

A STUDY OF THE MACROINVERTEBRATE FAUNAS
OF TWO TEMPERATE SPRINGS,
LAND BETWEEN THE LAKES, STEWART COUNTY, TENNESSEE

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A STUDY OF THE MACROINVERTEBRATE FAUNAS
OF TWO TEMPERATE SPRINGS,
LAND BETWEEN THE LAKES, STEWART COUNTY, TENNESSEE

An Abstract
Presented to
the Graduate Council of
Austin Peay State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Deborah Lingle Gillis

December 1991

ABSTRACT

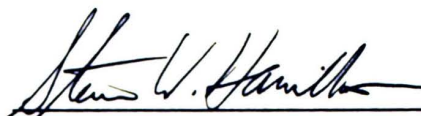
Aquatic springs are often limited in diversity and richness. Past studies have attributed this to the atypical non-seasonal stenothermal environment. Two temperate springs, Lost Creek Spring (LCS) and Pryor Creek Spring (PCS), in Land Between The Lakes in northwest Middle Tennessee were studied from September 1988 to September 1989. Mid-channel benthic samples collected bi-monthly and physicochemical data collected weekly were taken "upstream" (close to the spring source) and "downstream" (100 m from the upstream sites at LCS and 60 m from the upstream sites at PCS). Physicochemical parameters detected little difference between upstream and downstream. The average density of macroinvertebrates was 40,182 individuals/m² at LCS and 57,310 individuals/m² at PCS. For both springs, nearly 75% of the organisms were captured upstream with 86% of those individuals noninsect invertebrates. Downstream, 63% of the individuals captured at LCS and 73% at PCS were noninsect.

Of the total taxa identified (90 at LCS and 80 at PCS), the noninsect invertebrates comprised 14% of the taxa at LCS and 20% at PCS. The remainder of the invertebrates were insects. The number of insect taxa increased significantly downstream (over 43% at LCS and 87% at PCS) with the noninsect invertebrate richness decreasing. Overall, diversity was greater downstream at LCS and the evenness of the insect group varied less than upstream. Insect diversity at PCS was greater downstream and varied less than the upstream sites even though washouts from spates occurred throughout the study period at the downstream sites. At both sites, a wet weather creek joined the springbrooks above the downstream sites causing large increases in downstream discharge during storm events. During these spates, habitat was

altered as substrate and organic matter was shifted. Spates removed organisms, opened up new patches and allowed poor competitors but rapid colonizers (e.g. Simulium) to become established. Those insects adapted to spates probably escaped washout by moving into the hyporheic zone. Noninsects were unable to maintain their dominance due to their inability to escape increases in discharge. Upstream where spates did not occur, noninsect species such as Lirceus fontinalis and various gammarid amphipods excluded or restricted less competitive species and thus dominated the habitat. This suggests that disturbance increases diversity by limiting the abundance of certain species.

To the Graduate Council:

I am submitting herewith a Thesis written by Deborah Lingle Gillis entitled "A Study of the Macroinvertebrate Faunas of Two Temperate Springs, Land Between the Lakes, Stewart County, Tennessee." I recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science, with a major in Biology.



Major Professor

We have read this thesis and
recommend its acceptance:



Second Committee Member



Third Committee Member

Accepted for the
Graduate Council



Dean of the Graduate School

CHAPTER	PAGE
Macroinvertebrates	25
Analysis of Macroinvertebrate Samples	26
Community Similarity	26
Nonemergent and Emergent	27
Richness, Diversity and Evenness Indices	28
Functional Feeding Groups	29
Relative Abundance and Frequency of Occurrence	29
4. RESULTS	31
Site Descriptions	31
Discharge	31
Substrate and Water Velocity	34
Physicochemical Data	37
Macroinvertebrate Analysis	40
Community Similarity	40
Total Density	40
Nonemergent and Emergent Densities	45
Taxa Composition	63
Relative Abundance	67
Frequency of Occurrence	67
Taxa Diversity	70
Longitudinal Zonation	74
Functional Feeding Groups	78

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ACKNOWLEDGEMENTS

The author would like to thank those individuals of Austin Peay State University who unselfishly gave encouragement, advice and assistance, who treated me with respect and comradery, recognizing the challenges of my task. Special thanks go to Dr. Edward Chester for his aid in identification of aquatic plants and for his review of the manuscript; Dr. Mack Finley who gave helpful suggestions of the manuscript, plus encouragement and support throughout the study; Drs. Phillip Kemmerly and D.M.S. Bhatia who helped me to understand the geology of the study area; Mr. Robert Robison who donated many hours, including his free time, assisting in data manipulation and the use of computer software; Ms. Barbara Wilbur who encouraged me to begin my studies at Austin Peay and offered her friendship and concern. Sincere thanks to my major professor, mentor and comrade, Dr. Steven Hamilton, who through his example taught me determination and fortitude. He gave me countless hours of counsel, guidance and assistance in the field and laboratory. He also made this project bearable by making it a lot of fun.

Appreciation is also extended to all those invaluable undergraduate assistants who were involved in this project: Joe Barnes, Joey Forrester, Andy Hooper, Jenny Jordan, and Laurie Williams. Special thanks goes to Mike Stancil and Gwen Sunderland, fellow graduate students and unsung heroes.

The author is also very appreciative of the technical assistance of Dr. Peter Adler, Mr. Michael Heyn, Mr. Charles Watson, Clemson University; Dr. Joseph Beatty, Southern Illinois University at Carbondale; Dr. John Holsinger, Old Dominion University; Dr. Jerry Lewis, University of Louisville; and Dr. David Smith, University

of Tennessee at Knoxville for their aid in identification of various taxa. Thanks to Ms. Mickey Hill, Fort Donelson National Battlefield who supplied climatic data; to Ms. Carla Johnson, Drs. David White and Susan Hendricks of Hancock Biological Station for their assistance in analysis of various chemical and nutrient parameters.

Gratitude is expressed to Mr. Gregory Gillis who surveyed and mapped Lost Creek and Pryor Creek Spring. His desire for me to finish this project was often as great as mine. His moral and physical support is most deeply appreciated.

I would like to acknowledge Ruth Proctor and Vicki Eckart, friends that supported me through my graduate studies by providing their help to a busy mother. I especially want to thank my mother, Lois Lingle and my father, the late Clyde Lingle, who gave me the inner strength to persevere and finish this project. Their support through all my endeavors has been unfailing.

This study is dedicated to my daughter Hannah Elizabeth Gillis who played in the clean clear waters of these springs and marveled at the life within them. May her grandchildren have the same opportunity.

TABLE OF CONTENTS

CHAPTER	PAGE
1. INTRODUCTION AND REVIEW OF LITERATURE	1
Statement of the Problem	2
Importance of the Study	2
Review of Literature	3
Diversity	3
Longitudinal Zonation	4
Temperature	5
Cool Water Species	6
Springs as Refugia	7
Dominant Spring Species	8
Disturbance	9
Environment vs. Competition	10
Resilience	11
Synopsis	12
2. DESCRIPTION OF THE STUDY AREA	13
Land Between The Lakes	13
Lost Creek Spring	13
Pryor Creek Spring	18
3. MATERIALS AND METHODS	24
Physicochemical Parameters	24
Substrate Heterogeneity	25

5.	DISCUSSION	81
	Physicochemical Data	81
	Chemistry and Nutrient Data	81
	Substrate and Discharge	82
	Macroinvertebrate Analysis	83
	Similarity	83
	Habitat Preference and Availability	84
	Interstitial Space	86
	Spates	87
	Recolonization	90
	Disturbance and Competition	92
	Stability	92
	Differences Between the Springs	93
	Spring Limited Taxa	94
	Functional Feeding Groups	94
6.	SUMMARY	97

LITERATURE CITED	101
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APPENDIX

I.	Substrate composition (as % of total) in LCS and PCS	111
II.	Taxa list for Lost Creek Spring and Pryor Creek Spring	112
III.	Taxa list for Lost Creek Spring with month of collection and abundance rating	114

IV. Taxa list for Pryor Creek Spring with month of collection and
abundance rating 117

LIST OF TABLES

TABLE		PAGE
1.	Physicochemical data (means and ranges) for upstream (UP) and downstream (DOWN) sites of Lost Creek Spring (LCS) and Pryor Creek Spring (PCS), October 1988-October 1989	38
2.	Average, minimum and maximum values (ppm) of mineral and nutrients in water from springs in north-central Tennessee (Piper 1932)	39
3.	Density (individuals/m ²) of nonemergent and emergent invertebrates per sampling date for upstream (UP) and downstream (DOWN) sites of Lost Creek Spring (LCS) and Pryor Creek Spring (PCS)	46
4.	Number of taxa captured per sampling date for upstream (UP) and downstream (DOWN) sites at Lost Creek Spring (LCS) and Pryor Creek Spring (PCS)	64

LIST OF FIGURES

FIGURE	PAGE
1. Locations of Lost Creek Spring and Pryor Creek Spring in Land Between the Lakes	14
2. Location of Lost Creek Spring (LCS) in relation to Lost Creek and Kentucky Lake	15
3. Diagram of sampling sites within Lost Creek Spring	17
4. Location of Pryor Creek Spring (PCS) in relation to Pryor Creek and Lake Barkley	19
5. Diagram of sampling sites within Pryor Creek Spring	21
6. Mean monthly discharge (m^3/hr) at Lost Creek Spring Site 1 and Site 6 compared to mean monthly rainfall (cm) based on data from Fort Donelson National Battlefield	32
7. Mean monthly discharge (m^3/hr) at Pryor Creek Spring Site 1 and Site 6 compared to mean monthly rainfall (cm) based on data from Fort Donelson National Battlefield	33
8. Jaccard's coefficient of community similarity for six sampling sites, November 1988 to September 1989. A. Lost Creek Spring. B. Pryor Creek Spring	41
9. Morisita's index of community similarity for six sampling sites, November 1988 to September 1989. A. Lost Creek Spring. B. Pryor Creek Spring	42
10. Comparison of benthic macroinvertebrate densities from upstream and downstream sites. A. Lost Creek Spring. B. Pryor Creek Spring	43
11. Comparison of total number of individuals captured per sample date from upstream (UP) and downstream (DOWN) sites of Lost Creek (LCS) and Pryor Creek Spring (PCS)	44
12. Mean percent abundance of individuals in all samples from the upstream sites of Lost Creek Spring, November 1988 to September 1989. A. Nonemergent macroinvertebrates. B. All macroinvertebrates combined. C. Emergent macroinvertebrates	47

13. Mean percent abundance of individuals in all samples from the upstream sites of Pryor Creek Spring, November 1988 to September 1989. A. Nonemergent macroinvertebrates. B. All macroinvertebrates combined. C. Emergent macroinvertebrates 48

14. Mean percent abundance of individuals in all samples from the downstream sites of Lost Creek Spring, November 1988 to September 1989. A. Nonemergent macroinvertebrates. B. All macroinvertebrates combined. C. Emergent macroinvertebrates 49

15. Mean percent abundance of individuals in all samples from the downstream sites of Pryor Creek Spring, November 1988 to September 1989. A. Nonemergent macroinvertebrates. B. All macroinvertebrates combined. C. Emergent macroinvertebrates 51

16. Monthly sample densities of nonemergent macroinvertebrates for upstream and downstream sites at Lost Creek Spring 52

17. Frequency values of *Lirceus fontinalis* and *Gammarus pseudolimnaeus* were positively correlated ($r=0.742$, $p<0.042$) at Lost Creek Spring upstream. Frequency = percent of total capture/sampling period 53

18. Frequency values of *Gammarus pseudolimnaeus* and oligochaetes, the two dominant taxa from Lost Creek Spring downstream sites 55

19. Monthly sample densities of nonemergent macroinvertebrates for upstream and downstream sites at Pryor Creek Spring 56

20. Monthly sample densities of emergent macroinvertebrates for upstream and downstream sites at Lost Creek Spring 58

21. Monthly sample densities of emergent macroinvertebrates for upstream and downstream sites at Pryor Creek Spring 61

22. Number of individuals of four genera of dipterans considered to be opportunistic colonizers sampled from downstream sites of Pryor Creek Spring 62

23.	Taxa composition of macroinvertebrates from the upstream sites of Lost Creek Spring, September 1988 to September 1989. A. Number of nonemergent and emergent taxa (59 total taxa). B. Number of emergent taxa (47 total) among mayflies, stoneflies, megalopterans, caddisflies, chironomids and nonchironomid dipterans	65
24.	Taxa composition of macroinvertebrates from the upstream sites of Pryor Creek Spring, September 1988 to September 1989. A. Number of nonemergent and emergent taxa (45 total taxa). B. Number of emergent taxa (30 total) among caddisflies, chironomids and nonchironomid dipterans	65
25.	Taxa composition of macroinvertebrates from the downstream sites of Lost Creek Spring, November 1988 to September 1989. A. Number of nonemergent and emergent taxa (79 total taxa). B. Number of emergent taxa (67 total) among mayflies, stoneflies, megalopterans, caddisflies, beetles, odonates, chironomids and nonchironomid dipterans	66
26.	Taxa composition of macroinvertebrates from the downstream sites of Pryor Creek Spring, November 1988 to September 1989. A. Number of nonemergent and emergent taxa (69 total taxa). B. Number of emergent taxa (56 total) among mayflies, stoneflies, megalopterans, caddisflies, beetles, chironomids and nonchironomid dipterans	66
27.	Rarity/abundance distribution of taxa collected based on combined samples for upstream (UP) and downstream (DN) sites of Lost Creek (LCS) and Pryor Creek Spring (PCS). Abundance categories: Very Rare < 5, Rare = 5-49, Common = 5-249, Abundant = 250-1000, Very Abundant = 1000-5000, Exceptionally Abundant > 5000 individuals	68
28.	Number of times each taxa was found during the sampling year among the six sampling dates of the total taxa collected at the upstream (UP) and downstream (DN) sites of Lost Creek (LCS) and Pryor Creek Springs (PCS)	69
29.	Richness, heterogeneity and evenness in benthic macroinvertebrate samples from upstream and downstream sites at Lost Creek Spring. A. Margalef's taxa richness index. B. Shannon\Weiner diversity index. C. Pielou's evenness index	71

30. Richness, heterogeneity and evenness of emergent and nonemergent taxa in samples from upstream and downstream sites at Lost Creek Spring. A. Margalef's taxa richness index. B. Shannon-Weiner diversity index. C. Pielou's evenness index 72

31. Richness, heterogeneity and evenness in benthic macroinvertebrate samples from upstream and downstream sites at Pryor Creek Spring. A. Margalef's taxa richness index. B. Shannon\Weiner diversity index. C. Pielou's evenness index 73

32. Pielou's evenness of benthic macroinvertebrates from upstream and downstream sites of Pryor Creek Spring. A. Nonemergent taxa. B. Emergent taxa 75

33. Richness, heterogeneity and evenness in benthic macroinvertebrate samples from upstream and downstream sites at Pryor Creek Spring. A. Emergent and nonemergent, Margalef's taxa richness index. B. Shannon-Weiner diversity index of nonemergent taxa. C. Shannon-Weiner diversity of emergent taxa 76

34. Percent representation of functional feeding groups in all macroinvertebrate samples from Lost Creek Spring, November 1988 to September 1989, with gammarids considered as collectors-gatherers. A. Upstream sites. B. Downstream sites 79

35. Percent representation of functional feeding groups in all macroinvertebrate samples from Lost Creek Spring, November 1988 to September 1989, with gammarids considered as shredders. A. Upstream sites. B. Downstream sites 79

36. Percent representation of functional feeding groups in all macroinvertebrate samples from Pryor Creek Spring, November 1988 to September 1989, with gammarids considered as collectors-gatherers. A. Upstream sites. B. Downstream sites 80

37. Percent representation of functional feeding groups in all macroinvertebrate samples from Pryor Creek Spring, November 1988 to September 1989, with gammarids considered as shredders. A. Upstream sites. B. Downstream sites. 80

CHAPTER 1

INTRODUCTION AND REVIEW OF LITERATURE

The Greek philosopher Heraclitus wrote "You cannot step twice into the same river." Although intended as a metaphor of human life, this quote has been appropriated by stream ecologists to describe the dynamic systems they study (Resh et al. 1988).

The amount of water flowing in a stream normally reflects the quantity of precipitation that fell within the previous month, week, day, or hour. The discharge of a stream sometimes changes very quickly. A placid environment can be disrupted by a powerful torrent of water that rolls the substrate like marbles, moves tons of detritus and silt, and pulls rooted trees from banks. These fluctuations cause variations in every parameter within a stream: width, depth, current speed, discharge, temperature, light, dissolved oxygen, pH, chemistry, turbidity, nutrient level, substrate stability, and floral and faunal assemblages. Stream fauna must endure these often dramatic changes in their environment. Compared to these unstable and heterogenous stream environments, permanent freshwater springs would seem to be oases since they vary little in the above mentioned physicochemical aspects due to the perennial and rather even flow of water from underground aquifers. Water chemistry reflects the geologic formation through which the water flows and the near constant temperature approximates the mean annual temperature of the area. The lack of spates, rapid increases in discharge that can move substrate (Resh et al. 1988), would appear to be one of the greatest differences between springs and other flowing waters.

Statement of the Problem

When considering community structure, most spring surveys have not taken into account the lack of disturbance from spates. The purpose of this study was to look at the longitudinal zonation of biota within and between two springs by quantitatively and qualitatively describing the benthic faunas and physicochemical environments. Within each spring, the biota of the apparently undisturbed reach near the source is compared to the downstream reach which appears to be disturbed by spates.

