LAND USE IMPACTS ON LEAF PROCESSING AND INVERTEBRATE COMMUNITIES IN SOUTHERN APPALACHIAN STREAMS

A Thesis

by

ROBERT P. CHERRY

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APPROVED BY:

Dr. Robert P. Creed, Jr.
Chairperson, Thesis Committee

Dr. Howard S. Neufeld
Member, Thesis Committee

Dr. Ray S. Williams
Member, Thesis Committee

Dr. Vicki J. Martin,
Chairperson, Department of Biology

Dr. Judith E. Domer
Dean of Graduate Studies and Research

ABSTRACT

LAND USE IMPACTS ON LEAF PROCESSING AND INVERTEBRATE COMMUNITIES IN SOUTHERN APPALACHIAN STREAMS (December 2000)

Robert P. Cherry, B.S., Southern Illinois University at Carbondale

M.S., Appalachian State University

Thesis Chairperson: Dr. Robert P. Creed, Jr.

Land use impacts on leaf processing rates and macroinvertebrate communities were examined in Greene Creek and Sims Creek, headwater streams in the Southern Appalachian Mountains. In this study changes resulting from the conversion of a forested riparian zone to a grass pasture with just a few scattered trees were examined. There were three study sections in each stream: a downstream cattle-grazed pasture, an intermediate grazed forested section, and an upstream, ungrazed forest. Leaf-packs made of 5.0 g of dried yellow birch leaves were placed in each of the sections in Greene Creek in November 1997 and removed on six sampling dates over 56 d. The leaves were washed to remove macroinvertebrates, dried and weighed to determine loss of leaf matter. Leaf processing rates in Greene Creek were significantly different among sections with the fastest rates in the ungrazed, forested section and slowest in the grazed, pasture section. In Sims Creek, leaf pack breakdown in the pasture section was significantly slower than in the intermediate and forest sections.

Differences were also observed in the abundance of certain macroinvertebrate species among the sections in Greene Creek. The caddisfly *Pycnopsyche* was most common in the forest section and appeared to be the major leaf shredder in this headwater stream system. Leptophlebiid and ephemerellid mayflies were most abundant in the intermediate section.

These two groups of mayflies appeared to be important shredders in the intermediate section. In the pasture the stonefly *Allocapnia* was significantly more common than in the other sections but appeared to have little impact on leaf pack breakdown.

A *Pycnopsyche* enclosure experiment conducted in the pasture section of Greene Creek showed *Pycnopsyche* to be the dominant shredder in the creek. Their low numbers in the intermediate and pasture sections resulted in reduced leaf processing rates. The results of surveys for *Pycnopsyche* larvae in headwater streams in the New River watershed suggest that *Pycnopsyche* prefer forest sites over pasture sites, ungrazed over grazed sites, and sites not located below ponds over sites that are below ponds.

These results show that alterations in land cover and use along streams may result in reduced leaf processing rates and changes in the macroinvertebrate community. *Pycnopsyche*, the major shredder in these systems, was not abundant outside of undisturbed headwater stream systems. *Pycnopsyche* absence led to a significant reduction in the leaf processing rate in Greene Creek and should result in a reduction in the flow of energy to other trophic levels. As a result of these land cover and land use changes along these streams, there was not only a change in *Pycnopsyche* abundance but an alteration in the macroinvertebrate community overall.

ACKNOWLEDGEMENTS

To say that this thesis would not have been possible without the assistance and guidance of Dr. Robert Creed would be an understatement. Dr. Creed provided invaluable help from the design of the research all the way through to the editing of this thesis. But even more important than this technical assistance was his patience and encouragement when I was prepared to give up. His guidance kept me on track and kept me motivated when self-motivation was in short supply. His enthusiasm for aquatic ecology and quest for new ideas was not only infectious but also showed me that earning a degree was more than just attending classes and passing tests. For his friendship, his encouragement and his assistance I will always be grateful.

I would also like to thank Dr. Howard Neufeld and Dr. Ray Williams for their assistance with this thesis and with my research. Their input and comments helped greatly. Thanks also to Dr. Douglas Meikle, a member of my original thesis committee, who helped get me started and provided many helpful suggestions. Dr. Matt Rowe provided invaluable moral support many times during this seven-year effort and was always willing to stop what he was doing to have a talk. During those conversations his love of learning was contagious and his high expectations challenging. His friendship and guidance will always be treasured.

Several students assisted me with various parts of this research and helped to keep me from getting overwhelmed. I am grateful to Lee Echols for his assistance in spending many hours picking invertebrates out of sediment-filled vials. Without this help I would still be bent over a dissecting scope instead of writing this thesis. Ken Fortino and Brian Helms provided assistance with setting out the experiments on Sims and Greene Creeks. I am thankful for their help with this research, for their companionship in classes and for showing me that people really can complete their theses. I thank Rob McCorkle for helping me pick leaf after leaf for use in this study.

Thanks to Lynn Gordon, Joni Salzano and Mike Salzano for sacrificing their fingers while applying hundreds of binder clips to the leaf packs. You never know when friends are going to come through in the clutch, but that is what makes them true friends.

I was also fortunate to have the support of my supervisors on the Blue Ridge Parkway. Thanks to Bambi Teague, the Blue Ridge Parkway's Natural Resources Program Manager, for her support and encouragement while I worked to finish this thesis. I am grateful to former Chief Ranger Art Frederick and Highlands District Ranger Brent Pennington for supporting my efforts to attend class while working full-time on the Parkway. The National Park Service Albright-Wirth Employee Development Program provided valuable assistance with funding this research.

Most importantly I would like to acknowledge my wife, Jamie, and my children, Michael and Kelly. Through these last seven years they have put up with distractions to our family life as I took care of classes, research and writing. Thanks for putting up with everything and for being supportive of my efforts.

DEDICATION

To Michael and Kelly, who I hope will always enjoy learning new things as much as I have.

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INTRODUCTION

In small, woodland streams the primary input of energy is allochthonous material (Minshall 1967, Fisher and Likens 1973). Fisher and Likens (1973) noted that over 99% of the energy in Bear Brook was derived from allochthonous sources, with leaf litter alone representing 29% of the system's annual energy input. In a forested Danish stream, 71% of the allochthonous input was in the form of leaves (Iverson *et al.* 1982). In a Kentucky stream, Minshall (1967) found that allochthonous leaf detritus was the system's major energy component. As these leaves fall into the water and float downstream they are often caught up against logs or rocks, forming leaf packs as one leaf piles onto the previously retained leaves (Allan 1995).

These leaves form the base of the food chain in many stream systems (Fisher and Likens 1973, Petersen and Cummins 1974), serving as a food source for macroinvertebrates. Reice (1974) suggested that leaf packs also provide a microhabitat and offer varying protection to macroinvertebrates, though Richardson (1992) disagreed, arguing that the leaf packs are used by macroinvertebrates for food only.

Four different processes influence leaf breakdown rates. These four processes have been viewed as relatively distinct steps (but see Gessner *et al.* 1999). They are 1) leaching of soluble materials, 2) microbial conditioning, 3) invertebrate effects and 4) physical abrasion (Petersen and Cummins 1974, Webster and Benfield 1986). During the first 24 h after leaf fall approximately 5% - 30% of the initial weight is lost due to the leaching of water soluble materials (Petersen and Cummins 1974, Webster *et al.* 1999). This is followed by a microbial conditioning stage in which fungi and bacteria colonize and process the leaves (Petersen and

Cummins 1974). This conditioning increases the palatability of the leaves for macroinvertebrates (Benfield *et al.* 1977, Motyka *et al.* 1985). Macroinvertebrate consumption constitutes the next stage of leaf processing (Petersen and Cummins 1974). Physical processing is the fourth component of leaf breakdown and results from fragmentation of the leaf due to water flow, tumbling or other abiotic activities. Recently, Gessner *et al.* (1999) have argued that these processes do not occur in discrete stages but instead occur coincidentally and with overlap between the stages.

Some of the most abundant taxa in streams aggregate on this plant detritus (Egglishaw 1964, Griffith and Perry 1991). Mackay and Kalff (1969) found that about 30% of the total annual standing crop of macroinvertebrates in a small woodland stream could be found within leaf packs and other detritus.

This source of energy for these headwater systems can be easily altered by human activities, including the conversion of forest sites to pastures (Campbell *et al.* 1992a) and logging (Griffith and Perry 1991, Stout *et al.* 1993). Researchers have studied many of these human-caused impacts and their effects on lotic systems. These impacts include: habitat modification (O'Hop *et al.* 1984, Griffith and Perry 1991, Bunn *et al.* 1999), chemical changes to the water (Triska and Sedell 1976, Hall *et al.* 1980, Griffith and Perry 1993) and global climate changes (Hogg and Williams 1996). Allan and Flecker (1993) list six effects that are at least partially human-caused and that are of critical importance to lotic environments: habitat loss and degradation, the spread of exotic species, overexploitation, chemical and organic pollution, secondary extinction, and climate change.

Of the six factors listed by Allan and Flecker (1993), they considered degradation of stream habitat resulting from agricultural activity and human settlements to be the major cause of changes in aquatic fauna. Noss (1994) looked at the influences of agriculture on ecosystems in the Western US, stating that agriculture, especially livestock production, has exerted a greater impact on these systems than has development. Fleischner (1994) and Harding *et al.* (1999) warn that agricultural activities have been occurring for so long, and that the degradation has been accumulating so slowly, that it may no longer be noticeable. While this degradation can be long-term and cumulative, Ames (1977) compares even short-term grazing of riparian areas with "having the milk cow get in the garden for one night."

Along those Western streams, "natural" conditions disappeared long ago as cattle-grazing reduced stream bank vegetation (Platts and Nelson 1989, Quinn *et al.* 1992); increased thermal (Platts and Nelson 1989) and solar inputs (Rinne 1988b); increased sedimentation (Barton *et al.* 1985, Quinn *et al.* 1992, Harding *et al.* 1999); damaged stream banks (Platts and Nelson 1985, Rinne 1988b); and increased dissolved solids (Rinne 1988b). Platts and Nelson (1989) listed 20 impacts, including those listed above, that livestock grazing can have on aquatic and riparian habitats. Fleischner (1994) summarized the ecological consequences of livestock grazing as alterations of ecosystem structure, disruption of ecosystem functions and alteration of species community composition.

In studies of livestock-grazing along streams, Rinne (1988a) found that there was an increase in density and biomass of the more disturbance-tolerant aquatic insect species. Boreham *et al.* (1989) and Harding *et al.* (1999) reported a downstream increase in pollution-tolerant taxa of benthic macroinvertebrates. Quinn *et al.* (1992) noted marked changes in the

invertebrate community structure in small streams where cattle-grazing occurs. Bird and Kaushik (1992) and Reed *et al.* (1994) found differences in macroinvertebrate communities between forested and agricultural sections of a stream, with total invertebrate biomass greater in the forest sites than in the agricultural sites.

One of the primary concerns with changes in invertebrate communities is the effect on leaf processing and food chains. The invertebrate functional group that most directly processes leaves is shredders (Anderson and Sedell 1979, Cummins and Klug 1979). Several studies have looked at shredder response to the conversion of forested lands but the results of these studies are quite variable. Reed *et al.* (1994) and Tuchman and King (1993) found that the biomass of shredders is higher in forested streams than in streams flowing through pastures. Benfield *et al.* (1977) observed a similar reduction of macroshredders in a pastureland stream, noting that microbial decomposition and mechanical breakage were the main factors responsible for the breakdown of leaves and that shredders were unimportant. Hawkins *et al.* (1982), however, observed no difference in shredder abundance in streams in clear-cut forests compared with second growth forests. Stout *et al.* (1993) found shredder production greater in an 11-year-old clearcut than in a mature hardwood forest. Likewise, the land-use effects on leaf processing rates have not always been consistent between studies. Campbell *et al.* (1992b) and Bird and Kaushik (1992) found no difference in leaf processing rates between sections of forest and pasture streams. Tuchman and King (1993) and Young *et al.* (1994) found processing rates to be higher in agricultural sites.

In this study I examined whether the conversion of forested lands to pastures along small woodland streams in the Southern Appalachians affected the processing of leaf detritus and the benthic macroinvertebrates colonizing those leaf packs. I hypothesized that changes in land cover, i.e., forest to pasture, along the streams would affect benthic macroinvertebrate species composition and density on leaf packs. These changes would in turn influence the rate of detrital processing, specifically leaf pack breakdown.

Study Sites

The experiments were conducted in two headwater streams in the southern Appalachian Mountains near Blowing Rock, North Carolina. Both stream study sites were located along the Blue Ridge Parkway with Greene Creek at Milepost (MP) 291.6 and Sims Creek at MP 296.5. Both sites experience relatively mild weather throughout the year with summer maximum air temperatures averaging 24.3° C and winter lows of -6.4° C. Precipitation averages 166 cm annually.

The streams were selected because three different riparian types, i.e., land covers, were present along a short section of stream (Figures 1 & 2). The upstream sections of both streams consisted of intact mixed-hardwood forests from which cattle were excluded. The streams then flowed into forested sections of agricultural leases with open understories where cattle had free access; these were referred to as the Intermediate Sites. Finally the streams entered cattle-grazed pastures, which made up the downstream portions of both study sites. Specific descriptions of each site are presented below.

Greene Creek

Greene Creek is a tributary of the Middle Fork of the New River with headwaters at an elevation of 1080 m. The study site was at approximately 1050 m. The vegetation along the upper reaches consisted of mixed-hardwood forest with a canopy dominated by yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), and Eastern hemlock (*Tsuga canadensis*), while a thick layer of rosebay rhododendron (*Rhododendron maximum*) dominated the understory. At the intermediate site there was a canopy of yellow birch, red maple and Eastern hemlock but the understory was open, containing only widely scattered

