Short-term effects of defoliation by gypsy moth larvae on Appalachian headwater streams in Virginia

By Brett Douglas Marshall

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Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

Master of Science
in
Entomology

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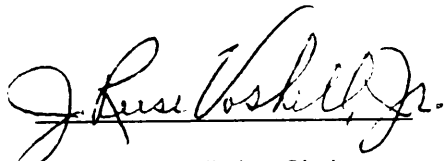

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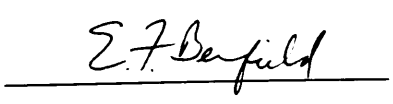
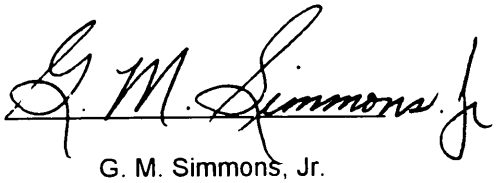


E. F. Benfield



G. M. Simmons, Jr.

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Blacksburg, Virginia

Short-term effects of defoliation by gypsy moth larvae on Appalachian headwater streams in Virginia

By Brett Douglas Marshall

J. Reese Voshell, Jr., Chairperson

Entomology

(Abstract)

This field study investigated the short-term effects of riparian defoliation by gypsy moth larvae on three aspects of headwater stream ecology, water quality, benthic macroinvertebrate community structure, and benthic macroinvertebrate function (expressed as secondary production). The experimental design was to compare measurements in three streams that were extensively defoliated by gypsy moth larvae (defoliated treatment), with three streams that were not affected by gypsy moth larvae (reference treatment). Although the riparian canopy became much more open after defoliation, I observed no significant differences in any water quality parameters except temperature, which was slightly elevated for a brief period after defoliation. There was a significant increase in the amount of detritus (frass and orts) falling into defoliated streams in the spring, which was followed by a significant decrease in the of amount detritus falling into defoliated streams in autumn. Many measures of community structure were analyzed, but only the Index of Biotic Similarity demonstrated a significant difference, indicating that, at most, only slight changes in community structure occurred. Secondary production of two representative aquatic insects, Peltoperlidae (shredder) and *Diplectrona modesta* (collector-filterer), was not affected by defoliation. *Glossosoma nigrior* (scraper) achieved higher production because of a second generation being induced by elevated temperature. I conclude that the short-term effects of riparian defoliation by gypsy moth larvae were minor.

Acknowledgments

This thesis is the result of several long years of work and would have never been possible without the assistance of many people. Every individual on my graduate committee provided their experience, insight, and resources towards the completion of this endeavor. I'm greatly indebted to them for their support. Dr. E. F. Benfield was always quick to remind me what frass truly is, and helped me weasel out new sources of motivation. Dr. George M. Simmons, Jr. was always able to accommodate my last-minute requests for information, nutrient analysis, and letters. In an academic environment teeming with stress and deadlines, the genuine kindness accompanying his input was truly appreciated. My major professor, Dr. J. Reese Voshell, Jr., provided financial support and cultivated my professional development. He provided a work environment with a strong "team player" atmosphere and made me feel more like a peer than just another student.

This study was funded by the National Park Service and the Division of Natural Resources and Sciences at Shenandoah National Park was very supportive throughout the study. Keith Watson and Tom Blount were particularly helpful. Despite the inconvenience they gladly provided 4-wheel drive vehicles, personnel, and housing to assist this project.

I was honored by receiving the J. McD. Grayson scholarship. The financial and motivational support provided by the award was extremely helpful. I thank Dr. Grayson and the members of the Grayson scholarship committee for selecting me as the recipient of the award in 1992.

Many friends helped in laboratory analyses and volunteered their time to assist in the field. I thank Michael West, Shane Evans, Susan Gale, Lourdes George, Billy Van Wart, Erik K. Gronning, and Ban-na Ang for their help and friendship. Stephen Hiner assisted in all aspects of this study and his experiences in the field and in life helped me with many difficulties before they got out of hand. Stephen helped me laugh at myself when I took myself entirely too seriously and bravely endured his PVC's under extreme circumstances.

The friends I met in Shenandoah National Park made the laborious field work associated with this project one of the most enjoyable experiences of my life. Special thanks to Mike Schrage, Amanda Allen, Martha Griffis, Laurie Clark, and Peg Hart for their friendship, and camaraderie across time and distance. The conclusion of this study holds the promise of returning to the field where the "big picture" is so much more apparent.

My mother, father and stepmother have been encouraging and supportive throughout my life, including this episode. I thank them for helping me when I stumble and allowing me take paths that promote stumbling. Thanks to my good dog, YoHo!, for reminding me there is more to life than computers and if it stinks, roll in it.

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INTRODUCTION

The gypsy moth (*Lymantria dispar* (L.)) has become a major forest pest in the eastern United States since its introduction in the 1860s. Repeated defoliation by gypsy moth larvae can cause tree mortality, especially in oaks (Houston 1981). Large scale defoliation by gypsy moth larvae has generated much research on life history, ecology, biology, distribution, control, and sampling of this pest species. (Fornbush and Fernald 1896, Doane and McMannus 1981). In addition, there has been research on the aquatic environmental effects of pesticides used to control gypsy moth larvae. For example, extensive use of diflubenzuron (Dimilin®) has lead to several recent reviews of its possible environmental impacts (Eisler 1992, Fischer and Hall 1992). While the biology of the pest and the ecological effects of pest suppression have been studied, there has been practically no research on the impacts to aquatic ecosystems from uncontrolled defoliation of riparian vegetation by insects, such as gypsy moth larvae.

Headwater streams are the aquatic ecosystems most likely to be affected by the feeding of gypsy moth larvae because physical, chemical, and biological characteristics of headwater streams are strongly influenced by riparian vegetation. These small streams are characterized by heavy shading during the warm months of the year. Primary production by algae and other photosynthesizing aquatic plants is very low for most of the year. The major source of energy for the macroinvertebrate community is coarse particulate organic matter (CPOM; >1 mm) that falls from the riparian vegetation (Vannote et al. 1980, Cummins 1989). The ratio of CPOM to fine particulate organic matter (FPOM; <1 mm) is high. As a result of shading and close proximity to groundwater discharge, water temperature remains constantly cool in headwaters. Water quality of headwaters is further characterized by low nutrient concentrations.

Severe defoliation by gypsy moth larvae could affect the physical, chemical, and biological characteristics of headwater streams in a number of ways. Defoliation by gypsy moth larvae is likely to decrease the quantity of CPOM entering streams. The success of

the macroinvertebrates that depend upon this material for food (shredders) could be reduced. Tree mortality and reduced regrowth may also reduce the food quality of the CPOM. Leaves of different tree species vary in nutritive quality, and changes in relative species composition of leaf material composing detritus inputs have been shown to alter the success of shredders (Smock and MacGregor 1988, Cummins et al. 1989, Stout et al. 1993). Several tree species have been found to respond to intensive defoliation by increasing the concentration of defensive chemicals and decreasing the carbohydrate concentration of their leaves to the extent that growth and reproduction of terrestrial insects are reduced (Valentine et al. 1983, Neuvonen and Haukioja 1984, Rossiter et al. 1988). Both of these changes could also lower the quality of CPOM entering the water and reduce the success of shredders. Furthermore, the timing of the CPOM inputs could be changed to the disadvantage of shredders. An autumn pulse of CPOM could be replaced by a late spring pulse, as gypsy moth larvae drop uneaten leaf fragments (orts) and damaged leaves fall off the branches. The life histories of most shredders in headwater streams are adapted so that a period of rapid growth follows the large detritus inputs in autumn (Cummins 1989). While a reduction in the amount of autumn CPOM could decrease the success of shredders, the magnitude of impact may be greatly reduced if their life histories are sufficiently flexible to allow them to utilize the spring CPOM.

Feeding gypsy moth larvae produce large amounts of frass (Leibhold and Elkinton 1987), which falls into streams when riparian canopies are being defoliated. Gypsy moth frass could increase the quantity of FPOM in headwater streams, thereby enhancing the success of macroinvertebrates that consume this material (collectors) in defoliated streams.

Defoliation by gypsy moth larvae would increase the amount of sunlight reaching the surface of the water, which could lead to an increase in the biomass of periphyton. This event could be enhanced by an increase in nutrients, especially nitrate, that might enter the water from gypsy moth frass, either by dropping directly into the water or by leaching from the surrounding watershed. Swank et al. (1981) showed that defoliation by an outbreak

population of fall cankerworm (*Alsophila pometaria* (Harris) (Lepidoptera: Geometridae)) increased nitrate export from a forest ecosystem and increased stream water nitrate concentration. Gypsy moth larvae caused changes in the dominant species and percent cover of macroalgae in a Rhode Island headwater stream by increasing the amount of solar radiation reaching the water surface (Sheath et al. 1986). Normally, macroinvertebrates that feed on periphyton (scrapers) are not very abundant in headwater streams, however, increased quantity or quality of periphyton as a result of the riparian canopy being defoliated by gypsy moth larvae could increase the success of scrapers.

Water temperatures could be raised because of more solar radiation reaching the surface and increased turbidity to absorb the heat. The macroinvertebrates that occur in headwater streams are physiologically adapted for consistent cool temperatures (cold stenotherms) and, therefore, could be less successful if water temperature rises.

These changes in the stream environment may cause changes in both benthic macroinvertebrate community structure and function. Different taxa may respond to changes in their environment by expressing different rates of survival, or voltinism than populations in undefoliated streams. These changes could result in changes in the relative species composition of benthic communities and ultimately in the addition or loss of species in defoliated streams (e.g., Kobuszewski and Perry 1993). Some changes may alter the success of entire functional feeding groups of organisms, altering energy flow pathways in defoliated streams (e.g., quantity, quality, or timing of CPOM could affect shredder-detritivores). Evidence of such functional changes may be manifested by more discrete community changes than those altering community structure, and may result in different rates of growth, production, or biomass of organisms in defoliated streams.

The purpose of this study was to determine the short-term effects of defoliation by gypsy moth larvae on the macroinvertebrates of headwater streams in Shenandoah National Park, Virginia. This study was initiated by the National Park Service to enable resource managers to make informed pest management decisions that will minimize

adverse impacts to aquatic resources. Although the study was conducted only in Shenandoah National Park, the results should apply to most Appalachian headwater streams. Specific objectives and hypotheses were as follows:

I: Determine the effects of defoliation by gypsy moth larvae on water quality of Appalachian headwater streams. H_{01}: Riparian defoliation by gypsy moth larvae has no effect on the water quality of headwater streams.

II: Determine the effects of defoliation by gypsy moth larvae on benthic community structure of Appalachian headwater streams. H_{02}: Riparian defoliation by gypsy moth larvae has no effect on the structure of benthic communities in headwater streams.

III: Determine the effects of defoliation by gypsy moth larvae on function of macroinvertebrates in Appalachian headwater streams. H_{03}: Riparian defoliation by gypsy moth larvae has no effect on the secondary production or growth of macroinvertebrates occupying different functional roles in headwater streams.

These objectives are addressed in separate chapters of this thesis.

Experimental Design

The design of this study was to use individual streams as replicates to avoid problems of pseudoreplication (Hurlbert 1984). With the assistance of National Park Service personnel, I conducted egg-mass surveys of riparian areas in February 1991 to select six streams as study sites. I selected three streams that were likely to have their riparian canopy heavily defoliated by gypsy moth larvae in the spring of 1991 (defoliated treatment), and I selected three other streams that would probably have their riparian canopies remain intact (reference treatment). The study's duration was 1 yr with different sampling frequency for each type of data collected (Table 0.1).

Study Sites

My study sites were first and second-order streams along the east slope of the Blue Ridge mountains in Shenandoah National Park. Appalachian headwater streams generally conform to the typical headwater streams described by the River Continuum Concept (Vannote et al. 1980). The forests of Shenandoah National Park are deciduous and comprised mainly of oak (*Quercus* spp.) species (Smith and Torbert 1990). The streams selected as study sites were heavily shaded by deciduous tree species (primarily *Quercus* spp., *Liriodendron tulipifera*, *Betula* spp, *Acer* spp, and *Tilia americana*). The land that now comprises Shenandoah National Park was logged extensively before gaining national-park status in 1935, but has remained undisturbed by the timber industry since . All of the streams selected as study sites had no previous defoliation of their riparian canopies by gypsy moth larvae, although most had some prior defoliation elsewhere in their watersheds (Table 0.2). While there were some differences size, geology, and elevation (Table 0.3), the study sites were as similar as possible without selecting streams that had a history of previous riparian defoliation by gypsy moth larvae.

Table 0.1. Sampling frequency for duration of study by parameter. The values are expressed as number of times each site was sampled each month. These values do not include sub-samples or replicates collected at each site.(*pH was measured once in April 1992)

Month	Terrestrial Measures	Physical / Chemical Measurements	Benthic Macroinvertebrates
March 1991	0	1	1
April	4	2	2
May	4	2	2
June	4	2	2
July	4	2	2
August	2	2	2
September	2	2	2
October	2	2	2
November	1	1	1
December	1	1	1
January 1992	1	1	1
February	1	1	1
March	1	1	1
*April		1	

Table 0.2. Defoliation histories of study site watersheds according to National Park Service Records. This table expresses the percent of the watershed draining through study sites that was defoliated.

YEAR	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
1987	0	0	1.5%	0	0	0
1988	0	0	51%	0	0	0
1989	0	48%	7.4%	0	0	0
1990	59%	2.6%	18%	38%	22%	0
1991	27%	0	0	78%	70%	39%

Table 0.3. Physical characteristics of study sites. Drainage area was deterimine by NPS personnel using GIS. Geologic formations were reported by Gathright (1976). Elevation and direction of flow were determined on USGS quad maps

YEAR	**South River**	**White Oak**	**Piney River**	**North Fork**	**Shop Run**	**South Fork**
Treatment	Reference	Reference	Reference	Defoliated	Defoliated	Defoliated
Drainage Area	364 ha	231 ha	276 ha	172 ha	75 ha	302 ha
Geologic formation	Catoctin	Catoctin	Catoctin	Hamton & Weaverton	Catoctin & Weaverton	Catoctin & Weaverton
Elevation	2400 ft	2800 ft	2500 ft	1800 ft	1600 ft	1800 ft
Direction of flow	NE	E	E	E	E	N

PART 1: SHORT-TERM EFFECTS OF DEFOLIATION BY GYPSY MOTH LARVAE ON THE WATER QUALITY OF APPALACHIAN HEADWATER STREAMS IN VIRGINIA

INTRODUCTION

This part of my thesis examines the effects of riparian defoliation by gypsy moth larvae on water chemistry, detritus inputs, and other physical parameters of headwater streams. The purpose of this study is to document changes in the stream environment that could explain any observed differences in benthic community structure or production in Parts 1 and 2. It addresses the first objective of the thesis and tests the null hypothesis: H_0: Defoliation by gypsy moth larvae does not affect water quality of headwater streams.

METHODS

Terrestrial Environment

I quantified several aspects of the terrestrial environment that would be affected by the feeding of gypsy moth larvae and might account for changes in water quality. I used a spherical densiometer (Lemmon 1956) to describe the intensity of defoliation occurring at each site as percent open canopy. Two observers recorded four densiometer readings at each of three locations at each study site (24 readings per site). This was done weekly from April to August, every 2 wk from August to November, and once in December 1991 (Table 1.1).

To follow changes in detritus inputs from the riparian canopy to the streams, I deployed three "funnel-type" frass traps at each site. These traps were similar to those described by Leibhold and Elkinton (1988), except that my traps sampled a larger area (funnel size 203 mm diameter), and the nylon mesh at the bottom of the trap was 100 μm. In April 1991, I suspended the traps about 2 to 3 m above each stream with three nylon cords that were tied to trees adjacent to streams. I collected the contents of frass traps weekly until activity of gypsy moths (both larvae and adults) ended in August (Table 1.1).

Table 1.1. Summary of sampling frequency by month and parameter. This table indicates the number of times (days) data was collected from each study site. Some parameters were measured more than once per sampling period (see methods).

Month	Defoliation	Detritus	Water Chem./Quality
March 1991	0	0	1
April	4	4	2
May	4	4	2
June	4	4	2
July	4	4	2
August	2	2	2
September	2	2	2
October	2	2	2
November	1	1	2
December	1	1	1
January 1992	0	0	1
February	0	0	1
March	0	0	1

The material collected in the frass traps was sorted into two categories, *frass* and *orts*, and dried in the lab. Herbivore-caused green litter fall has been collectively referred to as greenfall, and further divided into the classes "mined," "petiole-damaged," "clipped," and "orts" (Risley and Crossley 1988). Orts are leaf fragments that fall out of insects' mouths before that are macerated. I observed two constituents of greenfall, clipped leaves and orts. Orts were the most numerous and I refer to clipped leaves and orts collectively as orts in this study because they would be used the same in aquatic trophic dynamics. I used a Mettler AE 163 analytical balance to determine the dry mass of frass and orts to the nearest 0.1 mg. Other material collected by frass traps, primarily insects and spiders, was discarded.

Because frass collected in frass traps was potentially exposed to precipitation and leaching between periods of frass collection, I collected fresh frass as it fell for chemical analysis. Since this had to be done on a later date (June 23, 1992), another location that was being defoliated for the first time was chosen, because leaf chemistry changes after initial defoliation (Valentine et al. 1983, Rossiter et al. 1988). I placed 20, 19 x 30.5-cm enamel sorting pans, and a 2 x 2-m canvas on the ground at the leading edge of a first-year gypsy moth infestation near St. Marys River (FR 41, Augusta County, Virginia). I collected frass immediately as it fell onto the trays, canvas, and surface of my vehicle. I dried the frass in a Fisher model 55G lab oven at 65° C for 24 h and stored it in a desiccator to prevent the growth of mold. Several months later the National Park Service forwarded the "fresh" sample and a frass trap sample to Galbraith Laboratories, Inc. (Knoxville, TN 37950) for analysis of percent carbon, nitrogen, hydrogen, and ammonia (as nitrogen). Ammonia concentrations are reflective of ammonium salts because ammonia would have evaporated in the drying process.

In September, I replaced the frass traps with leaf-litter traps to compare the amount of autumn leaves falling into the streams. The leaf-litter traps were composed of 1-cm mesh hardware cloth arranged as an inverted tetrahedron with a sample area of 0.25 m^2

(Fig. 1.1). I suspended them at the same height and locations as the frass traps and removed the accumulated leaf material every 2 wk from September to November and once in December (Table 1.1). I allowed the leaf-litter samples to air dry in paper bags in the laboratory and kept them until they could be weighed.

Aquatic Environment

I used TempMentor™ thermographs (Ryan® Instruments, Redmond, Washington) to record the water temperature every 2 h in each stream. The thermographs were placed in pools where running water entered to ensure submergence during low flow and representative stream temperature records. To prevent vandalism, I placed the thermographs in 18-cm diameter steel well casing, which was cut into 50-cm lengths. The well casing was secured to the stream bottom with a 0.75 m long, 1.9-cm diameter concrete reinforcing bar (Fig. 1.2). In addition, the well casing was fastened to a tree with a 0.6-cm diameter steel cable to prevent loss during a flood. I downloaded the temperature data in the field with a lap-top computer. The 12 temperature measurements recorded each day were used to calculate daily mean temperature for each site for the entire year of the study.

I measured stream discharge by the six-tenths depth method (Buchanan and Somers 1969). Current velocity was measured every 10 cm along a transect with a Model 2000 digital portable flow meter (Marsh-McBirney Inc., Frederick, Maryland).

Water chemistry parameters that I measured included: pH, dissolved oxygen, alkalinity, hardness, conductivity, and nutrients. These were measured once in March 1991, every 2 wk from April to November 1991, and monthly from December 1991 to March 1992 (Table 1.1). I measured most water chemistry parameters in the field. I used an Orion SA250 pH meter, calibrated with pH 4.0 and 7.0 buffers, to measure pH. I measured dissolved oxygen with the same meter and an Orion 97-08 dissolved oxygen probe. I determined dissolved oxygen by the Winkler method when the meter or probe was not

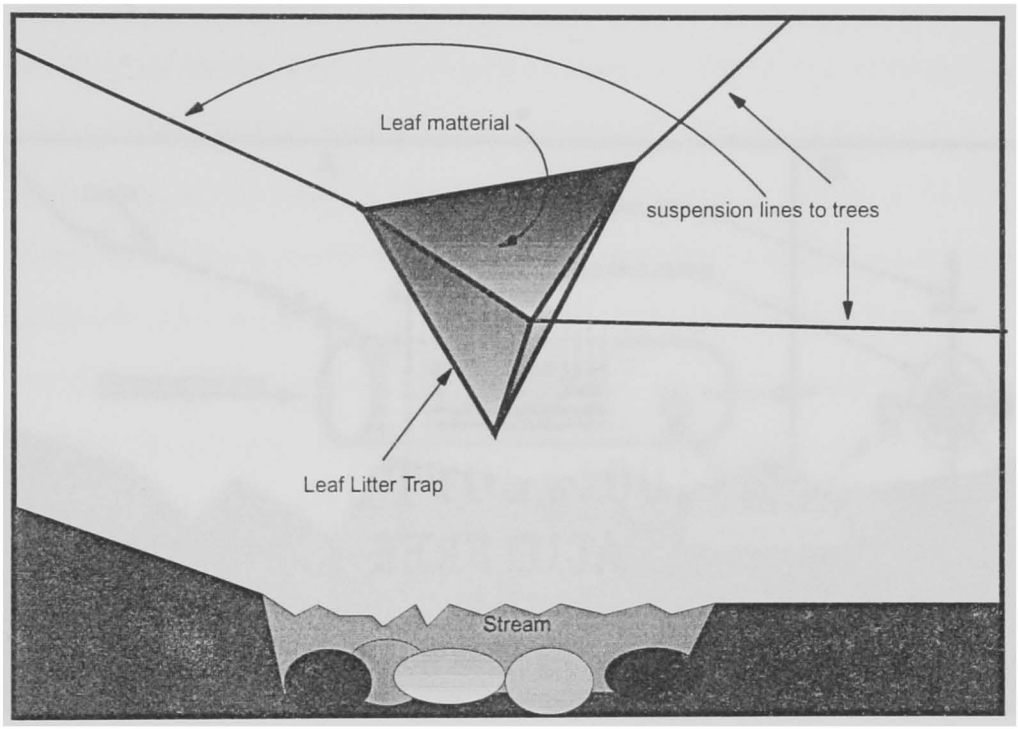


Fig. 1.1. Leaf-Litter Trap. Three leaf-litter traps were deployed at each site in September to quantify autumn coarse detritus inputs.

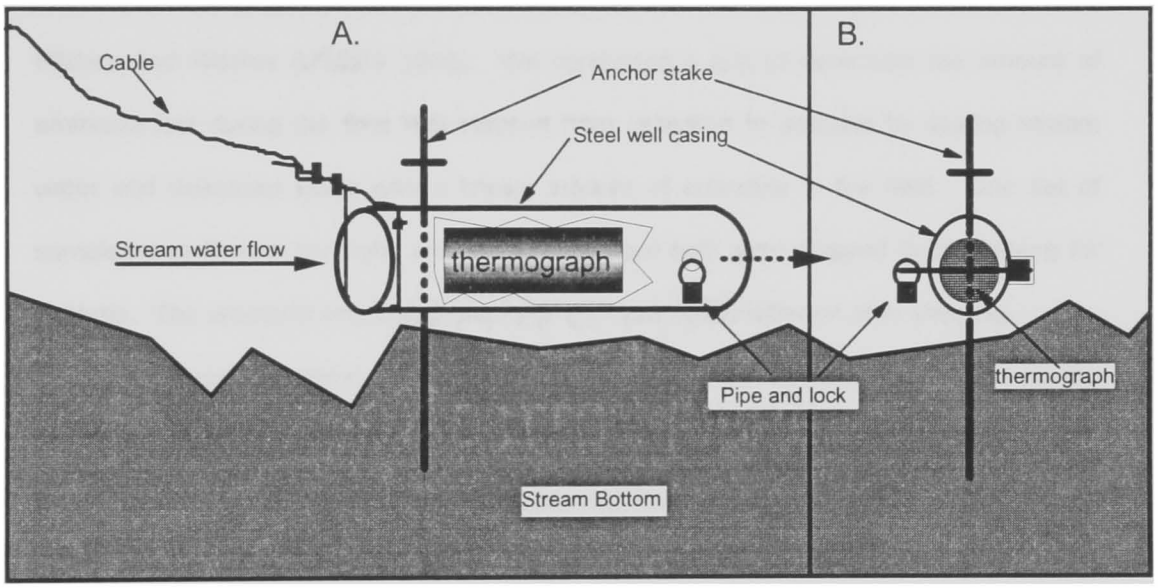


Fig. 1.2. Thermograph Deployment. This diagram illustrates the vandal-resistant deployment of thermographs at study sites from lateral (A.) and cross-sectional views (B (from the down-stream end))

functioning properly (USEPA 1983 (Method 360.2)). I collected 250 ml of stream water to determine alkalinity (mg/L $CaCO_3$) by titration with 0.02 *N* H_2SO_4, in accordance with the EPA's two-endpoint method (USEPA 1983 (Method 310.1)). I measured hardness (mg/L $CaCO_3$) with a Hach HA-71A kit. I measured conductivity with a YSI model 33 meter.

I collected 500 ml of water in acid-washed Nalgene® bottles for laboratory analysis of nutrient concentrations. The samples were kept on ice after collection and analyzed within 48 h. The analyses of nitrate, nitrite, ammonia, orthophosphate, and total phosphorous concentrations were done by persons in the Department of Biology at Virginia Tech. Nutrient analyses were done in accordance with *Methods for Chemical Analysis of Waters and Wastes* (USEPA 1983). We conducted a test to determine the amount of ammonia lost during the time that elapsed from collection to analysis by spiking stream water and deionized water with a known amount of ammonia in the field. One set of samples was fixed in the field, another was not, and both were shipped to Blacksburg for analysis. The ammonia concentrations were not significantly different after shipping.

To measure seston, four 1-L Nalgene® bottles were filled in riffles, stored on ice, and analyzed in the laboratory within 2 d. Two of these water samples were collected in translucent bottles and were used to determine the mass of organic seston (as ash-free dry mass, AFDM) by the same procedure as periphyton AFDM (see below). The other two water samples were collected in dark bottles and were used to determine the chlorophyll *a* concentration of seston by the same procedure as periphyton (see below).

The natural periphyton assemblage was sampled with a bar-clamp sampler that confined 10.2 cm^2 of rock surface (Hornick 1978). A sample was taken from each of six cobble-sized rocks at each study site . The surface of the rock within the sampler was scrubbed with a metal brush, then deionized water was added to the sampler. The dislodged material was removed from the sampler with a glass pipette and placed in a 60-ml dark Nalgene® bottle. The scrub and rinse cycle was repeated three times unless

periphyton could be seen in the sample area. If so, the process was repeated. Samples were put on ice immediately after collection and transported to the laboratory for analysis.

I filtered three periphyton samples through pre-ashed and tared Gelman type A/E glass fiber filters to determine periphyton biomass. The samples were dried in a Fisher Model 55G oven at 65° C for 24 h and allowed to cool in a desiccator for 1 h before being weighed to the nearest 0.1 mg with a Mettler AE 163 analytical balance. I ashed the samples at 500° C for 1 h in Fisher Model 186 ISOTEMP® muffle furnace. After ashing, I dehydrated the sample with deionized water to the point of run-off, then dried and weighed the sample as above. This procedure calculated the mass of organic material contained in the periphyton (as ash-free dry mass, AFDM). AFDM measurements include living and dead periphyton, associated organic sediment, and other epilithic biota (e.g., bacteria, fungi, microscopic invertebrates).

The other three periphyton samples were used to determine the chlorophyll *a* concentration, which measures the amount of living periphyton. They were filtered on Gelman type A/E glass fiber filters. The filter retaining the sample was folded in half with the sample on the inside of the fold. I placed the filters in 2-oz WhirlPacks® (Nasco Inc.) and froze them until they could be analyzed which was always within 3 wk. I determined chlorophyll *a* concentration by the spectrophotometric method described in *Standard Methods for the Examination of Water and Wastewater* (Clesceri et al. 1989.(section 10200-H.2)). I used the ratio of periphyton AFDM to chlorophyll *a* to determine the Autotrophic Index (AI) as an indicator of periphyton trophic quality (Clesceri et al. 1989, (section 10300-C.6)).

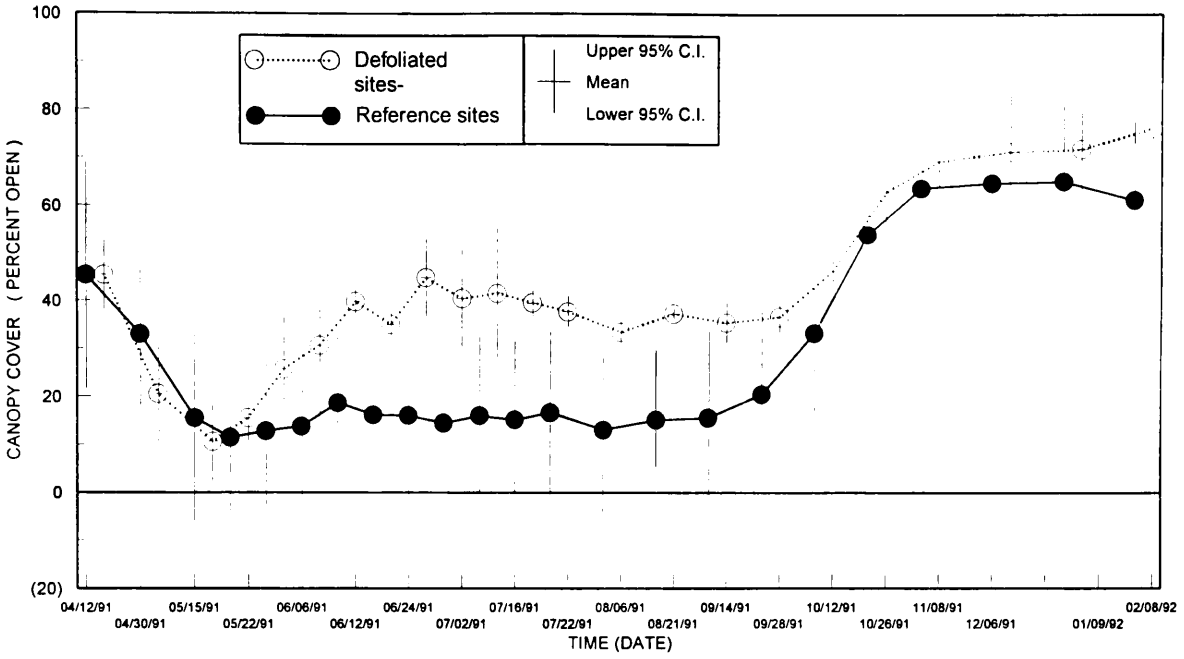
RESULTS

Terrestrial Environment

Eclosion of gypsy moth larvae began in mid-April, and defoliation ensued according to the study design (Fig. 1.3). While only about 40% of the canopy over the impacted streams was open to solar radiation, this corresponded to complete or nearly complete defoliation of all palatable trees in the area. Only tulip poplar (*Liriodendron tulipifera*), hemlock (*Tsuga canadensis*) , and striped maple (*Acer pensylvanicum*) kept their leaves all summer long. At the South Fork of the Moormans River, white pines (*Pinus strobus*) were defoliated. All gypsy moth larvae pupated by mid-June, and all adult activity ceased by mid-July. Only partial regrowth of the canopy occurred. Many oaks (*Quercus* spp.) did not produce a second flush of leaves, and those that did produced only small leathery leaves. Defoliated conifers did not produce regrowth. Only a few individual frass-pellets and orts were collected at the reference sites. The riparian canopy of reference streams remained intact for the duration of the 1991 growing season.

Large amounts of frass fell into the impacted streams during the period that gypsy moth larvae were feeding. The mean annual frass fall at the impacted sites was 131 g/m^2, compared to 13 g $/m^2$ at the reference sites (Fig. 1.4). Fresh frass was composed of 1.35% nitrogen and 45.11% carbon, which was similar in composition to frass collected in frass traps (Table 1.2). This represents a nitrogen load of about 1.77 g/m^2 in impacted streams compared to 0.17 g/m^2 in reference streams. The actual nitrogen input to defoliated streams was probably much higher than these values, because ammonia left the frass samples before they were analyzed and because orts and bodies of gypsy moth larvae were not included in the frass analyses. Large amounts of orts also fell into the impacted streams during gypsy moth feeding in late spring and continued to fall after the larvae pupated due to abscission of partially eaten leaves. The magnitude of combined frass and orts falling into impacted streams in late spring was comparable to the amount

(A) Mean Defoliation at Treatments with 95 % Confidence Interval



(B) Defoliation at Study Sites

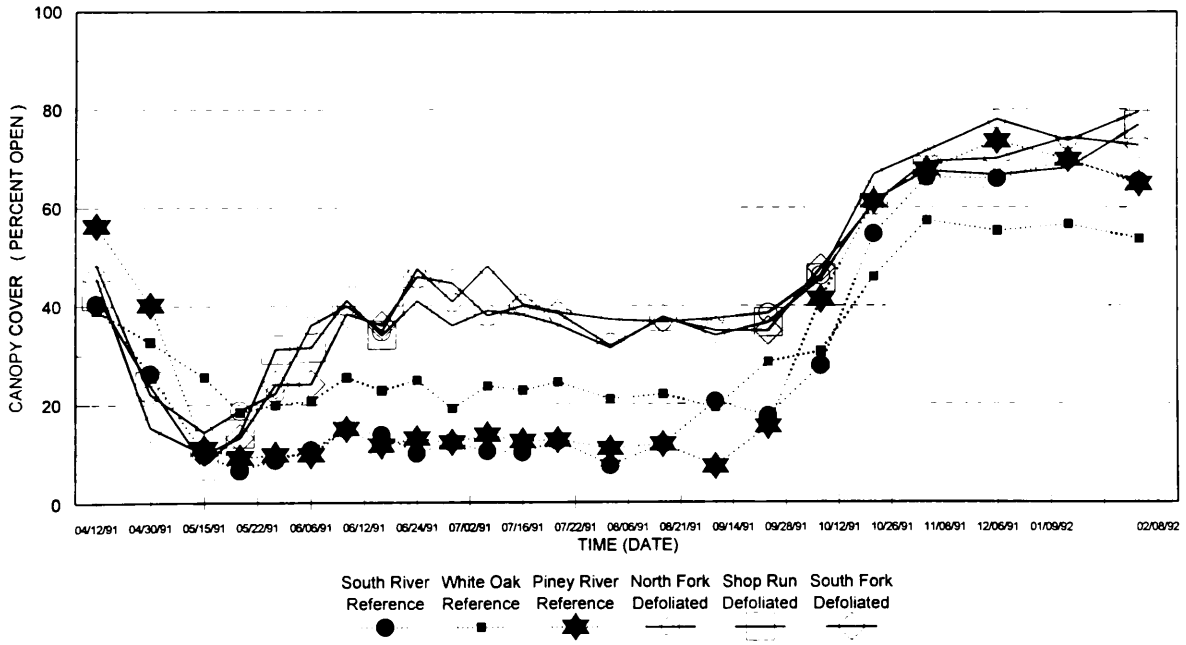
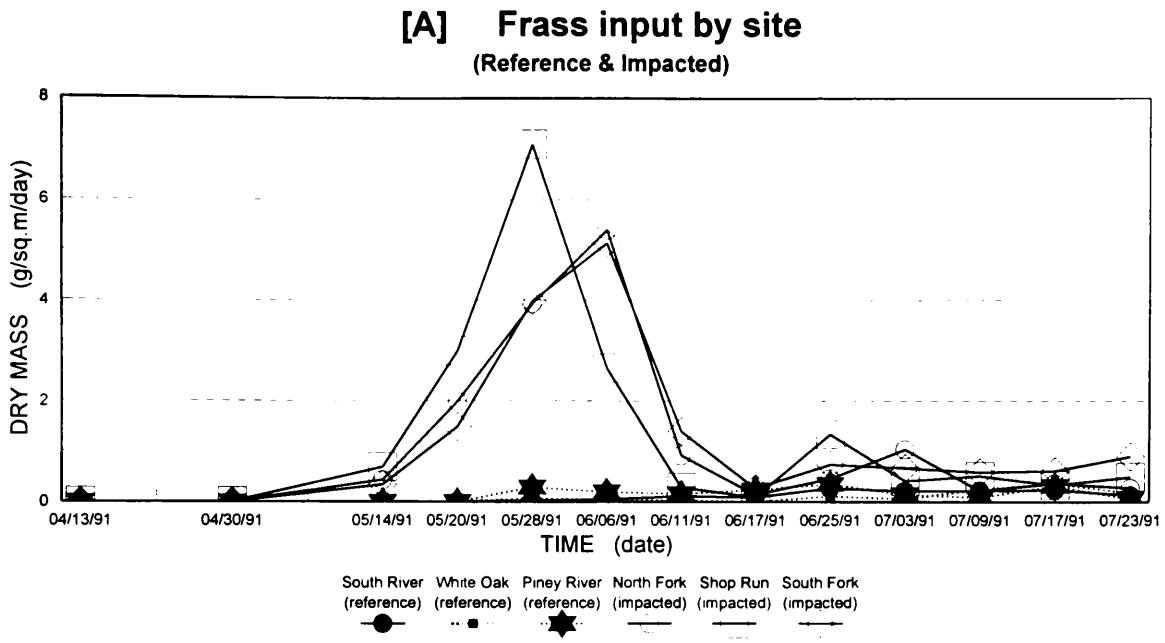


Fig. 1.3. Defoliation of study sites. The mean canopy cover by treatment is expressed with 95% confidence intervals (A). Defoliation at individual study sites is also illustrated (B).