Importance of the Study

Springs have received little scientific attention compared to other freshwater habitats. Similar to other aquatic systems, springs are affected by land management. Degradation of this type habitat may go unrecognized since their fauna is not well known. The loss of species due to groundwater pollution should be cause for concern. These species are often unique because of their restriction to cool headwater streams; relics of a cooler climate. The insect species may have abbreviated flight patterns or none at all which keeps them close to their native habitat and thus, limits their capacity to migrate. Once a spring has been damaged, recolonization is often difficult because springs are normally found in valleys separated by ridges and are often isolated from one another. O'Neill (1976 cited by Webster et al. 1983) determined that a spring is the aquatic ecosystem most sensitive to disturbance and one with very little resilience.

Recognizing the uniqueness of these aquatic habitats, Canada began a comprehensive study in 1983 to document that country's spring arthropod fauna (Williams 1983). Matthews et al. (1985) and Williams and Danks (1990) suggest that

the macroinvertebrate community of springs could be used to measure groundwater quality. Finding unpolluted aquatic environments to use as a reference comparison will become more difficult as land use continues to change making pristine springs even more important.

Review of Literature

Diversity. Although the environmental constancy of springs might appear idealic for macroinvertebrate residents, many studies have noted that springs have low diversity which frequently indicates a stressed community; low species richness along with a high number of individuals among a few species (Odum 1971, Williams 1983). Possible causes for low diversity in springs may include (1) environmental stability that reduces the availability of ecological niches (Sloan 1956, Armstrong and Williams 1971); (2) conditions in the spring deviate so far from normal wide ranging conditions of lotic environments that few animals have a developmental optima that falls within these narrow ranges (Sloan 1956, Minshall 1968, Hynes 1970); (3) various elements such as nutrient availability, temperature, substrate, discharge, dissolved oxygen, pH, or various chemical parameters limit the suitability of this type habitat.

Why is diversity important? Species of a community are actually a part of a food web rather than a food chain (Hutchinson 1959). They assume functional feeding roles at well-defined trophic levels (Cummins 1974, Vannote et al. 1980) that may change as they pass through the various life stages. This partitioning of habitat benefits the community as a whole. The more tightly the web is woven with many species as part of the community structure, the less chance that a breakage of any one of the

threads (loss of species) will cause the web to become less functional (a decrease in population and productivity) (MacArthur 1955, Hutchinson 1959, Green 1969, Patrick 1970). As diversity increases, the chance of preadaptations to environmental change also increases (Hutchinson 1959, Patrick 1970).

There has been little ecological research in spring habitats. However, many of the studies have shown that diversity was low at the spring source yet community composition changed longitudinally downstream (sometimes within short distances) with abundances becoming more evenly distributed among the taxa farther from the source.

Longitudinal Zonation. Davidson and Wilding's (1943) investigation of a cold spring community in southwestern Washington noted absences of expected species upstream at the resurgence. Noel (1954) studied a 70 m long springbrook in northeast New Mexico and found individuals in excess of 10,000/m² upstream, but only 2,228/m² downstream. On the west coast of Florida, Sloan (1956) identified 31 and 15 taxa at two springheads and approximately 50 taxa from each spring run around 800 m and 3200 m downstream, respectively. A comprehensive study by Minckley (1963) in Doe Run, a large spring in northcentral Kentucky, found a different faunal assemblage upstream than downstream. Hales (1967) identified a total of 52 taxa of Ephemeroptera, Plecoptera and Trichoptera in a 1200 meter springbrook in northcentral Utah with 18 taxa at the spring source, and 24, 27, and 31 taxa at sites progressively further downstream. Minshall (1968), in Morgan's Creek in northcentral Kentucky, identified 19 taxa at the spring source and counted 67,681 individuals/m², while 460 m downstream abundance dropped to 35,325/m² and taxa number increased to 31. Hynes

(1971) determined that there was a definite faunal zonation in a uniform temperature stream in Trinidad. Fahy (1972) found a different taxa composition one kilometer downstream in a spring in western Ireland. Thorup (1970) identified longitudinal succession of three species of Simuliidae in a spring in Denmark. In a spring in the foothills of northern Colorado, Ward and Dufford (1979) found densities of 2,512 individuals/m² and a diversity of 1.8 while 600 m downstream, diversity increased to 3.5 and density decreased to 1,685/m². In northwestern Colorado, Martinson et al. (1982), found diversity and densities to be lower at a spring source (3.0 and 23,937 individuals/m²) than 100 m downstream (4.0 and 14,543/m²).

Temperature. Most of the preceding studies have attributed the faunal differences longitudinally within springs to the nonseasonal constant water temperature at the source. Possibly the spring's relatively cool summer and warm winter temperatures alter the life cycles of many invertebrates, causing them to be unable to complete their life cycles during the appropriate time. They also theorize that many invertebrates have optimum growth temperatures not found in springs (Davidson and Wilding 1943, Dudley 1953, Sloan 1956, Teal 1957, Minckley 1963, Hales 1967, Minshall 1968, Tilly 1968, Stern and Stern 1969, Fahy 1972, Ward and Dufford 1979, Martinson et al. 1982, Williams 1983, Williams and Hogg 1988).

Temperature and photoperiod regulate many poikilothermic physiological processes including growth, adult size, fecundity, and diapause (Sweeney 1984). Diapause, a period of dormancy between growth stages, synchronizes the life stages of many aquatic insect species in order that the population may reach reproductive maturity

at the same time (Saunders 1976). Adult emergence must occur in mass since their aerial stage is often short-lived, often just a few hours or days. This brief adult stage may be an evolutionary response to predation, reducing the likelihood of capture by overwhelming the capture mechanism (spider webs, birds) (Edmunds and Edmunds 1979).

Although most of their life is aquatic, benthic insects have maintained their link to the terrestrial world through emergence. Seasonal timing of emergence and extended emergence through multiple cohorts enables aquatic insects to escape some catastrophes (e.g., floods or droughts) (Hynes 1961, Anderson and Wallace 1984).

Synchronized emergence has been shown to occur during the proper season in stenothermal environments in spite of the apparent lack of thermal cues (Odum 1957, Teal 1957, Thorup 1963). Hynes (1970) and Sweeney (1984) hypothesized that invertebrates in the stenothermal environment of a spring use other developmental cues such as photoperiod (which in an evolutionary sense is a more reliable and less irregular cue than temperature) to synchronize their growth stages. Changes in food quality or quantity or slight changes in water temperature (Williams 1981) and turbidity (Ziser 1985) during heavy summer rains may also be used as cues for timing developmental stages.

Cool Water Species. Although the cool summer temperatures typically found in a spring have been considered non-seasonal, many species among some of the more primitive orders of insects (Ephemeroptera, Plecoptera, and Trichoptera) are abundant in cool, headwater streams (Cummins 1975). Along with megalopterans and the

nematocerous Diptera, these groups are primitive in that they are, as immatures, wholly aquatic and highly adapted for aquatic life with extensive diversification within the groups (Hynes 1984). Williams and Williams (1987) have compiled over 175 records of caddisfly species from cold water springs throughout Canada with virtually all families represented. It has been hypothesized that ancestors of many freshwater insects evolved in cool lotic habitats (cf. Anderson and Wallace 1984). Adaptation to the low oxygen concentrations found in water (8,000 times less than in equal amounts of air) might have been the most limiting factor to the evolution and adaptation of terrestrial insects to aquatic environments (Eriksen et al. 1984). This transition may have occurred in cool waters where dissolved oxygen levels are higher than warm waters (Eriksen et al. 1984). Brundin (1956 cited by Oliver 1971) and Hynes (1984) theorize that chironomids evolved in cool spring-fed streams. Williams and Hynes (1974) found chironomid larvae deep in the substrate suggesting that the larvae seek cool optimum growth temperatures.

Springs as Refugia. According to Odum (1971) "there is little doubt that springs have provided refuges for many organisms." Nielsen (1950) identified several spring species of aquatic insects that are glacial relics far from their normal cooler geographic range. At the same time, some species found within springs were left behind from warmer times. They are crenobionts (species confined to springs), finding refuge from the cold winters (warmer climate species) or warm summers (cooler climate species) (Hynes 1970).

Within the Interior Low Plateau and eastern North America, uplift during the late Tertiary and early Quaternary caused once quiet waters to become rapidly flowing streams. The lotic but quieter waters of springs and cave streams may have provided an escape for intolerant species (Barr 1968, Holsinger 1988). Troglophilic and troglobitic salamanders, crayfish, fish, isopods, and amphipods were probably spring inhabitants prior to the invasion of caves (cf. Barr 1973).

Dominant Spring Species. Isopods and gammarid amphipods are the most commonly found arthropods in springs (Minckley 1963, Minckley and Cole 1963). These nonemergent (lacking an adult terrestrial stage), noninsect invertebrates are so well adapted to the spring environment that many species are strictly limited to that type habitat. As cold stenotherms, many gammarids are unable to reproduce in temperatures above 18°C (Smith 1973, Pennak 1978, Marchant 1981). Due to their intolerance of swift flow conditions (Ailee 1929, Marchant 1981), isopods and amphipods are usually found in quiet, oxygen rich waters with high levels of calcium carbonate, the latter used for their calcified exoskeletons (Pennak 1978). The isopod Asellus and amphipod Gammarus have been noted to work their way upstream and congregate in large aggregations in areas where they can no longer move against the current (Ailee 1929, Minckley 1964). Isopods and amphipods have life cycles of a year or two with at least two overlapping generations (Minckley 1963, Pennak 1978) and a high reproductive rate with up to ten individuals per brood (Culver 1971). These two groups often appear to dominate the spring habitats possibly preventing other species from existing in similar abundances. Insects do not compete as well as the nonemergent benthos because their

instream populations fluctuate due to adult emergence (Sousa 1984). However, adult emergence is advantageous in that it allows insects to recolonize new and disturbed habitats (Gray and Fisher 1981).

Disturbance. Several studies (McAuliff 1984, Clifford 1982, Hemphill and Cooper 1983, Sousa 1979) have shown that disturbance by spates reduces populations of dominant organisms. For purposes of this study disturbance is defined as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment" (White and Pickett 1985). Disturbances can cause different levels of disruption. The more extreme the disruption, the longer the recovery time (Gore et al. 1990, Yount and Niemi 1990).

Spates are thought to play an important role in shaping the community assemblages within streams. They allow diversity to increase or be maintained (Hoopes 1974, Abugov 1982, Ward and Stanford 1983, Fisher 1983, Hughes 1986, Robinson and Minshall 1986, Sousa 1984, Menge and Sutherland 1987, Resh et al. 1988) by rearranging the habitat (shifting substrate and organic matter) and removing dominant organisms such as isopods and amphipods as well as those that are not overly dominant. Spates allow new patches of habitat to open up and enables fugitive species (opportunistic colonizers), such as chironomids, baetid mayflies, and simuliids to establish themselves (Hutchinson 1953, Abugov 1982, Hemphill and Cooper 1983, McAuliffe 1984). These so called "wave" species (Loucks 1970), rather than being highly competitive, have high vagility and reproductive rate, rapid growth, and

recruitment throughout the year (Margalef 1963, Hemphill and Cooper 1983, Gurtz and Wallace 1984, Resh et al. 1988). These colonizers are usually generalists, being able to utilize a variety of available nutrients. As time passes and no further disturbance occurs, specialists with longer life cycles colonize the disturbed reaches (Hynes 1970, Gore and Milner 1990). These colonizers arrive from less disturbed patches of the reach, headwaters via drift, upstream migration, vertically from the hyporheic zone and oviposition by aerial adults (Williams and Hynes 1976, Gurtz and Wallace 1984).

When the periods between disturbances increases and no disruption of the ecosystem or community occurs, biotic interactions become important (Resh et al. 1988). In this stable environment, those species capable of utilizing the habitat most efficiently, dominate and replace the less efficient species (Hutchinson 1959, Connell 1978, Hart 1983). Their numbers increase because inter-specific competition is lessened (Patrick 1970). In a stable environment, organisms can use more energy for reproduction since less energy is needed for regulatory activities (Connell and Orias 1964). The high population density of only one or two species continues to lower diversity because of increased interactions (Hynes 1970, Huston 1979). Huston (1979) calls this "the paradox of enrichment"; stable environments allow high productivity which cause lower diversity.

Environment vs. Competition. A predominant topic among stream ecologists today is whether the community is shaped to a greater degree by the environment or by species interactions. These competing factors also have been variously termed density dependent vs. density independent (Shiozawa 1983); equilibrium vs. nonequilibrium

(Ward 1975, Huston 1979); predictability vs. spatial heterogeneity (Resh et al 1988); autogenic vs. allogenic (Fisher 1983); and/or endogenous vs. exogenous (White and Pickett 1985).

Past literature suggests that diversity is a product of competitive exclusion (Green 1969, Allan 1975). Today many ecologists hypothesize that diversity is increased by prevention of competitive exclusion (Menge and Sutherland 1987). Disturbances by spates and other environmental fluctuations interrupt the population growth and prevent species exclusion (Connell 1978). The greatest diversity occurs at an intermediate level of disturbance; too much disturbance will only allow fugitive species to exist and too little disturbance will only allow the superior competitive species to prevail (Connell 1978).

Resilience. Many ecologists have suggested that greater environmental heterogeneity leads to higher diversity (Green 1969, Ward 1975). High diversity denotes a mature community which also has high resilience; recovery from a disturbance can occur quickly (Connell 1964, Patrick 1970, Odum 1981, Webster et al. 1983). Diversity is maintained even though the community assemblage of species may be different (Patrick 1970). With greater diversity, more species are available to fill vacated niches and keep the food web from weakening (Hutchinson 1959, Green 1969). In an immature community (i.e., one with low diversity) recovery may take years. O'Neill (1976 cited by Webster et al. 1983) determined that a spring source is probably the ecosystem most sensitive to disturbance and has very little resilience. Late successional species which have long life cycles have less resilience since they cannot

recover quickly from population disturbance (Margalef 1963, Poff and Ward 1989). They usually have slower metabolic rates and fewer, more protected offspring (Patrick 1970).

Synopsis. The disturbances that occur in a stream, if not catastrophic (e.g., a once every 100 year flood), are predictable and organisms' life histories have been shaped by the responses to those conditions (Loucks 1970). If those predictable disturbances do not occur, as might be the case if a stream was impounded, the community deteriorates (Ziser 1985). Disturbance is a reset mechanism which allows the local coexistence of many species (Robinson and Minshall 1986), increases diversity and prevents extinction (Andrewartha and Birch 1954). On an evolutionary time scale, most species will not adapt to environmental changes. However, with increased diversity there is a greater possibility that some members of the community will persist. The few species that live in a less rigorous environment, such as a spring, possibly could be considered senescent (cf. Hutchinson 1959, Barr 1968) since the constancy disallows natural selection (Huheey 1962). Yet, competition may maintain the diversity of the individual species' gene pool.

CHAPTER 2

DESCRIPTION OF THE STUDY AREA

Land Between The Lakes

Lost Creek and Pryor Creek springbrooks are located in Land Between The Lakes (LBL) (Figure 1), an approximately 69,000 hectare multi-use demonstration area managed by the Tennessee Valley Authority (TVA). LBL is bordered to the east by Lake Barkley, the impounded lower Cumberland River, and to the west by Kentucky Lake, the impounded lower Tennessee River. The drainage divide for these two major rivers runs the length of LBL, splitting it into an eastern and western half. Pryor Creek springbrook is in the Cumberland River drainage and Lost Creek springbrook is in the Tennessee River Drainage.

Lost Creek Spring

Lost Creek Spring (LCS) is in the southwest corner of LBL (Figure 1) at an elevation of 119 m ($36^{\circ}28'28''\text{N}$, $88^{\circ}01'33''\text{W}$). LCS is actually two primary resurgences that form a springbrook which flows west (ca. 156 m) to the confluence with Lost Creek which flows northwest into Kentucky Lake (Figure 2). These resurgences are called rheocrenes, a term used to describe a spring resurgence with rapidly moving water forming a channel (Hynes 1970).