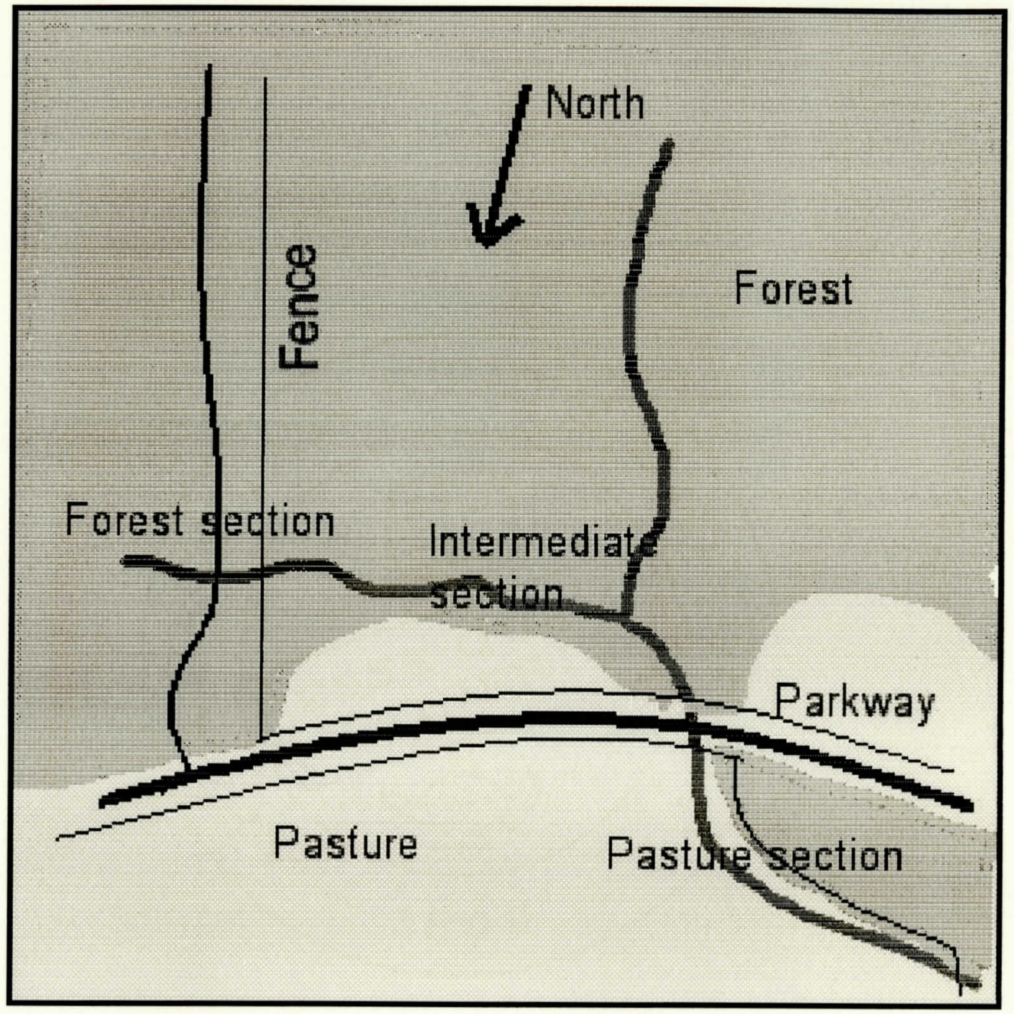
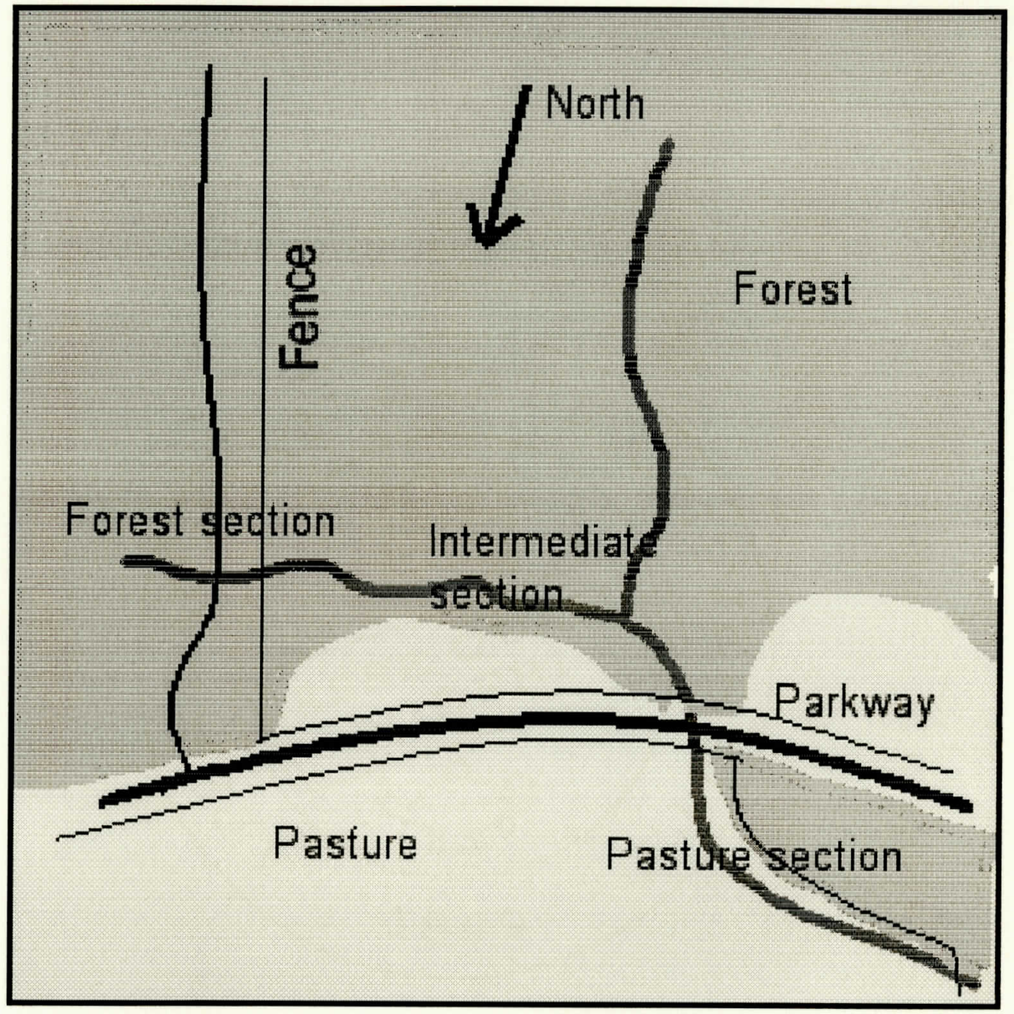


Figure 1. Greene Creek study site at Milepost 291.6 on the Blue Ridge Parkway.

Figure 2. Sims Creek study site at Milepost 296.5 on the Blue Ridge Parkway.



rhododendron. The pasture section consisted of grasses and forbs with widely scattered birch trees. Each study section (i.e., where the leaf packs were placed) was about 25 m long with 30 m between the ungrazed and grazed forest sections and 70 m between the grazed forest (intermediate section) and the pasture sections. The forested study site and the intermediate section of Greene Creek were in a first order section of the creek; the pasture site was in a second order section immediately below the confluence with another first order stream. Greene Creek is 1 - 2 m wide and the mean depth was 8.2 cm (range 5 – 17 cm). The substrate in each section was primarily a mix of gravel and cobble, with smaller patches of sand. The grazing lands have been in pasture and grazed by cattle since at least 1950.

Sims Creek

Sims Creek, a second order tributary of the Watauga River, has its headwaters at 1060 m. The study site was at 1030 m. A mixed-hardwood forest was present along the upper reaches with the canopy dominated by yellow birch, red maple, and Eastern hemlock. Rosebay rhododendron formed a thick understory. The intermediate site had a solid canopy of yellow birch, red maple and Eastern hemlock with an open understory of widely scattered rhododendron. In the Sims Creek pasture section there were birch trees and rhododendron bushes on the west bank while the east side of the stream was a pasture covered with a mix of grasses and forbs. Each study section was about 40 m long with approximately 100 m between sections. The creek was 1 - 2 m wide with a mean depth of 7.8 cm (range 5 – 13 cm). The substrate of Sims Creek consisted primarily of gravel and cobble, with smaller sections of bedrock and sand. The Sims Creek study site was located 200 m downstream of

Sims Pond, a 1/2 ha reservoir with a spillway overflow. The pasture section along Sims Creek has been grazed since at least 1950.

Materials and Methods

Leaf Pack Experiments

Greene Creek

I collected yellow birch leaves along Greene Creek in late-October and early-November 1997. Leaves were collected after the abscission layer formed but before the leaves fell from the trees. The collected leaves were air-dried on wire racks for at least four days. Packs of 5.0 g, air-dried leaves (approximately 40-50 leaves) were soaked in de-chlorinated water until pliable enough to be stacked without breaking. The petiole ends of the leaves were placed in a binder clip to form a leaf pack. These leaf packs were attached to bricks using cable ties and placed in riffles in the stream with the leaf pack facing upstream and with the leaf pack completely underwater. Current velocities (n=5) and stream depths (n=12) were measured on 9 November 1997 in each section. Water velocity was fastest in the pasture (16.20 cm/s, ± 4.14), slowest in the forest (9.80 cm/s ± 2.97) and intermediate in the middle section (16.00 cm/s ± 6.86). Mean stream depths were 9.17 cm (± 0.97) in the forest, 7.33 cm (± 0.36) in the intermediate section, and 8.17 cm (± 0.58) in the pasture. The experimental design was a completely randomized design with a factorial combination of treatments (date and section).

On 13 November 1997 I placed 48 leaf packs in each of the three study sections for a total of 144 packs. An additional six packs were placed in the creek for one minute and removed to determine how much material was lost due to the handling and placement of the packs (Day 0 sample). Six leaf packs in each of the three sections were randomly chosen and were removed on each sampling date (Days 1, 7, 14, 28, 42 and 56) with the last set of leaf

packs removed on 4 January 1998. Packs were to have been removed on Days 70 and 84 but a flood occurred on Day 60 and washed away many of the bricks. Upon removal from the creek the leaf packs were cut from the bricks, immediately placed in resealable plastic bags and taken back to the lab. There they were gently rinsed to remove debris and macroinvertebrates and then dried at 60° C for 4 d. The dried leaf packs were weighed to the nearest 0.1 g. The debris and macroinvertebrates from the leaf packs were placed in vials with 70% ethanol for later separation and identification. Macroinvertebrates were identified to the lowest taxonomic level possible, which was usually genus. Leaf pack mass and macroinvertebrate data were analyzed using a MANOVA and univariate ANOVAs (Program, SAS). Section means for leaf pack mass and macroinvertebrate abundance were compared using Tukey's test using pooled data from all six collection dates. Macroinvertebrate data were log transformed to homogenize the variances.

Sims Creek

The following year (1998) I repeated this experiment in Sims Creek to see if the results from Greene Creek could be replicated in a different stream. I collected yellow birch leaves along Sims Creek in late-October and early-November 1998. Leaves were collected, dried and placed in the stream on 15 November 1998 using the same methods as those described for the Greene Creek experiment. Stream depths were measured at several locations in each section (pasture mean depth 9.00 cm, range 6 – 10 cm; intermediate 7.17 cm, range 5 – 9; forest 7.17, range 5 – 10).

Forty-eight leaf packs were placed in each of three study sections for a total of 144 packs in the stream. Six additional packs were set out and removed the same day to determine how much leaf mass was lost during handling (Day 0). Six packs in each of the three sections were chosen randomly and were removed on a given sampling date (Days 1, 7, 14, 28, 42, 56, and 68). Packs were to have been removed on Day 84 but due to a flood the bricks and packs had been disturbed enough that I felt they were no longer useable for the study.

The leaf packs were removed from the stream and processed as described above in the Greene Creek section. Leaf pack mass data were analyzed using a two-way analysis of variance. I did not identify the macroinvertebrates associated with these leaf packs.

***Pycnopsyche* Enclosure Experiment**

The results of the leaf-pack breakdown experiment conducted in Greene Creek indicated that *Pycnopsyche* caddisflies might be responsible for the increased leaf processing rate in the ungrazed forested section of the stream (see Results). I set up an experiment in an attempt to see whether the decreased processing rate in the pasture was due to the lack of *Pycnopsyche* or possibly due to differences in physical factors (e.g., faster current velocities) in the pasture. By transplanting *Pycnopsyche* into the pasture section I could determine which was the cause. This experiment employed a randomized block design with three treatments and five replicates per treatment.

In the pasture section of Greene Creek I placed leaf packs made of 5.0 g of air-dried yellow birch leaves inside ten enclosures constructed from Rubbermaid© containers. The fronts and backs of these containers were removed and replaced with 1 mm mesh wire screens to allow water to flow through the containers while excluding large invertebrates. An additional 5 leaf packs were attached to exposed bricks with cable ties. I placed two enclosures and one brick randomly in each of five rows in a 15 m stretch of the pasture section

of Greene Creek. All of the treatments were placed so that the leaf packs were completely underwater. After a conditioning period of 2 weeks I placed six *Pycnopsyche* larvae on the leaf pack in one of the enclosures in each row (*Pycnopsyche* enclosure treatment). No *Pycnopsyche* larvae were added to the other enclosure that served as a cage control. The exposed brick treatment was used to evaluate any possible enclosure effects on leaf breakdown rates. All the leaf packs were collected after an additional 19 d in the creek. The leaf packs were removed from the containers and from the bricks and placed in resealable plastic bags. In the lab the leaves were rinsed to remove sediment and invertebrates and then dried at 60 °C for 4 d. The dried leaf packs were weighed to the nearest 0.1 g. Leaf pack mass data were analyzed using a two way analysis of variance. Any macroshredders (e.g., *Tallaperla*, *Tipula*, *Pycnopsyche*) associated with the leaf packs in the enclosures and those attached to the bricks were noted.

***Pycnopsyche* Surveys**

Observations made at Greene Creek indicated that *Pycnopsyche* were important shredders in sections of streams running through ungrazed forests but not in stream sections running through grazed forests or through pastures. Based on these results I decided to conduct surveys of *Pycnopsyche* larvae in nearby streams with land cover and use patterns similar to Greene and Sims Creeks. The purpose of these surveys was to determine if the distribution pattern of *Pycnopsyche* observed in Greene Creek occurred in other streams.

I surveyed five streams along the Blue Ridge Parkway between 27 February and 6 March, 2000: Sandpit Branch (MP 283.6), Weaver Creek (MP 287.3), Shoals Creek (MP 287.8), Aho Creek (MP 288.8), and Stringfellow Creek (MP 294.0). All of these streams were in Watauga County and in the watershed of the South Fork of the New River. All forested sections along these streams consisted of mixed hardwood forests. In the pasture sections the vegetation was a mix of grasses and forbs with few, if any, trees. Substrate in all streams was generally cobble and gravel, with occasional patches of sand. All surveyed streams were usually less than 15 cm deep in the areas sampled.

The forested section of Sandpit Branch was a first-order stream and was accessible to cattle. The pasture section of Sandpit Branch was a second order stream. I searched for *Pycnopsyche* in both sections. Weaver Creek, a first order tributary of Shoals Creek, flowed through an ungrazed forest and an open pasture above and below a small pond. I looked for *Pycnopsyche* in the forested section as well as in the pastures above and below the pond. In Shoals Creek, a first order stream, I searched for *Pycnopsyche* in sections of stream flowing through an ungrazed forest and an open pasture. In Aho Creek, a first order stream, I looked for *Pycnopsyche* in the stream in a grazed forest, in a section flowing through an ungrazed forest and in an open pasture with few scattered trees. All three sites on Aho Creek were downstream of a pond. Stringfellow Creek is a first order stream. I searched for *Pycnopsyche* in sections of this stream flowing through a grazed forest and an open pasture.

I also surveyed Sims Creek for *Pycnopsyche* cases. One survey site was located above Sims Pond in an ungrazed forest. The other three sites were all below Sims Pond, with one survey in each of the three sections used in the leaf pack study.

During surveys I searched through leaf litter in each of the streams. The leaves were removed from the stream and inspected for *Pycnopsyche* cases. I timed each of these surveys to determine the number of larvae collected per minute of searching.

Results

Greene Creek

In Greene Creek there were highly significant effects of both date and stream section on leaf pack breakdown and macroinvertebrate abundance (MANOVA: date – Wilk's Lambda=0.0285, $F_{80,350.9}=4.80$, $p<0.0001$; stream section – Wilk's Lambda=0.0780, $F_{32,144}=11.62$, $p<0.0001$). The date and section interaction was also significant (Wilk's Lambda=0.0520, $F_{160,634.1}=1.64$, $p<0.0001$). Both date and section significantly affected leaf pack breakdown (ANOVA: date $F_{5,2}=57.60$, $p<0.001$; section $F_{5,2}=14.53$, $p<0.001$, Table 1). Leaf packs broke down at a significantly faster rate in the forest section than in both the pasture and the intermediate section (Tukey's test (across dates), $p<0.05$) (Table 2, Figure 3). Overall there was no significant difference between the pasture and intermediate sections, although the mass of leaf packs in the intermediate section was less than that observed in the pasture at the end of the experiment. There was no change in leaf mass in the forest section between Day 42 (1.47 g ± 0.17) and Day 56 (1.53 g ± 0.27) possibly due to the remaining leaf material being made inaccessible by the binder clip compressing the petiole ends of the leaves and preventing the invertebrates from getting to them. During this same period the leaf packs in the intermediate section, which had leaf material still accessible to invertebrates, were reduced from 2.50 g (± 0.38) to 1.72 g (± 0.29).

A total of 21,355 invertebrates were recovered from the leaf packs in Greene Creek, with 6,190 from the pasture section, 8,069 from the intermediate section and 7,096 from the forested section. Of these 3,437 were classified as shredders (Appendix A) with 713 shredders collected in the pasture, 1,819 in the intermediate section and 905 in the forest.

