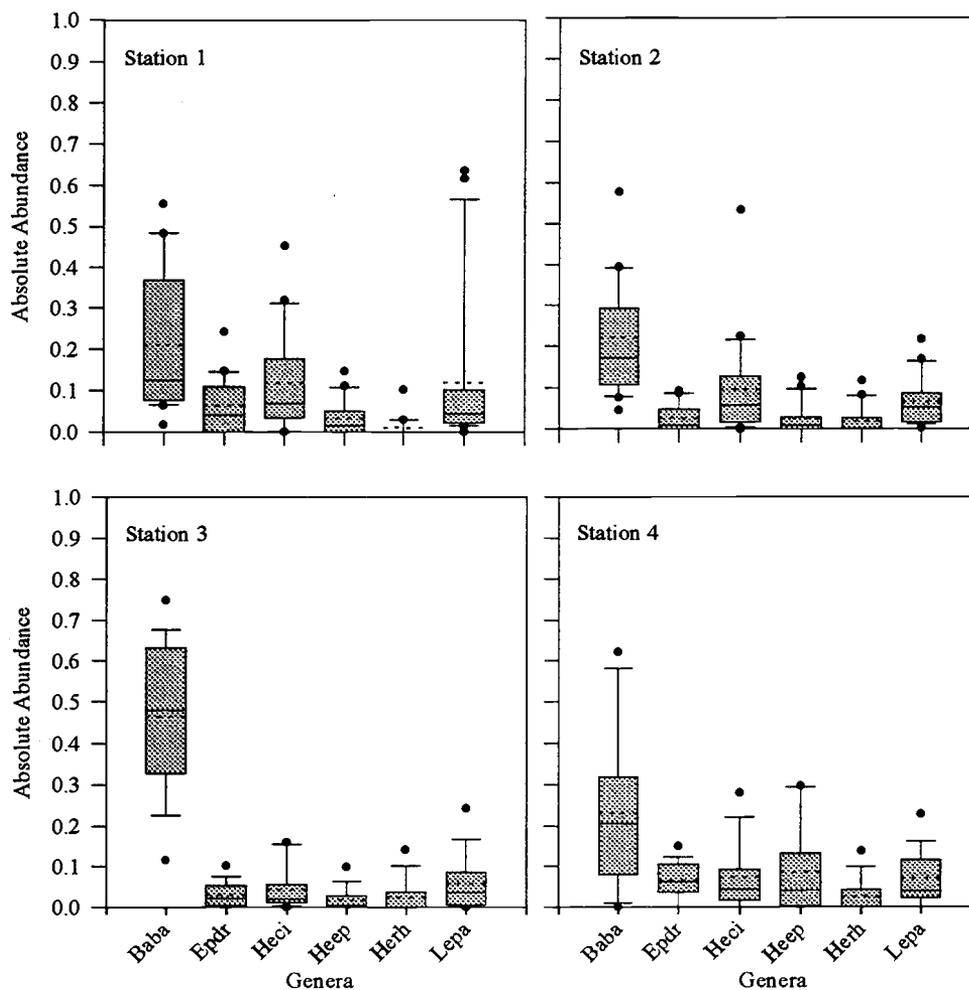
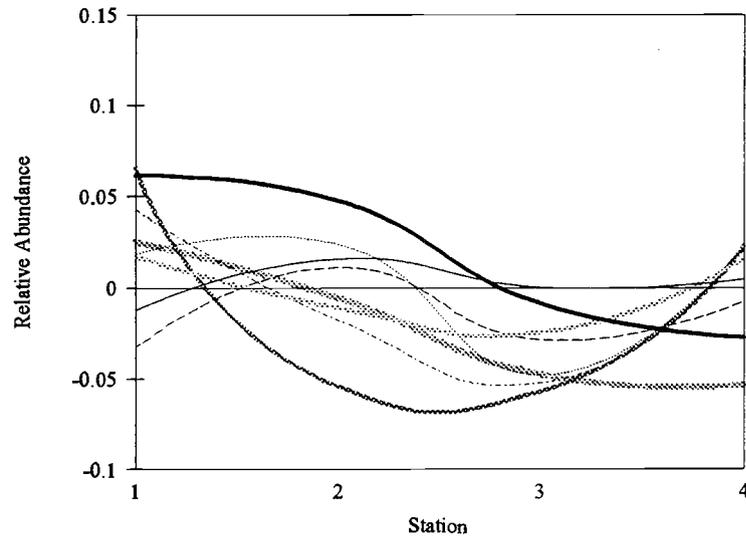


Figure 17. Population distributions for mayfly relative abundance by station in 1994. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (•) represents data points greater than the 10th and 90th percentiles. Baba=*Baetis*, Epdr=*Drunella*, Heci=*Cinygmula*, Heep=*Epeorus*, Herh=*Rhithrogena*, and Lepa=*Paraleptophlebia*.

a)



b)

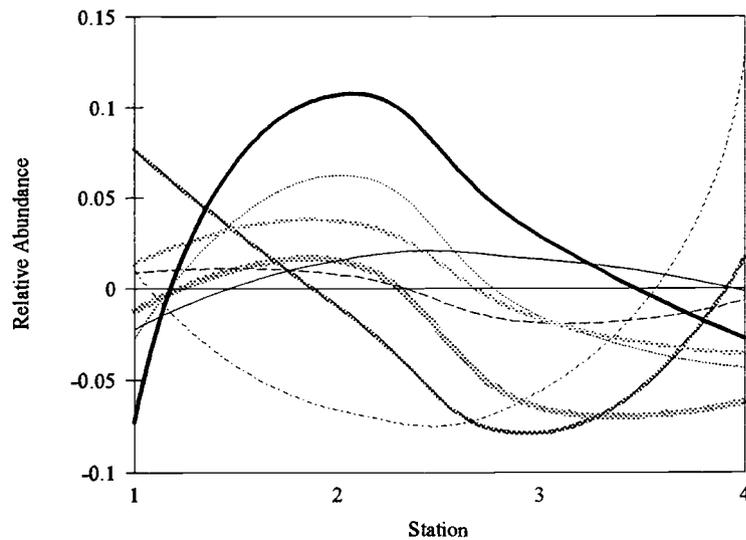


Figure 18a and 18b. Deviations of caddisfly relative abundance from the expected mean response at each station for 1993 (a) and 1994 (b). The center zero line represents the expected mean response given habitat characteristics, such as stream substrate, that correlated with each genus. Increases above or below the zero line signify population variance not explained by environmental parameters and, therefore, potentially introduced by treatment effects. —=*Micrasema*; —=*Glossosoma*;=*Arctopsyche*;=*Hydropsyche*;=*Lepidostoma*;=*Wormaldia*;=*Rhyacophila*;=*Neothremma*.

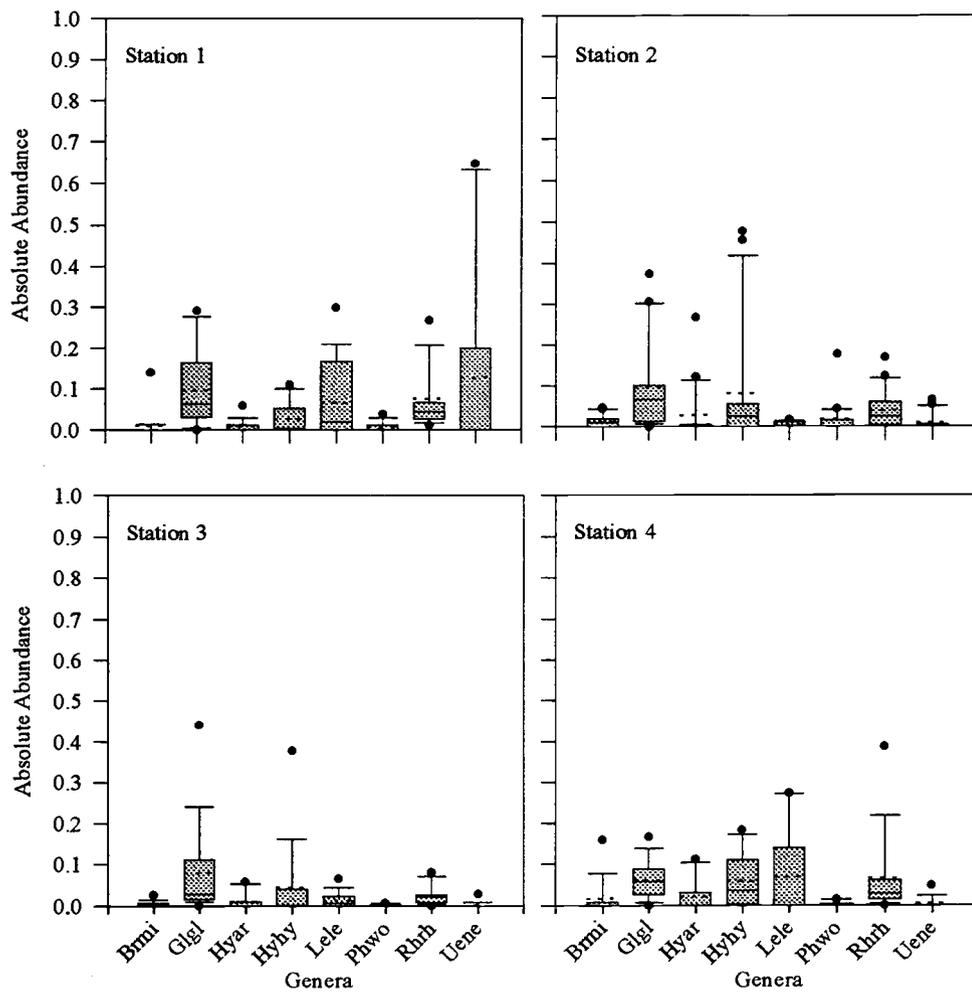


Figure 19. Population distributions for caddisfly relative abundance by station in 1993. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (●) represents data points greater than the 10th and 90th percentiles. Brmi=*Micrasema*, Glgl=*Glossosoma*, Hyar=*Arctopsyche*, Hyhy=*Hydropsyche*, Lele=*Lepidostoma*, Phwo=*Wormaldia*, Rhrh=*Rhyacophila*, and Uene=*Neothremma*.

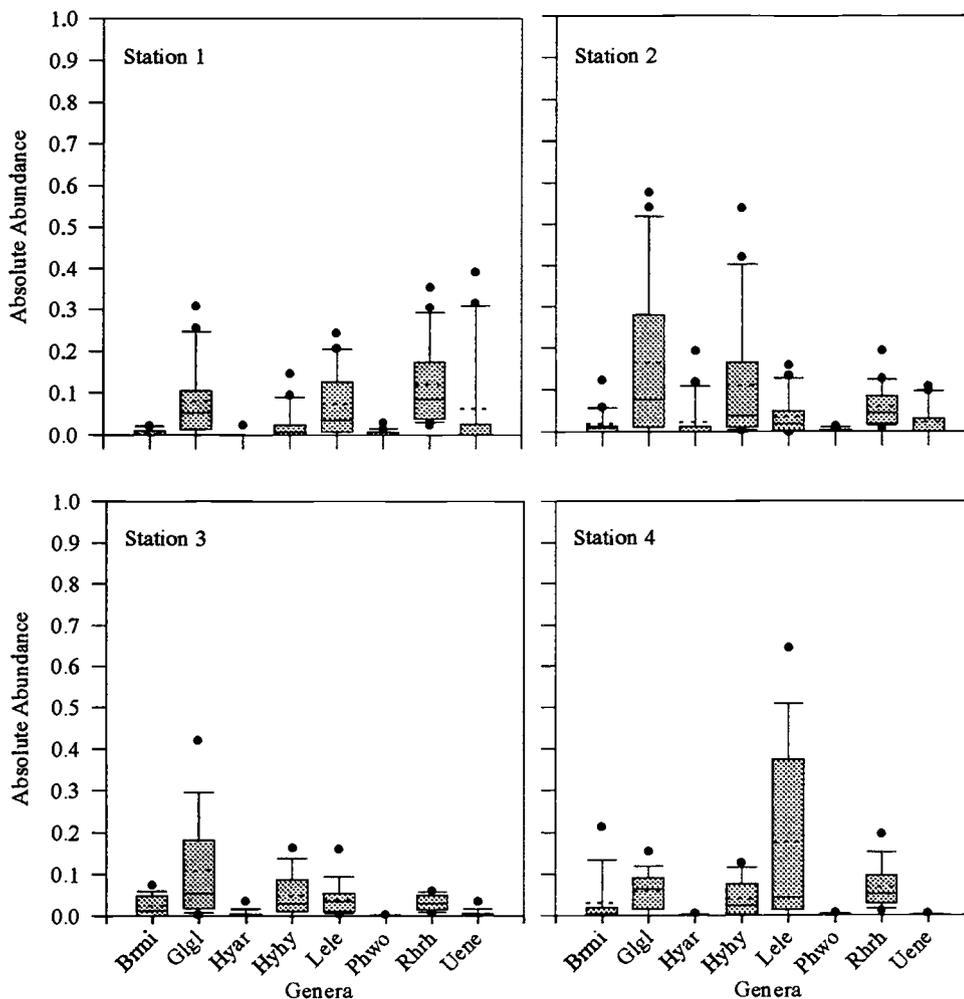


Figure 20. Population distributions for caddisfly relative abundance by station in 1994. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (•) represents data points greater than the 10th and 90th percentiles. Brmi=*Micrasema*, Glg=*Glossosoma*, Hyar=*Arctopsyche*, Hyhy=*Hydropsyche*, Lele=*Lepidostoma*, Phwo=*Wormaldia*, Rhrh=*Rhyacophila*, and Uene=*Neothremma*.

There were no significant differences in *Rhyacophila* absolute abundance between stations 2 and 3, so the increase in relative abundance may reflect proportional increases in other taxa at station 3 (Figure 18b). Using relative abundance reveals shifts in the generic

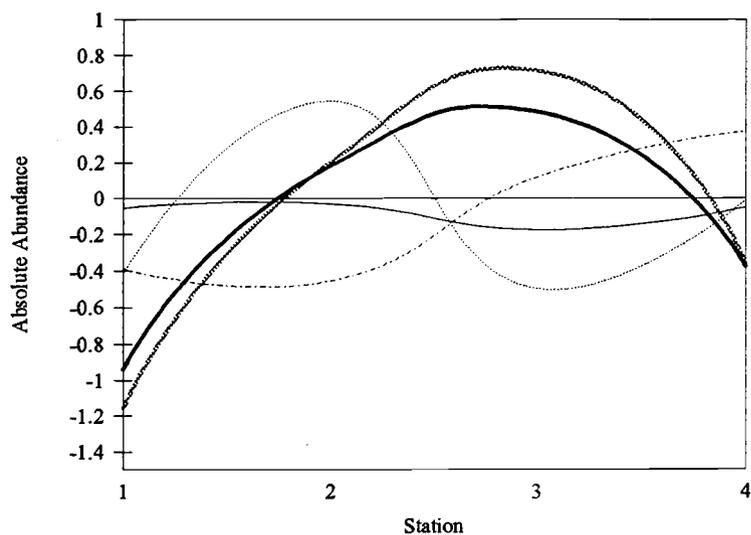
structure as a result of treatments by relativizing mayfly and caddisfly abundance among stations and streams.

Functional feeding groups. Absolute counts of predators and shredders did not differ significantly between any stations for both 1993 and 1994, although predators generally increased in abundance in a downstream direction (Figures 21a & 21b). In 1993, shredders had the highest absolute abundance at station 1 (Figure 21a). In 1994, collector-gatherers have the highest absolute abundance at station 1 (Figure 21b). Scrapers and collector-gatherers differed among all stations in 1993 with downstream stations having higher absolute abundance than the reference station and station 3 having higher absolute abundance than all others. Collector-gatherers and scrapers were significantly greater at station 3 in 1994 than in 1993. Station 4 had higher abundance of scrapers and collector-gatherers than station 1 in 1993, but the two stations did not differ for any functional feeding groups in 1994 (Table 11, Figure 21b). Among stations, collector-filterers showed highest abundance at station 2, but did not differ significantly between stations 1 and 4. It is therefore uncertain if the seston collector-filterers harvest from the water column increased overall as a result of silvicultural treatments.

Table 11. Significant differences for functional feeding group (FFG) absolute abundance between stations. The station with the greater abundance is listed. **=p-values<0.01, *=p-values<0.05.

FFG	1 vs. 4		1 vs. 3		1 vs. 2		2 vs. 3		2 vs. 4		3 vs. 4	
	93	94	93	94	93	94	93	94	93	94	93	94
Scraper	4**		3**	3**	2**	2*		3*	2**		3**	3**
Collector-gath.	4**		3**	3**	2**		3**	3*	2**		3**	3**
Collector-filter					2*	2*	2**			2*		

a)



b)

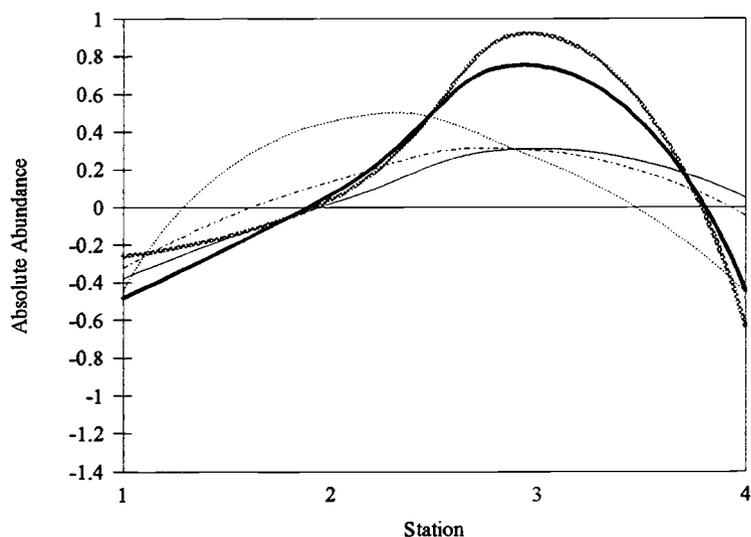


Figure 21a and 21b. Deviations of functional feeding group (FFG) absolute abundance from the expected mean response at each station for 1993 (a) and 1994 (b). The center zero line represents the expected mean response given habitat characteristics, such as stream substrate, that correlated with each FFG. Increases above or below the zero line signify population variance not explained by environmental parameters and, therefore, potentially introduced by treatment effects. —=Shredder; —=Scraper;=Collector-gatherer;=Collector-filterer; -.-.-=Predator.

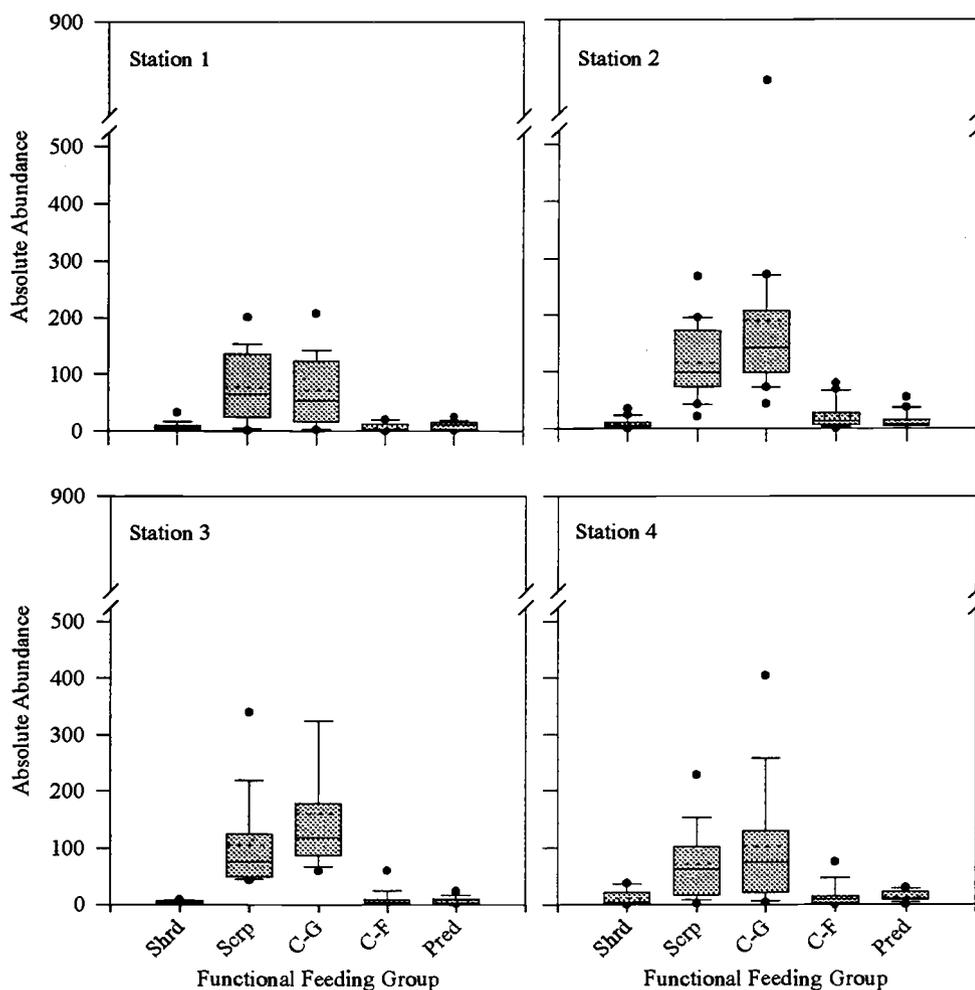


Figure 22. Population distributions for functional feeding group absolute abundance by station in 1993. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (●) represents data points greater than the 10th and 90th percentiles. Shrd=Shredders, Scrp=Scrapers, C-G=Collector-gatherers, C-F=Collector-filterers, Pred=Predators.

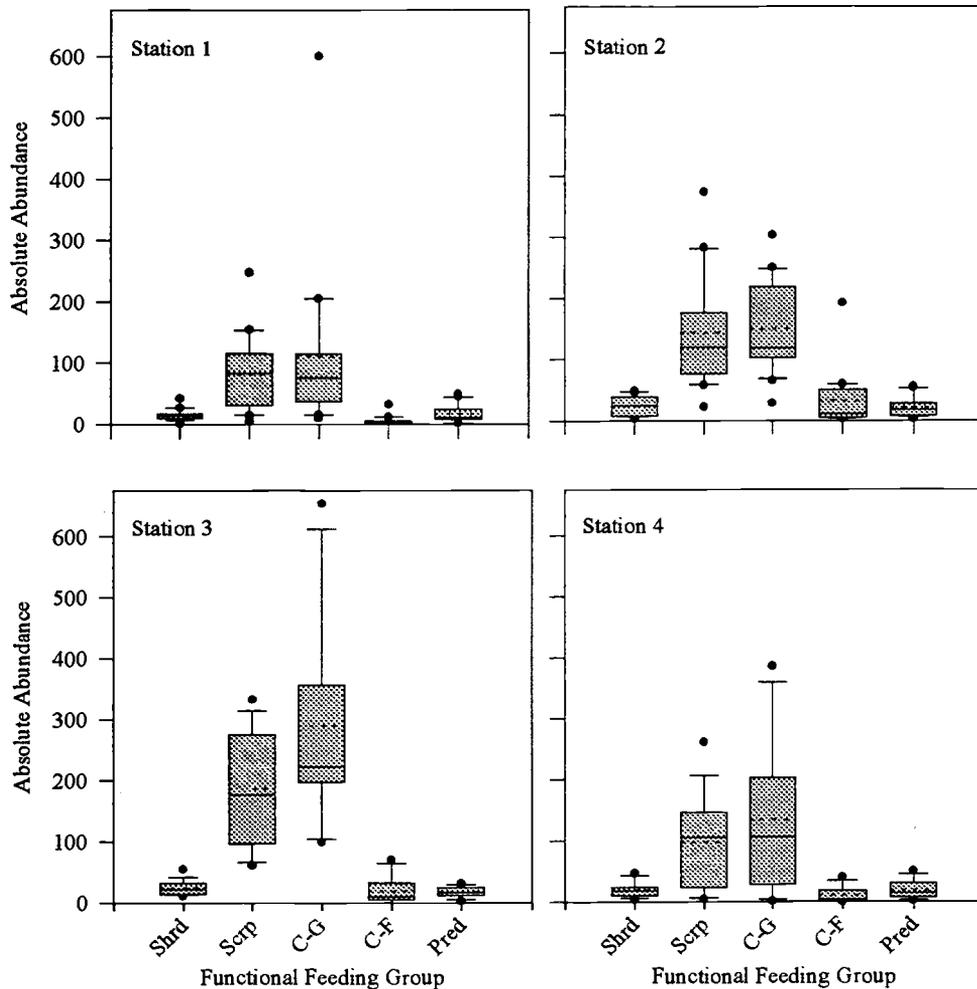


Figure 23. Population distributions for functional feeding group absolute abundance by station in 1994. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (●) represents data points greater than the 10th and 90th percentiles. Shrd=Shredders, Scrp=Scrapers, C-G=Collector-gatherers, C-F=Collector-filterers, Pred=Predators.

However, collector-filterers are highly sensitive to suspended particle size and competition for space (Edington 1965, Gordon & Wallace 1975, Wallace 1975, England 1993). Increases in material that would clog or wash away a silk spun net or favor competitors would also decrease abundance at a station. Predator populations peaked

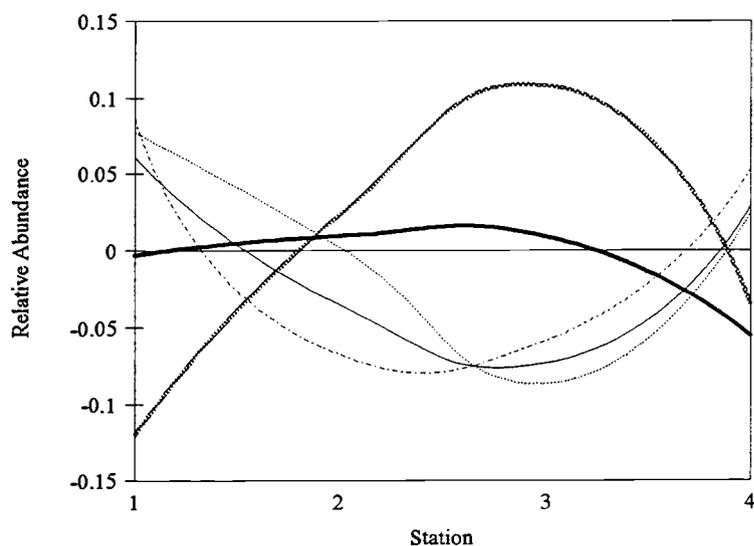
slightly, though not significantly at station 3 in 1994 (Figure 21b). In 1994, station 1 appeared to have less variation among the functional feeding groups than the treated stations, especially station 3 (Figures 21b). Figures 22 and 23 show the functional feeding group absolute abundance data distributions for both sampling seasons.

Relative abundance of functional feeding groups differed much more widely across stations. Because a number of genera makes up one functional feeding category, absolute changes in taxa do not often fully reflect changes in functional feeding groups. A large proportion of taxa would have to enter or disappear from a station community to reveal significant differences between absolute numbers of functional feeding groups. By describing shifts in the allocation of pieces of the functional feeding group community pie, relative abundance better describes shifts in community function. Predators and shredders decreased in relative abundance from station 1 to stations 2 and 3 (Table 12, Figures 24a & 24b). In 1994, however, shredders increased in abundance at station 4 compared to the reference station. They were not statistically different from the reference station in 1993. The caddisfly, *Lepidostoma*, a shredder, is at its highest relative abundance at station 4 compared to all other stations. This may explain why the shredder functional feeding group also has its greatest relative abundance at station 4.