The groundwater resurgence of LCS occurs at exposed bedrock of the Fort Payne formation, the oldest exposed limestone formation in LBL and lowest level of the group called the Mississippian sequence. It is recognized by its thin-beddedness and near lack

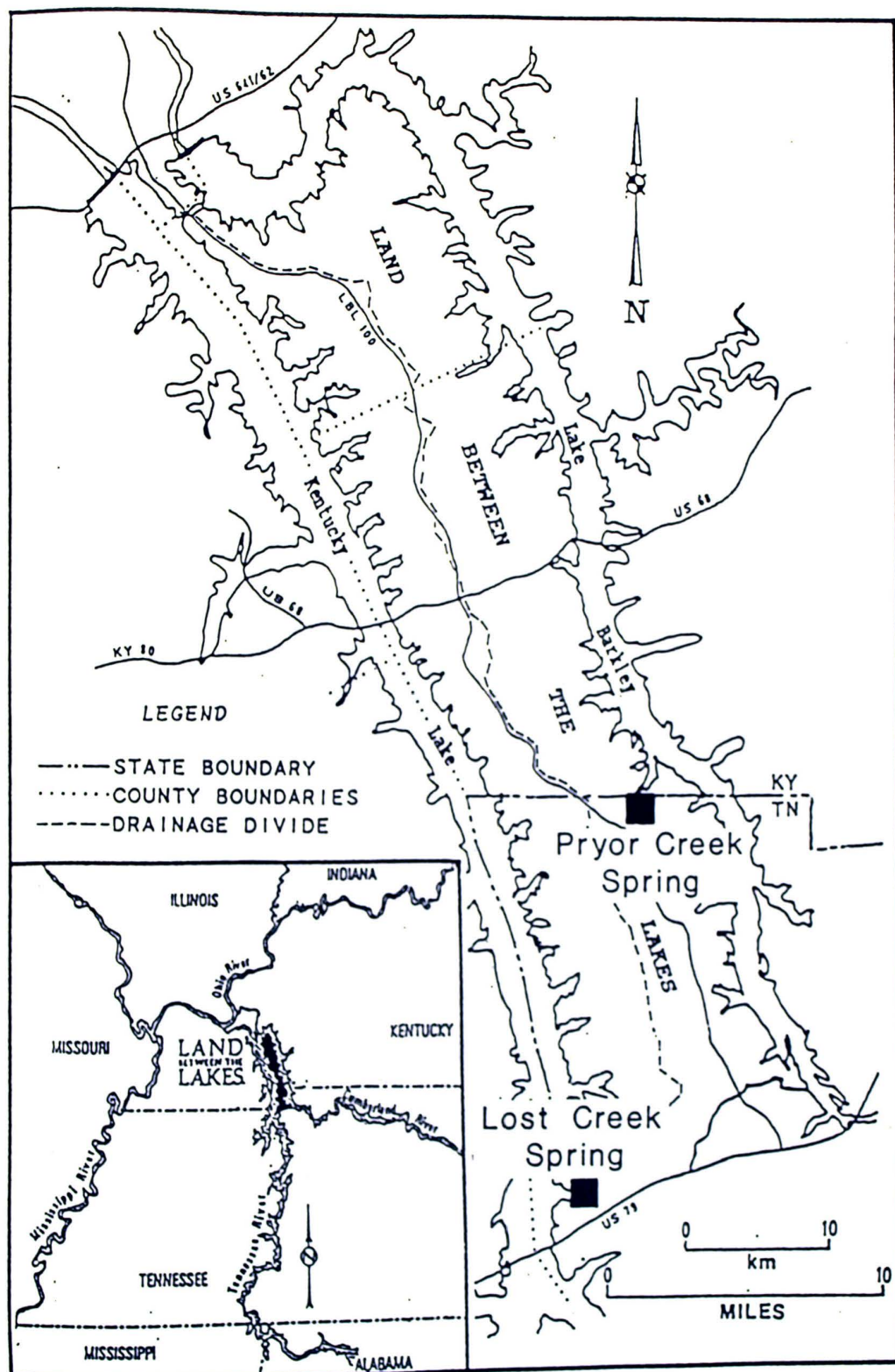


Figure 1. Locations of Lost Creek Spring and Pryor Creek Spring in Land Between The Lakes.

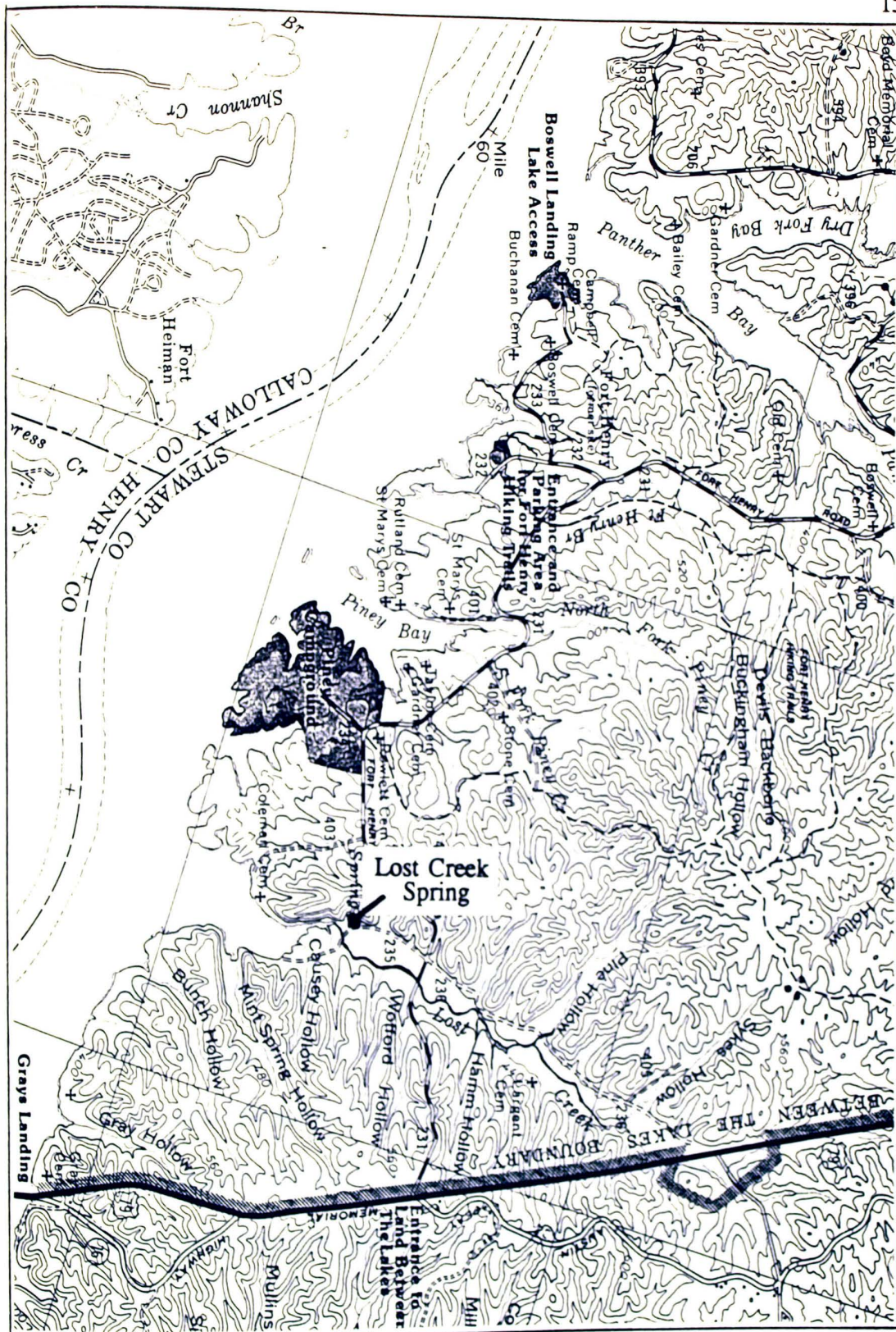


Figure 2. Location of Lost Creek Spring (LCS) in relation to Lost Creek and Kentucky Lake.

of fossilization. At least 50% of the formation is angular, blady chert found often in layers 10 to 30 cm thick that vary from light gray to yellowish (Harris 1988). The Fort Payne formation is underlain by the Chattanooga Shale formation of the Devonian age (P. Kemmerly pers. comm.). It is at this contact that many springs can be found due to this impermeable shale (P. Kemmerly and D. M. S. Bhatia pers. comm.).

Sites 1, 2, and 3, collectively called the "upstream" sites, were closest to the groundwater resurgence (Figure 3). The southerly exposure of the hillside from which the spring emanates along with the lack of forest canopy results in all three sites receiving direct sunlight throughout most of the day.

Site 1 approximately 2 m from the lower of the two spring sources, had an average width of 2 m and an average depth of 8 cm and can be characterized as a riffle. The red alga *Batrachospermum* sp., the aquatic moss *Amblystegium tenax*, the liverwort *Riccia fluitans*, and the duckweed *Lemna* sp. were found interspersed throughout this site. Acorns and white oak leaves fell from the hillside into the site in the fall.

Site 2, on a riffle, was approximately 7 m from the source and was much wider than the other two upper sites. It had an average width of 9 m and a depth of 10 cm. This site was often choked with the exotic, semi-aquatic peppermint, *Mentha piperita*. Duckweed and liverwort were also found here.

Site 3 was on a riffle and was approximately 22 m from the source. Similar to site 1, it contained cobbles covered with red alga and aquatic moss but was free of the peppermint.

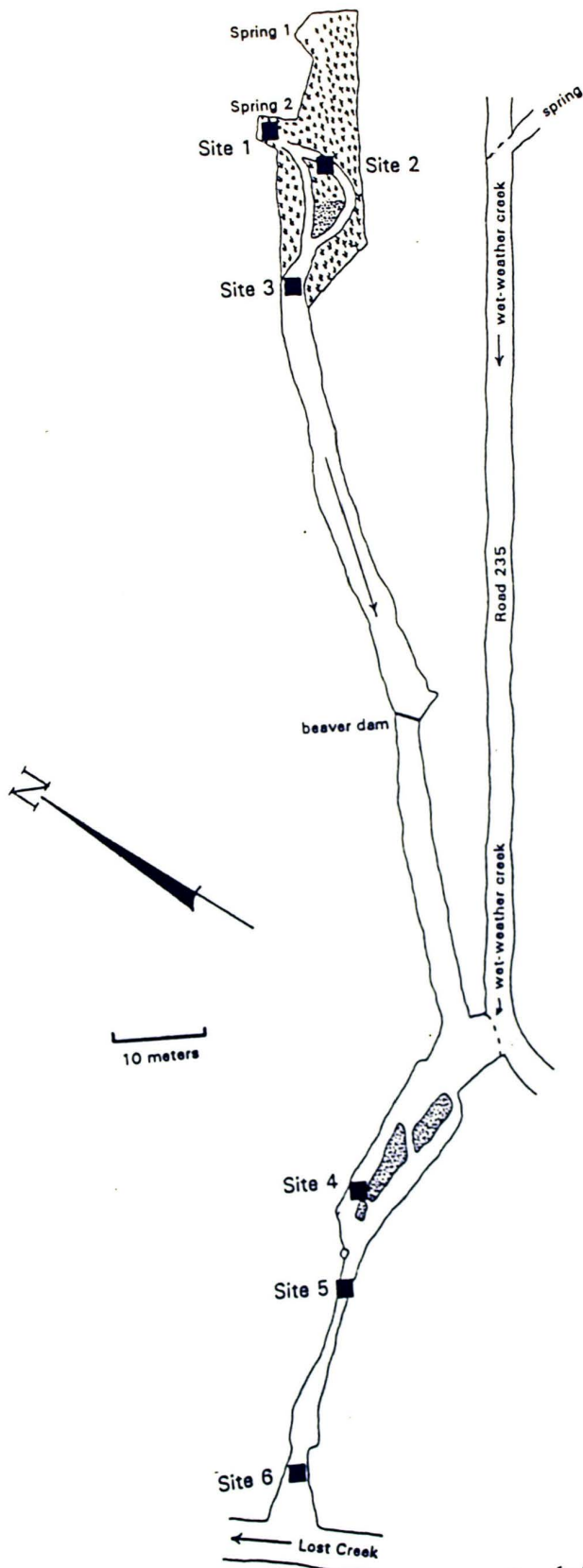


Figure 3. Diagram of sampling sites within Lost Creek Spring.

Sites 4, 5, and 6, collectively called the "downstream" sites, were visually much different than the upstream sites since there was little aquatic vegetation present during the sampling period. The stream bank canopy was sparse so the sites were exposed to full sun during a large portion of the day. Trees, including sycamore (*Platanus occidentalis*), red maple (*Acer rubrum*), red bud (*Cercis canadensis*), hornbeam (*Ostrya virginiana*), alder (*Alnus* sp.), birch (*Betula* sp.) and ironwood (*Carpinus caroliniana*), grew along the banks. A beaver population had denuded the area of many trees and bushes.

Just above these downstream sites, a wet weather creek flowed along LBL road 235 and joined the springbrook above the downstream sites (Figure 3). An unnamed spring also flowed down this road which joined LCS at this point. Sites 4 and 6 were on riffles and were 119 and 152 m, respectively, from the source (Figure 3). Both sites averaged 2-2.5 m in width and 7-8 cm deep. Site 5 on the shoal in a pool was approximately 129 m from the source. Here the springbrook averaged 3.5 m in width and 11 cm in depth.

Pryor Creek Spring

Pryor Creek Spring (PCS) is on the east side of LBL (Figure 1) near the Kentucky/Tennessee border (36°39'58"N, 87°57'44"W) at an elevation of 116 m. Drainage from this spring flows west (ca. 90 m) to the confluence with Pryor Creek. Pryor Creek flows north into Pryor Bay, an arm of Lake Barkley (Figure 4). PCS is

characterized as a seep, which is the most common type of spring in north-central Tennessee. Water is deflected upwards after it comes into contact with an impermeable layer of rock (Piper 1932).

The recharge area for PCS is the St. Louis limestone formation, a highly soluble rock which often contains many solution channels, caverns, and sinkholes. The clastic residuum is a bright orange clay with many fragments of two genera of fossil coral (*Lithostrotion* and *Lithostrotionella*) which are characteristic of this uppermost or youngest layer of the Mississippian sequence (Miller 1974). Between the St. Louis and Fort Payne formations lies the Warsaw formation. Oftentimes, there is an impermeable layer of chert at the contact between the St. Louis and Warsaw; this causes a spring to form (P. Kemmerly, pers. comm.).

The groundwater resurgence at PCS is a sandy bottomed limnocrene. Limnocrenes are characterized as resurging water that flows into a pool before overflowing into a channel (Hynes 1970). Site 1 was located in this pool (Figure 5), which averaged 4.8 m wide and 16 cm in depth. Filamentous algae (*Spirogyra* spp. and *Chladophora* spp.) were abundant throughout the year. The pool received diffused sunlight most of the day. A large sycamore tree (*Platanus occidentalis*) provided some shading. A fire occurred in the area approximately two years before this study began, killing or damaging many of the surrounding trees. The trees on the slope behind the spring source were harvested near the end of the study, further exposing the spring to sunlight.

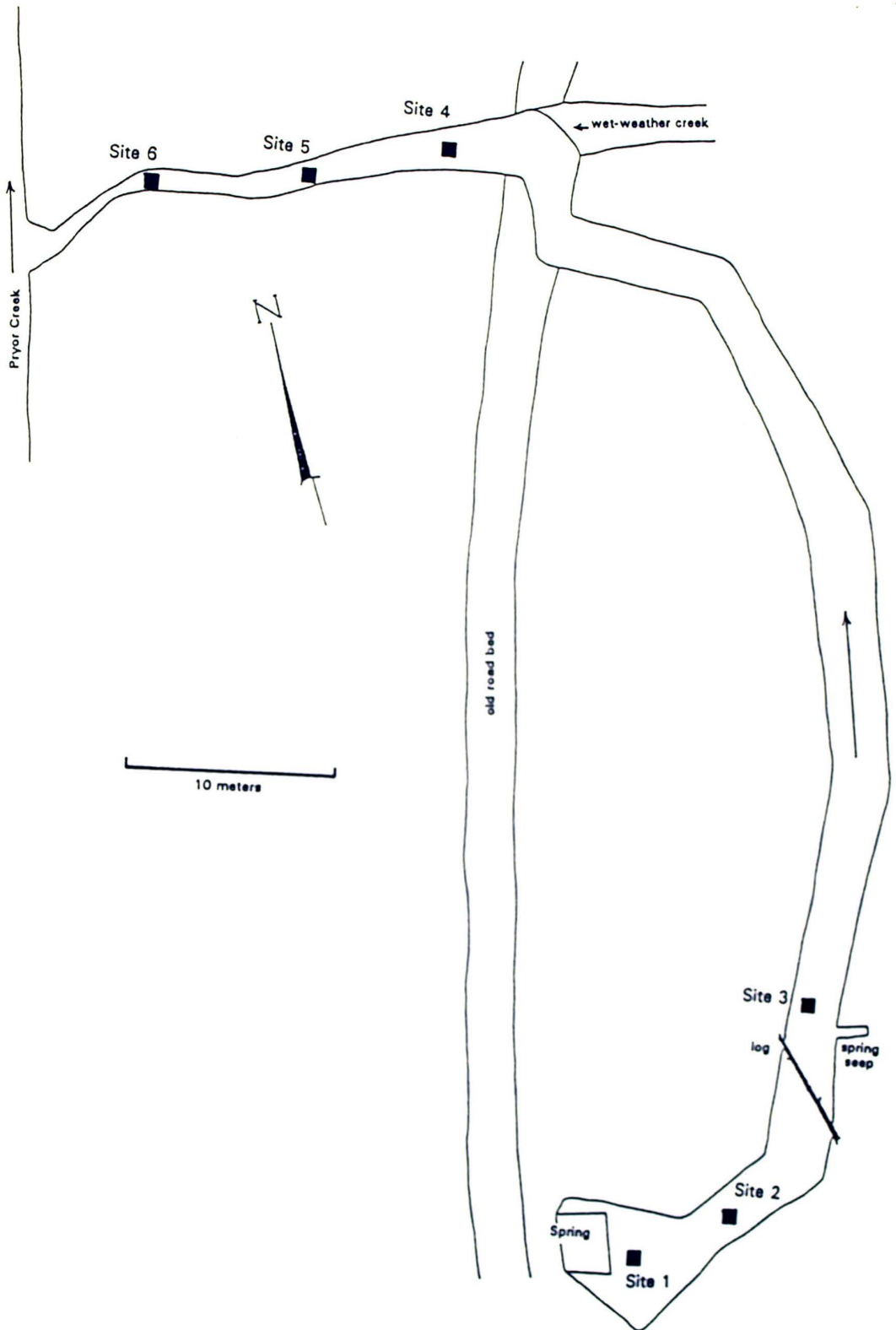


Figure 5. Diagram of sampling sites within Pryor Creek Spring.