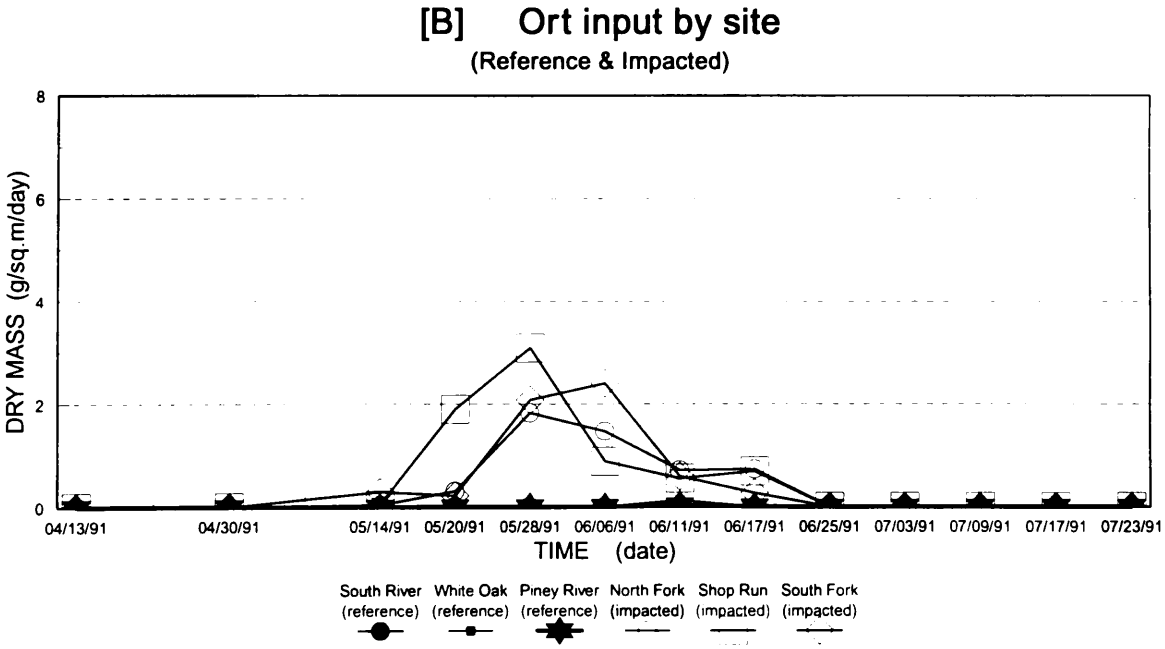


Fig. 1.4. Detritus collected by frass traps. Frass (A) and ort (B) input at individual study sites is expressed as mean daily input per square meter in grams.

Table 1.2. Chemical Composition of frass. This table displays the percent composition (by mass) of gypsy moth frass. The St. Marys River sample was collected as it fell, and the Shop Run sample was collected by a frass trap over a 1 wk period.

Sample	% Carbon	% Hydrogen	% Nitrogen	NH_4 - N
St. Marys 1992	45.11	5.96	1.35	0.32
Shop Run 1991	35.11	4.66	1.07	0.30

detritus entering reference streams in autumn and many green leaf packs were observed in impacted streams following defoliation. In autumn the amount of leaf material was significantly reduced in impacted streams (Fig. 1.5).

Aquatic Environment

Impacted streams had higher temperatures than reference streams before gypsy moth larvae hatched, and this trend continued throughout the year (Fig. 1.6). The temperature difference between treatments was often statistically significant (Fig. 1.7). This difference is probably evidence of some influence other than riparian defoliation (e.g. slope, orientation, etc.) gypsy moth feeding because temperatures were different before defoliation and during winter. There is a period of time accompanying defoliation when the impacted streams warmed faster than reference streams. This rate of temperature change is unlikely to stress cool stenotherms because its magnitude is less than summer temperatures in reference streams (Figs. 1.6, 1.7), but could influence life histories of aquatic insects as accumulated degree-days (Table 1.3).

No statistically significant change in discharge occurred after defoliation (Fig. 1.8a). The impacted sites exhibited a different trend than the reference sites during the period of low flow, but this trend was obscured by scale. When the annual discharge data are observed on a logarithmic scale (Fig. 1.8b) the impacted sites showed elevated discharge from June 24, 1991 until August 5, 1991. The elevated discharge was probably due to decreased transpiration in defoliated watersheds. The trend did not continue because drought conditions prevailed during late summer and fall 1991. The dry weather may have contributed to the sparse regrowth and mortality of the riparian canopy.

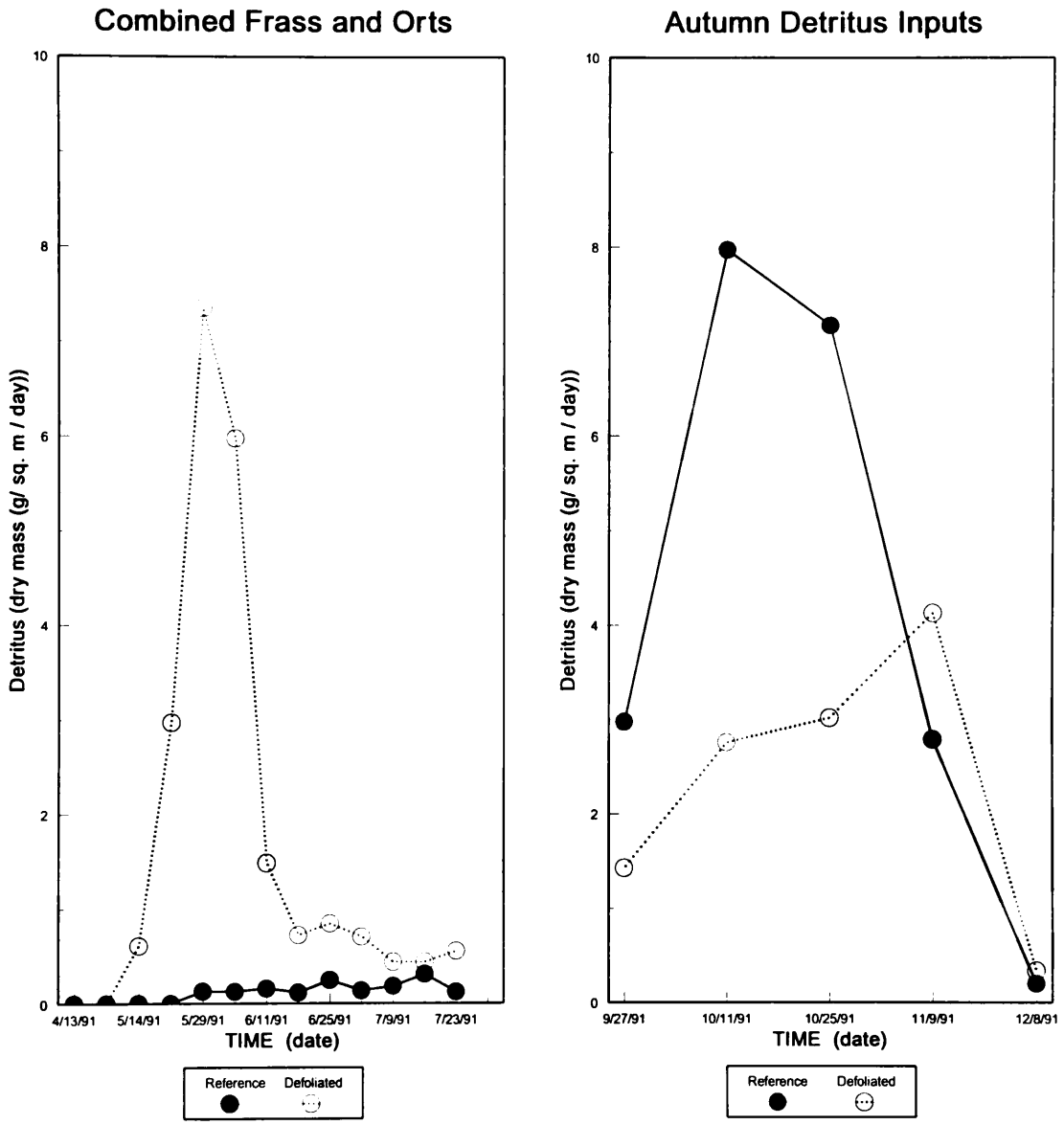


Fig. 1.5. Seasonal changes in the input of detritus at the study sites. Detritus inputs in the defoliated streams were larger than in reference streams in the spring (A), but smaller than reference streams in Autumn (B). The magnitude of peak frass and ort input in defoliated streams was comparable to the magnitude of peak leaf-fall at the reference sites.

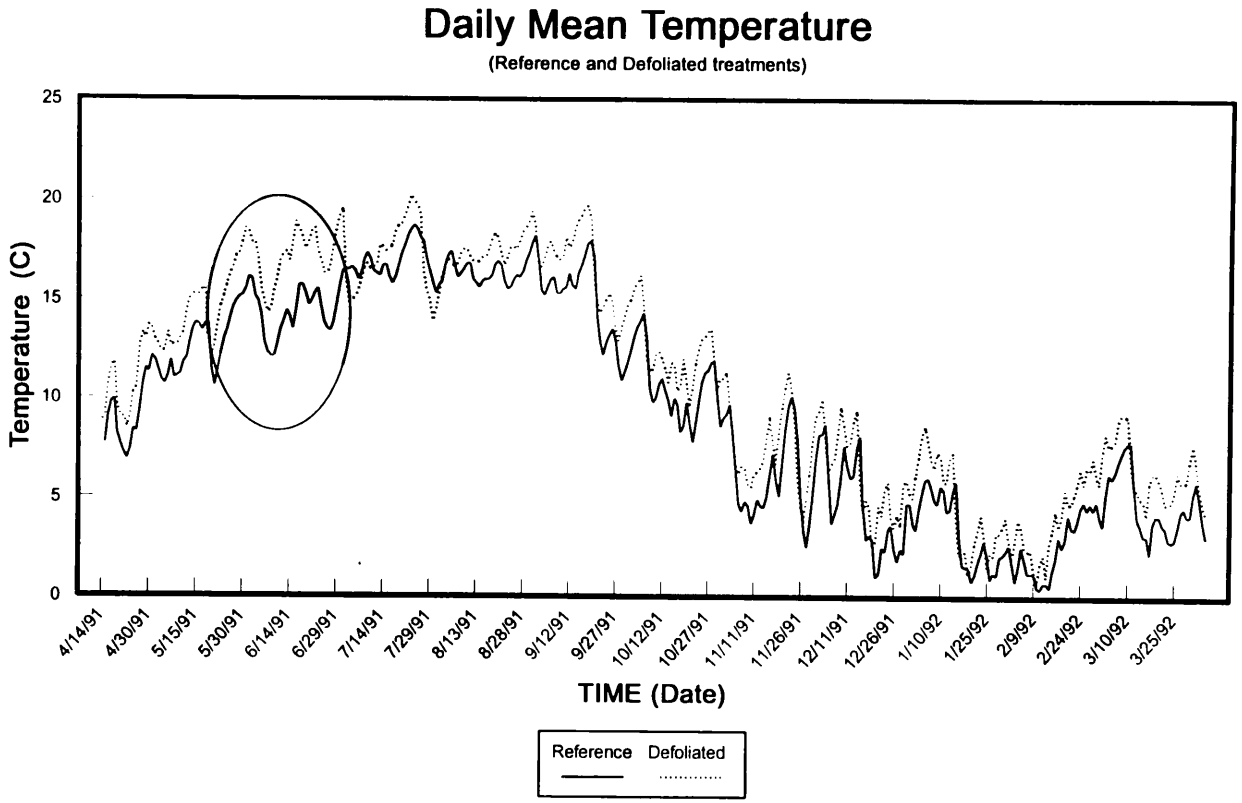


Fig. 1.6. Daily mean Temperature. This graph displays the daily mean temperature of the reference and defoliated treatments. The defoliated streams warmed at a greater rate (note the different slopes) during the period of time highlighted in the unshaded area. The daily mean temperature is calculuated from 12 measurements each day.

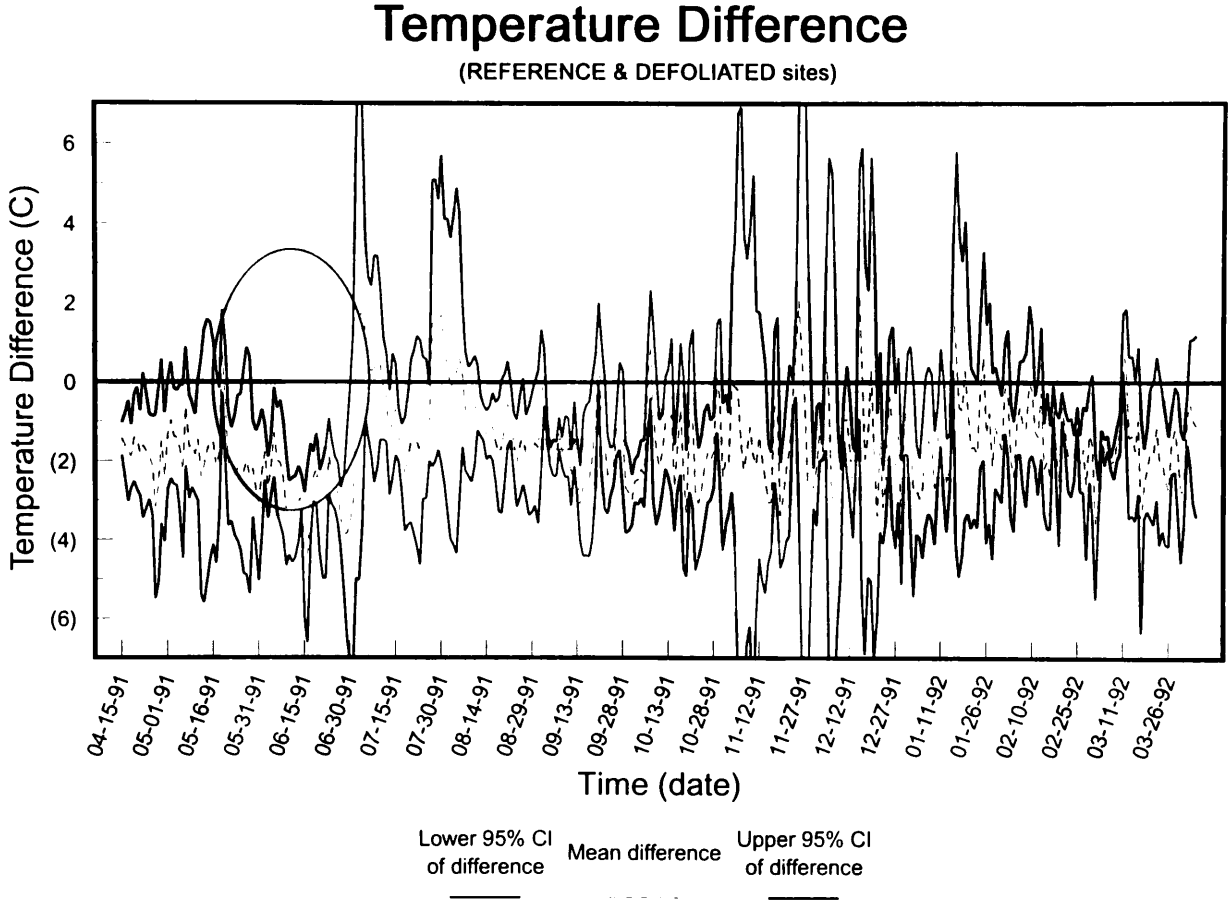
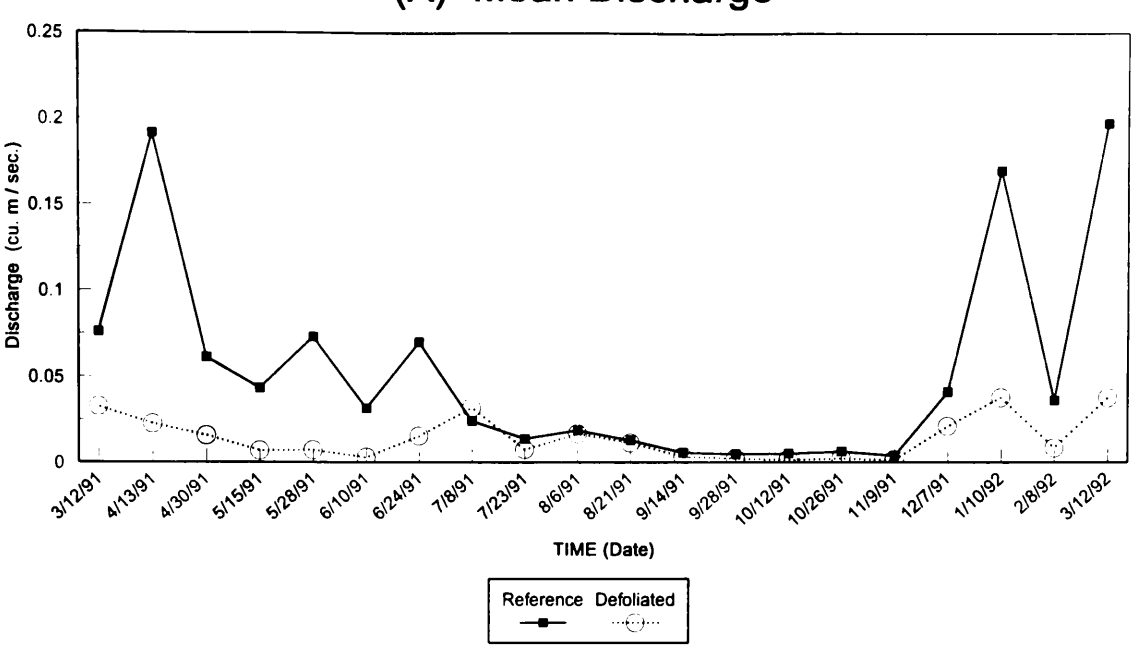


Fig. 1.7. Temperature difference. This graph displays the 95 % confidence interval for the mean temperature differenceof the study sites each day for the entire year. If the "X" axis (zero) is between the upper and lower confidence intervals, the temperatures of the treatments are NOT significantly different (i.e. the difference in treatment temperatures is not significantly different from zero) (Kleinbaum et al. 1988). Difference was calculated as reference - defoliated, so negative values indicate that the defoliated sites are warmer than the reference sites.



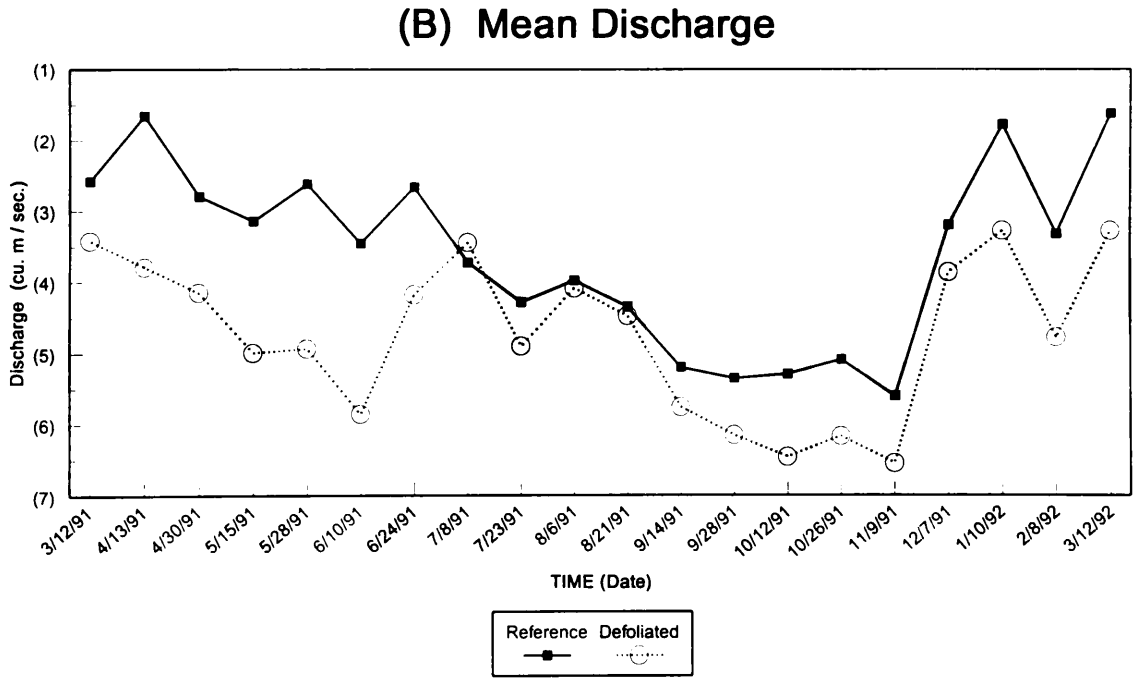


Fig. 1.8. Mean discharge at reference and defoliated treatments. Treatment mean discharge in Cubic meters per second is shown on both a linear (A) and logarithmic (base *e*) (B) scales.

Table 1.3. Temperature at individual study sites.

Site	Annual Mean Temperature	Maximum daily mean Temperature	Minimum daily mean temperature	Annual accumulated degree-days
South River	9.99	18	1.1	3546
White Oak	9.18	18.4	-0.1	3262
Piney River	9.83	19.4	0.2	3488
North Fork	11.18	20.6	0.4	3970
Shop Run	11.24	19.5	1.3	3991
South Fork	11.1	20.3	0.6	3942

I did not observe any significant changes in pH, dissolved oxygen, alkalinity, hardness, or conductivity associated with defoliation. Throughout the study two impacted streams, North Fork of the Moormans River and Shop Run, had lower conductivity, hardness, and alkalinity than all other sites. These values remained relatively constant all year, and most of the differences can be attributed to geology (Figs. 1.09 - 1.12). The alkalinity at Shop Run (defoliated) dropped markedly on one sample date (May 28; Fig. 1.11). A change of this magnitude should be accompanied by similar change in pH, but pH appeared normal at that time (Fig 1.9). On the day that water samples were collected, the pH meter was not operating properly, and the pH measurement had to be recorded 2 d later. These data suggest that any effects of gypsy moth larvae on the acid neutralizing capacity are ephemeral (Appendices 1.3, 1.5).

Nitrate concentrations were higher at reference streams before defoliation by gypsy moth larvae (Figs. 1.13, 1.14). The stream with the highest concentration of nitrate (South River, Reference) had a large stand of black locust (*Robinia pseudoacacia*) in the root nodules. Leaching of nitrate from black locusts and previous defoliation histories in reference watersheds may have elevated background nitrate concentrations making it difficult to compare absolute values of nitrate concentrations. The data are still useful for comparing annual trends in nitrate concentration. I did not observe a significant increase in nitrate concentration corresponding to peak frass fall. Rapid changes in nitrate concentrations may have been buffered by the growth of periphyton on the peritrophic membrane of frass particles. The general trend of nitrate observed in the reference streams was a decrease in concentration during spring and summer and an increase following autumn leaf fall. Nitrate concentrations in impacted streams did not follow this pattern and increased slightly after defoliation. These trends were similar to those observed in the stream water discharge data (Fig. 1.15). The only stream in the study with no previous defoliation in the watershed was South Fork of the Moormans River, which

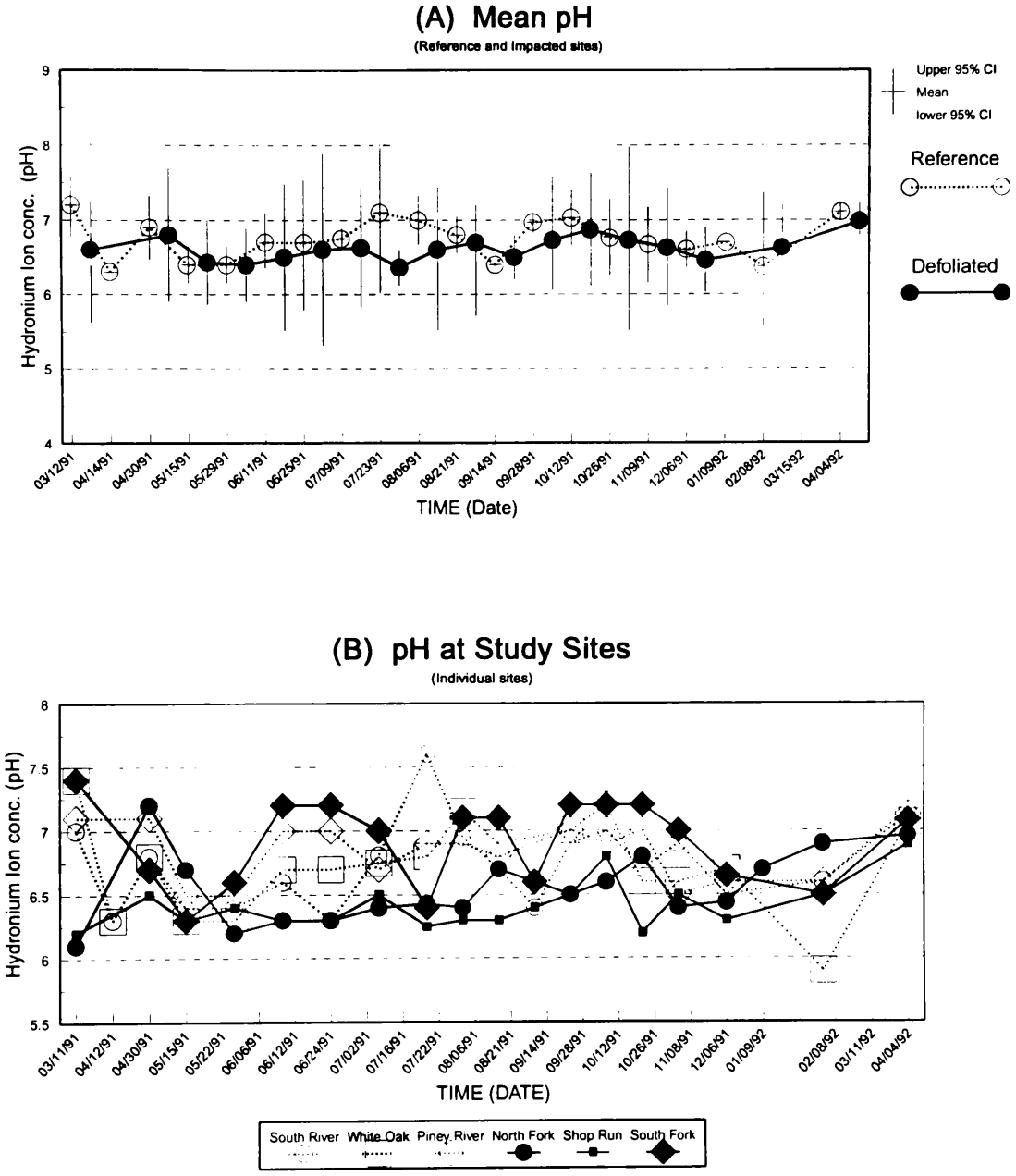
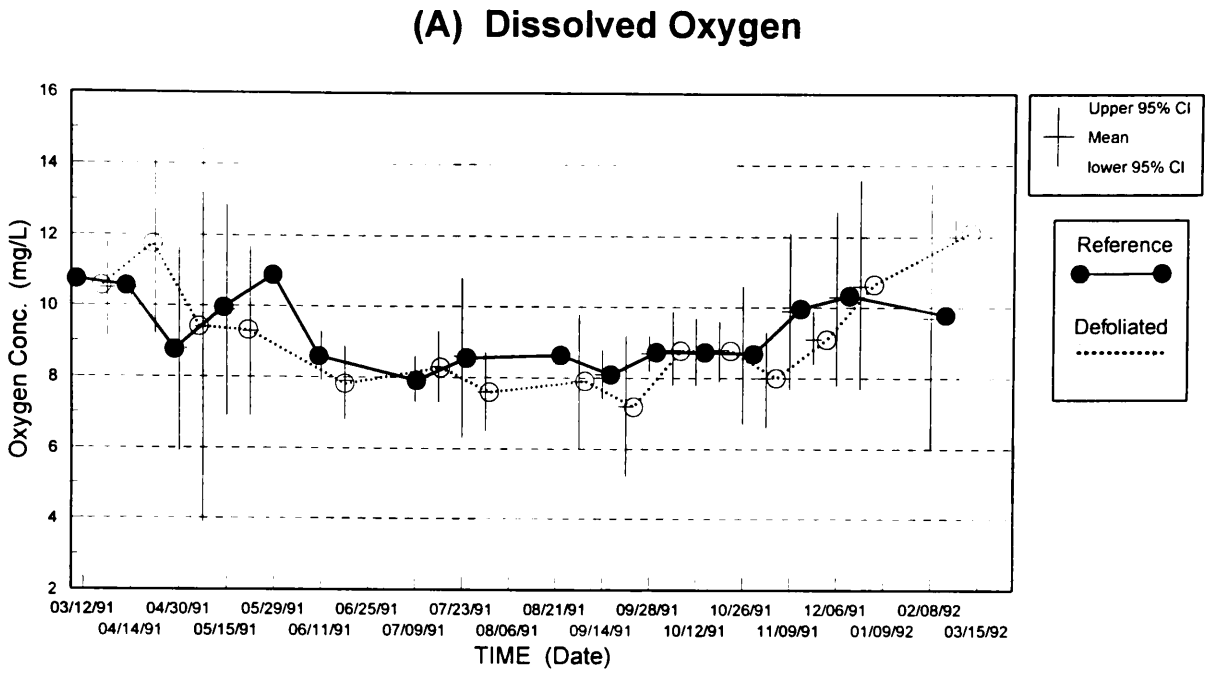


Fig. 1.9. Hydronium ion concentration. Hydronium ion concentration (pH) is expressed as treament means with 95 % confidence intervals (A) and as pH at individual study sites (B).



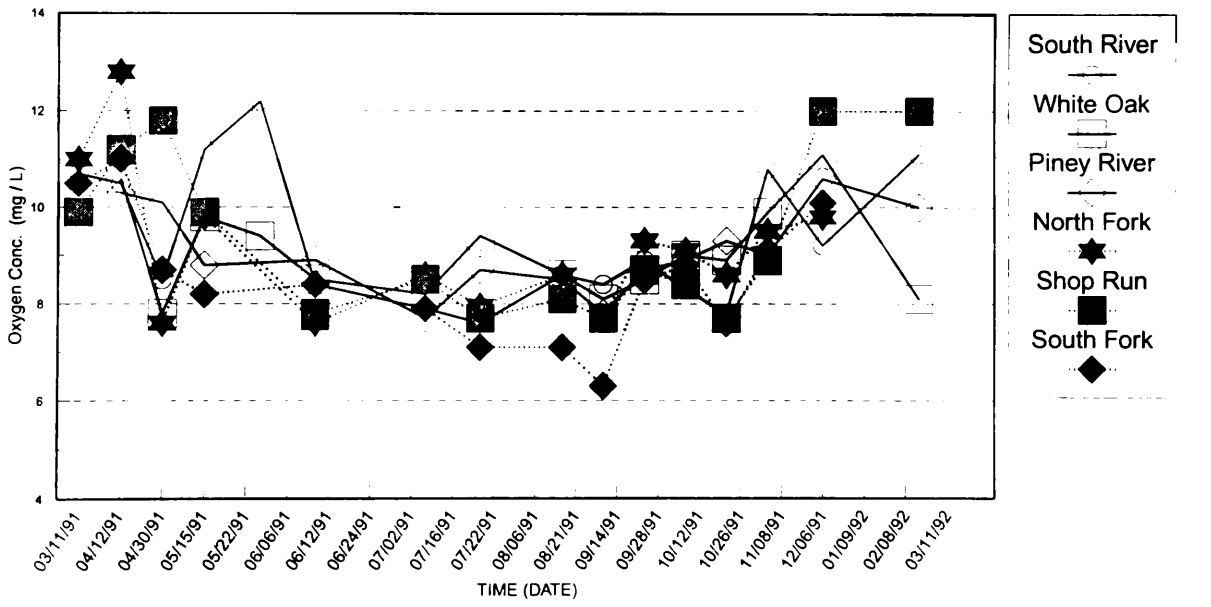


Fig. 1.10. Dissolved oxygen. Dissolved oxygen concentrations (mg/L) are expressed as treatment means with 95 % confidence interval (A), and as concentrations at individual study sites (B).

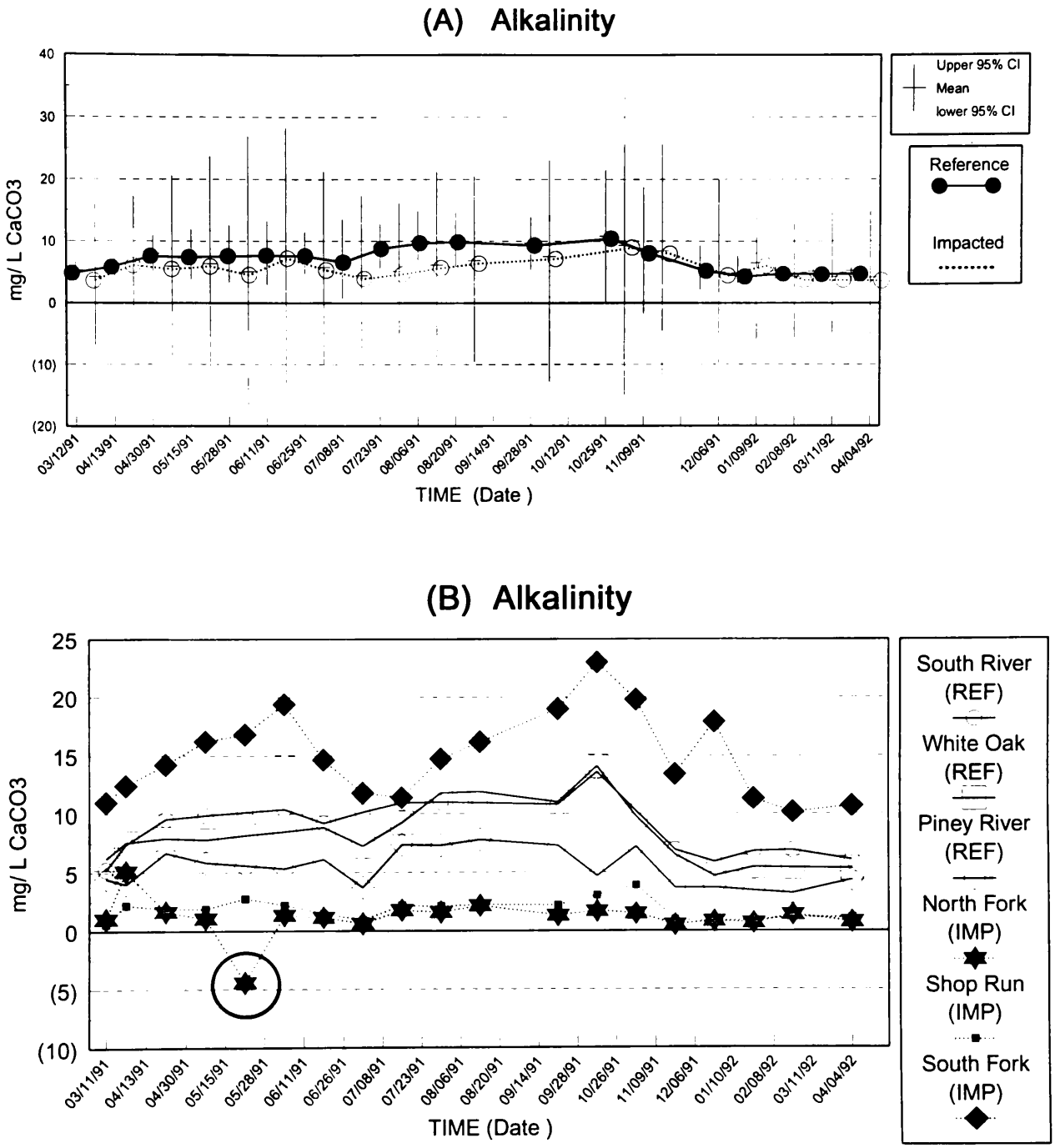
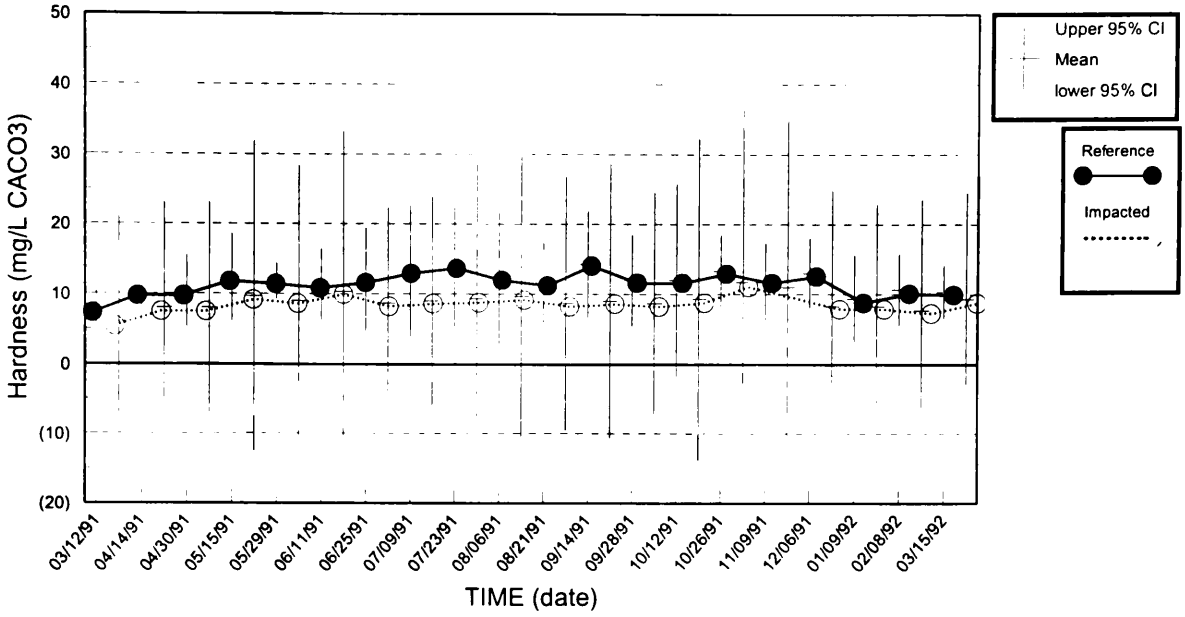


Fig. 1.11. Alkalinity. Alkalinity is expressed as treatment mean (mg / L CaCO3) with 95 % confidence interval (A), and alkalinity at individual study sites (B). The low alkalinity at shop run in May (circled value) was not accompanied by a depressed pH (Fig. 1.9) because pH was measured two days after alkalinity during that sampling period, suggesting that low alkalinity is a temporary phenomenon.