Table 12. Significant differences for functional feeding group (FFG) relative abundance between stations. The station with the greater abundance is listed. **=p-values<0.01, *=p-values<0.05.

FFG	1 vs. 4		1 vs. 3		1 vs. 2		2 vs. 3		2 vs. 4		3 vs. 4	
	93	94	93	94	93	94	93	94	93	94	93	94
Shredder		4**	1*	1*		1*				4**	4*	4**
Scraper						2*			2*	2*	3*	
Collector-gath.			3**		2**						3**	
Collector-filter			1**		1*	2*	2**	2**		2**	4**	
Predator			1*	1**	1*	1**						

a)



b)

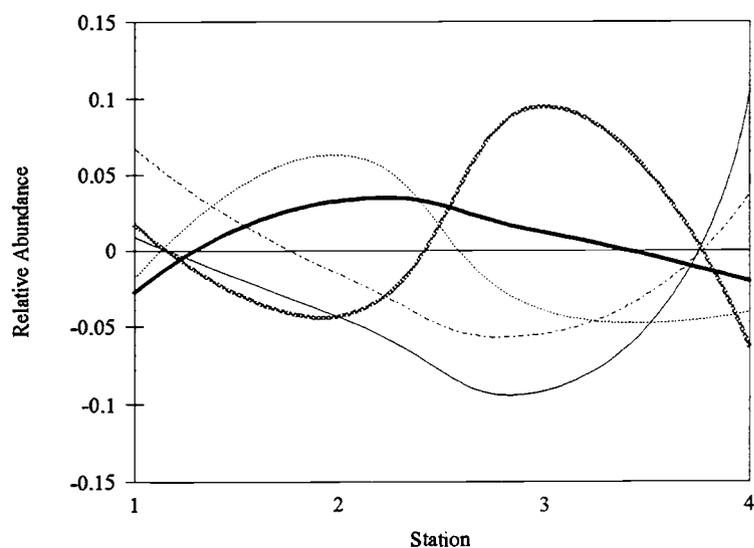


Figure 24a and 24b. Deviations of functional feeding group (FFG) relative abundance from the expected mean response at each station for 1993 (a) and 1994 (b). The center zero line represents the expected mean response given habitat characteristics, such as stream substrate, that correlated with each FFG. Increases above or below the zero line signify population variance not explained by environmental parameters and, therefore, potentially introduced by treatment effects. —=Shredder; —=Scraper; —=Collector-gatherer;=Collector-filterer; -.-.-=Predator.

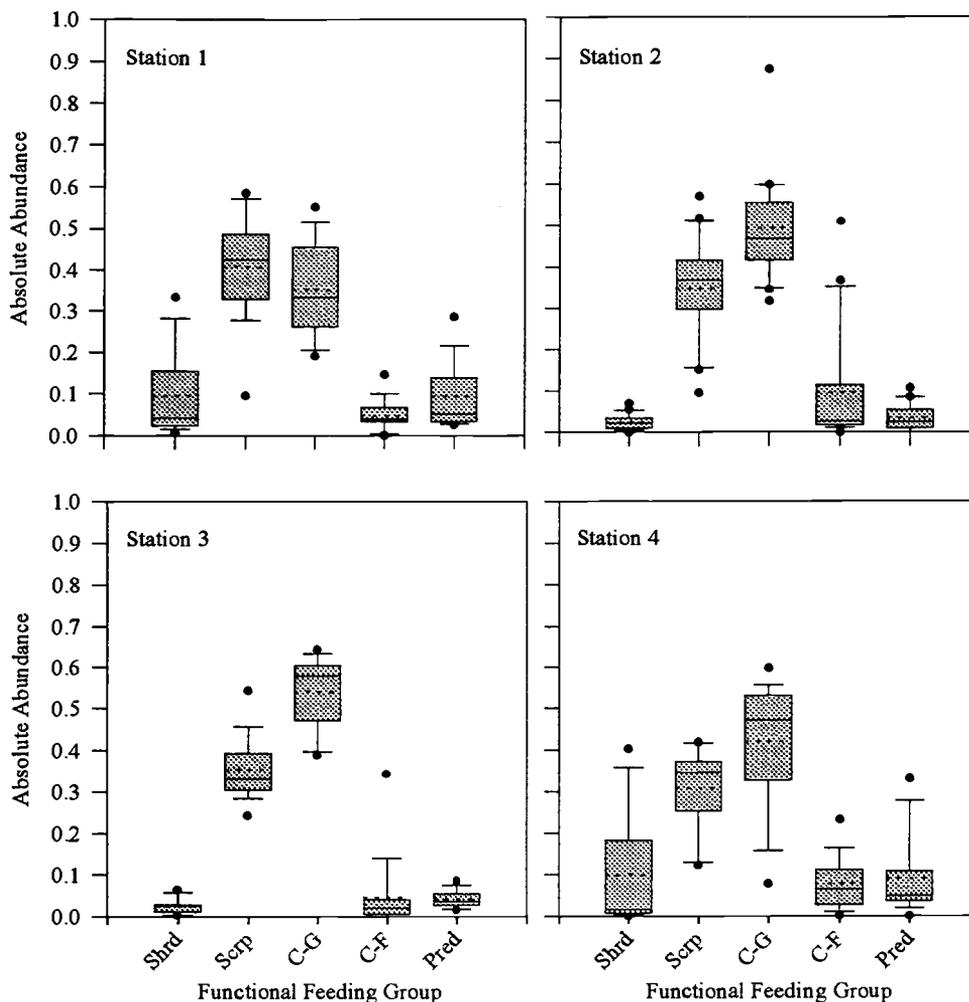


Figure 25. Population distributions for functional feeding group relative abundance by station in 1993. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (●) represents data points greater than the 10th and 90th percentiles. Shrd=Shredders, Scrp=Scrapers, C-G=Collector-gatherers, C-F=Collector-filterers, Pred=Predators.

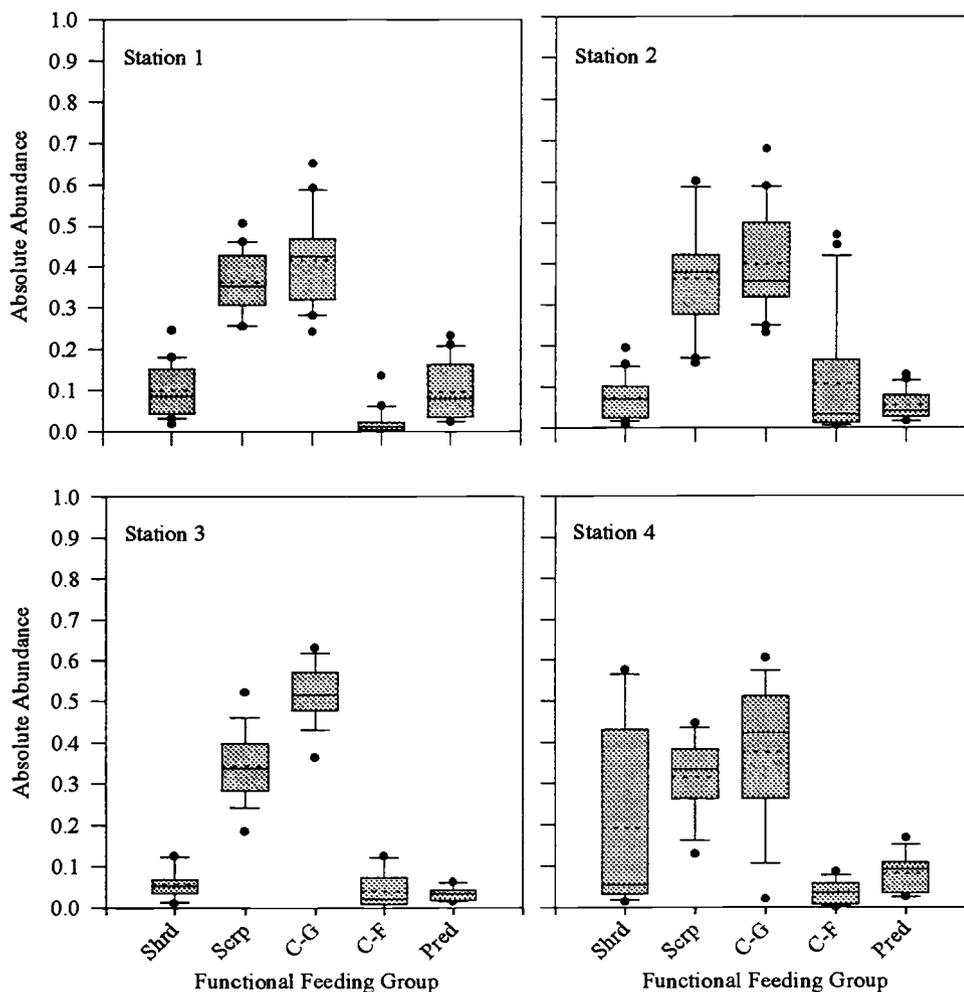


Figure 26. Population distributions for functional feeding group relative abundance by station in 1994. The solid line within the box represents the population median, the broken line represents the population mean, and each box encompasses the 25th through the 75th data percentiles. Line caps represent the 10th and 90th percentiles. (•) represents data points greater than the 10th and 90th percentiles. Shrd=Shredders, Scrp=Scrapers, C-G=Collector-gatherers, C-F=Collector-filterers, Pred=Predators.

Shredders did not compose a robust functional feeding group at any of the four streams and significant changes of one taxa within the group may affect the statistical behavior of the entire functional group. Collector-filterers had the lowest relative abundance at station 3 in 1993 and the highest abundance at station 2 in 1994. Collector-gatherers exhibited

significant increases at stations 2 and 3 in 1993 and increased at station 3 in 1994, although not significantly (Figures 24a & 24b). Figures 25 and 26 show the functional feeding group relative abundance data distributions for both sampling seasons. Stations 2 and 3 and stations 1 and 4, however, did not differ in the relative abundance of collector-gatherers in either years. Scrapers exhibited higher abundance at station 2 and at station 3 compared to station 4 and did not differ in relative abundance between stations 3 and 2 or 3 and 1 either year despite exposure to increased sunlight. This lack of significant response in relative abundance may be a result of the dramatic increases in collector-gatherers at station 3.

Diversity. Measures of diversity are given in Table 13 for each station for both years. Alpha (α) diversity is a measure of the number of species within each station and is a result of the combined effects of moderate, stable habitat and resource conditions, evolutionary and successional time, and the associated community which developed in that time under those conditions (Whittaker 1972). Alpha diversity is highest at station 1 although the difference may not be significant. Station 4's α -diversity was similar to the reference station's and station 2 and 3's α were similar to each other. Gamma (δ) diversity is a total measure of the alpha diversities of all four stations and so was the same at all four stations.

Table 13. Genera diversity of Ephemeroptera and Trichoptera at stations 1, 2, 3, and 4. Alpha, beta, and gamma diversity are defined in the text.

Station	N	Alpha	Beta	Gamma
1	32	30	1.13	34
2	32	27	1.26	34
3	24	26	1.31	34
4	24	29	1.17	34

Beta (β) diversity is a measure of species replacement among the four stations and is equal to δ/α (Whittaker 1972). Beta values approaching or equal to one indicate that the alpha diversity of a sample unit nearly reflects the gamma diversity of the entire sampled population. Beta diversity was relatively small in this study because the mayfly and caddisfly community did not differ dramatically across the longitudinal landscape described by the four stations nor across the environments of the four streams. However, station 3 showed the greatest degree of change from the general landscape diversity while station 1 showed little change.

The Shannon-Wiener (H') index incorporates species richness and evenness into one index, while the Shannon evenness index gives a more direct view of sample evenness (see Literature Review). The values of the Shannon-Wiener index usually fall between 1.5 and 3.5 while the Shannon evenness index is constrained between 0 and 1.0 with 1.0 representing a perfectly even sample (Magurran 1988). Index values and Shannon evenness values are given in Table 14 for each station. In 1993, there were significant differences in caddisfly and mayfly diversity (H') for stations 1 and 3 ($p=0.0008$) and 1 and 2 ($p=0.0016$) with station 1 having greater species diversity than the downstream treated stations (Table 14).

Table 14. Shannon-Wiener (H') index values and Shannon evenness (E) values averaged for stations 1, 2, 3, and 4 for 1993 and 1994. Standard errors are in parentheses.

Station	H'		E	
	1993	1994	1993	1994
1	1.77 (0.07)	1.80 (0.09)	0.50 (0.03)	0.56 (0.03)
2	1.47 (0.09)	1.82 (0.07)	0.41 (0.04)	0.50 (0.03)
3	1.30 (0.14)	1.60 (0.10)	0.48 (0.03)	0.56 (0.02)
4	1.58 (0.10)	1.80 (0.10)	0.56 (0.02)	0.54 (0.03)

Stations 2 vs. 4 ($p=0.03$) and 3 vs. 4 ($p=0.02$) also differed, with station 4 having higher diversity. There were no significant differences in diversity between stations 2 and

3 or stations 1 and 4. In 1993, station 3 had the lowest mean diversity of all the stations. In 1994, there were no significant differences between diversity at any station. After accounting for the variation caused by maximum temperature and cobbled substrate, diversity increased in a downstream direction so that station 3 had higher diversity than stations 1 and 2. Station diversity was significantly different between 1993 and 1994 ($p=0.002$) with mean diversity in 1994 higher at stations 2 and 3. Station's 1 and 4 had higher diversity in 1993, although station 4's diversity was not different in 1993 than in 1994 (Figure 27).

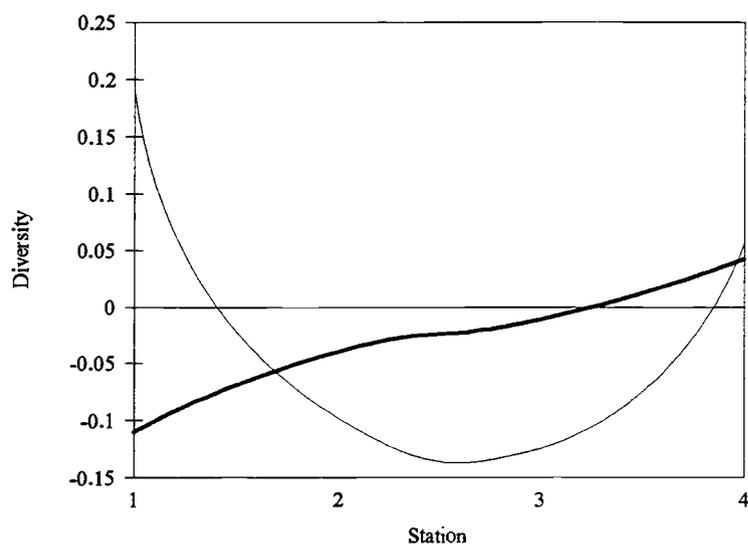


Figure 27. Deviations of the Shannon-Wiener diversity index (H') from the expected mean response at each station for 1993 and 1994. The center zero line represents the expected mean response given habitat characteristics, such as stream substrate, that correlated with diversity. Increases above or below the zero line signify population variance not explained by environmental parameters and, therefore, potentially introduced by treatment effects. —=1993; —=1994.

4.3. Reference Streams

Absolute counts. Reference stream data indicated little significant difference between the pseudo-stations in either 1992 or 1993 (Table 15). Only mayflies exhibited any significant differences between these stations. Although some genera, such as *Cinygmula*, showed strong consistent downstream trends, the “stations” are near enough to each other that it is unlikely that the majority of the significant differences are real and not a result of the probability of finding a false positive. Consequently, the results of the reference stream analysis provide a picture of the frequency of false significant differences. If results on the treated streams showed a greater number of genera with significant differences, then we may assume that these differences are a result of conditions not present in the untreated streams. *Cinygmula* exhibited consistent differences in both 1992 and 1993 between stations 1 and 4 and stations 1 and 2. The “downstream” stations 2 and 4 both had significantly higher abundance of *Cinygmula* than station 1 (Figure 26).

Table 15. Significant differences for reference stream mayfly and caddisfly absolute abundance between arbitrary stations. The “station” with the greater abundance is listed. **=p-values<0.01, *=p-values<0.05.

Genus	1 vs. 4		1 vs. 2		2 vs. 4	
	92	93	92	93	92	93
<i>Cinygmula</i>	4*	4*	2*	2*		
<i>Epeorus</i>					2*	
<i>Rhithrogena</i>		4*				
<i>Paraleptophlebia</i>				2*		

This pattern also occurred in the treated streams although station 4 had slightly higher abundance than station 2 on the reference streams. Because *Cinygmula* responses were strongly consistent on both reference and treated streams, this mayfly may commonly increase in abundance in a downstream direction. Other reference stream taxa's responses

appeared more a result of either natural variability or false positives within the statistical analysis.

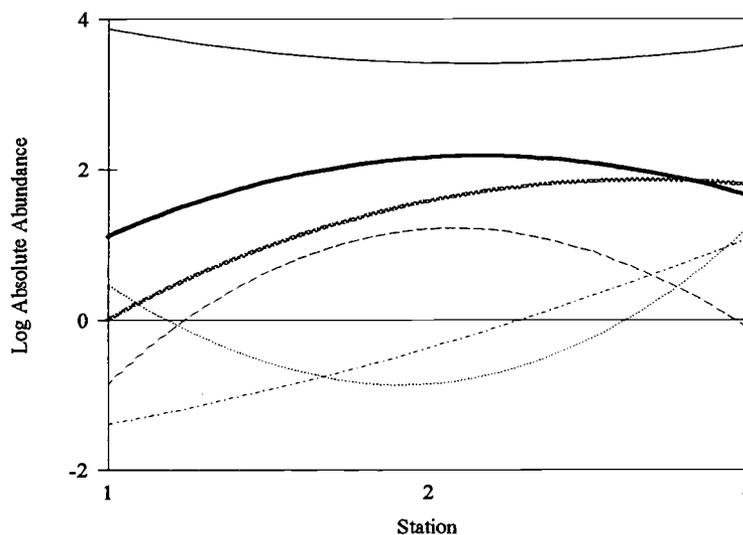


Figure 28. Log transformed absolute abundance for reference stream mayflies by arbitrary stations 1, 2, and 4 for 1993. —=*Baetis*; —=*Drunella*;=*Cinygmula*;=*Epeorus*;=*Rhithrogena*;=*Paraleptophlebia*.

Relative abundance. Reference stream relative abundance differed for most of the same taxa and in the same direction as differences raised with absolute mayfly and caddisfly count comparisons. This did not occur on the treated streams. *Cinygmula*, increased in relative abundance in a downstream direction between stations 1 and 2 and stations 1 and 4 in 1993 (Table 16). Using relative abundance, only one more mayfly genera exhibited a significant difference at the reference streams than did using absolute counts. *Baetis* had a strongly significant higher abundance at station 1 than at either 2 or 4. This was opposite what was observed in the treated streams where *Baetis* relative abundance increased consistently in a downstream direction. However, this variation between closely spaced sampling points likely expressed a range of natural variability within *Baetis* populations in a stream system. Because the treated stream consistently

contradicted this expression of natural variability, it can be assumed that the responses of treatment stream *Baetis* populations were in response to treatment.

Table 16. Significant differences for reference stream mayfly and caddisfly relative abundance between arbitrary stations. The "station" with the greater abundance is listed. **=p-values<0.01, *=p-values<0.05.

Genus	1 vs. 4		1 vs. 2		2 vs. 4	
	92	93	92	93	92	93
<i>Baetis</i>		1**		1**		
<i>Cinygmula</i>		4*	2*	2*		
<i>Rhithrogena</i>		4*				
<i>Paraleptophlebia</i>				2**		2*

Functional feeding groups. Reference streams did not show any significant differences in functional feeding group absolute abundance between "stations" in 1992 and 1993. Collector-gatherers and scrapers were the most abundant functional feeding groups, but no differences in the short downstream direction were detected. When relative abundance of reference stream functional feeding groups were analyzed, there were no significant differences between relative abundance at stations in 1992. In 1993, however, collector-gatherers had significantly higher relative abundance upstream at station 1 than at just a short distance downstream at stations 2 ($p=0.008$) and 4 ($p=0.03$) (Figure 27). This differs from the treated streams where collector-gatherers exhibited increased relative abundance at station 2 and did not differ at station 4 compared to 1. Again, because collector-gatherers consistently contradicted this pattern of natural variability in the treated streams, collector-gatherer response may also have been an artifact of treatment. Collector-filterers played a minor role in the reference stream functional feeding group community, in contrast to their noticeable presence on the treated streams.

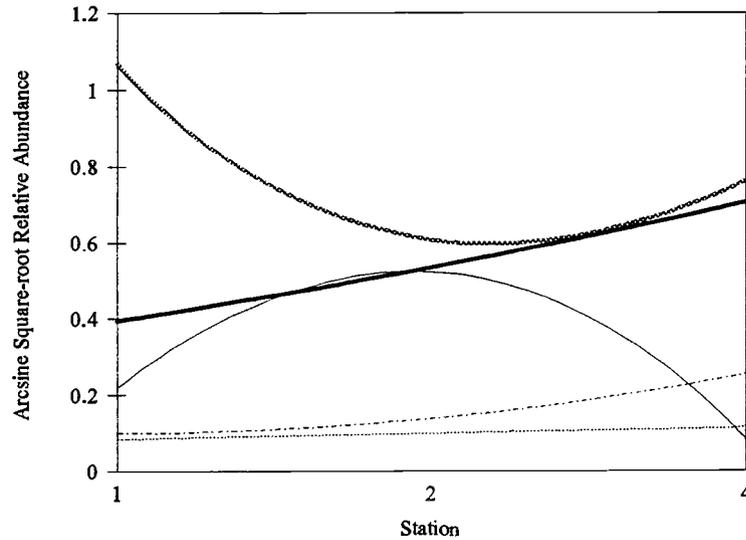


Figure 29. Arcsine square-root transformed relative abundance for reference stream functional feeding groups by arbitrary station for 1993. —=Shredder; —=Scraper;=Collector-gatherer;=Collector-filterer; -.-.-=Predator.

Diversity. Reference stream diversity showed no significant differences between station comparisons for 1992. In 1993, however, all the station comparisons differed significantly, with downstream stations having higher diversity than the upstream station. Diversity was highest at the middle station (Figure 28). This between year shift in diversity indicates that community diversity measured with the Shannon-Wiener index can be highly variable between years. Increases in diversity between 1993 and 1994 on the treated streams may fall into the range of natural variability and not reflect a real increase in mayfly and caddisfly community diversity a year after treatment.

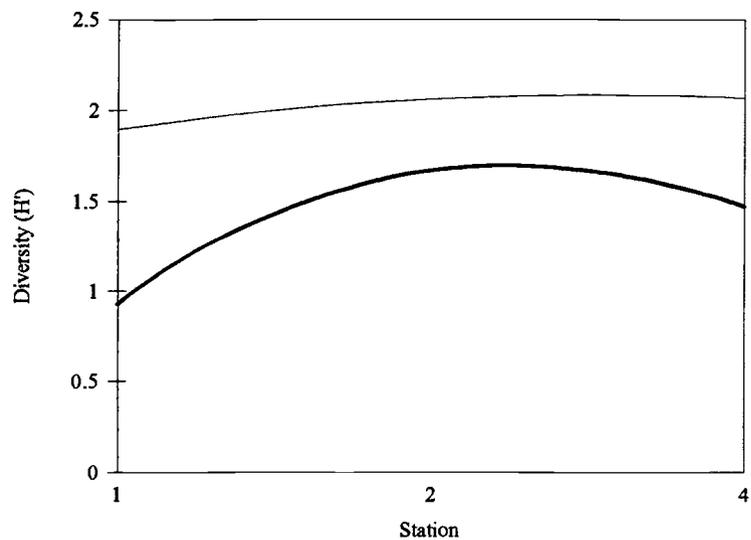


Figure 30. Shannon-Wiener diversity index (H') for arbitrary stations 1, 2, and 4 on reference streams in 1992 and 1993. —=1992; —=1993.

5. DISCUSSION

5.1. Environmental Effects

Changes in stream temperature and solar radiation loads affect aquatic invertebrates by altering food sources, life cycles, and habitat (Minshall 1968, Hansmann & Phinney 1973, Murphy & Hall 1981, Noel et al. 1986, Saleem & Iftikhar 1987, Tait et al. 1994). Riparian forest and vegetation removal, especially timber harvest, can increase stream temperature and solar radiation loading in the short term (Brown & Krygier 1970, Lee & Samuel 1976, Rishel et al. 1982, Noel et al. 1986, Holtby 1988, Brown 1991, Holopainen & Huttunen 1992, Tait et al. 1994). Aquatic insects grow, reproduce, and feed in a temperature buffered environment where, because of water's heat capacity, temperatures fluctuate less than air temperatures. Changes in stream temperature directly affect aquatic insects through changes in instar numbers, egg diapause, fecundity, body size, emergence phenology, and diurnal patterns (Merritt & Cummins 1984, Newbold et al. 1990, Rader & Ward 1990). Changes in stream temperature indirectly affect aquatic insects through oxygen saturation levels, respiration rates, food availability and nutritive value, and competition from other insects (see Literature Review).

Low order streams may be temperature limited. Moderate increases in stream temperature in these streams may raise the productivity of the general mayfly and caddisfly community by increasing food sources and food processing rates, speeding up life cycles, and increasing the number of reproductive cycles a prolific mayfly and caddisfly can go through in a season. In the meantime, dissolved oxygen levels rarely decline below tolerable limits, especially in flowing mountain streams. Not all insects, because of rigid life histories and sensitivity to competition from increasing mayfly and caddisfly numbers, respond positively to slight temperature increases with increases in abundance. Negative or neutral responses may be masked by surges in other taxa.

During 1993 and 1994, patch clearcuts which removed 25% of riparian forest stream cover along a 1600-m reach did not appear to raise maximum and mean stream temperatures above biologically lethal limits. The relatively small stream expanses exposed by the small 200- and 100-m patchcuts may have limited potential increases in stream temperature because the water passed through the clearcuts rapidly enough to avoid lengthy exposure to incident radiation. Twenty-five percent harvest removals on longer stream reaches using different sized clearcuts or on a number of streams within the same basin may not be expected to generate the same moderate aquatic insect responses to stream temperature or other treatment effects. The study results apply only to a single mile-long stream reach using a combination of medium to small sized patchcuts.

Moderate temperature increases in these cool streams may have been beneficial for some aquatic taxa although evidence of stress was not sampled for. Average mean temperature ranged between 9°C and 19°C for both years and maximum temperatures ranged between 18°C and 24°C for both years. *Rhithrogena* and *Baetis* have been found in streams at temperatures up to 21°C (Saleem & Ifikhar 1987). Noel et al. (1986) sampled mayflies in a fast flowing 1200-m clearcut reach where maximum temperatures reached 29°C. Caddisfly populations have been sampled at maximum temperatures of 26.5°C (Gordon & Wallace 1975). Maximum stream temperature, however, was negatively correlated with mayfly and caddisfly diversity. Highest temperatures may have proportionally favored only a very few of the taxa, thereby reducing proportions within the general mayfly and caddisfly community and lowering diversity.