Site 2 was in the brook on a riffle 8 m from the western most edge of the pool (Figure 5). The channel averaged 1.9 m wide and 4.6 cm deep. There was no aquatic vegetation except for unidentified diatoms growing on the rocks. This site was also mostly exposed to sunlight with little canopy cover.

Just below site 2, logs, detritus, and leaves from surrounding sycamores gathered in front of a large fallen cottonwood that spanned the springbrook. Site 3 was located below this jam on a riffle around 10 m from site 2 (Figure 5). The water averaged 2.2 m wide and 5.8 cm deep. Like site 2, it was free of aquatic vegetation. However, riparian vegetation from a few medium and large-sized trees including sycamore (*Platanus occidentalis*), sweet gum (*Liquidambar styraciflua*), sugar maple (*Acer saccharum*), and black gum (*Nyssa sylvatica*), along with winged elm (*Ulmus alata*) and mulberry (*Morus* sp.) formed a more dense canopy than that found at the other upper sites. Only filtered light reached the site.

Downstream, the springbrook joined Pryor Creek around 92 m from the source (Figure 5). Just above site 4, approximately 71 m from the source, a wet weather stream joined the springbrook. Site 5 was 76 m from the source and site 6 was 85 m from the source. All three sites averaged around 1.1-1.5 m in width. Sites 4 and 6, located on a riffle, had an average depth of 3.6 and 4.5 cm, respectively. Site 5 was on the shoals of a small pool and averaged 6.1 cm in depth. All three sites had a riparian canopy of small trees such as hornbeam (*Ostrya virginiana*), sycamore (*Platanus occidentalis*), pawpaw (*Asimina triloba*), black walnut (*Juglans nigra*), black cherry (*Prunus serotina*), red bud (*Cercis canadensis*), and sugar maple (*Acer*

saccharum). The sites received only diffused sunlight, had no aquatic vegetation, and little algal growth.

In both LCS and PCS, site 5 was significantly altered during the year of this study. These sites fluctuated between a more pool-like and later a more riffle-like condition as gravel deposits were alternately washed into and taken out of the pools. Other sites tended to be more stable in overall structure, width and depth, throughout the study.

MATERIALS AND METHODS

Physicochemical Parameters

Dissolved oxygen (D.O.), water temperature, and physical data (width, flow and depth) were measured at each of the twelve sites. The pH was measured at one upstream and one downstream site. Air temperature was recorded at the beginning of the sampling day. All measurements were made weekly from September 1988 through October 1989. Temperature and DO were measured with a YSI model 54A field meter. pH was measured with a Cole-Parmer pH meter (model 5985-80).

Flow was determined by the "cork float" method. The timed rate that a float traveled one meter was computed as seconds per meter, then converted to meters per second to determine current velocity. Weekly measurements of flow, width of the stream and depth of the water were taken at each site. Each measurement was replicated three times and averaged. Discharge was determined by the calculation $w \cdot d \cdot a \cdot l / t$ (w = mean width, d = mean depth, l = distance over which the float traveled, t = time for float to travel distance l , a = a constant 0.8 for rough stream or 0.9 for smooth stream bed) (cf. Hynes 1970). Velocity was characterized using the descriptions in Macan (1963): "very swift," over 1 m/sec; "swift," 0.5-1 m/sec; "moderate," 0.25-0.5 m/sec; "slight," 0.10-0.25 m/sec; "very slight," <0.10 m/sec.

Water samples were collected montly from upstream and downstream at each springbrook (at the resurgence in both springs as the upstream site, site 6 at LCS and site 4 at PCS as the downstream site). From each of these sites approximately two liters of water were collected in an acid-washed glass container, placed in ice and maintained

at 4°C, transported to the laboratory, and analyzed within 24 hours. Standard methods (APHA et al. 1983) were used to measure levels of phosphate, nitrate, total iron, sulphate, calcium, and magnesium.

Substrate Heterogeneity

Substrate type at each site was determined by selecting a representative area of the stream, sorting and grouping the particles by eye and with the aid of a ruler into size classes, and figuring the relative contribution of each. Size classes were determined by the use of Lane's (1947, cited in Platts et al. 1983) description of particle size: small cobble (128-64 mm), very coarse gravel (64-32 mm), coarse gravel (32-16 mm), medium gravel (16-8 mm), fine gravel (8-4 mm), very fine gravel (4-2 mm), very coarse sand (2-1 mm), and coarse sand (1.0-0.5 mm).

Macroinvertebrates

Mid-channel benthic samples were collected bi-monthly at each of the six sites from November 1988 to September 1989 (six sets of six samples) for each springbrook. In addition, two sets of preliminary samples were collected at the upstream sites during September and October 1988 (two sets of three samples for each springbrook). Samples were collected using the English PVC T-joint benthic sampler with a 363 μ net (English 1987). The sampler collects from a 380 cm² area to a depth of approximately 10 cm. The sampler was placed quickly onto the substrate to avoid loss of escaping invertebrates and twisted into the substrate to the greatest depth possible, usually at least 8 cm. The substrate within the sampler was swirled by hand and attached organisms were removed from rocks and vegetation. Organisms and debris were carried by the

current into the net which was directly downstream. The samples were placed in a one liter jar, preserved in formalin, and returned to the laboratory for sorting and identification using a binocular dissection microscope. Chironomid larvae were slide mounted in CMCP-10 for determination under a compound microscope. Aquatic macroinvertebrates, except for oligochaetes, Hydracarina, and chironomid pupae, were identified to genus and, when possible, to species.

Analysis of Macroinvertebrate Samples

Community Similarity. Throughout this study in both springbrooks, sites 1, 2, and 3 were collectively called "upstream", being closer to the resurgence, and sites 4, 5, and 6 were collectively called "downstream", being farther from the resurgence and below the confluence with a wet weather creek. Two indices of community similarity (Jaccard's and Morisita's) were used to determine if these three sites upstream of each springbrook were more alike than they are like the downstream sites and thus could be collectively designated "upstream". Similarly the three downstream sites should be more alike to each other than they are to the upstream sites to be accurately called "downstream". Jaccard's coefficient of similarity is based on the presence or absence of taxa within a sample and is determined as follows:

$$Jaccard's = \frac{c}{s_1 + s_2 - c}$$

where c = number of taxa in common in both communities, s_1 = number of taxa in community 1, and s_2 = number of taxa in community 2. Morisita's Index of

community similarity takes into account not only the presence or absence of taxa, but the numbers of individuals in those taxa. Morisita's index is determined by the following formula:

$$Morisita's = \frac{2 \sum_{i=1}^s X_i Y_i}{(s_1 + s_2) N_1 N_2}$$

where $s_1 = \sum X_i(X_i-1)/N_1(N_1-1)$, $s_2 = \sum Y_i(Y_i-1)/N_2(N_2-1)$, X_i = number of individuals from community 1 in the i^{th} taxa, Y_i = number of individuals from community 2 in the i^{th} taxa, $N_1 = \sum X_i$, $N_2 = \sum Y_i$, s = the number of taxa in all sample units.

Nonemergent and Emergent. The aquatic macroinvertebrates were placed into the groups "nonemergent" or "emergent" to further recognize the possible differences between upstream and downstream. Nonemergent invertebrates are noninsects including planariids, oligochaetes, sphaeriid clams, physid and pleurocerid snails, gammarid amphipods, asellid isopods, and hydracarina mites. These invertebrates complete their entire life cycle in the water and do not emerge to become terrestrial or aerial. The emergent invertebrates are aquatic insects that spend most of their life as aquatic immatures. Most aquatic insects, however, emerge as aerial adults during their reproductive stage. These emergent invertebrates include odonates, hemipterans, mayflies, stoneflies, caddisflies, megalopterans, coleopterans, and dipterans. Hemiptera and coleoptera were included in this category although many of the species remain in the water throughout their development.

Richness, Diversity and Evenness Indices. Margalef's species richness index (1958, cited in Ludwig and Reynolds 1988), Shannon's Diversity index (cf. Cox 1990), and Pielou's Evenness Index (cf. Cox 1990) were calculated for each of the samples. Shannon's Diversity index (H'), calculated as:

$$H' = - \sum_{i=1}^S \frac{n_i}{N} \log \left(\frac{n_i}{N} \right)$$

where n_i = the number of individuals in the i^{th} species, N = total number of individuals of all taxa in the sample, and S = the number of taxa in all sample units. Shannon's diversity index incorporates taxa richness (the number of taxa in the sample) and species evenness (how the abundances are distributed among the taxa). Using diversity indices alone may obscure the contribution of taxa richness or taxa evenness. Two communities may have similar diversity although one has low taxa richness but has high evenness while the other community may have high taxa richness and low evenness. Therefore the components of diversity were examined also. Margalef's species richness (R) index was calculated as follows:

$$R = \frac{S-1}{\log N}$$

where S = total number of taxa in all sampling units and N = total number of individuals in all sample units. Pielou's evenness (J') was calculated as:

$$J' = \frac{H'}{\log S}$$

where H' = Shannon's diversity and S = total number of taxa in all sampling units (approximates the maximum possible H' for the sample size).

Functional Feeding Groups. In order to recognize the relationship between the habitat and the organisms, the taxa were placed into the functional feeding group classification (ffg) which is a system that groups taxa together that use a similar feeding strategies. Indirectly, it may also identify the most available food source. The invertebrates were characterized as shredders, collectors-filterers, collectors-gatherers, scrapers, herbivores, predators, scavengers or omnivores. A shredder is dependent on coarse particulate organic matter (CPOM) such as leaves and vascular plant tissue; collectors-filterers filter suspended fine particulate organic matter (FPOM); collectors-gatherers are FPOM sediment feeders; scrapers scrape off aufwuch (attached algae, fungi and bacteria) from rocks; herbivores feed upon living plant tissues; predators feed upon living animal tissue; and scavengers and omnivores are nonspecific feeders (Merritt and Cummins 1984). The relative contribution of each group to the whole trophic community is determined by computing the number of individuals of each ffg in relation to the total number of individuals.

Relative Abundance and Frequency of Occurrence. The number of individuals of any one taxon captured over the entire one year sampling period was called the relative abundance. Each taxon was designated as: exceptionally abundant = >5000

specimens were captured; very abundant = 1000 to 5000 specimens; abundant = 250 to 999 specimens; common = 50 to 249 specimens; rare = 5 to 49 specimens; or, very rare = <5 specimens. Frequency of occurrence, defined here as the number of times each taxon was found during the sampling year, was shown as a percentage. Out of the six sampling periods (November, January, March, May, July and September) for both upstream and downstream reaches, each taxon was characterized by the number of sampling months it was found (possible 1 to 6). If the taxon was found in only one sampling month it was found 17% of the time; 2 sampling periods = 33% of the time; 3 sampling periods = 50% of the time; 4 sampling periods = 67% of the time; 5 sampling periods = 83% of the time; 6 sampling periods = 100% of the time. In both relative abundance and frequency of occurrence, taxa were separated as upstream or downstream captures.

RESULTS

Site Descriptions

Discharge. Temporal rainfall recharge had no significant effect on the average monthly discharge at LCS (upstream $r=0.24$, $p>0.40$; downstream $r=0.12$, $p>0.60$), indicating that rain and snow melt had entered the ground many months to years prior or at some distance away. Discharge was greater downstream and not correlated with upstream ($r=0.21$, $p>0.40$, Figure 6)

Average monthly discharge at PCS was correlated with temporal rainfall ($r=0.58$, $p<0.05$). Therefore, groundwater discharge increased with monthly rainfall increases indicating that recharge of the groundwater was recent and within relatively close proximity to the resurgence (Figure 7). Turbidity of the spring was noted after recent heavy rainfalls. PCS discharge upstream and downstream were correlated ($r=0.67$, $p=0.01$).

PCS had much lower discharge than LCS. Mean discharge at LCS ($226 \text{ m}^3/\text{hr}$) was greater than three times the mean discharge at PCS ($70 \text{ m}^3/\text{hr}$).

Both springbrooks were joined by wet weather creeks just above the downstream sites. On 18 November just before sampling on 25 November, LCS downstream discharge was measured during a high flow event causing the peak in discharge shown in Figure 6. Although the water level was not measured or observed at PCS downstream on 13 November, the rise in water was indicated by floating emergence traps being washed from the downstream sites and deposited on the meter high stream bank.

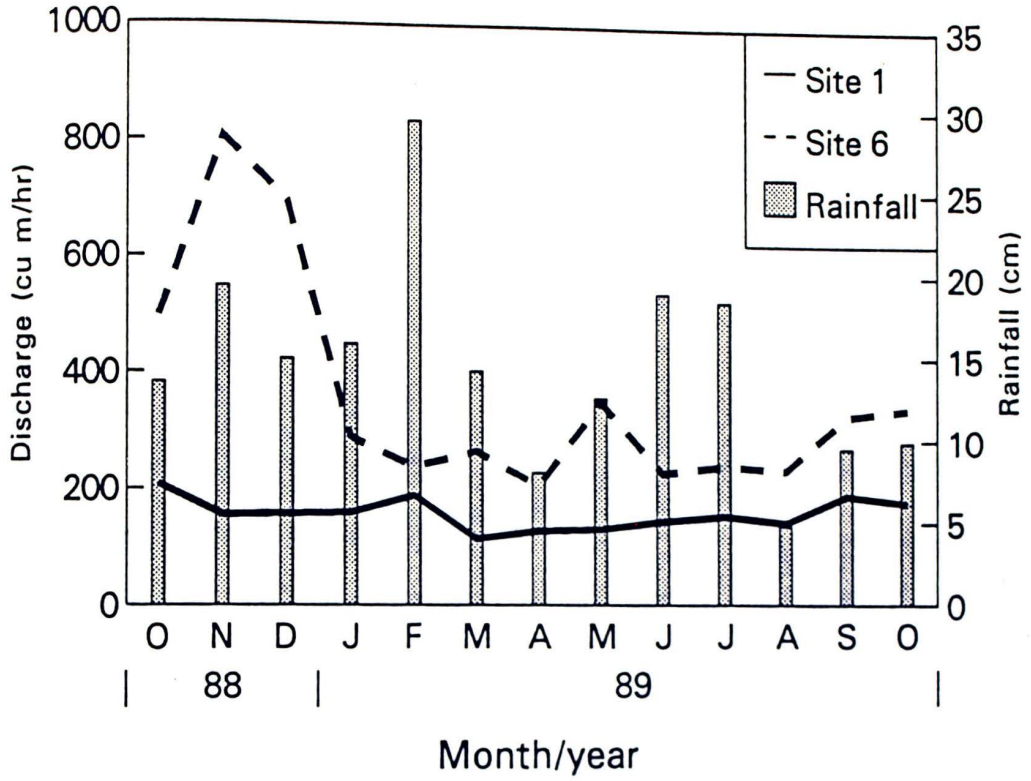


Figure 6. Mean monthly discharge (m^3/hr) at Lost Creek Spring Site 1 and Site 6 compared to mean monthly rainfall (cm) based on data from Fort Donelson National Battlefield.

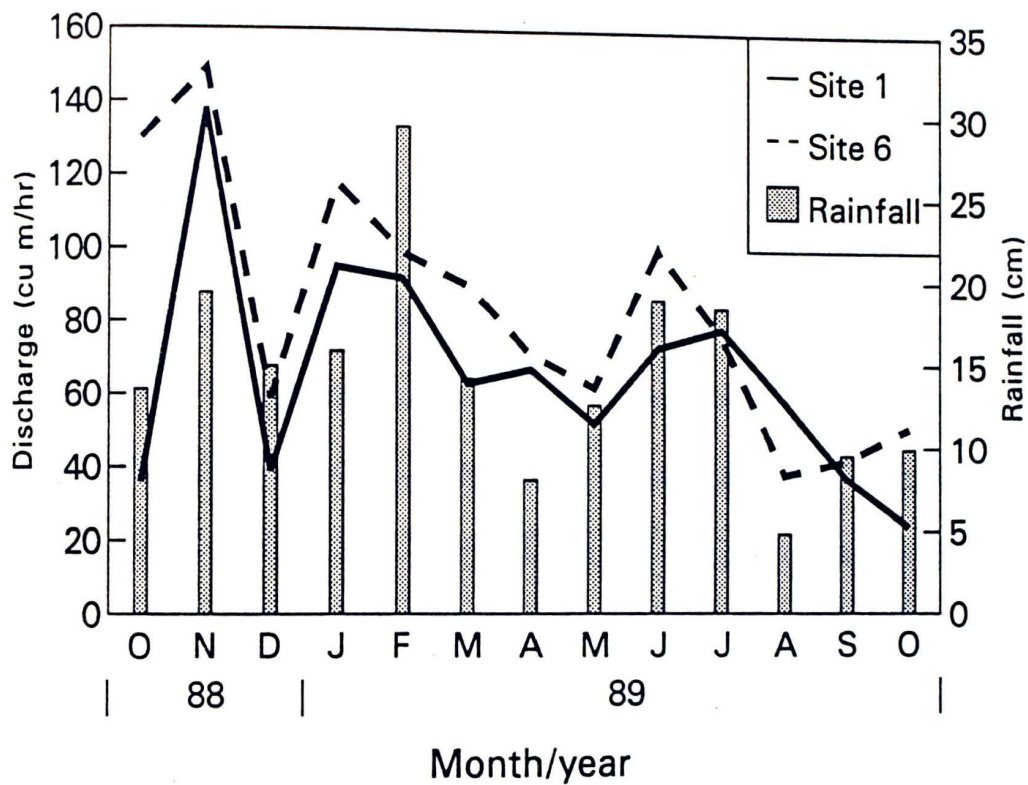


Figure 7. Mean monthly discharge (m^3/hr) at Pryor Creek Spring Site 1 and Site 6 compared to mean monthly rainfall (cm) based on data from Fort Donelson National Battlefield.