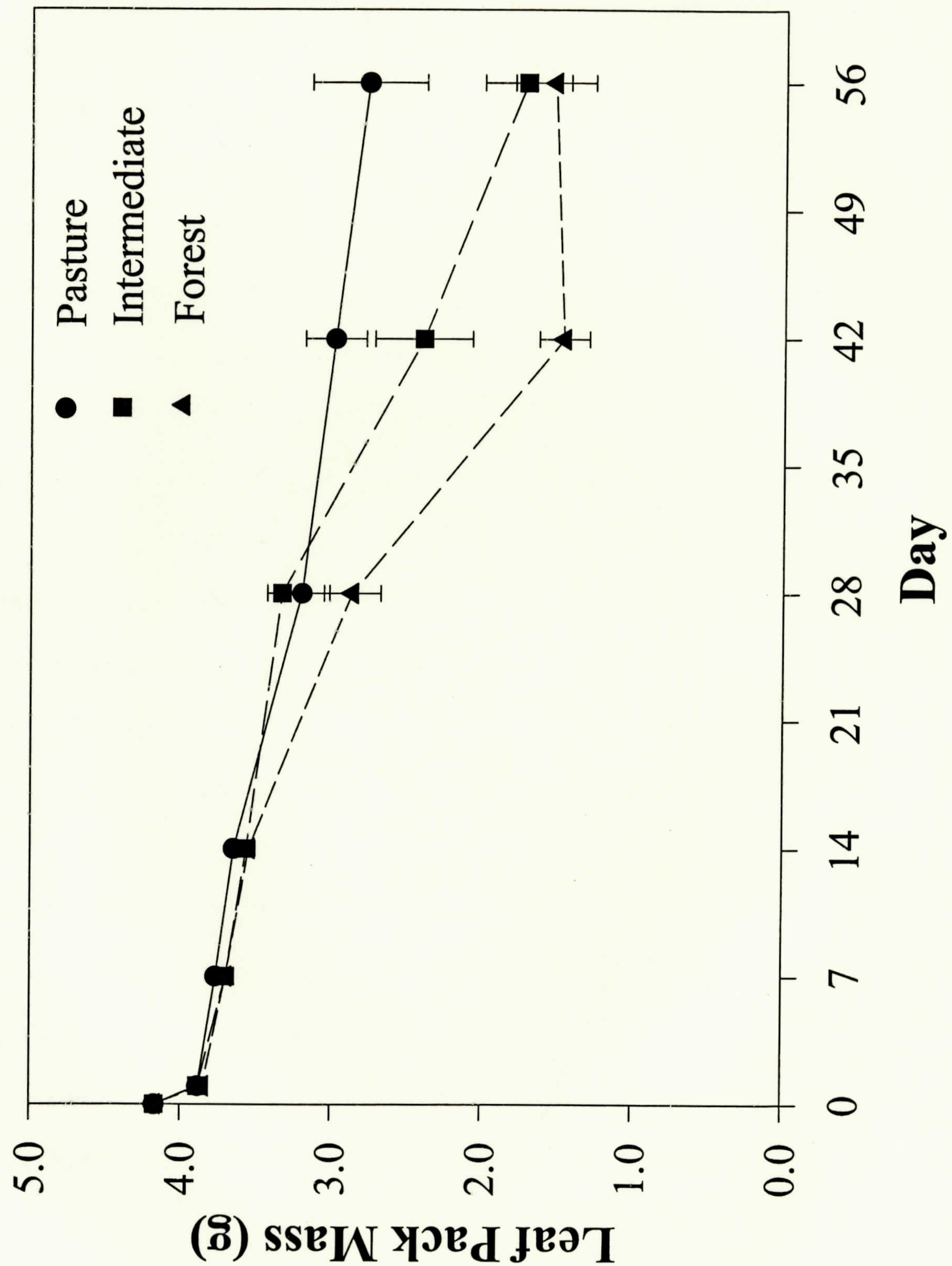
Table 1. Results of the univariate ANOVAs for leaf pack mass and common taxa to Date, Section and the Date x Section interaction in the Greene Creek experiment. Date refers to when the leaf packs were collected from the stream. Section refers to the pasture, intermediate and forest sections of the study stream. Significance at $p \leq 0.05$. n.s. = no significant response

Taxon	Functional Group	Date		Section		Date x Section	
		$F_{(5,87)}$	P	$F_{(2,87)}$	P	$F_{(10,87)}$	P
Leaf Pack Mass		57.60	0.0001	14.53	0.0001	4.29	0.0001
Ephemerellidae	S	9.31	0.0001	31.90	0.0001	7.50	0.0001
Epeorus	C-G	1.48	0.0485	2.72	0.0082	1.86	0.0125
Leptophlebiidae	C-G	6.73	0.0001	7.52	0.0010	3.04	0.0143
Ameletus	C-G	1.06	n.s.	0.02	n.s.	1.42	n.s.
Allocapnia	S	4.54	0.0004	27.11	0.0001	1.92	n.s.
Nemouridae	S	5.55	0.0001	6.46	0.0013	2.13	0.0454
Peltoperlidae	S	1.42	n.s.	7.69	0.0087	1.25	n.s.
Perlodidae	P	1.59	0.0324	3.06	0.0026	1.12	n.s.
Chironomidae	C-G	30.31	0.0001	1.88	n.s.	3.74	0.0025
Tipula	S	5.62	0.0002	2.42	n.s.	1.24	n.s.
Pycnopsyche	S	3.11	0.0216	14.62	0.0001	3.52	0.0009
Rhyacophilidae	P	1.17	n.s.	0.53	n.s.	0.93	n.s.
Cyclopoida	C-G	7.93	0.0001	5.20	0.0025	2.16	0.0471
Harpacticoidae	C-G	11.56	0.0001	0.41	n.s.	0.94	n.s.
Oligochaeta	C-G	11.34	0.0001	1.71	n.s.	1.42	n.s.

Table 2. Results of Tukey's Test for differences among the three sections of Greene Creek for leaf pack mass and abundance of common taxa. Sections with same letter were not significantly different ($p \leq 0.05$).

Response Variable	Pasture	Intermediate	Forest
Leaf Pack Mass	A	A	B
Ephemerellidae	A	B	A
Epeorus	A	B	B
Leptophlebiidae	A	B	A
Ameletus	A	A	A
Allocapnia	A	B	B
Nemouridae	A	B	A/B
Peltoperlidae	A	B	A/B
Perlodidae	A	B	A
Chironomidae	A	A	A
Tipula	A	A	A
Pycnopsyche	A	A	B
Rhyacophilidae	A	A	A
Cyclopoida	A	B	B
Harpacticoida	A	A	A
Oligochaeta	A	A	A

Figure 3. Change in leaf pack mass for the Greene Creek experiment. The points represent mean dry mass of leaf packs (± 1 SE) (n=6).



Chironomids were the most abundant taxon in each section with 9,276 collected overall. Total invertebrates per g leaf pack ranged from 5 in the intermediate section after 1 d up to 231 in the forest section on Day 42.

In the Greene Creek pasture section I collected and identified 6,190 macroinvertebrates, which was 29.0% of the total collected for the study. There was an average 51 macroinvertebrates per g leaf material in this section, ranging from just 6 per g on Day 1 up to 198 per g on Day 28. Chironomids made up 49% of the total number of organisms collected in the pasture section. The largest functional group in the pasture was the collector-gatherers with 79.5% of the total invertebrates.

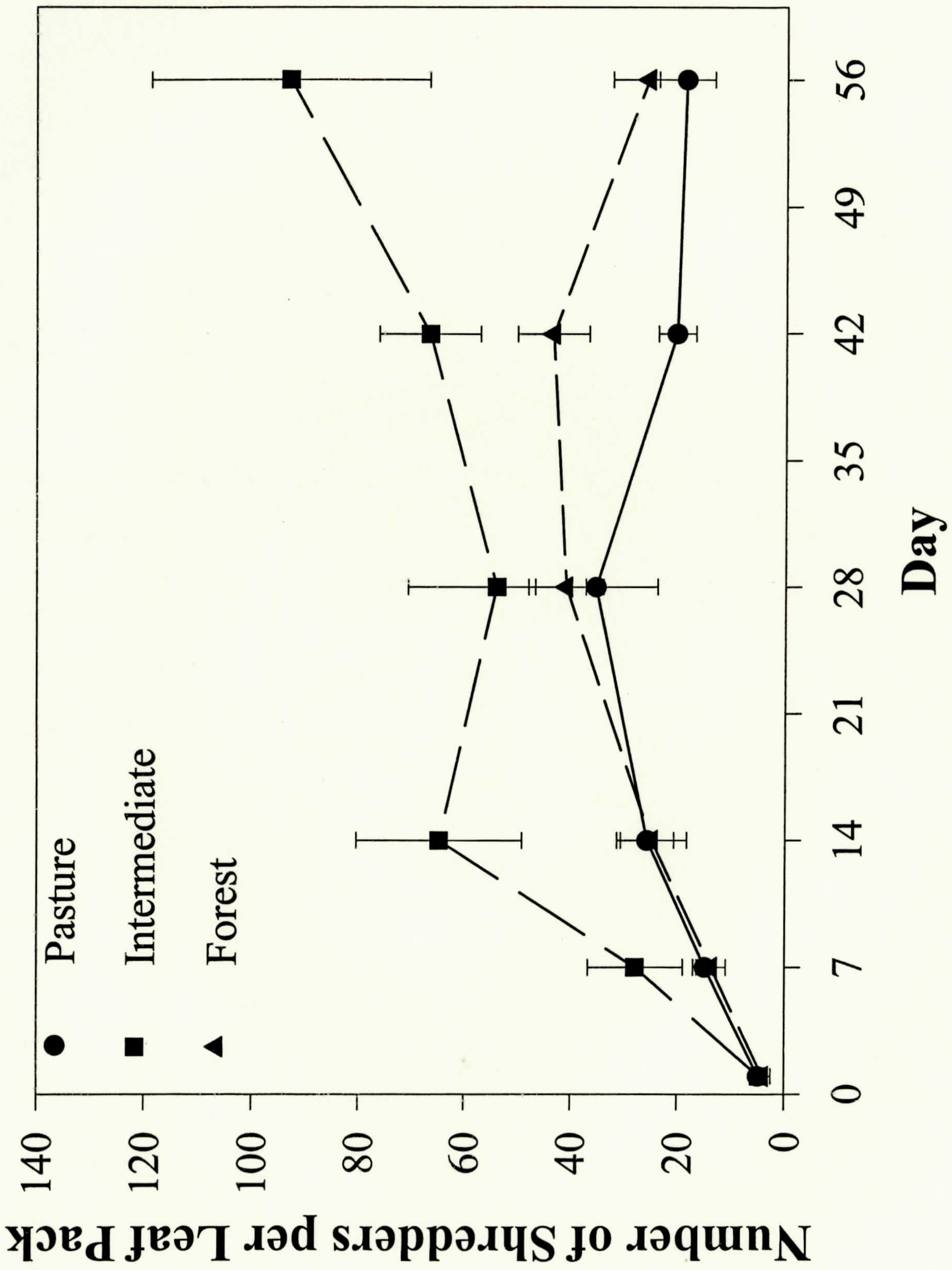
The intermediate section had 8,069 invertebrates (37.8% of the total). Collector-gatherers were also the most common functional group with 5,294 individuals (66% of the total organisms in the intermediate section). Organisms per g leaf pack ranged from 5 on Day 1 up to 215 per g on Day 56.

I collected 7,096 macroinvertebrates in the forest section (33.2% of the total). Of this total 62.2% were collector-gatherers. The number of invertebrates per g leaf pack ranged from 6 on Day 1 up to 231 on Day 56.

The number of invertebrates per g leaf pack increased on each sampling date in the intermediate and forest sections and on five of the six dates in the pasture section. Twelve of the 15 macroinvertebrates showed a significant response to date, including 5 of the 6 shredders and 6 of the 7 collector-gatherers, and 1 of the 2 predator taxa.

Total shredders were more abundant in the intermediate section than in the other two sections on four of the six dates (Figure 4). In both the pasture and forest sections shredders

Figure 4. Total number of shredders per leaf pack in Greene Creek on each sampling date. Points represent mean number of shredders per leaf pack (± 1 SE) (n=6). Ephemerellidae, Capniidae, Nemouridae, Peltoperlidae and *Tipula* (Tipulidae) were counted as shredders for this figure.



generally increased in number per g leaf pack through Day 28 and then decreased to Day 56. Shredders also increased in the leaf packs over the course of the experiment.

Several macroinvertebrate taxa showed a significant response to section in the Greene Creek experiment (Table 2) with the abundance differing significantly among the three sites. The forest section had significantly more *Pycnopsyche* caddisflies than either the pasture or intermediate sections (Table 2, Figure 5). On every sampling date there were more *Pycnopsyche* per g leaf mass in the forest section than in the other two sections. Ephemerellid and leptophlebiid mayflies were found in significantly higher numbers in the intermediate section (Table 2, Figures 6 & 7). Ephemerellids were more abundant in the intermediate section on each sampling date, with their abundance increasing rapidly after Day 28, and least abundant in the pasture section. Their numbers never exceeded 0.25 ± 0.15 per g leaf pack in the pasture while in the intermediate section their total reached 39.83 ± 10.22 (Figure 6). On Day 42 there were twice as many leptophlebiids in the intermediate section than in the other two sections and five times as many on Day 56 (Figure 7). Overall the intermediate section had significantly more *Tallaperla* and Nemouridae stoneflies than the pasture section, but numbers of neither species in the intermediate section differed significantly from the forest section (Table 2, Figures 8 & 9). The pasture section contained significantly more *Allocapnia* stoneflies (86.5% of the total) than in either the intermediate or forest sections with more found in the pasture on all of the sampling dates (Figure 10). *Tipula* was the only shredder taxon that showed no significant difference in abundance between the sections (Table 2, Figure 11).

Figure 5. Mean number (± 1 SE) of *Pycnopsyche* per gram of leaf pack in Greene Creek on each sampling date (n=6).