Solar radiation indirectly affects aquatic mayfly and caddisfly populations by both increasing water temperatures and increasing primary production within a creek (Lyford & Gregory 1975, Hawkins et al. 1982, Fuller et al. 1986, Feminella et al. 1989, Brown 1991). Third-order mountain streams obtain energy inputs from allochthonous sources. Riparian canopy and streamside vegetation provide detritus to coarse organic particulate matter (CPOM) processors. Insects which depend on autochthonous energy sources in these systems usually rely on diatoms and algae living on stream substrates, particularly gravel and leaves (Hansmann & Phinney 1973, Mayer & Likens 1987). After removal of the riparian canopy, algae and aquatic macrophytes respond to increases in sunlight and

create abundant, easily digestible, nutritious autochthonous food sources as well as habitat for particular taxa that cling or sprawl within the velocity slowing mats and fronds (Dudley et al. 1986). Some substrate habitat is eliminated by the coverage of filamentous algae (Hansmann & Phinney 1973). I observed heavy algal blooms in only Mosby Creek. The dense filamentous mats appeared to limit the abundance and diversity of much of the local stream community except for early mayfly instars and Chironomidae. However, in general, the dominant taxa of the local stream community responds to increases in autochthonous food sources by increasing in density and absolute abundance (Hawkins et al. 1982, Rounick et al. 1982, Fuller et al. 1986, Noel et al. 1986).

Increases in abundance of certain taxa were expected from increases in radiation load at station 3, specifically *Baetis* (Newbold et al. 1980, Noel et al. 1986, Wallace & Gurtz 1986). *Baetis* did increase significantly in both absolute and relative abundance at station 3. However, because primary productivity was not directly measured it is uncertain if this increase was in direct response to increasing sunlight or a result of a combination of related treatment factors, including local increases in stream temperature and adjacent riparian disturbance. When determining the correlation of environmental factors and population measures in the analysis, incident solar radiation did not correlate significantly with any mayfly and caddisfly taxa, including *Baetis*. This likely was a function of radiation being significantly different only at station 3.

Remaining environmental parameters were monitored as covariates of mayfly and caddisfly microhabitat because there was little likelihood that harvest treatments would affect the parameter's conditions. Velocity accounted for mayfly and caddisfly variation among stations on our four streams in western Oregon. Harvest treatments adjacent to the stream channel may affect stream velocity by decreasing local transpiration temporarily and slightly increasing flow (Harr 1979). However, because of the small size of the installed clearcut reaches, the adjacent, intact riparian forest between clearcuts, and the moderate stream gradients, measurable increases in stream velocity during the summer were unlikely as a result of clearcutting. Stream velocity, which was highest in June and declined through the sampling season, did correlate significantly with certain mayfly and caddisfly taxa. *Hydropsyche* and *Arctopsyche* were positively affected by velocity while

Lepidostoma, *Glossosoma*, *Paraleptophlebia*, and *Rhyacophila* were negatively associated with velocity. Remaining taxa were not significantly correlated with velocity.

Substrate type explained a large proportion of mayfly and caddisfly variance among stations. More taxa exhibited a positive association with complex substrates than smoother substrates, which explained less variance for all taxa (Pennak & Van Gerpen 1947, Allan 1975a, Minshall 1968, De March 1976, Gurtz & Wallace 1984, Brown & Brussock 1991). Cobbled substrates were positively associated with the most mayfly and caddis genera. *Baetis*, *Drunella*, *Glossosoma*, *Cinygmula*, *Rhithrogena*, and *Rhyacophila* were positively associated with cobbles. Only the caddis, *Neothremma*, was negatively associated with cobbles. Gurtz and Wallace (1984) found that after forest clearcutting, cobble substrates were the only substrates to not exhibit significant declines in benthic leaf detritus and, Reice (1985) observed that the invertebrates in cobbled environments were the most resilient to disturbance. This indicates that cobble riffles remain relatively supportive habitats after clearcutting disturbance. This is likely a combined function of food particle retention, habitat availability, and dissolved oxygen levels caused by increased mixing and associated current velocities (Minshall & Minshall 1977).

Although boulders and gravel are also complex substrates, boulders are associated with higher flows and tend to retain less detritus and have lower habitat heterogeneity. Gravel retains large quantities of detritus, but is also limited in habitat heterogeneity and may tend to have higher fine particle deposition rates. Sand, silt and bedrock were associated with a few taxa. *Wormaldia* and *Neothremma* positively identified with sand. *Wormaldia* is a filter feeder with an extremely small net size and prefers habitat with lower flows. Sand substrates would be characteristic of depositional areas with lower velocities. In a study by Ogilvie and Clifford (1986), populations of *Neothremma alicia* were positively associated with rock substrates in fast-flowing currents. Comparison with *Neothremma* spp. sampled in our western Oregon streams is difficult because mayflies and caddisflies were not identified to species. However, according to Anderson (1976), *N. alicia* has been found only in streams of northeastern Oregon. More likely, the *Neothremma* in our streams were either *N. andersoni* Wiggins or *N. didactyla* Ross, and

more likely the later. All *Neothremma* construct their cases from sand grains which may explain the link to substrate type. *Lepidostoma* was positively linked with silt substrates. Grafius and Anderson (1979) observed *Lepidostoma* inhabiting pools and pool-end areas more frequently than riffles. The Hydropsychids and *Micrasema* were positively associated with bedrock substrates (Smith-Cuffney & Wallace 1987, Huryn & Wallace 1988).

5.2. Treatment Effects

After accounting for within site variance, mayfly and caddisfly communities on four streams in western Oregon exhibited faunal changes that were likely a response to riparian forest clearcutting. The spatial and temporal longevity of these changes, however, varied. With minor fluctuations between seasons, abundant mayfly and caddisfly taxa in undisturbed systems with relatively stable climate conditions have a high degree of stability over periods of several years. Changes in species composition attributable to immigration and chance extinction are minor. Instead, significant changes in mayfly and caddisfly community composition result from biological, environmental, and anthropogenic events occurring over relatively large spatial and temporal scales (Richards & Minshall 1992).

Clearcutting introduces large spatial and temporal disturbances to stream systems (Newbold et al. 1980). Over a two-year period following harvesting of 25% of the riparian forest along a 1600-m reach in four streams, abundant mayflies and caddisflies responded with increases in abundance, changes in dominance of functional feeding groups, and stabilization of decreases in diversity. Mayfly and caddisfly community variability and changes were evaluated by comparisons to upstream reference stations and to reference streams. The relative constancy of reference stream populations was in sharp contrast to the number of significant differences observed on the treated streams.

Both absolute and relative abundance tended to maximize halfway through the treatment reach (as measured by stations 2 and 3) and then to decline to reference station

levels below the two lower 100-m clearcuts. Diversity declined continually from the reference station through the treatment stations in 1993. In 1994, there were no significant differences between diversity at all four stations and the Shannon-Wiener index was higher for most stations the second year. Those insects with longer life cycles, such as *Neothremma* whose adults would not have laid the next generation's eggs until the end of the first summer, may have, by 1994, responded to increases in food availability or habitat favorability by increasing in abundance (Ogilvie & Clifford 1986). On the reference streams, diversity also differed significantly between years indicating that the difference between years on the treated streams may have been a result of natural variability and not a recovery from possible treatment effects.

Station 2. The middle, canopied station exhibited the greatest significant increases in absolute abundance for more taxa and functional feeding groups than any other treated station. Relative abundance at stations 2 and 3 increased equally. Increases, however, did not continue downstream below station 2. Once absolute abundance rose from reference station levels it either did not increase beyond that level or fell again to not differ significantly from reference station levels. Significant differences between station 2 and the other stations were numerous in both 1994 and 1993. Scrapers and collector-gatherers increased far above other functional feeding groups at station 2. Mayflies are primarily collector-gatherers and scrapers and the large increases in mayfly taxa at station 2 would explain the increases in the relative abundance of these functional feeding groups. By 1994, differences between scraper and collector-gatherer abundance at the reference station and station 2 had diminished possibly because of upstream oviposition from the 200-m clearcut or general increases in habitat favorability. Decreases in predator and shredder relative abundance at station 2 are most likely explained by large absolute increases in collector-gatherers and scrapers (i.e., mayflies). Collector-filterers peaked in absolute abundance at station 2 compared to the other stations possibly in response to primary production within the 200-m clearcut and potentially related increases in seston delivery downstream. Towns (1981) also noted that collector-filterers were relatively more abundant beneath canopies next to exposed stream reaches.

In view of rapid increases in certain taxa and decreases in diversity at station 2, it can be hypothesized that the 200-m clearcut influenced the downstream mayfly and caddisfly communities for at least some distance under the riparian buffer. Because there was no statistical difference between the absolute abundance of the caddisfly and mayfly communities at station 2 and station 3 in 1993, it may be assumed that there was little difference between the community upstream in the 200-m clearcut and at station 2. Increases in taxa that are prone to drifting at station 2, such as *Baetis* or *Hydropsyche*, may have been a result of increases in populations at the 200-m clearcut which drifted downstream. However, station 2 was often more than 500 m from the downstream edge of the upstream 200-m clearcut, so measurable increases in taxa abundance caused by drift were unlikely. More likely, increases in taxa abundance at 2 may have resulted from upstream oviposition of taxa flourishing in the nearby exposed clearcut (station 3).

Increased populations require increased food availability in order to successfully colonize and support a site. Towns (1981) recorded that detritus weight sampled underneath a riparian canopy increased downstream of canopy openings where autochthonous production had increased. The increase in weight was a result of decayed algae floating downstream and becoming trapped in the substrate. Downstream transportation of high quality algal material generated in the upper 200-m clearcut may have increased food availability at station 2. Possible colonization by populations from surrounding clearcut reaches combined with moderate increases in water temperature, deposition of detrital material from harvest disturbance, and increased seston from autochthonous production may have caused facilitated increases in absolute abundance at station 2. Using the variability observed at "station 2" within the reference stream caddis and mayfly populations as a measure of natural background population fluctuations, the sheer number of significant changes in mayfly and caddisfly abundance and functional groups observed on the treated streams indicates that treated genera responses exceeded "normal" population variability. At station 2, these divergences were likely a local function of the riparian harvest removal and not longitudinal variation because farther downstream at station 4 (a greater longitudinal distance), populations vary less.

Station 3. The station located in the exposed upper 100-m clearcut differed most from the reference station. The absolute abundance of all significant taxa exhibited increases at station 3 with more taxa showing significant differences in 1994. This may indicate a lag caused by taxa's uni- or semivoltine life cycles. Despite the delay, these taxa may still have responded to increases in primary production and local stream temperature. *Baetis* exhibited increases in both absolute and relative abundance for both 1993 and 1994. No other mayflies and caddisflies showed as quick a response to changes in habitat. *Baetis* is most frequently recorded as the initial and highly successful colonizer of streams disturbed by logging (Newbold et al. 1980, Haefner & Wallace 1981). Colonization is typically accomplished by drift dispersal which is stimulated by increasing food abundance in another section of stream (Richards & Minshall 1988). *Drunella* also increased significantly. However, it increased to "normal" levels from low population levels at station 2. *Baetis* and *Drunella doddsi* were identified by Rader and Ward (1987b) as diatom consumers with high within group overlap of habitat (rock surfaces) and food preferences. Simultaneous increases in both these taxa in our streams may have indicated similar responses to habitat conditions.

Because *Baetis* suffers both little energy expenditure from entering drift and mortality at higher population densities, they readily abandon periphyton patches with relatively high food densities in search of less crowded periphyton patches (Kohler 1992). Therefore, *Baetis* is more likely to leave an area before other more tolerant and efficient taxa. *Glossosoma*, for example, is an efficient scraper which does not abandon food resources readily and can survive at lower resource levels. *Glossosoma* must transport its case or construct a new one when it leaves an area and so, experiences high energy costs to change location. *Glossosoma* levels were among the highest of the caddis taxa at station 3. However, abundance levels were lower at station 3 than at station 2 in 1993. Not until 1994 were increases in *Glossosoma* observed at station 3.

Baetis is also primarily a collector-gatherer and secondarily a scraper. Collector-gatherers increase in response to clearcutting and other disturbances (Towns 1981). Scrapers, on the other hand, have shown decreases in disturbed areas (Towns 1981, Kondratieff et al. 1984). Particular scrapers, such as *Glossosoma*, may not respond as

readily to clearcutting despite increases in primary production. Hawkins and Sedell (1981) observed that scrapers fed primarily on thin periphyton films and avoided filamentous algae communities because they are not harvested as efficiently. *Glossosoma* in particular prefers diatoms which are proportionally more abundant in shaded stream reaches (Kohler 1992).

More caddisflies and fewer mayflies significantly changed in relative abundance at station 3. All caddisflies, except for *Lepidostoma* and *Micrasema* in 1994 showed significant declines in relative abundance in the exposed clearcut when compared to the reference station. These decreases were likely a result of significant increases in mayfly taxa at station 3. However, ecological stimuli such as food abundance and quality, competition, habitat availability, and local temperature maxima may have contributed to declines in caddis populations. Station 3 had the lowest diversity in both 1993 of all stations and exhibited increasing diversity in 1994. Diversity differences among stations were not significant in 1994 however. In view of the constancy of treatments among stations in 1993 and 1994, the shifts in diversity between years appear a function of random shifts in time and microenvironment.

Absolute functional feeding group abundance showed significant increases in scrapers and collector-gatherers at station 3. However, relative scraper abundance increased only compared to station 4 in 1993 and was not significantly different from reference station populations. Again, scrapers may not necessarily respond to disturbance with increases in abundance, even when disturbance increases primary production. Accumulation of macroalgae restricts some scrapers' foraging habits (Hawkins & Sedell 1981, Dudley et al. 1986). Shredders and collector-filterers decreased in relative abundance at station 3. In 1994, relative abundance differences were minimal because of increases in collector-gatherers and decreases in other functional groups at each station. The excellent oviposition behavior of mayflies and their multivoltine life cycles (Brittain 1982) as well as increased second year responses of caddis, such as *Lepidostoma* and *Neophylax*, may have succeeded in evening out the relative abundances in 1994 and reducing significant differences that year. Murphy (1979) observed increases in species richness and mean total density of predators within clearcut reaches as compared to old-

growth reaches. Predators on our streams, however, exhibited higher relative abundance underneath the riparian canopy compared to the clearcut section and no difference in absolute abundance between any stations.

Station 4. The farthest downstream station was installed to reflect cumulative changes in the mayfly and caddisfly community as a result of the entire 25% harvest removal. Few differences were significant between the reference station and station 4. Increases at middle stations often had decreased again by this point. Potentially, the smaller 100-m clearcuts with riparian buffer in between did not affect the mayfly and caddisfly communities as dramatically as the larger cut. One of the few taxa showing significant differences at station 4 on both the treated and reference streams was *Cinygmula* which increased consistently in 1993 compared to the upstream stations. It is unlikely that increases in *Cinygmula* abundance at station 4 were a result of treatment, but more likely a reflection of genera-specific downstream increases. The number of remaining taxa that showed a significant difference between the reference station and station 4 was not greater than the natural variation that may be expected between stations as evidenced by variation observed on the reference streams. In short, clearing of 25% of a 1600-m reach did not provide evidence of a major cumulative effect that expressed itself in the mayfly and caddisfly communities at the bottom of the entire treatment reach.

6. CONCLUSIONS

6.1. Summary

Research conclusions. Timber harvesting alongside streams can cause significant changes within aquatic invertebrate communities (Newbold et al. 1980). However, when timber harvesting removes only 25% of the riparian canopy and the rest of the streamside riparian vegetation remains intact, the effects on caddisfly and mayfly populations are not clear. Spatially, absolute populations in almost every common genus increase in a downstream direction with population peaks within the exposed clearcut reach and under the buffer in the center of the 1600-m treatment reach. Abundance increases, however, appear to span short longitudinal distances and most taxa return to levels observed in upstream reference stations by the bottom of the 1600-m harvest reach. Those few taxa that still differed exhibited higher abundance than the reference station. However, even in the short distances between reference stream "stations," some mayfly and caddisfly populations increased in a downstream direction. Longitudinal increases in specific taxa abundance may be a "normal" function of downstream movement through a basin. A few differences between the reference station and bottom station were not necessarily a direct result of harvest treatments, but more likely a reflection of "normal" downstream variability.

Increases in relative abundance were not observed over long distances. Relative abundances through the 1600-m treatment reach varied, with mayflies, such as *Baetis*, Heptageniidae, and *Paraleptophlebia*, increasing downstream in general and specifically at stations 2 and 3, and caddisflies, such as *Lepidostoma*, *Rhyacophila*, and *Wormaldia*, decreasing through patchcut and buffered stream sections. Other, often more abundant caddisfly genera, such as Hydropsychidae, *Glossosoma*, and *Neothremma*, however, exhibited increases through the treated reaches. The relative abundance of some members of the caddisfly and mayfly community may decline because of a dramatic increase in a

few taxa, specifically *Baetis*. Using absolute and relative abundance and functional feeding groups to compare communities from the top to the bottom of a 1600-m stream reach revealed little difference in the communities entering and exiting the affected distance.

Temporally, decreases and/or increases in the caddisfly and mayfly communities also appeared to be short lived and/or variable. Over the two-year sample period, most mayflies and caddisflies increased in abundance. Diversity decreased the first year after harvesting in a downstream direction. In 1994, however, two years after harvesting, diversity equalized between stations and increased above 1993 levels for most stations. Whether 1994 diversity exceeded pretreatment conditions or was returning to pretreatment levels is uncertain. Because reference stream diversity varied significantly between years, diversity increases in 1994 on the treated streams may merely reflect normal variability in community diversity. Increases in diversity and absolute mayfly and caddisfly abundance during the second year may be more attributable to warmer temperatures, less cloud cover, and lower current velocities in 1994 than to a definitive recovery from treatment effects.

By the end of the second year, a pattern of population peaks in the center of the unit followed by a decline in the bottom half was evident. Whether longitudinal mayfly and caddisfly communities were positively affected by the 200-m clearcut and negatively affected by the two 100-m clearcuts or were negatively affected by the 200-m clearcut and then positively affected by the two 100-m clearcuts depends on the philosophy of the observer. The end result of the riparian silviculture manipulation is that, two years after harvesting, abundances were similar to reference station levels below the 1600-m reach and diversity did not differ beyond expected variability below or within the clearcuts.

Changes in stream maximum temperature did not significantly influence individual mayfly and caddisfly genera as measured in this study. Maximum stream temperature did have a negative correlation with diversity but did not appear to exceed thermal death points of the mayflies and caddis. Solar radiation did not explain the variance of individual taxa but may have been a factor in increasing primary productivity in the exposed reach and therefore, indirectly, influencing increases in certain taxa. Exposing

the stream to increased solar radiation may have increased absolute abundance of *Baetis*. It did not, in the span of a 100-m opening, appear to have affected other genera. However, Rounick et al. (1982) did not observe significant responses of mayfly and caddisfly taxa to increased primary production until 5 years after harvesting. Two years after harvesting, insects were still responding to stores of allochthonous material within the stream channel that had not been flushed downstream. A two-year post-harvest period is likely not sufficient to measure responses to increases in primary production caused by streamside harvesting. Stream substrate appeared to have the greatest effect on mayfly and caddisfly presence and resiliency.

Management applications. Increases in mayflies and caddisflies that are prone to drift, such as *Baetis* and *Hydropsyche*, may be beneficial for salmonid populations that feed primarily on drifting insects. Both these insects increased in the treated reaches. Small, patch clearcuts carefully installed to minimize channel and herbaceous vegetation disturbance may offer short-term and long-term benefits to salmonid populations. In the short-term, small patch clearcuts appear to increase the absolute and relative abundance of the drifting mayfly and caddisfly food supply without dramatically increasing stream temperature or altering the composition of the mayfly and caddisfly community a short distance downstream. Patchcut locations should be planned with considerations for stream substrate and flow. For example, locating patchcuts alongside riffle habitats may enhance mayfly and caddisfly abundance more and be less “stressful” for the stream system than beside slow flowing water or pools (Murphy 1979). Riffles contain high proportions of cobbles and exhibit fast accumulation rates of algal biomass when exposed to light (Busch 1978). Cobbles are preferred by *Baetis* and other abundant taxa populations, so that riffles exposed to light also show higher faunal biomass export rates. Salmon appear to feed preferentially below riffles in forest streams because they support high drift. Riffles also have relatively high current velocities which may prevent water from warming beyond tolerable biological levels and maintain adequate concentrations of dissolved oxygen. However, managers must be careful to not manage for one or two aquatic invertebrate taxa, such as *Baetis*. Community diversity is critical for maintaining stream ecosystem functions.

In the long-term, patch clearcuts may facilitate the growth and succession of conifers in currently hardwood-dominated plant communities. Conifers would provide year-long microclimate modification, long-term sources of nutrient litter, and a long-term source of large woody debris. It is important to the mayfly and caddisfly community, however, to retain a mix of deciduous and coniferous species. High nitrogen content and rapid processing of red alder leaves balances the low nutrient content and slow conditioning rates of conifer detritus (Swanson et al. 1982). First, however, riparian forests must reach a point where tree species diversity is possible. In the Douglas-fir region, it is virtually impossible to exclude deciduous cover over streams on the resilient environments along low-elevation streams. Conifers are therefore the species that require re-introduction. However, under current conditions, the red alder/salmonberry community does not provide conditions suitable for natural conifer regeneration. Managers must weigh the consequences between waiting for possible natural succession to restore conifers to riparian areas and acting with current knowledge to attempt to restore conifers in moderate sized patches along riparian corridors.

Management of riparian conifer sections after regeneration should be undertaken with both the salmonid and aquatic insect populations in mind. Between short-term responses of mayfly and caddisfly taxa to increased primary production and the long-term benefits of mature conifer riparian forests lies a gray area where habitat conditions and mayfly and caddisfly responses are less certain. Second-growth deciduous and coniferous forests up to 100 years of age may foster nutrient poor stream systems because of dense shading, slowly conditioned detritus, and lack of large woody debris delivery (Murphy 1979, Murphy & Hall 1981, Sedell & Swanson 1982). Streamside conifer forests with characteristics more similar to old-growth systems, including patchy openings (increases primary production), large wood delivery (increases channel complexity), and frequently disturbed streamside areas (maintains nutrient rich plant material) appear to support a more diverse mayfly and caddisfly community. Higher levels of mayfly and caddisfly and macrophyte production and greater physical heterogeneity within the stream system may support healthy salmonid populations. However, results from this research effort emphasized "reach scale" mayfly and caddisfly responses. Riparian management

conducted throughout a stream network system or basin may contribute to different and possibly greater cumulative responses within the aquatic insect community. Issues of scale and frequency should be considered when planning management activities. Forestry to achieve riparian and stream health goals before, during, and after conifers are established is possible with sound planning, foresight, and an understanding of the complex terrestrial and aquatic systems operating within the riparian zone.

6.2. Lessons Learned

Although a goal of the master's thesis is to contribute an original body of research to the scientific community, it differs from a Ph.D. dissertation or a research grant proposal in that its primary purpose is to give a beginning scientist a forum for trial and error without professional consequences. Consequently, the lessons learned for a "better next time" are critical to the thesis process. The areas of research where I realized and envisioned possible improvements to this study are in experimental design and sampling. Improvements to these two areas would facilitate a more powerful and clear analysis as well as a more direct interpretation of mayfly and caddisfly response to the silviculture treatments.

Experimental design. The treatment clearcuts were not randomly installed on the streams, so that, the 200-m patchcut was always upstream of the two 100-m patchcuts. Also, although the proposed objectives were to test the removal of 25% of the riparian canopy, effectively we tested the removal of 200 meters of stream canopy and 100 meters of stream canopy. In future studies which test a percentage removal of stream canopy, I would randomize the location of different sized patchcuts and, if enough streams were available, I would vary the form in which the 25% removal occurred. For example, if some of our streams had had a 100-m clearcut upstream, I could have tested if the increase in mayfly and caddisfly abundance at station 2 was an effect of the 200-m clearcut or a characteristic response of mayfly and caddisfly communities in upstream reaches. Or, I could have tested whether the 200-m clearcut would have had a greater or

lesser effect on mayfly and caddisfly communities if it were downstream from the 100-m clearcuts. Variations of this type of question are possible by randomizing the location of the patchcuts.

If the clearcuts had varied in sizes that still created an overall 25% removal, such as one 400-m clearcut, a 100- and 300-m patchcut, or four 100-m patchcuts, etc., the results may have given forest managers applying the techniques in the field greater flexibility in their application and provided greater insight to the actual effects of a 25% removal on aquatic communities: were they consistent or did they vary with clearcut size? Randomization in these forms with a slightly different temporal sampling scheme would have facilitated a complete randomized block analysis which would have simplified and strengthened the statistical analysis. Each of these experimental design options would have realistically necessitated more than four treatment streams in order to preserve replication, which would have demanded greater time and effort in sampling.

Had I not been instructed to attempt to determine the responses of the mayflies and caddisflies in both the western Cascades and Oregon Coast Range, I might have also intensified my sampling by focusing on the responses of the mayflies and caddisflies to treatments on only one stream in either georegion. Although doing so limits the validity of the conclusions on streams in other geographical areas and creates an even more "case study" thesis, sample number and stations could have been increased on one stream, intensifying the strength of the results without adding many more total samples. More stations would have improved the measurement of downstream longitudinal shifts in mayfly and caddisfly abundance and diversity and better shown potential recovery or continued long-distance effects. Streams differ greatly between basins within the same area and therefore require much greater replication than even four streams could provide to show measurable and significant geographic differences.

Sampling. As discussed in the Literature Review, sample variability can be a significant source of error in aquatic mayfly and caddisfly studies. However, in order to effectively evaluate the responses of the mayfly and caddisfly community, the number of samples collected and how they are collected is critical. Had I had the experience I have now when I began this project, I would have planned to collect more samples because 1) I

would be able to process and identify them more rapidly and, 2) during the analysis it became apparent that those mayflies and caddisflies with the largest abundance exhibited a more normal population distribution and greater significant responses to the treatments. Collecting more samples either within stations or for more stations may have increased the normalcy of rarer mayfly and caddisfly genera, improved the power of the analysis, and reduced the Type II error. Rare taxa are seldom included in community studies because of limited sample size compared to the sample area. However, if changes in rare taxa could be analyzed without bias, it seems that their disappearance or increase would be a more sensitive index of community change. Unfortunately, because I pooled the six samples collected at each station before identifying and counting them, the sample variance per station cannot be calculated. However, in general, the range of the coefficient of variation across all genera, stations, and streams for 1993 was -270 to 5664% and for 1994 was -1199 to 321% around the expected mean. More samples would likely have reduced that variance and increased the power of the study because taxa with the greatest normal population distributions, such as *Baetis* and *Rhyacophila* had coefficient of variances in the range of 18 to 39%. I would have improved sample variance and increased power by:

- adding more streams to the sample population to increase treatment replication and improve between-sample variation.
- realistically increasing the number of samples collected at each station from 6 to 12 based on sample variance research in other studies (see Literature Review) to improve within-sample variation.
- adding a station at each test area so that stations would be replicated on each stream.
- having two upstream reference station locations, so that I could test for differences between reference stations as well as differences between reference stations and the treated stations.
- gathering preliminary data through at least one season and preferably two on all treatment streams. Or otherwise,
- sampling on reference streams in the same basin as the treated streams over the same longitudinal distance and for the same years of the study.