Disturbance of these traps often helped in pinpointing weeks when spates had occurred. On two occasions (21 January before the sampling on 28 January and again on 3 July, two weeks before the sampling on 14 July) spates were noted. According to weather data supplied by the National Park Service at Fort Donelson, Tennessee (Mickey Hill, pers. comm.), another storm event occurred 6 March about three weeks before sampling on 28 March. These data indicate that 1.6 inches of rain fell in approximately four hours. Scouring of the substrate downstream below the wet weather creek was noted in both March and July at both springbrooks.

Substrate and Water Velocity. In both LCS and PCS, substrate complexity varied between the upstream sites but was more similar at all three sites downstream (Appendix I). The absence of sorting was the most obvious difference between the upstream and downstream areas. These differences were readily noted while trying to push the benthic sampler at least 8 cms into the substrate. Penetration of the substrate with the sampler was very difficult at the upstream sites and much easier downstream. Upstream, sand was compacted between the larger gravel pieces and all sizes were mixed together as in a matrix. There was little interstitial space between the particles. Downstream, tumbling of the substrate caused by spates sorted the particles into layers. The upper-most layer consisted of larger gravel and cobble. Vertically below the larger pieces were smaller gravel particles. Further down were the smallest particles such as fine sand. The result was a less compact substrate.

At LCS site 1, the point of groundwater resurgence, the substrate consisted of very coarse, coarse, and medium gravel with some small cobble interspersed. Velocity

was "moderate" at 0.29 m/sec. Dissolved oxygen (D.O.) was lower here than the other sites (6.4 ppm).

Site 2, located at the junction of the two major LCS sources, had a different substrate composed of coarse to medium fine sand and some medium to fine gravel. At this site the water flowed through a wide braided channel. That, along with the stems and roots of the aquatic peppermint that grows throughout the wide upper portion of the springbrook, slowed the velocity (0.23 m/sec, "slight"). D.O. increased to 6.8 ppm.

From LCS site 2 to site 3, the channel narrowed and water flow was unconstrained by peppermint, causing the velocity to double (0.57 m/sec, "swift"). D.O. was at its highest for the three sites (7.0 ppm). Here, the substrate was composed of large pieces of gravel (very coarse and coarse) with some cobble interspersed, small gravels and sand intermingled.

LCS site 4 and 6 had similar substrate consisting of mainly very coarse gravel with coarse and medium gravel, and some small cobble. Water velocity was moderate at 0.40 m/sec. D.O. at the lower sites was higher at 8.2-8.6 ppm. The substrate yielded readily to the sampler.

Site 5 of LCS, at the pools edge, had a "slight" velocity (0.21 m/sec) and a substrate consisting of mostly coarse and medium gravel along with various grades of sand. There was little substrate compaction at this site.

Site 1 at PCS, a limnocrane, had a very slight water velocity (0.05 m/sec). The substrate was almost entirely sand with some silt. D.O. was relatively low at 6.5 ppm.

Located in the narrow channel below the limnocrene pool, PCS site 2 had a moderate water velocity (0.30 m/sec) and D.O. increased to 7.0 mg/l. With the increased velocity, a lot of the sand was washed further downstream exposing substrate of mostly coarse and medium gravel, with some fine and very fine gravel and sand. Immediately below the gravelly surface the substrate was highly compacted.

A large downed cottonwood lay across the channel below site 2 causing the velocity to slow (0.17 m/sec, "slight") at PCS site 3. The substrate consisted of mostly sand particles and silt which settled out due to the reduced velocity. There were a few exposed pieces of cobble and coarse gravel. D.O. increased to 7.6 mg/l.

At PCS site 4 approximately 53 meters downstream and immediately below the confluence with the wet-weather creek, particle size changed substantially and D.O. increased to 9.1 mg/l. Site 4 had moderate velocity (0.40 m/sec) and the substrate was mostly coarse and very coarse gravel with some medium to fine gravel and cobble. The substrate was still somewhat compacted.

The velocity at site 5, located in a pool averaged only 0.18 m/sec ("slight"). D.O. averaged 9.4 mg/l. The gravel substrate, much less compacted here, consisted of smaller pieces, mostly coarse and medium with some fine and very fine.

Finally at PCS site 6, the channel narrowed causing the velocity to increase (0.56m/sec, "swift"). D.O. averaged 9.5 mg/l. The substrate was mainly very coarse, coarse, and medium gravel with interspersed sand. The substrate was not very compacted and yielded readily to the benthic sampler.

Physicochemical Data. Comparing upstream to downstream, mean temperature was nearly the same at both LCS and PCS (Table 1). Although monthly variation downstream ($CV=7\%$) was greater than upstream ($CV=3\%$) at LCS the temperature never fell below 12°C nor rose above 17°C . PCS upstream (12.7°C) and downstream (13.1°C) temperatures were very similar and had little variation within the year ($CV=5\%$). PCS was considerably cooler than LCS and the mean water temperature was cooler than the ambient mean air temperature of 15°C .

Dissolved oxygen levels were greater for the downstream sites at both springbrooks (Table 1). Variation in monthly oxygen was greater at the source (CV : LCS up= 12% , down= 6% ; PCS up= 13% , down= 6%). The upstream monthly measurements at LCS did not correlate ($r=0.51$, $p>0.10$) with the downstream samples although PCS upstream and downstream were similar in variation ($r=0.75$, $p<0.05$).

The pH was lower upstream than downstream at both springbrooks (Table 1). Variations in pH measurements at upstream and downstream reaches were correlated at PCS ($r=0.75$, $p<0.05$), but were not at LCS ($r=0.52$, $p>0.10$).

Mineral and nutrient levels were average or below average compared to other springs in north-central Tennessee (Tables 1 and 2). Upstream and downstream levels were very similar. The only obvious difference between the two springs was hardness (CaCO_3) which was greater at PCS yet was still below the regional average. Total dissolved carbon was similar to other findings of second and third order streams in LBL (Carla Johnson, pers. comm.).

Table 1. Physicochemical data (means and ranges) for upstream (UP) and downstream (DOWN) sites of Lost Creek Spring (LCS) and Pryor Creek Spring (PCS), October 1988-October 1989.

Parameter	Sites			
	LCS UP	LCS DOWN	PCS UP	PCS DOWN
Temp.(°C) range	14.7 (3%)* (14.2-15.8)	14.9 (7%) (12.5-16.4)	12.7 (5%) (11.6-13.8)	13.1 (5%) (12.1-13.8)
O ₂ (ppm) range	6.6 (12%) (5.2-8.3)	8.3 (6%) (7.0-10.0)	7.0 (13%) (5.5-9.0)	9.3(6%) (6.5-9.0)
pH(median) range	6.6 (3%) (6.1-6.9)	6.8 (3%) (6.4-7.4)	6.6 (4%) (5.9-7.0)	6.8 (5%) (6.2-7.5)
Fe (ppm) range	0.22 (52%) (0-0.32)	0.27 (12%) (0.24-0.33)	0.28 (17%) (0.26-0.39)	0.29 (14%) (0.25-0.37)
SO ₄ (ppm) range	2.1 (32%) (1.2-3.6)	2.9 (47%) (1.8-5.8)	3.5 (38%) (1.3-6.5)	4.2 (29%) (3.0-7.0)
Ca (ppm) range	34.0 (17%) (24-40)	33.5 (21%) (20-40)	35.3 (51%) (10-57)	36.1 (47%) (13-57)
Mg (ppm) range	3.1 (80%) (0-5.8)	3.4 (70%) (0-5.6)	1.9 (101%) (0-4.7)	1.9 (112%) (0-5.4)
CaCO ₃ (ppm) range	91.6 (24%) (55-112)	91.8 (35%) (32-114)	112.7 (28%) (51-142)	97.0 (45%) (39-142)
NO ₃ (ppm) range	0.21 (164%) (0-0.94)	0.16 (178%) (0.03-0.96)	0.22 (204%) (0.05-1.57)	0.20 (211%) (0.04-1.32)
Ortho-PO ₄ ^b (ppm)	0.097		0.024	
TDC ^c (ppm)	0.40	0.55	0.73	0.55
Discharge (m ³ /hr)	157 (17%) (105-209)	295 (52%) (147-694)	62 (47%) (24-138)	78 (41%) (31-149)

* Coefficient of variation (CV) as percent = $(s^2/\text{mean}) \times 100$

^b Analysis done by Hancock Biological Station, May 1989

^c TDC=total dissolved carbon analysis, done by Hancock Biological Station, July 1990

Table 2. Average, minimum and maximum values (ppm) of mineral and nutrients in water from springs in north-central Tennessee (Piper 1932).

Mineral	Average	Minimum	Maximum
Fe	0.6	0.02	4.6
SO ₄	10.9	3.7	31.0
Ca	49.0	8.6	93.0
Mg	6.3	4.0	14.0
NO ₃	1.9	0.2	8.0
CaCO ₃	139.0	31.0	272.0

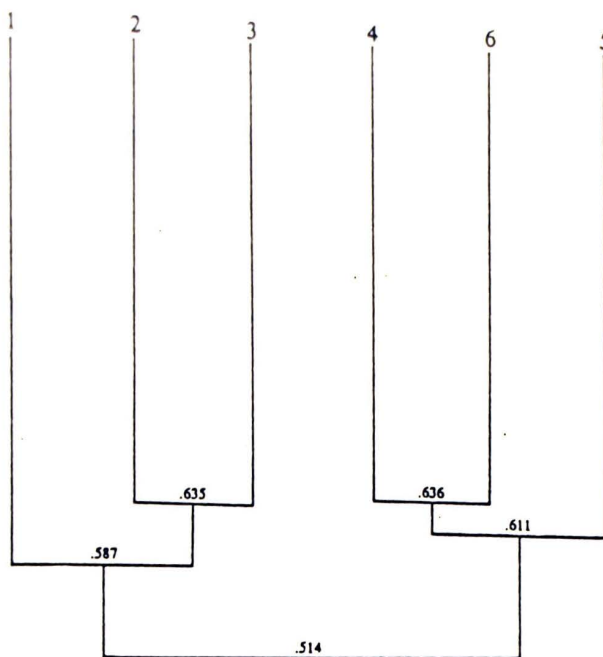
Macroinvertebrate Analysis

Community Similarity. Jaccard's coefficient of similarity determines similarities between communities based on the presence or absence of shared taxa. It demonstrated that at both springs, sites 1, 2, and 3 (upstream) are more similar to each other than they are similar to sites 4, 5, and 6 (downstream) and that the downstream sites are more similar to each other than they are to the upstream sites (Figure 8). Morisita's index also considers the presence or absence of shared taxa as a determination of similarity but also incorporates in the calculation the abundances of each of those taxa. It found similar results at LCS with upstream and downstream sites clustering. At PCS, sites 4, 5, and 6 cluster together while 3, 2, and 1 cluster progressively less closely with the lower sites (Figure 9). Densities of some of the abundant taxa were very different among the three PCS upstream sites. For example oligochaete density, 28% of the upstream samples, varied 98% among the three sites. Most of the oligochaetes (68%) were found in site 1, 27% at site 3, and only 5% in site 2.

Total Density. Total capture during the sampling year from 80 samples was 31,335 individuals at LCS and 54,492 individuals at PCS. The difference between upstream and downstream macroinvertebrate densities was substantial (Figure 10). The mean density of LCS upstream, $2.7 \times 10^4/\text{m}^2$, was significantly greater than the $1.0 \times 10^4/\text{m}^2$ downstream ($p \leq 0.001$). PCS upstream mean density of $4.9 \times 10^4/\text{m}^2$ was also significantly greater than the downstream density of $1.5 \times 10^4/\text{m}^2$ ($p < 0.05$).

Comparing the two streams (Figure 11), LCS macroinvertebrate sample densities were relatively more consistent over time than they were in PCS. Coefficients of

A



B

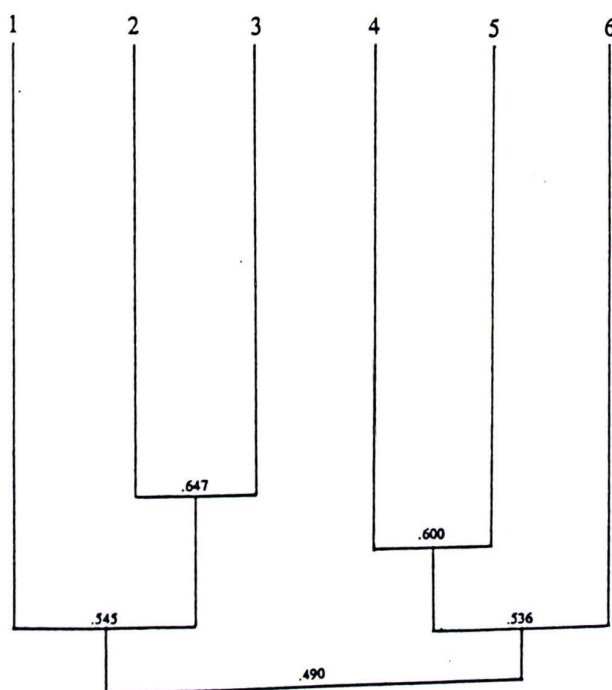


Figure 8. Jaccard's coefficient of community similarity for six sampling sites, November 1988 to September 1989. A. Lost Creek Spring. B. Pryor Creek Spring.

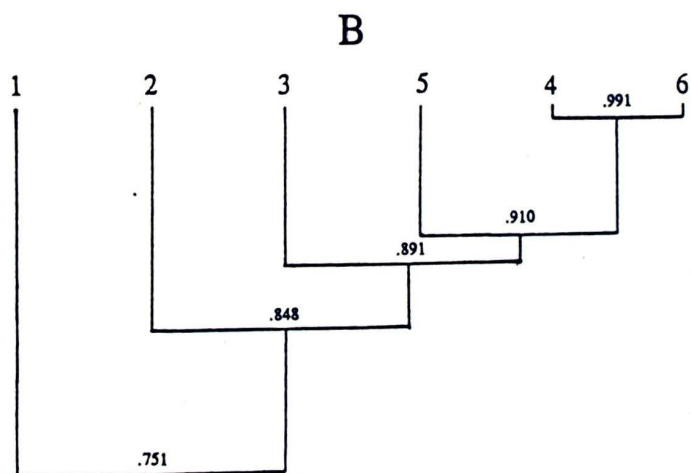
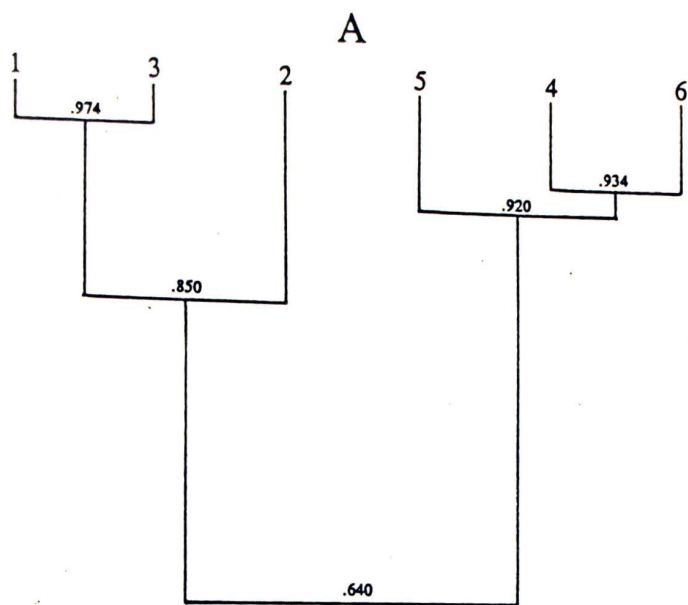


Figure 9. Morisita's index of community similarity for six sampling sites, November 1988 to September 1989. A. Lost Creek Spring. B. Pryor Creek Spring.