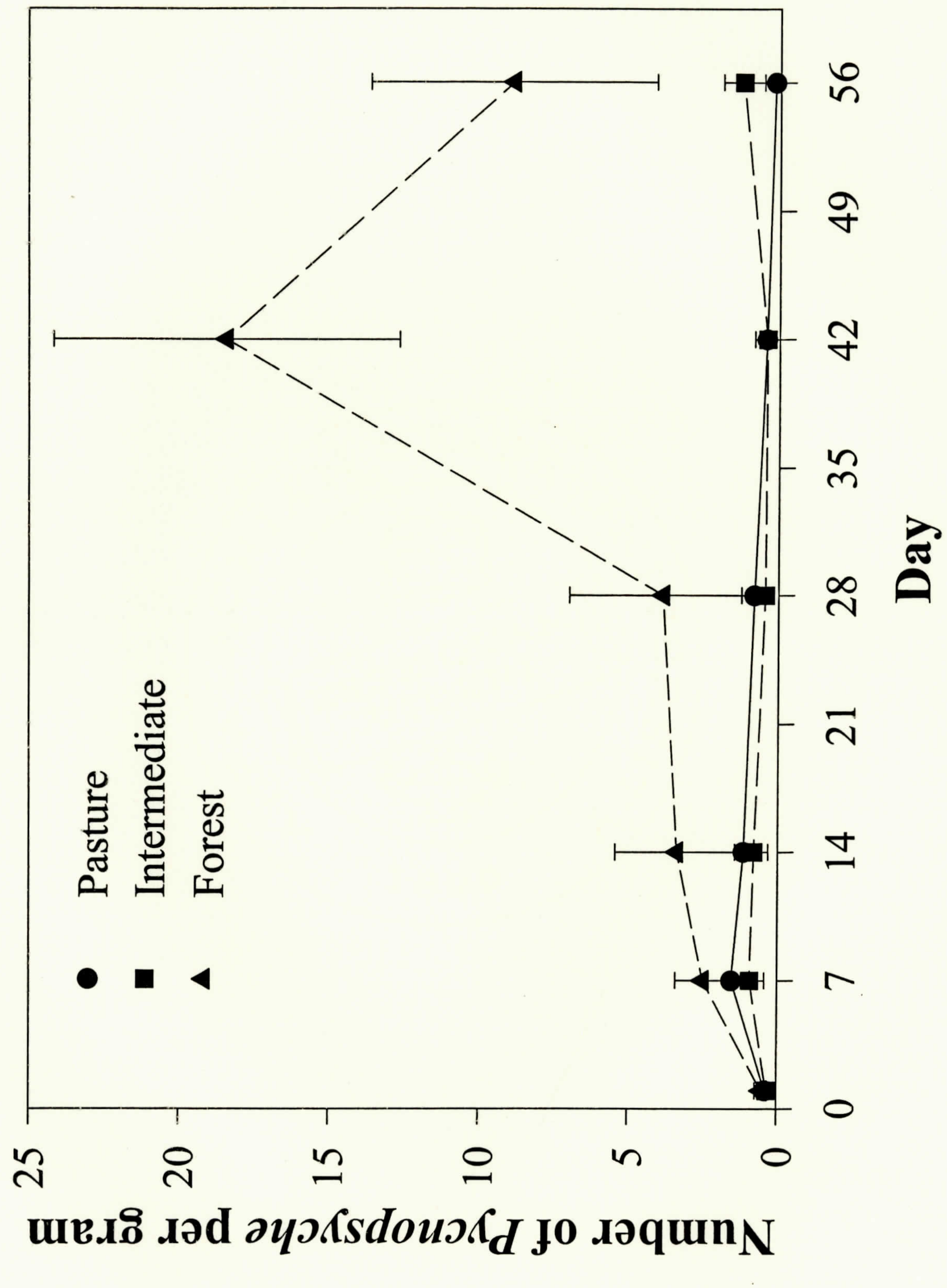


Figure 6. Mean number (± 1 SE) of Ephemerellidae per gram of leaf pack in Greene Creek on each sampling date (n=6).

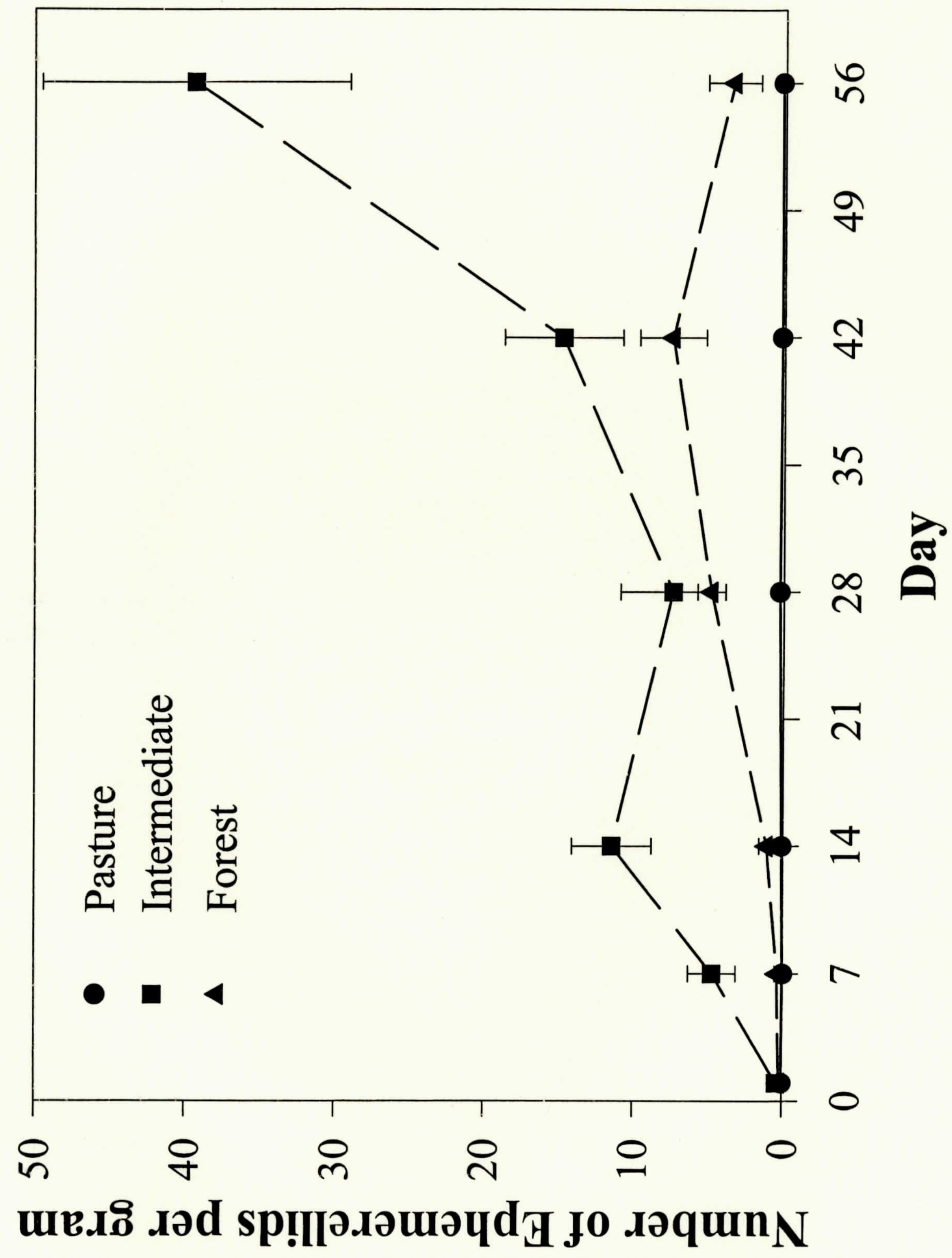


Figure 7. Mean number (± 1 SE) of Leptophlebiidae per gram of leaf pack in Greene Creek on each sampling date (n=6).

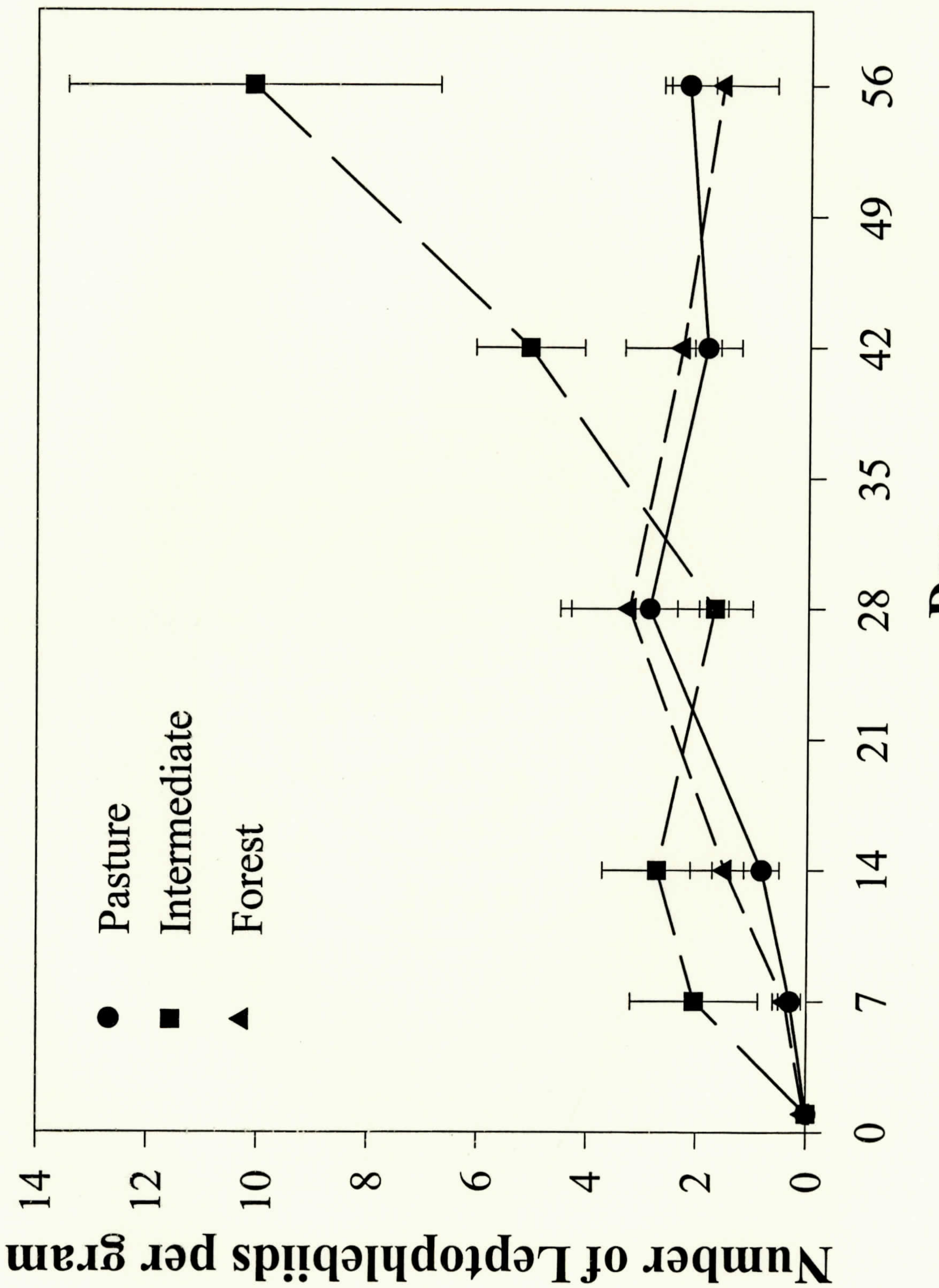


Figure 8. Mean number (± 1 SE) of *Tallaperla* per gram of leaf pack in Greene Creek on each sampling date (n=6).

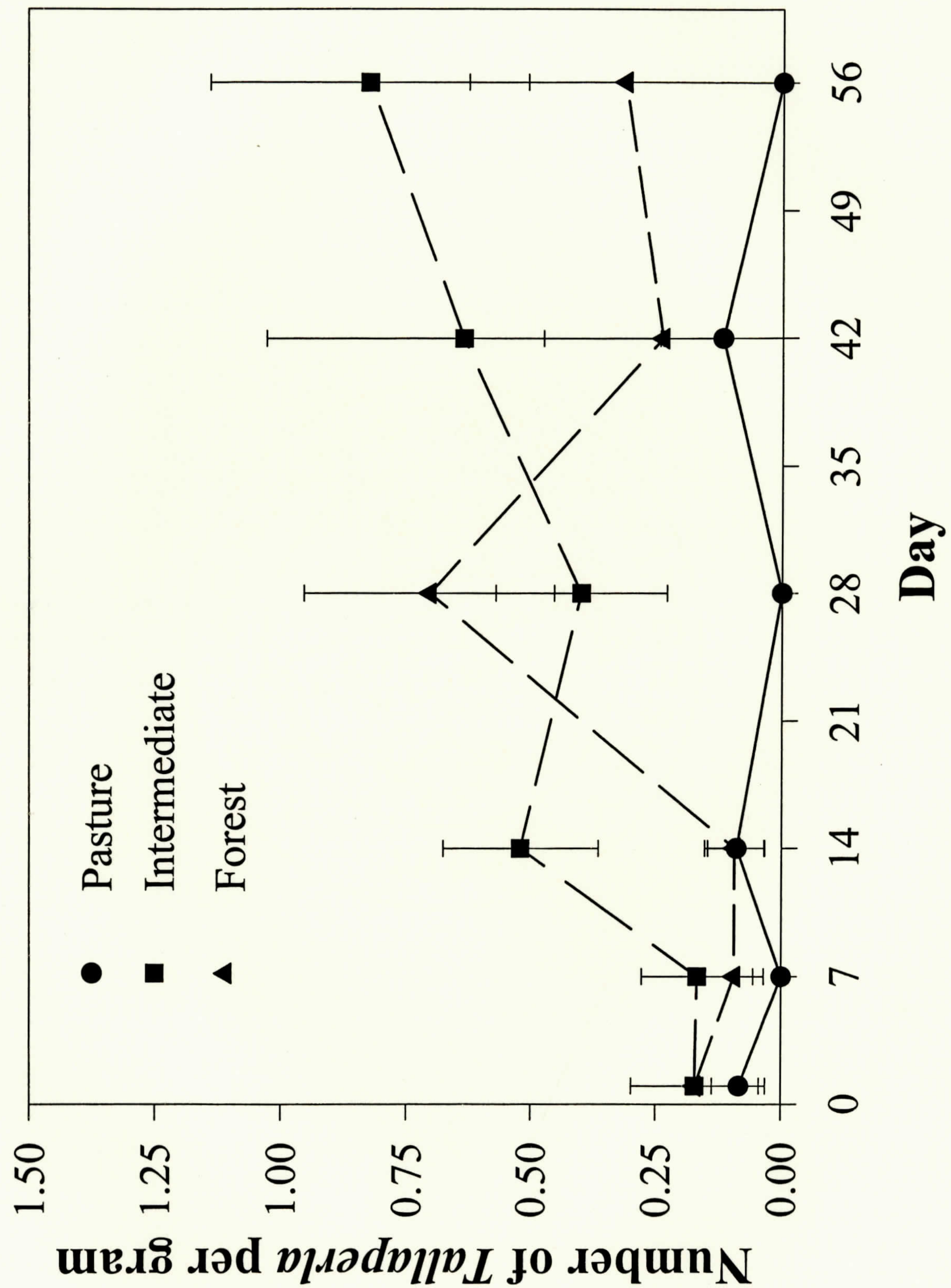


Figure 9. Mean number (± 1 SE) of Nemouridae per gram of leaf pack in Greene Creek on each sampling date (n=6)

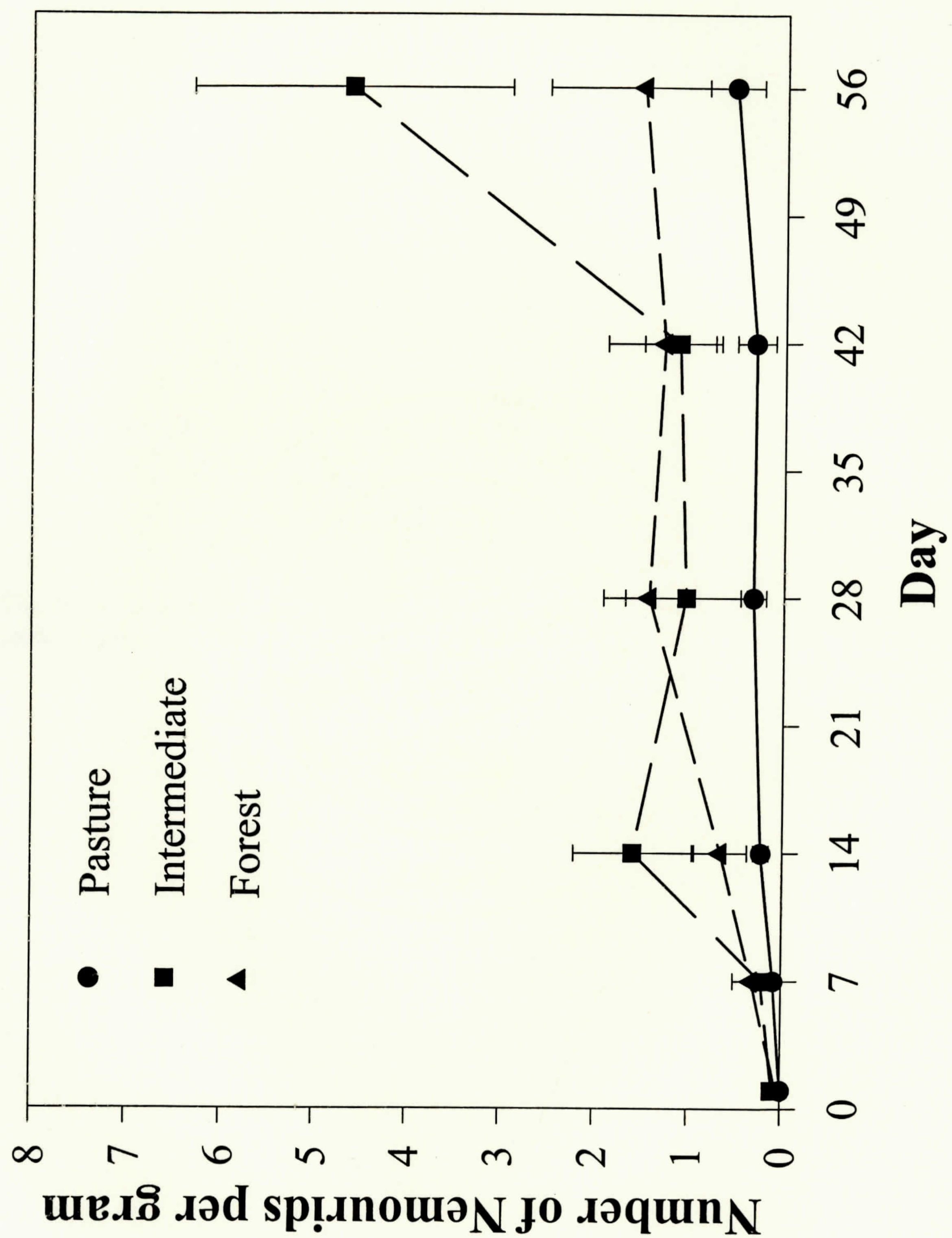


Figure 10. Mean number (± 1 SE) of *Allocapnia* per gram of leaf pack in Greene Creek on each sampling date (n=6).