I feel confident in my choice of monthly sampling dates despite the possibility of monitoring repeated measures effects. Without knowing the specific life histories of the mayflies and caddisflies in the four streams, sampling through the life cycle incorporated the natural fluctuations of the populations into my analysis. Sporadic sampling once a summer may have captured short-term peaks or depressions in populations which would have biased results. However, sampling through April and May and then September and October would also be a viable sampling option because it would capture the peaks in population of most of the insects in our streams and avoid the period through mid-summer where many insects are either adults, eggs, in diapause, or are such small instars that thorough collection and accurate identification are a concern. This discontinuous seasonal sampling would have increased the independence of sample units, eliminated the effects of repeated measures, and therefore allowed the use of easily analyzed experimental designs such as randomized complete block.

As well as improving mayfly and caddisfly sample power by increasing sample number, I would try to reduce the variability within the samples by distinguishing among pool, riffle, and glide environments in order to test if certain habitats are more resilient to silviculture treatments than others. In order to construct more thorough correlations with environmental parameters, I would have measured velocity closer to the boundary layer, collected stream temperatures within the clearcut reaches, and attempted to actually measure changes in primary production to directly test the relationship between increases in abundance and increases in solar radiation striking the stream. I feel confident in my choice of the two mayfly and caddisfly orders as a sampling community because the two orders are relatively diverse and yet also specific enough to capture possible treatment effects. They also constitute primary sources of fish food and nutrient processing within the stream. Some may argue, however, that including Diptera, Plecoptera, Hemiptera, Coleoptera, Megaloptera, and Odonata into the abundance and diversity measurements would have facilitated a better picture of the overall effects of the silviculture treatments. Had I been analyzing biomass, I would have agreed. Including these orders may have provided a better picture of functional feeding group response, however. Others may argue that the results provided by mayflies and caddisflies are not specific enough and that

a more focused picture would have been provided by the analysis of just one genera or species.

Because of the limitations of the study design and relatively low sample number and the different climatic conditions between 1993 and 1994, responses observed in the Ephemeroptera and Trichoptera communities on these four streams are applicable to western Oregon, third-order streams at low elevations harvested with small patchcuts which remove only 25% of the stream side overstory vegetation. Streamside herbs and forbs must be left intact. Higher elevations, larger or smaller order streams, and larger harvest treatments may cause significantly different responses in the mayfly and caddisfly genera over time. For those mayflies and caddisflies that did respond to the harvest treatments, their responses are likely characteristic of the same insects in similar streams under similar treatments. However, those mayflies and caddisflies that did not respond to the treatments, that were rare, or that were not found in our four streams (i.e., Siphonuridae which was found in the reference streams in high abundance), may respond to similar treatments in other streams. A null response in such a study with small samples and limited replication does not necessarily reflect no treatment effect. More accurately, it may reflect a failure of the research to measure the effect. Despite these caveats, on the four streams in western Oregon, two and a half years after installing streamside patchcuts, mayfly and caddisfly absolute and relative abundance, functional feeding group abundance, and diversity were similar between the reference station and the bottom monitoring station. Abundance measures changed within the 1600-m reach however and, overall, the treated stream mayflies and caddisflies exceeded the patterns of variability observed within reference stream caddisfly and mayfly communities.

BIBLIOGRAPHY

- Ahtiainen, M. 1992. The effects of forest clearcutting and scarification on the water quality of small brooks. *Hydrobiologia* 243/244: 465-473.
- Allan, J.D. 1975a. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 56: 1040-1053.
- Allan, J.D. 1975b. Components of diversity. *Oecologia* 18: 359-367.
- Allan, J.D. 1984. Hypothesis testing in ecological studies of aquatic insects. *In* Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 484-507.
- Alstad, D.N. 1987. Particle size, resource concentration, and the distribution of net-spinning caddisflies. *Oecologia* 71: 525-531.
- Amaranthus, M., H. Jubas, and D. Arthur. 1989. Stream shading, summer streamflow and maximum water temperature following intense wildfire in headwater streams. U.S.D.A. Forest Service General Technical Report. Pacific Southwest Forest Research Station. PSW-109.
- Anderson, N.H. 1976. The Distribution and Biology of the Oregon Trichoptera. Agriculture Experiment Station, Technical Bulletin 134. Oregon State University, Corvallis, Oregon. 152 pp.
- Anderson, N.H. 1992. Influence of disturbance on insect communities in Pacific Northwest streams. *Hydrobiologia* 248: 79-92.
- Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by stream macroinvertebrates in stream ecosystems. *Annual Review of Entomology* 24: 351-377.
- Andrus, C. and H.A. Froehlich. 1988. Riparian forest development after logging or fire in the Oregon Coast Range: wildlife habitat and timber value. *In* *Streamside Management: Riparian Wildlife and Forestry Interactions*. College of Forest Resources, University of Washington, Seattle. Institute of Forest Resources Contribution 59. 139-152.
- Andrus, C.W., B.A. Long, and H.A. Froehlich. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. *Canadian Journal of Fisheries and Aquatic Science* 45: 2080-2086.

- Barton, D.R., W.D. Taylor, and R.M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in Southern Ontario streams. *North American Journal of Fisheries Management* 5: 364-378.
- Becker, G. 1994. Food preferences by five Trichopteran scrapers. *Hydrobiologia* 273: 171-178.
- Benke, A.C. 1984. Secondary production of aquatic insects. *In* Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 289-322.
- Bergersen, R. 1989. Zoobenthos and food of Atlantic salmon (*Salmo salar* L.) fry in Alta River, North Norway - and notes on the measurement of faunal resemblance. *Nordic Journal of Freshwater Research* 65: 99-115.
- Bergey, E.A. and J.V. Ward. 1989. Upstream-downstream movements of aquatic invertebrates in a Rocky Mountain stream. *Hydrobiologia* 185: 71-82.
- Beschta, R.L., R.E. Bilby, G.W. Brown, L.B. Holtby, and T.D. Hofstra. 1987. Stream temperature and aquatic habitat: Fisheries and forestry interactions. *In* Salo, E.C. and T.W. Cundy (eds.). *Streamside Management: Forestry and Fisheries Interactions*. College of Forest Resources, No. 57, University of Washington, Seattle. 191-232.
- Beschta, R.L., W.S. Platts, and B. Kauffman. 1991. Field review of fish habitat improvement projects in the Grande Ronde and John Day River basins of eastern Oregon. U.S. Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife. P.O. Box 3621, Portland, Oregon 97208. 53 pp.
- Bilby, R.E. 1984. Post-logging removal of woody debris affects stream channel stability. *Journal of Forestry* 82: 609-613.
- Bisson, P.A., R.E. Bilby, M.D. Bryant, C.A. Dolloff, G.B. Grette, R.A. House, M.L. Murphy, K.V. Koski, and J.R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. *In* Salo, E.C. and T.W. Cundy (eds.). *Streamside Management: Forestry and Fisheries Interactions*. College of Forest Resources, No. 57, University of Washington, Seattle. 143-190.
- Bisson, P.A., T.P. Quinn, G.H. Reeves, and S.V. Gregory. 1992. Best management practices, cumulative effects, and long-term trends in fish abundance in Pacific Northwest River systems. *In* R.J. Naiman, (ed.). *Watershed Management: Balancing sustainability and environmental change*. NY: Springer-Verlag. 189-232.

- Boulton, A.J., C.G. Peterson, N.B. Grimm, and S.G. Fisher. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* 73(6): 2192-2207.
- Bowles, D.E. and R.T. Allen. 1992. Life histories of six species of caddisflies (Trichoptera) in an Ozark stream, U.S.A. *Journal of the Kansas Entomological Society* 65(2): 174-184.
- Brittain, J.E. 1982. Biology of mayflies. *Annual Review of Entomology* 27: 119-147.
- Brönmark, C., J. Herrmann, B. Malmqvist, C. Otto, and P. Sjöström. 1984. Animal community structure as a function of stream size. *Hydrobiologia* 112: 73-79.
- Brown, A.V. and P.P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia* 220: 99-108.
- Brown, G.W. 1969. Predicting temperatures of small streams. *Water Resources Research* 5(1): 68-75.
- Brown, G.W. 1970. Predicting the effect on clearcutting on stream temperature. *Journal of Soil and Water Conservation* 25: 11-13.
- Brown, G.W. 1991. *Forest and Water Quality*. Corvallis, OR: Oregon State University Book Stores, Inc. 142 pp.
- Brown, G.W. and J.T. Krygier. 1970. Effects of clearcutting on stream temperature. *Water Resources Research* 6(4): 1133-1140.
- Brussock, P.P. and A.V. Brown. 1991. Riffle-pool geomorphology disrupts longitudinal patterns of stream benthos. *Hydrobiologia* 220: 109-117.
- Busch, D.E. 1978. *Successional Changes Associated with Benthic Assemblages in Experimental Streams*. Ph.D. Thesis. Oregon State University, Corvallis, Oregon.
- Butler, M.G. 1984. Life histories of aquatic insects. In Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 24-55.
- Carlson, P.H. 1981. *Aquatic Insects as Indicators of Environmental Health*. Ph.D. Dissertation. Clemson University, Clemson, South Carolina. 99 pp.
- Carlton, G.C. 1988. *The Structure and Dynamics of Red Alder Communities in the Central Coast Range of Western Oregon*. M.S. Thesis. Oregon State University, Corvallis, Oregon.

- Christensen, M. J. 1996. Effects of Stream Restoration on Macroinvertebrate Communities in an Oregon Coast Range Stream. M.S. Thesis. Oregon State University, Corvallis, Oregon. 120 pp.
- Chutter, F.M. 1972. A reappraisal of Needham and Usinger's data on the variability of a stream fauna when sampled with a Surber sampler. *Limnology and Oceanography* 17: 139-141.
- Chutter, F.M. and R.G. Noble. 1966. The reliability of a method of sampling stream invertebrates. *Arch. Hydrobiol.* 62(1): 95-103.
- Ciborowski, J.J.H. 1983. Influence of current velocity, density, and detritus on drift of two mayfly species (Ephemeroptera). *Canadian Journal of Zoology* 61: 119-125.
- Clements, W.H. 1987. The effect of rock surface area on distribution and abundance of stream insects. *Journal of Freshwater Ecology* 4(1): 83-91.
- Clifford, H.F. 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. *Quaestiones Entomologicae* 18: 15-90.
- Connell, J.H. and W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *The American Naturalist* 121(6): 789-815.
- Corkum, L.D. 1989. Patterns of benthic invertebrate assemblages in rivers of northwestern North America. *Freshwater Ecology* 21: 191-205.
- Cummins, K.W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *The American Midland Naturalist* 67(2): 477-504.
- Cummins, K.W. and G.H. Lauff. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* 34: 145-181.
- Cummins, K.W. and M.J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Entomology* 10: 147-12.
- Cummins, K.W., M.A. Wilzbach, D.M. Gates, J.B. Perry and W.B. Taliferro. 1989. Shredders and riparian vegetation. *BioScience* 39(1): 24-29.
- DeJong, T.M. 1975. A comparison of three diversity indices based on their components of richness and evenness. *Oikos* 26: 222-227.
- De March, B.G.E. 1976. Spatial and temporal patterns in macrobenthic stream diversity. *Journal of the Fisheries Research Board of Canada* 33: 1261-1270.

- De Moor, F.C. 1991. The influence of fish on the structure and behavior of macroinvertebrates in a second-order headwater stream. *Verh. Internat. Verein. Limnol.* 24: 2050-2055.
- Dent, E.F. 1995. Influence of small clearcut openings in riparian areas on summer stream temperatures on Coastal Oregon and Western Cascade streams. Coastal Oregon Productivity Enhancement Program, Hatfield Marine Science Center, Newport, Oregon. COPE Report 8(3): 4-8.
- Downes, B.J., P.S. Lake, and E.S.G. Shreiber. 1993. Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization. *Freshwater Biology* 30: 119-132.
- Dudgeon, D. 1989. The influence of riparian vegetation on the functional organization of four Hong Kong stream communities. *Hydrobiologia* 179: 183-194.
- Duncan, W.F.A., M.A. Brusven, and T.C. Bjornn. 1989. Energy-flow response models for evaluation of altered riparian vegetation in three southeast Alaskan streams. *Water Resources* 23(8): 965-974.
- Edington, J.M. 1965. Some observations on stream temperatures. *Oikos* 15(2): 265-273.
- Edington, J.M. 1968. Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. *Journal of Animal Ecology* 37: 675-692.
- Edmunds, G.F., Jr., S.L. Jensen, and L. Berner. 1976. *The Mayflies of North and Central America*. University of Minnesota Press: Minneapolis.
- Englund, G. 1993. Effects of density and food availability on habitat selection in a net-spinning caddis larvae, *Hydropsyche siltalai*. *Oikos* 68: 473-480.
- Feminella, J.W., M.E. Power, and V.H. Resh. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. *Freshwater Biology* 22: 445-457.
- Franklin, J.R. and C.T. Dyrness. 1973. *Natural Vegetation of Oregon and Washington*. Oregon State University Press: Corvallis, Oregon.
- Froyd, C.A. 1993. The Effect of Riparian Buffer Strips on Salmonberry (*Rubus spectabilis*) Community Structure in Alder Stands of the Oregon Coast Range. M.S. Thesis. Oregon State University, Corvallis, Oregon.

- Fuller, R.L., J.L. Roelofs, and T.J. Fry. 1986. The importance of algae to stream invertebrates. *Journal of the North American Benthological Society* 5(4): 290-296.
- Fuller, R.L. and T.J. Fry. 1991. The influence of temperature and food quality on the growth of *Hydropsyche betteni* (Trichoptera) and *Simulium vittatum* (Diptera). *Journal of Freshwater Ecology* 6(1): 75-86.
- Gaufin, A.R., E.K. Harris, and H.J. Walter. 1956. A statistical evaluation of stream bottom sampling data obtained from three standard samplers. *Ecology* 37(4): 643-648.
- Gecy, J.L. and M.V. Wilson. 1990. Initial establishment of riparian vegetation after disturbance by debris flows in Oregon. *The American Midland Naturalist* 123: 282-291.
- Georgian, T. and J.B. Wallace. 1984. Seasonal production dynamics of six species of periphyton-grazing stream insects. *BioScience* 34(1): 42-44.
- Gilpin, B.R. and M.A. Brusven. 1970. Food habits and ecology of mayflies of the St. Maries River in Idaho. *Melandria* 4: 19-40.
- Gordon, A.E. and J.B. Wallace. 1975. Distribution of the family Hydropsychidae (Trichoptera) in the Savannah River Basin of South Carolina and Georgia. *Hydrobiologia* 46: 405-423.
- Grafius, E. and N.H. Anderson. 1979. Population dynamics, bioenergetics and role of *Lepidostoma quercina* Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. *Ecology* 60(2): 433-441.
- Gregory, S.V. 1983. Plant-herbivore interactions in stream systems. In Barnes, J.R. and G.W. Minshall (eds.). *Stream Ecology: Application and Testing of General Ecological Theory*. Plenum Press: NY. 157-189.
- Gurtz, M.E., J.R. Webster, and J.B. Wallace. 1980. Seston dynamics in southern Appalachian streams: Effects of clearcutting. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 624-631.
- Gurtz, M.E. and J.B. Wallace. 1984. Substrate-mediated response of stream invertebrates to disturbance. *Ecology* 65(5): 1556-1569.
- Haefner, J.D. and J.B. Wallace. 1981. Shifts in aquatic insect populations in a first-order Southern Appalachian stream following a decade of old field succession. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 353-359.

- Hansmann, E.W. and H.K. Phinney. 1973. Effects of logging on periphyton in coastal streams of Oregon. *Ecology* 54(1): 194-199.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack, Jr., and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133-302.
- Harr, R.D. 1979. Changes in streamflow following timber harvest in Southwestern Oregon. United States Department of Agriculture Forest Service Research Paper PNW-249. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 22p.
- Harr, R.D. 1980. Streamflow after patch logging in small drainages within the Bull Run municipal watershed, Oregon. United States Department of Agriculture Forest Service Research Paper PNW-268. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 16p.
- Hawkins, C.P. 1988. Effects of watershed vegetation and disturbance on invertebrate community structure in western Cascade streams: implications for stream ecosystem theory. *Verh. Internat. Verein. Limnol.* 23: 1167-1173.
- Hawkins, C.P. and J.R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62(2): 387-397.
- Hawkins, C.P., M.L. Murphy, and N.H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63(6): 1840-1856.
- Hawkins, C.P., M.L. Murphy, N.H. Anderson, and M.A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences* 40(8): 1173-1185.
- Healey, M. 1984. Fish predation on aquatic insects. In Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 255-288.
- Henderson, J.A. 1970. Biomass and Composition of the Understory Vegetation in some *Alnus Rubra* Stands in Western Oregon. M.S. Thesis. Oregon State University, Corvallis, Oregon.
- Hogue, J.N. and C.P. Hawkins. 1991. Morphological variation in adult aquatic insects: associations with developmental temperature and seasonal growth patterns. *Journal of the North American Benthological Society* 10(3): 309-321.

- Holomuzki, J., S. Messier, and T. Short. 1990. Effect of substrate distribution and current on the habitat distribution of a stream-dwelling mayfly. *American Zoology* 30: 18A.
- Holopainen, A-L. and P. Huttunen. 1992. Effects of forest clearcutting and soil disturbance on the biology of small forest brooks. *Hydrobiologia* 243/244: 457-464.
- Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 45: 502-515.
- House, R.A. and P.L. Boehne. 1987. The effect of stream cleaning on salmonid habitat and populations in a coastal Oregon drainage. *Western Journal of Applied Forestry* 2(3): 84-87.
- Hury, A.D. and J.B. Wallace. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology* 68(6): 1932-1942.
- Illies, J. and E.C. Masteller. 1977. A possible explanation of emergence patterns of *Baetis vernus* Curtis (Ins.: Ephemeroptera) on the Breitenbach-Schlitz studies on Productivity, Nr. 22-. *Int. Revue ges. Hydrobiol.* 62(2): 315-321.
- Irons, J.G. III, M.W. Oswald, and J.P. Bryant. 1988. Consumption of leaf detritus by a stream shredder: influence of tree species and nutrient status. *Hydrobiologia* 160: 53-61.
- Jamieson-Dixon, R.W. and F.J. Wrona. 1992. Life history and production of the predatory caddisfly *Rhyacophila vao* Milne in a spring-fed stream. *Freshwater Biology* 27: 1-11.
- Johnson, R.K., T. Wiederholm, and D.M. Rosenberg. 1993. Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. *In* Rosenberg, D.M. and V.H. Resh (eds.). *Freshwater Biomonitoring and Benthic Macroinvertebrates*. Chapman and Hall: London. 40-158.
- 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 Alaskan streams. *North American Journal of Fisheries Management* 6: 532-537.
- Kellog, L. D., S.J. Pilkerton, and A. Skaugset. 1993. Harvesting for active riparian zone management and the effects on multiple forest resources. *In* *Environmentally*

Sensitive Forest Engineering, Proceedings of the 16th Annual Meeting of the Council on Forest Engineering. August 8-11, 1993, Savannah, Georgia. 6-21.

- Kerans, B.L. 1992. Season and body size influence movement of Hydropsychid caddisfly larvae (Trichoptera: Hydropsychidae). *Canadian Journal of Fisheries and Aquatic Sciences* 49: 259-265.
- Kerans, B.L., J.R. Karr, and S.A. Ahlstedt. 1992. Aquatic invertebrate assemblages: spatial and temporal differences among sampling protocols. *Journal of the North American Benthological Society* 11(4): 377-390.
- Kimmins, H. 1992. *Balancing Act: Environmental issues in forestry*. UBC Press: Vancouver. 244 pp.
- Kohler, S.L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. *Ecology* 66(6): 1749-1761.
- Kohler, S.L. 1992. Competition and the structure of a benthic stream community. *Ecological Monographs* 62(2): 165-188.
- Kondratieff, P.F., R.A. Mathews, and A.L. Buikema, Jr.. 1984. A stressed stream ecosystem: macroinvertebrate community integrity and microbial trophic response. *Hydrobiologia* 111: 81-94.
- Koski, K.V., J. Heifetz, S. Johnson, M. Murphy, and J. Thedinga. 1984. Evaluation of buffer strips for protection of salmonid rearing habitat and implications for enhancement. *In* T.J. Hassler (ed.). *Pacific Northwest Stream Habitat Management Workshop: proceedings*. American Fisheries Society. October 10-12, Humboldt State University, Arcata, California. 138-155.
- Lamberti, G.A. and V.R. Resh. 1979. Substrate relationships, spatial distribution patterns, and sampling variability in a stream caddisfly population. *Environmental Entomology* 8(3): 561-567.
- Lamberti, G.A., and J.W. Moore. 1984. Aquatic insects as primary consumers. *In* Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 164-195.
- Lamberti, G.A., S.V. Gregory, C.P. Hawkins, R.C. Wildman, L.R. Ashkenas, and D.M. Denicola. 1992. Plant-herbivore interactions in streams near Mount St. Helens. *Freshwater Biology* 27: 237-247.
- Lancaster, J. and A.G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society* 12(4): 385-393.

- Lealand, H.V., S.V. Fend, J.L. Carter, and A.D. Mahood. 1986. Composition and abundance of periphyton and aquatic insects in a Sierra Nevada, California stream. *Great Basin Naturalist* 46(4): 595-611.
- Lee, R. and D.E. Samuel. 1976. Some thermal and biological effects of forest cutting in West Virginia. *Journal of Environmental Quality* 5(4): 362-366.
- Lehmkuhl, D.M. 1972. Change as a cause or reduction of benthic fauna downstream of a reservoir. *Journal of the Fisheries Research Board of Canada* 29: 1329-1332.
- Levno, A. and J. Rothacher. 1967. Increases in maximum stream temperatures after logging in old-growth Douglas-fir watersheds. U.S.D.A. Forest Service Research Note, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. PNW-65.
- Lienkaemper, G.W. and F.J. Swanson. 1987. Dynamics of large woody debris in streams in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* 17: 150-156.
- Linduska, J.P. 1942. Bottom type as a factor influencing the local distribution of mayfly nymphs. *Canadian Entomologist* 74(2): 26-36.
- Linklater, W. and M.J. Winterbourn. 1993. Life histories and production of two trichopteran shredders in New Zealand streams with different riparian vegetation. *New Zealand Journal of Marine and Freshwater Research* 27: 61-70.
- Lorensen, T., C. Andrus, K. Mills, J. Runyon, D. Morman, K. Birch, G. Copley, and S. Martin. 1993. Report on the Analysis of Proposed Water Classification and Protection Rules, September 3, 1993. Oregon Department of Forestry. Salem, Oregon. 85 pp.
- Lyford, J.H., Jr. and S.V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade mountain streams. *Verh. Internat. Verein, Limnol.* 19: 1610-1616.
- Magurran, A.E. 1988. *Ecological Diversity and Its Measurements*. Princeton: Princeton University Press. 179 pp.
- Malmqvist, B. and C. Otto. 1987. The influence of substrate stability on the composition of stream benthos: an experimental study. *Oikos* 48: 33-38.
- Mattingly, R.L. 1987. Handling of coarse and fine particulate organic matter by the aquatic insects *Paraleptophlebia gregalis* and *P. temporalis* (Ephemeroptera: Leptophlebiidae). *Freshwater Biology* 18: 255-265.

- Mayer, M.S. and G.E. Likens. 1987. The importance of algae in a shaded headwater stream as food for an abundant caddisfly (Trichoptera). *Journal of the North American Benthological Society* 6(4): 262-269.
- McAuliffe, J.R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65(3): 894-908.
- McCune, B. 1995. Community Structure and Analysis. Notes for Biology 570, Winter Quarter. Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon. 150 pp.
- McElravy, E.P and R.H. Resh. 1987. Diversity, seasonality, and annual variability of caddisfly (Trichoptera) adults from two streams in the California Coast Range. *Pan-Pacific Entomologist* 63(1): 75-91.
- McElravy, E.P., G.A. Lamberti, and V.R. Resh. 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the North American Benthological Society* 8(1): 51-63.
- Meehan, W.R., F.J. Swanson, and J.R. Sedell. 1977. Influences of riparian vegetation on aquatic ecosystems with particular reference to salmonid fishes and their food supply. *In* R.R. Johnson and D.A. Jones (eds.). Importance, preservation, and management of riparian habitat: a symposium. U.S.D.A. Forest Service General Technical Report. RM-43. 137-145.
- Meffe, G.K. and W.L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *The American Midland Naturalist* 117: 177-191.
- Merritt, R.W. and K.W. Cummins (eds.). 1984. *An Introduction to the Aquatic Insects of North America*. Second edition. Kendall/Hunt: Dubuque, Iowa. 722 pp.
- Merritt, R.W., K.W. Cummins, and T.M. Burton. 1984. The role of aquatic insects in the processing and cycling of nutrients. *In* Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 134-163.
- Minshall, G.W. 1968. Community dynamics of the benthic fauna in a woodland springbrook. *Hydrobiologia* 32: 305-339.
- Minshall, G.W. 1978. Autotrophy in stream ecosystems. *BioScience* 28(12): 767-771.
- Minshall, G.W. 1984. Aquatic insect-substratum relationships. *In* Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 358-400.

- Minshall, G.W. 1988. Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society* 7(4): 263-288.
- Minshall, G., W. and J.N. Minshall. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (U.S.A.) stream. *Hydrobiologia* 55(3): 231-249.
- Minshall, G.W., K.W. Cummins, R.C. Petersen, C.E. Cushing, D.A. Bruns, J.R. Sedell, and R.L. Vannote. 1985. Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1045-1055.
- Molles, M.C., Jr. 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. *Ecology* 63(1): 1-6.
- Murphy, M.L. 1979. Predator Assemblages in Old-Growth and Logged Sections of Small Cascade Streams. M.S. Thesis. Oregon State University, Corvallis, Oregon. 72 pp.
- Murphy, M.L. 1984. Primary production and grazing in freshwater and intertidal reaches of a coastal stream, Southeast Alaska. *Limnol. Oceanogr.* 29(4): 805-815.
- Murphy, M.L., C.P. Hawkins, and N.H. Anderson. 1981. Effects of canopy modifications and accumulated sediment on stream communities. *Transactions of the American Fisheries Society* 110: 469-478.
- Murphy, M.L. and K.V. Koski. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. *North American Journal of Fisheries Management* 9(4): 427-436.
- Murphy, M.L. and W.R. Meehan. 1991. Stream ecosystems. Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats. *American Fisheries Society Special Publication* 19: 17-46.
- Nakamura, F. and Dokai, T. 1989. Estimation of the effect of riparian forest on stream temperature based on heat budget. *Journal of the Japanese Forest Society* 71: 387-394.
- Needham, J.G., J.R. Traver, and Y. Hsu. 1935. *The Biology of Mayflies: With a systematic account of North American species.* Comstock: Ithaca, NY. 759 pp.
- Needham, P.R. and R.L. Usinger. 1956. Variability in the macrofauna of a single riffle in Prosser Creek, California, as indicated by the Surber sampler. *Hilgardia* 24(14): 383-397.