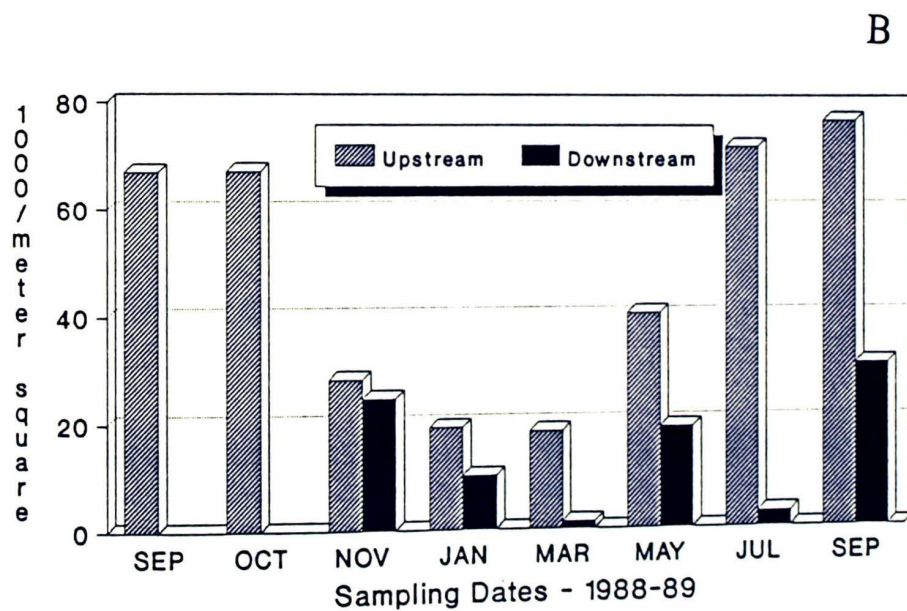
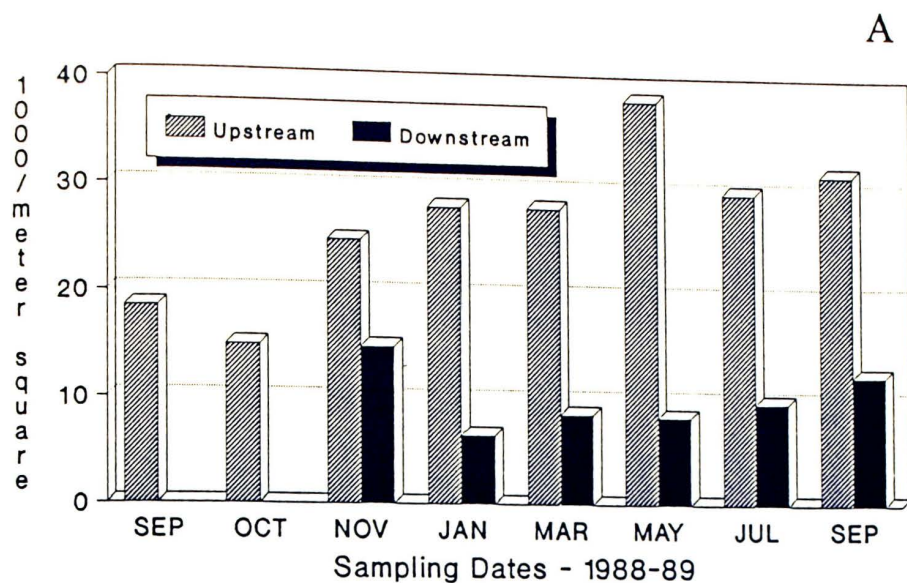


Figure 10. Comparison of benthic macroinvertebrate densities from upstream and downstream sites. A. Lost Creek Spring. B. Pryor Creek Spring.

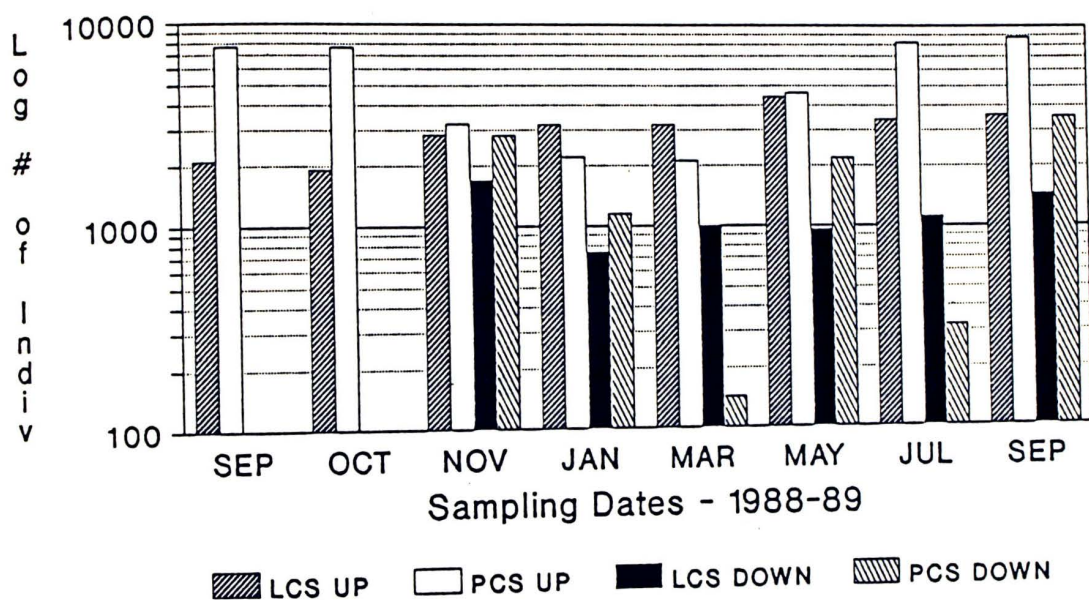


Figure 11. Comparison of total number of individuals captured per sample date from upstream (UP) and downstream (DOWN) sites of Lost Creek (LCS) and Pryor Creek Spring (PCS).

variation (CV) were high for PCS and relatively low for LCS. LCS upstream densities (Figure 10) ranged from $1.5 \times 10^4/\text{m}^2$ in October to $3.8 \times 10^4/\text{m}^2$ in May (CV=15%) and downstream densities ranged from $0.65 \times 10^4/\text{m}^2$ in January to $1.5 \times 10^4/\text{m}^2$ in November (CV=30%). These monthly densities were not significantly different ($p > 0.10$) over the year for either upstream or downstream sites. PCS upstream densities (Figure 10) ranged from $1.8 \times 10^4/\text{m}^2$ in March to $7.7 \times 10^4/\text{m}^2$ in September 1989 (CV=61%) and downstream densities ranged from $0.12 \times 10^4/\text{m}^2$ in March to $3.1 \times 10^4/\text{m}^2$ in September 1989 (CV=81%). Unlike LCS, this variation was significantly different over time at both upstream ($p < 0.05$) and downstream ($p < 0.01$) sites.

Nonemergent and Emergent Densities. The density of the nonemergent macroinvertebrate group was much greater upstream than downstream at both streams ($p < 0.001$ LCS; $p < 0.05$ PCS; Table 3). An average of 80.3% of the nonemergent macroinvertebrates was found upstream at LCS and 77.3% in the upstream samples at PCS. However, the emergent macroinvertebrates were not significantly different between upstream and downstream (at LCS, 52.4% up vs. 47.6% down, $p > 0.70$; at PCS, 58.8% up vs. 41.2% down, $p > 0.60$).

The nonemergent macroinvertebrates accounted for the greatest percentage of the total individuals captured from the upstream sites in both spring streams (86% in both, range=78-93% in LCS, range=74-97% in PCS) (Figure 12 and 13). The difference between densities of nonemergent and emergent macroinvertebrates was significant (LCS $p < 0.001$; PCS $p < 0.01$). While downstream, nonemergent macroinvertebrates were not a significantly greater ($p > 0.10$) percentage of the population at LCS (Figure 14)

Table 3. Density (individuals/m²) of nonemergent and emergent invertebrates per sampling date for upstream (UP) and downstream (DOWN) sites of Lost Creek Spring (LCS) and Pryor Creek Spring (PCS).

DATE	Nonemergent				Emergent			
	LCS		PCS		LCS		PCS	
	UP	DOWN	UP	DOWN	UP	DOWN	UP	DOWN
NOV	23,140	11,860	27,439	18,570	1,737	2,921	842	6,140
JAN	25,912	5,132	18,316	7,947	2,175	1,368	912	2,123
MAR	21,982	4,825	16,509	790	6,105	3,736	1,877	456
MAY	32,333	5,544	30,982	16,438	6,175	2,789	9,482	2,675
JUL	25,263	5,456	53,333	2,544	4,447	4,281	18,465	263
SEP	27,702	5,509	73,754	18,351	3,842	7,173	3,088	12,579
Mean	26,055	6,388	36,722	10,773	4,080	3,711	5,778	4,037
%	80.3	19.7	77.3	22.7	52.4	47.6	58.8	41.2
UP/DN	p<0.001*		p<0.05*		p>0.70		p>0.60	

*Anova significant at $p < 0.05$

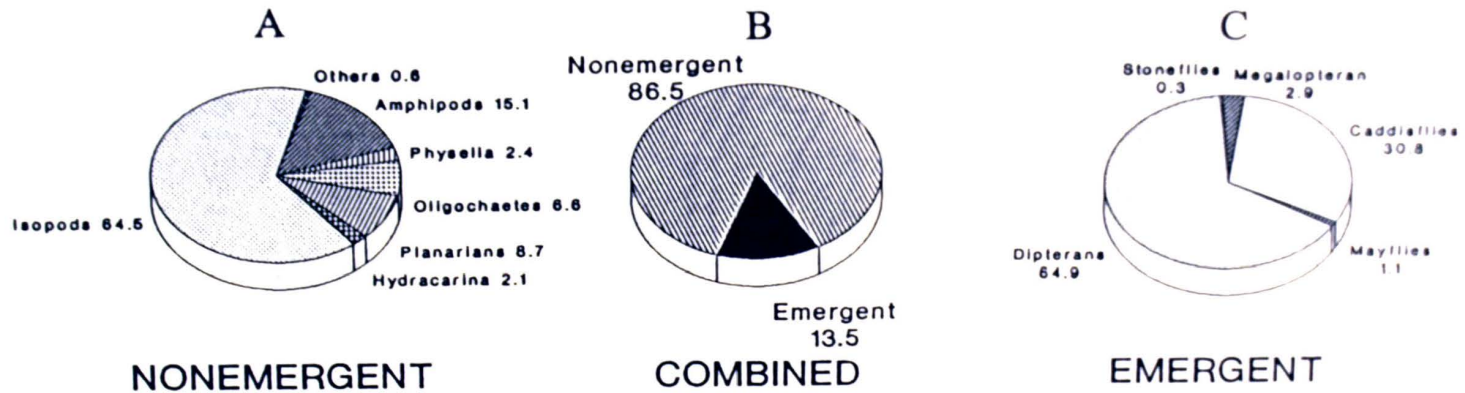


Figure 12. Mean percent abundance of individuals in all samples from the upstream sites of Lost Creek Spring, November 1988 to September 1989. A. Nonemergent macroinvertebrates. B. All macroinvertebrates combined. C. Emergent macroinvertebrates.

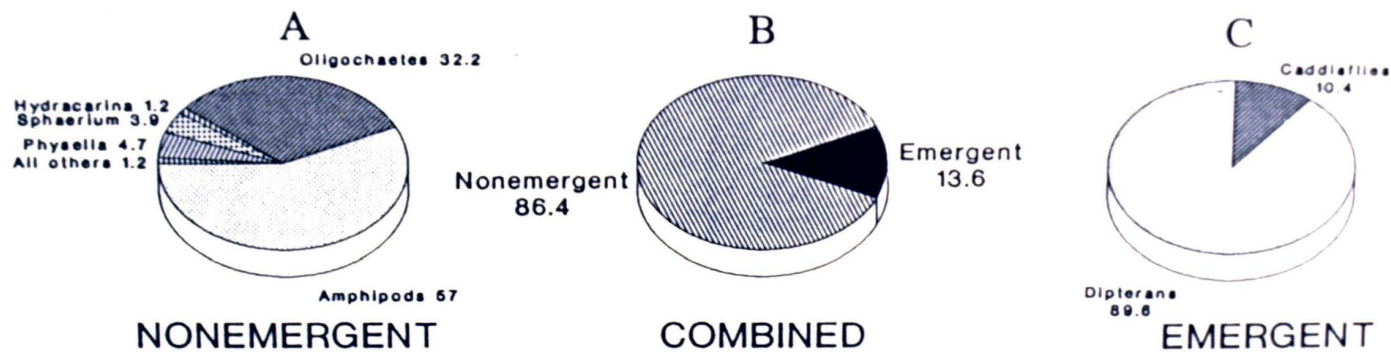


Figure 13. Mean percent abundance of individuals in all samples from the upstream sites of Pryor Creek Spring, November 1988 to September 1989. A. Nonemergent macroinvertebrates. B. All macroinvertebrates combined. C. Emergent macroinvertebrates.

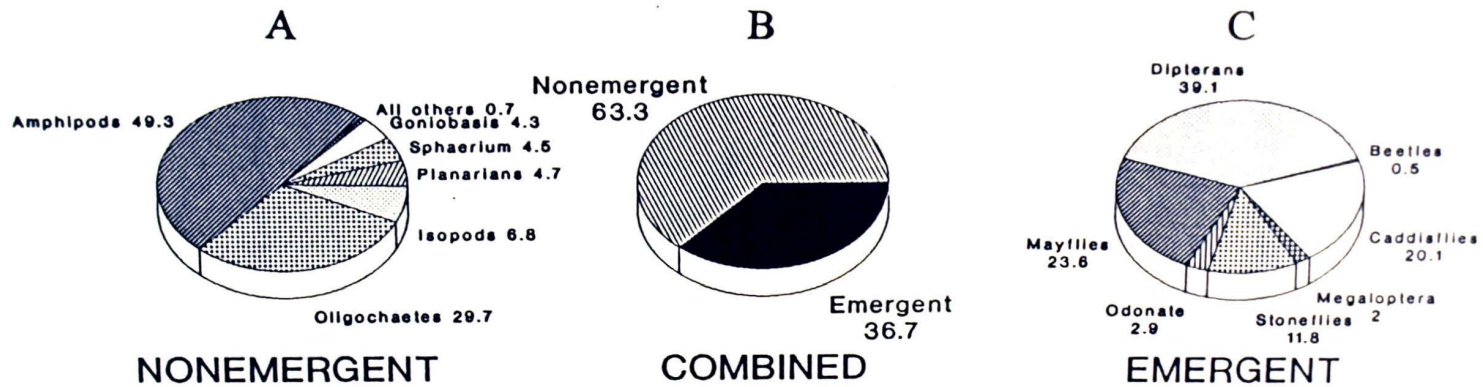


Figure 14. Mean percent abundance of individuals in all samples from the downstream sites of Lost Creek Spring, November 1988 to September 1989. A. Nonemergent macroinvertebrates. B. All macroinvertebrates combined. C. Emergent macroinvertebrates.

with a relative abundance of 63.3% (range 43-80%). However, at PCS downstream (Figure 15), the nonemergent macroinvertebrates maintained the numerical dominance over the emergent macroinvertebrates ($p < 0.05$) comprising 72.8% of the relative abundance (range 59-91%).

The isopod *Lirceus fontinalis* constituted 64.5% (range=62.0-71.0%) of the nonemergent invertebrates upstream at LCS (Figure 12) ranging from 14,148 to 20,105/m². The amphipod *Gammarus pseudolimnaeus* was second in dominance at 11.2% (range=7.3-24.6%) with densities ranging from 1,535 to 5,193/m². Five taxa (*L. fontinalis*, *G. pseudolimnaeus*, *Phagocata gracilis*, *Crangonyx* spp., and Oligochaeta) made up 95% of the relative abundance of the nonemergent individuals captured over the year. The monthly densities are presented in Figure 16.

Figure 17 demonstrates the correlation ($r=0.74$ $p < 0.05$) between *L. fontinalis* and *G. pseudolimnaeus*. Although it appears that the two taxa were equally abundant at the same time of the year, they were equally important (*G. pseudolimnaeus* (42%) and *L. fontinalis* (58%)) at only site 2 where the habitat was dissimilar to the other two upstream sites and appeared to favor *G. pseudolimnaeus*. At sites 1 and 3, *L. fontinalis* was dominant (94% and 91%, respectively, of the relative abundance).

Of the nonemergent macroinvertebrates captured at LCS downstream (63.3% of the total macroinvertebrates), amphipods (1,280 to 6,035/m²), primarily *G. pseudolimnaeus*, and oligochaetes (877-3,088/m²) were most abundant accounting, respectively, for 49.3% (range=23.5-53.1%) and 29.7% (range=18.2-53.3%) of the total captures. *Lirceus fontinalis* decreased to 6.8% (range=0-11.2%) of the nonemergent

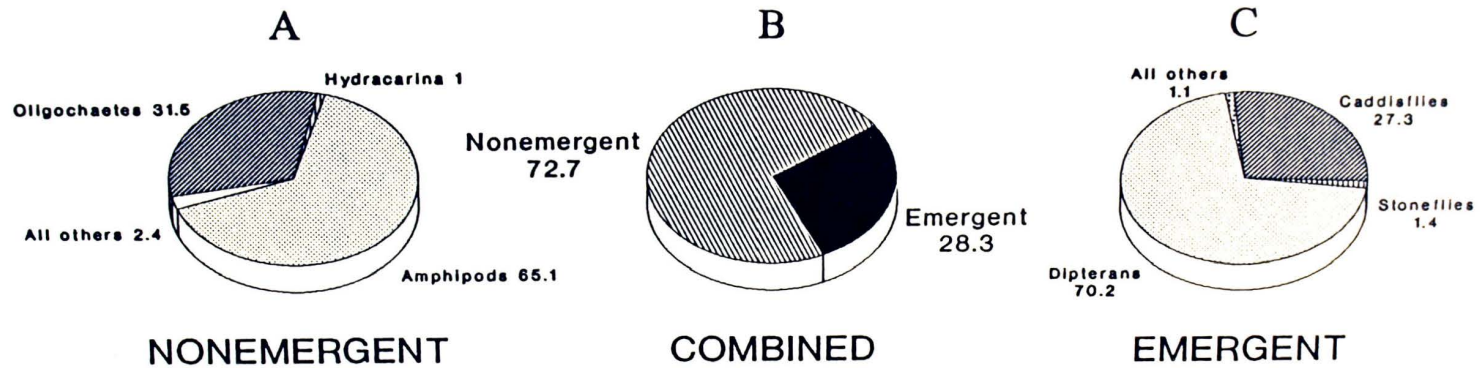


Figure 15. Mean percent abundance of individuals in all samples from the downstream sites of Pryor Creek Spring, November 1988 to September 1989. A. Nonemergent macroinvertebrates. B. All macroinvertebrates combined. C. Emergent macroinvertebrates.