(A) Hardness



(B) CONDUCTIVITY

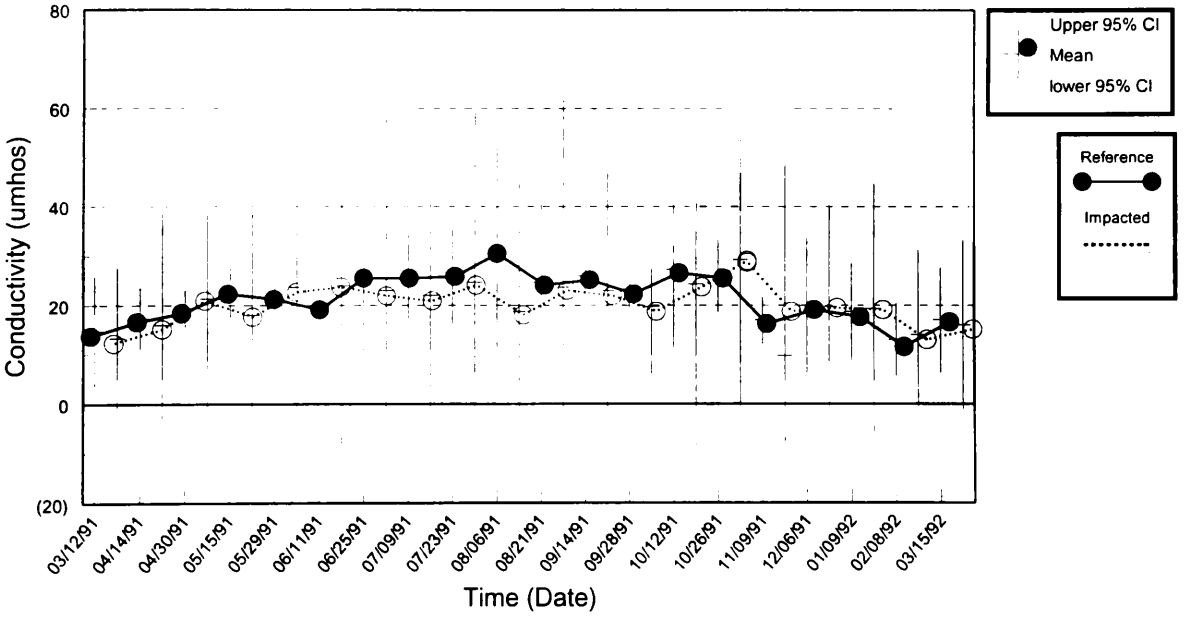


Fig. 1.12. Hardness and Conductivity. Hardness (A) (mg/L CaCO3) and conductivity (B) (μmhos) are expressed as treatment mean with a 95 % confidence intervals.

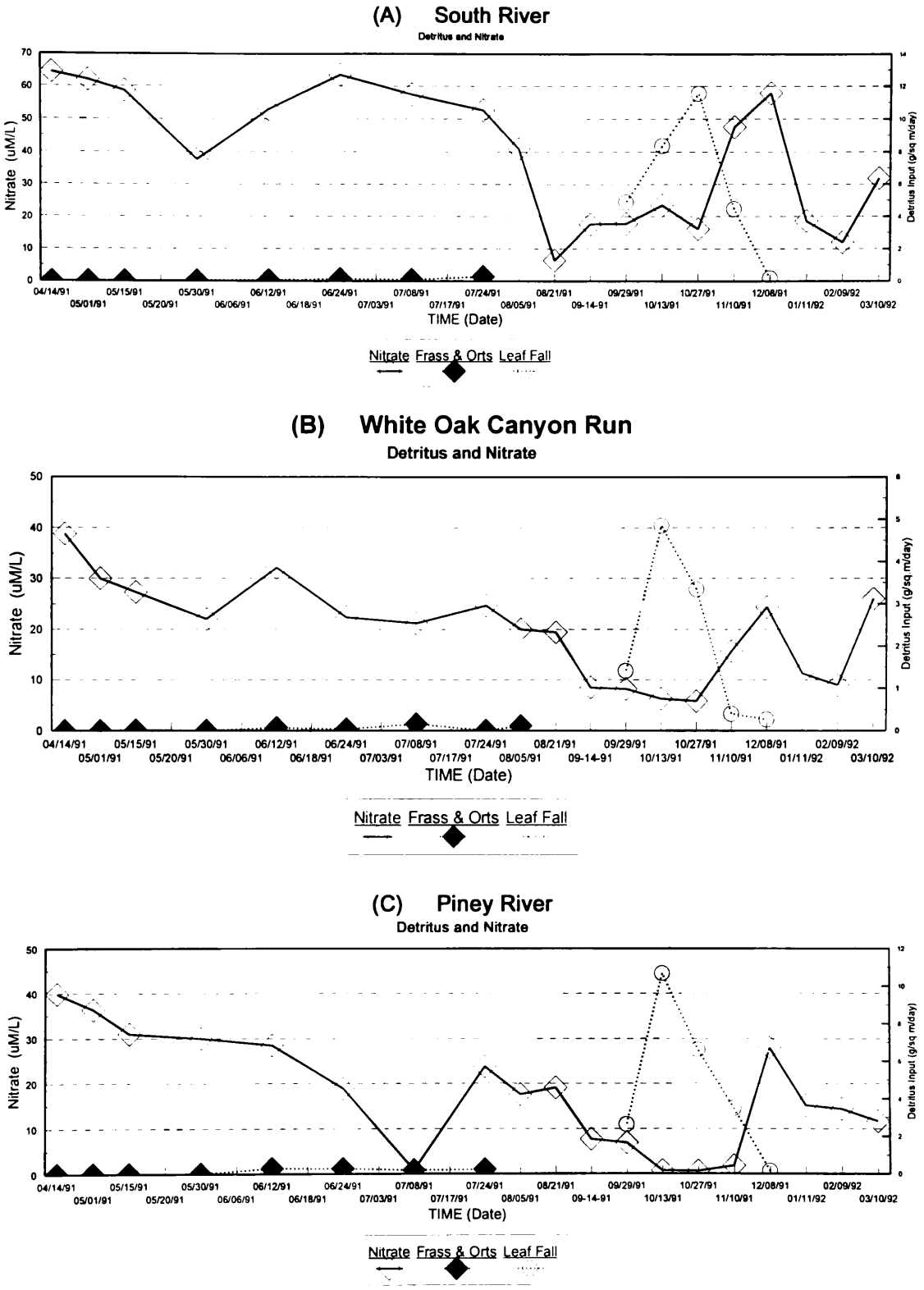


Fig. 1.13. Nitrate and detritus at reference sites. The nitrate concentrations (μM / L) at reference study sites with detritus inputs (g / sq.m / day). (A) South River. (B) White Oak Canyon Run, (C) Piney River.

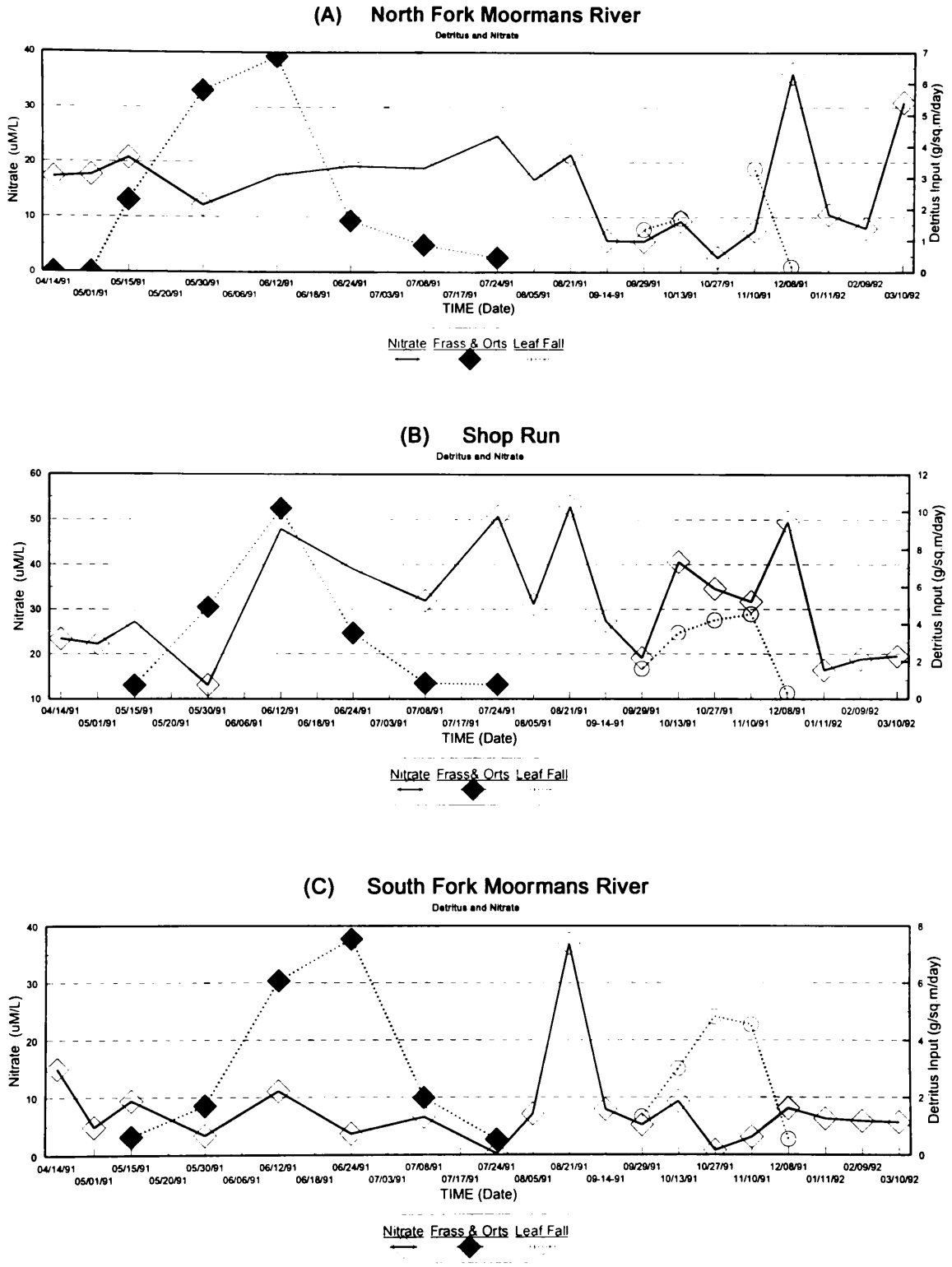
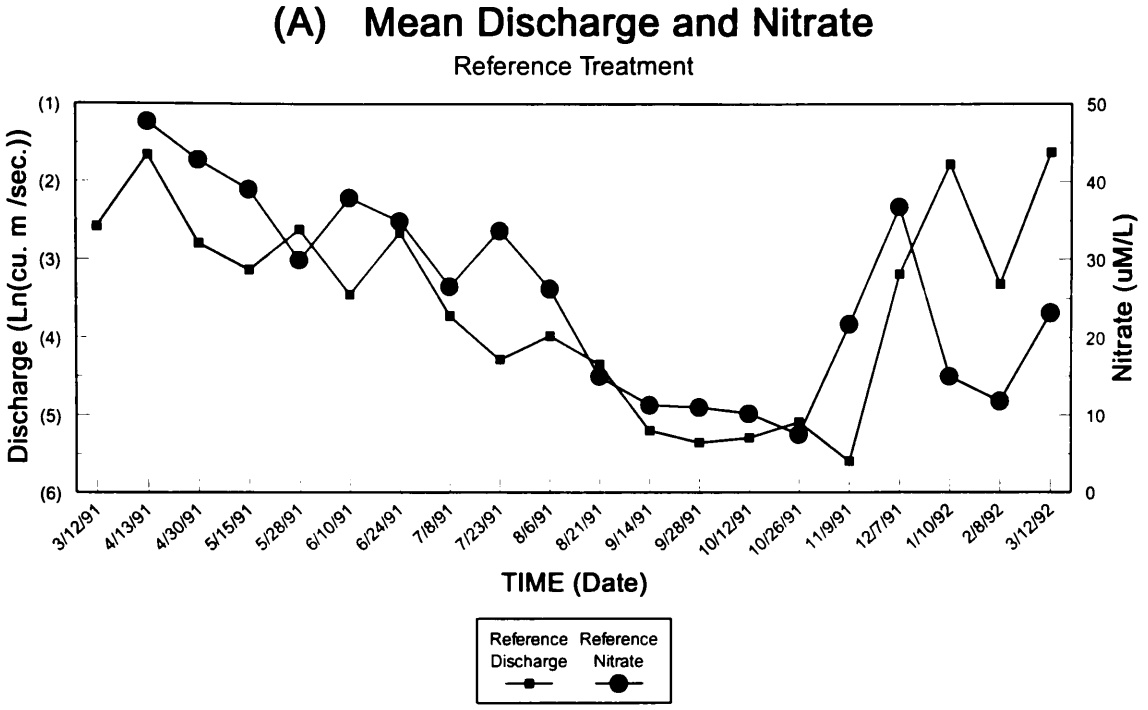


Fig. 1.14. Nitrate and detritus at defoliated sites. The nitrate concentrations (μM / L) at defoliated study sites with detritus inputs (g / sq.m / day). (A) North Fork Moormans River, (B) Shop Run, (C) South Fork Moormans River.]



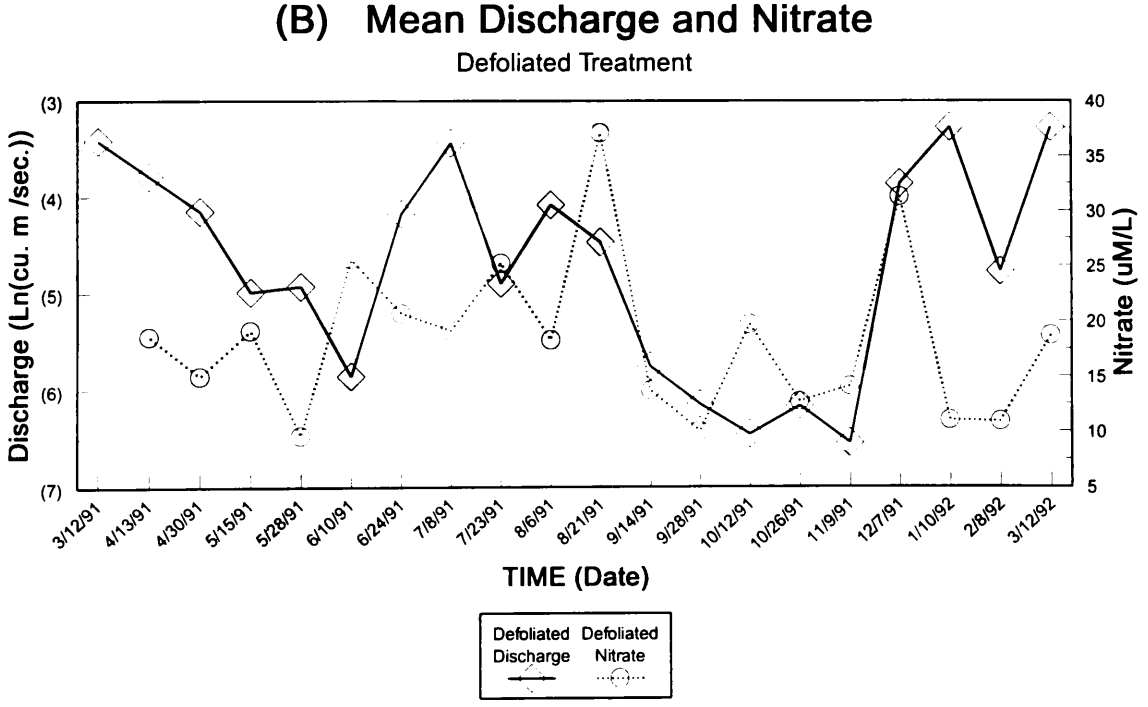


Fig. 1.15. Nitrate and discharge. Mean nitrate and discharge for the (A) reference and (B) defoliated treatments.

showed a large pulse of nitrate in August followed by a return to concentrations below those at the beginning of the study. This was probably the best example of short-term effects of defoliation on stream water nitrate, as the other sites may all be exhibiting long-term effects of cumulative frass fall in their watersheds (Table 1.4).

Other nitrogenous nutrients, nitrite and ammonia, were not significantly different between treatments. Nitrite concentrations were often below detection of the analytical method used and remained below detection in all sites after November (Fig. 1.16 (B)). Ammonia was not affected by defoliation as impacted stream ammonia concentrations mirrored those at reference streams for the duration of the study (Fig. 1.16 (A))

Total phosphorus concentrations were not significantly different between treatments, and I did not observe any trends in concentrations during the study (Fig. 1.17 A). While orthophosphate concentrations were not significantly different during the study (Fig. 1.17 B), there was a trend of increased phosphate concentrations coinciding with frass and ort input among the impacted sites (Fig. 1.18).

Despite large inputs of frass to defoliated treatment , the amount of seston did not appear to vary in relation to defoliation (Fig. 1.19). Stream water was hypotonic relative to frass, so the frass particles expanded within their peritrophic membranes. These swollen frass particles retained the star-shaped cross section typical of gypsy moth frass and tumbled along the stream bottom. Rather than breaking into fine particles and increasing seston concentrations, they accumulated in eddies and pools and became substrates for algal growth as shown by their bright green color (Fig. 1.20). Despite the eventual breakup of periphyton-coated frass, concentrations of chlorophyll *a* in 1 L of seston remained below detection by the spectrophotometric method I used for analysis. Most of the visible frass particles were purged from the impacted sites by two spates in June. If a pulse of seston occurred, it may have occurred during the spates and remained unobserved.

Table 1.4: Defoliation histories of study site watersheds according to National Park Service Records. This table expresses the percent of the watershed draining through study sites that was defoliated.

YEAR	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
1987	0	0	1.5%	0	0	0
1988	0	0	51%	0	0	0
1989	0	48%	7.4%	0	0	0
1990	59%	2.6%	18%	38%	22%	0
1991	27%	0	0	78%	70%	39%

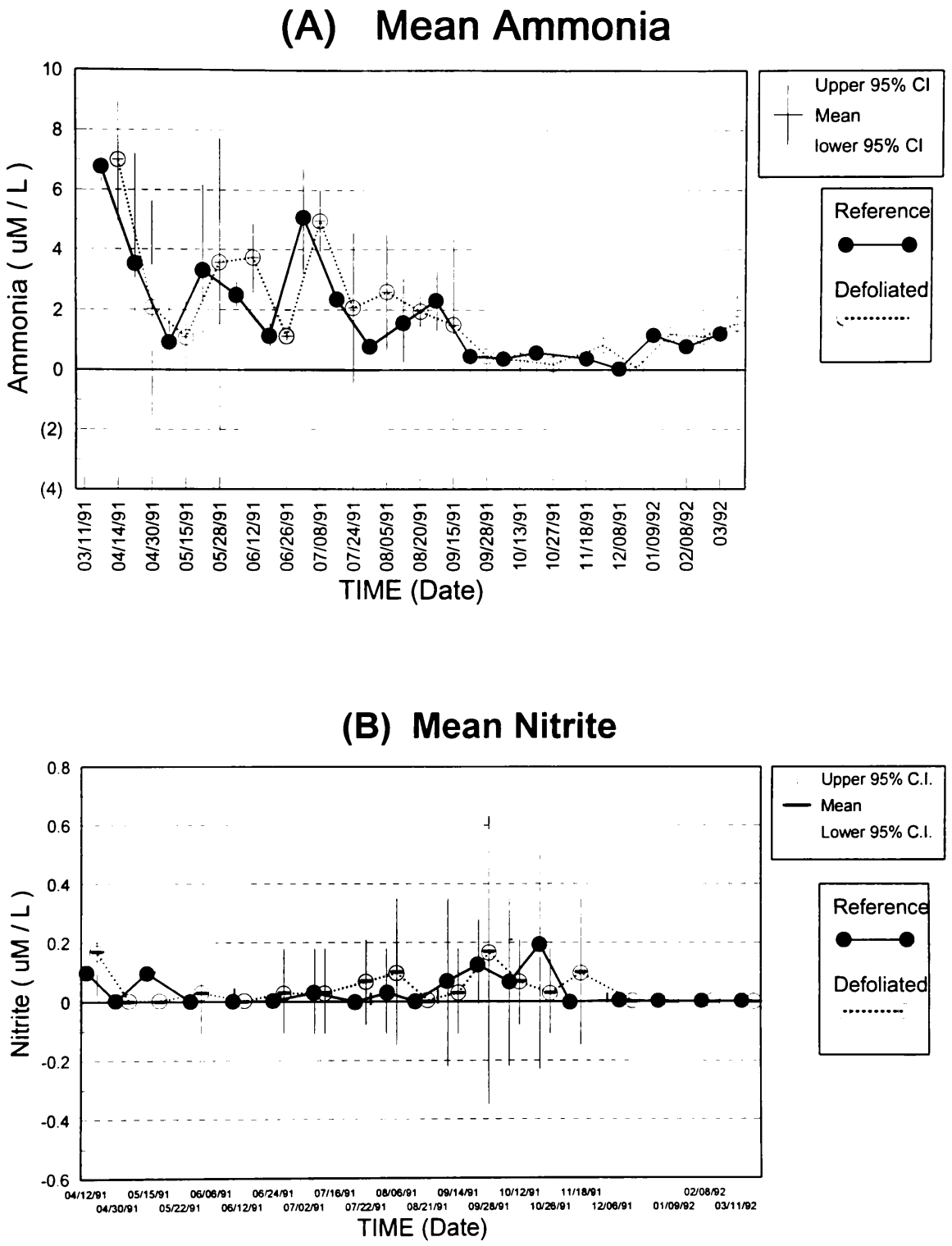


Fig. 1.16. Ammonia and Nitrite. Ammonia concentrations (uM/L) are expressed as treatment means with 95 % confidence intervals (A). Nitrite concentrations (uM/L) are expressed as treatment means with 95 % confidence intervals (B). After November, Nitrite remained below detection of the analyitical method used in this study.

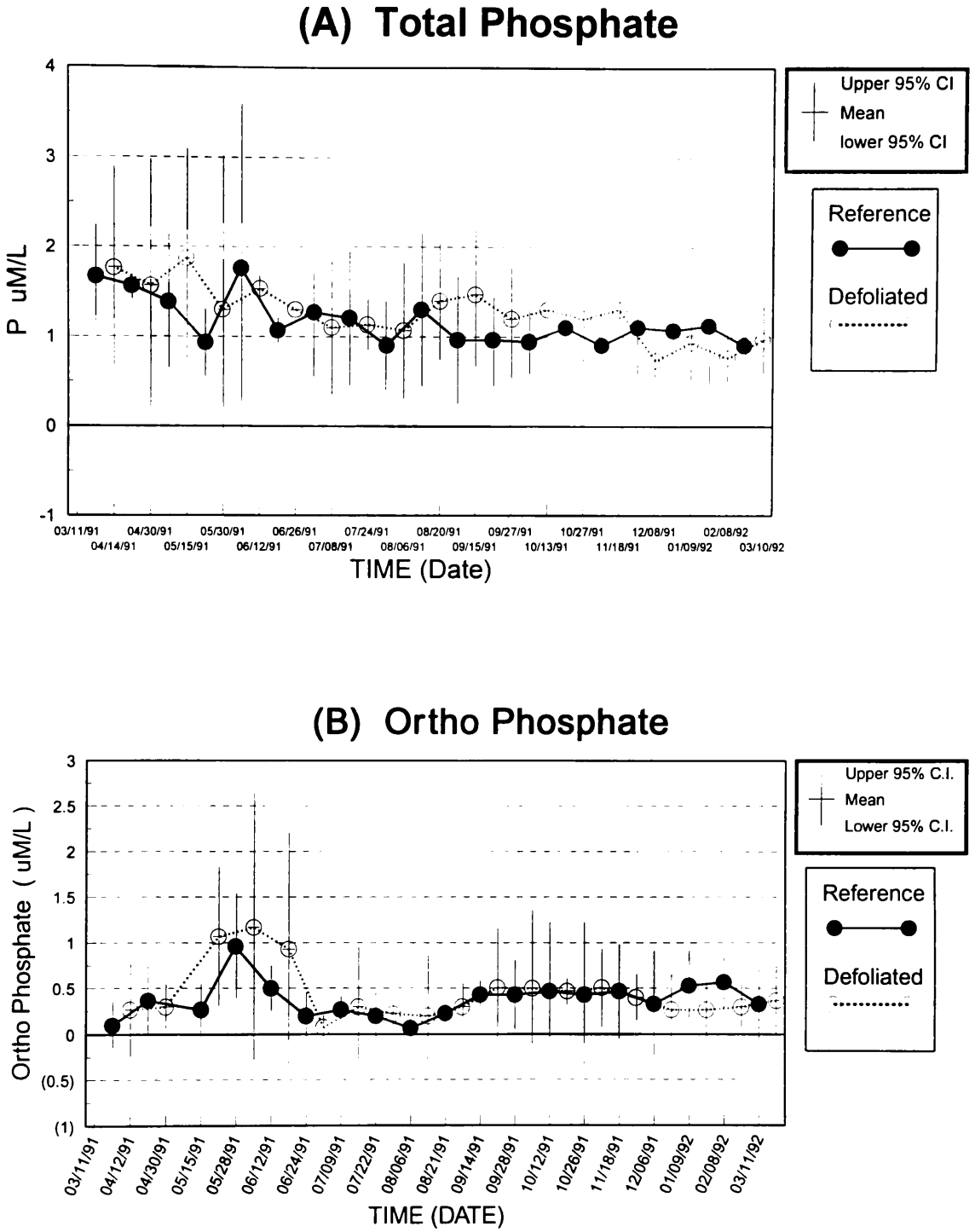
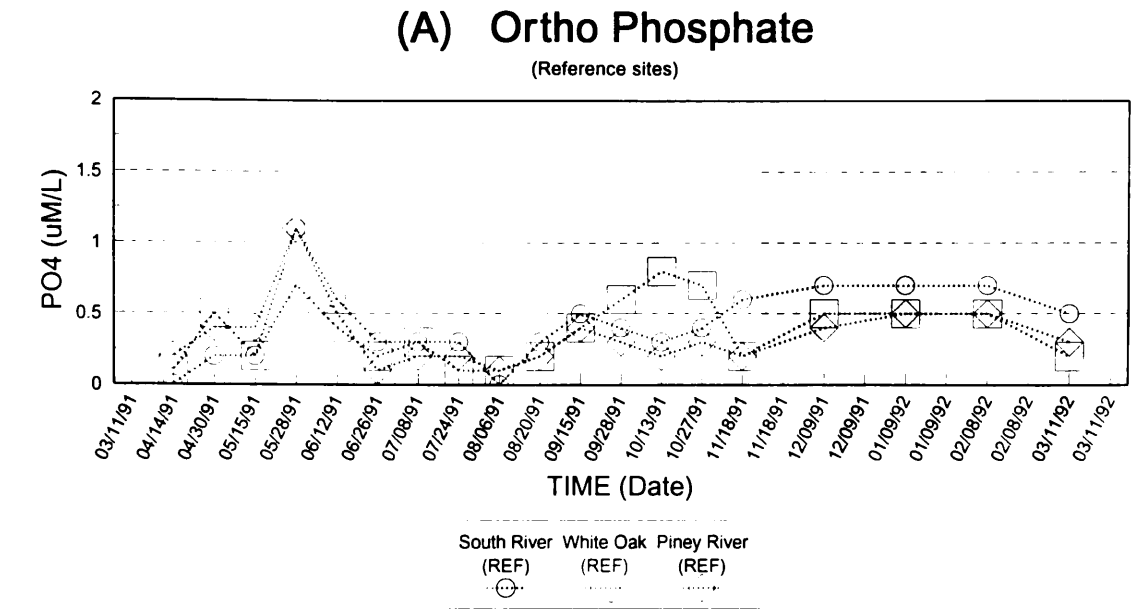


Fig. 1.17. Total phosphorous and orthophosphate. Total phosphorous (A) and orthophosphate (B) concentrations (uM/L) are presented as treatment means with 95 % confidence intervals



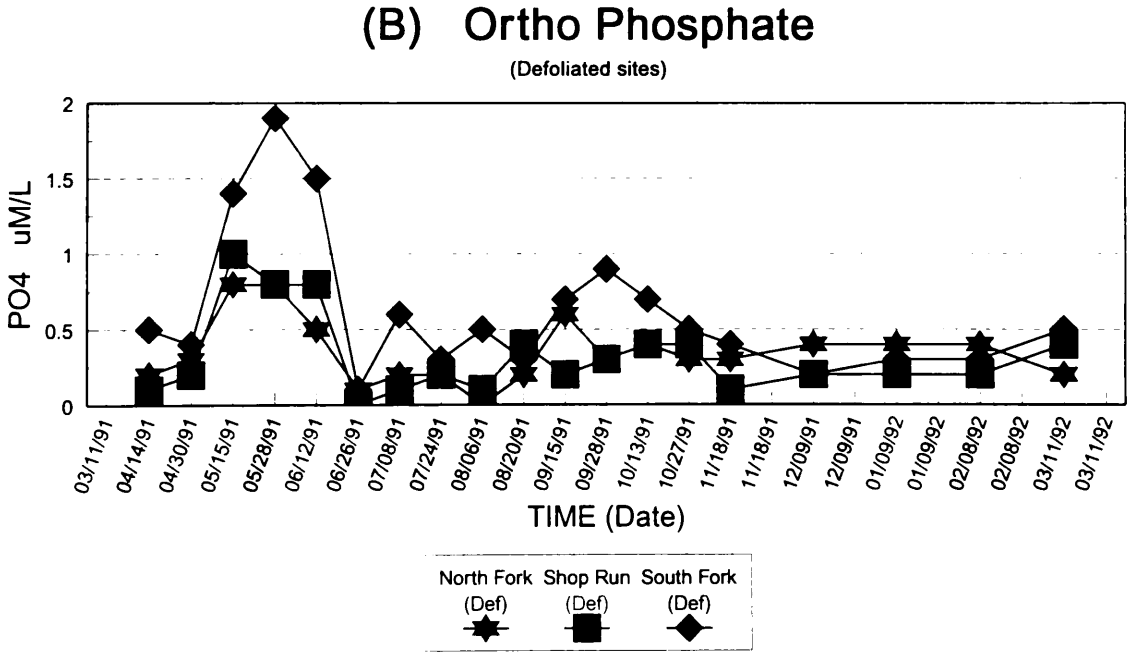


Fig.1.18. Orthophosphate. Orthophosphate concentrations at individual Reference (A) sites and defoliated sites (B) are expressed in uM/L. There was a trend of slightly elevated phosphate concentrations coinciding with green fall.

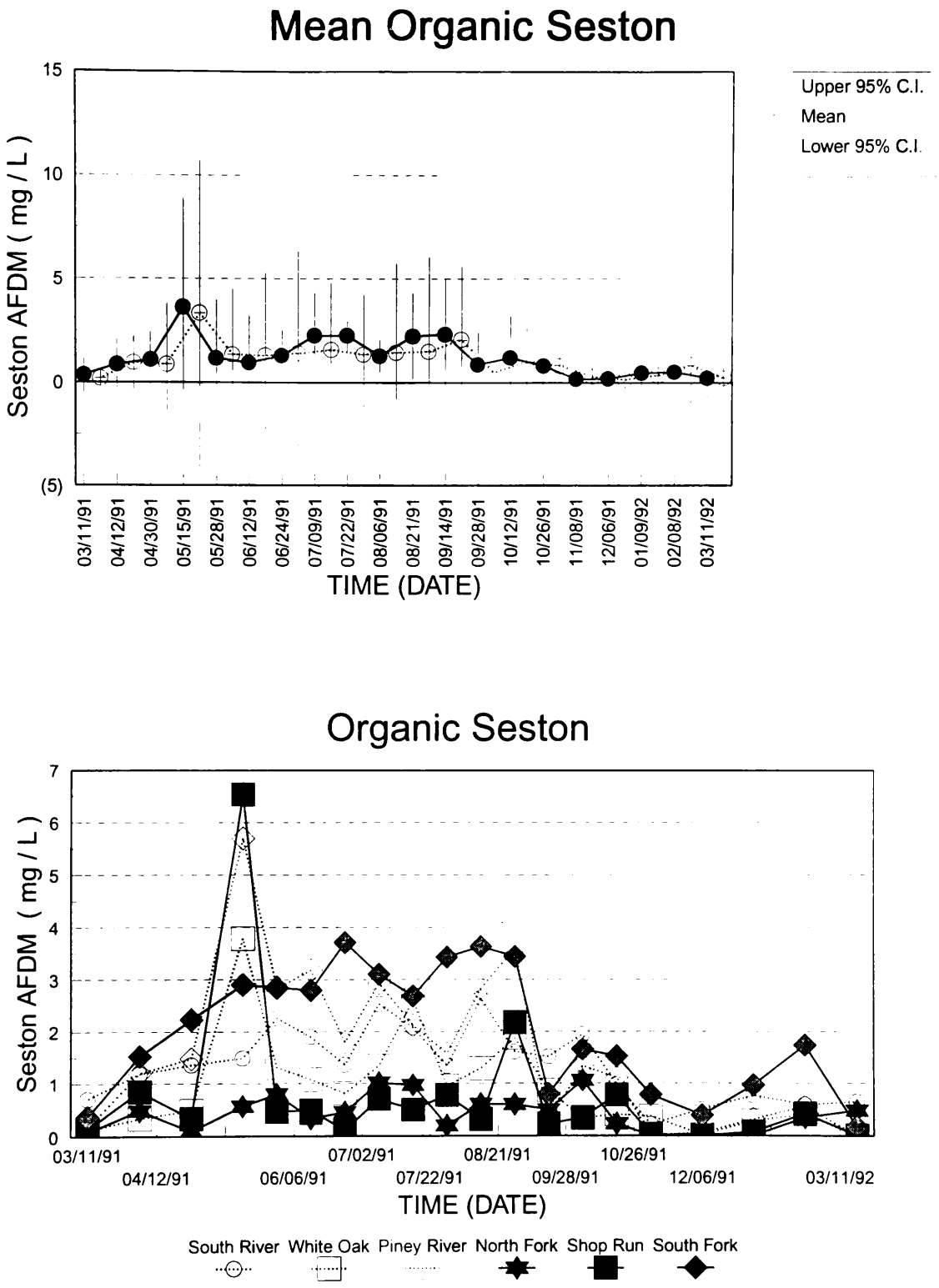


Fig. 1.19. Seston. Seston concentration (mg/L organic mass) is expressed as treatment means with 95 % confidence intervals (A). Concentrations at individual study sites show the lack of trends in the amount of seston between the treatments (B).