- Newbold, J.D., D.C. Erman, and K.B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. *Canadian Journal of Fisheries and Aquatic Science* 37: 1076-1085.
- Newbold, J.D., B.W. Sweeney, and R.L. Vannote. 1994. A model of seasonal synchrony in stream mayflies. *Journal of the North American Benthological Society* 13(1): 3-18.
- Newton, M., B.A. El Hassan, and J. Zavitkovski. 1968. Role of red alder in western Oregon forest succession. *In* Trappe, J.M, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (eds.). *Biology of Alder, Proceedings of a Symposium*. Northwest Scientific Association, April 14-15, 1967. U.S.D.A. Forest Service. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 73-84.
- Newton, M., R.L. Beschta, and M. Zwieniecki. 1995. Unpublished data. Oregon State University Forest Science Department. Oregon State University, Corvallis, Oregon.
- Noel, D.S., C.W. Martin, and C.A. Federer. 1986. Effects of forest clearcutting in New England on stream macroinvertebrates and periphyton. *Environmental Management* 10(5): 661-670.
- Norris, R.H. and A. Georges. 1993. Analysis and interpretation of benthic macroinvertebrate surveys. *In* Rosenberg, D.M. and V.H. Resh (eds.). *Freshwater Biomonitoring and Benthic Macroinvertebrates*. Chapman and Hall: London. 234-287.
- Ogilvie, G.A. and H. F. Clifford. 1986. Life histories, production, and microdistribution of two caddisflies (Trichoptera) in a Rocky Mountain stream. *Canadian Journal of Zoology* 64: 2706-2716.
- Osenberg, C.W., R.J. Schmitt, S.J. Holbrook, K.E. Abu-Saba, and A.R. Flegal. 1994. Detection of environmental impacts: natural variability, effect size, and power analysis. *Ecological Applications* 4(1): 16-30.
- Pennak, R.W. and E.D. Van Gerpen. 1947. Bottom fauna production and physical nature of the substrate in a northern Colorado trout stream. *Ecology* 28(1): 42-48.
- Perry, S.A., W.B. Perry, and J.A. Stanford. 1986. Effects of stream regulation on density, growth, and emergence of two mayflies (Ephemeroptera: Ephemerellidae) and a caddisfly (Trichoptera: Hydropsychidae) in two Rocky Mountain rivers (U.S.A.). *Canadian Journal of Zoology* 64: 656-666.

- Philipson, G.N. 1954. The effect of water flow and oxygen concentration on six species of caddis fly (Trichoptera) larvae. *Proceedings of the Zoological Society of London* 124: 547-564.
- Pickett, S.T. A. and P.S. White (eds.). 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida.
- Rabeni, C.F. and G.W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos* 29: 33-43.
- Rader, R.B. and J.V. Ward. 1987a. Mayfly production in a Colorado mountain stream: an assessment of methods for synchronous and non-synchronous species. *Hydrobiologia* 148: 145-150.
- Rader, R.B. and J.V. Ward. 1987b. Resource utilization, overlap, and temporal dynamics in a guild of mountain stream insects. *Freshwater Biology* 18: 521-528.
- Rader, R.B. and J.V. Ward. 1990. Mayfly growth and population density in constant and variable temperature regimes. *The Great Basin Naturalist* 50(2): 97-106.
- Ralph, S.C., G.C. Poole, L.L. Conquest, and R.J. Naiman. 1994. Stream channel morphology and woody debris in logged and unlogged basins of western Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 51(1): 37-51.
- Reice, S.R. 1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. *Ecology* 61(3): 580-590.
- Reice, S.R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia* 67: 90-97.
- Reice, S.R. and M. Wohlenberg. 1993. Monitoring freshwater benthic macroinvertebrates and benthic processes: measures for assessment of ecosystem health. *In* Rosenberg, D.M. and V.H. Resh (eds.). *Freshwater Biomonitoring and Benthic Macroinvertebrates*. Chapman and Hall: London. 207-305.
- Resh, V.H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. *Journal of the Fisheries Research Board of Canada* 36: 290-311.
- Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R.C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7(4): 433-455.

- Resh, V.H. and D.M. Rosenberg. 1989. Spatial-temporal variability and the study of aquatic insects. *The Canadian Entomologist* 121: 941-963.
- Resh, V.H. and E.P. McElvay. 1993. Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. In Rosenberg, D.M. and V.H. Resh (eds.). *Freshwater Biomonitoring and Benthic Macroinvertebrates*. Chapman and Hall: London. 159-233.
- Richards, C. and G.W. Minshall. 1988. The influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream. *Journal of the North American Benthological Society* 7(2): 77-86.
- Richards, C. and G.W. Minshall. 1992. Spatial and temporal trends in stream macroinvertebrate communities: the influence of catchment disturbance. *Hydrobiologia* 241: 173-184.
- Rishel, G.B., J.A. Lynch, and E.S. Corbett. 1982. Seasonal stream temperature changes following forest harvesting. *Journal of Environmental Quality* 11(1): 112-116.
- Robinson, C.T., G.W. Minshall, and S.R. Rushforth. 1990. Seasonal colonization of macroinvertebrates in an Idaho stream. *Journal of the North American Benthological Society* 9(3): 240-248.
- Robison, E.G. and R.L. Beschta. 1990. Identifying trees in riparian areas that can provide coarse woody debris to streams. *Forest Science* 36(3): 790-801.
- Roeding, C.E. and L.A. Smock. 1989. Ecology of macroinvertebrate shredders in a low-gradient sandy-bottomed stream. *Journal of the North American Benthological Society* 8(2): 149-161.
- Rosillon, D. 1989. The influence of abiotic factors and density-dependent mechanisms on between-year variations in a stream invertebrate community. *Hydrobiologia* 179: 25-38.
- Rossiter, A. 1988. A modified Surber sampler of use in monitoring the distribution of benthic macroinvertebrates. *Physiological Ecology of Japan* 25: 39-42.
- Rounick, J.S., M.J. Winterbourn, and G.L. Lyon. 1982. Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. *Oikos* 39: 191-198.
- Saleem, P.M. and Ifikhar A. 1987. The effect of substratum, speed and temperature on the distribution of mayflies (nymphs) in Swat District (NWFP) Pakistan. *Biologia* 33(1): 139-148.

- Sedell, J.R. and F.J. Swanson. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. *In* W.R. Meehan, T.R. Merrell, Jr. and T.A. Hanley (eds.), *Fish and Wildlife Relationships in Old-Growth Forests, Proceedings from a Symposium*. 12-15 April 1982, Juneau, Alaska. American Institute of Fisheries Research Biologists. 9-16.
- Sedell, J.R., G.H. Reeves, F.R. Hauer, J.A. Stanford, and C.P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management* 14(5): 711-724.
- Smith-Cuffney, F.L. and J. B. Wallace. 1987. The influence of microhabitat on availability of drifting invertebrate prey to a net-spinning caddisfly. *Freshwater Biology* 17: 91-98.
- Stafford, S.G. and T.E. Sabin. 1994. *Statistical Analysis for the Natural Resources and Ecological Sciences with the SAS Programming Language*. Course notes for Forest Science 523. Department of Forest Science, Oregon State University, Corvallis, Oregon.
- Stark, J.D. 1993. Performance of the Macroinvertebrate Community Index: effects of sampling method, sample replication, water depth, current velocity, and substratum on index values. *New Zealand Journal of Marine and Freshwater Research* 27: 463-478.
- Statzner, B. and B. Higler. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology* 16: 127-139.
- Statzner, B., J.A. Gore, and V.H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* 7(4): 307-360.
- Steel, R.G.D. and J.H. Torrie. 1960. *Principles and Procedures of Statistics with Special References to the Biological Sciences*. McGraw-Hill: NY. 481 pp.
- Steinman, A.D. and C.D. McIntire. 1986. Effects of current velocity and light energy on the structure of periphyton assemblages in laboratory streams. *Journal of Phycology* 22: 352-361.
- Strommer J.L. and L.A. Smock. 1989. Vertical distribution and abundance of invertebrates within the sandy substrate of a low-gradient headwater stream. *Freshwater Biology* 22: 263-274.
- Sullivan, K., T.E. Lisle, C.A. Dolloff, G.E. Grant, and L.M. Reid. 1987. Stream channels: the link between forests and fishes. *In* Salo, E.C. and T.W. Cundy

- (eds.). *Streamside Management: Forestry and Fisheries Interactions*. College of Forest Resources, No. 57, University of Washington, Seattle. 39-97.
- Sullivan, K., J. Tooley, K. Doughty, J.E. Caldwell, P. Knudsen. 1990. Evaluation of prediction models and characterization of stream temperature regimes in Washington. *Timber/Fish/Wildlife Rep. No. TFW-WQ3-90-006*. Washington Department of Natural Resources, Olympia, Washington. 224 pp.
- Swanson, F.J., S.V. Gregory, J.R. Sedell, and A.G. Campbell. 1982. Land-water interactions: the riparian zone. *In* R.L. Edmonds (ed.), *Analysis of Coniferous Ecosystems in the Western United States*. Hutchinson Ross: Stroudsburg, PA. 267-291.
- Sweeney, B.W. 1984. Factors influencing life-history patterns of aquatic insects. *In* Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 56-100.
- Tait, C.K., J.L. Li, G.A. Lamberti, T.N. Pearsons, and H.W. Li. 1994. Relationships between riparian cover and the community structure of high desert streams. *Journal of the North American Benthological Society* 13(1): 45-56.
- 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(8): 1383-1391.
- Tikkanen, P., P. Laasonen, T. Muotka, A. Huhta, and K. Kuusela. 1994. Short-term recovery of benthos following disturbance from stream habitat rehabilitation. *Hydrobiologia* 273: 121-130.
- Towns, D.R. 1979. Composition and zonation of benthic invertebrate communities in a New Zealand kauri forest stream. *Freshwater Biology* 9: 251-262.
- Towns, D.R. 1981. Effects of artificial shading on periphyton and invertebrates in a New Zealand stream. *New Zealand Journal of Marine and Freshwater Research* 15: 185-192.
- Towns, D.R. 1985. Life history patterns and their influence on monitoring invertebrate communities. *In* *Biological Monitoring in Freshwaters: proceedings of a seminar*. Pridmore, R.D. and A.B. Cooper, eds. Water and Soil Directorate, Ministry of Works and Development for the National Water and Soil Conservation Authority, Wellington. Water and Soil Miscellaneous Publication 83.

- Townsend, C.R., A.G. Hildrew, and K. Schofield. 1987. Persistence of stream invertebrate communities in relation to environmental variability. *Journal of Animal Ecology* 56: 597-613.
- Triska, F.J., J.R. Sedell, and S.V. Gregory. 1982. Coniferous forest streams. In R.L. Edmonds (ed.), *Analysis of Coniferous Forest Ecosystems in the Western United States*. Hutchinson Ross, Stroudsburg, PA. 292-332.
- Trotter, E.H. 1990. Woody debris, forest-stream succession, and catchment geomorphology. *Journal of the North American Benthological Society* 9(2): 141-156.
- Underwood, A.J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications* 4(1): 3-15.
- United States Weather Bureau. 1993. *Climatological Data: a national summary*. National Oceanic and Atmospheric Administration. Environmental Data and Information Service, National Climatic Center. Asheville, North Carolina.
- United States Weather Bureau. 1994. *Climatological Data: a national summary*. National Oceanic and Atmospheric Administration. Environmental Data and Information Service, National Climatic Center. Asheville, North Carolina.
- 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 Science* 37: 130-137.
- Van Sickle, J. and S.V. Gregory. 1990. Modeling inputs of large woody debris to streams from falling trees. *Canadian Journal of Forest Research* 20: 1593-1601.
- Wallace, J.B. 1975. Food partitioning in net-spinning Trichoptera larvae: *Hydropsyche venularis*, *Cheumatopsyche etrona*, and *Macronema zebratum* (Hydropsychidae). *Annals of the Entomological Society of America* 68(3): 463-472.
- Wallace, J.B. and R.W. Merritt. 1980. Filter-feeding ecology of aquatic insects. *Annual Review of Entomology* 25: 103-132.
- Wallace, J.B., J.R. Webster, and T.F. Cuffney. 1982. Stream detritus dynamics: regulation by invertebrate consumers. *Oecologia* 53: 197-200.
- Wallace, J.B. and M.E. Gurtz. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. *The American Midland Naturalist* 115(1): 25-41.

- Wallace, J.B., D.S. Vogel, and T.F. Cuffney. 1986. Recovery of a headwater stream from an insecticide-induced community disturbance. *Journal of the North American Benthological Society* 5(2): 115-126.
- Walsh, J.B.S. 1992. The Effects of Timber Harvesting on Benthic Macroinvertebrates in Southwestern Virginia. Virginia Department of Forestry, Charlottesville, Virginia. 53 pp.
- Ward, J.V. and J.A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* 27: 97-117.
- Waters, T.F. 1964. Recolonization of denuded stream bottom areas by drift. *Transactions of the American Fisheries Society* 93: 311-315.
- Weatherly, N.S. and S.J. Ormerod. 1990. Forests and the temperature of upland streams in Wales: a modeling exploration of the biological effects. *Freshwater Biology* 24: 109-122.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21:213-251.
- Wiggins, G.B. Larvae of the North American Caddisfly Genera (Trichoptera). 1977. Toronto: University of Toronto Press. 401pp.
- Wiley, M.J. and S.L. Kohler. 1984. Behavioral adaptations of aquatic insects. In Resh, V.H. and Rosenberg, D.M. (eds.). *The Ecology of Aquatic Insects*. Praeger: New York. 101-133.
- Williams, D.D. and H.B. Hynes. 1976. The recolonization mechanisms of stream benthos. *Oikos* 27: 265-272.
- Wilzbach, P. T.L. Dudley, and J.D. Hall. 1983. Recovery patterns in stream communities impacted by the Mt. St. Helens eruption. Final Technical Completion Report, U.S. Department of the Interior. Water Resources Research Institute, Oregon State University, Corvallis, Oregon. WRRRI-83. 33 pp.

APPENDICES

APPENDIX A. Insect Genus List for Treatment Streams. Taxa sampled on fewer than all four streams are identified with the first initial of the stream to the right above the taxa. A=Ames, B=Buttermilk, M=Mosby, P=Pancake. * indicates that the genus was used within the absolute count dataset.

Order	Family	Genus	
Ephemeroptera	Baetidae	<i>Baetis</i> *	
	Ephemerellidae	<i>Caudatella</i> ^M	
		<i>Drunella</i> *	
		<i>Euryophylla</i> ^B	
		<i>Serratella</i> *	
		<i>Timpanoga</i>	
	Heptageniidae	<i>Cinygmula</i> *	
		<i>Epeorus</i> *	
		<i>Heptagenia</i> ^{A,M,P}	
		<i>Ironodes</i> *	
		<i>Rhithrogena</i> *	
	Trichoptera	Leptophlebiidae	<i>Paraleptophlebia</i> *
		Brachycentridae	<i>Micrasema</i> *
		Glossosomatidae	<i>Glossosoma</i> *
Hydropsychidae		<i>Arctopsyche</i> ^{*A,P}	
		<i>Hydropsyche</i> *	
		<i>Parapsyche</i>	
Hydroptilidae		<i>Agrayalea</i> ^M	
		<i>Hydroptila</i> ^M	
Lepidostomatidae		<i>Lepidostoma</i> *	
Limnephilidae		<i>Dicosmoecus</i> ^{B,M}	
		<i>Ecclisomyia</i> ^{B,M,P}	
		<i>Homophylax</i> ^P	
		<i>Hydatophylax</i> ^B	
		<i>Onocosmoecus</i> ^B	
	<i>Psychoglypha</i>		
Philopotamidae	<i>Wormaldia</i> *		
Polycentropoidae	<i>Polycentropus</i>		
Rhyacophilidae	<i>Rhyacophila</i> *		
Uenoidae	<i>Neophylax</i> *		
	<i>Neothremma</i> ^{*A,B,P}		

APPENDIX B. Insect Genus List for Reference Streams. Taxa sampled on fewer than all four streams are identified with the first initial of the stream to the right above the taxa. C=Southfork Crabtree, E=Ennis, M=Mack. * indicates that the genus was used within the absolute count dataset.

Order	Family	Genus	
Ephemeroptera	Baetidae	<i>Baetis</i> *	
	Ephemerellidae	<i>Attenella</i> ^{E,C}	
		<i>Caudatella</i>	
		<i>Drunella</i> *	
		<i>Serratella</i> *	
		Heptageniidae	<i>Cinygma</i> ^C
			<i>Cinygmula</i> *
			<i>Epeorus</i> *
	<i>Heptagenia</i> ^M		
	<i>Ironodes</i> *		
	<i>Rhithrogena</i> ^{*E,C}		
	Leptophlebiidae	<i>Paraleptophlebia</i> *	
	Trichoptera	Brachycentridae	<i>Micrasema</i> *
		Calamoceratidae	<i>Heteroplectron</i>
Glossosomatidae		<i>Glossosoma</i> *	
Hydropsychidae		<i>Hydropsyche</i> *	
Lepidostomatidae		<i>Lepidostoma</i> *	
Limnephilidae		<i>Ecclisomyia</i> ^M	
		<i>Hydatophylax</i> ^E	
Philopotamidae		<i>Wormaldia</i> ^E	
Polycentropoidae		<i>Polycentropus</i>	
Rhyacophilidae		<i>Rhyacophila</i> *	
Uenoidae	<i>Neothremma</i> ^{*M}		
Siphonuridae	<i>Ameletus</i>		

APPENDIX C. ANOVA tables for genera and functional feeding group absolute abundance and diversity.

Absolute Insect Counts.

Baetidae Baetis:

1993:

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	91.2137	2.6828	4.84	0.0003
Error	19	10.5291	0.5541		
Corrected Total	53	101.7428			

R-Square	C.V.	Root MSE	RBABA Mean
0.8965	9999.99	0.7444	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	8.0097	2.6699	4.82	0.0117
STATION	3	41.5283	13.8428	3.23	0.0910
STREAM*STATION	7	29.9681	4.2812	7.73	0.0002
MONTH	3	0.1691	0.0564	0.08	0.9692
STREAM*MONTH	9	6.3427	0.7047	1.27	0.3133
STATION*MONTH	9	4.8735	0.5415	0.98	0.4883

1994:

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	82.5761	2.4287	5.36	0.0001
Error	21	9.5206	0.4534		
Corrected Total	55	92.0967			

R-Square	C.V.	Root MSE	RBABA Mean
0.8966	9999.99	0.6733	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	1.5176	0.5059	1.12	0.3650
STATION	3	34.1436	11.3812	2.62	0.1324
STREAM*STATION	7	30.3732	4.3390	9.57	0.0001
MONTH	3	0.9589	0.3196	0.21	0.8855
STREAM*MONTH	9	13.5599	1.5067	3.32	0.0112

STATION*MONTH 9 3.8041 0.4227 0.93 0.5182

Brachycentridae *Micrasema*:

1993:

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	50.3868	1.4820	1.43	0.2053
Error	19	19.66244	1.0349		
Corrected Total	53	70.0492			

R-Square	C.V.	Root MSE	RBRMI Mean
0.7193	-9999.99	1.0173	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	0.9398	0.3133	0.30	0.8231
STATION	3	7.6148	2.5383	1.32	0.3419
STREAM*STATION	7	13.4608	1.9230	1.86	0.1339
MONTH	3	0.4392	0.1464	0.09	0.9652
STREAM*MONTH	9	15.0816	1.6757	1.62	0.1799
STATION*MONTH	9	13.3459	1.4829	1.43	0.2428

1994:

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	57.6780	1.6964	1.78	0.0836
Error	21	20.0360	0.9541		
Corrected Total	55	77.7140			

R-Square	C.V.	Root MSE	RBRMI Mean
0.7422	-9999.99	0.9768	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	5.5329	1.8443	1.93	0.1552
STATION	3	14.9506	4.9835	2.03	0.1977
STREAM*STATION	7	17.1444	2.4492	2.57	0.0445
MONTH	3	0.5223	0.1741	0.17	0.9150
STREAM*MONTH	9	9.3024	1.0336	1.08	0.4144
STATION*MONTH	9	12.6497	1.4055	1.47	0.2215

Ephemerellidae *Drunella*:

1993:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	35.2248	1.0360	1.64	0.1269
Error	19	11.9890	0.6310		
Corrected Total	53	47.2138			

R-Square	C.V.	Root MSE	REPDR Mean
0.7461	9999.99	0.7944	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	1.9491	0.6497	1.03	0.4018
STATION	3	10.5433	3.5144	2.24	0.1715
STREAM*STATION	7	11.0005	1.5715	2.49	0.0539
MONTH	3	0.1097	0.0366	0.06	0.9802
STREAM*MONTH	9	5.6154	0.6239	0.99	0.4802
STATION*MONTH	9	6.5848	0.7316	1.16	0.3727

1994:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	51.8901	1.5261787	3.00	0.0050
Error	21	10.6673	0.5079669		
Corrected Total	55	62.5574			

R-Square	C.V.	Root MSE	REPDR Mean
0.8295	9999.99	0.7127	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	5.1595	1.7198	3.39	0.0372
STATION	3	13.3971	4.4657	1.62	0.2702
STREAM*STATION	7	19.3497	2.7642	5.44	0.0011
MONTH	3	0.4689	0.1563	0.40	0.7550
STREAM*MONTH	9	3.4977	0.3886	0.77	0.6489
STATION*MONTH	9	11.5298	1.2811	2.52	0.0388

Glossosomatidae *Glossosoma*:**1993:**

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	30.7237	0.9036	1.46	0.1926

Error	19	11.7598	0.6189
Corrected Total	53	42.4835	

R-Square	C.V.	Root MSE	RGLGL Mean
0.7232	-9999.99	0.7867	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	1.7570	0.5856813	0.95	0.4380
STATION	3	5.8562	1.9520804	5.65	0.0276
STREAM*STATION	7	2.4179	0.3454210	0.56	0.7802
MONTH	3	0.8309	0.2769736	0.28	0.8392
STREAM*MONTH	9	8.9329	0.9925484	1.60	0.1845
STATION*MONTH	9	12.0667	1.3407398	2.17	0.0748

1994:

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	93.6123	2.7533	3.60	0.0015
Error	21	16.0690	0.7652		
Corrected Total	55	109.6813			

R-Square	C.V.	Root MSE	RGLGL Mean
0.8535	9999.99	0.8748	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	3.0430	1.0143	1.33	0.2927
STATION	3	35.9005	11.9668	2.46	0.1474
STREAM*STATION	7	34.0596	4.8657	6.36	0.0004
MONTH	3	0.5578	0.1859	0.32	0.8086
STREAM*MONTH	9	5.1753	0.5750	0.75	0.6599
STATION*MONTH	9	15.5966	1.7330	2.26	0.0590

Heptageniidae Cinygmula:**1993:**

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	71.6258	2.1066	2.82	0.0096
Error	19	14.1687	0.7457		
Corrected Total	53	85.7945			

R-Square	C.V.	Root MSE	RHECI Mean
0.8349	-9999.99	0.8636	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	32.1267	10.7089	14.36	0.0001
STATION	3	16.1923	5.3974	4.23	0.0530
STREAM*STATION	7	8.9348	1.2764	1.71	0.1660
MONTH	3	0.8790	0.2930	0.18	0.9051
STREAM*MONTH	9	14.3904	1.5989	2.14	0.0774
STATION*MONTH	9	22.1685	2.4632	3.30	0.0136

1994:

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	87.9914	2.5880	3.22	0.0032
Error	21	16.8609	0.8029		
Corrected Total	55	104.8523			

R-Square	C.V.	Root MSE	RHECI Mean
0.8392	-9999.99	0.8961	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	38.0911	12.6970	15.81	0.0001
STATION	3	8.3117	2.7706	0.97	0.4605
STREAM*STATION	7	20.0843	2.8692	3.57	0.0109
MONTH	3	0.06430	0.0214	0.01	0.9985
STREAM*MONTH	9	19.2671	2.1408	2.67	0.0308
STATION*MONTH	9	4.1288	0.4588	0.57	0.8052

Heptageniidae Epeorus:**1993:**

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	56.9144	1.6740	1.53	0.1652
Error	19	20.8245	1.0960		
Corrected Total	53	77.7390			

R-Square	C.V.	Root MSE	RHEEP Mean
0.7321	-9999.99	1.0469	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
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STREAM	3	2.1996	0.7332	0.67	0.5815
STATION	3	3.1367	1.0456	0.36	0.7857
STREAM*STATION	7	20.4726	2.9247	2.67	0.0420
MONTH	3	0.4902	0.1634	0.08	0.9710
STREAM*MONTH	9	19.1446	2.1272	1.94	0.1071
STATION*MONTH	9	13.5150	1.5017	1.37	0.2683

1994:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	43.9550	1.2928	1.26	0.2904
Error	21	21.4950	1.0236		
Corrected Total	55	65.4500			

R-Square	C.V.	Root MSE	RHEEP Mean
0.6716	-9999.99	1.0117	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	5.3923	1.7974	1.76	0.1864
STATION	3	2.6669	0.8890	0.31	0.8197
STREAM*STATION	7	20.2555	2.8936	2.83	0.0306
MONTH	3	0.4061	0.1354	0.36	0.7830
STREAM*MONTH	9	3.3777	0.3753	0.37	0.9384
STATION*MONTH	9	11.6203	1.2911	1.26	0.3133

Heptageniidae Rhithrogena:

1993: Repeated measures

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	33.3680	11.1227	10.45	0.0085
STATION	3	3.7756	1.2585	1.18	0.3922
Error	6	6.3847	1.0641		

Source: MONTH

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
3	0.7995	0.2665	0.15	0.9284	0.7604	0.9256

Source: MONTH*STREAM

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	25.7094	2.8566	1.61	0.1873	0.2692	0.1895

Source: MONTH*STATION

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	15.6229	1.7359	0.98	0.4905	0.4694	0.4900

Source: Error(MONTH)

DF	Type III SS	Mean Square
18	32.0107	1.7784

1994:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	87.9015	2.5853	2.63	0.0111
Error	21	20.6228	0.9820		
Corrected Total	55	108.5244			

R-Square	C.V.	Root MSE	RHERI Mean
0.8100	9999.99	0.9910	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	16.0900	5.3633	5.46	0.0062
STATION	3	15.9481	5.3161	1.70	0.2535
STREAM*STATION	7	21.9072	3.1296	3.19	0.0184
MONTH	3	0.3993	0.1331	0.12	0.9430
STREAM*MONTH	9	9.5881	1.0653	1.08	0.4135
STATION*MONTH	9	11.3912	1.2657	1.29	0.2997

Hydropsychidae Arctopsyche:

1993:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	43.0284	1.2655	4.02	0.0011
Error	19	5.9806	0.3148		
Corrected Total	53	49.0090			

R-Square	C.V.	Root MSE	RHYAR Mean
0.8780	9999.99	0.5610	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
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STREAM	3	17.5999	5.8666	18.64	0.0001
STATION	3	1.2312	0.4104	0.20	0.8933
STREAM*STATION	7	14.3787	2.0541	6.53	0.0005
MONTH	3	0.0306	0.0102	0.01	0.9975
STREAM*MONTH	9	6.4812	0.7201	2.29	0.0617
STATION*MONTH	9	3.1623	0.3514	1.12	0.3980

1994: Repeated Measures

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	4.8095	1.60316	2.14	0.1833
STATION	3	5.5958	1.86526	2.49	0.1444
Error	7	5.2417	0.74881		

Source: MONTH

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
3	0.0844	0.0281	0.06	0.9784	0.9071	0.9784