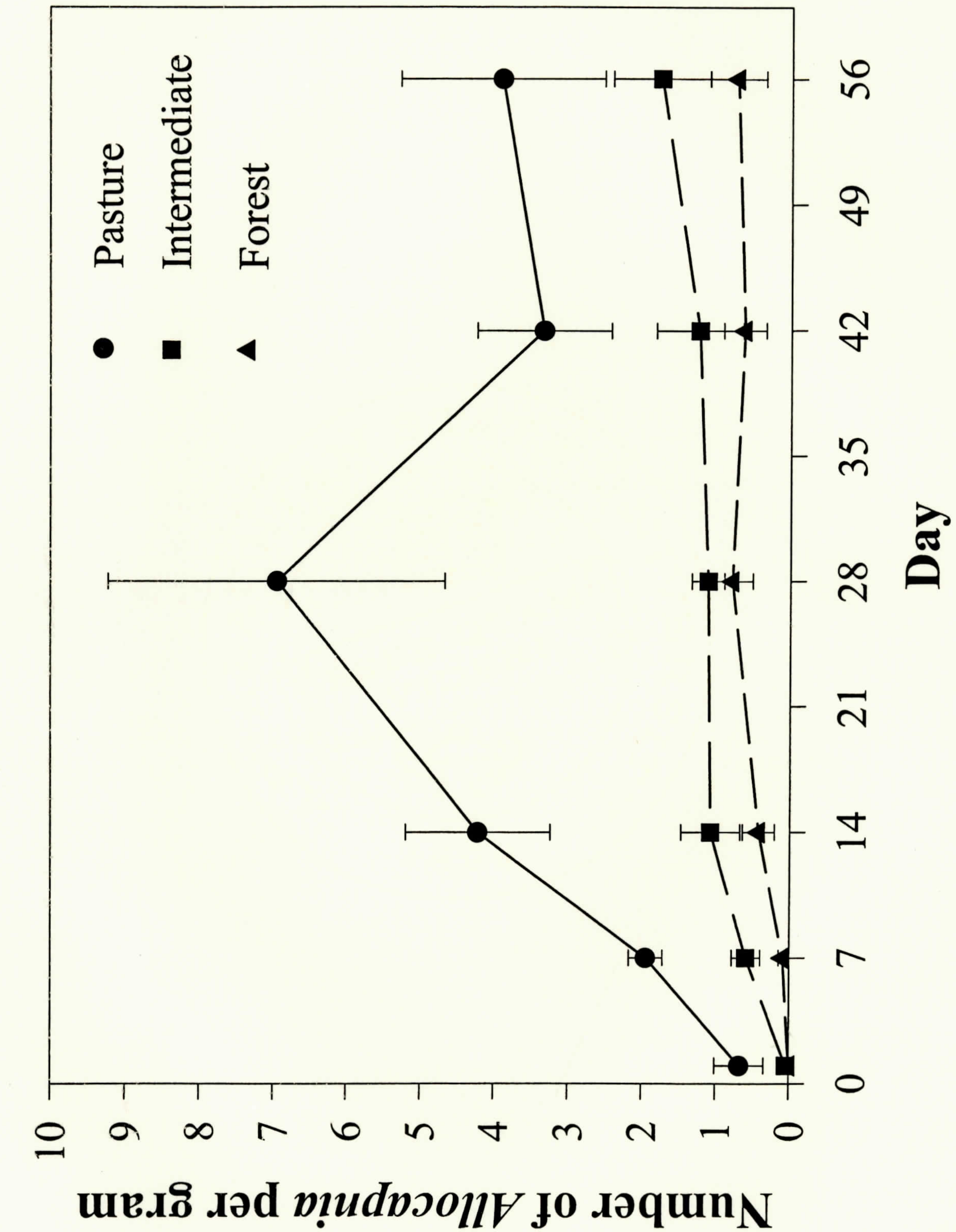
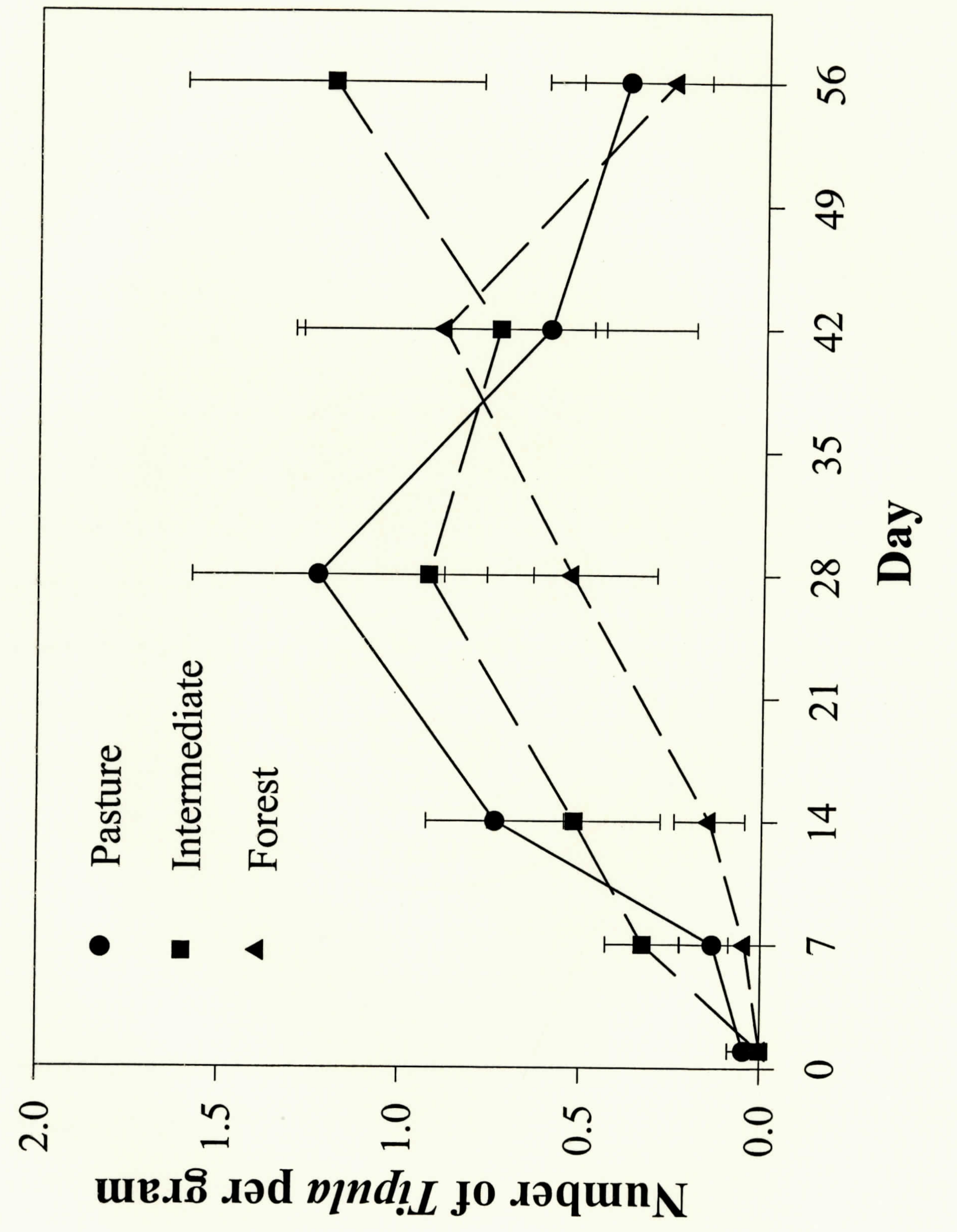


Figure 11. Mean number (± 1 SE) of *Tipula* per gram of leaf pack in Greene Creek on each sampling date (n=6).



Sims Creek

In Sims Creek there was an overall significant effect of both date and section on leaf processing, with leaf pack mass decreasing over time ($F_{6,2}=71.18$, $p<0.0001$) and leaf packs in the pasture breaking down significantly slower ($F_{6,2}=12.91$, $p<0.0001$) than the intermediate and forest sections (Tukey's test, $p<0.05$) (Figure 12). There was no difference in processing rates between the intermediate and forest sections. The rate of leaf loss in all three sections was similar to that observed in the pasture in Greene Creek (Figure 3).

Pycnopsyche Enclosure Experiment

There was significantly less leaf material remaining in the *Pycnopsyche* enclosures than in the other two treatments in this experiment (Figure 13). The masses of the leaf packs in the containers without caddisflies and on the exposed bricks were similar. No *Pycnopsyche* larvae were found on the leaf packs in the exclosure treatment or on the leaf packs attached to the exposed bricks.

Pycnopsyche Surveys

Both land-use cover and location of the survey site relative to a pond significantly affected number of *Pycnopsyche* larvae (ANOVA: cover $F_{1,7}=14.96$, $p<0.006$; pond $F_{1,7}=37.90$, $p<0.000$, Table 3). The highest numbers of *Pycnopsyche* were found in streams running through forests rather than through pastures, in ungrazed areas rather than grazed areas, and above ponds rather than below ponds (Table 4, Figures 14, 15 & 16)). There was one outlier (determined using Dixon's test) in this data set from the Weaver Creek survey (Weaver Creek 2). This site was located in a short section of stream ~15 m below a forested section and above a pond. I conducted this survey 5 March 1999 when there appeared to be

Figure 12. Change in leaf pack mass for the Sims Creek experiment. The points represent mean dry mass of leaf packs (± 1 SE) (n=6).

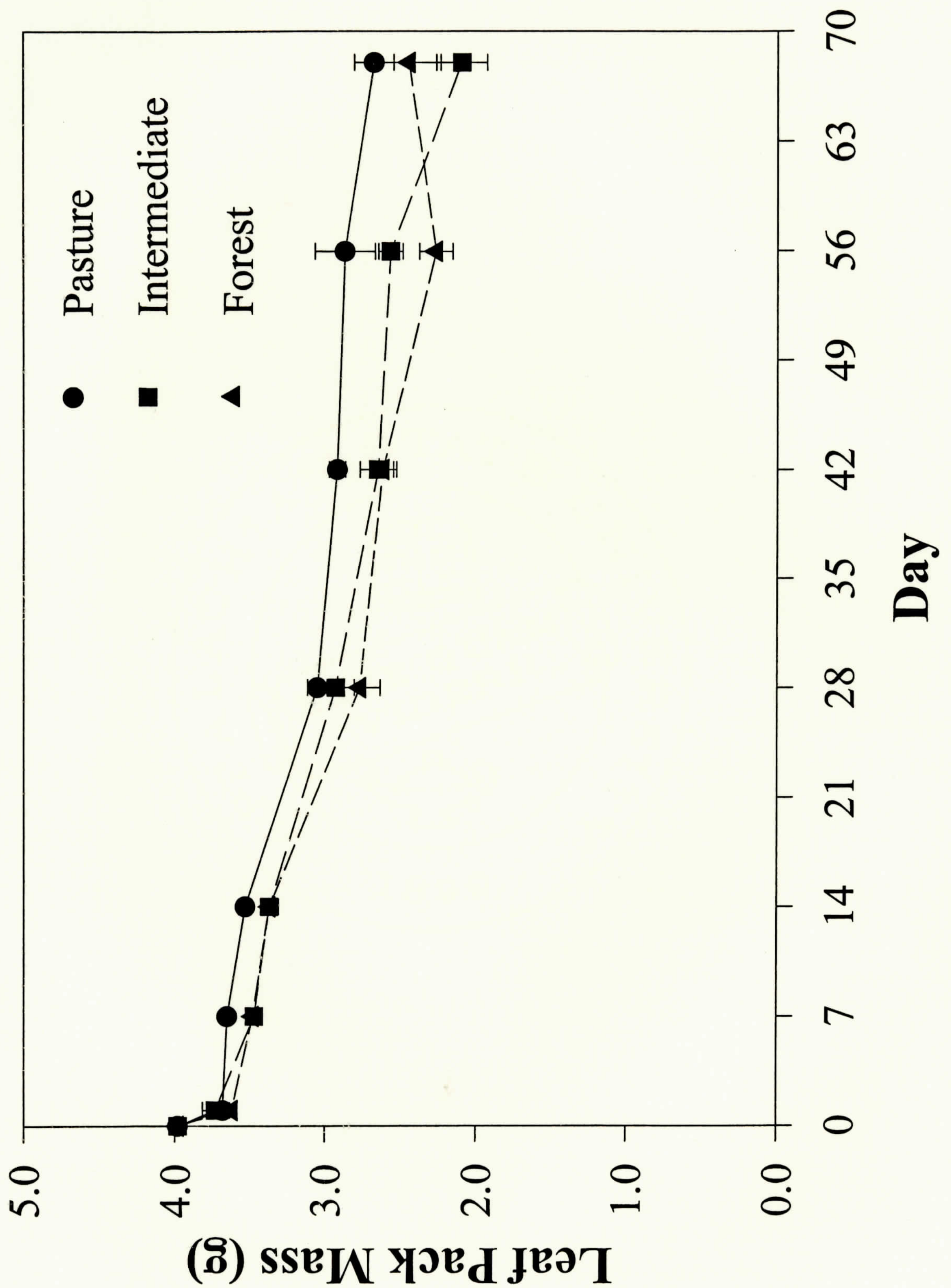


Figure 13. Results of the *Pycnopsyche* enclosure experiment. Bars represent the mean (± 1 SE) dry mass of leaves remaining for the three treatments on Day 33. "Exp. Brick" = leaf pack attached to exposed brick. "No Caddis" = container with no caddflies added to leaf pack. "Caddis" = container with *Pycnopsyche* larvae added to leaf pack. Sections with same letter were not significantly different ($p > 0.05$).