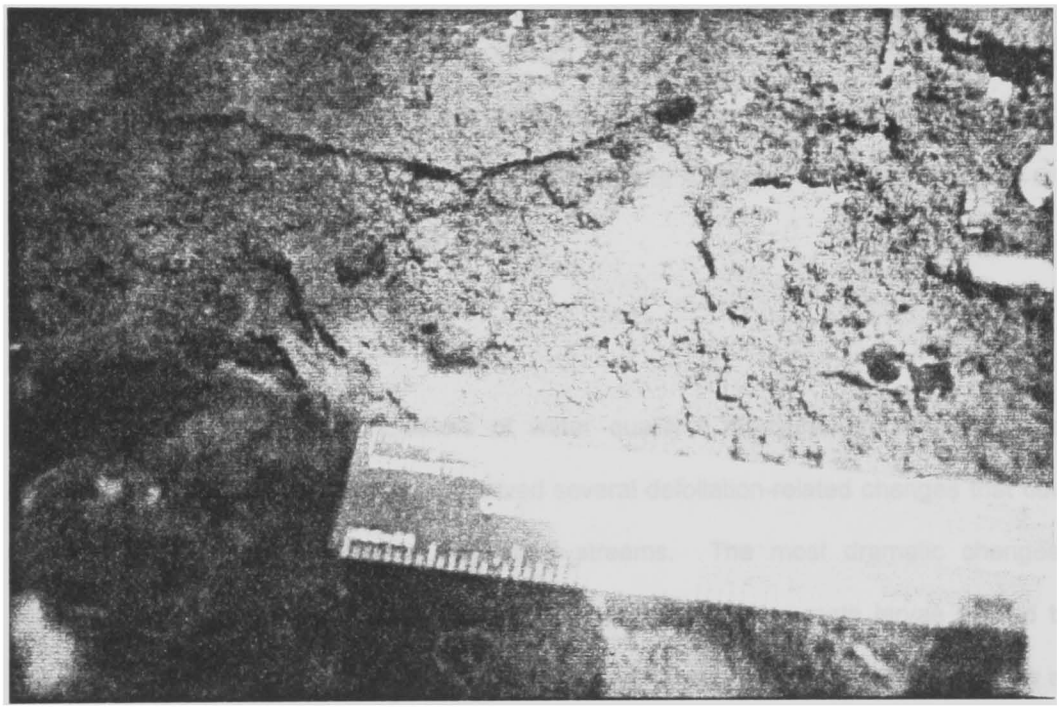


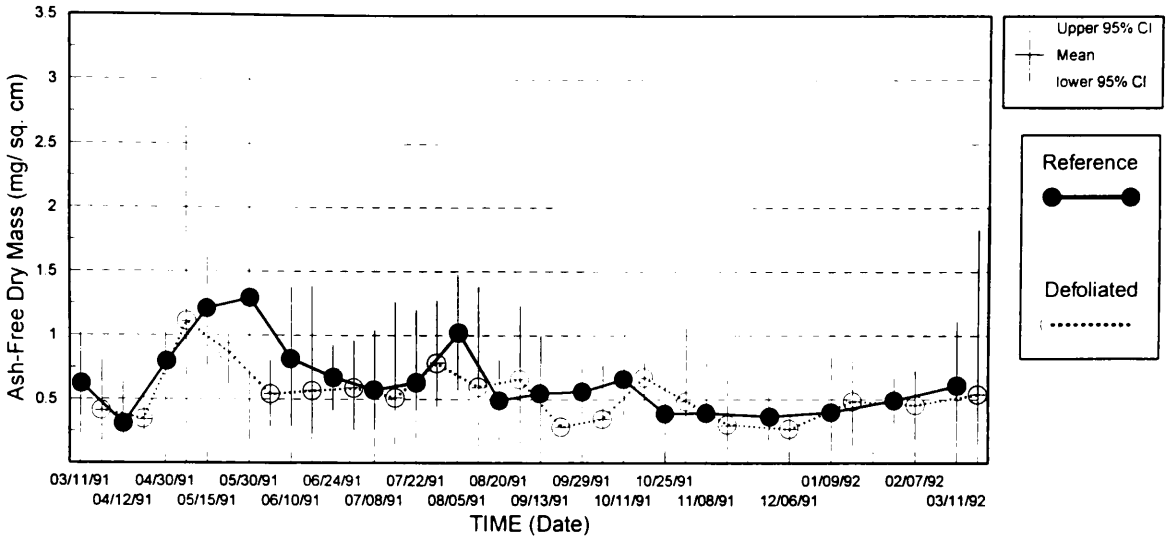
Fig. 1.20. Frass in Stream. The Frass did not break up upon entering the stream. It expanded within the peritrophic membrane, rolled along the stream bottom, and accumulated in eddies and pools. The frass particles provided substrata for the growth of algae, which buffered the streams from elevated nitrate concentrations.

Periphyton ash-free dry mass (AFDM) and chlorophyll *a* concentration varied greatly at all sites throughout the year. Differences between treatments were not statistically significant and no clear pattern was discernible (Fig. 1.21). High autotrophic index (AI) values indicate that both reference and impacted sites are strongly heterotrophic (Clesceri et al. 1989, (section 10300-C.6)), which is expected to occur in forested headwater streams (Fig. 1.22). Large AI values are caused by a high mass of organic material or low concentrations of chlorophyll *a* in periphyton. The disproportionally large AI value (~91,000) observed at Shop Run on April 30, 1991 was due to very low chlorophyll *a* concentrations and normal mass of periphyton. I would attribute the large AI value at that site to shading and the natural patchiness of headwater streams, because it occurred on a date before defoliation of the riparian canopy.

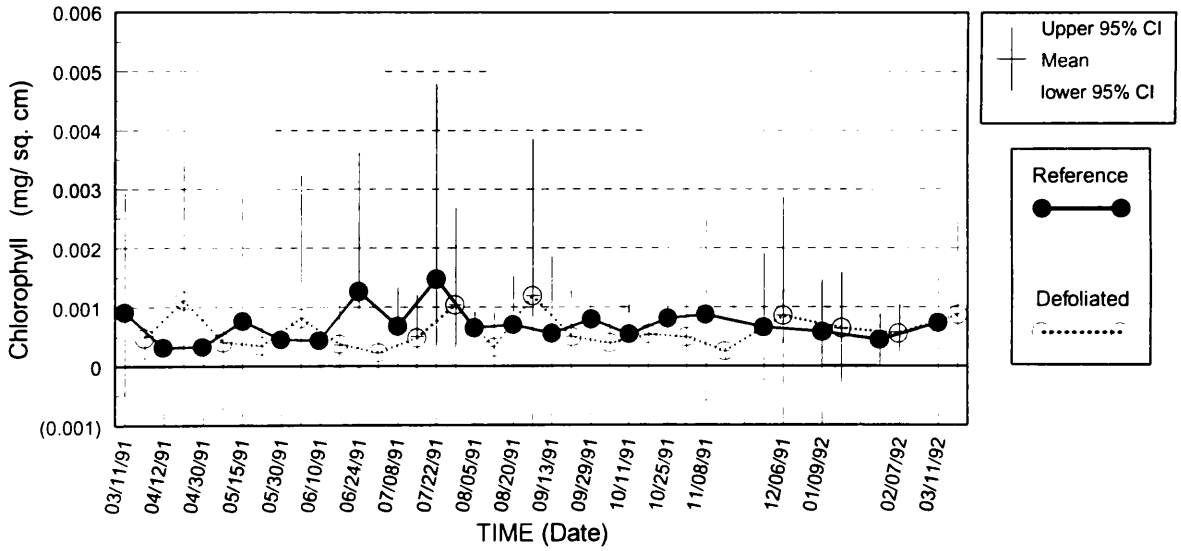
Discussion

While most of the indicators of water quality I measured in this study were unaffected by riparian defoliation, I observed several defoliation-related changes that could markedly impact the ecology of headwater streams. The most dramatic changes I observed involved detritus inputs. Riparian defoliation by gypsy moth larvae altered the timing, form, and amount of detritus falling into the defoliated streams. Most shredders are adapted to follow an autumn pulse of allocthonous detritus with a period of rapid growth and development. While the feeding of gypsy moth larvae greatly reduced the magnitude of this autumn pulse, it greatly increased the amount of detritus entering defoliated streams in the spring. The falling of frass and orts into defoliated streams occurs at a period of low CPOM availability. If shredder life histories allow exploitation of this supplementary detritus input, they may not be negatively impacted by reduced detritus inputs in autumn. As a result of only partial regrowth of the riparian canopy, and selective feeding by gypsy moth larvae, the relative species composition of autumn detritus was probably also altered. Other studies

(A) Periphyton Organic Mass (AFDM)



(B) Periphyton Chlorophyll Content



To estimate biomass multiply chlorophyll by 67.

Fig. 1.21. Periphyton. Periphyton ash-free dry mass (AFDM) (A) and chlorophyll *a* concentration (B) are expressed as treatment means with 95% Confidence intervals.

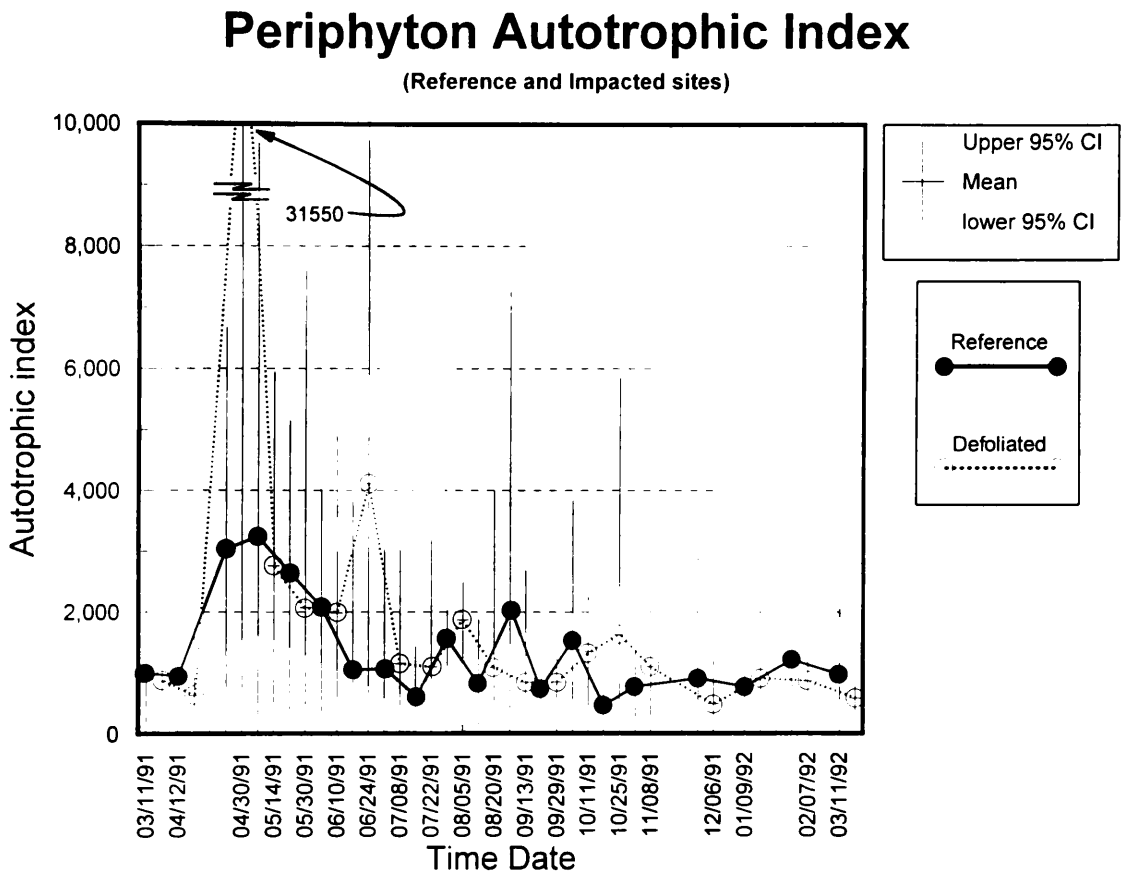


Fig. 1.22. Autotrophic Index. The Autotrophic Index (Periphyton AFDM / Chlorophyll *a*) is expressed as treatment means with 95 % confidence intervals. The extreamly high AI values indicate a heterotrophic condition, which is typical of Appalachian headwater streams.

(e.g. Smock and MacGregor 1988, Stout et al. 1993) reported that the species composing detritus inputs significantly affects the success of shredders.

Many of the insects composing the benthic community of headwater streams are adapted to consistent, cool temperatures (i.e., cool stenotherms) and their life-history patterns are often regulated by temperature (Sweeny 1984). The change in the thermal regime I observed could affect the success and life-history patterns of aquatic insects.

Epidemic populations of gypsy moth larvae have been postulated to increase the export of nitrate from forested watersheds, causing elevated nitrate concentrations in stream water. Because nitrate leaches through the soil as nitric acid, intensive defoliation by gypsy moth larvae is expected to have an impact on stream communities similar to that of acid rain (i.e, reduced alkalinity and pH). Some investigators suspect that repeated years of defoliation cause frass accumulations in the watershed and associated pH (and alkalinity) changes from continual leaching (Downey et al. 1992, Webb 1992, personal contact). My experimental design did not allow me to address the effects of long-term leaching, but the only indication of reduced alkalinity I observed occurred in May and was ephemeral. The peak period of frass fall was not accompanied with a sudden increase in stream water nitrate concentration. Algae using the peritrophic membrane of the frass as substrata buffered defoliated streams from increasing nitrate concentrations until the frass was exported during spate conditions. While this buffering prevented increased nitrate from frass falling into the stream, the possibility of leaching from the surrounding watershed exists. I could not assess the effects of defoliation elsewhere in the watershed because defoliation occurred in some reference watersheds. Another study (Swank et al. 1981) has observed a similar phenomenon caused by epidemic populations of fall cankerworm (*Alsophila pometetaria* (Harris)) at Coweeta National Hydrologic Laboratory. Stream-water nitrite concentrations increased during years of cankerworm outbreaks but returned to normal during endemic population levels. I did observe a seasonal difference in nitrate

concentrations. Differences in temperature and nitrate availability could alter periphyton community sufficiently to affect scrapers.

Defoliated streams exhibited a rotten odor from decaying organic material dropped into them, but rapid stream flow kept the water aerated with dissolved oxygen concentrations near saturation. I did not study any changes in the microbial community associated with defoliation, but changes in abundance or species of microbes could have caused the rotten odor and could alter the quality of various food material available to benthic macroinvertebrates.

This section of my thesis addressed the effects of riparian defoliation on the physical and chemical characteristics of headwater stream ecosystems. The following sections examine the effects of defoliation on the benthic macroinvertebrates inhabiting headwater streams.

PART 2: SHORT-TERM EFFECTS OF DEFOLIATION BY GYPSY MOTH LARVAE ON COMMUNITY STRUCTURE OF BENTHIC MACROINVERTEBRATES IN APPALACHIAN HEADWATER STREAMS IN VIRGINIA

INTRODUCTION

This part of my thesis examines the effects of riparian defoliation by gypsy moth larvae on the benthic community structure of headwater streams. I compared the benthic community structure of the study streams during the early phases of defoliation with the community structure 1 yr later. This section addresses my second objective and tests the null hypothesis: H_0: *Riparian defoliation by gypsy moth larvae causes no short term effects on the benthic community structure of headwater streams.*

METHODS

I sampled benthic macroinvertebrates from three riffles in each stream in mid-May 1991 (concurrent with defoliation) and 1992 (one year after defoliation) with a Portable Invertebrate Box Sampler (PIBS (sample area = $0.1m^2$)). I preserved the entire sample shortly after collection with 95 % ethanol. I separated all benthic macroinvertebrates from debris in the laboratory, and identified insects to the lowest taxonomic level possible using the keys provided by Wiggins (1977), Merrit and Cummins (1984), Stewart and Stark (1988). Chironomidae were only identified to family. I identified other macroinvertebrates to class, order, or family using Pennak (1989). I used the mean density of each taxon collected from all three riffles to represent the density at each stream and each individual stream as a statistical replicate to avoid pseudoreplication.

I used the mean abundance data to calculate several metrics commonly used for the description of benthic macroinvertebrate community structure. I calculated taxa richness (the number of different taxa), Simpson's Index of Diversity (Simpson 1949), EPT Index (the number of taxa from the orders Ephemeroptera, Plecoptera, Trichoptera), and Hilsenhoff's

Biotic Index (HBI)(Hilsenhoff 1987). I compared the mean value of each metric for both treatments with a Mann-Whitney Rank Sum (U) test before and after defoliation.

I assigned each taxon to a functional feeding group based on its role in processing organic matter (Merrit and Cummins 1984), and used the relative abundance of invertebrates in each functional feeding group to estimate the percent contribution of functional groups to the community. I used the percent contribution of functional groups at each site as statistical replicates for analysis of variance (ANOVA), after arcsin-transforming the values (Krebs 1987). I used the Least Significant Difference test to explain any differences indicated by ANOVA.

The mean abundance of each taxon at each site was compared to the other sites with several indices of similarity. The Bray-Curtis Coefficient (Bray and Curtis 1957) may be expressed as percent similarity (PS) or percent dissimilarity (PD) (Ludwig and Reynolds 1988). Percent similarity of community *a* and community *b* (PS_{ab}) is calculated as follows:

$$PS_{ab} = \left(\frac{2W}{A+B}\right)(100)$$

where

$$W = \sum_{i}^{k}[\min(X_{ia}, X_{ib})]$$

$$A = \sum_{i}^{k} X_{ia}$$

$$B = \sum_{i}^{k} X_{ib}$$

X_{ia} and X_{ib} = abundance of the i^{th} species in communities a and b, respectively.

k = number of taxa compared.

PS_{ab} ranges from 0 - 100, with 0 indicative of two communities which no taxa in common, and 100 indicative of identical communities. To keep PS comparable to other indices I, chose to express PS between 0 and 1 (Ludwig and Reynolds 1988).

One disadvantage of the Bray-Curtis Coefficient is that changes in the abundance of rare taxa may be obscured by a few dominant taxa. Because changes in rare taxa could be ecologically significant, I also used a similarity index that is more sensitive to changes in rare taxa. The Index of Biotic Similarity, *B*, (Pinkham and Pearson 1974) weights all taxa equally, thereby preventing dominant taxa from obscuring differences in communities due to changes in the abundance of rare taxa (Pearson and Pinkham, 1992). The authors proposed the use of a "weighting factor" to assign more importance to dominant taxa, but because my purpose was to de-emphasize dominant taxa I chose not to use it (Pearson and Pinkham, 1992). Biotic Similarity varies between 0 and 1, with 0 indicative of completely different communities, and 1 indicative of identical communities. *B* is calculated by the following equation:

$$B = \frac{1}{k} * \sum_{i}^{k} \frac{\min(X_{ia}, X_{ib})}{\max(X_{ia}, X_{ib})}$$

The third index of similarity I employed uses the relative abundance of each taxon and ignores the effects of absolute density. Chord distance projects the data onto a unit circle in *k*-dimensional taxa-space. The relative Euclidean distance between points on the circle is chord distance (CRD_{ab}) and values vary between 0 and ~1.41, with larger numbers indicative of greater dissimilarity. Chord distance is highly recommended for the comparison of communities when the samples are quantitative (Ludwig and Reynolds 1988, Pielou 1984) and is calculated with the following equation:

$$CRD_{ab} = \sqrt{2 * (1 - ccos_{ab})}$$

where the Chord cosign, $ccos_{ab}$ is:

$$ccos_{ab} = \frac{\sum_{i}^{k} (X_{ia} * X_{ib})}{\sqrt{\sum_{i}^{k} X^2_{ia} * \sum_{i}^{k} X^2_{ib}}}$$

I grouped the similarity values into treatments based on the type of sites being compared: RR= similarity of a reference site to another reference site; RD = similarity of a reference site to a defoliated site; DD = similarity of a defoliated site to another defoliated site). This grouping scheme produced 6 treatments (3 before defoliation; 3 after defoliation) with an unequal number of replicates (3 in each RR and DD treatment, 9 in each RD treatment) (Fig. 2.1). I arcsin-transformed similarity estimates (Krebs 1987) before subjecting the data to Analysis of Variance (ANOVA) because the similarity indices I used vary between a fixed range (0-1 for Bray-Curtis and Index of Biotic Similarity, 0-1.41 for chord distance) and are not necessarily normally distributed within that range. If ANOVA revealed a significant difference ($p < 0.05$) in the level of similarity of the treatments with a particular similarity index, I conducted a pairwise comparison of the treatment means with a Least Significant Difference (LSD) test. This statistical analysis of similarity indices is similar to that of Hruby (1987) except that he performed t-tests on each treatment combination.. Using individual t-tests, the probability of rejecting a null hypothesis exceeds the level of significance of the ANOVA (in this case 0.05). The LSD test I used avoids this problem (Kleinbaum et al. 1988).

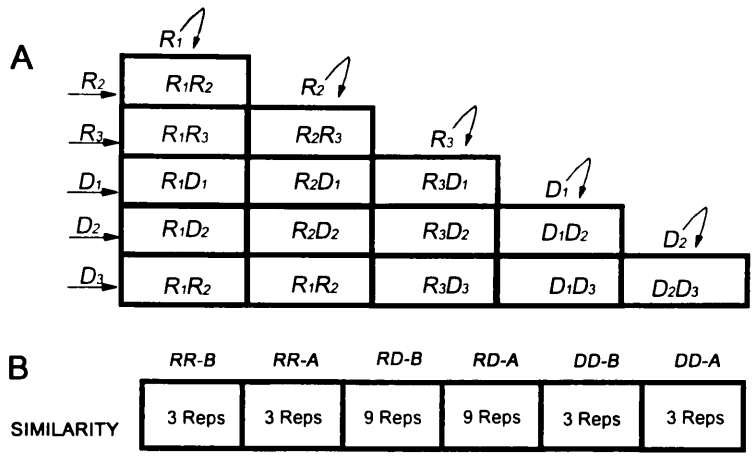


Fig. 2.1. (A) Similarity matrix. This similarity matrix was developed before and after defoliation by applying taxa abundance data from each site to similarity indices. R1-3 and D1-3 refer to reference and defoliated sites 1-3 respectively. The values in the matrix are the similarity of the two sites compared. R1R2 refers to the similarity of reference site 1 to reference site 2, and R2D2 refers to the similarity of reference site 2 to defoliated site 2 (etc.). (B) Breakdown of treatments for statistics. The similarity values were grouped into treatments for analysis of variance (ANOVA) according to the type of sites compared. The RR-B treatment consists of the three similarity values which compare reference sites to reference sites before defoliation (i.e. R1R2; R1R3; R2R3), and the RD-A treatment consists of the 9 similarities comparing reference to defoliated sites after defoliation (etc.)

Dendrograms generated by cluster analysis are useful tools for visualizing trends among community similarity data. Unfortunately, cluster analysis has an inherent shortcoming in that it lacks statistical inference power. Clusters are formed until all communities are clustered (or linked) so that linkages formed may not be based on any community similarity. A recent development is the application of bootstrap procedures to taxa abundance data to generate 95% confidence intervals for the linkages formed by cluster analysis. These confidence intervals test the null hypothesis: *The Communities or groups of communities clustered are similar enough to be considered the same community.* I applied this procedure to the taxa abundance data of the study sites before and after defoliation by sampling the mean abundance matrix 500 times and using the Bray-Curtis Coefficient of similarity to generate clusters (Nemec and Brinkhurst 1988).

RESULTS

Mean density of the taxa collected from each site before and after defoliation is presented in Tables 2.1 and 2.2, respectively. I observed no statistically significant changes in taxa richness, Hilsenhoff's Biotic Index, nor in the EPT Index one year after defoliation by gypsy moth larvae (Figs. 2.2, 2.3). Before defoliation the reference and defoliated treatments were not significantly different, but one year after defoliation, the defoliated streams were significantly more diverse than reference streams (Fig. 2.4 A). Diversity of all This difference was due to a decrease in the variance between defoliated sites in 1992, not due to a trend of changing diversity in defoliated streams (Fig. 2.4 B).

The relative abundance of insects in different-functional feeding groups was not significantly different before or after defoliation. The relative proportions of collector-filterers, collector-gatherers, and predators remained similar in both years (Figs. 2.5, 2.6). There was a slight increase in the proportion of scrapers and a slight decrease in the

Table 2.1. Mean abundance of individual taxaper sample (0.1 sq. m) at study sites in May 1991

1991	REFERENCE			DEFOLIATED		
	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
CLASS OLIGOCHAETA	2.3	2.3	0.3	--	--	3.0
ORDER AMPHIPODA	--	--	--	11.3	7.0	--
CAMBARIDAE	0.3	--	0.3	--	0.3	--
ORDER PLECOPTERA						
Pteronarcys	1.3	4.3	5.7	--	--	2.7
Peltoperla	--	--	--	--	4.0	--
Tallaperla	4.7	1.0	1.7	4.3	--	7.7
Amphinemura	1.7	0.3	4.3	0.3	4.0	--
Perlidae	1.3	1.0	0.7	0.3	--	2.3
Hansonoperla	--	--	--	--	--	0.3
Acroneuria	0.7	1.3	1.7	--	--	1.7
Eccoptura xanthenes	--	0.3	--	0.3	--	0.3
Perlesta	3.7	3.3	--	3.0	--	--
Perlodidae	0.7	4.0	1.0	2.7	1.0	6.0
Remenus bilobatus	--	--	--	--	0.7	--
Isoperla	0.3	0.7	4.3	0.3	--	1.7
Chloroperidae	14.7	18.3	1.3	41.7	21.7	10.3
Suwallia	--	--	--	--	--	--
Haploperla brevis	5.0	8.3	0.7	--	6.7	1.0
Leuctra	20.3	41.7	63.7	114.3	6.7	93.0
ORDER EPHEMEROPTERA						
Drunella cornutella	--	--	--	0.3	--	0.3
Ephemerella	5.0	6.7	2.3	4.3	2.0	8.7
Eurylophella	--	--	0.3	--	--	--
Leptophlebiidae	--	--	--	6.0	--	--
Paraleptophlebia	16.7	13.3	9.0	4.0	12.7	4.3
Habrophlebia vibrans	--	--	--	2.0	--	--
Habrophlebiodes	--	--	--	11.7	--	3.3
Baetis	4.7	22.0	18.7	6.0	--	6.7
Stenonema	2.3	--	2.0	0.3	0.7	0.3
Epeorus	27.3	66.3	16.3	1.0	7.0	4.0
Cinygmula	--	1.3	1.3	0.3	--	--
Leucrocuta	--	0.7	0.7	--	0.7	0.7
ORDER ODONATA						
Gomphidae	0.3	--	--	--	--	0.7
Lanthus	--	0.3	--	--	--	--
ORDER MEGALOPTERA						
Nigronia serricornis	--	--	--	--	--	0.3
ORDER TRICHOPTERA						
Hydroptila	--	--	--	0.7	--	--
Hydropsyche	0.3	0.7	0.7	6.3	--	2.3
Diplectrona modesta	5.7	6.3	19.7	2.0	1.7	2.7
Rhyacophila	0.7	3.0	1.3	0.3	1.0	1.7
Philopotamidae	--	--	--	--	0.3	--
Dolophilodes distinctus	1.7	1.0	22.7	2.7	--	5.7
Adicrophleps hitchcocki	--	--	--	0.3	0.3	--
Lepidostoma	--	--	2.0	--	0.3	--

continued

continued

Table 2.1 (cont.). Mean abundance of individual taxa per sample (0.1 sq. m) at study sites in 1991

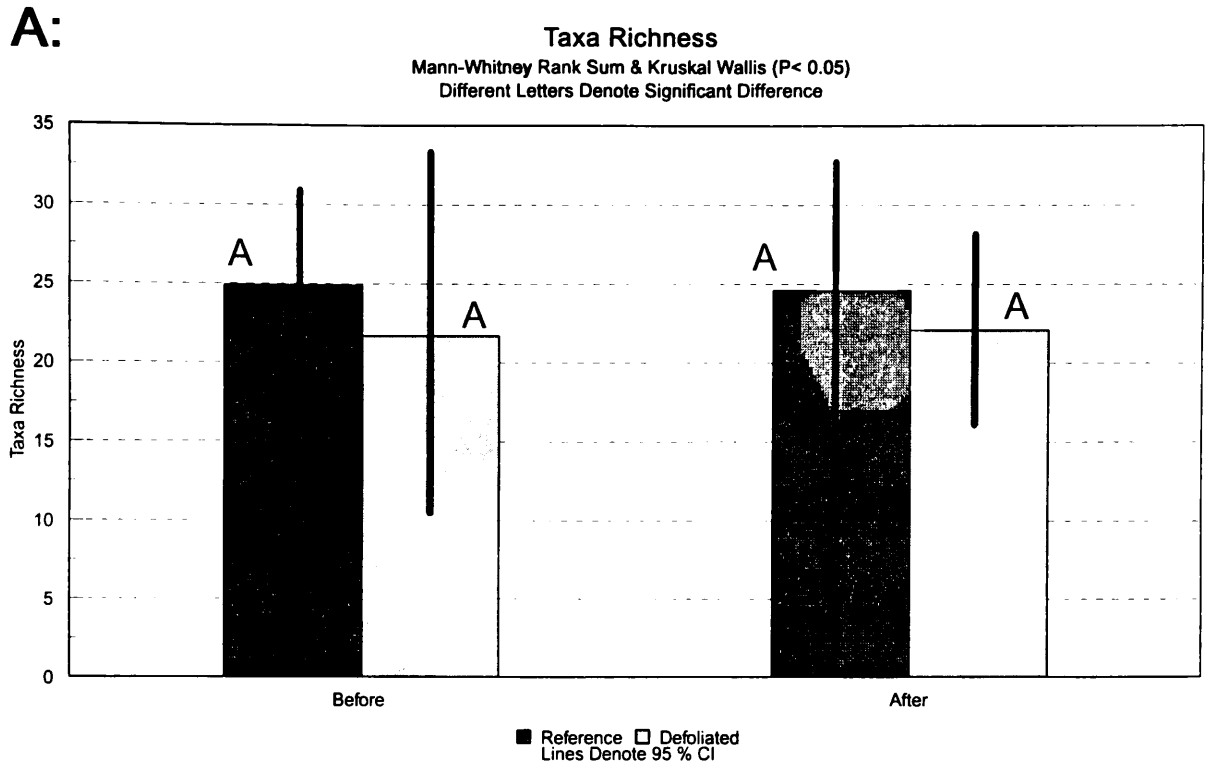
1991	REFERENCE			DEFOLIATED		
	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
Glossosoma nigrior	3.7	--	2.3	3.3	--	1.0
Limnephilidae	--	--	--	--	0.3	--
Neophylax	--	--	0.3	--	--	--
Polycentropus	0.3	1.0	1.0	0.3	2.0	2.3
ORDER COLEOPTERA	--	--	--	--	--	--
Psephenus herricki	1.3	1.0	--	--	--	7.0
Optioservus	1.3	2.3	0.3	0.3	--	1.0
Oulimnus latiusculus	14.3	10.3	1.3	27.0	3.7	13.0
Ectopria	--	--	0.3	0.7	--	0.3
ORDER DIPTERA						
Blepharcera	--	1.0	--	--	--	--
Antocha	1.3	0.3	--	1.3	--	--
Dicranota	--	3.7	1.7	--	--	--
Hexatoma	0.3	2.0	1.0	3.3	3.7	3.0
Limnophila	--	--	--	--	--	0.7
Ormosia	0.7	--	--	--	--	0.7
Dixa	--	--	--	--	0.7	2.7
Prosimulium	--	0.3	--	--	--	--
Simulium	0.7	25.3	1.0	1.0	0.3	2.7
Chironomidae	25.7	57.0	87.3	159.7	96.0	67.7
Ceratopogonidae	2.7	1.0	1.0	2.3	--	2.7
ORDER COLEMBOLA	0.3	0.3	0.7	1.7	0.3	0.7
NEMOTODA	--	--	--	--	--	0.3
Mean total abundance	174.3	314.3	281.0	428.0	185.7	277.3
Taxa Richness	35	37	37	37	27	41

Table 2.2. Mean abundance of individual taxa per sample (0.1 sq. m) at study sites in May 1992

1992	REFERENCE			DEFOLIATED		
	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
CLASS OLIGOCHAETA	--	--	0.5	0.3	0.3	1.0
ORDER AMPHIPODA	--	--	--	22.0	7.7	0.3
ORDER DECAPODA	--	--	--	--	3.0	--
CAMBARIDAE	0.3	--	1.5	--	1.3	--
ORDER PLECOPTERA						
Pteronarcys	14.3	2.0	21.5	--	--	3.0
Peltoperla	--	--	--	--	0.3	--
Tallaperla	24.3	1.3	47.0	28.0	--	--
Amphinemura	0.3	0.7	9.5	4.0	0.3	--
Perlidae	0.3	0.3	2.0	--	1.3	0.7
Acroneuria	1.3	0.7	4.5	0.7	--	1.7
Eccoptura xanthenes	--	--	--	1.0	--	--
Perlesta	2.3	0.7	--	1.0	--	--
Perlodidae	--	1.0	--	1.0	0.7	2.0
Isoperla	1.3	1.0	3.5	--	--	--
Chloroperidae	4.0	2.3	4.5	12.0	27.3	3.0
Suwallia	--	--	--	--	0.3	--
Haploperla brevis	11.3	1.0	2.0	--	0.3	2.7
Leuctra	5.3	6.3	73.0	81.0	19.0	33.3
ORDER EPHEMEROPTERA						
Ephemera	--	--	--	--	--	2.0
Drunella cornutella	--	--	--	--	--	0.3
Ephemerella	10.0	13.0	9.5	12.3	3.3	7.3
Eurylophella	--	0.3	--	--	--	--
Ameletus	--	--	--	--	0.3	--
Leptophlebiidae	--	--	--	--	10.3	0.7
Paraleptophlebia	12.7	7.0	4.0	0.3	--	1.7
Habrophlebiodes	--	--	--	47.3	--	3.0
Baetis	6.3	1.7	3.0	2.7	1.7	7.0
Stenonema	--	0.7	2.0	2.3	5.7	0.3
Epeorus	50.7	36.7	52.5	7.0	15.3	22.0
Cinygmula	--	10.7	1.0	--	--	0.7
Leucrocuta	--	1.7	--	--	0.7	--
ORDER ODONATA						
Lanthus	0.3	--	0.5	--	--	--
ORDER MEGALOPTERA						
Nigronia serricornis	--	--	1.0	--	--	0.7
Nigronia fasciatus	--	--	--	--	0.3	--
ORDER TRICHOPTERA						
Hydropsyche	0.7	2.3	--	4.0	0.3	1.0
Diplectrona modesta	21.3	10.7	23.0	4.3	6.3	3.3
Rhyacophila	0.3	0.3	1.0	0.3	--	0.7
Dolophilodes distin	19.0	--	9.5	4.0	0.3	47.3
Adicrophleps hitchc	--	--	--	--	--	--
Lepidostoma	0.3	0.3	4.0	1.0	--	--
Glossosoma nigrior	--	--	--	0.7	0.3	1.3
Limnephilidae	--	--	--	--	--	--
Neophylax	1.0	0.3	--	--	1.3	1.0
		continued			continued	

Table 2.2 (cont.). Mean Abundance of individual taxa per sample (0.1 sq. m) at study sites in 1992

1992	REFERENCE			DEFOLIATED		
	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
Optioservus	--	1.0	0.5	--	0.7	--
Oulimnus latiusculus	2.3	2.0	7.0	23.3	--	26.0
Ectopria	0.7	--	0.5	--	--	--
ORDER DIPTERA						
Blepharcera	0.7	1.7	1.0	--	--	5.0
Tipulidae	--	--	--	0.7	--	--
Tipula	--	--	0.5	--	--	--
Antocha	--	0.3	--	0.7	--	0.3
Dicranota	2.3	1.0	3.0	--	--	0.7
Hexatoma	1.0	0.3	0.5	2.7	3.0	4.0
Limnophila	--	0.3	--	--	--	--
Dixa	--	--	--	0.3	0.3	0.7
Prosimulium	--	0.3	--	--	--	--
Simulium	2.7	1.7	11.0	3.0	2.3	--
Chironomidae	36.7	31.0	119.5	146.0	86.7	106.7
Ceratopogonidae	1.0	--	0.5	--	0.7	0.3
Hemerodromia	0.3	--	--	0.3	--	--
Chelifera	--	--	--	0.7	--	--
ORDER COLEMBOLA	--	--	--	3.0	--	--
CLASS GASTROPODA						
Planorbidae	--	0.3	--	--	--	--
Mean total abundance	235.7	143.0	424.0	395.7	194.0	290.3
Taxa Richness	31	35	32	30	29	32



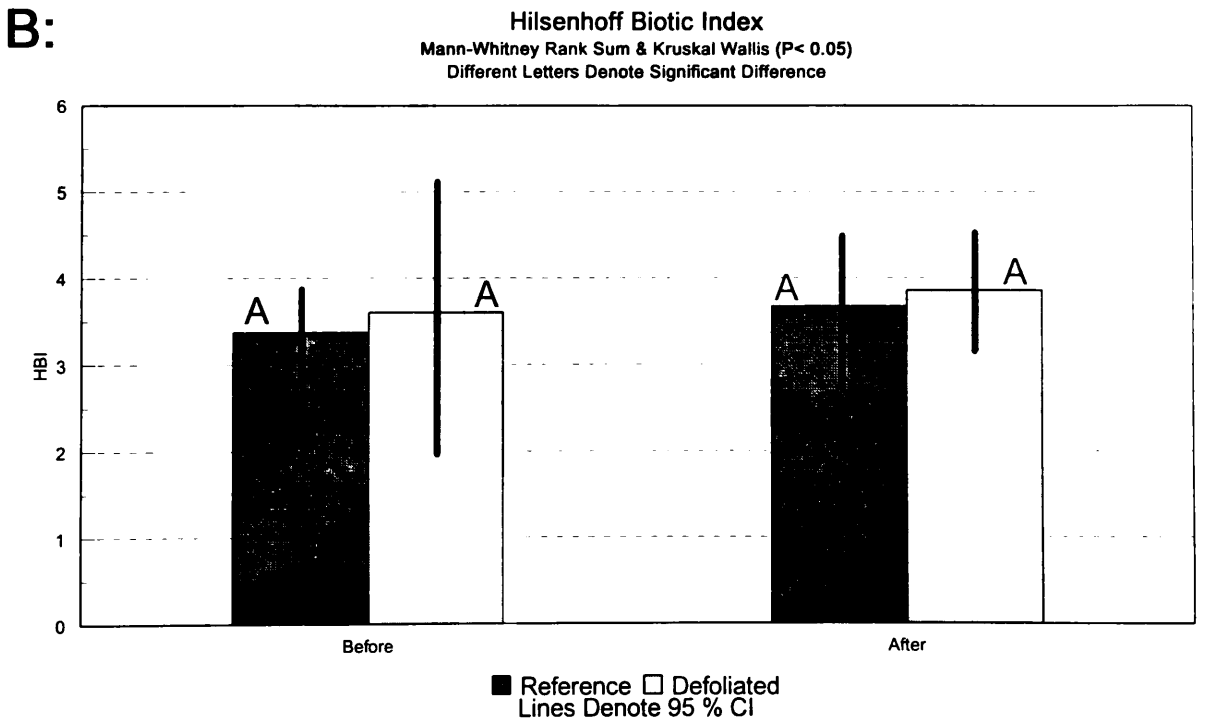


Fig. 2.2. Taxa richness and Hilsenhoff Biotic Index. The mean taxa richness **(A)** of reference and defoliated treatments was not significantly different before or after defoliation. The Hilsenhoff Biotic Index (HBI) **(B)** of the treatments was not significantly different before or after defoliation.