Source: MONTH*STREAM

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	3.4350	0.3817	0.87	0.5680	0.5301	0.5680

Source: MONTH*STATION

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	4.3586	0.4843	1.10	0.4042	0.4112	0.4042

Source: Error(MONTH)

DF	Type III SS	Mean Square
21	9.2489	0.4404

Hydropsychidae *Hydropsyche*:**1993:**

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	55.5111	1.6327	1.02	0.4970
Error	19	30.4424	1.6022		
Corrected Total	53	85.9535			

R-Square C.V. Root MSE RHYHY Mean

	0.6458	9999.99	1.2658	0.00000	
Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	4.0658	1.3553	0.85	0.4858
STATION	3	10.4156	3.4719	1.00	0.4456
STREAM*STATION	7	24.2114	3.4588	2.16	0.0864
MONTH	3	0.1183	0.0394	0.04	0.9883
STREAM*MONTH	9	8.6898	0.9655	0.60	0.7796
STATION*MONTH	9	12.2927	1.3659	0.85	0.5801

1994:

		Residual Sum of Mean			
Source	DF	Squares	Square	F Value	Pr > F
Model	34	110.4433	3.2483	2.63	0.0112
Error	21	25.9525	1.2358		
Corrected Total	55	136.3958			

R-Square	C.V.	Root MSE	RHYHY Mean
0.8097	9999.99	1.1117	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	17.3965	5.7988	4.69	0.0117
STATION	3	36.5129	12.1710	3.38	0.0836
STREAM*STATION	7	25.1977	3.5997	2.91	0.0271
MONTH	3	0.2705	0.0902	0.04	0.9866
STREAM*MONTH	9	18.1812	2.0201	1.63	0.1692
STATION*MONTH	9	12.7446	1.4161	1.15	0.3763

Lepidostomatidae *Lepidostoma*:**1993:**

		Residual Sum of Mean			
Source	DF	Squares	Square	F Value	Pr > F
Model	34	38.6833	1.1377	0.73	0.7976
Error	19	29.7922	1.5680		
Corrected Total	53	68.4755			

R-Square	C.V.	Root MSE	RLELE Mean
0.5649	9999.99	1.2522	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
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STREAM	3	6.0725	2.0242	1.29	0.3063
STATION	3	0.4522	0.1507	0.14	0.9318
STREAM*STATION	7	7.4434	1.0633	0.68	0.6886
MONTH	3	0.6551	0.2184	0.15	0.9302
STREAM*MONTH	9	13.5414	1.5046	0.96	0.5007
STATION*MONTH	9	9.7966	1.0885	0.69	0.7063

1994: Repeated Measures

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	14.9539	4.9846	2.62	0.1328
STATION	3	6.2386	2.0795	1.09	0.4131
Error	7	13.3241	1.9034		

Source: MONTH

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
3	0.3306	0.1102	0.10	0.9567	0.8486	0.9567

Source: MONTH*STREAM

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	7.9544	0.8838	0.84	0.5916	0.5423	0.5916

Source: MONTH*STATION

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	9.5993	1.0666	1.01	0.4633	0.4526	0.4633

Source: Error(MONTH)

DF	Type III SS	Mean Square
21	22.1906	1.0567

Leptophlebiidae Paraleptophlebia:**1993:**

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	73.4350	2.1599	1.48	0.1852
Error	19	27.7787	1.4620		
Corrected Total	53	101.2138			

R-Square	C.V.	Root MSE	RLEPA Mean
0.7255	-9999.99	1.2092	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	1.4825	0.4942	0.34	0.7981
STATION	3	18.2487	6.0829	3.43	0.0815
STREAM*STATION	7	12.4301	1.7757	1.21	0.3424
MONTH	3	2.2700	0.7567	0.35	0.7898
STREAM*MONTH	9	19.4170	2.1574	1.48	0.2267
STATION*MONTH	9	16.2298	1.8033	1.23	0.3326

1994:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	55.1120	1.6209	2.07	0.0407
Error	21	16.4089	0.7814		
Corrected Total	55	71.5209			

R-Square	C.V.	Root MSE	RLEPA Mean
0.7706	-9999.99	0.8840	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	5.8277	1.9426	2.49	0.0886
STATION	3	9.8098	3.2699	2.02	0.2000
STREAM*STATION	7	11.3413	1.6202	2.07	0.0927
MONTH	3	0.7296	0.2432	0.16	0.9223
STREAM*MONTH	9	13.9138	1.5460	1.98	0.0950
STATION*MONTH	9	15.4549	1.7172	2.20	0.0660

Philopotamidae Wormaldia:**1993:**

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	47.4961	1.3969	1.17	0.3669
Error	19	22.7080	1.1952		
Corrected Total	53	70.2041			

R-Square	C.V.	Root MSE	RPHWO Mean
0.6765	9999.99	1.0932	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
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STREAM	3	17.8225	5.9408	4.97	0.0103
STATION	3	3.7756	1.2585	1.63	0.2669
STREAM*STATION	7	5.3993	0.7713	0.65	0.7137
MONTH	3	0.7113	0.2371	0.21	0.8871
STREAM*MONTH	9	10.1718	1.1302	0.95	0.5106
STATION*MONTH	9	5.6278	0.6253	0.52	0.8399

1994:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	22.2900	0.6556	0.79	0.7407
Error	21	17.5258	0.8346		
Corrected Total	55	39.8158			

R-Square	C.V.	Root MSE	RPHWO Mean
0.5598	9999.99	0.9135	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	1.7737	0.5912	0.71	0.5577
STATION	3	2.0924	0.6975	2.43	0.1503
STREAM*STATION	7	2.0087	0.2870	0.34	0.9241
MONTH	3	0.9262	0.3087	0.20	0.8951
STREAM*MONTH	9	14.0276	1.5586	1.87	0.1144
STATION*MONTH	9	3.1384	0.3487	0.42	0.9110

Rhyacophilidae *Rhyacophila*:**1993:**

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	38.0802	1.1200	1.35	0.2493
Error	19	15.8108	0.8321		
Corrected Total	53	53.8910			

R-Square	C.V.	Root MSE	RRHRH Mean
0.7066	-9999.99	0.9122	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	10.4584	3.4861	4.19	0.0196
STATION	3	2.9429	0.9810	0.46	0.7218
STREAM*STATION	7	15.0790	2.1541	2.59	0.0469
MONTH	3	0.2372	0.0791	0.12	0.9471

STREAM*MONTH	9	6.0197	0.6689	0.80	0.6182
STATION*MONTH	9	4.5011	0.5001	0.60	0.7809

1994:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	13.9747	0.4110	1.08	0.4344
Error	21	7.9834	0.3802		
Corrected Total	55	21.9581			

R-Square	C.V.	Root MSE	RRHRH Mean
0.6364	-9999.99	0.6166	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	0.3005	0.1002	0.26	0.8509
STATION	3	1.6469	0.5490	0.49	0.7023
STREAM*STATION	7	7.8985	1.1284	2.97	0.0250
MONTH	3	0.0961	0.0320	0.14	0.9324
STREAM*MONTH	9	2.0347	0.2261	0.59	0.7871
STATION*MONTH	9	2.3338	0.2593	0.68	0.7167

Uenoidae Neothremma:**1993:**

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	63.0898	1.8556	1.71	0.1086
Error	19	20.6219	1.0854		
Corrected Total	53	83.7117			

R-Square	C.V.	Root MSE	RUENE Mean
0.7537	9999.99	1.0418	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	16.0647	5.3549	4.93	0.0106
STATION	3	1.6247	0.5416	0.24	0.8673
STREAM*STATION	7	15.9385	2.2769	2.10	0.0944
MONTH	3	0.8715	0.2905	0.26	0.8546
STREAM*MONTH	9	10.1788	1.1310	1.04	0.4445
STATION*MONTH	9	6.4563	0.7174	0.66	0.7331

1994:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	101.3698	2.9815	3.52	0.0018
Error	21	17.7942	0.8473		
Corrected Total	55	119.1641			

R-Square	C.V.	Root MSE	RUENE Mean
0.8507	9999.99	0.92051	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	54.3076	18.1025	21.36	0.0001
STATION	3	6.1528	2.0509	1.44	0.3094
STREAM*STATION	7	9.9445	1.4206	1.68	0.1693
MONTH	3	0.1265	0.0422	0.06	0.9783
STREAM*MONTH	9	6.0625	0.6736	0.79	0.6247
STATION*MONTH	9	11.3119	1.2569	1.48	0.2178

Functional Feeding Group Absolute Counts.**Collector-Gatherers:****1993:**

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	44.6675	1.3138	7.72	0.0001
Error	19	3.2329	0.1702		
Corrected Total	53	47.9004			

R-Square	C.V.	Root MSE	RGATH Mean
0.9325	-9999.99	0.4125	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	3.3282	1.1094	6.52	0.0032
STATION	3	18.8892	6.2964	2.37	0.1567
STREAM*STATION	7	18.6072	2.6582	15.62	0.0001
MONTH	3	0.4774	0.1591	0.16	0.9195
STREAM*MONTH	9	8.8585	0.9843	5.78	0.0006
STATION*MONTH	9	2.6909	0.2990	1.76	0.1440

1994:

Residual Sum of Mean

Source	DF	Squares	Square	F Value	Pr > F
Model	34	45.2856	1.3319	2.29	0.0243
Error	21	12.2088	0.5814		
Corrected Total	55	57.4944			

R-Square	C.V.	Root MSE	RGATH Mean
0.7877	-9999.99	0.7625	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	2.9015	0.9672	1.66	0.2052
STATION	3	15.6576	5.2192	1.78	0.2377
STREAM*STATION	7	20.4831	2.9262	5.03	0.0018
MONTH	3	0.1636	0.0545	0.12	0.9454
STREAM*MONTH	9	4.0533	0.4504	0.77	0.6411
STATION*MONTH	9	1.4524	0.1614	0.28	0.9739

Scraper:**1993:**

Source	DF	Squares	Residual Sum of Mean Square	F Value	Pr > F
Model	34	28.9324	0.8510	4.76	0.0003
Error	19	3.3931	0.1786		
Corrected Total	53	32.3256			

R-Square	C.V.	Root MSE	RSCRAP Mean
0.8950	-9999.99	0.4226	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	4.0555	1.3519	7.57	0.0016
STATION	3	9.9168	3.3056	2.59	0.1355
STREAM*STATION	7	8.9405	1.2772	7.15	0.0003
MONTH	3	0.5415	0.1805	0.24	0.8629
STREAM*MONTH	9	6.6323	0.7369	4.13	0.0045
STATION*MONTH	9	4.9791	0.5532	3.10	0.0182

1994:

Source	DF	Squares	Residual Sum of Mean Square	F Value	Pr > F
Model	34	31.4791	0.9259	2.74	0.0089
Error	21	7.1079	0.3385		

Corrected Total 55 38.5871

R-Square	C.V.	Root MSE	RSCRAP Mean
0.8158	9999.99	0.5818	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	2.1381	0.7127	2.11	0.1300
STATION	3	10.9468	3.6489	1.62	0.2692
STREAM*STATION	7	15.7633	2.2519	6.65	0.0003
MONTH	3	0.0816	0.0272	0.10	0.9584
STREAM*MONTH	9	2.4645	0.2738	0.81	0.6134
STATION*MONTH	9	0.7855	0.0873	0.26	0.9795

Collector-Filterer:**1993:**

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	52.1551	1.5340	1.87	0.0750
Error	19	15.5763	0.8198		
Corrected Total	53	67.7315			

R-Square	C.V.	Root MSE	RFILT Mean
0.7700	9999.99	0.9054	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	16.9652	5.6551	6.90	0.0025
STATION	3	8.5489	2.8496	1.52	0.2915
STREAM*STATION	7	13.1350	1.8764	2.29	0.0717
MONTH	3	0.1127	0.0376	0.12	0.9462
STREAM*MONTH	9	2.8251	0.3139	0.38	0.9290
STATION*MONTH	9	9.8628	1.0959	1.34	0.2829

1994:

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	58.8513	1.7309	1.99	0.0499
Error	21	18.2702	0.8700		
Corrected Total	55	77.1215			

R-Square	C.V.	Root MSE	RFILT Mean
0.7631	9999.99	0.9327	0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	12.1883	4.0628	4.67	0.0119
STATION	3	12.7474	4.2491	2.94	0.1083
STREAM*STATION	7	10.1057	1.4437	1.66	0.1737
MONTH	3	0.9194	0.3065	0.19	0.9010
STREAM*MONTH	9	14.5683	1.6187	1.86	0.1158
STATION*MONTH	9	11.2533	1.2504	1.44	0.2351

Shredder:

1993:

Source	DF	Residual Sum of Squares	Mean Square	F Value	Pr > F
Model	34	24.9329	0.7333211	0.63	0.8847
Error	19	22.2094	1.1689166		
Corrected Total	53	47.1423			

R-Square	C.V.	Root MSE	RSHRED Mean
0.5289	-9999.99	1.0812	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	6.1275	2.0425	1.75	0.1914
STATION	3	0.1578	0.0526	0.04	0.9867
STREAM*STATION	7	8.3814	1.1973	1.02	0.4463
MONTH	3	0.0440	0.0147	0.04	0.9889
STREAM*MONTH	9	3.3612	0.3735	0.32	0.9583
STATION*MONTH	9	4.0728	0.4525	0.39	0.9267

1994: Repeated Measures

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	0.2344	0.0781	0.11	0.9523
STATION	3	3.7134	1.2378	1.72	0.2492
Error	7	5.0350	0.7193		

Source: MONTH

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
3	0.0149	0.0050	0.01	0.9977	0.9855	0.9977

Source: MONTH*STREAM

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	4.2241	0.4693	1.29	0.2969	0.3225	0.2969

Source: MONTH*STATION

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	1.6471	0.1830	0.50	0.8546	0.7921	0.8546

Source: Error(MONTH)

DF	Type III SS	Mean Square
21	7.6134	0.3625

Predator:**1993: Repeated Measures**

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	2.2244	0.7415	1.04	0.4414
STATION	3	3.3201	1.1067	1.55	0.2967
Error	6	4.2935	0.7157		

Source: MONTH

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
3	0.4819	0.1606	0.23	0.8731	0.6972	0.8731

Source: MONTH*STREAM

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	8.0542	0.8949	1.29	0.3071	0.3528	0.3071

Source: MONTH*STATION

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	8.9150	0.9906	1.43	0.2478	0.3123	0.2478

Source: Error(MONTH)

DF	Type III SS	Mean Square
18	12.4801	0.6933

1994: Repeated Measures

Source	DF	Type III SS	Mean Square	F Value	Pr > F
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STREAM	3	0.3066	0.1022	0.13	0.9398
STATION	3	2.0714	0.6905	0.87	0.4994
Error	7	5.5413	0.7916		

Source: MONTH

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
3	0.1455	0.0485	0.17	0.9158	0.8058	0.9158

Source: MONTH*STREAM

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	0.8009	0.0890	0.31	0.9626	0.8950	0.9626

Source: MONTH*STATION

DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
9	2.006	0.2229	0.78	0.6379	0.5831	0.6379

Source: Error(MONTH)

DF	Type III SS	Mean Square
21	6.0112	0.2862

Diversity.

1993:

Source	DF	Residual Sum of Mean		F Value	Pr > F
		Squares	Square		
Model	34	3.4353	0.1010	2.53	0.0177
Error	19	0.7595	0.0400		
Corrected Total	53	4.1948			

R-Square	C.V.	Root MSE	RH93 Mean
0.8189	-9999.99	0.1999	-0.00000

Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	1.1508	0.3836	9.60	0.0005
STATION	3	0.6844	0.2281	2.20	0.1765
STREAM*STATION	7	0.7274	0.1039	2.60	0.0462
MONTH	3	0.0272	0.0091	0.13	0.9397
STREAM*MONTH	9	0.6264	0.0696	1.74	0.1478
STATION*MONTH	9	0.5404	0.0600	1.50	0.2173

1994:

Source	Residual Sum of Mean				
	DF	Squares	Square	F Value	Pr > F
Model	34	2.2462	0.0661	0.86	0.6590
Error	21	1.6107	0.0767		
Corrected Total	55	3.8569			
	R-Square	C.V.	Root MSE	RH94 Mean	
	0.5824	9999.99	0.2770	0.00000	
Source	DF	Type III SS	Mean Square	F Value	Pr > F
STREAM	3	0.5901	0.1967	2.56	0.0819
STATION	3	0.1490	0.0497	0.64	0.6155
STREAM*STATION	7	0.5472	0.0782	1.02	0.4466
MONTH	3	0.0214	0.0071	0.13	0.9373
STREAM*MONTH	9	0.4785	0.0532	0.69	0.7076
STATION*MONTH	9	0.5853	0.0650	0.85	0.5826

APPENDIX D. Regression equations of correlated environmental variables with log-transformed absolute genera counts, functional feeding groups, and diversity by month and year. Standard errors are in parentheses.

Absolute Insect Counts.

Baetidae *Baetis*:

$$\text{Jun/93: } Y = 3.92 + 1.44_{\text{COBBLE}} - 3.14_{\text{SILT}}$$

(2.16) (2.87) (3.33)

$$\text{Aug/93: } Y = 3.25 + 1.14_{\text{COBBLE}} - 4.50_{\text{SILT}}$$

(1.38) (1.14) (2.06)

$$\text{Jun/94: } Y = 4.67 - 1.97_{\text{SILT}}$$

(0.35) (1.15)

$$\text{Aug/94: } Y = 4.18 - 4.71_{\text{SILT}}$$

(0.54) (1.62)

$$\text{Jul/93: } Y = 4.27 + 0.31_{\text{COBBLE}} - 3.33_{\text{SILT}}$$

(1.41) (1.88) (2.45)

$$\text{Sept/93: } Y = 2.11 + 3.31_{\text{COBBLE}} - 2.74_{\text{SILT}}$$

(1.73) (2.46) (2.72)

$$\text{Jul/94: } Y = 4.27 - 3.17_{\text{SILT}}$$

(0.58) (2.13)

$$\text{Sept/94: } Y = 3.63 - 2.20_{\text{SILT}}$$

(0.47) (1.56)

Brachycentridae *Micrasema*:

$$\text{Jun/93: } Y = 1.47 - 5.30_{\text{SAND}}$$

(1.36) (3.49)

$$\text{Aug/93: } Y = -0.24 - 0.23_{\text{SAND}}$$

(0.90) (2.26)

$$\text{Jun/94: } Y = 1.94 - 5.60_{\text{SAND}} - 0.77_{\text{GRAVEL}}$$

(1.12) (3.32) (1.28)

$$\text{Aug, 1994: } Y = 3.99 - 9.13_{\text{SAND}} - 0.75_{\text{GRAVEL}}$$

(1.14) (3.60) (1.56)

$$\text{Jul/93: } Y = 1.33 - 6.06_{\text{SAND}}$$

(0.84) (2.31)

$$\text{Sept/93: } Y = 1.84 - 5.28_{\text{SAND}}$$

(1.11) (3.12)

$$\text{Jul/94: } Y = 3.17 - 2.24_{\text{SAND}} - 4.03_{\text{GRAVEL}}$$

(0.93) (3.02) (1.21)

$$\text{Sept/94: } Y = 3.29 - 1.81_{\text{SAND}} - 4.95_{\text{GRAVEL}}$$

(1.30) (4.88) (3.51)

EphemereIIDae *Drunella*:

$$\text{Jun/93: } Y = 0.19 + 4.57_{\text{BOULDER}} + 3.64_{\text{BOULDER}^2} - 0.72_{\text{COBBLE}}$$

(1.28) (5.82) (10.22) (1.73)

$$\text{Jul/93: } Y = -0.48 + 2.15_{\text{BOULDER}} + 4.90_{\text{BOULDER}^2} + 1.69_{\text{COBBLE}}$$

(0.92) (6.59) (8.01) (0.75)

$$\text{Aug/93: } Y = -0.71 + 9.79_{\text{BOULDER}} - 5.05_{\text{BOULDER}}^2 - 1.40_{\text{COBBLE}}$$

(0.65) (4.08) (4.95) (1.59)

$$\text{Jun/94: } Y = 1.27 + 2.10_{\text{BOULDER}} + 1.13_{\text{BOULDER}}^2 - 3.39_{\text{SILT}}$$

(0.95) (7.26) (12.01) (2.22)

$$\text{Aug/94: } Y = 0.32 + 5.77_{\text{BOULDER}} - 1.87_{\text{BOULDER}}^2 - 1.18_{\text{SILT}}$$

(0.81) (4.99) (7.24) (1.69)

$$\text{Sept/93: } Y = -2.58 + 3.07_{\text{BOULDER}} + 6.17_{\text{BOULDER}}^2 - 2.80_{\text{COBBLE}}$$

(0.84) (5.08) (9.29) (1.63)

$$\text{Jul/94: } Y = 0.47 + 4.64_{\text{BOULDER}} - 1.11_{\text{BOULDER}}^2 - 3.49_{\text{SILT}}$$

(0.59) (4.34) (6.26) (1.65)

$$\text{Sept/94: } Y = 0.07 + 16.04_{\text{BOULDER}} - 18.34_{\text{BOULDER}}^2 - 2.32_{\text{SILT}}$$

(0.68) (3.72) (5.48) (1.59)

Glossosomatidae *Glossosoma*:

$$\text{Jun/93: } Y = -0.01 + 3.58_{\text{COBBLE}} - 0.65_{\text{BEDROCK}}$$

(1.86) (2.57) (1.74)

$$\text{Aug/93: } Y = -0.10 + 3.34_{\text{COBBLE}} - 0.94_{\text{BEDROCK}}$$

(0.63) (0.98) (0.74)

$$\text{Jun/94: } Y = 3.64 - 1.08_{\text{COBBLE}} - 1.57_{\text{BEDROCK}}$$

(0.80) (1.44) (0.85)

$$\text{Aug/94: } Y = 0.40 + 3.36_{\text{COBBLE}} - 2.15_{\text{BEDROCK}}$$

(1.59) (2.61) (1.58)

$$\text{Jul/93: } Y = 2.04 + 1.57_{\text{COBBLE}} - 1.11_{\text{BEDROCK}}$$

(0.83) (1.39) (0.90)

$$\text{Sept/93: } Y = -2.12 + 6.12_{\text{COBBLE}} - 0.05_{\text{BEDROCK}}$$

(1.35) (2.07) (1.16)

$$\text{Jul/94: } Y = 3.01 + 1.05_{\text{COBBLE}} - 3.36_{\text{BEDROCK}}$$

(1.31) (2.26) (1.30)

$$\text{Sept/94: } Y = -0.30 + 3.08_{\text{COBBLE}} - 0.23_{\text{BEDROCK}}$$

(1.68) (2.19) (1.45)

Heptageniidae *Cinygmula*:

$$\text{Jun/93: } Y = 0.11 - 1.05_{\text{BEDROCK}}$$

(0.51) (1.43)

$$\text{Aug/93: } Y = 1.92 - 3.75_{\text{BEDROCK}}$$

(0.41) (1.03)

$$\text{Jun/94: } Y = 1.59 + 0.78_{\text{COBBLE}} - 1.73_{\text{BEDROCK}}$$

(0.67) (1.21) (0.72)

$$\text{Aug/94: } Y = 1.20 + 2.98_{\text{COBBLE}} - 1.64_{\text{BEDROCK}}$$

(1.32) (2.16) (1.30)

$$\text{Jul/93: } Y = 2.51 - 3.40_{\text{BEDROCK}}$$

(0.24) (0.65)

$$\text{Sept/93: } Y = 1.49 - 3.21_{\text{BEDROCK}}$$

(0.48) (1.16)

$$\text{Jul/94: } Y = 1.27 + 2.32_{\text{COBBLE}} - 1.56_{\text{BEDROCK}}$$

(0.83) (1.43) (0.83)

$$\text{Sept/94: } Y = 1.39 + 1.84_{\text{COBBLE}} - 1.40_{\text{BEDROCK}}$$

(2.46) (3.20) (2.13)

Heptageniidae *Epeorus*:

$$\text{Jun/93: } Y = -0.27 + 3.58_{\text{BOULDER}}$$

$$\text{Jul/93: } Y = -0.28 + 1.04_{\text{BOULDER}}$$

(0.66) (1.98)
 Aug/93: $Y = -1.28 + 1.85_{\text{BOULDER}}$
 (0.41) (0.99)
 Jun/94: $Y = 1.52 + 3.56_{\text{BOULDER}}$
 (0.43) (1.19)
 Aug/94: $Y = -0.94 + 3.55_{\text{BOULDER}}$
 (0.40) (1.05)

(0.53) (1.34)
 Sept/93: $Y = -2.24 + 9.71_{\text{BOULDER}}$
 (0.62) (1.91)
 Jul/94: $Y = -0.19 + 5.00_{\text{BOULDER}}$
 (0.46) (1.13)
 Sept/94: $Y = -1.37 + 3.92_{\text{BOULDER}}$
 (0.46) (1.35)

Heptageniidae *Rhithrogena*:

Jun/93: $Y = -2.31 + 2.17_{\text{COBBLE}}$
 (0.59) (0.90)
 Aug/93: $Y = -1.90 + 6.41_{\text{COBBLE}}$
 (1.10) (1.73)
 Jun/94: NA
 Aug/94: $Y = 0.74 + 0.02_{\text{COBBLE}} - 2.04_{\text{BEDROCK}}$
 (1.67) (2.74) (1.65)

Jul/93: $Y = -2.07 + 4.17_{\text{COBBLE}}$
 (1.17) (2.17)
 Sept/93: $Y = -2.11 + 7.73_{\text{COBBLE}}$
 (1.57) (2.70)
 Jul/94: $Y = 1.37 - 3.11_{\text{COBBLE}} - 2.18_{\text{BEDROCK}}$
 (1.08) (1.86) (1.07)
 Sept/94: $Y = -0.83 + 3.74_{\text{COBBLE}} - 0.69_{\text{BEDROCK}}$
 (2.17) (2.82) (1.87)

Hydropsychidae *Hydropsyche*:

Jun/93: $Y = -0.72 - 0.58_{\text{VELOCITY}} + 1.18_{\text{GRAVEL}}$
 (2.79) (1.21) (5.21)
 Aug/93: $Y = 3.20 + 0.77_{\text{VELOCITY}} - 2.95_{\text{GRAVEL}}$
 (1.37) (1.07) (3.73)
 Jun/94: $Y = 1.76 + 1.08_{\text{VELOCITY}}$
 (0.69) (0.94)
 Aug/94: $Y = 4.24 + 2.34_{\text{VELOCITY}}$
 (1.21) (0.99)

Jul/93: $Y = -1.55 - 0.61_{\text{VELOCITY}} + 1.40_{\text{GRAVEL}}$
 (1.53) (0.79) (2.98)
 Sept/93: $Y = 7.60 + 1.49_{\text{VELOCITY}} - 6.97_{\text{GRAVEL}}$
 (1.45) (0.59) (2.72)
 Jul/94: $Y = 1.36 + 0.73_{\text{VELOCITY}}$
 (0.66) (0.68)
 Sept/94: $Y = 4.27 + 2.10_{\text{VELOCITY}}$
 (1.23) (1.08)