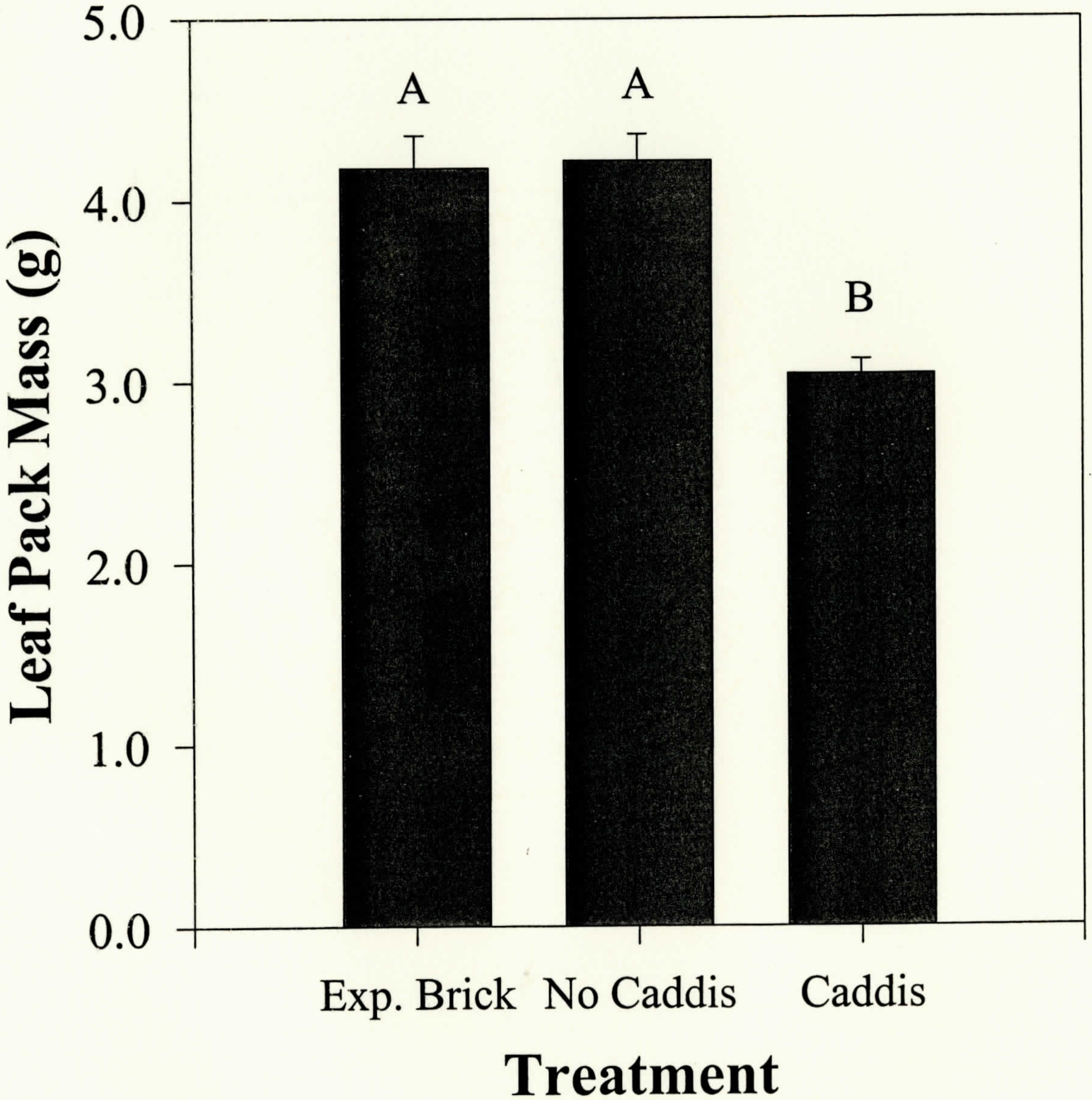


Table 3. Results of the two-way analysis of variance examining the effects of pond location and land-use cover on *Pycnopsyche* abundance. Data are from the *Pycnopsyche* surveys. Surveys were conducted in headwater streams of the New River drainage.

Source	df	SS	MS	F	P
Pond	1	0.81493	0.81493	37.90	0.000
Cover	1	0.32160	0.32160	14.96	0.006
Pond * Cover	1	0.50884	0.50884	23.66	0.002
Error	7	0.15053	0.02150		
Total	10				

Table 4. Results of *Pycnopsyche* surveys in headwater streams of the New River drainage. Surveys were conducted between 27 February and 6 March 2000 by looking through leaf detritus in the streams for indicated time. Results are given in mean Cases Found per Minute of Searching. F = Forest, P = Pasture, B = Below pond, N = Not below pond, U = Ungrazed, G = Grazed

Site	Type of Site			Occupied	Total Time
	Vege-tation	Pond	Grazed	Cases Found/Min	Searching (Min.)
Aho Creek 1	F	B	G	0.233	30
Aho Creek 2	F	B	U	0.300	30
Aho Creek 3	P	B	G	0.167	30
Sandpit branch 1	F	N	G	1.300	30
Sandpit branch 2	P	N	G	0.367	30
Shoals Creek 1	F	N	U	1.300	30
Shoals Creek 2	P	N	G	0.533	30
Stringfellow Ck. 1	F	N	G	1.100	30
Stringfellow Ck. 2	P	N	G	0.533	15
Weaver Creek 1	F	N	U	1.433	30
Weaver Creek 2	P	N	U	2.600	10
Weaver Creek 3	P	B	U	0.550	20

Figure 14. Mean number (± 1 SE) of *Pycnopsyche* larvae found per minute of searching during surveys in streams above ponds for different land uses. This figure does not include the data from Weaver Creek (Site 2), which was the outlier. The numbers in parentheses above the bars indicates the number of sites surveyed. "UnGr" = ungrazed, "Gr" = grazed

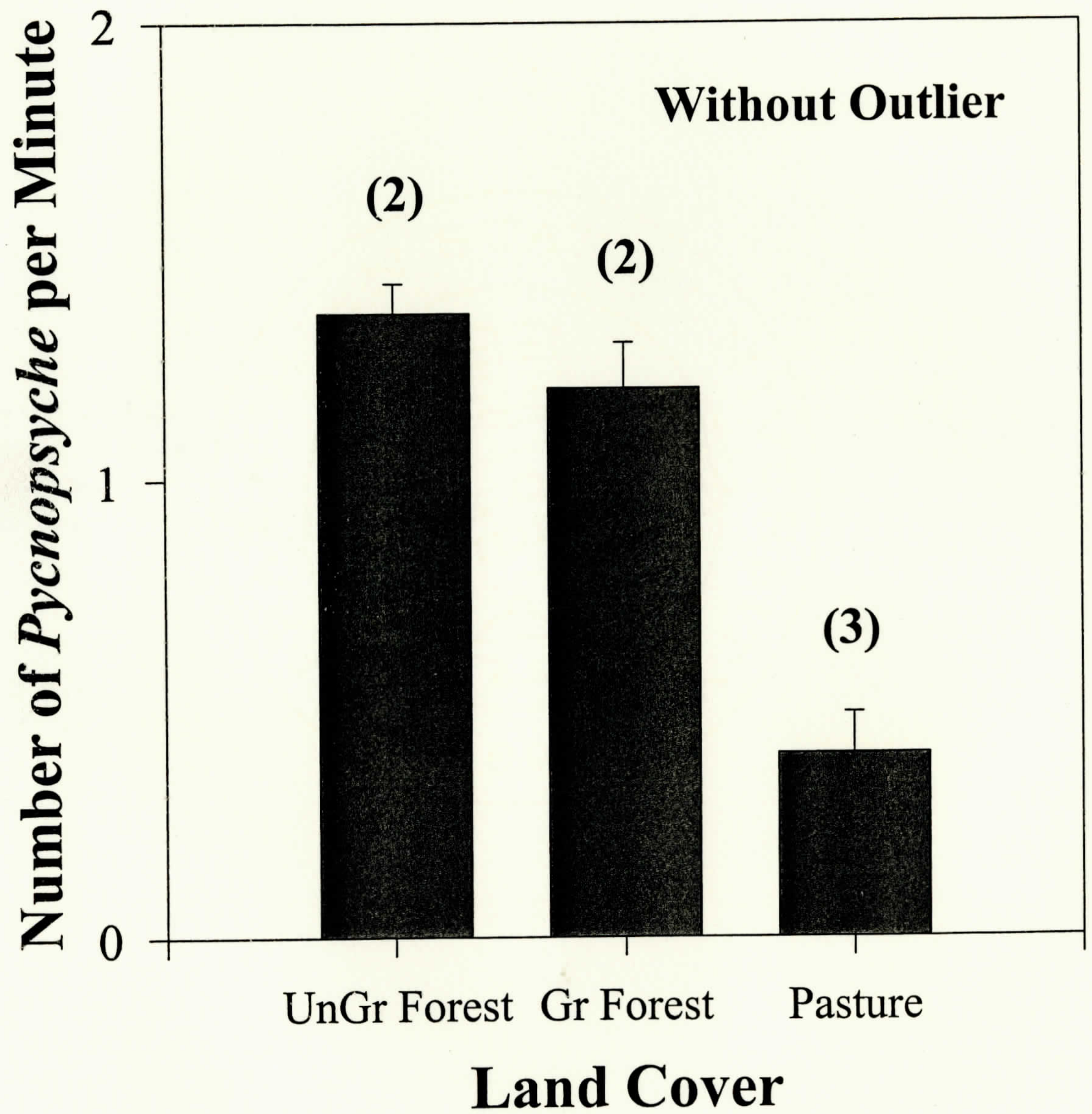


Figure 15. Mean number (± 1 SE) of *Pycnopsyche* larvae found per minute of searching during surveys in streams above ponds for different land uses. This figure does include the data from Weaver Creek (Site 2), which was the outlier. The numbers in parentheses above the bars indicates the number of sites surveyed. “UnGr” = ungrazed, “Gr” = grazed.

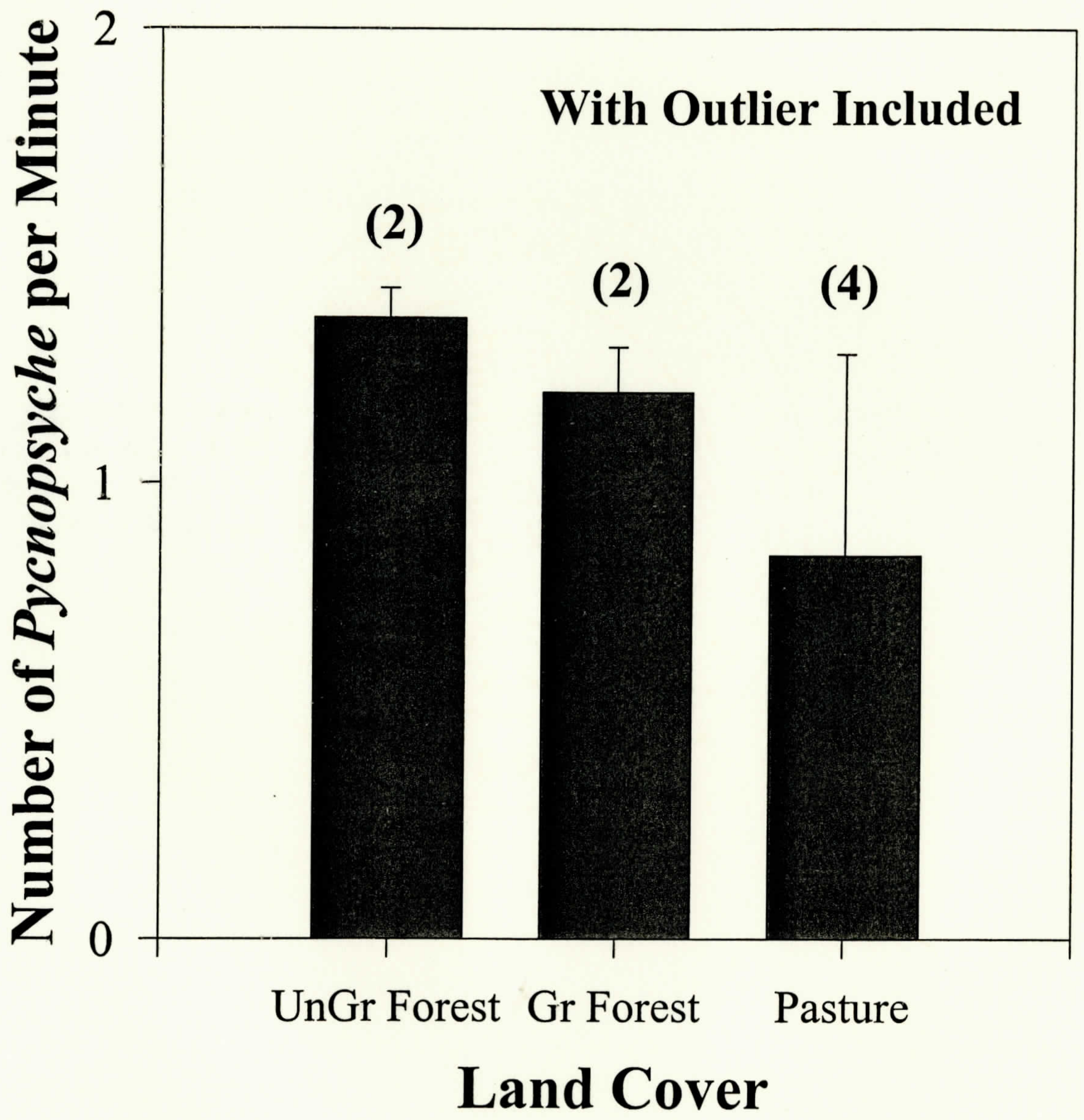
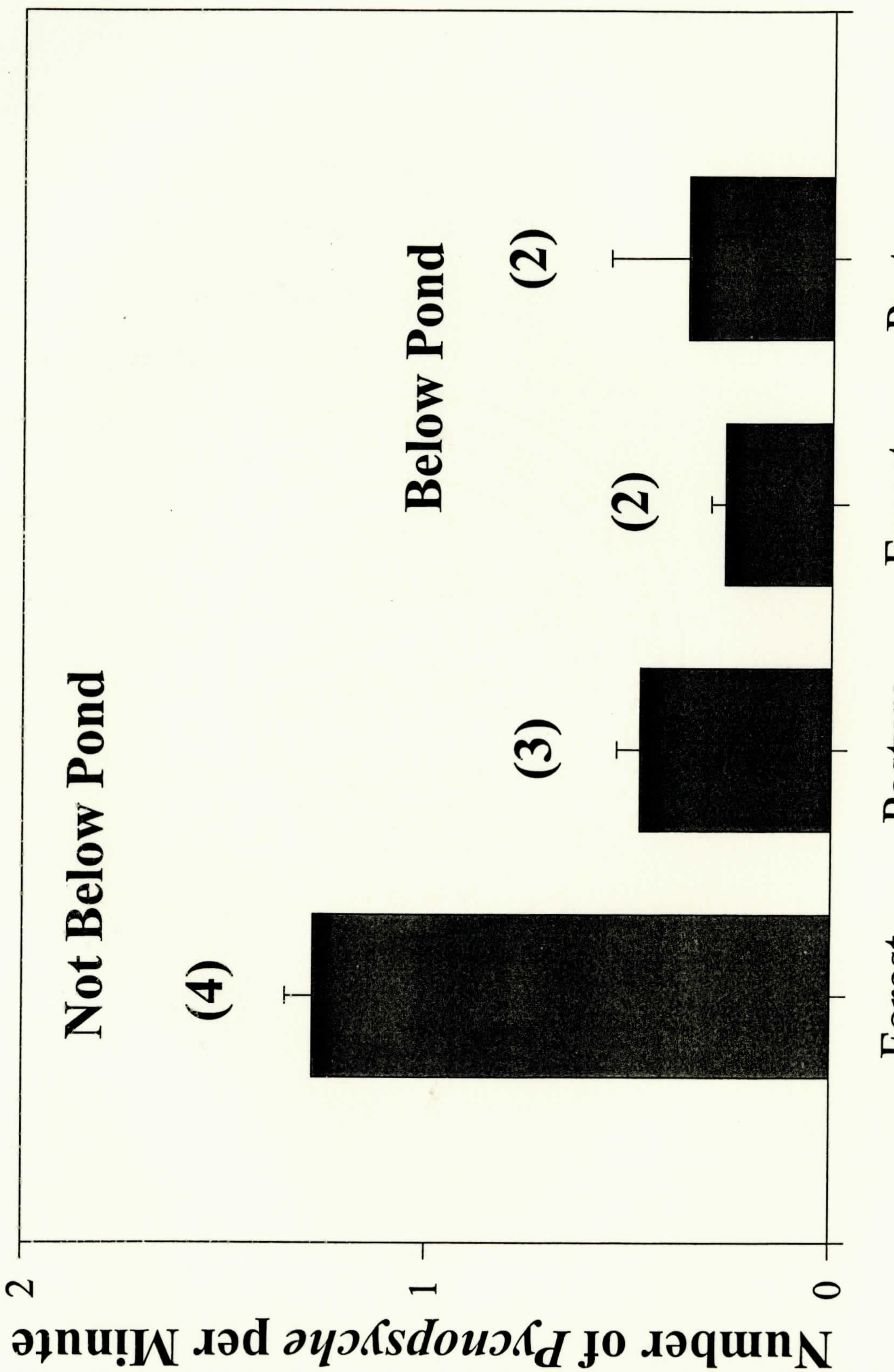


Figure 16. Effects of ponds on the mean number of *Pycnopsyche* in streams flowing through areas with different land uses. Bars represent mean number (± 1 SE) of *Pycnopsyche* collected per minute. The numbers in parentheses above the bars represent the number of sites surveyed. Figure does not include the Weaver Creek 2 site under Not Below Pond Pasture.



little detritus available in the forested section but more available in this section, possibly due to high water flows washing leaves downstream from the forest. Because this number is so much higher than any other site I have presented the survey results with and without this outlier, in Figures 14 & 15. The data from Weaver Creek 2 are omitted from Figure 16.