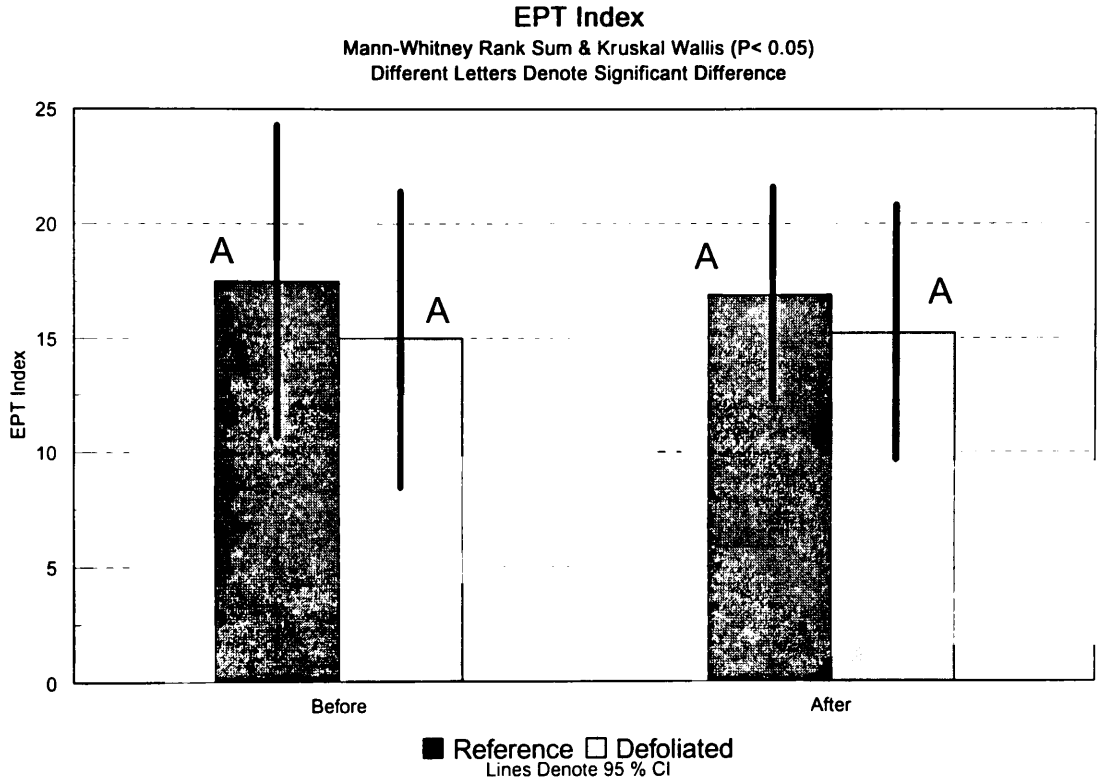
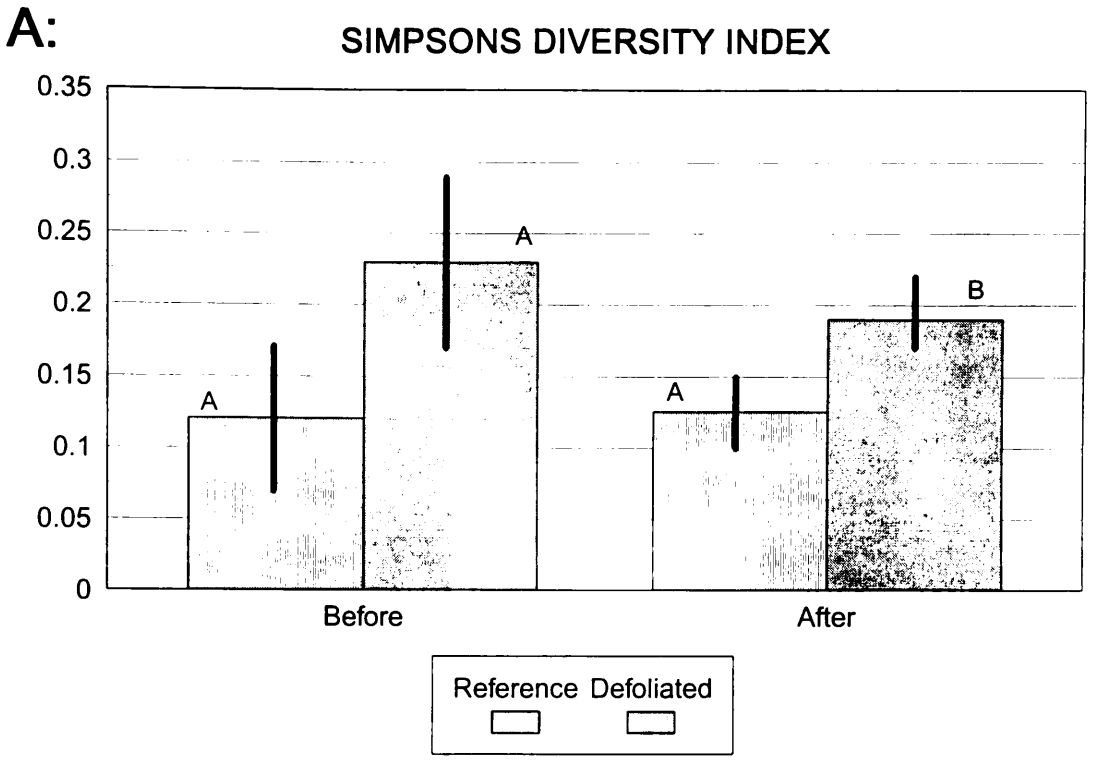


Fig. 2.3. EPT index. I observed no significant difference in the number of taxa from the orders Ephemeroptera, Plecoptera, or Trichoptera (the EPT Index) before or after defoliation.



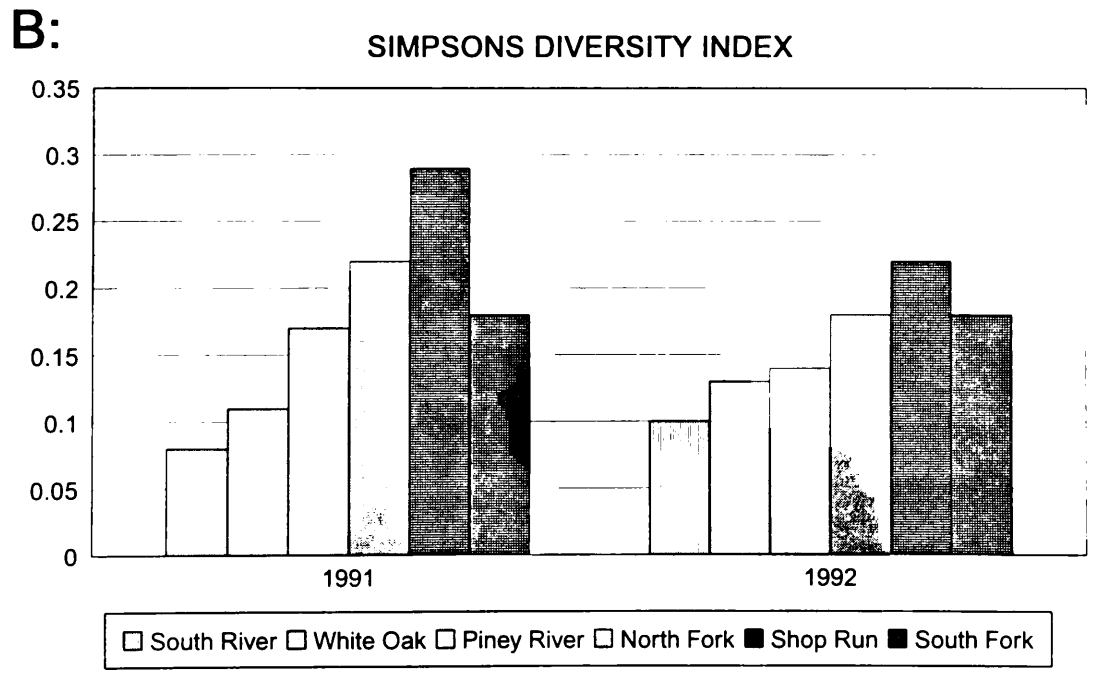
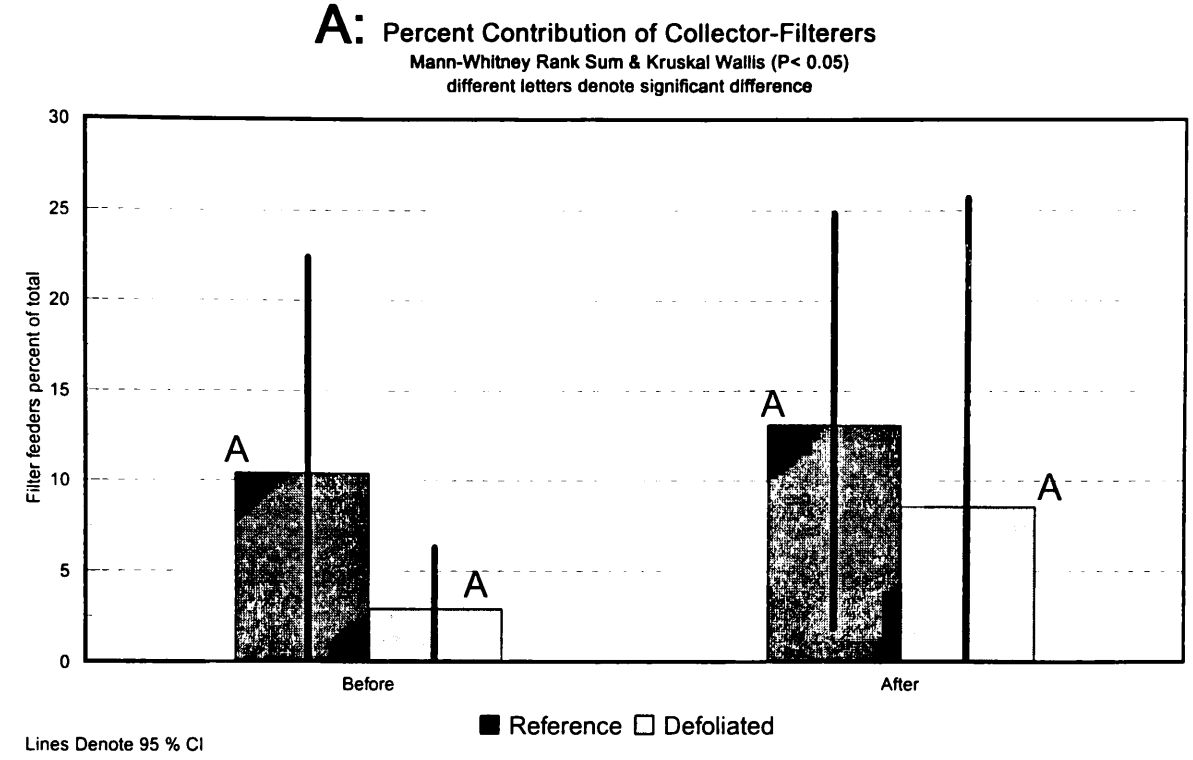


Fig. 2.5. Simpsons Index of diversity. The defoliated streams were significantly less diverse (i.e. Simpsons diversity higher) than reference streams after 1 yr after defoliation, but not significantly different before defoliation **(A)**. The diversity of the treatments was more similar after defoliation and the statistical significance seems to be due to a reduction in the variance of observed diversity values **(B)**, not due to a trend of changing diversity.



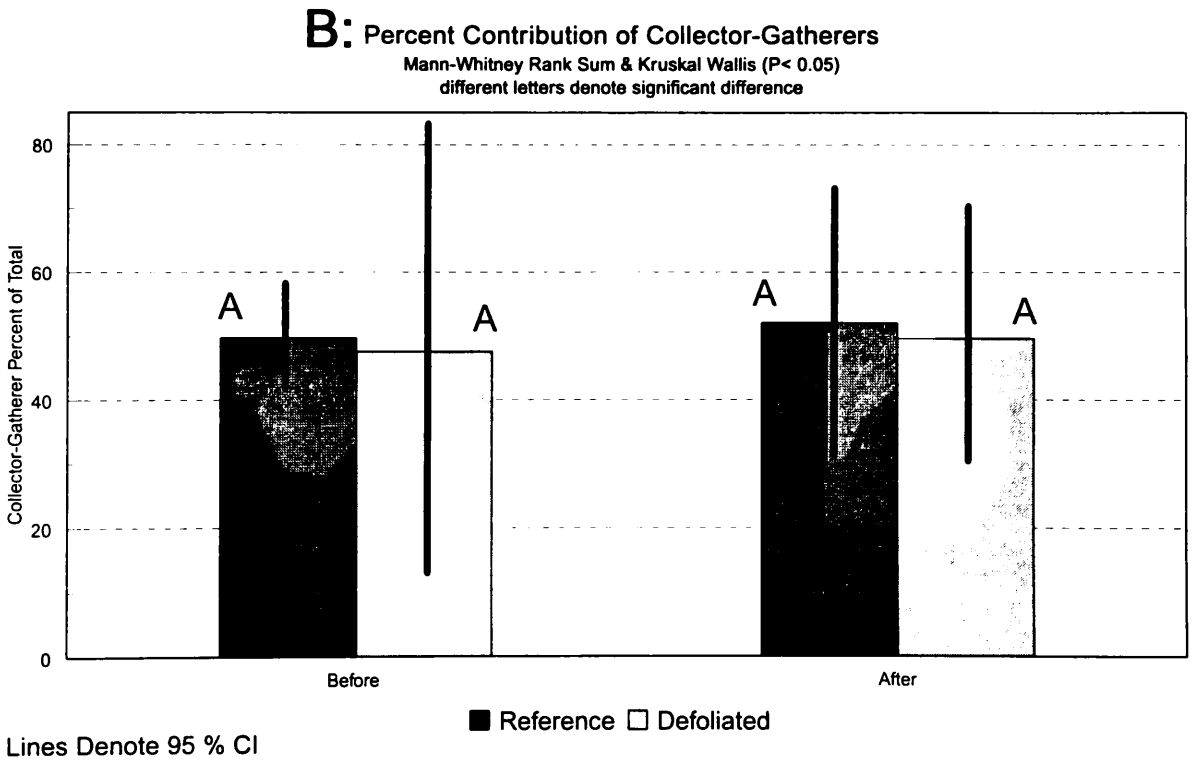


Fig. 2.5. Percent contribution of collectors. There was no significant difference in the contribution of **(A)** collector-filterers or **(B)** collector-gatherers to the benthic community before or after defoliation.

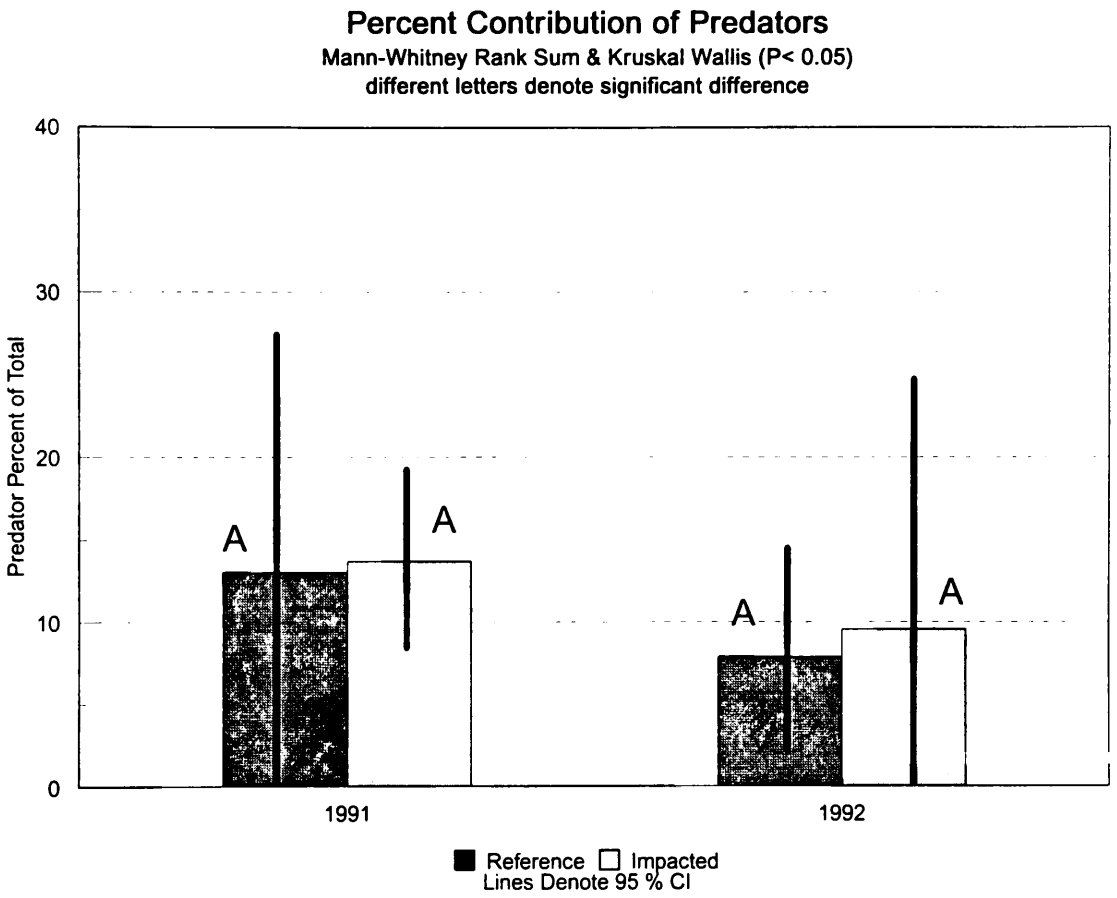


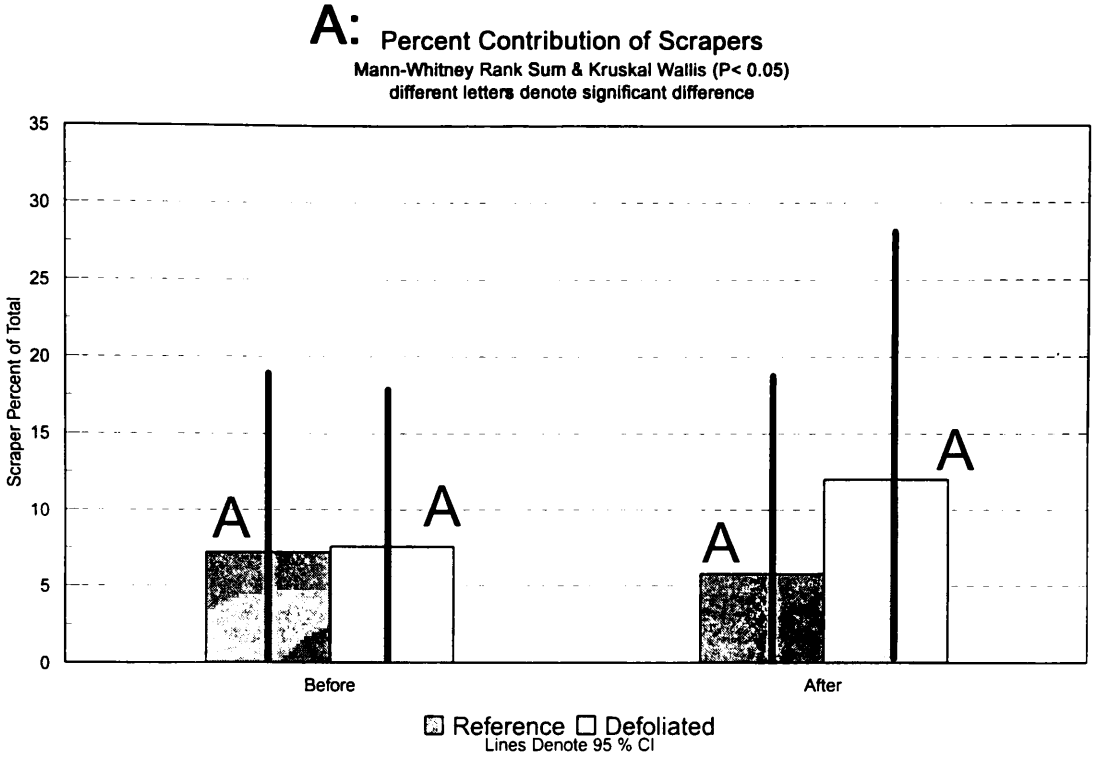
Fig 2.6. Percent contribution of predators. There was no significant difference in the percent contribution of predators to the benthic community before or after defoliation.

proportion of shredder-detritivores in defoliated streams 1 yr after defoliation. The increase in the contribution of scrapers to the benthic community was observed at all defoliated sites (Fig. 2.7). The decrease in the contribution of shredders was also observed in all defoliated streams, but the treatment mean was influenced primarily by a large reduction in the number of shredders in South Fork of the Moormans River (defoliated) after defoliation. The other defoliated sites only showed slight decreases in shredder abundance (Fig. 2.8). The observed differences in relative abundance of the shredder and scraper functional groups are probably due to the natural variability of sampling headwater streams.

I observed no statistically significant difference in the similarity of treatments by use of the Bray-Curtis Coefficient (Table 2.3, Fig. 2.9), nor in dissimilarity expressed as chord distance (Table 2.4, Fig. 2.10).

Results of ANOVA revealed a significant difference in the similarity of the treatments as expressed by the Index of Biotic similarity (Table 2.5). Pairwise comparison of means by LSD showed that the similarity of defoliated to reference streams was significantly lower after defoliation than before (Fig. 2.11)

The application of bootstrap analysis to similarity clusters generated by the Bray-Curtis coefficient of similarity did not cause the null hypothesis to be rejected for any linkages formed, indicating benthic community structure of all study sites was similar enough to be considered the same community before and after defoliation (Fig. 2.12).



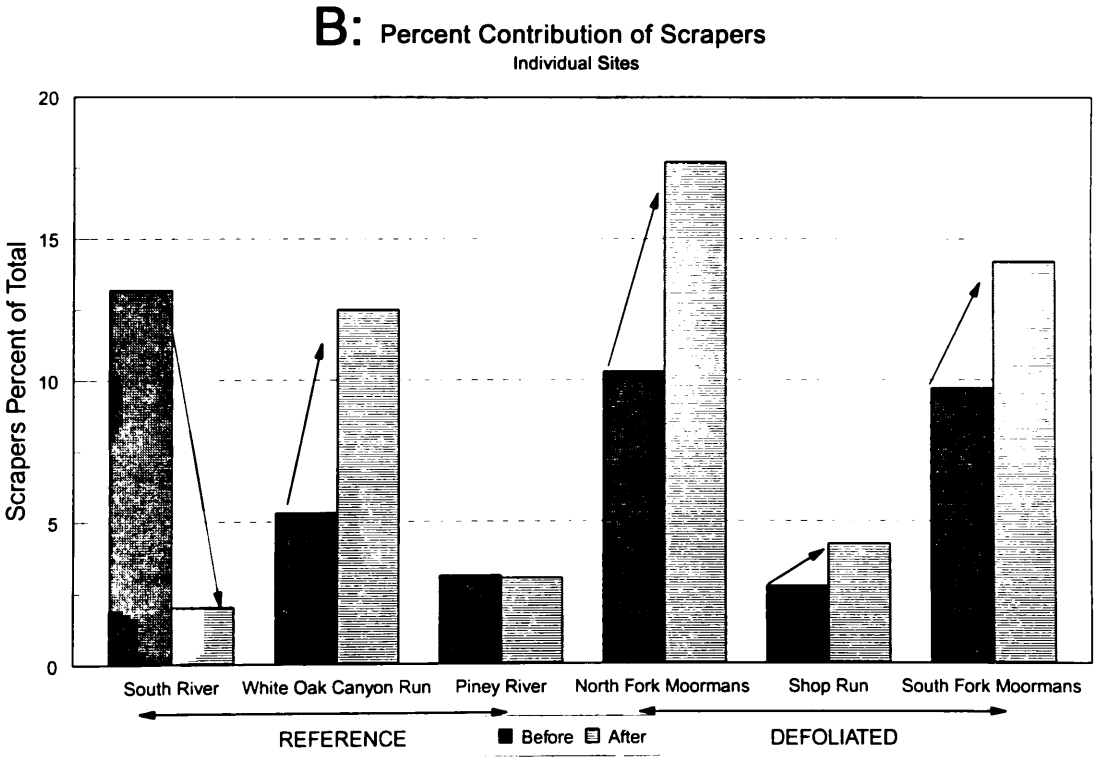
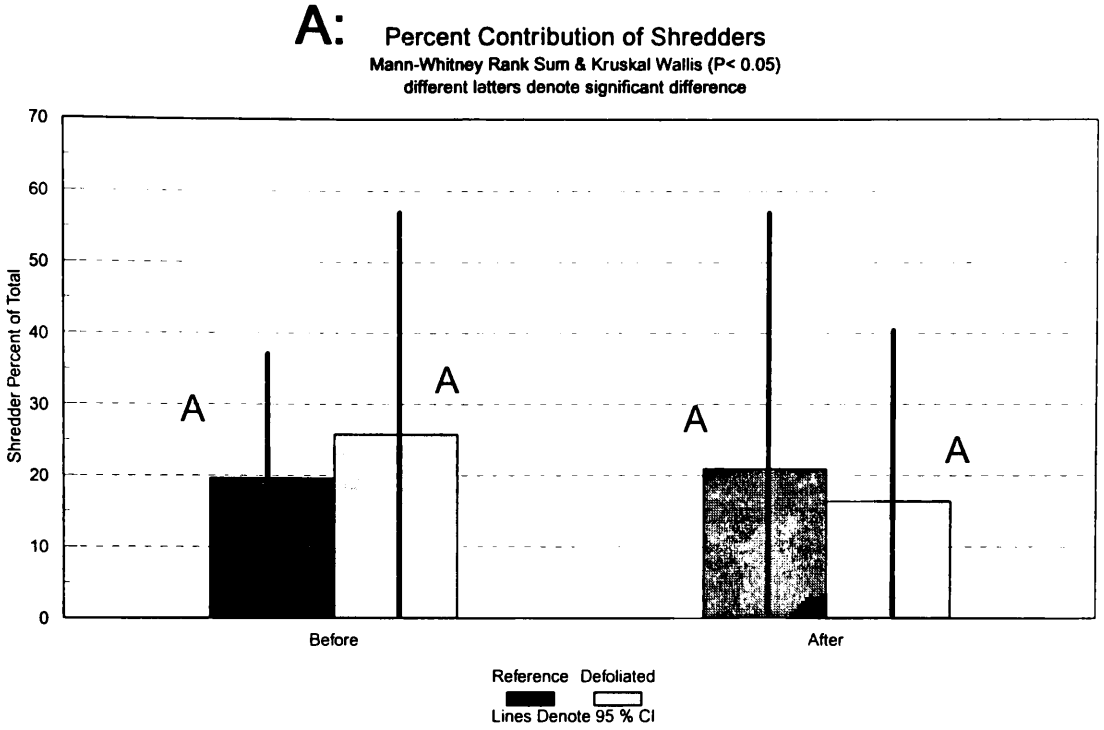


Fig.2. 7. Percent contribution of scrapers. There was no significant difference in the percent contribution of scrappers in the benthic community before or after defoliation **(A)**. All Impacted sites showed an increase in the relative abundance of scrapers **(B)**. While not statistically significant, this increase could be indicative of a trend.



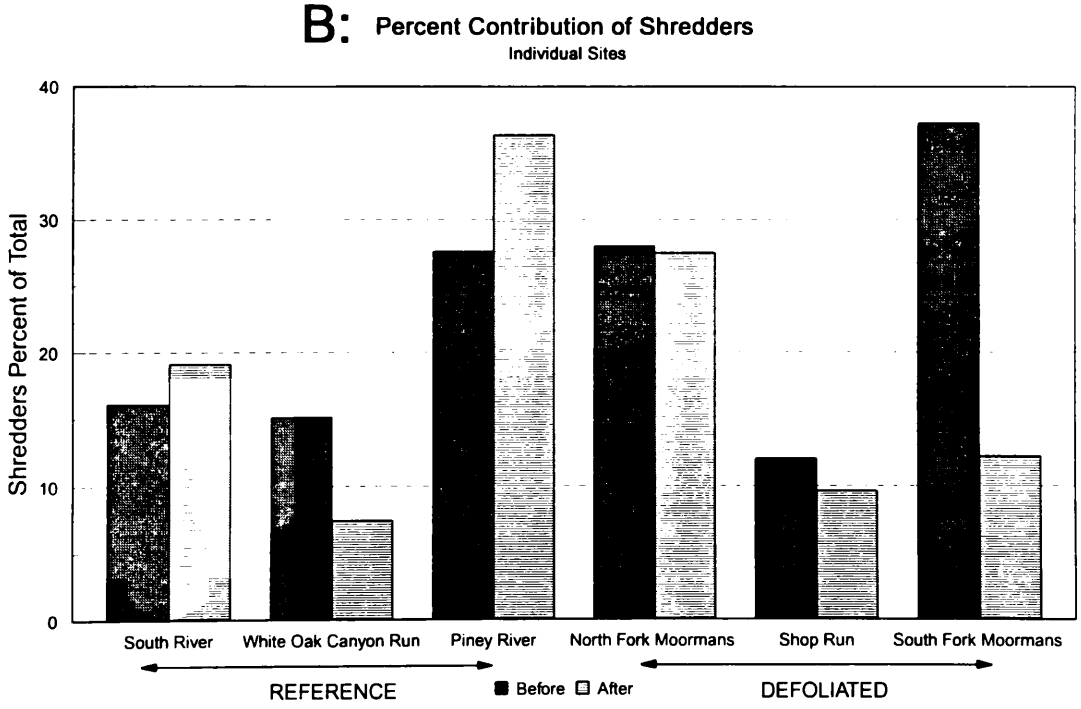


Fig. 2.8. Percent contribution of shredders. There was no significant difference in the percent contribution of shredders to the benthic community before or afterdefoliation **(A)**. The slight decrease in the abundance of shredder taxa in the defoliated treatment after defoliation was due to a large change at only one site (South Fork of the Moormans River) **(B)**.

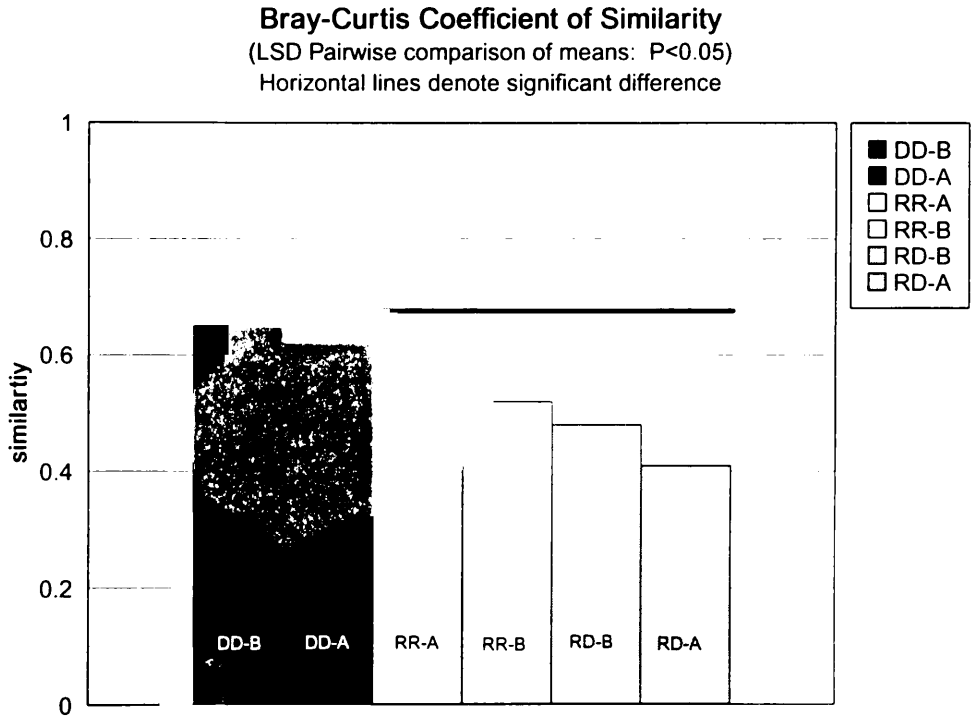


Fig. 2.9. Bray-Curtis Similarity. There was no significant difference in the Bray-Curtis coefficient of similarity of the treatments compared by ANOVA (see Fig.2.1 for treatment identification).

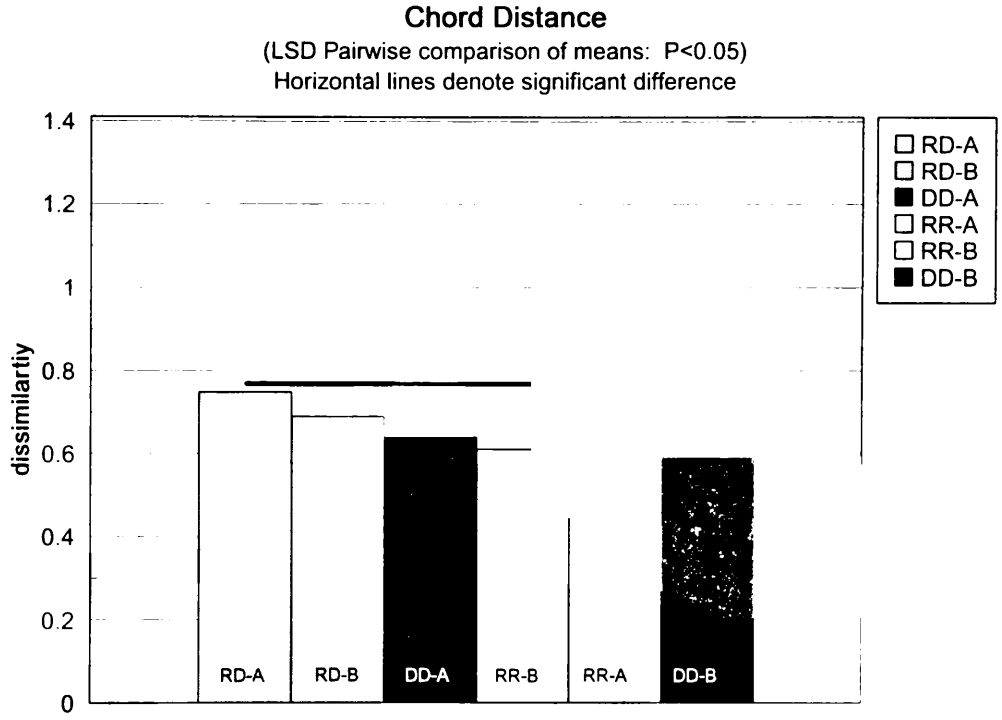


Fig. 2.10. Chord distance. There was no significant difference in the Chord distance (dissimilarity) of the treatments compared by ANOVA (see Fig.2.1 for treatment identification)

Table 2.3. Results of ANOVA for comparison of similarity of study sites (Bray-Curtis)

Source	df	Sums of Squares	Mean Square	F	P
Between	5	887.0	117.4	1.13	0.374
Within	24	3783.4	157.6		
Total	29	4670.4			

Table 2.4. Results of ANOVA for comparison of dissimilarity of study sites (Chord Distance)

Source	df	Sums of Squares	Mean Square	F	P
Between	5	564.94	112.98	0.96	0.460
Within	24	2816.7	117.36		
Total	29	3381.7			

Table 2.5. Results of ANOVA for comparison of the Index of Biotic Similarity of study sites

Source	df	Sums of Squares	Mean Square	F	P
Between	5	255.3	51.1	5.29	0.0021
Within	24	231.7	9.66		
Total	29	487.1			

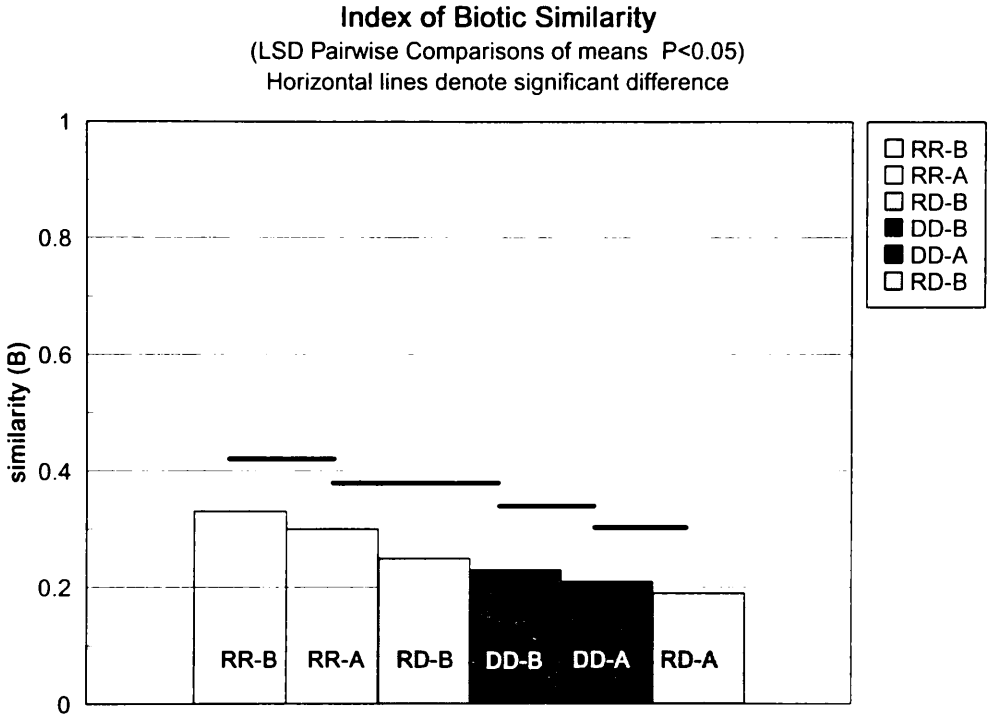


Fig. 2.11. Index of Biotic Similarity. ANOVA indicated there was a significant difference in the Index Biotic Similarity among the treatments (see fig. 2.1 for treatment identification). There several statistically distict groups of treatments, but it is noteworthy that the similarity of reference to defoliated sites is significantly less after defloliation (RD-B) than before (RD-A).