Hydropsychidae *Arctopsyche*:

$$\text{Jun/93: } Y = -0.71 + 0.55_{\text{VELOCITY}} + 2.28_{\text{BEDROCK}}$$

(0.43) (0.89) (1.26)

$$\text{Aug/93: } Y = -1.03 + 0.21_{\text{VELOCITY}} + 3.70_{\text{BEDROCK}}$$

(0.42) (0.41) (0.74)

$$\text{Jun/94: } Y = -0.91 + 0.24_{\text{VELOCITY}} + 2.52_{\text{BEDROCK}}$$

(0.45) (0.56) (0.73)

$$\text{Aug/94: } Y = -1.33 + 0.15_{\text{VELOCITY}} + 3.26_{\text{BEDROCK}}$$

(0.50) (0.37) (0.49)

$$\text{Jul/93: } Y = -0.67 + 0.35_{\text{VELOCITY}} + 3.25_{\text{BEDROCK}}$$

(0.50) (0.68) (1.23)

$$\text{Sept/93: } Y = -1.22 - 0.03_{\text{VELOCITY}} + 0.86_{\text{BEDROCK}}$$

(0.51) (0.37) (0.60)

$$\text{Jul/94: } Y = -1.08 + 0.43_{\text{VELOCITY}} + 1.80_{\text{BEDROCK}}$$

(0.66) (0.62) (0.79)

$$\text{Sept/94: } Y = -0.84 + 0.55_{\text{VELOCITY}} + 1.48_{\text{BEDROCK}}$$

(0.56) (0.44) (0.43)

Lepidostomatidae *Lepidostoma*:

$$\text{Jun/93: } Y = -0.48 + 2.71_{\text{SILT}} - 1.76_{\text{BOULDER}}$$

(0.76) (2.20) (1.74)

$$\text{Aug/93: } Y = 0.85 + 0.62_{\text{SILT}} - 2.65_{\text{BOULDER}}$$

(0.79) (1.71) (1.52)

$$\text{Jun/94: } Y = 1.25 - 1.56_{\text{SILT}} - 2.54_{\text{BOULDER}} + 3.24_{\text{BOULDER}}^2$$

(0.54) (0.56) (4.54)(7.64)

$$\text{Aug/94: } Y = 1.26 - 0.65_{\text{SILT}} - 3.57_{\text{BOULDER}} + 2.79_{\text{BOULDER}}^2$$

(1.31) (0.89) (5.66)(8.77)

$$\text{Jul/93: } Y = -1.46 + 5.12_{\text{SILT}} + 3.03_{\text{BOULDER}}$$

(1.88) (3.96) (2.80)

$$\text{Sept/93: } Y = 1.13 - 0.83_{\text{SILT}} - 0.16_{\text{BOULDER}}$$

(0.94) (2.24) (2.10)

$$\text{Jul/94: } Y = 1.38 - 1.63_{\text{SILT}} - 9.10_{\text{BOULDER}} + 9.85_{\text{BOULDER}}^2$$

(0.76) (0.69) (4.40) (6.35)

$$\text{Sept/94: } Y = 0.45 - 0.86_{\text{SILT}} - 0.97_{\text{BOULDER}} + 0.02_{\text{BOULDER}}^2$$

(1.54) (1.17) (6.19) (9.64)

Leptophlebiidae *Paraleptophlebia*:

$$\text{Jun/93: } Y = 0.93 - 1.44_{\text{BEDROCK}}$$

(0.34) (0.97)

$$\text{Aug/93: } Y = 0.34 - 2.08_{\text{BEDROCK}}$$

(0.48) (1.21)

$$\text{Jun/94: } Y = 2.42 - 0.44_{\text{BEDROCK}}$$

(0.25) (0.56)

$$\text{Aug/94: } Y = 2.03 - 2.07_{\text{BEDROCK}}$$

(0.48) (1.11)

$$\text{Jul/93: } Y = 0.75 - 1.64_{\text{BEDROCK}}$$

(0.44) (1.17)

$$\text{Sept/93: } Y = 2.03 - 2.35_{\text{BEDROCK}}$$

(0.54) (1.29)

$$\text{Jul/94: } Y = 1.93 - 0.45_{\text{BEDROCK}}$$

(0.41) (0.91)

$$\text{Sept/94: } Y = 2.92 - 2.72_{\text{BEDROCK}}$$

(0.32) (0.62)

Philopotamidae *Wormaldia*:

Jun/93: $Y = -0.03 - 1.40_{\text{SAND}}$
(1.18) (3.03)

Aug/93: $Y = -1.75 + 3.35_{\text{SAND}}$
(0.79) (1.97)

Jun/94: $Y = -2.17 + 3.91_{\text{SAND}}$
(0.71) (2.09)

Aug/94: $Y = -0.17 - 1.84_{\text{SAND}}$
(0.78) (2.39)

Jul/93: $Y = -3.59 + 8.62_{\text{SAND}}$
(1.19) (3.28)

Sept/93: $Y = -2.82 + 6.30_{\text{SAND}}$
(1.23) (3.48)

Jul/94: $Y = -1.40 + 2.24_{\text{SAND}}$
(0.83) (2.52)

Sept/94: $Y = -0.03 - 1.40_{\text{SAND}}$
(0.54) (1.90)

Rhyacophilidae *Rhyacophila*:

Jun/93: $Y = -3.16 + 5.76_{\text{COBBLE}} + 1.16_{\text{BEDROCK}}$
(1.70) (2.34) (1.58)

Aug/93: $Y = 1.77 + 0.33_{\text{COBBLE}} - 2.51_{\text{BEDROCK}}$
(0.66) (1.03) (0.77)

Jun/94: $Y = 1.48 + 0.42_{\text{COBBLE}} + 0.43_{\text{BEDROCK}}$
(0.50) (0.90) (0.53)

Aug/94: $Y = 2.21 + 1.10_{\text{COBBLE}} - 1.26_{\text{BEDROCK}}$
(0.62) (1.02) (0.61)

Jul/93: $Y = 2.52 - 1.61_{\text{COBBLE}} - 1.17_{\text{BEDROCK}}$
(1.23) (2.06) (1.34)

Sept/93: $Y = 1.00 + 1.59_{\text{COBBLE}} - 1.33_{\text{BEDROCK}}$
(1.52) (2.34) (1.30)

Jul/94: $Y = 2.98 - 0.80_{\text{COBBLE}} - 1.48_{\text{BEDROCK}}$
(0.51) (0.87) (0.50)

Sept/94: $Y = 0.59 + 3.02_{\text{COBBLE}} + 0.01_{\text{BEDROCK}}$
(0.82) (1.07) (0.71)

Uenoidae *Neothremma*:

Jun/93: $Y = -2.03 + 2.18_{\text{SAND}}$
(0.58) (1.50)

Aug/93: $Y = -2.81 + 7.93_{\text{SAND}}$
(0.95) (2.38)

Jun/94: $Y = 0.15 - 1.78_{\text{COBBLE}}$
(0.71) (1.38)

Aug/94: $Y = 1.57 - 3.73_{\text{COBBLE}}$
(1.14) (2.06)

Jul/93: $Y = -3.78 + 9.36_{\text{SAND}}$
(1.98) (5.45)

Sept/93: $Y = -3.82 + 9.16_{\text{SAND}}$
(1.07) (3.01)

Jul/94: $Y = 1.53 - 3.66_{\text{COBBLE}}$
(1.01) (1.95)

Sept/1994: $Y = 1.54 - 3.20_{\text{COBBLE}}$
(1.00) (1.50)

Functional Feeding Group Absolute Abundance.

Collector- Gatherers:

Jun/93: $Y=5.06-3.76_{\text{SILT}}$
(0.45) (2.03)

Aug/93: $Y=4.88-3.15_{\text{SILT}}$
(0.34) (1.09)

Jun/94: $Y=5.31-1.78_{\text{SILT}}$
(0.26) (0.87)

Aug/94: $Y=4.91-2.64_{\text{SILT}}$
(0.50) (1.51)

Jul/93: $Y=4.69-1.50_{\text{SILT}}$
(0.46) (1.38)

Sept/93: $Y=5.51-5.08_{\text{SILT}}$
(0.36) (1.38)

Jul/94: $Y=5.21-3.09_{\text{SILT}}$
(0.35) (1.29)

Sept/94: $Y=5.19-2.99_{\text{SILT}}$
(0.41) (1.37)

Scrapers:

Jun/93: $Y=2.94+2.54_{\text{COBBLE}}-1.67_{\text{SILT}}$
(1.17) (1.57) (2.04)

Aug/93: $Y=3.62+1.30_{\text{COBBLE}}-2.00_{\text{SILT}}$
(0.72) (1.03) (1.08)

Jun/94: $Y=4.43+0.81_{\text{COBBLE}}-0.69_{\text{SILT}}$
(0.51) (0.87) (0.85)

Aug/94: $Y=4.65+0.26_{\text{COBBLE}}-1.86_{\text{BEDROCK}}$
(0.90) (1.36) (1.24)

Jul/93: $Y=4.49+0.47_{\text{COBBLE}}-1.49_{\text{SILT}}$
(0.87) (1.16) (1.34)

Sept/93: $Y=3.55+2.41_{\text{COBBLE}}-3.70_{\text{SILT}}$
(0.98) (1.40) (1.55)

Jul/94: $Y=4.43+1.06_{\text{COBBLE}}-1.92_{\text{SILT}}$
(0.80) (1.32) (1.42)

Sept/94: $Y=3.93+1.35_{\text{COBBLE}}-2.26_{\text{SILT}}$
(0.78) (0.99) (1.36)

Collector-Filterers:

Jun/93: $Y=0.96+0.22_{\text{VELOCITY}}+1.59_{\text{SILT}}$
(0.51) (0.92) (2.51)

Aug/93: $Y=2.84+0.75_{\text{VELOCITY}}-1.06_{\text{SILT}}$
(0.45) (0.57) (1.45)

Jun/94: $Y=2.01+0.20_{\text{VELOCITY}}-2.40_{\text{SILT}}$
(0.66) (1.22) (2.62)

Jul/93: $Y=-0.31+1.01_{\text{VELOCITY}}+6.85_{\text{SILT}}$
(0.98) (1.26) (4.07)

Sept/93: $Y=4.44+1.51_{\text{VELOCITY}}-1.88_{\text{SILT}}$
(0.68) (0.77) (2.51)

Jul/94: $Y=2.04+0.46_{\text{VELOCITY}}-3.03_{\text{SILT}}$
(0.71) (0.93) (2.20)

$$\text{Aug/94: } Y=4.27+1.10_{\text{VELOCITY}}-4.24_{\text{SILT}}$$

$$(0.58) \quad (0.56) \quad (1.13)$$

$$\text{Sept/94: } Y=4.71+1.39_{\text{VELOCITY}}-4.20_{\text{SILT}}$$

$$(0.82) \quad (0.74) \quad (1.49)$$

Shredders:

$$\text{Jun/93: } Y=-0.16+1.81_{\text{GRAVEL}}$$

$$(1.80) \quad (3.33)$$

$$\text{Aug/93: } Y=0.52+2.64_{\text{GRAVEL}}$$

$$(0.71) \quad (1.42)$$

$$\text{Jun/94: } Y=1.58+1.60_{\text{GRAVEL}}$$

$$(0.39) \quad (0.62)$$

$$\text{Aug/94: } Y=2.53+1.00_{\text{GRAVEL}}$$

$$(0.26) \quad (0.44)$$

$$\text{Jul/93: } Y=1.48-0.86_{\text{GRAVEL}}$$

$$(1.06) \quad (1.88)$$

$$\text{Sept/93: } Y=0.87+2.09_{\text{GRAVEL}}$$

$$(0.87) \quad (1.48)$$

$$\text{Jul/94: } Y=2.15+1.33_{\text{GRAVEL}}$$

$$(0.38) \quad (0.60)$$

$$\text{Sept/94: } Y=0.53+0.74_{\text{GRAVEL}}$$

$$(0.77) \quad (1.56)$$

Predators:

$$\text{Jun/93: } Y=-2.39+5.43_{\text{COBBLE}}+2.04_{\text{BEDROCK}}$$

$$(2.07) \quad (2.85) \quad (1.93)$$

$$\text{Aug/93: } Y=1.70+1.34_{\text{COBBLE}}-2.24_{\text{BEDROCK}}$$

$$(0.61) \quad (0.94) \quad (0.71)$$

$$\text{Jun/94: } Y=1.30+1.81_{\text{COBBLE}}+0.86_{\text{BEDROCK}}$$

$$(0.52) \quad (0.93) \quad (0.55)$$

$$\text{Aug/94: } Y=2.19+1.74_{\text{COBBLE}}-1.13_{\text{BEDROCK}}$$

$$(0.45) \quad (0.74) \quad (0.45)$$

$$\text{Jul/93: } Y=2.70-0.15_{\text{COBBLE}}-1.52_{\text{BEDROCK}}$$

$$(0.67) \quad (1.13) \quad (0.73)$$

$$\text{Sept/93: } Y=1.94+1.20_{\text{COBBLE}}-1.87_{\text{BEDROCK}}$$

$$(1.19) \quad (1.83) \quad (1.02)$$

$$\text{Jul/94: } Y=2.51+0.68_{\text{COBBLE}}-1.12_{\text{BEDROCK}}$$

$$(0.45) \quad (0.77) \quad (0.44)$$

$$\text{Sept/94: } Y=0.64+3.32_{\text{COBBLE}}+0.67_{\text{BEDROCK}}$$

$$(0.69) \quad (0.90) \quad (0.60)$$

Diversity.

$$\text{Jun/93: } Y=2.64+0.30_{\text{COBBLE}}-0.12_{\text{MAXTEMP}}$$

$$(0.68) \quad (0.41) \quad (0.05)$$

$$\text{Aug/93: } Y=1.33+0.44_{\text{COBBLE}}+0.01_{\text{MAXTEMP}}$$

$$(0.90) \quad (0.32) \quad (0.04)$$

$$\text{Jun/94: } Y=2.89-0.51_{\text{COBBLE}}-0.06_{\text{MAXTEMP}}$$

$$\text{Jul/93: } Y=1.67+0.67_{\text{COBBLE}}-0.03_{\text{MAXTEMP}}$$

$$(0.83) \quad (0.47) \quad (0.05)$$

$$\text{Sept/93: } Y=0.84+1.46_{\text{COBBLE}}+0.00_{\text{MAXTEMP}}$$

$$(0.74) \quad (0.47) \quad (0.04)$$

$$\text{Jul/94: } Y=3.12-0.19_{\text{COBBLE}}-0.08_{\text{MAXTEMP}}$$

$$\begin{array}{l} \text{Aug/94: } Y=1.62+0.81_{\text{COBBLE}}-0.01_{\text{MAXTEMP}} \\ \quad (0.65) \quad (0.33) \quad (0.04) \\ \quad (0.49) \quad (0.38) \quad (0.02) \end{array}$$

$$\begin{array}{l} \text{Sept/94: } Y=1.81+0.49_{\text{COBBLE}}-0.02_{\text{MAXTEMP}} \\ \quad (0.74) \quad (0.41) \quad (0.04) \\ \quad (0.85) \quad (0.33) \quad (0.04) \end{array}$$

APPENDIX E. Raw genus count dataset by stream, month, year, and station.

STREAM	DATE	STATION	<i>Baetis</i>	<i>Micrasema</i>	<i>Caudatella</i>	<i>Drunella</i>	<i>Euryophella</i>	<i>Serratella</i>	<i>Timpanoga</i>
Ames	Jun-93	1	115	0	0	14	0	0	0
Ames	Jun-93	2	207	0	0	4	0	9	0
Ames	Jun-93	3	120	7	0	8	0	3	0
Ames	Jun-93	4	26	7	0	1	0	0	0
Ames	Jul-93	1	52	0	0	9	0	0	0
Ames	Jul-93	2	109	0	0	0	0	0	0
Ames	Jul-93	3	70	1	0	0	0	0	0
Ames	Jul-93	4	3	0	0	8	0	0	0
Ames	Aug-93	1	46	0	0	12	0	0	0
Ames	Aug-93	2	66	1	0	1	0	0	0
Ames	Aug-93	3	35	3	0	0	0	5	0
Ames	Aug-93	4	9	0	0	7	0	0	0
Ames	Sep-93	1	50	0	0	8	0	3	0
Ames	Sep-93	2	101	3	0	0	0	2	0
Ames	Sep-93	3	83	8	0	0	0	1	0
Ames	Sep-93	4	29	0	0	13	0	1	0
Ames	Jun-94	1	50	0	0	14	0	0	1
Ames	Jun-94	2	344	5	0	52	0	259	0
Ames	Jun-94	3	106	5	0	0	0	172	0
Ames	Jun-94	4	60	0	0	14	0	2	0
Ames	Jul-94	1	23	0	0	12	0	2	0
Ames	Jul-94	2	155	4	0	4	0	21	0
Ames	Jul-94	3	63	2	0	1	0	28	0
Ames	Jul-94	4	3	1	0	4	0	0	0
Ames	Aug-94	1	25	0	0	19	0	0	0
Ames	Aug-94	2	265	22	0	7	0	5	0
Ames	Aug-94	3	16	4	0	1	0	0	0
Ames	Aug-94	4	8	1	0	8	0	0	0
Ames	Sep-94	1	39	0	0	21	0	0	0
Ames	Sep-94	2	83	7	0	8	0	0	0
Ames	Sep-94	3	42	42	0	7	0	8	0
Ames	Sep-94	4	6	1	0	12	0	0	0

STREAM	DATE	STATION	<i>Glossosoma</i>	<i>Agraylea</i>	<i>Hydroptila</i>	<i>Cinygmula</i>	<i>Epeorus</i>	<i>Heptagenia</i>	<i>Ironodes</i>
Ames	Jun-93	1	8	0	0	4	6	0	0
Ames	Jun-93	2	4	0	0	2	7	0	0
Ames	Jun-93	3	1	0	0	0	6	0	2
Ames	Jun-93	4	5	0	0	0	1	0	1
Ames	Jul-93	1	6	0	0	3	6	0	0
Ames	Jul-93	2	2	0	0	1	5	0	0
Ames	Jul-93	3	7	0	0	0	0	0	0
Ames	Jul-93	4	14	0	0	8	2	0	0
Ames	Aug-93	1	4	0	0	0	1	0	2
Ames	Aug-93	2	2	0	0	0	0	0	2
Ames	Aug-93	3	0	0	0	0	0	0	0
Ames	Aug-93	4	2	0	0	5	0	0	0
Ames	Sep-93	1	10	0	0	1	16	0	5
Ames	Sep-93	2	0	0	0	0	0	0	0
Ames	Sep-93	3	1	0	0	0	0	0	0
Ames	Sep-93	4	4	0	0	1	0	0	2
Ames	Jun-94	1	29	0	0	6	56	0	0
Ames	Jun-94	2	18	0	0	4	38	0	0
Ames	Jun-94	3	2	0	0	0	6	0	0
Ames	Jun-94	4	14	0	0	2	26	0	0
Ames	Jul-94	1	11	0	0	9	33	0	0
Ames	Jul-94	2	20	0	0	3	7	0	0
Ames	Jul-94	3	0	0	0	2	0	0	1
Ames	Jul-94	4	12	0	0	3	3	0	0
Ames	Aug-94	1	14	0	0	19	9	4	0
Ames	Aug-94	2	1	0	0	5	0	0	1
Ames	Aug-94	3	0	0	0	1	3	0	0
Ames	Aug-94	4	4	0	0	11	1	1	0
Ames	Sep-94	1	6	0	0	10	6	0	0
Ames	Sep-94	2	4	0	0	9	0	0	0
Ames	Sep-94	3	0	0	0	1	0	0	6
Ames	Sep-94	4	3	0	0	5	0	3	0

STREAM	DATE	STATION	<i>Rhithrogena</i>	<i>Arctopsyche</i>	<i>Hydropsyche</i>	<i>Parapsyche</i>	<i>Lepidostoma</i>	<i>Paraleptophlebia</i>
Ames	Jun-93	1	0	8	7	0	0	0
Ames	Jun-93	2	0	5	3	0	2	3
Ames	Jun-93	3	0	6	0	1	2	1
Ames	Jun-93	4	0	3	0	1	1	2
Ames	Jul-93	1	0	10	3	0	0	0
Ames	Jul-93	2	0	8	0	0	9	0
Ames	Jul-93	3	0	32	0	3	1	1
Ames	Jul-93	4	0	1	0	1	0	6
Ames	Aug-93	1	8	11	20	1	0	0
Ames	Aug-93	2	0	7	52	0	0	0
Ames	Aug-93	3	0	14	55	0	0	0
Ames	Aug-93	4	3	0	0	0	1	0
Ames	Sep-93	1	22	2	12	0	0	17
Ames	Sep-93	2	0	0	8	0	0	1
Ames	Sep-93	3	0	1	79	0	0	0
Ames	Sep-93	4	2	1	10	0	0	5
Ames	Jun-94	1	0	1	14	0	5	5
Ames	Jun-94	2	0	6	56	0	7	2
Ames	Jun-94	3	0	12	46	0	1	13
Ames	Jun-94	4	0	4	26	0	11	12
Ames	Jul-94	1	0	0	4	0	4	4
Ames	Jul-94	2	0	0	9	0	13	2
Ames	Jul-94	3	0	32	7	0	3	3
Ames	Jul-94	4	0	0	0	0	9	1
Ames	Aug-94	1	9	0	20	0	23	21
Ames	Aug-94	2	0	15	54	0	18	1
Ames	Aug-94	3	0	11	39	0	5	1
Ames	Aug-94	4	0	0	0	0	19	9
Ames	Sep-94	1	26	0	7	0	10	22
Ames	Sep-94	2	0	1	25	0	7	0
Ames	Sep-94	3	1	8	184	0	7	1
Ames	Sep-94	4	2	0	4	0	11	10

STREAM	DATE	STATION	<i>Psychoglypha</i>	<i>Dicosmoecus</i>	<i>Ecclisomyia</i>	<i>Homophylax</i>	<i>Hydatophylax</i>	<i>Onocosmoecus</i>
Ames	Jun-93	1	0	0	0	0	0	0
Ames	Jun-93	2	0	0	0	0	0	0
Ames	Jun-93	3	0	0	0	0	0	0
Ames	Jun-93	4	0	0	0	0	0	0
Ames	Jul-93	1	0	0	0	0	0	0
Ames	Jul-93	2	0	0	0	0	0	0
Ames	Jul-93	3	0	0	0	0	0	0
Ames	Jul-93	4	0	0	0	0	0	0
Ames	Aug-93	1	0	0	0	0	0	0
Ames	Aug-93	2	0	0	0	0	0	0
Ames	Aug-93	3	0	0	0	0	0	0
Ames	Aug-93	4	0	0	0	0	0	0
Ames	Sep-93	1	0	0	0	0	0	0
Ames	Sep-93	2	0	0	0	0	0	0
Ames	Sep-93	3	0	0	0	0	0	0
Ames	Sep-93	4	0	0	0	0	1	0
Ames	Jun-94	1	0	0	0	0	0	0
Ames	Jun-94	2	0	0	0	0	0	0
Ames	Jun-94	3	0	0	0	0	0	0
Ames	Jun-94	4	0	0	0	0	0	0
Ames	Jul-94	1	0	0	0	0	0	0
Ames	Jul-94	2	1	0	0	0	0	0
Ames	Jul-94	3	0	0	0	0	0	0
Ames	Jul-94	4	1	0	0	0	0	0
Ames	Aug-94	1	0	0	0	0	0	0
Ames	Aug-94	2	0	0	0	0	0	0
Ames	Aug-94	3	0	0	0	0	0	0
Ames	Aug-94	4	0	0	0	0	0	0
Ames	Sep-94	1	0	0	0	0	0	0
Ames	Sep-94	2	0	0	0	0	0	0
Ames	Sep-94	3	0	0	0	0	0	0
Ames	Sep-94	4	0	0	0	0	0	0

STREAM	DATE	STATION	<i>Pseudostenophylax</i>	<i>Wormaldia</i>	<i>Polycentropus</i>	<i>Rhyacophila</i>	<i>Neophylax</i>	<i>Neothremma</i>
Ames	Jun-93	1	0	0	0	1	0	0
Ames	Jun-93	2	0	0	0	0	2	0
Ames	Jun-93	3	0	0	0	1	0	0
Ames	Jun-93	4	0	0	0	1	1	0
Ames	Jul-93	1	0	0	0	1	0	0
Ames	Jul-93	2	0	0	0	3	1	0
Ames	Jul-93	3	0	0	0	2	2	0
Ames	Jul-93	4	0	0	1	2	1	1
Ames	Aug-93	1	0	1	0	2	1	0
Ames	Aug-93	2	0	1	0	1	0	4
Ames	Aug-93	3	0	0	0	0	0	3
Ames	Aug-93	4	0	0	5	12	1	0
Ames	Sep-93	1	0	0	0	4	0	0
Ames	Sep-93	2	0	0	2	1	1	0
Ames	Sep-93	3	0	0	0	0	0	0
Ames	Sep-93	4	0	0	17	1	2	0
Ames	Jun-94	1	0	0	0	2	4	1
Ames	Jun-94	2	0	0	0	6	5	3
Ames	Jun-94	3	0	0	0	7	0	4
Ames	Jun-94	4	0	2	0	4	0	0
Ames	Jul-94	1	0	0	0	9	2	0
Ames	Jul-94	2	0	0	0	3	0	2
Ames	Jul-94	3	0	0	0	7	0	18
Ames	Jul-94	4	0	0	0	9	0	1
Ames	Aug-94	1	0	1	0	16	2	0
Ames	Aug-94	2	0	1	0	11	0	15
Ames	Aug-94	3	0	1	0	2	0	9
Ames	Aug-94	4	0	0	2	13	0	1
Ames	Sep-94	1	0	0	3	37	2	0
Ames	Sep-94	2	0	0	2	7	0	1
Ames	Sep-94	3	0	0	0	3	0	32
Ames	Sep-94	4	0	0	0	25	0	0

STREAM	DATE	STATION	<i>Baetis</i>	<i>Micrasema</i>	<i>Caudatella</i>	<i>Drunella</i>	<i>Euryophella</i>	<i>Serratella</i>	<i>Timpanoga</i>
Buttermilk	Jun-93	1	3	0	0	0	1	0	0
Buttermilk	Jun-93	2	84	1	0	1	0	1	0
Buttermilk	Jun-93	3	138	5	0	0	0	6	0
Buttermilk	Jun-93	4							
Buttermilk	Jul-93	1	0	0	0	0	0	1	0
Buttermilk	Jul-93	2	44	0	0	0	0	4	0
Buttermilk	Jul-93	3	57	0	0	0	0	2	0
Buttermilk	Jul-93	4							
Buttermilk	Aug-93	1	0	10	0	2	0	9	0
Buttermilk	Aug-93	2	51	0	0	0	0	6	0
Buttermilk	Aug-93	3	117	0	0	0	0	5	0
Buttermilk	Aug-93	4	0	0	0	0	0	0	0
Buttermilk	Sep-93	1	0	3	0	0	0	2	0
Buttermilk	Sep-93	2	32	1	0	0	0	17	0
Buttermilk	Sep-93	3	69	0	0	0	0	8	0
Buttermilk	Sep-93	4	1	0	0	0	0	0	0
Buttermilk	Jun-94	1	8	0	0	0	0	0	0
Buttermilk	Jun-94	2	80	0	0	1	0	5	1
Buttermilk	Jun-94	3	85	5	0	0	0	9	0
Buttermilk	Jun-94	4	27	0	0	0	0	1	0
Buttermilk	Jul-94	1	1	1	0	2	0	0	0
Buttermilk	Jul-94	2	159	0	0	0	0	5	0
Buttermilk	Jul-94	3	54	0	0	0	0	2	0
Buttermilk	Jul-94	4	6	0	0	0	0	0	0
Buttermilk	Aug-94	1	0	2	0	3	0	0	0
Buttermilk	Aug-94	2	114	0	0	0	0	1	0
Buttermilk	Aug-94	3	109	6	0	0	0	7	0
Buttermilk	Aug-94	4	1	0	0	0	0	0	0
Buttermilk	Sep-94	1	2	6	0	0	0	0	0
Buttermilk	Sep-94	2	109	0	0	0	0	0	0
Buttermilk	Sep-94	3	26	0	0	0	0	2	0
Buttermilk	Sep-94	4	2	0	0	0	0	0	0