All of the Sims Creek sites produced fewer *Pycnopsyche* larvae per minute of searching than found in any of the New River headwater sites (Table 5). Unlike the New River streams, Sims Creek forest and pasture sites contained similar numbers of *Pycnopsyche*, as did the grazed and ungrazed sites.

Table 5. Results of *Pycnopsyche* surveys per minute of searching in Sims Creek. Surveys were conducted by looking through leaf detritus for indicated time. Results are given in mean Cases Found per Minute of Searching. F = Forest, P = Pasture, B = Below pond, N = Not below pond, U = Ungrazed, G = Grazed

Site	Type of Site			Occupied Cases Found/Min	Total Time Searching (Min.)
	Vege-tation	Pond	Grazed		
Sims Creek 1	F	N	U	0.050	30
Sims Creek 2	F	B	U	0.133	30
Sims Creek 3	F	B	G	0.100	30
Sims Creek 4	P	B	G	0.067	30

Discussion

Leaf Pack Processing in Blue Ridge Streams

Leaf processing in the forest section was significantly faster than that observed in the other two sections of Greene Creek. In the forest section the leaf processing rate was at a relatively steady rate through Day 14, presumably a period of microbial colonization and leaf conditioning (Cummins 1974). Leaf pack breakdown rate differed little from the other two sections during this period. Differences in rates became more apparent at Day 28 and were quite marked by Day 42. *Pycnopsyche* caddisflies were the only shredders found significantly more often in the forest section than in the other two sections and the only one to increase greatly from Day 28 to Day 42. Seventy-one percent of the *Pycnopsyche* were collected from leaf packs in the forest section. The other shredders found in the forest section were more abundant in the pasture (*Allocapnia*) or in the intermediate section (Nemouridae and *Tallaperla*) or did not vary among sections (*Tipula*). There were almost as many *Allocapnia* stoneflies in the pasture section (348) as *Pycnopsyche* in the forest section (388) though their impact as shredders evidently is much less important.

Of the 15 common taxa that were collected in Greene Creek, 12 showed a significant increase in the leaf packs over time. For the shredders this was probably largely in response to microbial conditioning and increased palatability of the leaves. In feeding tests, two species of detritivorous *Pycnopsyche* ate colonized and conditioned leaves more rapidly than uncolonized leaves (Motyka *et al.* 1985). At some point the leaves become "post-conditioned" making the leaves less palatable to shredders (Hutchens *et al.* 1997). Petersen and Cummins (1974) noted a lag time in which macroinvertebrates were not initially present on the leaf packs, possibly due to lack of conditioning by microbes. This preference for conditioned leaves may explain the marked increase in numbers of *Pycnopsyche* in the leaf packs in the forest section after Day 28.

The distributions of *Allocapnia*, Nemouridae and *Tallaperla* do not support the idea that any of these other taxa are responsible for the significantly faster detrital processing in the forest. Their higher abundances in the intermediate and pasture sections, where leaf pack breakdown was slower, suggests that their relative contribution to leaf processing in Greene Creek is minimal.

Pycnopsyche played a significant role in the processing of leaves in the forest section and their low numbers in the pasture and intermediate sections appears to be a likely cause of the slower rates of leaf breakdown in those sections. This is in agreement with Bird and Kaushik (1992) who found that during the autumn *Pycnopsyche* were significantly more common in a forest site, where they were the main leaf processor, than the pasture site. Leaf packs were processed more rapidly, though not significantly, in the forest section than in the pasture section (Bird and Kaushik 1992).

The *Pycnopsyche* enclosure experiment was designed to separate shredder effects (low densities of *Pycnopsyche*) from abiotic effects (differences in steam flow, depth, etc. between the sections). The leaf packs in the containers with the added *Pycnopsyche* larvae lost significantly more mass than the other two treatments during this 33-day experiment. The mean mass of the enclosure leaf packs was 3.04 ± 0.1 g, which was similar to the 2.87 ± 0.2 g in the forest section of Greene Creek on Day 28 in the original experiment. The higher processing rate of the leaf packs in the *Pycnopsyche* enclosure support the conclusion that

Pycnopsyche is the dominant shredder in this stream. These data also indicate that the faster processing rate in the forest section was not due to abiotic conditions. In fact, the slower water velocities in the forest section should result in slower processing rates (Campbell *et al.* 1992b), not faster rates as was observed.

Eggert and Wallace (1999) excluded litter in an Appalachian headwater stream and found that *Pycnopsyche* production stopped within 3 years. This decline in *Pycnopsyche* was attributed primarily to the loss of food, though there was also an effect from larvae being forced to construct cases out of alternate materials. Campbell *et al.* (1992a) and Reed *et al.* (1994) found that forested sites had more organic matter entering the streams than pasture sites. Campbell *et al.* (1992a) also found that forest sites had more litter accession than the pasture sites. The removal of large woody debris, as typically happens in agricultural sites, results in a reduction in organic matter storage and an inability to retain leaf-sized organic matter in the system (Bilby and Likens 1980). This decrease in the abundance of allochthonous leaf litter resulting from conversion of forest to pasture could result in the same decline in *Pycnopsyche* production as observed by Eggert and Wallace (1999). This is one possible explanation for why there were fewer *Pycnopsyche* larvae in the Green Creek pasture study site.

Removal of woody vegetation along streams can result in changes in leaf detritus quality as well as decreased amounts of litter entering streams. Stout *et al.* (1993) found that streams flowing through second-growth forests contained significantly less leaf material but had more litter from fast-processing tree species. There was significantly more shredder production in the streams flowing through second-growth forests, with *Pycnopsyche gentilis* larvae present at higher densities and achieving significantly greater annual biomass. Hutchens and Benfield (2000) believe that similar changes in leaf quality resulting from gypsy moth defoliation may have negative effects on shredders. Second-flush leaves following gypsy moth defoliation were found to be higher quality food for macroinvertebrates and were broken down faster than natural spring-flush leaves (Hutchens and Benfield 2000). In a food-limited system such as these headwater streams (Richardson 1991) this may leave a shortage of food resources available to invertebrates in the spring when slow processing leaves from other tree species would normally be available

The leaf processing in the intermediate section was significantly slower overall than in the forest section but faster, though not significantly, than in the pasture section. Through Day 28 there was little change in the rate of leaf loss in the intermediate section. This rate increased after Day 28, and by the last sampling date the mean leaf pack mass was not significantly different from that in the forest site. Total shredder numbers in the intermediate section show an increase from Day 28 through Day 56, which corresponds well with the increased loss in leaf mass in the intermediate section during this period. Except for *Tallaperla*, other shredder taxa (*Tipula,* Nemouridae, *Allocapnia* and *Pycnopsyche*) did not show a correlation between increased leaf loss and increased numbers of shredders in the intermediate section. While *Tallaperla* did increase from Day 28 to Day 56, their numbers never exceeded 1 per g leaf mass and they probably did not contribute greatly to leaf loss.

The two macroinvertebrate taxa that were highly abundant in the intermediate site were the mayfly families Ephemerellidae and Leptophlebiidae. Over 80% of the ephemerellid mayflies were found in the intermediate section, 15.7% in the forest section and just 1.0% in

the pasture section. The leptophlebiid mayflies were also most common in the intermediate section with 52% of the total found there and the remainder evenly split between the other two sections. Numbers of individuals in both families showed a large increase in the intermediate section beginning with Day 28 and continuing through Day 56, which corresponded well with the period of rapid leaf loss in this section. While ephemerellid and leptophlebiid mayflies are generally considered to be collector-gatherers (Edmunds and Waltz 1996, Merritt and Cummins 1996), Hawkins (1985) found many species of ephemerellid to be at least part-time shredders. One genus (*Attenella*), which was common in Greene Creek, feeds almost exclusively on detritus (Hawkins 1985). In the initial analysis of the macroinvertebrate shredder effects it was not obvious which taxa were responsible for this leaf loss in the intermediate section. Only 25.2% of the shredders collected were from the intermediate section while 37% of the shredders were found in each the pasture and forest sections (Table 6). Treating ephemerellids as shredders increased the percentage of the total Greene Creek shredders found in the intermediate section from 25% up to 53% and increased the percentage of shredders in the macroinvertebrate community in the intermediate section from 4.6% to 18.6%. The importance of large numbers of shredders for leaf processing is supported by Kirby *et al.* (1983) and Benfield and Webster (1985) whose data suggest shredder abundance on the leaves largely governs species-specific leaf breakdown rates. The 1,131 ephemerellid mayflies found on leaf packs in the intermediate section were likely the cause of the increased leaf processing rates observed after Day 28 in this section.

Benfield *et al.* (1977) reported similarly high densities of ephemerellid mayflies in their study of leaf processing in a pastureland stream with a narrow band of riparian vegetation

Table 6: Macroinvertebrate numbers and percentages for functional groups for each section. Ephemerellidae are listed under Shredder category or as Collector-Gatherers as noted. Shredders are Capniidae, Nemouridae, Peltoperlidae and *Tipula* (Tipulidae). Collector-Gatherers are *Epeorus* (Heptageniidae), Leptophlebiidae, *Ameletus* (Siphlonuridae), Chironomidae, Copepoda and Oligochaeta. Predators are Perlodidae and Rhyacophilidae. Total invertebrates are all organisms collected including others not listed as Shredder, Collector-Gatherer or Predator.

	Shredders (without Ephemerellidae)	Shredders (including Ephemerellidae)	Collector-Gatherers (including Ephemerellidae)	Collector-Gatherers (without Ephemerellidae)	Predators	Total Invertebrates
Total of functional group in pasture section	556	570	4934	4920	28	6190
% Total of functional group in pasture section	37.6%	20.1%	30.4%	33.1%	9.8%	29.0%
% Total of pasture section organisms that are in functional group	9.0%	9.2%	79.7%	79.5%	0.4%	
#/g leaf pack in pasture section	4.59	5.30	40.74	40.63	0.23	51.11
Total of functional group in intermediate section	373	1504	6425	5294	144	8069
% Total of functional group in intermediate section	25.2%	53.0%	39.6%	35.6%	50.5%	37.8%
% Total of intermediate section organisms that are in functional group	4.6%	18.6%	79.6%	65.6%	1.8%	
#/g leaf pack in intermediate section	3.34	13.46	53.06	43.72	1.29	72.24
Total of functional group in forest section	551	765	4857	4643	113	7096
% Total of functional group in forest section	37.2%	26.9%	30.0%	31.3%	39.6%	33.2%
% Total of forest section organisms that are in functional group	4.7%	10.8%	68.4%	62.2%	1.8%	
#/g leaf pack in forest section	5.41	7.51	43.46	38.34	1.11	69.71
Total	1480	2839	16216	14857	285	21355

along each bank. A stonefly, *Allocapnia*, was dominant until Day 70 when large numbers of *Ephemerella*, an ephemerellid mayfly, began to replace them as the dominant taxon. *Ephemerella* either dominated or shared dominance with chironomids through Day 161 when the experiment ended. Because of the relative absence of known macroshredders after Day 70, Benfield *et al.* (1977) concluded that there was little invertebrate feeding occurring and that leaves were being processed by mechanical breakage, primarily by water currents. My data, along with that of Hawkins (1985), suggest that ephemerellid mayflies can be important shredders and may be responsibie for a significant amount of leaf processing in pasture streams and streams at the interface between pastures and forests.

Leaf processing in the pasture section was the slowest of the three sections at the Greene Creek study site. The loss of leaf mass was at a relatively steady rate throughout the experiment, unlike the processing rates observed in the intermediate and forest sections. This is likely due to continued microbial conditioning and the absence of an important shredder, e.g., *Pycnopsyche*. The slow processing rate in the pasture section is even more striking considering that the abiotic conditions in the pasture section should cause faster leaf loss than in the other two sites. Higher water currents, as found in the pasture section, have been shown to increase breakdown rates (Campbell *et al.* 1992b) due to greater physical force on the leaves. Increased solar input resulting from the loss of the canopy can increase water temperatures (Platts and Nelson 1989, Quinn *et al.* 1992), though probably not significantly, in short sections of streams (Quinn *et al.* 1992), which could increase microbial respiration. The increased microbial colonization increases palatability of the leaves and thus invertebrate shredding (Murphy *et al.* 1981, Short and Smith 1989).

The results of the leaf pack experiment and the *Pycnopsyche* enclosure experiment demonstrated that *Pycnopsyche* is a major shredder in Greene Creek and is abundant in undisturbed forests but not in pasture sites or disturbed forest sites. The surveys of headwater streams in the New River drainage showed that *Pycnopsyche* were more common in forested sections of streams, in ungrazed sections and in streams not below ponds. With only one exception, streams above ponds held more *Pycnopsyche* than streams that were below ponds. The only exception was an ungrazed pasture section below a pond (Weaver Creek 3), which contained more larvae than three sites in grazed pasture above ponds. Forest sites always contained more larvae than pasture sites except when the forest was below a pond. More *Pycnopsyche* were always found in ungrazed sites if other stream characteristics were the same. By affecting the distribution of the dominant shredder in this system, changes in land cover and land use can affect leaf processing and energy flows.

Surveys of Sims Creek showed much lower numbers of *Pycnopsyche* compared to Greene Creek and the other sites in the New River drainage. The highest abundance of *Pycnopsyche* in Sims Creek was smaller than the lowest abundance found in surveys of the New River headwater sites. The trends in abundance observed in the grouping of New River sites by stream characteristics did not hold in Sims Creek, possibly due to the low numbers of *Pycnopsyche* found in the surveys of this stream. Numbers of *Pycnopsyche* in the forest section were equal to those in the pasture site. The ungrazed stream sites were equal to the grazed sites in *Pycnopsyche* numbers. In the streams surveyed in the New River drainage, stream sites below ponds had fewer larvae than the stream site not below ponds. All three sites in the Sims Creek experiment were below Sims Pond. The low overall abundance of

Pycnopsyche in Sims Creek may explain why the leaf processing rates were slower in the Sims forest and intermediate sections than at the Greene Creek sites. Without this dominant shredder there was less leaf processing by shredders occurring in this stream.