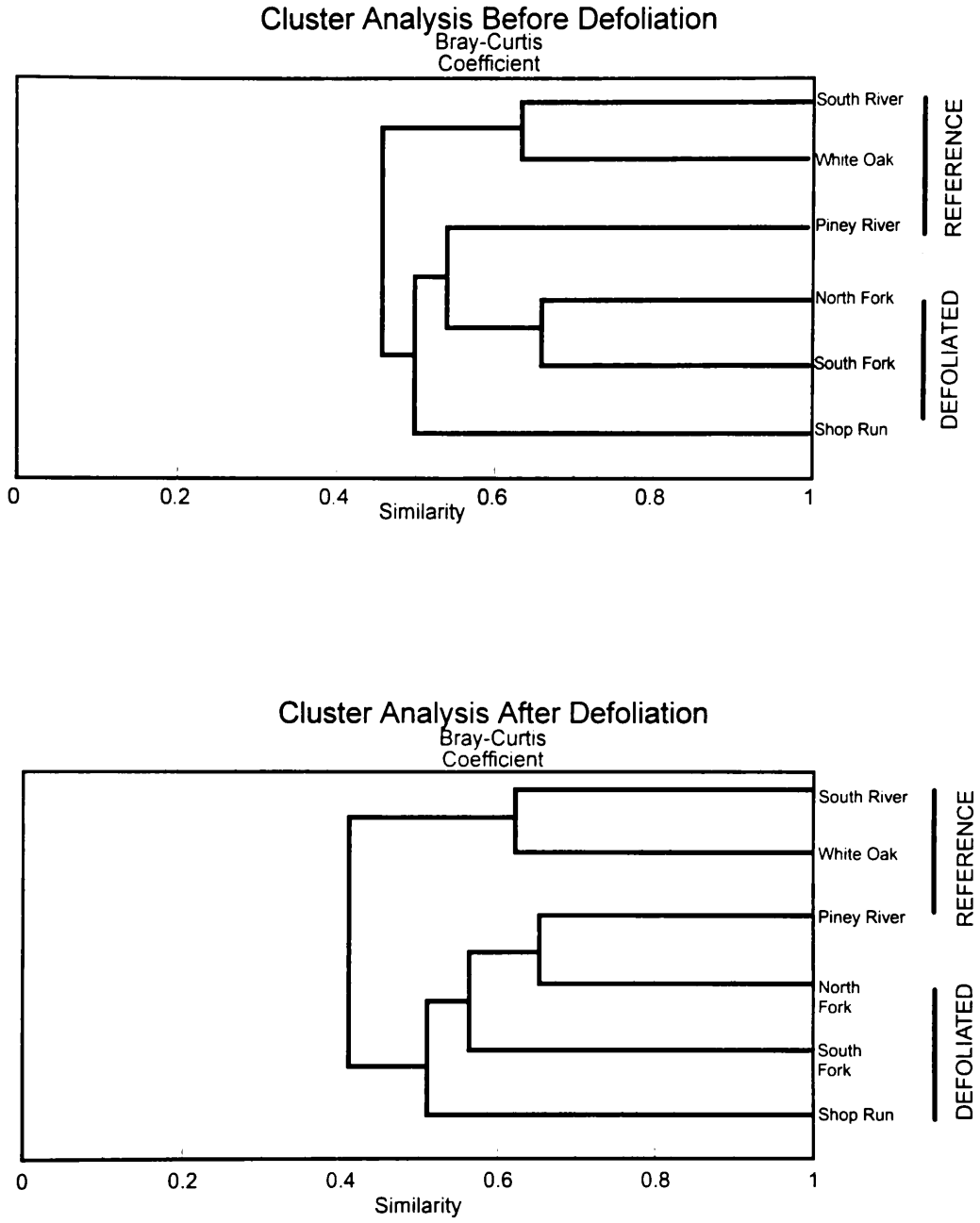


Fig. 2. 12. Cluster analysis. These dendrograms were produced by application of Bootstrap procedures to cluster analysis. The Null hypothesis tested was : "The communities or groups of communities joined by forming a linkage are similar enough to be considered the same community". This null hypothesis was not rejected (ie. P> 0.05) for any linkage before or after defoliation, indicating that the communities are similar before and after defoliation.

Discussion

Almost all of the measures of community structure and function did not change after defoliation by gypsy moth larvae. The only measure significantly affected by defoliation, the Index of Biotic Similarity, is sensitive to changes in rare taxa. This indicates that, at most, there were only subtle changes in community structure during the first year of defoliation. This study only compared the benthic community structure of streams over a 1-yr period, which may not be enough time to resolve trends of change in benthic community structure. Comparison of communities for several years after defoliation could provide greater insight into the effects of extensive defoliation by gypsy moth larvae on the ecology of headwater streams.

The indices of community structure I employed reflect changes in survival, but they do not allow observation of changes in the condition of individuals. Individual growth is not reflected in taxa abundance data, but it may be ecologically important for subsequent generations because fecundity is strongly influenced by growth and condition of adult insects (Sweeney 1984). The third part of this document examines the short-term effects of defoliation by gypsy moth larvae on the benthic macroinvertebrates of headwater streams with greater resolution than gross community structure by estimating the secondary production of insects representing different functional feeding groups.

PART 3: SHORT-TERM EFFECTS OF DEFOLIATION BY GYPSY MOTH LARVAE ON GROWTH AND PRODUCTION OF AQUATIC INSECTS OCCUPYING DIFFERENT FUNCTIONAL FEEDING GROUPS IN APPALACHIAN HEADWATER STREAMS

INTRODUCTION

Part 3 of this thesis examines the effects of gypsy moth defoliation on the ecology of benthic insects with greater resolution than any of the previous sections. I compared the secondary production and growth of taxa representative of the shredder-detritivore, collector-filterer, and scraper functional-feeding groups in the impacted streams with the reference streams. This section addresses the third objective of my thesis and tests the null-hypothesis: Ho: Riparian defoliation by gypsy moth larvae has no effect on the function of benthic macroinvertebrates in headwater streams.

METHODS

I sampled benthic macroinvertebrates periodically from three riffles in each stream with a Portable Invertebrate Box Sampler (PIBS (sample area = $0.1m^2$)), starting in March 1991 and continuing through March 1992. I collected benthos once in March, once every 2 wk from April through October, and monthly from November through March 1992. I preserved the entire sample shortly after collection with 95 % ethanol, and later separated all benthic macroinvertebrates from debris in the laboratory. I identified members of the family Peltoperlidae (Plecoptera) to genus by the key provided by Stewart and Stark (1988), and used them to represent the shredder-detritivore functional-feeding group (Merrit and Cummins 1984). Peltoperlidae occurred at all study sites but was represented by different proportions of two genera. One site (Shop Run) had exclusively *Peltoperla* sp., two others (Piney River and White Oak Canyon Run) had exclusively *Tallaperla* sp., and the remaining sites (South River, North and South Forks of the Moormans River) had mostly *Tallaperla* sp. with some *Peltoperla* sp. The diagnostic character used to separate these two genera is a pair of dark spots on the meso- and metanota (Stewart and Stark, 1988), but this character

was not apparent in the specimens I collected until nymphs attained a Head-Capsule Width (HCW) of ≅ 900 μm. I collected nymphs as small as HCW ≅ 300 μm and as large as HCW ≅ 2300 μm. There was a significant period when larvae of the two genera were indistinguishable. They occupied a similar ecological niche and their life-histories appeared to be synchronous. Therefore, I believe that family-level production, by the size-frequency method, was the only method valid for comparing peltoperlid success in defoliated and reference streams. Huryn and Wallace (1987) experienced a similar problem with Peltoperlidae and circumvented it by calculating family-level secondary production in a stream containing three peltoperlid genera.

I identified all Hydropsychidae larvae to the lowest taxonomic level possible (Wiggins 1977) and light-trapped adults to identify species occurring at study sites. I sent the adults to Dr. Oliver S. Flint at the U. S. National Museum to confirm species identifications. All streams contained several species of *Hydropsyche*, and *Diplectrona modesta* Banks. Two streams had very low densities of *Homoplectra (= Aphropsyche) moticola* (Flint). I used *D. modesta* to represent the collector-filterer functional-feeding group because it was most abundant and *Diplectrona* was a monotypic genus in the streams examined.

The genus *Glossosoma* (Trichoptera: Glossosomatidae) is a scraper (Merrit and Cummins, 1984) and is represented by only one species, *Glossosoma nigrior* Banks, in the state of Virginia (Parker and Voshell 1981). It was collected from all study sites and was used as a representative of the scraper functional-feeding group in this study.

Environmental conditions of a study treatment may favor the development of some insect species more than the other treatment. Insects growing under favorable conditions (e.g., food quantity / quality, temperature, etc.) may accumulate more lipids than individuals in a less-hospitable environment. Ethanol preservative could obscure differences in mass by dissolving lipids and other soluble constituents of insects. Additionally, benthos samples collected with the PIBS are often badly damaged. To circumvent these potential errors in

mass, I collected individuals qualitatively from each stream for regression of the head capsule width - dry mass (HCW - DM) relationship occasionally from July of 1991 through August of 1992. I carefully removed individuals insects from surfaces of stream debris with soft forceps, or a dropper, and placed them in 10-ml plastic vials containing stream water. I kept the vials on ice in the field and froze them upon return to the laboratory. I measured the widest distance across the dorsal surface of head capsules of ~200 individuals from each taxon with a Zeiss / Boeckler filar eyepiece which was interfaced with an IBM-PC. I determined the dry mass of completely intact individuals of a given size class by drying them at 60 °C for 24 h and weighing them with a Mettler AE163 electronic microbalance. I calculated separate regression equations for each taxon in the reference and defoliated treatment using a $\log_e$-$\log_e$ transformation (Smock 1980). I estimated the dry mass of preserved individuals by measuring their HCW (as above) and applying the data to the appropriate regression equation.

I estimated secondary production of each taxon in each stream by the size-frequency method (Hynes and Coleman 1968, Hamilton 1969, Benke 1984, Benke 1993) and compared annual secondary production of each taxon in the reference treatment with the defoliated treatment with a two-sample t-test. There were some differences in life-history patterns between the different taxa. Their effect on secondary production calculation is discussed with the life-history results of each taxon.

I estimated the dry mass of individuals collected in the quantitative samples with the appropriate regression equation and used the values to calculate the annual growth rate of each taxon, in each stream, by the instantaneous growth method (Mackay 1972), as follows:

$$IGR = \frac{(\ln(M_t) - \ln(M_0))}{t}$$

where M_t = mean individual mass at time = t,

M_0 = mean individual mass at time = zero,

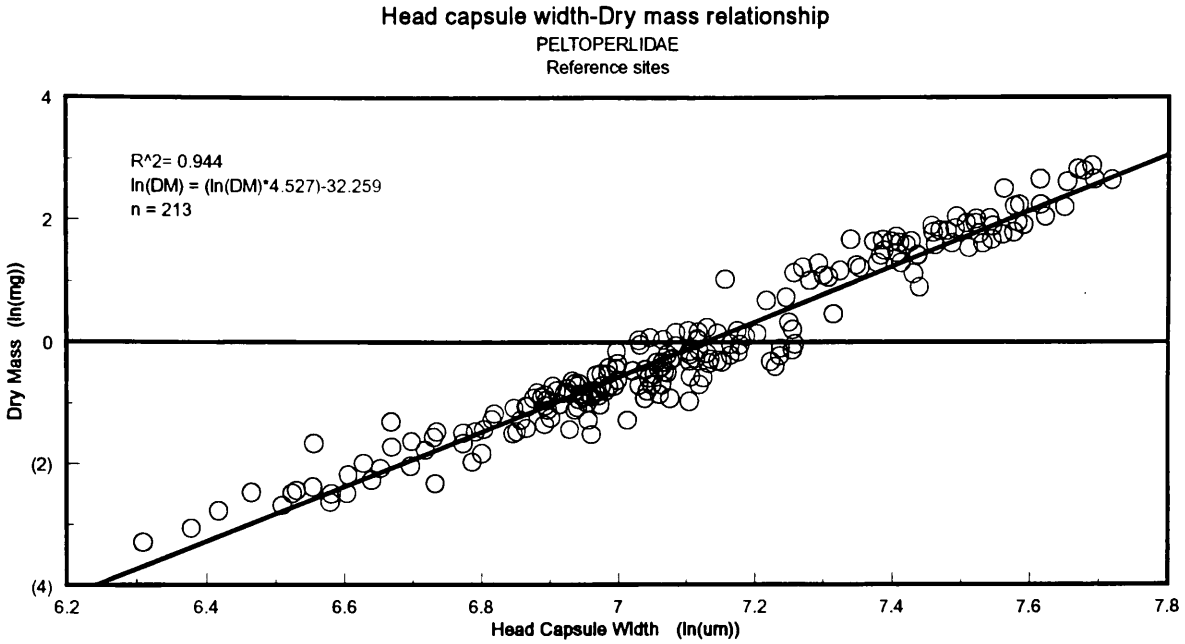
t = elapsed time.

I used regression analysis to fit an equation to the mean individual dry mass ($\log_e$) through time from the beginning of the cohort for both treatments. Because the instantaneous growth rate is actually the slope of the line described by the above regression, I used "the method of comparing two straight lines using separate regression fits" (Method I, Kleinbaum et al. 1988) to test for significance of differences in growth. This procedure is analogous to analysis of covariance.

RESULTS

Peltoperlidae

Head capsule-width measurements did not reveal any discrete patterns in size-distribution of Peltoperlidae, so arbitrary size classes of 300 μm (beginning at 200 μm) were set for life-history description and size-frequency calculation of secondary production. The HCW-DM relationships of Peltoperlidae populations were similar between treatments (Fig. 3.1). The HCW - DW relationships of reference and defoliated Peltoperlidae populations were best described by the equations:



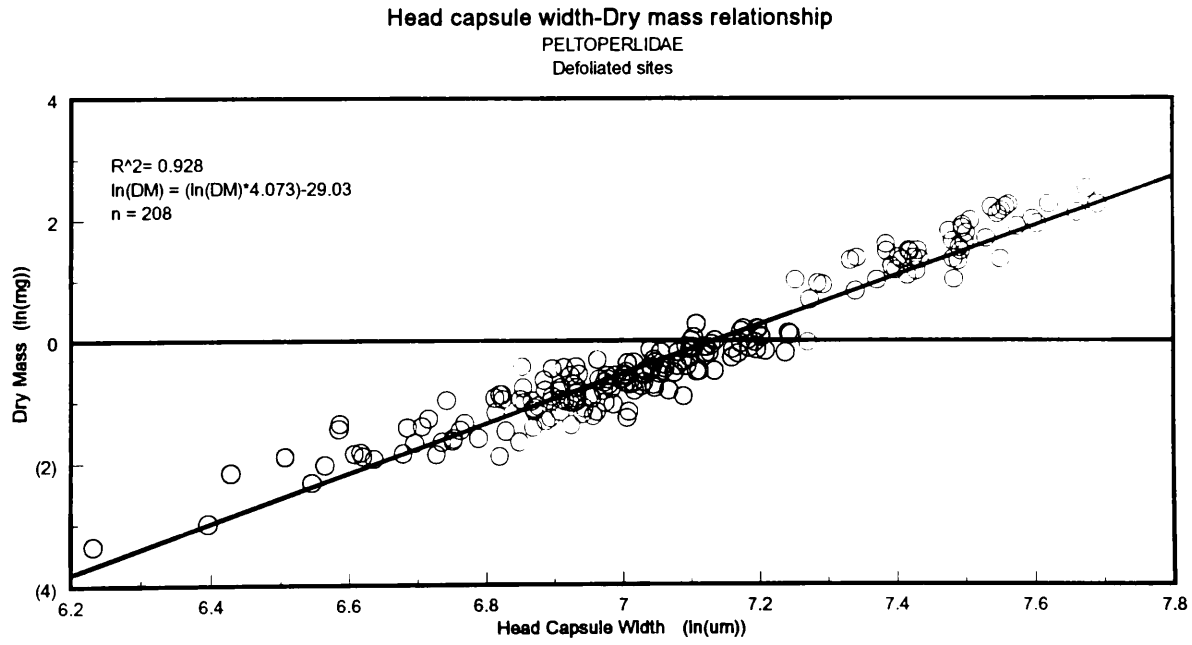


Fig. 3.1. Head Capsule Width-Dry Mass Relationship of Peltoperlidae in reference and defoliated streams.

Reference

$\ln(DM) = (\ln(HCW) \times 4.527) - 32.259$

$R^2 = 0.944$

$n = 213$

Defoliated

$\ln(DM) = (\ln(HCW) \times 4.073) - 29.03$

$R^2 = 0.928$

$n = 208$

Peltoperlidae exuviae were observed on stream-side stones and vegetation in April, and adults were collected and observed in May. Both genera, *Tallaperla* and *Peltoperla*, began a synchronous, univoltine life cycle in May and appeared to have a Cohort Production Interval (CPI) of 1 yr (Fig. 3.2).

The Peltoperlidae in reference and defoliated treatments grew at significantly different rates ($P < 0.05$). Reference treatment Peltoperlidae had an annual instantaneous growth rate of 0.016 mg / d compared to 0.012 mg / d for Peltoperlidae of the defoliated treatment. This difference appears to be due to lower mass of nymphs near the end of cohort development (Fig. 3.3).

Annual secondary production for Peltoperlidae in reference and defoliated treatments averaged 135 and 208 mg / m^2 respectively, and was not significantly different (Table 3.1). Mean annual Biomass ($\overline{B}$) of Peltoperlidae in reference and defoliated treatments was 24.4 mg and 40.3 mg respectively, yielding mean $P / \overline{B}$ ratios of 5.3 and 5.2, respectively. These differences were not statistically significant.

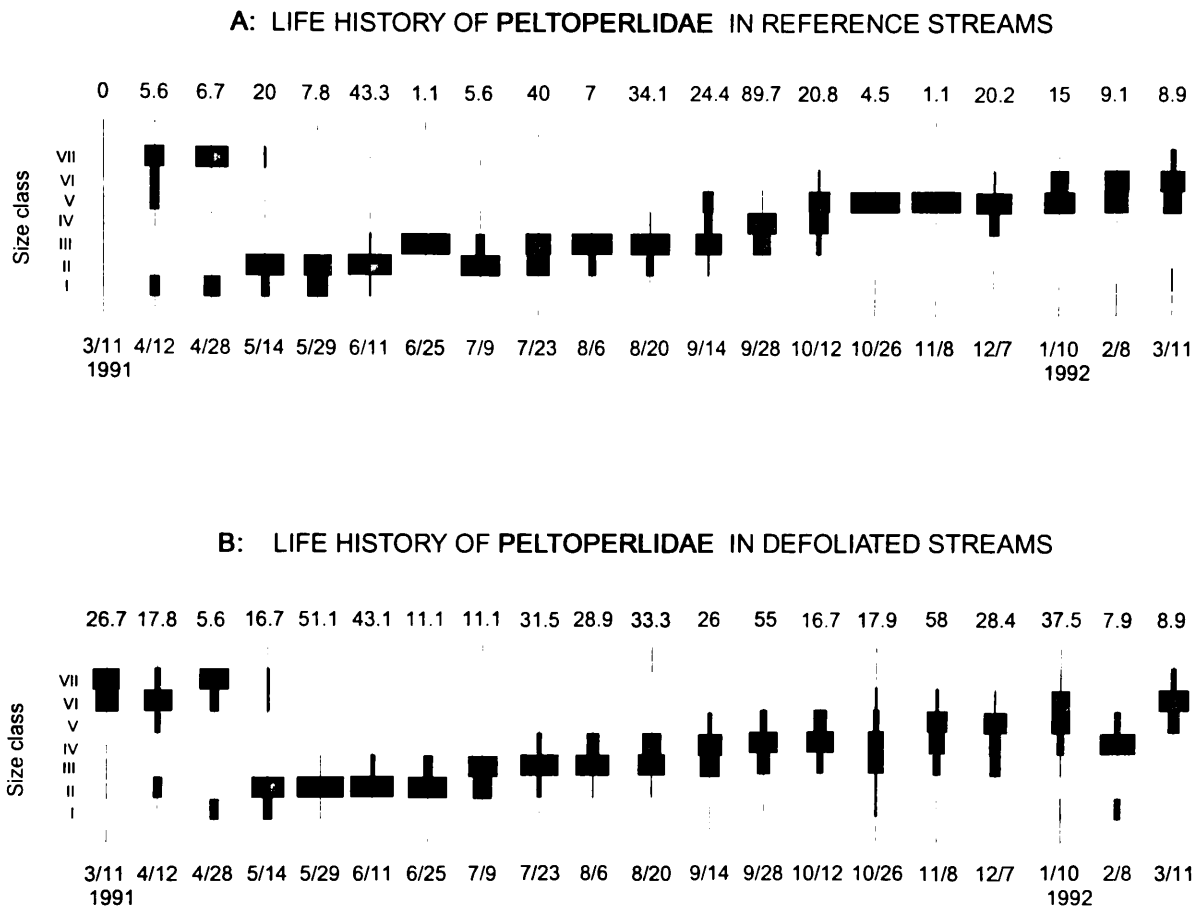


Fig. 3.2. Life-history of Peltoperlidae in (A) reference streams and (B) defoliated streams. The bars represent the relative abundance of collected individuals in each size-class. Each sampling date has an axis and the numbers along the top of the figures represent the mean density (No. / sq. m) of individuals. ■ = 100%

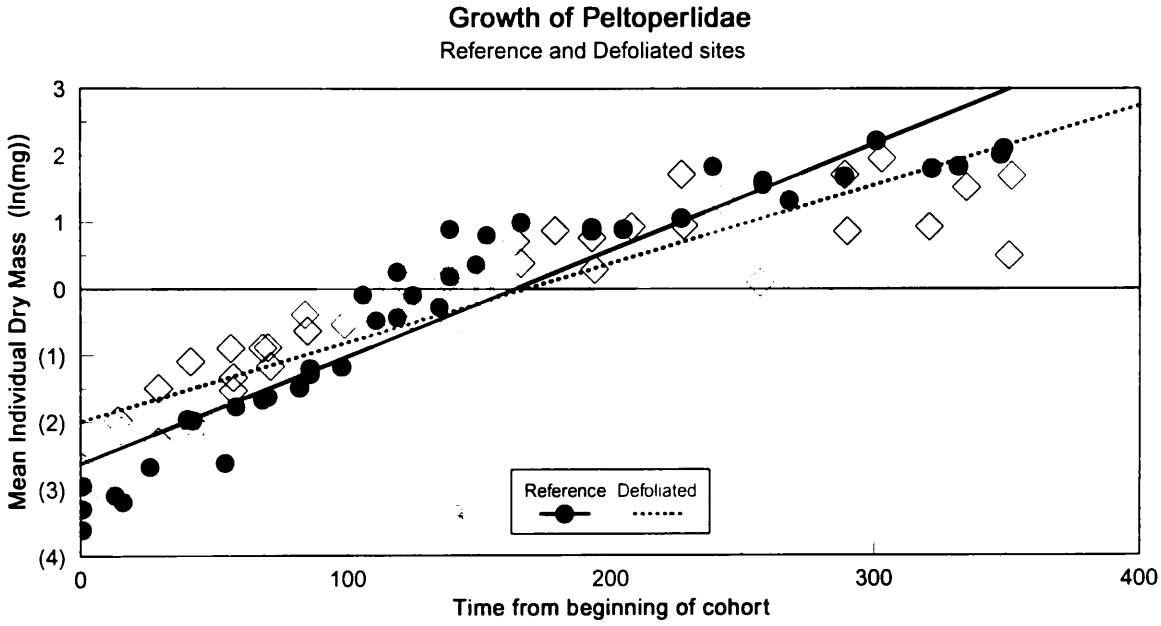


Fig. 3.3. Growth of Peltoperlidae in refernce and impacted streams. The Peltoperlidae in reference streams grew significantly faster than those in the defoliated streams.

Table 3.2. Secondary production and annual mean biomass of *D. modesta* by site and treatment. *D. modesta* populations in reference streams had significantly greater secondary production than those in defoliated streams (P=0.00075). Annual mean biomass and P/$\overline{B}$ ratios were not significantly different between treatments (P=0.054 and P=0.504 respectively).

Site	Treatment	Site Production	Treatment Production	Annual mean Biomass	mean $\overline{B}$	P/$\overline{B}$ ratio	mean P / $\overline{B}$
South River	Reference	355		53.4		6.64	
White Oak Canyon	Reference	394	389 [a]	48.8	60.5[a]	8.06	6.7[a]
Piney River	Reference	419		79.3		5.28	
North Fork Moormans	Defoliated	207		32.0		6.48	
Shop Run	Defoliated	196	207 [b]	37.0	34.6[a]	5.29	6.0[a]
South Fork Moormans	Defoliated	218		34.8		6.27	

Diplectrona modesta

Measurement of head-capsule widths for determination of HCW-DM relationship reviled five distinct size classes corresponding to the five instars of *D. modesta*'s larval life-stage. Too few individuals were collected to permit determination of the mean dry mass of the first instar (HCW ≅ 150 μm). The HCW-DM relationships were similar in each treatment and the four clusters of points (Fig. 3.4) correspond to instars II through V. The five instars were used as size classes for estimation of secondary production. The HCW-DW relationships of reference and defoliated *D. modesta* populations were best described by the equations:

Reference

$\ln(DM) = (\ln(HCW) \times 4.02) - 27.60$

$R^2 = 0.838$

$n = 176$

Defoliated

$\ln(DM) = (\ln(HCW) \times 4.25) - 29.16$

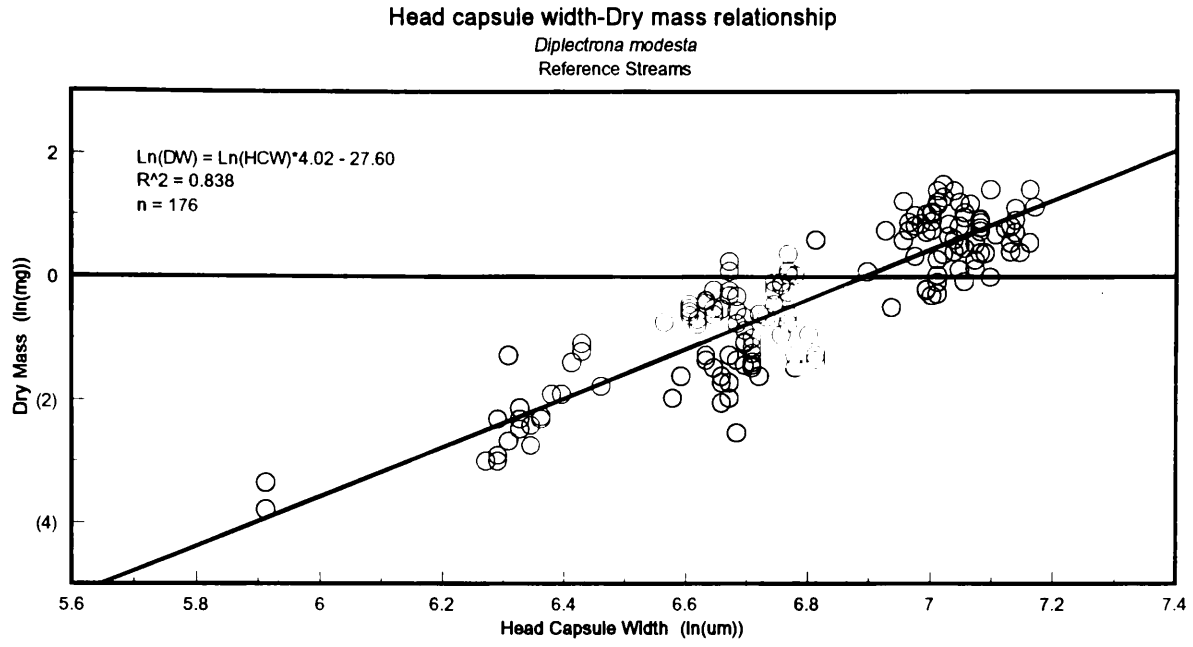
$R^2 = 0.841$

$n = 184$

Diplectrona modesta populations in reference streams exhibited a synchronous, univoltine life cycle beginning in June. In the defoliated streams, early-instar larvae occurred earlier and cohort development appeared less synchronous than in reference streams. Fifth instar larvae did not occur until December in reference streams, but were collected as early as September in defoliated streams (Fig. 3.5).

The annual IGR of *D. modesta* larvae was not significantly different between treatments and the lack of synchrony in larval development resulted in reduced R^2 values for the growth model of defoliated streams (Fig. 3.6).

Secondary production and annual mean biomass of *D. modesta* were significantly greater in reference than defoliated streams (Table 3.2).



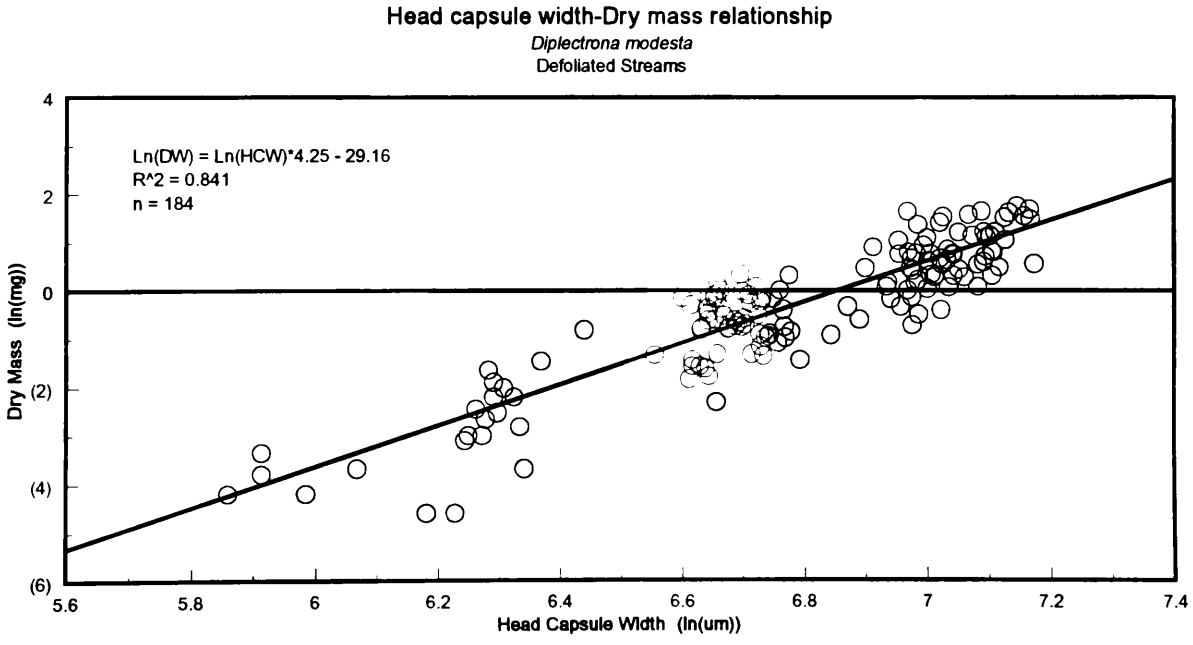


Fig. 3.4. Head Capsule Width-Dry Mass Relationship of *Diplectrona modesta* in reference and defoliated streams

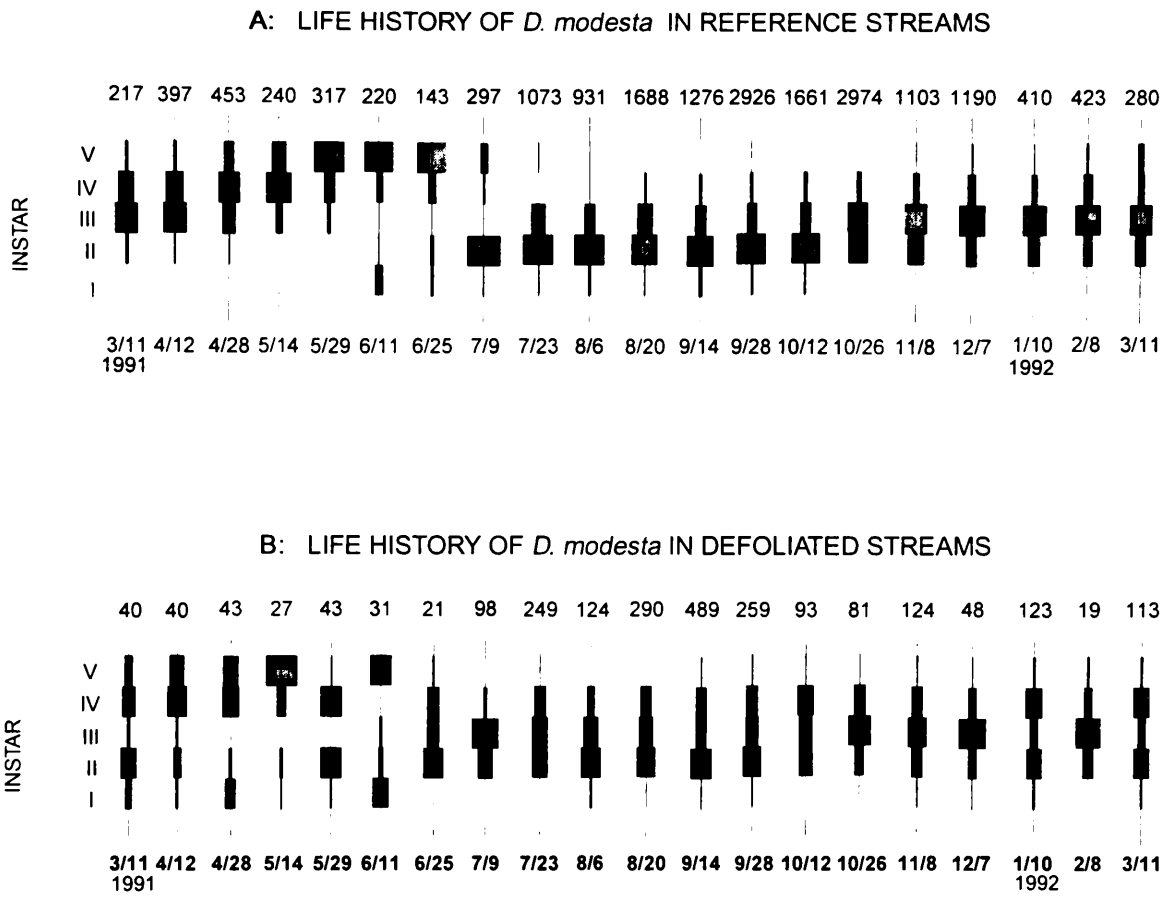


Fig. 3.5. Life-history of *Diplectrona modesta* in (A) reference streams and (B) defoliated streams. The bars represent the relative abundance of collected individuals in each size-class. Each sampling date has an axis and the numbers along the top of the figures represent the mean density (No. / sq. m) of individuals. ☐ = 100 %

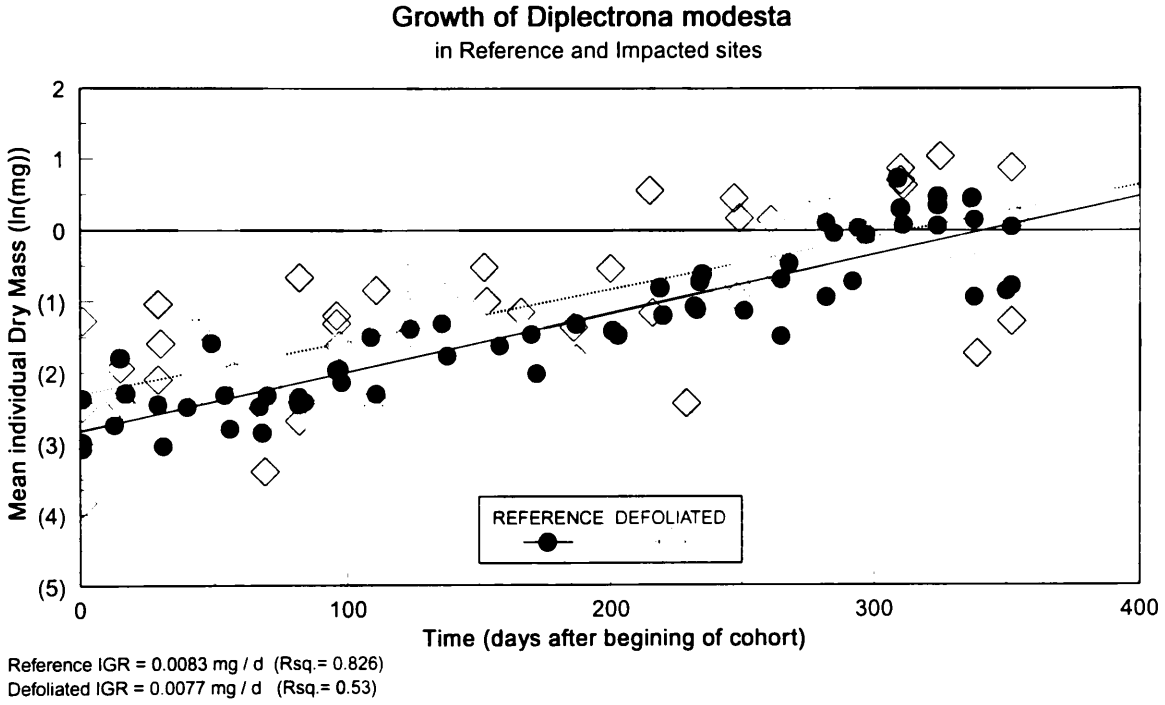


Fig. 3.6. Growth of *Diplectrona modesta* in refernce and impacted streams. There was no significant difference in the annual instantaneous growth rate between treatments.