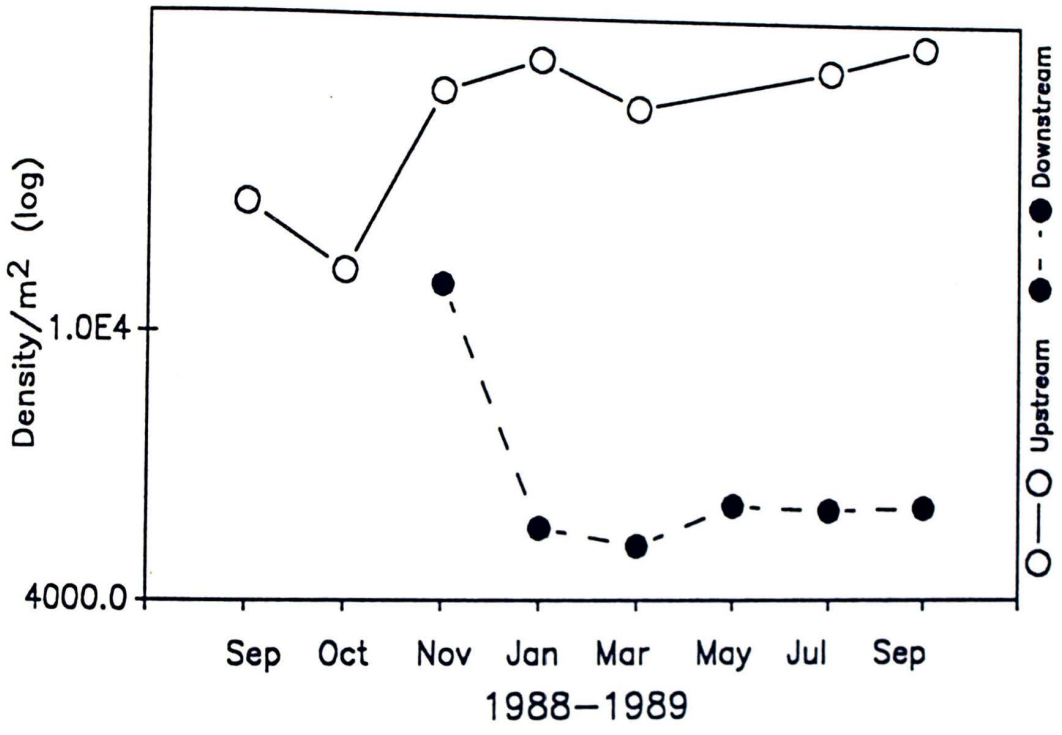


Figure 16. Monthly sample densities of nonemergent macroinvertebrates for upstream and downstream sites at Lost Creek Spring.

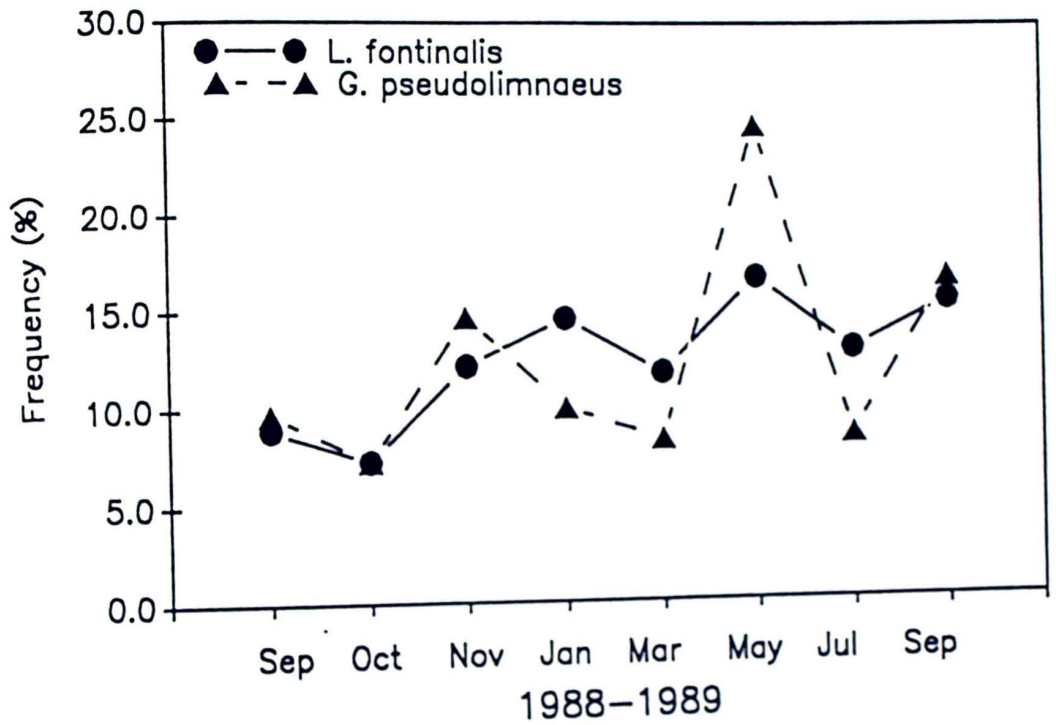


Figure 17. Frequency values of *Lirceus fontinalis* and *Gammarus pseudolimnaeus* were positively correlated ($r=0.742$, $p<0.042$) at Lost Creek Spring upstream. Frequency = percent of total capture/sampling period.

macroinvertebrates. In the downstream sites, the nonemergent group was at its greatest density in November (Figure 16) although for most of the year it remained considerably lower than at the upstream sites. Most of the year the two dominant taxa (amphipods and oligochaetes) appeared to be in competition. Their frequencies (Figure 18) were negatively correlated, although not significantly at the 0.05 level ($r = -0.78$, $p = 0.10$).

The nonemergent faunas of PCS at both upstream (Figure 13) and downstream sites (Figure 15) were comprised of amphipods, mainly *G. pseudolimnaeus* and *Gammarus minus*, and oligochaetes. *Gammarus minus* was more abundant (83 %) at site 2 averaging 15,763/m². They were nearly equally abundant at site 3 (12,500/m² for *G. minus*, 15,428/m² for *G. pseudolimnaeus*). *Gammarus pseudolimnaeus* dominated (71 %) at site 1 with 10,395/m². Overall, the amphipods made up 57 % (range = 35.1-69.8 %) of the nonemergent abundance upstream and 65.1 % (range = 42.3-85.3 %) downstream. Oligochaetes comprised 32.2 % (range = 23.5-52.4 %) of the abundance upstream and 31.5 % (range = 8.4-75.7 %) downstream.

Fahy (1972) found gammarids in an isothermic spring to be acyclic. There appeared to be a cyclic pattern to their abundance in this study at least at the upstream sites. The three dominant taxa were found most abundantly upstream in September and October, 1988, and again in September 1989 (Figure 19). They were most abundant downstream in the fall months of November and September 1989. The greatest percentage of the peak in May (Figure 19) was oligochaetes, comprising 76 % of the relative abundance with a density of 12,436/m².

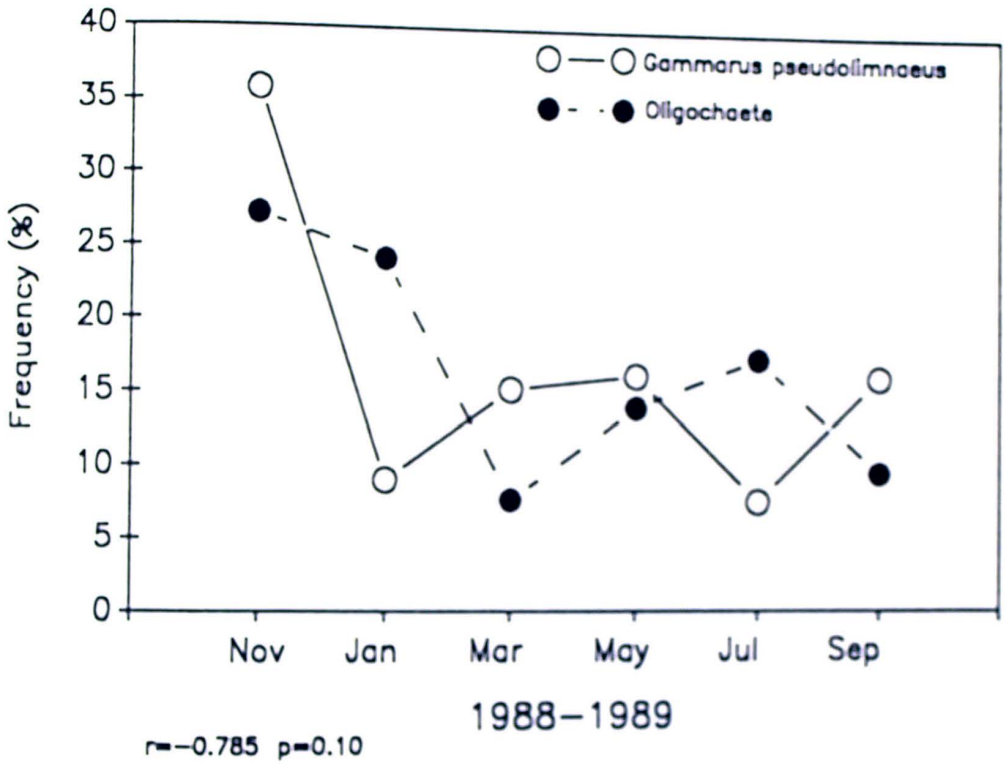


Figure 18. Frequency values of *Gammarus pseudolimnaeus* and oligochaetes, the two dominant taxa from Lost Creek Spring downstream sites.

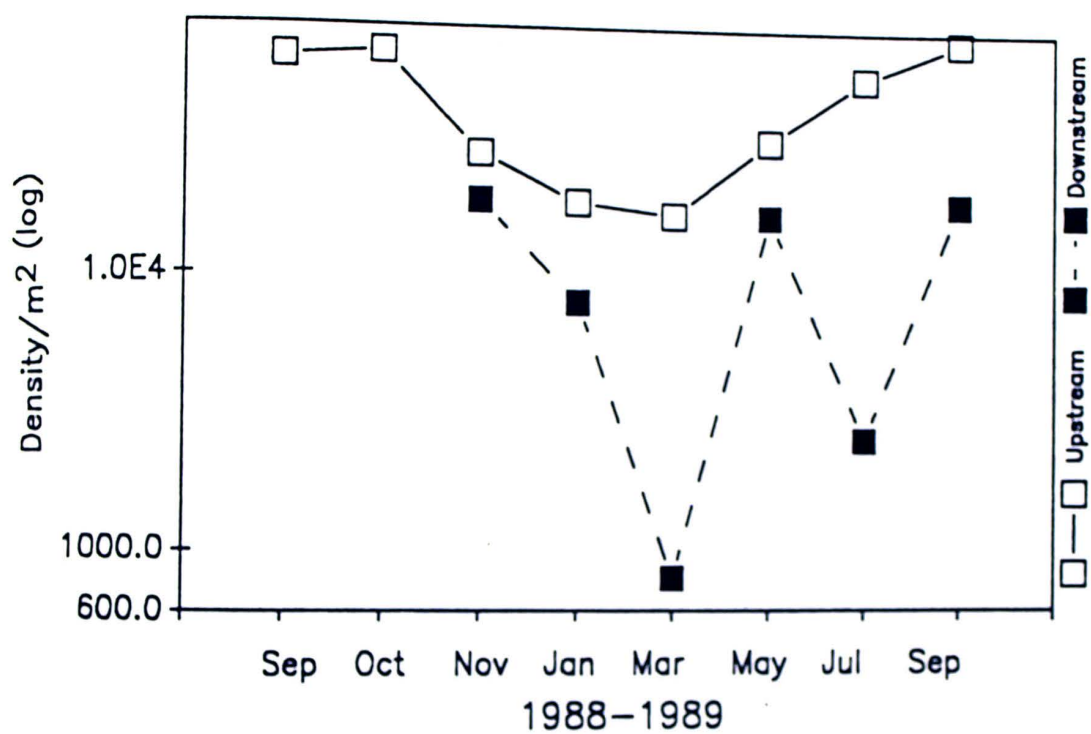


Figure 19. Monthly sample densities of nonemergent macroinvertebrates for upstream and downstream sites at Pryor Creek Spring.

The low densities for nonemergent macroinvertebrates during March and July (Figure 19) were correlated with spates that occurred during those months. Oligochaete densities recovered to 12,436/m² by May from a low of 281/m² in March taken after the March washout. By the September sampling, *G. minus* densities had increased to 13,509/m² from the low 1,719/m² sampled in July after the spate which had occurred that month.

Similar to the nonemergent group, only a few emergent taxa made up a large percentage of the upstream emergent group abundance. The density of the emergent macroinvertebrates varied considerably over the sampling period at LCS upstream ranging from 1,737 to 6,105 individuals/m² (Figure 20). All of the samples were dominated ($\geq 20\%$) by one taxon. Most of the relative abundance of individuals (Figure 12) were dipterans (64.9%) mainly chironomid midge larvae (91%). Three taxa, *Tvetenia*, *Parametriocnemus*, and *Rheotanytarsus*, accounted for 66.7% of the chironomid abundance. The orthocladiine *Tvetenia* dominated the upstream samples ($> 30\%$) in October (947/m²), November (544/m²), and May (2,192/m²). *Ochrotrichia eliaga* and *Glossossoma nigrior* made up 73% of the trichopterans which comprised 30.8% of the emergent macroinvertebrates. *Ochrotrichia eliaga* comprised 42.8% of the sample in March (2,614/m²), and *G. nigrior* appeared in high percentages twice; 21.7% (623/m²) in September 1988 and 32% (1,421/m²) in July. Megalopterans, stoneflies, and one ephemeropteran taxon were present, but in relatively low abundance (Figure 12). Increases in emergent abundance occurred through the spring months with a decrease in

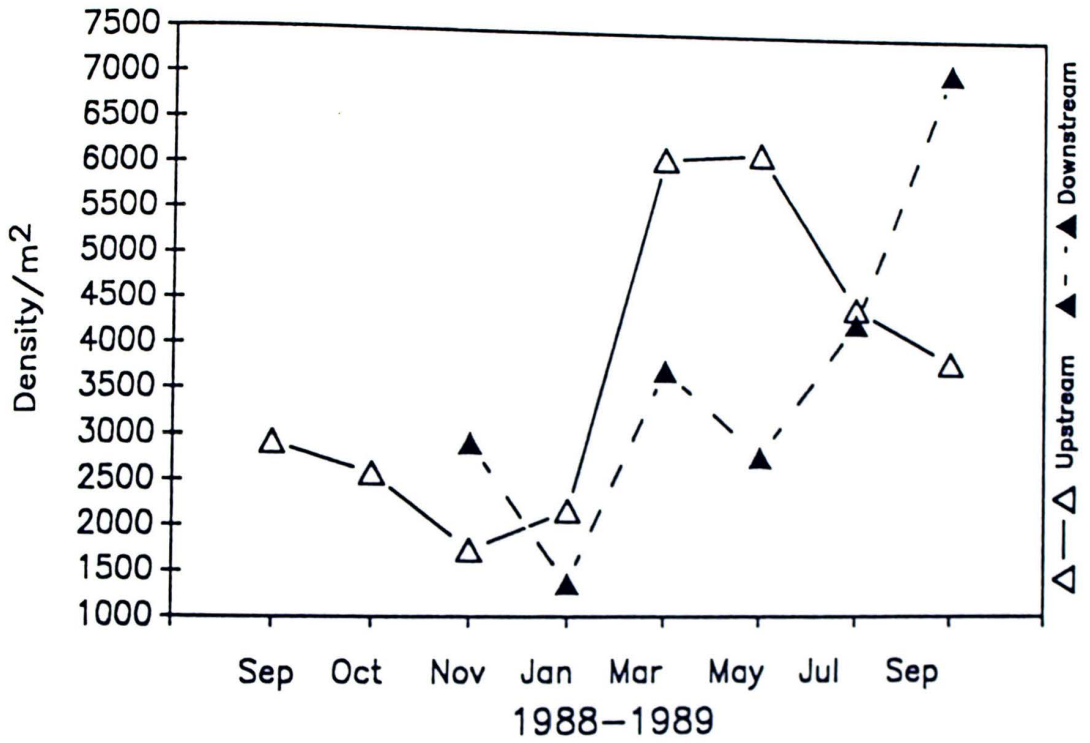


Figure 20. Monthly sample densities of emergent macroinvertebrates for upstream and downstream sites at Lost Creek Spring.

abundance in July and September which may correspond to emergence of the winged aerial adults.

Downstream at LCS, the emergent invertebrate abundances were divided more evenly among the orders (Figure 14). Most of the samples consisted of $\leq 20\%$ of any one taxon. Dipterans comprised only 39.1% and the chironomids were a smaller percentage (75%) of the dipterans than they were upstream. Compared to upstream, several orders increased in abundance including mayflies (23.6%, up from 1.1%) and stoneflies (11.8% up from 0.3%). Beetles and odonates were present in downstream samples, but were not found upstream. The mayfly *Baetis* was the most commonly sampled emergent invertebrate at 17%, comprising 37.9% (2,702/m²) of the September sample. The chironomid *Rheotanytarsus* made up 14.1% (2,140/m²) of the January sample. Otherwise, the chironomids were less dominant per sample than upstream. The stonefly *Leuctra*, which was not captured upstream, was the dominant taxa captured in the downstream samples for March at 20% (754/m²) and July at 15% (649/m²). Abundances peaked in September for the emergent group (Figure 20).