Pycnopsyche caddisflies were the dominant shredder in Greene Creek, but only appeared to play a significant role in the forest section of the study site. In the forest site on Day 42 *Pycnopsyche* numbers per g leaf mass were almost 20 times that found in each of the other two sites and on Day 56 there were still 5-10 times the numbers found in the intermediate and pasture sites. Why *Pycnopsyche* were the dominant shredder in this section is not clear from my data. Williams and Smith (1996) suggested that biotic interactions at times might be more important than abiotic influences in determining invertebrate communities. It is possible that the *Pycnopsyche* were competing with other taxa for prime *Pycnopsyche* habitat in the forest and were preventing other taxa from inhabiting leaf packs that they were using. Wissinger *et al.* (1996) found competition and predation to be the case with a detritivorous caddisfly *Asynarchus nigriculus*. *Asynarchus* larvae dominated certain habitats by preying upon another caddisfly, *Limnephilus externus,* and driving them away by this aggressive behavior. Kohler (1992) found that the grazing caddisfly *Glossosoma nigrior* was able to influence the abundance of filter feeders through physiological, behavioral (non-aggressive), and life cycle attributes. Either of these mechanisms may explain the dominance of *Pycnopsyche,* at least with respect to some of the smaller shredder taxa. More than one-third of the *Tallaperla* larvae, which are slightly smaller than the *Pycnopsyche*, were collected in the forest section, suggesting that the *Pycnopsyche* were not significantly excluding them from the forest site. *Allocapnia* and ephemerellid larvae, about one-fourth the size of the

Pycnopsyche, were found in much lower numbers in the forest than they were in the pasture and intermediate sections respectively, possibly as a result of competition from the *Pycnopsyche* in the forest. Despite this possibility of a competitive effect by *Pycnopsyche*, it is also possible that there were one or more abiotic factors involved and that competition is not important in determining the distribution of these other shredders. Reice (1980) determined that for highly mobile aquatic macroinvertebrates the community varies constantly depending on many factors that are always changing. Williams and Smith (1996) also suggested that multiple factors may be involved, including both biotic and abiotic influences and that how a species responds varies with the species.

Land Cover and Use and Leaf Pack Processing

As hypothesized, changes in land cover along these southern Appalachian streams resulted in changes in detrital processing rates. Specifically, the conversion of forested riparian vegetation to pasture on both Greene and Sims Creeks resulted in a decrease in the leaf processing rate. Leaf mass was lost significantly faster in the forest site and slower in the intermediate and pasture sites on Greene Creek. On Sims Creek leaf processing was significantly faster in both the forest and intermediate sections than it was in the pasture section, though these rates were slower than those observed in Greene Creek. As discussed above, these changes in breakdown rates appear to be due to differences in the abundance of a particular shredder taxon, *Pycnopsyche*.

While I expected that the changes in land use along these headwater streams would lead to alterations in leaf processing rates, the results of my experiment differ from what other

researchers have found in similar experiments. Tuchman and King (1993) compared two agricultural sites, one with all riparian vegetation removed and the other with trees extending 9 m out from the stream banks, with a wooded site and found that leaves were processed faster in the agricultural sites. Similarly, Young *et al.* (1994) found that streams in catchments with increasing agricultural activity had faster processing rates. However, no significant differences were found in the rates of leaf processing in agricultural and forested sites in studies by Bird and Kaushik (1992) and Campbell *et al.* (1992b), despite differences in invertebrate communities among the sites in the study by Bird and Kaushik. The results of my experiment appear to be the first to show significantly faster processing rates in the undisturbed forest section of a stream.

At forested sites Bird and Kaushik (1992) felt that weight loss was mainly a biological process, while at an agricultural site the loss was governed by physical abrasion and microbial activity, a finding similar to the conclusions of Benfield *et al.* (1977) and Tuchman and King (1993). Bird and Kaushik (1992) concluded that leaf breakdown at agricultural sites was primarily due to discharge, while in wooded sites it was due to microbial decay and macroinvertebrate shredding. Based on the results of the studies mentioned above, abiotic leaf processing appears to be more of an agricultural site effect rather than one of the intermediate or forested sections. As argued by Suberkropp *et al.* (1976), the lack of variability in weight loss rates indicates a steadier biological processing rather than an erratic, stochastic loss more commonly associated with abiotic activity. Leaf loss in both Sims and Greene Creeks had fairly steady rates, especially in the agricultural sections, which indicates that abiotic breakdown was a minor component of loss of leaf material.

Reed *et al.* (1994) found no difference in total biomass of invertebrates between forest and pasture sites but observed a significantly higher biomass of shredders in the forest sites. Young *et al.* (1994) found very low shredder numbers in pasture sites. My data show highest total numbers of shredders in the pasture and forest sites without including ephemerellid mayflies, but highest numbers (53% of all shredders) in the intermediate site when Ephemerellidae are included in the shredder count. While I did not determine shredder biomass, the high numbers of the large *Pycnopsyche* in the forest section of Greene Creek might also result in higher shredder biomass in the forest section.

Conclusions and Suggestions for Future Research

The results of this study have shown the importance of *Pycnopsyche* caddisflies to leaf processing in the undisturbed portions of these headwater stream systems in the southern Appalachian Mountains. *Pycnopsyche* is the major shredder in these systems and its absence leads to a significant reduction in leaf processing rates. Reduced *Pycnopsyche* abundance should lead to a reduction in the flow of energy in these headwater streams. As a result of these land cover and land use changes along these streams, there was not only a change in *Pycnopsyche* abundance but an alteration in the macroinvertebrate community overall.

While the results of this study provide interesting information about detrital processing in these stream systems, a change in how the leaf packs are constructed may be beneficial. It is likely that if the leaf packs had been constructed differently there would have been a greater contrast in leaf mass remaining in the intermediate and forest sites in Greene Creek on Day 56. In constructing the leaf packs in this study, binder clips were placed over the petiole end of

the leaves, covering approximately 1 g of leaf material and making it inaccessible to macroinvertebrates. By Day 42 virtually all of the remaining leaf material in the packs in the forest section was covered by the clips, preventing any further loss of leaf material on Day 56. In the other two sections, notably in the intermediate section, processing continued, allowing the intermediate section to catch up with the forest section. Using 10 g leaf packs, large mesh leaf bags with loose leaves, or placing the binder clip over a smaller portion of the leaf packs, may have allowed processing of the forest packs to continue through Day 56 with a continued significant difference from the intermediate section on that date.

Abiotic influences on the leaf processing rates should be more thoroughly examined in future experiments. Due to time and monetary restraints I was unable to conduct water chemistry testing for the three sections. Temperature recordings for Sims Creek were attempted but were incomplete due to equipment malfunctions. Researchers have found that processing rates can be affected by pH levels, phosphorous concentrations, presence of aluminum and water temperatures.

Why the *Pycnopsyche* seem to avoid the pasture section should be determined. Possible causes include differences in abiotic conditions, such as increased light or temperature, or a shortage of case building material as suggested by Eggert and Wallace (1999). *Pycnopsyche* may be more sensitive to cattle trampling and the disruption of the leaf packs.

The invertebrates in this study were examined by looking at the abundance of individuals rather than determining their biomass. Biomasses of the invertebrates would provide additional data when looking at effects caused by different taxa. There is a large size difference in organisms not only within a taxon but also among taxa. Smaller numbers of a large-sized taxon, such as *Tipula*, may have a greater leaf processing effect than many more small-sized *Allocapnia*. The biomasses of invertebrates collected in this study, or in future studies, need to be determined for more complete data analysis.

Why there is such a difference in the macroinvertebrate communities in the three sections is not clear from this study. Future research is needed to see if *Pycnopsyche* are competing with other invertebrates for desired sites in the undisturbed forest and are causing other shredders (e.g., Ephemerellidae, Leptophlebiidae, and *Allocapnia*) to relocate to less desirable downstream sites. Abiotic factors may be responsible for certain taxa being found in one section in greater numbers than in other sections.

Ephemerellid mayflies were an unexpected shredder in the intermediate section. Leptophlebiid mayflies were also significantly more abundant in the intermediate section and should be examined to see if they may be contributing to leaf loss by being part-time shredders. It may be that leptophlebiid mayflies are also important leaf processors in this section. Research is needed to determine the functional group(s) to which this taxon should be assigned.

Direct impacts of livestock grazing were not examined in this study. Changes in land use along the two study streams resulted from agricultural activities, specifically clearing the land for livestock grazing. This study only looked at impacts resulting from change in land cover and use, not impacts caused directly by cattle. Future research is needed to determine whether cattle directly influence leaf processing and aquatic invertebrate communities by such

activities as walking and standing in the streams and by introducing nutrients to the aquatic system.

Since completion of this experiment cattle have been excluded from the study sites by the erection of barbed wire fences. There will be opportunities to monitor changes in the streams as succession of the vegetation proceeds in the pasture and intermediate sections. Long-term studies may reveal whether processing rates and the macroinvertebrate communities in the three sections become increasingly similar over time or if the differences between the sites remain.

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Appendix A

Species List and Functional Groups of Invertebrates Collected in Greene Creek

Species List and Functional Groups of Invertebrates Collected in Greene Creek

Introduction. I collected and identified a wide variety of macroinvertebrates in the Greene Creek study. Determining which organisms were shredders was important to aid in identifying which organisms were responsible for the processing of leaf packs. In stream research the standard classification of stream invertebrates is by functional groups, as determined by Cummins (1973) based on the food eaten and the feeding mechanism. The main problem with assigning organisms to a functional group is that most aquatic insects are opportunistic feeders or change their feeding habits in different life stages (Anderson and Sedell 1979). While agreeing that many organisms alter feeding habits in response to environmental changes and in different life stages, Cummins and Merritt (1996) argued that assigning organisms to functional groups avoided having to classify most organisms as omnivores, and that it established links to food resource categories. Despite these shortcomings, there is no better alternative and so I used functional groups in this study to identify the taxa responsible for leaf processing.

I used definitions provided by Allan (1995) for the various functional groups. Shredders chew on non-woody coarse particulate organic matter (> 1 mm), especially leaves, and on the associated microbiota. The collector-gatherers collect fine particulate organic matter (< 1 mm) and microbiota, especially bacteria and the organic microlayer. Collector-filterers consume similar resources but filter the materials out of the water rather than collect it. Grazers scrape periphyton and the organic microlayer. Predators consume animal matter.

Methods. I removed the leaf packs from the bricks at the stream and placed them in resealable plastic bags. The bags and leaf packs were taken to the lab where the sediments

and macroinvertebrates were washed off the leaves using tap water. I collected the invertebrates and sediment in vials containing 70% ethanol for later processing. Using Wiggins (1977), Brigham *et al.* (1982), and Merritt and Cummins (1996), I identified the invertebrates to the lowest taxonomic level possible.

Results. I collected 21,355 macroinvertebrates from the leaf packs in Greene Creek. I was able to identify 18 different species and 32 genera. There were four Ephemeropteran families (2,767 individuals), seven Plecopteran families (1,821 individuals), seven Trichopteran families (1,436 individuals) and six Dipteran families (9,432 individuals).

Table 1. – Species list for all taxa collected from leaf packs in the Greene Creek study. Functional groups are defined using Cummins and Klug (1979). Functional Groups: C-G = Collector-Gatherer; C-F = Collector-Filterer; Sh = Shredder; P = Predator; Sc = Scraper; Pi = Piercer, Gr = Grazer. References: 1 = Merritt and Cummins (1996); 2 = Thorp and Covich (1991); 3 = Hawkins (1985).

Taxon	Functional Group	Reference
Ephemeroptera		
Ephemerellidae	Sc, Sh, C-G	1, 3
Attenella sp	Sc, Sh, C-G	1, 3
A. attenuata		
Danella sp.	Gr	1
D. lita		
Drunella sp.	Sh, Sc, C-G, P(?)	1, 3
Serratella sp.	Sc, Sh, C-G	1, 3
S. deficiens		
S. serratoides		
S. sordida		
Heptageniidae	Sc, C-G	1
Epeorus sp.	C-G, S	1
Heptagenia sp.	Sc, C-G	1
Stenonema sp.	Sc, C-G	1
S. carlsoni		
S. femoratum		
Leptophlebiidae	C-G, Sc	1
Habrophlebia vibrans		
Leptophlebia sp.	C-G	1
Paraleptophlebia sp.	C-G, Sh	1
Siphlonuridae	C-G	1
Ameletus sp.	C-G	1
A. lineatus		
Plecoptera		
Capniidae	Sh	1
Allocapnia sp.	Sh	1
Chloroperlidae	P, Sc, C-G	1
Alloperla sp.	P	1
Hastaperla brevis	P	1
Utaperla sp.	P	1
Leuctridae	Sh	1
Leuctra sp.	Sh	1
Nemouridae	Sh, C-G	1
Amphinemura	Sh, C-G	1
A. nigritta		

Table 1. Continued

Taxon	Functional Group	Reference
Plecoptera (continued)		
Peltoperlidae	Sh	1
Tallaperla sp.	Sh	1
Perlodidae	P	1
Isoperla	P	
I. similis		
Malirekus hastatus		
Helopicus subvarians	P	1
Taeniopterygidae	Sh, C-G, Sc	1
Strophopteryx	Sc, Sh	1
S. limata		
Trichoptera		
Hydropsychidae	C-F, P	1
Parapsyche sp.	C-F	1
P. apicalis		
Hydroptilidae	Pi, H, Sc, C-G	1
Limnephilidae	Sh, C-G, Sc	1
Hydatophylax argus	Sh, C-G	1
Pycnopsyche sp.	Sh, Sc	1
Odontoceridae	Sh	1
Polycentropodidae	C-F, P	1
Nyctiophylax sp.	P	1
Polycentropus sp.	P, C-F, Sh	1
Psychomyiididae	C-G	1
Rhyacophilidae	P	1
Rhyacophila sp.	P, Sc, C-G, Sh	1
R. nigrita		
Diptera		
Ceratopogonidae	P, C-G	1
Chironomidae	C-G, P	1
Dixidae	C-G	1
Psychodidae	C-G	1
Pericoma sp.	C-G	1
Simuliidae	C-F	1
Tipulidae	Sh, C-G	1
Dicranota sp.	P	1
Erioptera sp.	C-G	1
Tipula sp.	Sh, C-G, P	1

Table 1. Continued

Taxon	Functional Group	Reference
Collembela	C-G	1
Isotomidae		
Copepoda	C-G, P	2
Cyclopoida	C-G, P	2
Harpacticoida	C-G, P	2
Turbellaria	C-G, P	2
Ostracodes	C-G	2
Oligochaeta	C-G, P	2

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VITAE

Robert Paul Cherry was born August 30, 1956, in Chicago, Illinois. After moving to Park Ridge, Illinois, he attended Maine Township High School South until graduating in May 1974. He attended the University of Illinois at Chicago Circle for two years and then Southern Illinois University at Carbondale where he graduated in the spring of 1979 with a Bachelor of Science degree in Forestry, specializing in forest resource management.

That same year in October he began his career with the National Park Service as an interpreter at Lincoln Home National Historic Site. There he met Jamie Sue Leigh who he wed on March 13, 1982. His career with the National Park Service has taken him to Boston (MA), Corpus Christi (TX), Deer Lodge (MT), Whiskeytown (CA) and Boone (NC). He is currently a Resource Management Specialist for the Highlands District on the Blue Ridge Parkway. His son Michael Cherry-Leigh was born in 1987 in Corpus Christi (TX) and his daughter Kelly Cherry-Leigh in Redding (CA) in 1989.

Mr. Cherry began working towards a Master of Science degree at Appalachian State University in June 1993, which he completed in December 2000. He currently resides in Boone, North Carolina with his wife and children.