Table 3.1. Annual secondary production (dry mass mg / m^2) and annual mean biomass of Peltoperlidae by site and treatment. There was no significant difference between the reference and defoliated treatments in annual production (P=0.41), annual mean biomass (P=0.36), P/$\overline{B}$ ratio (P=0.81). Treatment (Ref. = Reference; Def = Defoliated)

Site	Treatment	Site Production	Treatment Production	Annual mean Biomass	mean $\overline{B}$	P/$\overline{B}$ ratio	mean P / $\overline{B}$
South River	Reference	240		41.2		5.8	
White Oak Canyon	Reference	78.0	135 [a]	15.6	24.4[a]	5.0	5.3 [a]
Piney River	Reference	87.6		16.4		5.3	
North Fork Moormans	Defoliated	297		63.3		4.7	
Shop Run	Defoliated	231	208 [a]	39.8	40.3[a]	5.8	5.2 [a]
South Fork Moormans	Defoliated	97.0		18.0		5.3	

Glossosoma nigrior

Regression analysis described the HCW-DM relationship of *G. nigrior* as shown below and identified five distinct instars. Three first-instar individuals were measured to have a HCW ≅ 115 - 125 μm, but did not weigh enough to determine dry mass. The other four instars appear as clusters of points on the regression plots (Fig. 3.7). The five instars were used as the size-classes for estimation of secondary production. The HCW-DW relationships of reference and defoliated *G. nigrior* populations were best described by the equations:

Reference

$\ln(DM) = (\ln(HCW) \times 3.925) - 26.11$

$R^2 = 0.794$

$n = 199$

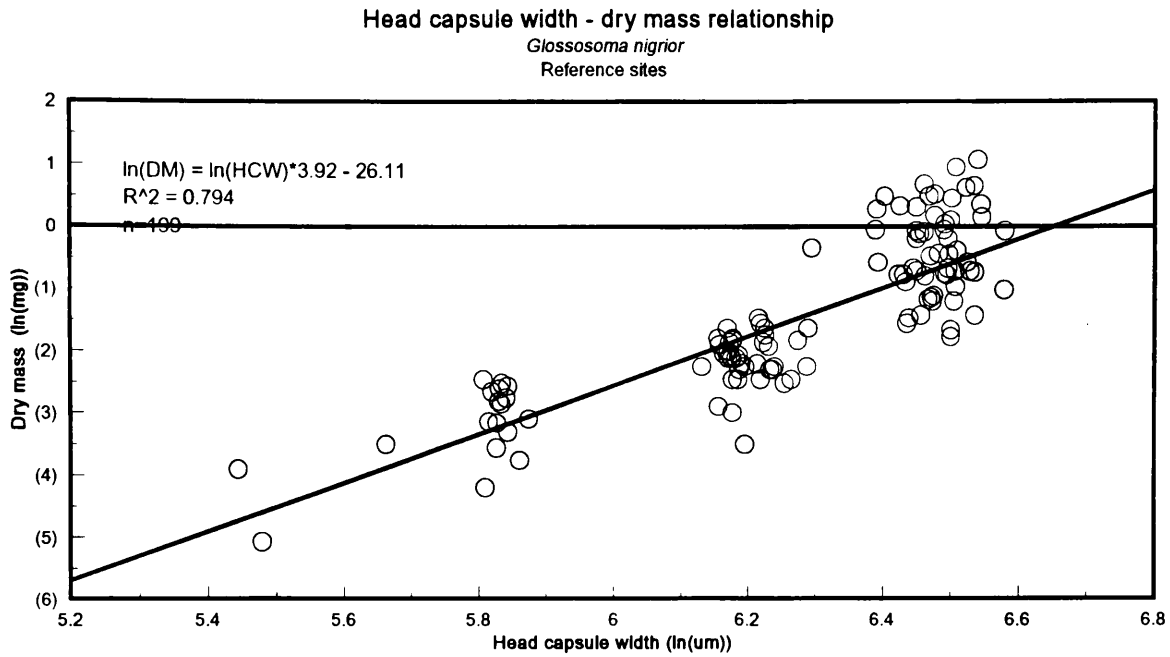
Defoliated

$\ln(DM) = (\ln(HCW) \times 4.255) - 27.89$

$R^2 = 0.81$

$n = 239$

Larval development of *G. nigrior* is asynchronous (Figs. 3.8 - 3.10), so field data did not permit easy identification of individual cohorts or calculation of annual instantaneous growth rates. Populations of *G. nigrior* in South River, White Oak Canyon Run, Piney River, and Shop Run showed a pattern of larval development similar to the univoltine population described by Trapp and Hendricks (1984). Populations in the North and South Forks of the Moormans River resembled the bivoltine populations described by Trapp and Hendricks (1984). They attributed these differences in voltinism to different temperature regimes at their study sites but did not consider any other parameters which could have affected larval development (e.g., periphyton quality or quantity). Oemke (1989) found that temperature had a stronger influence on larval growth than did food quality. The population in White Oak Canyon Run may have been intermediate of the univoltine and bivoltine populations because first-instar larvae were collected in October, after all late-instar larvae had pupated. Although this coincided with development of the second cohort in the bivoltine populations,



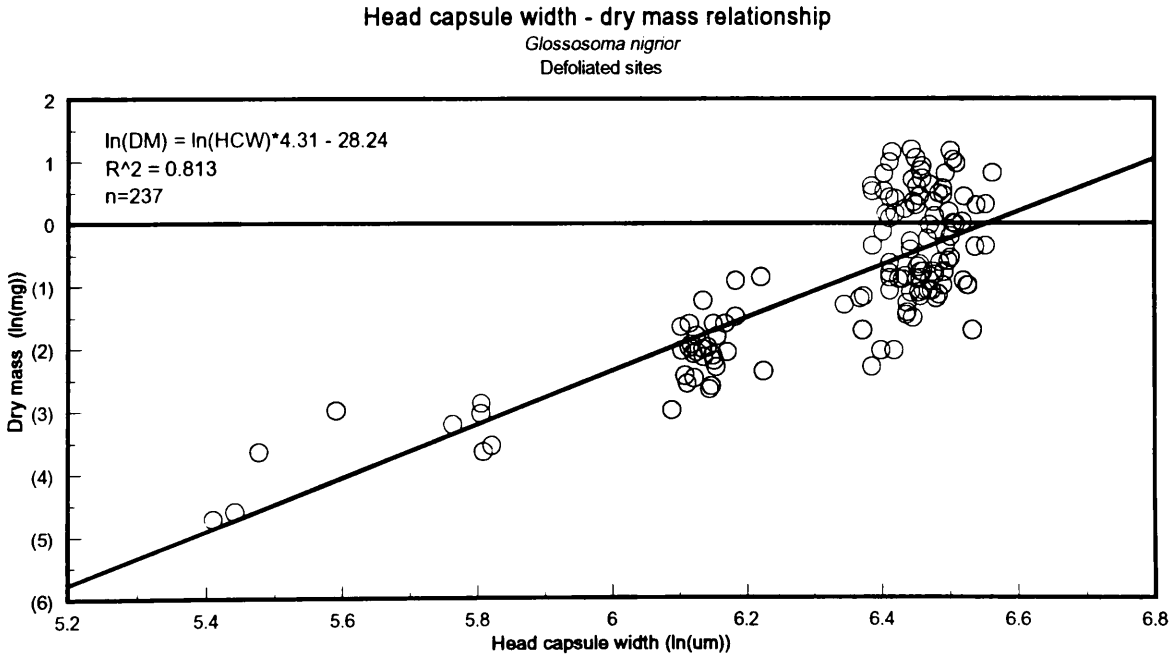


Fig. 3.7. Head Capsule Width-Dry Mass Relationship of *Glossosoma nigrior* in reference and defoliated streams.

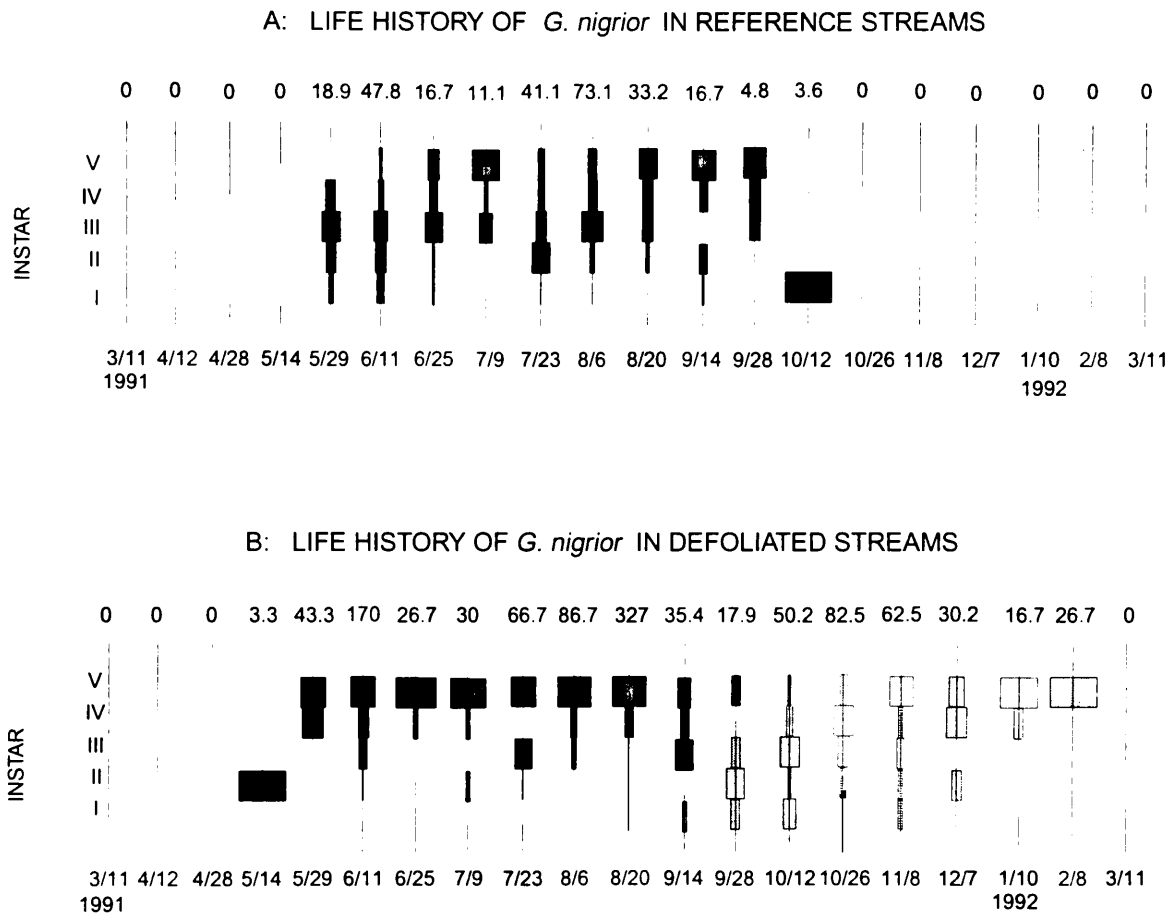


Fig. 3.8. Life-history of *Glossosoma nigrior* in (A) reference streams and (B) defoliated streams.The bars represent the relative abundance of collected individuals in each size-class. Each sampling date has an axis and the numbers along the top of the figures represent the mean density (No. / sq. m) of individuals. ■ = 100%

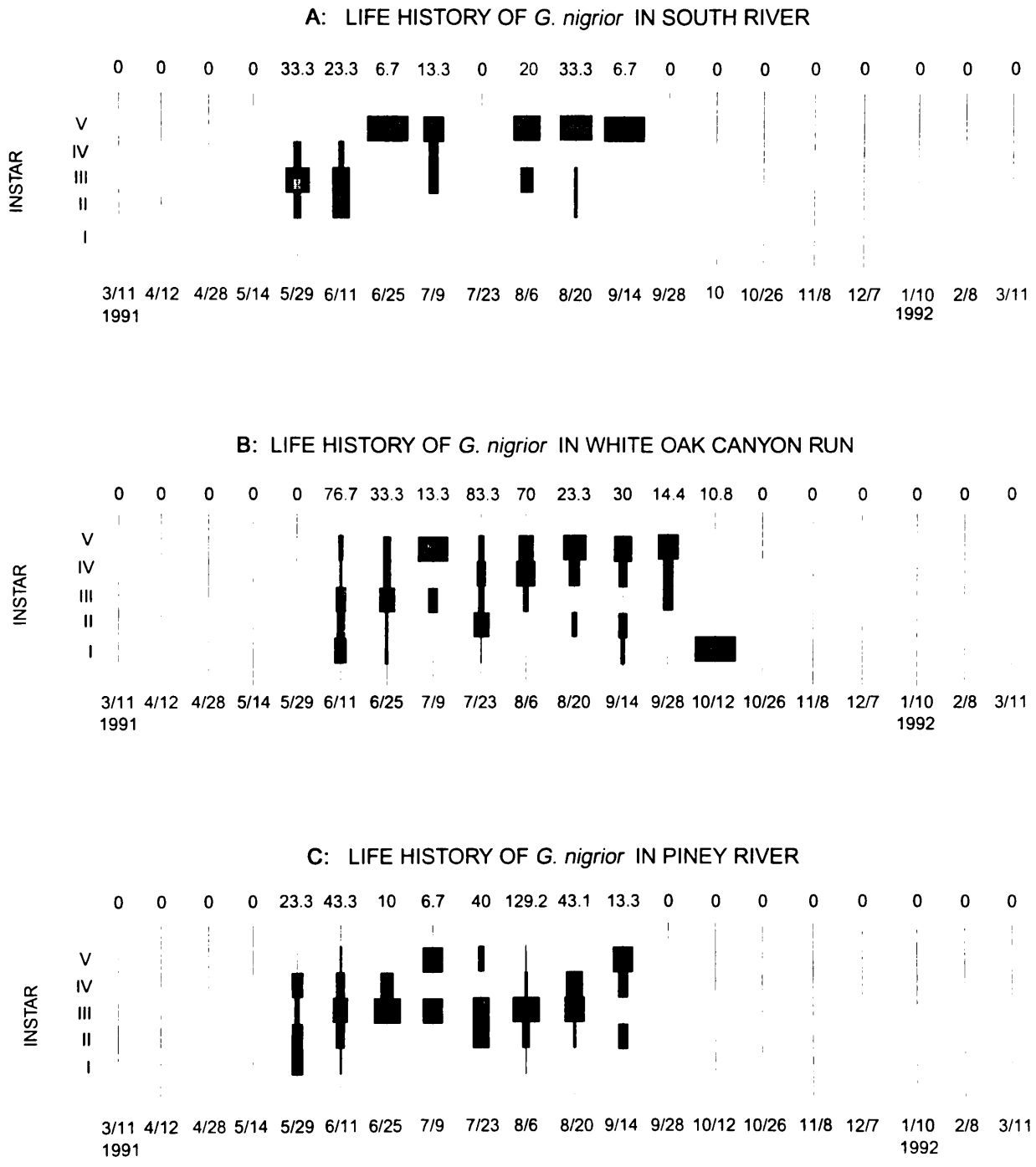


Fig. 3.9. Life-history of *Glossosoma nigrior* in reference streams [(A)South River; (B) White Oak Canyon Run; and (C) Piney River]. The bars represent the relative abundance of collected individuals in each size-class. Each sampling date has an axis and the numbers along the top of the figures represent the mean density (No. / sq. m) of individuals. ■ = 100%

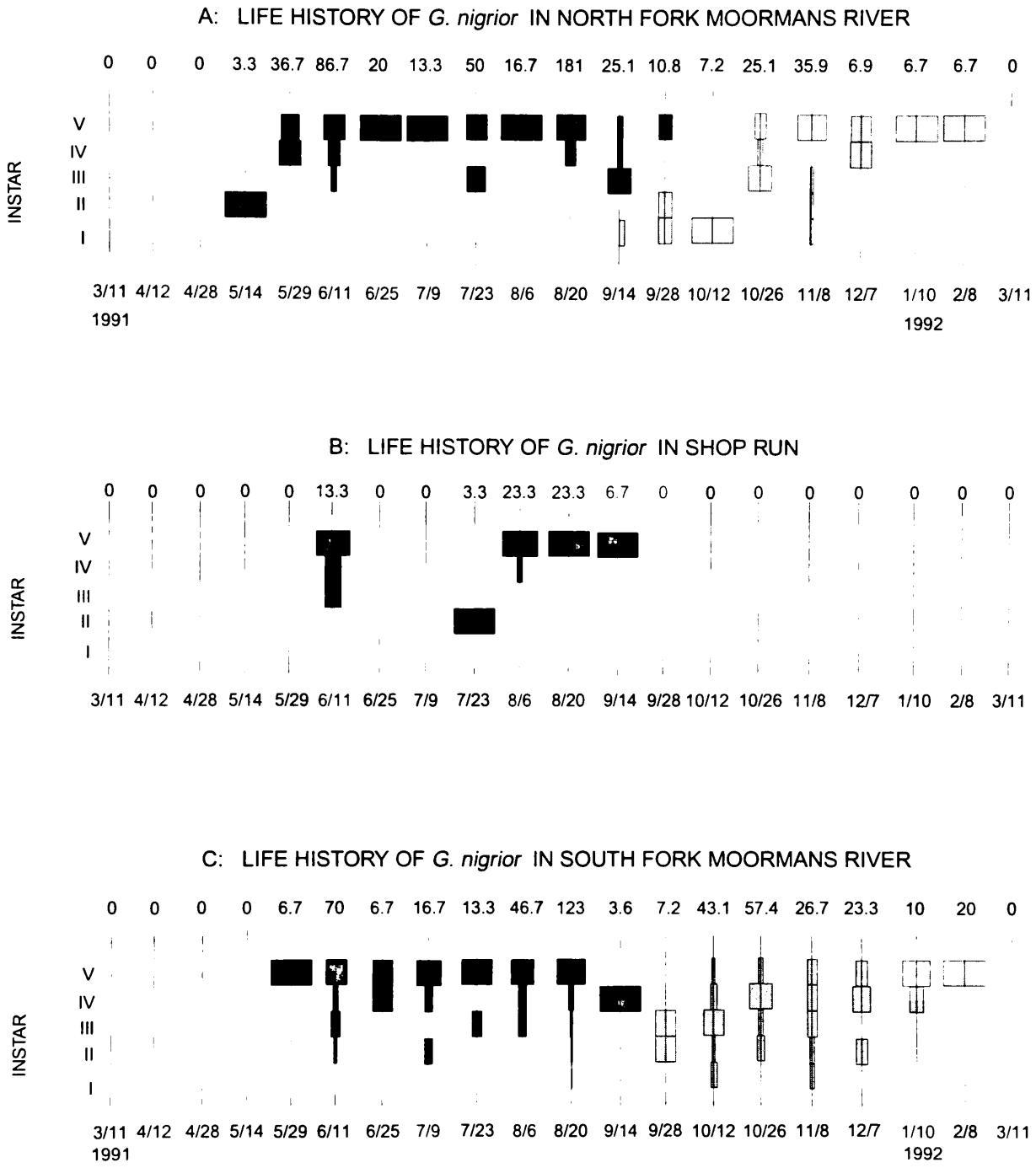


Fig. 3.10. Life-history of *Glossosoma nigrior* in defoliated streams [(A) North Fork of the Moormans R.; (B) Shop Run; South Fork of the Moormans R.]. The bars represent the relative abundance of collected individuals in each size-class. Each sampling date has an axis and the numbers along the top of the f igures represent the mean density (No. / sq. m) of individuals. ■ = 100%

larvae were not collected from White Oak Canyon Run after this date, suggesting that conditions were not favorable for continued development of a second cohort.

The size frequency method of estimating secondary production assumes that an equal amount of time is spent in each of the size classes, an assumption which usually does not result in large errors if violated (Benke 1984). *G. nigrior* larvae accumulate as much as 90 % of their mass in the last instar (Trapp and Hendricks 1984, Trapp 1991), and very little growth occurs before the fourth instar (Oemke 1986). Larval development takes ~ 4 mo and most of the time is spent in the last instar (Trapp 1991). Rather than having many early and few late instar larvae, *G. nigrior* had many late and few early instars (i.e., the size distribution was "top-heavy" rather than "bottom-heavy"). This pattern of larval development confounds estimation of secondary production by the size-frequency method because all early size classes produce negative production values. Hamilton (1969) provided the means to correct for this type of life history with his N_g column, but this calculation requires knowledge of the relative amount of time spent in each instar. There is no detailed information on the proportion of time *G. nigrior* larvae spend in each instar and it was impossible to resolve this information from my field observations because of asynchronous development of larvae. It was necessary to make some assumptions regarding life history to allow correction of *G. nigrior* production estimates. I began with the assumption that larval development takes ~ 4 mo (Trapp and Hendricks 1986, Trapp 1991); therefore, I estimated the CPI to be 120 days. Sweeney (personal contact) placed second instar larvae in artificial streams and found fourth and fifth instars 2 wk later. He stressed the rapid rate of development and mentioned the possibility of trivoltine populations. My field observations yielded similar results. The first samples containing *G. nigrior* occurred when the interval between samples was 2 wk and contained instars I through IV (Fig. 3.8A), so I assumed larval development to fourth instar took ~ 2 wk. *D. modesta* takes ~ 7 d to reach second instar and I assumed that the first instar of *G. nigrior* to have a stadium similar to other members of the same order in the same type of habitat. There was no information available

on the stadia of instars II and III, so I split the remaining time (~1 week) evenly both instars (4 d each). The samples collected 2 wk after the first occurrence of *G. nigrior* included fifth instar larvae (Fig. 3.8), so I assumed that development from fourth to fifth instar larvae took 2 wk and the rest of the CPI (~ 90 days) was spent in the fifth instar (Table 3.3). While all these assumptions may not be accurate, they correct for the irregular pattern of larval development and were applied uniformly to reference and defoliated streams. These assumptions should not alter conclusions regarding the effects of defoliation on *G. nigrior* production, but they should be considered when comparing these production values to those of other studies. The Hamilton correction (N_g (1969)) was applied as follows:

$$N_g = N \times b\left(\frac{P_e}{P_a}\right)$$

Where N = annual mean density of a given size class

b = number of generations per year

P_e = expected portion of the CPI spent in the size class

P_a = actual portion of the CPI spent in the size class

Table 3.3. Derivation of values used to calculate the Hamilton Correction (N_g) for size-frequency calculation of secondary production for *G. nigrior* populations in reference and defoliated streams.

Stage	days after hatch	stadium (days)	P_a	P_e	b = 1 $b(P_e/P_a)$	b = 2 $b(P_e/P_a)$
instar I to II	7	7	0.06	0.20	3.43	6.86
instar II to III	11	4	0.03	0.20	6.00	12.00
instar III to IV	15	4	0.03	0.20	6.00	12.00
instar IV to V	30	15	0.13	0.20	1.60	3.20
instar V to pupa	120	90	0.75	0.20	0.27	0.53

Secondary production was not significantly different (Table 3.4, P=0.305) between treatments because of extremely low density of *G. nigrior* in Shop Run (defoliated). *G. nigrior* may have been under represented in Shop Run for accurate estimation of secondary production, so it may be prudent to exclude Shop Run. The populations in other defoliated

streams had extremely high values of secondary production because they initiated a second generation in the autumn. Trapp (1981) attributed differences in *G. nigrior* voltinism to differences in temperature, and riparian defoliation by gypsy moth larvae caused an increase of accumulated degree-days in defoliated streams similar in magnitude to the differences she studied. Shop Run populations did not respond to temperature changes the same as populations of other defoliated streams. Shop Run is by far the smallest stream, in terms of both watershed area and discharge, and it could have a naturally low abundance of scrapers. Annual mean biomass and P/B ratios were also influenced by the low abundance of *G. nigrior* in Shop Run and were not significantly different ($P=0.184$ and $P=0.222$ respectively).

Table 3.4. Secondary production and annual mean biomass of *G. nigrior* by site and treatment. There was no significant difference in the annual production (P=.302), annual mean biomass (P=0.184), or P/B ratio (P=0.222).

Site	Treatment	Site Production	Treatment Production	Annual mean Biomass	mean $\overline{B}$	P/$\overline{B}$ ratio	mean P / $\overline{B}$
South River	Reference	21.6		0.61		35.3	
White Oak Canyon	Reference	51.8	44.3a	1.77	1.04a	29.2	48.0a
Piney River	Reference	59.5		0.75		79.4	
North Fork Moormans	Defoliated	154		7.12		21.7	
Shop Run	Defoliated	15.4	116a	1.11	5.24a	13.8	19.8a
South Fork Moormans	Defoliated	179		7.5		23.9	

Discussion

Peltoperlidae

Huryn and Wallace (1987) found Peltoperlidae in an Appalachian headwater stream in Coweeta Hydrologic Laboratory (Macon County, North Carolina) to have an annual secondary production of 298 mg / m^2. The community they studied consisted of three genera of Peltoperlidae, which appeared to have a CPI of 540 days. Annual production of Peltoperlidae reported in this study (Table 3.1) is similar to the production reported by Huryn and Wallace (1987) despite the difference in CPIs (365 d vs. 540 d) and the occurrence of only two perltoperlid genera among my study sites.

Secondary production and annual mean biomass were not significantly different despite lower annual IGRs in defoliated streams. Growth rates appeared to be decreased by reduced growth of nymphs in autumn and winter, and corresponded to a period of significantly reduced detritus inputs in defoliated streams. Survival and growth of early instar nymphs may have been increased by the accumulation of green leaf material in defoliated streams, thereby compensating for decreased growth later in the season. Peltoperlidae did not appear to be negatively impacted by riparian defoliation in this study.

Diplectrona modesta

Benke and Wallace (1980) reported annual secondary production of *D. modesta* in a fourth order southern Appalachian stream to be 53 mg m^{-2} yr^{-1} (ash-free dry mass (AFDM)), corresponding to 58.8 mg dry mass m^{-2} $yr.^{-1}$ (Benke 1993). The higher production in this study may be due to the absence of *Arctopsyche irrorata*, a larger insect that dominated Hydropsychidae productivity in the stream studied by Benke and Wallace. *A. irrorata* larvae may have excluded *D. modesta* from preferred habitat through territorial interactions, thereby reducing the success of the *D. modesta* population examined by Benke and Wallace (1980).

Cushman et al. (1977) reported annual secondary production of *D. modesta* in Walker Branch, Tennessee as 586 mg wet mass m^{-2} yr^{-1} (~ 117 mg dry mass m^{-2} yr^{-1} (Benke 1993)). While the community studied in Walker Branch was composed of two populations of *D. modesta*, this production estimate is much more similar to production values reported in this study than are those reported by Benke and Wallace (1980).

D. modesta larvae had significantly greater production in the reference treatment, probably because of the greater stream flow, not because of adverse effects of riparian defoliation. I did not observe any changes in organic seston associated riparian defoliation by gypsy moth larvae, suggesting that the food resources available to filter-feeders remained unchanged. The reference streams had a greater flow than the impacted streams. Within limits, greater stream flow is analogous to increasing the availability of seston to filter-feeders because they remove more particles from the water column per unit time. This allows Hydropsychidae larvae to build smaller capture-nets, in turn reducing the frequency of territorial interactions between larvae, allowing hydropsychids to attain grater densities in streams with greater flow (Matczak and Mackay 1990). Another possible explanation for the lower production of *D. modesta* in is the slightly elevated temperature of defoliated streams. I exclude this possibility because the difference in production was primarily due to higher abundance of individuals in reference streams and the magnitude of this difference remained constant before and after defoliation (Fig. 3.5). The temperature change was slight but did not affect the growth rate of *D. modesta* larvae.

Larval development appeared to progress more rapidly, but less synchronously than reference streams. Annual IGRs were not significantly different between treatments, but the accelerated rate of larval development caused greater variation in the size of larvae present at any given time, reducing the r^2 of the IGR regression fit.

Glossosoma nigrior

Georgian and Wallace (1983) estimated secondary production of *G. nigrior* in Lower Shope Fork, Macon County North Carolina (USDA Forest Service: Coweeta Hydrologic

Laboratory), by the instantaneous growth method. The bivoltine population of *G. nigrior* in Lower Shope Fork had annual secondary production of 612 mg AFDM m^{-2} yr^{-1} (~ 679 mg dry mass m^{-2} yr^{-1} (Benke 1993)). Productivity in lower Shope Fork was much higher than observed in my study sites because it is a larger, open-canopy stream.

While the differences in production of *G. nigrior* populations was not significantly different between treatments, productivity was much greater in two of the defoliated streams because *G. nigrior* initiated a second generation. Other studies (Trapp and Hendricks 1984, Trapp 1991) have shown that increased temperature can cause *G. nigrior* to initiate a second generation, and defoliation by gypsy moth larvae caused a significant increase in accumulated degree-days. It appears that the greatest potential for defoliation by gypsy moth larvae to affect the success of scrapers lies in the magnitude of the temperature changes that accompany removal of the riparian canopy.

Of the functional groups examined in this study, the scrapers appeared most-affected by riparian defoliation. Thermal changes accompanying defoliation allowed the species studied (*Glossosoma nigrior* Banks) to initiate a second generation after defoliation, increasing productivity of populations in defoliated streams. Other species with temperature-sensitive life histories may display similarly increased success in streams defoliated gypsy moth larvae. While the changes in temperature observed in this study were extreme enough to enhance the success of G. nigrior, they were not extreme enough to decrease the success of Peltoperlidae nymphs (cool stenotherms). Differences in the production of *Diplectrona modesta* (Banks) populations were statistically significant, but the differences were probably due to natural differences in stream flow, not to defoliation by gypsy moth larvae. Defoliation by gypsy moth larvae did not appear to negatively affect the short-term success of the insects examined in this study.

Summary

This field study investigated the short-term effects of riparian defoliation by gypsy moth larvae on three aspects of headwater stream ecology: water quality, benthic macroinvertebrate community structure, and benthic macroinvertebrate function (expressed as secondary production). The experimental design used six streams in Shenandoah National Park as study sites. Three of the streams were extensively defoliated by gypsy moth larvae (defoliated treatment), whereas the riparian canopies of the other three streams were not affected by gypsy moth larvae (reference treatment). Weekly defoliation measurements which were made with a spherical densiometer, indicated that the canopies of defoliated streams became significantly more open than those of reference streams after eclosion of gypsy moth larvae. I did not observe significant differences in pH, dissolved oxygen, alkalinity, conductivity, hardness, nutrient concentrations (nitrate, nitrite, ammonia, orthophosphate, and total phosphorus), or seston as a result of defoliation. Ash-free dry mass and chlorophyll *a* content of periphyton also remained unchanged after defoliation. There was a significant increase in the amount of detritus (frass and orts) falling into defoliated streams in the spring, which was followed by a significant decrease in the amount of detritus falling into defoliated streams in autumn. Temperature of defoliated streams was slightly elevated for a brief period after defoliation.

I observed only slight changes in benthic community structure. Taxa richness, EPT index, Hilsenhoff Biotic Index, and diversity did not change significantly after defoliation. Likewise, changes in the percent contribution of different functional-feeding groups were not statistically significant. Bray-Curtis Coefficient and chord distance did not reveal any significant changes in the structure of defoliated and reference streams after defoliation. Only the Index of Biotic Similarity demonstrated a significant difference, indicating that, at most, only slight changes in community structure occurred.

I estimated secondary production by the size-frequency method for selected aquatic insects in different functional-feeding groups. Production of Peltoperlidae (shredder) and *Diplectrona modesta* Banks (collector-filterer) were not significantly affected by defoliation. *Glossosoma nigrior* Banks larvae initiated a second generation in two of the defoliated streams because of temperature changes. Secondary production was much higher in streams having bivoltine populations of *G. nigrior*. Other species with temperature-sensitive life histories may be affected similarly.

I concluded that the short-term effects of riparian defoliation by gypsy moth larvae were minor. I arrived at this conclusion by comparing the measures of community structure commonly used to detect environmental perturbations and finding almost all of them to be statistically not significant. Long-term effects may result from defoliation-induced tree mortality and accompanying forest succession. Current gypsy moth Integrated Pest Management (IPM) strategies in Virginia rely heavily on the use of Dimilin® (Carrol and Ravlin 1993). During this study, IPM programs in Shenandoah National Park involved both Dimilin® and *Bacillus thurengensis* (Watson 1993). Recent research (Swift, Smucker and Cummins 1988, Swift, Cummins and Smucker 1988, Harrahy et al. 1993, Whimmer et al. 1993) suggests that diflubenzuron (Dimilin®) may enter streams as residues on allocthonous detritus. The high level of shredder mortality (>90% mortality in *Tipula* (Swift, Smucker and Cummins 1988)) caused by Dimilin® residues on CPOM is likely to have a greater impact on headwater stream ecology than single-season riparian defoliation by gypsy moth larvae.

Some researchers have speculated that the adverse effects of defoliation by gypsy moth larvae may be analogous to the effects of acid deposition (Downey et al. 1992, Webb 1992). The experimental design of this study did not allow me to examine the possibility of long-term leaching of nitrate (as nitric acid) from defoliated watersheds. Swank et al. (1981) described the effects of defoliation by an out break of fall cankerworm larvae on stream water nitrate concentration. Nitrate export was elevated during the 10 yr period cankerworm

larvae defoliated the watersheds studied, but returned to normal after the cankerworm larval populations returned to endemic levels. Because the fall cankerworm is native to the Appalachian Mountains, including Shenandoah National Park (Watson, 1992), Appalachian headwater streams should be adapted to periodic defoliation-induced nitrate export.