STREAM	DATE	STATION	<i>Glossosoma</i>	<i>Agraylea</i>	<i>Hydroptila</i>	<i>Cinygmula</i>	<i>Epeorus</i>	<i>Heptagenia</i>	<i>Ironodes</i>
Buttermilk	Jun-93	1	1	0	0	0	0	0	0
Buttermilk	Jun-93	2	78	0	0	0	0	0	0
Buttermilk	Jun-93	3	109	0	0	0	5	0	0
Buttermilk	Jun-93	4							
Buttermilk	Jul-93	1	4	0	0	4	0	0	0
Buttermilk	Jul-93	2	14	0	0	4	0	0	0
Buttermilk	Jul-93	3	78	0	0	57	4	0	0
Buttermilk	Jul-93	4							
Buttermilk	Aug-93	1	2	0	0	2	0	0	0
Buttermilk	Aug-93	2	3	0	0	7	0	0	0
Buttermilk	Aug-93	3	5	0	0	14	0	0	5
Buttermilk	Aug-93	4	1	0	0	0	0	0	0
Buttermilk	Sep-93	1	0	0	0	0	0	0	0
Buttermilk	Sep-93	2	4	0	0	7	0	0	0
Buttermilk	Sep-93	3	49	0	0	0	0	0	1
Buttermilk	Sep-93	4	0	0	0	0	0	0	0
Buttermilk	Jun-94	1	5	0	0	3	10	0	0
Buttermilk	Jun-94	2	17	0	0	3	1	0	0
Buttermilk	Jun-94	3	271	0	0	10	12	0	0
Buttermilk	Jun-94	4	21	0	0	1	1	0	0
Buttermilk	Jul-94	1	0	0	0	0	0	0	0
Buttermilk	Jul-94	2	188	0	0	9	2	0	0
Buttermilk	Jul-94	3	199	0	0	9	1	0	0
Buttermilk	Jul-94	4	3	0	0	2	1	0	0
Buttermilk	Aug-94	1	0	0	0	0	0	0	0
Buttermilk	Aug-94	2	70	0	0	16	0	0	0
Buttermilk	Aug-94	3	139	0	0	38	1	0	0
Buttermilk	Aug-94	4	0	0	0	0	0	0	0
Buttermilk	Sep-94	1	2	0	0	0	0	0	0
Buttermilk	Sep-94	2	97	0	0	0	0	0	0
Buttermilk	Sep-94	3	84	0	0	6	0	0	0
Buttermilk	Sep-94	4	0	0	0	0	0	0	0

STREAM	DATE	STATION	<i>Rhithrogena</i>	<i>Arctopsyche</i>	<i>Hydropsyche</i>	<i>Parapsyche</i>	<i>Lepidostoma</i>	<i>Paraleptophlebia</i>
Buttermilk	Jun-93	1	0	0	1	0	0	0
Buttermilk	Jun-93	2	0	0	0	0	1	2
Buttermilk	Jun-93	3	1	0	0	1	0	8
Buttermilk	Jun-93	4						
Buttermilk	Jul-93	1	0	0	0	0	15	0
Buttermilk	Jul-93	2	0	0	0	0	3	11
Buttermilk	Jul-93	3	23	0	15	0	5	14
Buttermilk	Jul-93	4						
Buttermilk	Aug-93	1	3	0	1	0	17	0
Buttermilk	Aug-93	2	13	0	0	0	3	6
Buttermilk	Aug-93	3	0	0	10	2	2	1
Buttermilk	Aug-93	4	0	0	1	0	3	1
Buttermilk	Sep-93	1	13	0	0	0	19	2
Buttermilk	Sep-93	2	45	0	0	0	1	45
Buttermilk	Sep-93	3	177	0	11	0	2	160
Buttermilk	Sep-93	4	0	0	0	0	1	0
Buttermilk	Jun-94	1	0	0	1	0	35	12
Buttermilk	Jun-94	2	0	0	0	0	24	15
Buttermilk	Jun-94	3	0	0	2	0	14	62
Buttermilk	Jun-94	4	0	0	0	0	7	6
Buttermilk	Jul-94	1	0	0	0	0	45	16
Buttermilk	Jul-94	2	12	0	6	0	24	14
Buttermilk	Jul-94	3	7	0	4	0	15	25
Buttermilk	Jul-94	4	1	0	0	0	7	0
Buttermilk	Aug-94	1	0	0	0	0	9	0
Buttermilk	Aug-94	2	25	0	3	0	8	40
Buttermilk	Aug-94	3	21	0	4	0	13	32
Buttermilk	Aug-94	4	0	0	0	0	7	37
Buttermilk	Sep-94	1	0	0	0	0	10	3
Buttermilk	Sep-94	2	57	0	10	0	2	97
Buttermilk	Sep-94	3	23	0	5	0	18	61
Buttermilk	Sep-94	4	0	0	0	0	0	7

STREAM	DATE	STATION	<i>Psychoglypha</i>	<i>Dicosmoecus</i>	<i>Ecclisomyia</i>	<i>Homophylax</i>	<i>Hydatophylax</i>	<i>Onocosmoecus</i>
Buttermilk	Jun-93	1	0	0	0	0	0	0
Buttermilk	Jun-93	2	0	0	0	0	0	0
Buttermilk	Jun-93	3	0	0	0	0	0	0
Buttermilk	Jun-93	4						
Buttermilk	Jul-93	1	1	0	0	0	0	0
Buttermilk	Jul-93	2	0	1	0	0	0	0
Buttermilk	Jul-93	3	0	0	0	0	0	0
Buttermilk	Jul-93	4						
Buttermilk	Aug-93	1	1	0	0	0	0	0
Buttermilk	Aug-93	2	0	0	1	0	0	0
Buttermilk	Aug-93	3	0	0	0	0	0	0
Buttermilk	Aug-93	4	0	0	0	0	0	0
Buttermilk	Sep-93	1	0	0	0	0	0	0
Buttermilk	Sep-93	2	0	0	0	0	0	0
Buttermilk	Sep-93	3	0	0	0	0	0	0
Buttermilk	Sep-93	4	0	0	0	0	1	0
Buttermilk	Jun-94	1	0	1	0	0	0	0
Buttermilk	Jun-94	2	0	0	0	0	0	0
Buttermilk	Jun-94	3	0	0	0	0	0	0
Buttermilk	Jun-94	4	0	0	0	0	0	0
Buttermilk	Jul-94	1	0	0	1	0	0	0
Buttermilk	Jul-94	2	0	0	0	0	0	0
Buttermilk	Jul-94	3	0	0	0	0	0	1
Buttermilk	Jul-94	4	0	0	0	0	0	1
Buttermilk	Aug-94	1	0	0	3	0	0	0
Buttermilk	Aug-94	2	0	0	1	0	0	0
Buttermilk	Aug-94	3	0	0	0	0	0	2
Buttermilk	Aug-94	4	0	0	0	0	0	5
Buttermilk	Sep-94	1	0	0	0	0	0	0
Buttermilk	Sep-94	2	0	0	0	0	0	0
Buttermilk	Sep-94	3	0	0	0	0	0	0
Buttermilk	Sep-94	4	0	0	0	0	0	0

STREAM	DATE	STATION	<i>Psuedostenophylax</i>	<i>Wormaldia</i>	<i>Polycentropus</i>	<i>Rhyacophila</i>	<i>Neophylax</i>	<i>Neothremma</i>
Buttermilk	Jun-93	1	0	0	0	0	0	0
Buttermilk	Jun-93	2	0	1	4	3	1	0
Buttermilk	Jun-93	3	0	4	0	7	8	0
Buttermilk	Jun-93	4						
Buttermilk	Jul-93	1	0	0	22	8	0	0
Buttermilk	Jul-93	2	0	0	3	6	0	0
Buttermilk	Jul-93	3	0	5	0	37	3	0
Buttermilk	Jul-93	4						
Buttermilk	Aug-93	1	0	0	8	5	0	3
Buttermilk	Aug-93	2	0	0	1	8	0	0
Buttermilk	Aug-93	3	0	8	0	7	0	10
Buttermilk	Aug-93	4	0	0	0	2	0	2
Buttermilk	Sep-93	1	1	1	1	27	0	1
Buttermilk	Sep-93	2	1	0	2	4	0	0
Buttermilk	Sep-93	3	0	0	1	32	0	0
Buttermilk	Sep-93	4	0	0	2	1	0	0
Buttermilk	Jun-94	1	0	0	0	12	3	0
Buttermilk	Jun-94	2	0	0	0	3	0	0
Buttermilk	Jun-94	3	0	2	0	23	6	0
Buttermilk	Jun-94	4	0	2	0	2	0	0
Buttermilk	Jul-94	1	0	0	0	2	2	0
Buttermilk	Jul-94	2	0	0	0	25	2	0
Buttermilk	Jul-94	3	0	1	0	27	1	0
Buttermilk	Jul-94	4	0	0	0	12	0	1
Buttermilk	Aug-94	1	0	0	2	1	0	0
Buttermilk	Aug-94	2	2	0	0	16	0	0
Buttermilk	Aug-94	3	0	0	0	55	7	0
Buttermilk	Aug-94	4	0	0	0	10	0	0
Buttermilk	Sep-94	1	0	0	4	1	0	0
Buttermilk	Sep-94	2	3	0	0	24	1	0
Buttermilk	Sep-94	3	0	0	0	54	0	0
Buttermilk	Sep-94	4	0	0	0	2	0	0

STREAM	DATE	STATION	<i>Baetis</i>	<i>Micrasema</i>	<i>Caudatella</i>	<i>Drunella</i>	<i>Euryophella</i>	<i>Serratella</i>	<i>Timpanoga</i>
Mosby	Jun-93	1	171	0	0	19	0	7	0
Mosby	Jun-93	2	529	0	0	40	0	5	0
Mosby	Jun-93	3	94	0	0	17	0	1	0
Mosby	Jun-93	4	108	0	0	25	0	3	0
Mosby	Jul-93	1	113	2	0	21	0	0	0
Mosby	Jul-93	2	184	2	3	18	0	4	0
Mosby	Jul-93	3	52	1	0	33	0	1	0
Mosby	Jul-93	4	43	0	1	18	0	0	0
Mosby	Aug-93	1	38	0	0	19	0	0	0
Mosby	Aug-93	2	64	1	0	16	0	0	0
Mosby	Aug-93	3	60	3	0	7	0	0	0
Mosby	Aug-93	4	40	0	0	18	0	1	0
Mosby	Sep-93	1	171	3	0	20	0	54	0
Mosby	Sep-93	2	55	2	0	8	0	35	0
Mosby	Sep-93	3	53	3	0	14	0	3	0
Mosby	Sep-93	4	22	0	0	5	0	2	0
Mosby	Jun-94	1	125	0	4	11	0	3	3
Mosby	Jun-94	2	484	5	0	34	0	16	0
Mosby	Jun-94	3	153	1	0	23	0	18	0
Mosby	Jun-94	4	130	1	0	8	0	8	3
Mosby	Jul-94	1	299	11	0	20	0	11	3
Mosby	Jul-94	2	336	21	0	14	0	13	3
Mosby	Jul-94	3	118	3	0	25	0	11	0
Mosby	Jul-94	4	199	3	0	48	0	3	0
Mosby	Aug-94	1	117	2	0	22	0	0	0
Mosby	Aug-94	2	88	15	0	30	0	11	4
Mosby	Aug-94	3	18	14	0	22	0	5	0
Mosby	Aug-94	4	16	3	0	33	0	0	0
Mosby	Sep-94	1	99	5	0	23	0	56	0
Mosby	Sep-94	2	41	26	0	14	0	93	0
Mosby	Sep-94	3	13	3	0	10	0	8	0
Mosby	Sep-94	4	20	1	0	37	0	1	0

STREAM	DATE	STATION	<i>Glossosoma</i>	<i>Agraylea</i>	<i>Hydroptila</i>	<i>Cinygmula</i>	<i>Epeorus</i>	<i>Heptagenia</i>	<i>Ironodes</i>
Mosby	Jun-93	1	2	1	0	9	0	0	0
Mosby	Jun-93	2	13	0	0	6	14	0	0
Mosby	Jun-93	3	2	0	0	1	8	0	0
Mosby	Jun-93	4	15	0	0	0	6	0	0
Mosby	Jul-93	1	25	0	0	8	1	0	0
Mosby	Jul-93	2	35	0	0	14	2	0	0
Mosby	Jul-93	3	50	0	0	10	1	0	0
Mosby	Jul-93	4	25	0	0	18	0	0	0
Mosby	Aug-93	1	14	0	0	2	0	0	0
Mosby	Aug-93	2	17	4	2	16	0	0	0
Mosby	Aug-93	3	12	0	0	15	4	0	0
Mosby	Aug-93	4	30	0	0	12	4	0	0
Mosby	Sep-93	1	11	0	2	16	23	0	9
Mosby	Sep-93	2	6	0	2	13	18	0	1
Mosby	Sep-93	3	16	0	0	11	78	0	0
Mosby	Sep-93	4	7	0	0	24	30	0	0
Mosby	Jun-94	1	4	0	0	18	34	0	0
Mosby	Jun-94	2	9	0	0	10	64	0	0
Mosby	Jun-94	3	7	0	0	7	33	0	0
Mosby	Jun-94	4	6	0	0	12	26	0	0
Mosby	Jul-94	1	50	2	0	16	33	0	0
Mosby	Jul-94	2	65	1	2	12	14	0	0
Mosby	Jul-94	3	51	0	0	34	31	0	0
Mosby	Jul-94	4	42	0	0	43	34	0	0
Mosby	Aug-94	1	27	0	0	62	1	0	0
Mosby	Aug-94	2	8	0	18	47	1	0	0
Mosby	Aug-94	3	20	0	0	53	10	0	0
Mosby	Aug-94	4	15	0	0	29	5	0	0
Mosby	Sep-94	1	5	0	5	121	12	0	0
Mosby	Sep-94	2	3	0	25	54	0	0	0
Mosby	Sep-94	3	5	0	1	154	7	4	0
Mosby	Sep-94	4	5	0	0	123	4	6	0

STREAM	DATE	STATION	<i>Rhithrogena</i>	<i>Arctopsyche</i>	<i>Hydropsyche</i>	<i>Parapsyche</i>	<i>Lepidostoma</i>	<i>Paraleptophlebia</i>
Mosby	Jun-93	1	1	0	0	0	0	5
Mosby	Jun-93	2	0	0	1	0	0	2
Mosby	Jun-93	3	0	0	2	0	0	3
Mosby	Jun-93	4	2	0	1	0	0	10
Mosby	Jul-93	1	12	0	1	1	2	0
Mosby	Jul-93	2	2	0	0	0	5	2
Mosby	Jul-93	3	13	0	0	0	1	1
Mosby	Jul-93	4	7	0	0	0	28	3
Mosby	Aug-93	1	49	0	5	0	0	0
Mosby	Aug-93	2	41	0	5	0	3	3
Mosby	Aug-93	3	44	0	4	0	0	0
Mosby	Aug-93	4	53	1	8	0	0	1
Mosby	Sep-93	1	128	0	74	0	0	4
Mosby	Sep-93	2	29	0	10	0	0	1
Mosby	Sep-93	3	114	0	13	0	0	16
Mosby	Sep-93	4	126	0	16	0	1	11
Mosby	Jun-94	1	0	0	1	0	4	9
Mosby	Jun-94	2	0	0	0	0	3	11
Mosby	Jun-94	3	0	0	6	0	0	10
Mosby	Jun-94	4	0	0	6	0	7	14
Mosby	Jul-94	1	3	0	2	0	4	8
Mosby	Jul-94	2	0	0	5	0	5	21
Mosby	Jul-94	3	0	0	1	0	0	15
Mosby	Jul-94	4	0	0	3	0	0	11
Mosby	Aug-94	1	11	0	40	0	0	0
Mosby	Aug-94	2	14	0	10	0	6	21
Mosby	Aug-94	3	8	0	58	0	1	3
Mosby	Aug-94	4	0	0	13	0	0	6
Mosby	Sep-94	1	35	0	33	0	0	12
Mosby	Sep-94	2	8	0	38	0	23	17
Mosby	Sep-94	3	34	0	15	0	1	28
Mosby	Sep-94	4	28	0	6	0	0	12

STREAM	DATE	STATION	<i>Psychoglypha</i>	<i>Dicosmoecus</i>	<i>Ecclisomyia</i>	<i>Homophylax</i>	<i>Hydatophylax</i>	<i>Onocosmoecus</i>
Mosby	Jun-93	1	0	0	0	0	0	0
Mosby	Jun-93	2	0	0	0	0	0	0
Mosby	Jun-93	3	0	0	0	0	0	0
Mosby	Jun-93	4	0	0	0	0	0	0
Mosby	Jul-93	1	0	0	0	0	0	0
Mosby	Jul-93	2	0	0	0	0	0	0
Mosby	Jul-93	3	0	0	0	0	0	0
Mosby	Jul-93	4	0	0	0	0	0	0
Mosby	Aug-93	1	0	0	0	0	0	0
Mosby	Aug-93	2	0	0	0	0	0	0
Mosby	Aug-93	3	0	0	0	0	0	0
Mosby	Aug-93	4	0	0	0	0	0	0
Mosby	Sep-93	1	0	0	0	0	0	0
Mosby	Sep-93	2	0	0	0	0	0	0
Mosby	Sep-93	3	0	0	0	0	0	0
Mosby	Sep-93	4	0	0	0	0	0	0
Mosby	Jun-94	1	0	0	1	0	0	0
Mosby	Jun-94	2	0	0	0	0	0	0
Mosby	Jun-94	3	0	1	0	0	0	0
Mosby	Jun-94	4	0	0	4	0	0	0
Mosby	Jul-94	1	1	1	0	0	0	0
Mosby	Jul-94	2	0	1	0	0	0	0
Mosby	Jul-94	3	0	1	0	0	0	0
Mosby	Jul-94	4	0	0	0	0	0	0
Mosby	Aug-94	1	0	0	0	0	0	0
Mosby	Aug-94	2	0	3	0	0	0	0
Mosby	Aug-94	3	0	2	0	0	0	0
Mosby	Aug-94	4	0	0	0	0	0	0
Mosby	Sep-94	1	0	2	0	0	0	0
Mosby	Sep-94	2	0	1	0	0	0	0
Mosby	Sep-94	3	0	1	0	0	0	0
Mosby	Sep-94	4	0	0	0	0	0	0

STREAM	DATE	STATION	<i>Psuedostenophylax</i>	<i>Wormaldia</i>	<i>Polycentropus</i>	<i>Rhyacophila</i>	<i>Neophylax</i>	<i>Neothremma</i>
Mosby	Jun-93	1	0	0	2	7	1	0
Mosby	Jun-93	2	0	2	0	4	1	0
Mosby	Jun-93	3	0	0	0	0	0	0
Mosby	Jun-93	4	0	0	0	12	1	0
Mosby	Jul-93	1	0	3	0	8	0	0
Mosby	Jul-93	2	0	0	0	6	2	0
Mosby	Jul-93	3	0	0	0	0	0	0
Mosby	Jul-93	4	0	0	0	9	0	0
Mosby	Aug-93	1	0	0	4	3	0	0
Mosby	Aug-93	2	0	0	0	5	1	0
Mosby	Aug-93	3	0	0	0	4	0	0
Mosby	Aug-93	4	0	0	0	3	0	0
Mosby	Sep-93	1	0	0	3	17	0	0
Mosby	Sep-93	2	0	0	1	4	0	0
Mosby	Sep-93	3	0	0	0	4	1	0
Mosby	Sep-93	4	0	0	0	10	0	0
Mosby	Jun-94	1	0	0	0	4	0	0
Mosby	Jun-94	2	0	0	0	11	0	0
Mosby	Jun-94	3	0	0	0	4	2	0
Mosby	Jun-94	4	0	0	2	7	0	0
Mosby	Jul-94	1	0	1	0	13	4	0
Mosby	Jul-94	2	0	1	1	5	0	0
Mosby	Jul-94	3	0	0	2	5	3	0
Mosby	Jul-94	4	0	3	0	26	0	0
Mosby	Aug-94	1	0	0	0	32	1	0
Mosby	Aug-94	2	0	0	0	11	6	0
Mosby	Aug-94	3	0	1	0	19	3	0
Mosby	Aug-94	4	0	0	0	15	2	0
Mosby	Sep-94	1	0	0	0	23	2	0
Mosby	Sep-94	2	0	0	0	12	0	0
Mosby	Sep-94	3	0	0	0	5	0	0
Mosby	Sep-94	4	0	2	0	27	0	0

STREAM	DATE	STATION	<i>Baetis</i>	<i>Micrasema</i>	<i>Caudatella</i>	<i>Drunella</i>	<i>Euryophella</i>	<i>Serratella</i>	<i>Timpanoga</i>
Pancake	Jun-93	3	135	0	0	1	0	0	0
Pancake	Jun-93	4	8	0	0	2	0	1	0
Pancake	Jul-93	3	132	0	0	0	0	0	0
Pancake	Jul-93	4	10	0	0	4	0	1	0
Pancake	Aug-93	3	30	4	0	0	0	5	0
Pancake	Aug-93	4	20	0	0	1	0	1	0
Pancake	Sep-93	3	68	3	0	0	0	2	0
Pancake	Sep-93	4	66	0	0	3	0	5	0
Pancake	Jun-94	3	13	0	0	4	0	1	0
Pancake	Jun-94	4	74	0	0	7	0	0	1
Pancake	Jul-94	3	31	0	0	0	0	13	1
Pancake	Jul-94	4	13	0	0	2	0	2	0
Pancake	Aug-94	3	66	3	0	1	0	13	0
Pancake	Aug-94	4	21	0	0	2	0	3	0
Pancake	Sep-94	3	64	1	0	13	0	0	0
Pancake	Sep-94	4	19	0	0	0	0	4	0

STREAM	DATE	STATION	<i>Glossosoma</i>	<i>Agraylea</i>	<i>Hydroptila</i>	<i>Cinygmula</i>	<i>Epeorus</i>	<i>Heptagenia</i>	<i>Ironodes</i>
Pancake	Jun-93	3	21	0	0	9	1	0	5
Pancake	Jun-93	4	11	0	0	0	0	3	0
Pancake	Jul-93	3	17	0	0	24	1	0	0
Pancake	Jul-93	4	5	0	0	18	0	0	2
Pancake	Aug-93	3	24	0	0	35	0	0	0
Pancake	Aug-93	4	1	0	0	21	2	0	0
Pancake	Sep-93	3	2	0	0	7	0	0	23
Pancake	Sep-93	4	7	0	0	21	0	0	15
Pancake	Jun-94	3	6	0	0	20	1	0	0
Pancake	Jun-94	4	27	0	0	11	3	0	1
Pancake	Jul-94	3	51	0	0	29	2	0	0
Pancake	Jul-94	4	9	0	0	19	0	0	2
Pancake	Aug-94	3	58	0	0	21	0	0	7
Pancake	Aug-94	4	0	0	0	49	0	5	2
Pancake	Sep-94	3	15	0	0	19	0	0	18
Pancake	Sep-94	4	1	0	0	46	0	0	6

STREAM	DATE	STATION	<i>Rhithrogena</i>	<i>Arctopsyche</i>	<i>Hydropsyche</i>	<i>Parapsyche</i>	<i>Lepidostoma</i>	<i>Paraleptophlebia</i>
Pancake	Jun-93	3	0	0	11	2	0	1
Pancake	Jun-93	4	0	1	0	0	8	1
Pancake	Jul-93	3	0	1	0	2	3	2
Pancake	Jul-93	4	0	0	1	0	0	4
Pancake	Aug-93	3	87	0	8	0	4	66
Pancake	Aug-93	4	0	0	0	3	5	3
Pancake	Sep-93	3	1	0	13	0	0	17
Pancake	Sep-93	4	1	0	12	2	4	1
Pancake	Jun-94	3	0	0	5	1	19	24
Pancake	Jun-94	4	0	0	2	0	5	3
Pancake	Jul-94	3	0	0	2	0	31	13
Pancake	Jul-94	4	0	0	3	3	3	6
Pancake	Aug-94	3	0	0	10	8	1	3
Pancake	Aug-94	4	0	0	0	0	3	4
Pancake	Sep-94	3	0	0	45	0	1	12
Pancake	Sep-94	4	0	0	1	1	5	2

STREAM	DATE	STATION	<i>Psychoglypha</i>	<i>Dicosmoecus</i>	<i>Ecclisomyia</i>	<i>Homophylax</i>	<i>Hydatophylax</i>	<i>Onocosmoecus</i>
Pancake	Jun-93	3	0	0	0	0	0	0
Pancake	Jun-93	4	0	0	1	0	0	0
Pancake	Jul-93	3	0	0	1	0	0	0
Pancake	Jul-93	4	0	0	7	0	0	0
Pancake	Aug-93	3	0	0	0	0	0	0
Pancake	Aug-93	4	0	0	8	0	0	0
Pancake	Sep-93	3	0	0	0	0	0	0
Pancake	Sep-93	4	0	0	6	0	0	0
Pancake	Jun-94	3	0	0	32	0	0	0
Pancake	Jun-94	4	0	0	7	0	0	0
Pancake	Jul-94	3	0	0	2	0	0	0
Pancake	Jul-94	4	2	0	17	0	0	0
Pancake	Aug-94	3	2	0	6	0	0	0
Pancake	Aug-94	4	15	0	7	0	0	0
Pancake	Sep-94	3	0	0	0	0	0	0
Pancake	Sep-94	4	0	0	17	1	0	0

STREAM	DATE	STATION	<i>Psuedostenophylax</i>	<i>Wormaldia</i>	<i>Polycentropus</i>	<i>Rhyacophila</i>	<i>Neophylax</i>	<i>Neothremma</i>
Pancake	Jun-93	3	0	3	0	7	0	0
Pancake	Jun-93	4	0	1	0	1	0	2
Pancake	Jul-93	3	0	5	0	12	2	14
Pancake	Jul-93	4	0	2	0	7	0	105
Pancake	Aug-93	3	0	1	0	55	5	0
Pancake	Aug-93	4	0	9	0	11	0	156
Pancake	Sep-93	3	1	33	0	13	0	2
Pancake	Sep-93	4	0	6	0	15	0	60
Pancake	Jun-94	3	0	0	0	6	4	6
Pancake	Jun-94	4	0	0	0	5	7	0
Pancake	Jul-94	3	0	2	0	16	2	1
Pancake	Jul-94	4	8	0	0	12	1	65
Pancake	Aug-94	3	0	0	0	24	6	0
Pancake	Aug-94	4	16	3	0	11	0	65
Pancake	Sep-94	3	0	3	2	19	1	4
Pancake	Sep-94	4	0	1	0	6	0	34