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Appendix 1.1. Stream Discharge (cubic meters per second) at study sites

DATE	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
3/11/91	0.1073					
3/12/91				0.0395	0.0148	0.0442
3/13/91		0.0738	0.0472			
4/12/91	0.0699	0.0746				
4/13/91				0.0237	0.0067	0.0377
4/14/91			0.43			
4/29/91	0.0515	0.0853				
4/30/91				0.0154	0.0074	0.0246
5/1/91			0.0476			
5/14/91				0.0069	0.0037	0.0099
5/15/91		0.06548	0.0194			
5/16/91	0.0459					
5/28/91	0.0378	0.1109	0.0711			
5/29/91				0.0087	0.0055	0.0075
6/10/91	0.0189	0.0296				
6/11/91				0.0028	0.0023	0.0035
6/12/91			0.0467			
6/24/91	0.15624	0.0374	0.0168			
6/25/91				0.00648	0.0094	0.0302
7/8/91	0.0393	0.0244	0.009			
7/9/91				0.0372	0.0151	0.0441
7/22/91	0.0203	0.0162				
7/23/91				0.0107	0.0037	0.008
7/24/91			0.005			
8/5/91	0.0374	0.0143	0.0046			
8/6/91				0.0269	0.0126	0.0111
8/20/91				0.0091	0.0061	0.0191
8/21/91	0.0236	0.013	0.0024			
9/13/91	0.0101					
9/14/91				0.0037	0.0031	0.0027
9/15/91		0.0046	0.0019			
9/27/91	0.0087					
9/28/91				0.0017	0.0019	0.0028
9/29/91		0.0036	0.0019			
10/11/91	0.008					
10/12/91				0.0016	0.0019	0.0012
10/13/91		0.0054	0.0017			
10/25/91	0.0107					
10/26/91				0.0028	0.0004	0.0031
10/27/91		0.0059	0.0019			
11/8/91				0.002	0.0006	0.0017
11/9/91	0.0027	0.0063	0.0021			
12/6/91	0.0614	0.0468	0.0154			
12/7/91				0.0311	0.0222	0.01
1/9/92	0.1759	0.2372	0.0974			
1/10/92				0.043	0.04	0.031
2/7/92	0.0436	0.0492	0.01616			
2/8/92				0.0092	0.0051	0.0111
3/11/92	0.2247	0.2431	0.1249			
3/12/92				0.0449	0.02704	0.0416

Appendix 1.2. Mean organic seston concentration (mg/L) at study sites

DATE	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
3/11/91	0.712					
3/12/91				0.080	0.135	0.370
3/13/91		0.120	0.165			
4/12/91	1.190	0.340				
4/13/91				0.490	0.850	1.525
4/14/91			1.195			
4/29/91	1.360	0.490				
4/30/91				0.095	0.335	2.235
5/1/91			1.480			
5/14/91				0.570	6.535	2.900
5/15/91		3.790	5.690			
5/16/91	1.485					
5/28/91	2.260	1.305	2.825			
5/29/91				0.800	0.470	2.850
6/10/91	1.900	1.075				
6/11/91				0.335	0.490	2.790
6/12/91			3.175			
6/24/91	1.900	1.075	3.170			
6/25/91				0.455	0.115	3.710
7/8/91	2.530	1.340	2.930			
7/9/91				1.015	0.710	3.080
7/22/91	2.080	5.595				
7/23/91				0.970	0.505	2.675
7/24/91			2.120			
8/5/91	1.335	0.955	1.580			
8/6/91				0.200	0.780	3.425
8/20/91				0.610	0.320	3.630
8/21/91	2.640	1.285	2.825			
9/13/91	1.605					
9/14/91				0.605	2.175	3.440
9/15/91		1.880	3.600			
9/27/91	1.515					
9/28/91				0.500	0.230	0.800
9/29/91		0.870	0.270			
10/11/91	1.950					
10/12/91				1.055	0.350	1.655
10/13/91		0.340	1.335			
10/25/91	0.975					
10/26/91				0.235	0.780	1.525
10/27/91		0.405	1.110			
11/8/91				0.000	0.036	0.790
11/9/91	0.220	0.380	0.000			
12/6/91	0.510	0.020	0.065			
12/7/91				0.045	0.000	0.395
1/9/92	0.775	0.285	0.320			
1/10/92				0.000	0.080	0.970
2/7/92	0.595	0.415	0.560			
2/8/92				0.350	0.420	1.735
3/11/92	0.655	0.000	0.000			
3/12/92				0.485	0.010	0.170

Appendix 1.3. Mean periphyton chlorophyll 'a' content (ug / sq. cm.) at study sites
Multiply chlorophyll concentrations by 63 to approximate biomass

DATE	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
3/11/91	1.839					
3/12/91				0.236	0.684	0.601
3/13/91		0.684	0.283			
4/12/91	0.331	0.326				
4/13/91				0.551	0.273	2.543
4/14/91			0.327			
4/29/91	0.644	0.152				
4/30/91				0.947	0.002	0.266
5/1/91			0.239			
5/14/91				0.491	0.234	0.329
5/15/91		0.170	0.416			
5/16/91	1.742					
5/28/91	0.385	0.563	0.474			
5/29/91				0.445	0.009	1.925
6/10/91	0.682	0.488				
6/11/91				0.269	0.679	0.133
6/12/91			0.188			
6/24/91	0.214	1.436	0.279			
6/25/91				0.412	0.007	0.203
7/8/91	0.774	0.881	0.378			
7/9/91				0.820	0.275	0.422
7/22/91	0.833	0.591				
7/23/91				0.920	0.448	1.752
7/24/91			3.012			
8/5/91	0.663	0.755	0.538			
8/6/91				0.215	0.192	0.609
8/20/91				0.939	0.275	2.371
8/21/91	1.086	0.537	0.502			
9/13/91	1.158					
9/14/91				0.812	0.525	0.184
9/15/91		0.359	0.173			
9/27/91	0.591					
9/28/91				0.372	0.252	0.563
9/29/91		0.977	0.852			
10/11/91	0.328					
10/12/91				0.486	0.331	0.795
10/13/91		0.424	0.871			
10/25/91	0.645					
10/26/91				0.706	0.613	0.172
10/27/91		0.794	1.014			
11/8/91				0.185	0.297	0.284
11/9/91	1.423	1.021	0.161			
12/6/91	1.207	0.583	0.220			
12/7/91				1.790	0.309	0.498
1/9/92	0.828	0.754	0.188			
1/10/92				0.591	0.289	1.051
2/7/92	0.065	0.375	0.322			
2/8/92				0.517	0.791	0.426
3/11/92	1.105	0.709	0.456			
3/12/92				0.629	0.322	1.172

Appendix 1.4. Mean organic mass of periphyton (mg / sq. cm) at study sites

DATE	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
3/11/91	0.810					
3/12/91				0.243	0.430	0.563
3/13/91		0.542	0.517			
4/12/91	0.291	0.187				
4/13/91				0.431	0.267	0.324
4/14/91			0.450			
4/29/91	0.954	0.661				
4/30/91				0.813	1.853	0.670
5/1/91			0.796			
5/14/91				0.860	0.985	0.768
5/15/91		1.007	1.276			
5/16/91	1.350					
5/28/91	0.962	2.094	0.814			
5/29/91				0.563	0.426	0.638
6/10/91	0.948	0.947				•
6/11/91				0.331	0.945	0.445
6/12/91			0.551			
6/24/91	0.582	0.785	0.655			
6/25/91				0.540	0.477	0.759
7/8/91	0.624	0.373	0.736			
7/9/91				0.442	0.250	0.844
7/22/91	0.765	0.379				
7/23/91				0.903	0.895	0.562
7/24/91			0.773			
8/5/91	1.179	1.068	0.823			
8/6/91				0.424	0.395	0.961
8/20/91				0.427	0.672	0.883
8/21/91	0.356	0.615	0.491			
9/13/91	0.428					
9/14/91				0.267	0.269	0.312
9/15/91		0.473	0.761			
9/27/91	0.647					
9/28/91				0.196	0.250	0.583
9/29/91		0.498	0.536			
10/11/91	0.831					
10/12/91				0.665	0.563	0.775
10/13/91		0.576	0.598			
10/25/91	0.211					
10/26/91				0.215	0.630	0.610
10/27/91		0.525	0.417			
11/8/91				0.127	0.349	0.408
11/9/91	0.282	0.657	0.235			
12/6/91	0.277	0.425	0.396			
12/7/91				0.302	0.225	0.277
1/9/92	0.519	0.479	0.196			
1/10/92				0.387	0.423	0.644
2/7/92	0.498	0.423	0.571			
2/8/92				0.376	0.411	0.581
3/11/92	0.599	0.413	0.818			
3/12/92				0.302	0.192	1.136

Appendix 1.5. Mean conductivity (umhos) of stream water at study sites

DATE	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
3/11/91	15.000					
3/12/91				10.000	10.000	20.000
3/13/91		19.000	10.000			
4/12/91	20.000	17.000				
4/13/91				10.000	10.000	28.000
4/14/91			15.000			
4/29/91	21.000	19.000				
4/30/91				10.000	21.000	33.000
5/1/91			18.000			
5/14/91				10.000	12.000	32.000
5/15/91		22.000	21.000			
5/16/91	25.000					
5/28/91	24.000	22.000	21.000			
5/29/91				15.000	17.000	39.000
6/10/91	21.000	20 000				
6/11/91				13.000	20.000	39.000
6/12/91			19.000			
6/24/91	21.000	21.000	37.000			
6/25/91				12.000	18.000	39.000
7/8/91	29.000	27.000	22.000			
7/9/91				13.000	16.000	37.000
7/22/91	30.000	28.000				
7/23/91				14.000	18.000	42.000
7/24/91			22.000			
8/5/91	30.000	23.000	40.000			
8/6/91				12.000	13.000	31.000
8/20/91				12.000	18.000	41.000
8/21/91	30.000	27.000	17.000			
9/13/91	25.000					
9/14/91				15.000	20.000	34.000
9/15/91		28.000	25.000			
9/27/91	23.000					
9/28/91				14.000	20.000	25.000
9/29/91		25.000	22.000			
10/11/91	27.000					
10/12/91				13.000	21.000	39.000
10/13/91		34.000	21.000			
10/25/91	29.000					
10/26/91				18.000	21.000	39.000
10/27/91		23.000	26.000			
11/8/91				9.000	18.000	32.000
11/9/91	19.000	17.000	15.000			
12/6/91	26.000	19.000	15.000			
12/7/91				13.000	17.000	29.000
1/9/92	23.000	18.000	15.000			
1/10/92				12.000	15.000	31.000
2/7/92	16.000	10.000	13.000			
2/8/92				9.000	11.000	22.000
3/11/92	22.000	14.000	15.000			
3/12/92				11.000	13.000	24.000

Appendix 1.6. Mean Hardness (mg / L CaCO3) of stream water at study sites

DATE	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
3/11/91	9.000					
3/12/91				2.000	3.000	13.000
3/13/91		7.000	7.000			
4/12/91	12.000	9.000				
4/13/91				5.000	4.000	15.000
4/14/91			9.000			
4/29/91	12.000	11.000				
4/30/91				4.000	5.000	15.000
5/1/91			8.000			
5/14/91				4.000	5.000	20.000
5/15/91		12.000	10.000			
5/16/91	15.000					
5/28/91	13.000	11.500	11.000			
5/29/91				4.000	5.000	18.000
6/10/91	12.000	13.000				
6/11/91				4.000	6.000	21.000
6/12/91			9.000			
6/24/91	15.000	12.000	9.000			
6/25/91				5.000	6.000	15.000
7/8/91	16.000	15.000	9.000			
7/9/91				5.000	6.000	15.000
7/22/91	16.000	16.000				
7/23/91				3.000	7.000	18.000
7/24/91			10.000			
8/5/91	15.000	14.000	8.000			
8/6/91				4.000	6.000	19.000
8/20/91				3.000	6.000	17.000
8/21/91	13.000	13.000	9.000			
9/13/91	17.000					
9/14/91				3.000	6.000	18.000
9/15/91		15.000	11.000			
9/27/91	14.000					
9/28/91				4.000	6.000	16.000
9/29/91		13.000	9.000			
10/11/91	17.000					
10/12/91				3.000	5.000	20.000
10/13/91		13.000	6.000			
10/25/91	15.000					
10/26/91				4.000	7.000	24.000
10/27/91		11.000	14.000			
11/8/91				4.000	7.000	22.000
11/9/91	13.000	13.000	9.000			
12/6/91	15.000	13.000	11.000			
12/7/91				4.000	5.000	16.000
1/9/92	12.000	9.000	7.000			
1/10/92				4.000	6.000	15.000
2/7/92	10.000	13.000	9.000			
2/8/92				3.000	5.000	15.000
3/11/92	12.000	10.000	9.000			
3/12/92				4.000	8.000	16.000

Appendix 1.7. Mean pH of stream water at study sites

DATE	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
3/11/91	7					
3/12/91				6.1	6.2	7.4
3/13/91		7.4	7.1			
4/12/91	6.3	6.3				
4/13/91						
4/14/91						
4/29/91	6.8	6.8		7.2	6.5	6.7
4/30/91						
5/1/91			7.1			
5/14/91	6.4			6.7	6.3	6.3
5/15/91		6.3	6.5			
5/16/91						
5/28/91	6.4	6.3	6.5			
5/29/91				6.2		6.6
5/31/91					6.4	
6/10/91	6.6	6.7				
6/11/91				6.5	6.1	6.9
6/12/91			6.9			
6/24/91	6.3	6.7	7			
6/25/91				6.3	6.3	7.2
7/8/91	6.81	6.75	6.7			
7/9/91				6.4	6.5	7
7/22/91	7.6	6.8				
7/23/91				6.43	6.25	6.4
7/24/91			6.9			
8/5/91	6.95	7.15	6.9			
8/6/91				6.4	6.3	7.1
8/20/91				6.7	6.3	7.1
8/21/91	6.7	6.9	6.8			
9/13/91	6.4					
9/14/91					6.4	6.6
9/15/91						
9/27/91	6.9					
9/28/91				6.5	6.5	7.2
9/29/91		7	7			
10/11/91	7					
10/12/91				6.6	6.8	7.2
10/13/91		7.2	6.9			
10/25/91	6.7					
10/26/91				6.8	6.2	7.2
10/27/91		6.6	7			
11/8/91				6.4	6.5	7
11/9/91	6.9	6.6	6.5			
12/6/91	6.5	6.7	6.6			
12/7/91				6.44	6.3	6.65
1/9/92			6.7			
1/10/92						
2/7/92	6.6	5.9	6.6			
2/8/92				6.9	6.5	6.5
3/11/92						
3/12/92						
4/4/92	7.16	7.06	7.12	6.96	6.89	7.08

Appendix 1.8. Mean Alkalinity (mg / L CaCO3) of stream water at study sites

DATE	South River	White Oak	Piney River	North Fork	Shop Run	South Fork
3/11/91	5.26					
3/12/91				1	0.6	11
3/13/91		6.2	4.48			
4/12/91	7.4	7.56				
4/13/91				5.12	2.2	12.44
4/14/91			4			
4/29/91	9.56	7.92				
4/30/91				1.64	1.88	14.24
5/1/91			6.682			
5/14/91				1.04	1.88	16.2
5/15/91		7.8	5.84			
5/16/91	9.87					
5/28/91	10.16	8.18	5.6			
5/29/91				-4.416	2.76	16.8
6/10/91	10.4	8.48				
6/11/91				1.32	2.2	19.4
6/12/91			5.32			
6/24/91	9.2	8.84	6.12			
6/25/91				1.136	1.463	14.64
7/8/91	10.16	7.24	3.72			
7/9/91				0.6	0.92	11.8
7/22/91	10.96	9.24				
7/23/91				1.76	2.16	11.4
7/24/91			7.36			
8/5/91	11	11.8	7.3			
8/6/91				1.6	2.1	14.72
8/20/91				2.16	2.24	16.17
8/21/91	10.96	11.9	7.8			
9/13/91						
9/14/91						
9/15/91						
9/27/91	10.8					
9/28/91				1.32	2.2	19
9/29/91		11	7.28			
10/11/91	27					
10/12/91						
10/13/91		34	21			
10/25/91	13.6					
10/26/91				1.7	3.05	23
10/27/91		14.08	4.7			
11/8/91				1.5	3.9	19.8
11/9/91		9.8	7.2			
12/6/91	6.9	6.5	3.7			
12/7/91				0.52	0.96	13.4
1/9/92	5.9	4.7	3.7			
1/10/92				0.84	0.8	17.9
2/7/92	6.8	5.44	3.44			
2/8/92				0.68	0.92	11.3
3/11/92	6.88	5.4	3.2			
3/12/92				1.4	1.16	10.16
4/4/92	6.08	5.32	4.36	0.76	1.12	10.68

Appendix 2.1. Similarity matrix for Bray-Curtis similarity. The Bray-Curtis Coefficient compares the similarity of each study site to the others each other in 1991 and 1992 were used to construct community similarity matrices. Bray-Curtis Coefficient values of 1 indicate identical communities, and values near zero indicate dissimilar communities.

Reference sites:	South River	White Oak	Piney River	
Defoliated sites:	North Fork	Shop Run	South Fork	

Bray-Curtis 1991

	South River	White Oak	Piney River	North Fork	Shop Run
White Oak	0.62				
Piney River	0.35	0.59			
North Fork	0.31	0.45	0.52		
Shop Run	0.27	0.40	0.42	0.49	
South Fork	0.49	0.74	0.77	0.98	0.48

Bray-Curtis 1992

	South River	White Oak	Piney River	North Fork	Shop Run
White Oak	0.63				
Piney River	0.70	0.42			
North Fork	0.26	0.18	0.65		
Shop Run	0.26	0.24	0.48	0.49	
South Fork	0.47	0.35	0.84	0.81	0.57

Appendix 2.2. Similarity matrix for Chord Distance (dissimilarity). The Chord distance compares each of the study sites to the others in 1991 and 1992 to construct community similarity matrices. Chord distance values of zero indicate identical communities, and values near 1.4 indicate dissimilar communities.

Reference sites:	South River	White Oak	Piney River
Defoliated sites:	North Fork	Shop Run	South Fork

Chord Distance 1991

	South River	White Oak	Piney River	North Fork	Shop Run
White Oak	0.43				
Piney River	0.72	0.67			
North Fork	0.75	0.77	0.41		
Shop Run	0.83	0.84	0.65	0.56	
South Fork	0.77	0.78	0.44	0.36	0.86

Chord Distance 1992

	South River	White Oak	Piney River	North Fork	Shop Run
White Oak	0.51				
Piney River	0.66	0.67			
North Fork	0.98	0.91	0.49		
Shop Run	0.91	0.77	0.57	0.69	
South Fork	0.83	0.80	0.56	0.70	0.54

Appendix 2.3. Similarity matrix for The Index of Biotic Similarity. The Index of Biotic Similarity compares each of the study sites to the others in 1991 and 1992 to construct community similarity matrices. Index of Biotic Similarity values of 1 indicate identical communities, and values near zero indicate dissimilar communities.

Reference sites:	South River	White Oak	Piney River
Defoliated sites:	North Fork	Shop Run	South Fork

Index Biotic Similarity 1991

	South River	White Oak	Piney River	North Fork	Shop Run
White Oak	0.37				
Piney River	0.28	0.35			
North Fork	0.29	0.23	0.21		
Shop Run	0.20	0.18	0.24	0.17	
South Fork	0.30	0.31	0.29	0.33	0.18

Index of Biotic Similarly 1992

	South River	White Oak	Piney River	North Fork	Shop Run
White Oak	0.33				
Piney River	0.33	0.23			
North Fork	0.18	0.21	0.21		
Shop Run	0.15	0.16	0.18	0.22	
South Fork	0.20	0.22	0.24	0.21	0.19

Appendix 3.1: Annual secondary production of Peltoperlidae in South River (reference) as as esimated by the size-frequency method (see Benke 1984)

size-class CW in micron	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of size-classes *7	neg. exclud.
201 - 500	1.000	0.011	0.011					
				-7.000	0.037	-0.259	-1.812	-
501- 800	8.000	0.063	0.501					
				-0.500	0.202	-0.101	-0.705	-
01 - 1100	8.500	0.340	2.893					
				0.475	0.648	0.307	2.152	2
101 - 140	8.025	0.956	7.669					
				4.667	1.876	8.754	61.277	61
401 - 170	3.359	2.796	9.391					
				2.359	4.631	10.925	76.473	76
701 - 200	1.000	6.467	6.467					
				-0.167	9.334	-1.556	-10.890	-
001 - 230	1.167	12.202	14.235					
				1.167	12.202	14.235	99.647	100
	31.051		41.168			32.565	227.953	
	⇧		⇧					240 Production
	Annual Mean Density		Annual mean Biomass					5.82 P/B

20 sampling dates

Size classes with negative production excluded from total (Benke. 1984)

CPI assumed to = 1 year

Appendix 3.2: Annual secondary production of Peltoperlidae in White Oak Canyon Run (reference) as as esimated by the size-frequency method (see Benke 1984)

size-class CW in micron	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of size-classes *6	neg. exclud.
201 - 500	0.167	0.015	0.003	-0.667	0.040	-0.026	-0.159	-
501- 800	0.833	0.064	0.054	-1.513	0.216	-0.326	-1.956	-
01 - 1100	2.346	0.367	0.860	0.219	0.721	0.158	0.946	1
101 - 140	2.127	1.075	2.286	-0.962	1.861	-1.790	-10.740	-
401 - 170	3.089	2.647	8.178	2.243	3.825	8.579	51.477	51
701 - 200	0.846	5.003	4.232	0.846	5.003	4.232	25.395	25
001 - 230	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-
	9.409 ⇧ Annual Mean Density		15.613 ⇧ Annual mean Biomass			10.854	65.122	78 Production
								4.98 P/B

20 sampling dates

Size classes with negative production excluded from total (Benke. 1984)

CPI assumed to = 1 year

Appendix 3.3: Annual secondary production of Peltoperlidae in Piney River (reference) as as esimated by the size-frequency method (see Benke 1984)

size-class CW in micron	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of size-classes *6	negitive. excluded
201 - 500	0.666667	0.012383	0.008256	-4.02547	0.044476	-0.17904	-1.07423	-
501 - 800	4.692133	0.076569	0.359273	-1.06253	0.200694	-0.21324	-1.27947	-
801 - 1100	5.754667	0.324819	1.869225	4.344933	0.687657	2.987824	17.92694	17.9
101 - 140	1.409733	1.050495	1.480918	-0.61573	2.006182	-1.23527	-7.41164	-
401 - 170	2.025467	2.961869	5.999167	1.025467	4.81781	4.940504	29.64302	29.6
701 - 200	1	6.673751	6.673751	1	6.673751	6.673751	40.04251	40.0
001 - 230	0	0	0	0	0	0	0	-
	15.54867		16.391			13.154	78.921	
	⇧ Annual Mean Density		⇧ Annual mean Biomass					88 Production
								5.35 P/B

20 sampling dates

Size classes with negative production excluded from total (Benke. 1984)

CPI assumed to = 1 year

Appendix 3.4: Annual secondary production of Peltoperlidae in North Fork of the Moormans River (defoliated) as as esimated by the size-frequency method (see Benke 1984)

size-class CW in micron	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of size-classes *7	neg. exclud.
201 - 500	0.667	0.019	0.012					
				-8.667	0.048	-0.415	-2.905	-
501- 800	9.333	0.077	0.719					
				2.475	0.220	0.546	3.819	4
01 - 1100	6.859	0.364	2.496					
				1.091	0.635	0.693	4.854	5
101 - 140	5.767	0.907	5.230					
				2.332	1.670	3.895	27.268	27
401 - 170	3.435	2.434	8.361					
				-1.231	3.516	-4.330	-30.309	-
701 - 200	4.667	4.598	21.458					
				1.833	6.708	12.298	86.085	86
001 - 230	2.833	8.818	24.983					
				2.833	8.818	24.983	174.882	175
	33.561		63.259			38.085	266.597	
	⇧		⇧					297 Production
	Annual Mean Density		Annual mean Biomass					4.69 P/B

20 sampling dates

Size classes with negative production excluded from total (Benke. 1984)

CPI assumed to = 1 year

Appendix 3.5: Annual secondary production of Peltoperlidae in Shop Run (defoliated) as as esimated by the size-frequency method (see Benke 1984)

size-class CW in micron	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of size-classes *7	neg. exclud.
201 - 500	0.525	0.010	0.005					
				-3.935	0.049	-0.191	-1.338	-
501- 800	4.461	0.087	0.389					
				-4.806	0.236	-1.134	-7.941	-
01 - 1100	9.266	0.385	3.566					
				-0.666	0.709	-0.472	-3.304	-
101 - 140	9.932	1.034	10.266					
				3.166	1.587	5.025	35.173	35
401 - 170	6.766	2.141	14.486					
				4.806	3.202	15.389	107.725	108
701 - 200	1.961	4.264	8.360					
				1.615	6.107	9.861	69.024	69
001 - 230	0.346	7.950	2.751					
				0.346	7.950	2.751	19.260	19
	33.257		39.824			31.419	219.935	
	⇧		⇧					231
	Annual Mean Density		Annual mean Biomass					Production
								5.81 P/B

20 sampling dates

Size classes with negative production excluded from total (Benke. 1984)

CPI assumed to = 1 year

Appendix 3.6: Annual secondary production of Peltoperlidae in South Fork of the Moormans River (defoliated) as as esimated by the size-frequency method (see Benke 1984)

size-class CW in micron	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of size-classes *7	neg. exclud.
201 - 500	0.167	0.017	0.003	-5.500	0.040	-0.219	-1.532	-
501- 800	5.667	0.063	0.356	1.128	0.218	0.246	1.719	2
01 - 1100	4.538	0.372	1.690	1.270	0.652	0.828	5.795	6
101 - 140	3.269	0.932	3.045	1.743	1.472	2.566	17.962	18
401 - 170	1.525	2.013	3.070	0.192	3.656	0.702	4.917	5
701 - 200	1.333	5.300	7.066	1.000	6.810	6.810	47.673	48
001 - 230	0.333	8.321	2.774	0.333	8.321	2.774	19.416	19
	16.832 ⇧ Annual Mean Density		18.004 ⇧ Annual mean Biomass			13.926	97.482	97 Production
								5.41 P/B

20 sampling dates

Size classes with negative production excluded from total (Benke. 1984)

CPI assumed to = 1 year

Appendix 3.7: Annual secondary production of Diplectrona modesta in South River (reference) as estimated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negatives excluded
1	2.01	0.00	0.01					
				-111.30	0.01	-1.42	-7.12	-
2	113.31	0.02	2.52					
				15.92	0.06	0.89	4.44	4
3	97.39	0.09	8.71					
				63.17	0.27	16.92	84.61	85
4	34.22	0.45	15.27					
				21.05	1.24	26.20	130.98	131
5	13.17	2.04	26.90					
				13.17	2.04	26.90	134.48	134
	260.10		53.397			69.479	347.395	
	⇧ Annual Mean Density		⇧ Annual mean Biomass					355 Production
								6.64 P/B

20 sampling dates

Size-classes with negative production excluded from total (Benke 1984)

CPI assumed to = 1 year

Appendix 3.8: Annual secondary production of Diplectrona modesta in White Oak Canyon Run (reference) as estimated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negatives excluded
1	10.31	0.00	0.04	-154.48	0.01	-2.03	-10.14	-
2	164.78	0.02	3.61	48.77	0.06	2.73	13.66	14
3	116.01	0.09	10.46	79.10	0.27	21.00	104.99	105
4	36.92	0.44	16.27	28.31	1.29	36.57	182.84	183
5	8.60	2.14	18.43	8.60	2.14	18.43	92.14	92
	336.62		48.809			76.698	383.489	
	⇧ Annual Mean Density		⇧ Annual mean Biomass					394 Production
								8.06 P/B

20 sampling dates

Size-classes with negitive production values excluded from total (Benke 1984)

CPI assumed to = 1 year

Appendix 3.9: Annual secondary production of Diplectrona modesta in Piney River (reference) as estimated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negatives excluded
1	16.75	0.00	0.08					
				-123.19	0.01	-1.70	-8.50	-
2	139.94	0.02	3.19					
				49.29	0.06	2.87	14.35	14
3	90.66	0.09	8.49					
				56.37	0.27	15.34	76.69	77
4	34.29	0.45	15.45					
				10.30	1.31	13.52	67.58	68
5	23.99	2.17	52.13					
				23.99	2.17	52.13	260.67	261
	305.62		79.343			82.157	410.786	
	⇧		⇧					419 Production
	Annual Mean Density		Annual mean Biomass					5.28 P/B

20 sampling dates

Size-classes with negitive production values excluded from total (Benke 1984)

CPI assumed to = 1 year

Appendix 3.10: Annual secondary production of Diplectrona modesta in North Fork of the Moormans River (defoliated) as estimated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negatives excluded
1	5.19	0.00	0.02					
				-44.48	0.02	-0.78	-3.88	-
2	49.67	0.03	1.55					
				19.40	0.07	1.35	6.77	7
3	30.28	0.11	3.28					
				11.22	0.31	3.43	17.17	17
4	19.06	0.50	9.61					
				12.32	1.55	19.12	95.58	96
5	6.74	2.60	17.53					
				6.74	2.60	17.53	87.64	88
	110.95		31.989			40.657	203.287	
	⇧ Annual Mean Density		⇧ Annual mean Biomass					207 Production
								6.48 P/B

20 sampling dates

Size-classes with negitive production values excluded from total (Benke 1984)

CPI assumed to = 1 year

Appendix 3.11: Annual secondary production of Diplectrona modesta in Shop Run (defoliated) as estimated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negatives excluded
1	2.69	0.00	0.01					
				-29.90	0.02	-0.54	-2.69	-
2	32.59	0.03	1.07					
				11.94	0.07	0.85	4.23	4
3	20.65	0.11	2.25					
				3.38	0.31	1.06	5.31	5
4	17.27	0.52	8.96					
				7.91	1.58	12.51	62.57	63
5	9.36	2.65	24.75					
				9.36	2.65	24.75	123.77	124
	82.55		37.042			38.636	193.181	
	⇧		⇧					196 Production
	Annual Mean Density		Annual mean Biomass					5.29 P/B

20 sampling dates

Size-classes with negitive production values excluded from total (Benke 1984)

CPI assumed to = 1 year

Appendix 3.12: Annual secondary production of Diplectrona modesta in South Fork of the Moormans River (defoliated) as estimated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negatives excluded
1	1.50	0.00	0.01					
				-52.98	0.02	-0.92	-4.62	-
2	54.48	0.03	1.70					
				16.98	0.07	1.16	5.78	6
3	37.51	0.11	3.94					
				18.39	0.30	5.61	28.03	28
4	19.11	0.50	9.65					
				11.44	1.52	17.39	86.96	87
5	7.68	2.54	19.48					
				7.68	2.54	19.48	97.42	97
	120.28		34.773			42.714	213.570	
	⇧ Annual Mean Density		⇧ Annual mean Biomass					218 Production
								6.27 P/B

20 sampling dates

Size-classes with negitive production values excluded from total (Benke 1984)

CPI assumed to = 1 year

Appendix 3.13: Annual secondary production of Glossosoma nigrior in South River (reference) as calcuated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	Hammilton correction Nγ	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negative values excluded
1	0.00	0.00	0.00	0.00					
					-6.00	0.00	0.00	-0.01	-
2	1.00	6.00	0.00	0.00					
					-7.00	0.00	-0.01	-0.04	-
3	2.17	13.00	0.00	0.02					
					11.93	0.08	0.95	4.73	4.73
4	0.67	1.07	0.16	0.17					
					0.18	0.31	0.06	0.28	0.28
5	3.33	0.89	0.47	0.42					
					0.89	0.47	0.42	2.10	2.10
	7.17	20.96		0.61					7.10
	⇧			⇧					Interval Production
	Annual Mean Density			Annual mean Biomass					

20 sampling dates
size-classes with negative production are excluded from total (Benke 1984)
*CPI Correction assumes 4 months of production per cohort.
See discussion of Hamilton correction in text

7.10	x	3.04	**21.59**	35.27
IP		CPI corr*	**Annual P**	Annual P/B

Appendix 3.14: Annual secondary production of Glossosoma nigrior in White Oak Canyon Run (reference) as calcuated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	Hammilton correction Nγ	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negative values excluded
1	2.20	7.56	0.00	0.00					
					-11.44	0.00	0.00	-0.02	-
2	3.17	19.00	0.00	0.01					
					-0.08	0.00	0.00	0.00	-
3	3.18	19.08	0.00	0.03					
					12.39	0.08	0.94	4.71	4.71
4	4.18	6.69	0.15	1.00					
					5.26	0.33	1.73	8.67	8.67
5	5.36	1.43	0.51	0.73					
					1.43	0.51	0.73	3.64	3.64
	18.09	53.75		1.77					17.02
	⇧			⇧					Interval Production
	Annual Mean Density			Annual mean Biomass					

20 sampling dates
size-classes with negative production are excluded from total (Benke 1984)
*CPI Correction assumes 4 months of production per cohort.
See discussion of Hamilton correction in text

IP		CPI corr*	Annual P	Annual P/B
17.02	x	3.04	**51.76**	29.17

Appendix 3.15: Annual secondary production of Glossosoma nigrior in Piney River (reference) as calcuated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	Hammilton correction Nγ	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negative values excluded
1	0.68	2.33	0.00	0.00					
					-17.28	0.00	0.00	-0.02	-
2	3.27	19.61	0.00	0.01					
					-26.68	0.00	-0.03	-0.13	-
3	7.72	46.29	0.00	0.07					
					42.13	0.07	2.78	13.89	13.89
4	2.60	4.16	0.13	0.54					
					3.85	0.26	1.01	5.06	5.06
5	1.18	0.31	0.40	0.12					
					0.31	0.40	0.12	0.62	0.62
	15.44	72.71		0.75					19.57
	⇧			⇧					Interval Production
	Annual Mean Density			Annual mean Biomass					

20 sampling dates
size-classes with negative production are excluded from total (Benke 1984)
*CPI Correction assumes 4 months of production per cohort.
See discussion of Hamilton correction in text

IP		CPI corr*	Annual P	Annual P/B
19.57	x	3.04	**59.52**	79.54

Appendix 3.16: Annual secondary production of Glossosoma nigrior in North Fork of the Moormans River (defoliated) as calcuated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	hamilton correction Nγ	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negative values excluded
1	0.90	6.15	0.00	0.00					
					-0.15	0.00	0.00	0.00	-
2	0.53	6.31	0.00	0.00					
					-35.07	0.00	-0.04	-0.21	-
3	3.45	41.38	0.00	0.08					
					29.52	0.10	2.93	14.67	14.67
4	3.70	11.86	0.20	2.33					
					5.46	0.47	2.55	12.73	12.73
5	11.99	6.39	0.74	4.70					
					6.39	0.74	4.70	23.50	23.50
	20.56	72.08		7.12					50.90
	⇧			⇧					Interval Production
	Annual Mean Density			Annual mean Biomass					

20 sampling dates
size-classes with negative production are excluded from total (Benke 1984)
*CPI Correction assumes 4 months of production per cohort.
See discussion of Hamilton correction in text

50.90	x	3.04	154.81	21.76
IP		CPI corr*	Annual P	Annual P/B

Appendix 3.17: Annual secondary production of Glossosoma nigrior in Shop Run (defoliated) as calcuated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	hamilton correction Nγ	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negative values excluded
1	0.00	0.00	0.00	0.00					
					-2.00	0.00	0.00	0.00	-
2	0.17	2.00	0.00	0.00					
					0.00	0.00	0.00	0.00	-
3	0.17	2.00	0.00	0.00					
					0.93	0.08	0.08	0.39	0.39
4	0.33	1.07	0.17	0.18					
					-0.44	0.39	-0.17	-0.87	-
5	2.83	1.51	0.62	0.93					
					1.51	0.62	0.93	4.66	4.66
	3.50	6.58		1.11					5.06
	⇧			⇧					Interval Production
	Annual Mean Density			Annual mean Biomass					

20 sampling dates
size-classes with negative production are excluded from total (Benke 1984)
*CPI Correction assumes 4 months of production per cohort.
See discussion of Hamilton correction in text

5.06	x	3.04	15.38	13.79
IP		CPI corr*	Annual P	Annual P/B

Appendix 3.18: Annual secondary production of Glossosoma nigrior in South Fork of the Moormans River (defoliated) as calcuated by the size-frequency method (see Benke 1984)

instar	annual mean (No/sq.m) N	hamilton correction Nγ	mg ω	mg/sq.m β	ΔN	at loss (μ) ω	ωΔN	No. of INSTARS *5	negative values excluded
1	0.69	4.75	0.00	0.00					
					-22.02	0.00	-0.01	-0.03	-
2	2.23	26.76	0.00	0.01					
					-20.61	0.00	-0.02	-0.12	-
3	3.95	47.38	0.00	0.09					
					30.35	0.10	2.92	14.62	14.62
4	5.32	17.02	0.19	3.25					
					10.87	0.43	4.71	23.53	23.53
5	11.54	6.15	0.68	4.16					
					6.15	0.68	4.16	20.78	20.78
	23.73	102.06		7.50					58.93
	⇧			⇧					Interval Production
	Annual Mean Density			Annual mean Biomass					

20 sampling dates
size-classes with negative production are excluded from total (Benke 1984)
*CPI Correction assumes 4 months of production per cohort.
See discussion of Hamilton correction in text

58.93	x	3.04	179.24	23.89
IP		CPI corr*	Annual P	Annual P/B

VITAE

Brett Douglas Marshall was born on June 12 1965 in Cedar Falls, Iowa. His family moved to Duluth, Minnesota when he was 2 years old, and moved to Grand Rapids, Minnesota in 1980. While growing up among the lakes of northern Minnesota, Brett's interest in aquatic biology -- especially in aquatic invertebrates -- grew. He graduated from Grand Rapids Senior High School in 1983 without the means to pursue higher education and joined the U.S. Army. Three years with the army included tours of duty in West Germany and Fort Hood, Texas. Brett received an honorable discharge in 1986 and entered the undergraduate program at the University of Wisconsin's Superior campus (UWS). While attending classes, he assisted Dr. William Swenson with the fisheries portion of the Little Rock Lake acidification study and worked with the U.S. Environmental Protection Agency as a biology lab aide at the National Water Quality Laboratory in Duluth, Minnesota. Brett received his Bachelor of Science in Biology with an "aquatic / population biology focus" in 1990 and moved to Blacksburg Virginia to pursue graduate education at Virginia Polytechnic Institute and State University (Virginia Tech). His thesis research examined the effects of riparian defoliation by gypsy moth larvae on Appalachian headwater streams in Virginia. Most funding for Brett's MS degree was attained through various research assistantships which included identification of benthic macroinvertebrate samples for the National Park Service and the U.S. Forest Service. Brett's major advisor, Dr. J. Reese Voshell, Jr., introduced Brett to the joys of teaching by providing teaching assistantships for two senior-level undergraduate classes (Aquatic Entomology and Biomonitoring of Aquatic Ecosystems Using Aquatic Macroinvertebrates and Fish). Drs. E. Fred Benfield and George M. Simmons, Jr. were valuable members of his graduate committee.