At PCS upstream (Figure 13), the total relative abundance of the emergent groups was dominated by Diptera (89.6%), mostly chironomids (93% of Diptera). Two genera, *Micropsectra* and *Chaetocladius* accounted for 65.6% of the chironomids. One or the other or both genera made up a large percentage of the emergent abundance in all samples except in two where the ceratopogonid *Bezzia* comprised 46% (421/m²) of the sample in January and 56% (1,053/m²) in March. The caddisfly *Pycnopsyche* comprised the greatest percentage (29.2%) of capture (246/m²) in November, coinciding with leaf

fall. *Pycnopsyche* constructs its early instar case from leaf disks and later converts the case to one composed of rock fragments, bark, and twigs (Wiggins 1977). In the springbrook, many sycamore leaves were observed to have dime-sized holes. Similar to the emergence group at LCS upstream, a spring and summer rise in emergent abundance is noted in the curve (Figure 21) followed by a decrease in September corresponding to emergence of winged adults.

While still dominant among the emergent macroinvertebrates at PCS downstream, Diptera decreased in importance (89.6% upstream to 70.2% downstream) compared to upstream. Stoneflies, megalopterans, beetles and mayflies were found downstream and had not been found upstream. Caddisflies increased in abundance to 27.3% from 10.4% upstream. The caddisfly *Diplectrona*, found downstream only, was 58% of the trichopteran abundance. It comprised the main portion (43%) of the overall emergent invertebrate abundance in November. The two occurrences of very low density (Figure 21) of the downstream emergent fauna correspond to March and July spates. Many of the taxa dropped off to zero abundance during these two months and yet were able to reestablish themselves by the next sampling period of May and September. *Rheotanytarsus* had the most dramatic increase in density from no individuals captured in the July sample to 6,105/m² in September 1989 sample (Figure 22). The genus was far less common or absent in the other four sampling periods. Other Diptera, including the blackfly genus *Simulium*, and the chironomid genera *Cricotopus* and *Chaetocladius*, were found in samples for the first time after the washouts (Figure 22). Similar to

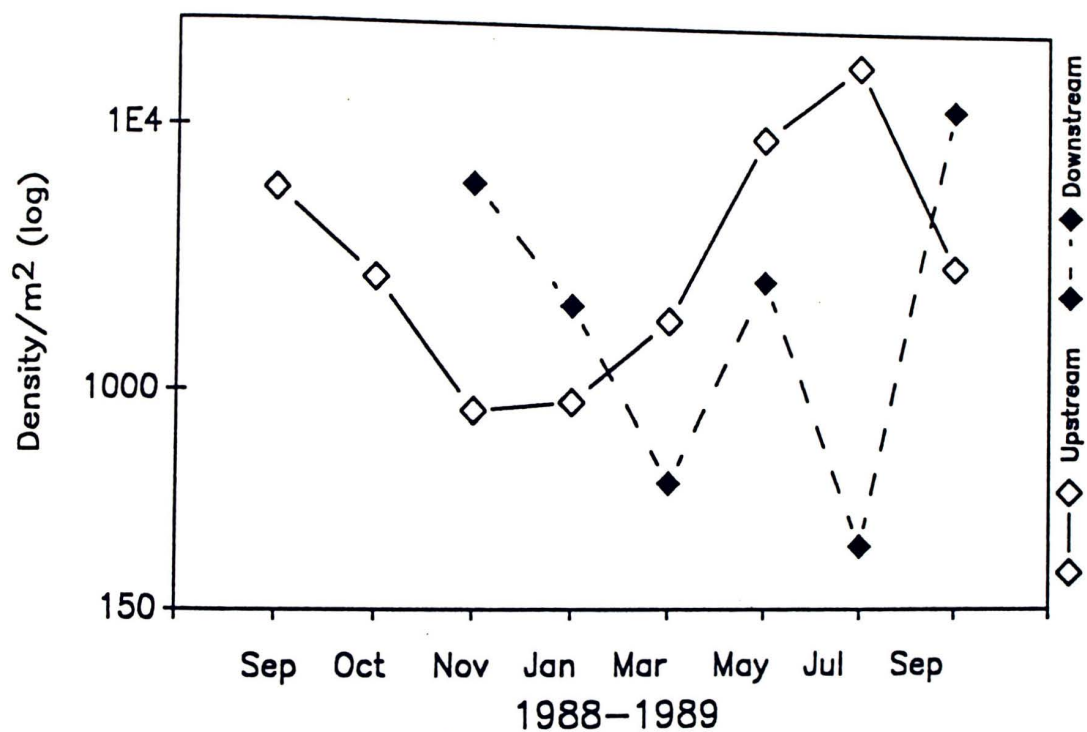


Figure 21. Monthly sample densities of emergent macroinvertebrates for upstream and downstream sites at Pryor Creek Spring.

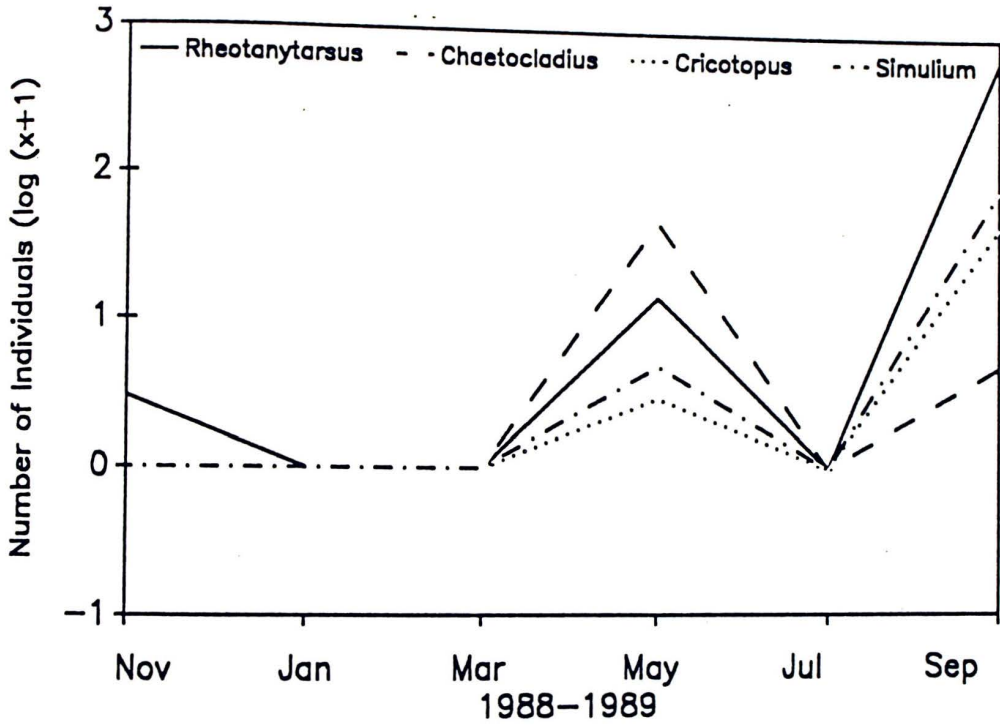


Figure 22. Number of individuals of four genera of dipterans considered to be opportunistic colonizers sampled from downstream sites of Pryor Creek Spring.

LCS downstream, density increased to the greatest numbers in September, 1989 (Figure 21).

Taxa Composition. A combined total of 117 taxa (51 families) were found in LCS and PCS; 53 of those taxa (28 families) common to both springs (Appendix II). Ninety taxa representing 43 families occurred at LCS (Appendix III) and 81 taxa in 39 families were identified from PCS (Appendix IV). The greatest number of taxa were found downstream in both springs (Table 4). LCS downstream had 79 taxa compared to 56 (59 with preliminary samples) upstream. PCS downstream had 69 taxa compared to 41 (45 with preliminary samples) upstream. This increase in taxa number was entirely due to emergent taxa. The number of nonemergent taxa was 12 both upstream and downstream at LCS, and decreased from 15 upstream to 13 downstream at PCS.

Figures 23-26 depict the taxa composition broken down into emergent and nonemergent groups. Although the nonemergent group was the greatest part of the density, they comprised a small percentage of the taxa; 14% at LCS and 20% at PCS. Of the 47 emergent taxa at LCS upstream (Figure 23), 51% were chironomid genera. Other diptera including crane flies (3 genera), dance flies (2 genera), dioxid midges (one genus) and black flies (3 genera) made up 21% of the emergent taxa. Eight genera of caddisflies comprised 17%. Two genera each of megalopterans and stoneflies and one genus (*Baetis*) of mayflies made up the remaining 10%. PCS upstream (Figure 24) had very similar results with most of the 30 emergent taxa consisting of chironomids (53%) and other diptera (31%). Two genera of caddisflies and one genus of Hemiptera were found.

Table 4. Number of taxa captured per sampling date for upstream (UP) and downstream (DOWN) sites at Lost Creek Spring (LCS) and Pryor Creek Spring (PCS)

DATE	LCS		PCS	
	UP	DOWN	UP	DOWN
NOV	33	41	20	44
JAN	27	32	19	23
MAR	31	48	19	18
MAY	27	41	21	31
JUL	36	46	21	17
SEP	29	44	22	29
TOTAL	56	79	41	69

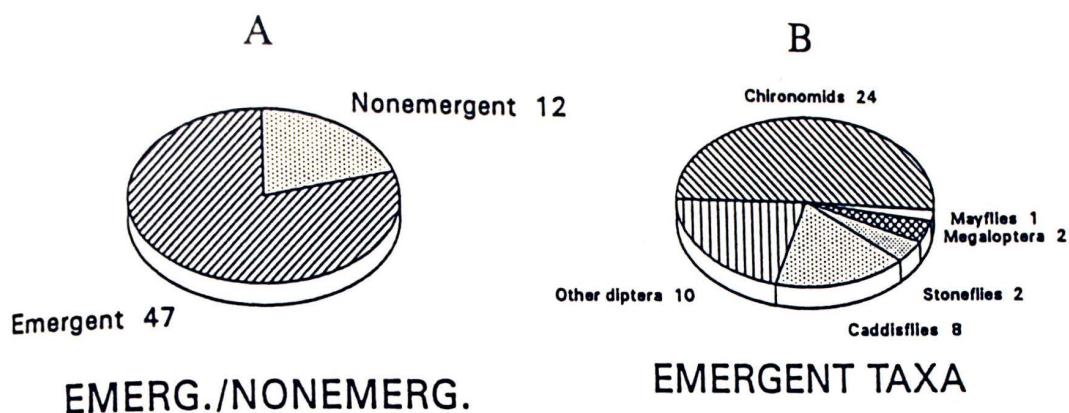


Figure 23. Taxa composition of macroinvertebrates from the upstream sites of Lost Creek Spring, September 1988 to September 1989. A. Number of nonemergent and emergent taxa (59 total taxa). B. Number of emergent taxa (47 total) among mayflies, stoneflies, megalopterans, caddisflies, chironomids and nonchironomid dipterans.

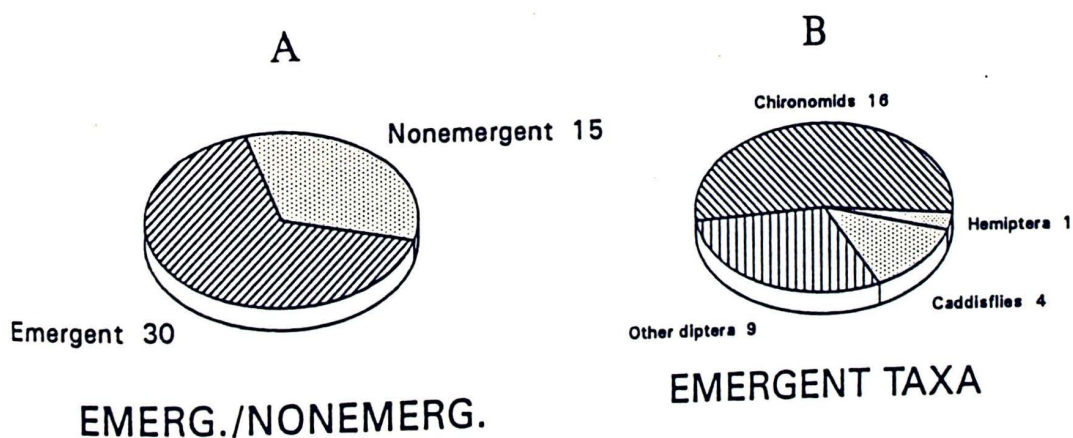


Figure 24. Taxa composition of macroinvertebrates from the upstream sites of Pryor Creek Spring, September 1988 to September 1989. A. Number of nonemergent and emergent taxa (45 total taxa). B. Number of emergent taxa (30 total) among caddisflies, chironomids and nonchironomid dipterans.

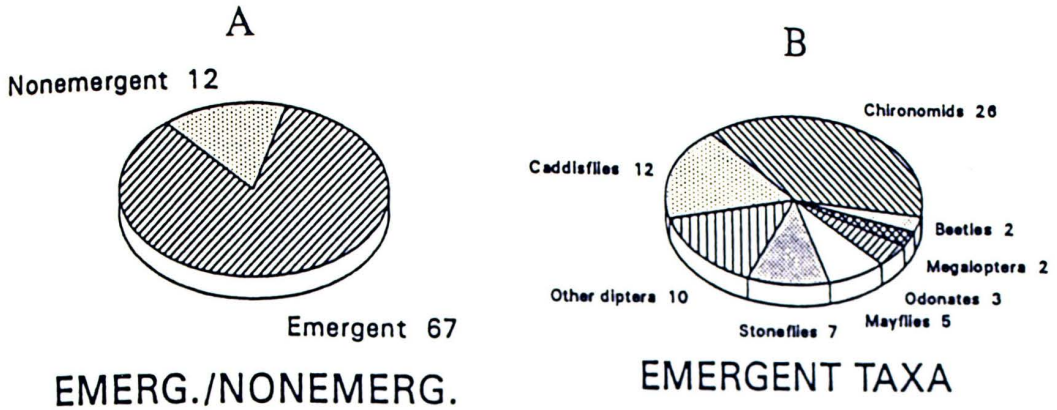


Figure 25. Taxa composition of macroinvertebrates from the downstream sites of Lost Creek Spring, November 1988 to September 1989. A. Number of nonemergent and emergent taxa (79 total taxa). B. Number of emergent taxa (67 total) among mayflies, stoneflies, megalopterans, caddisflies, beetles, odonates, chironomids and nonchironomid dipterans.

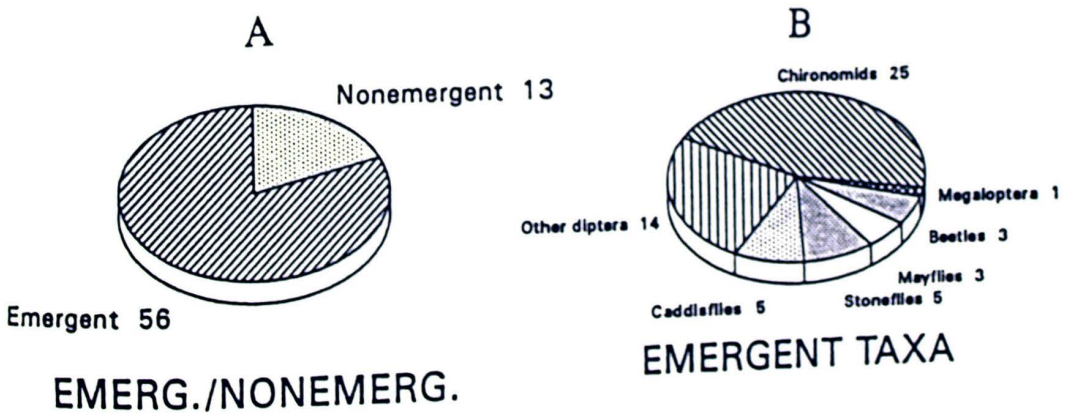


Figure 26. Taxa composition of macroinvertebrates from the downstream sites of Pryor Creek Spring, November 1988 to September 1989. A. Number of nonemergent and emergent taxa (69 total taxa). B. Number of emergent taxa (56 total) among mayflies, stoneflies, megalopterans, caddisflies, beetles, chironomids and nonchironomid dipterans.

Downstream, the emergent density remained nearly the same (Table 3) but the number of emergent taxa increased by 43% to 67 taxa at LCS (Figure 25) and increased 87% to 56 taxa at PCS (Figure 26). In both streams, chironomids remained the most diverse group, but comprised a smaller percentage of the total taxa (39% in LCS; 45% in PCS). Dipterans were also taxa rich, but were a smaller percentage downstream (15% in LCS; 25% in PCS) compared to upstream. Caddisflies increased in number of taxa from eight to 12 in LCS and from four to five in PCS, but increased little in relative percentages at LCS (from 17% to 18%) and decreased at PCS (from 13% to 9%). The number of stonefly and mayfly taxa increased at LCS, while odonates and beetles occurred for the first time. In PCS, many orders occurred only downstream, including stoneflies, mayflies, beetles and megalopterans.

Relative Abundance. A typical community has a few abundant taxa (in terms of number of individuals or biomass) and many rare species (Odum 1971). Many of LCS taxa (59% up; 68% down) were rare (5-49 individuals of the taxon captured) and very rare (<5 individuals captured) in the combined 24 samples upstream or 18 samples downstream (Figure 27). Approximately 25% of the taxa were common (50-249 individuals). At PCS most (60% up; 77% down) of the taxa were rare and very rare (Figure 27).

Frequency of Occurrence. Many of the taxa upstream in both springs (29% LCS; 39% PCS) occurred in only one of the 6 sampling periods. The next greatest percentage of occurrence was for taxa that occurred in all six samples (23% LCS; 24% PCS) (Figure 28). While the greatest percentage of occurrence was in only a single sample

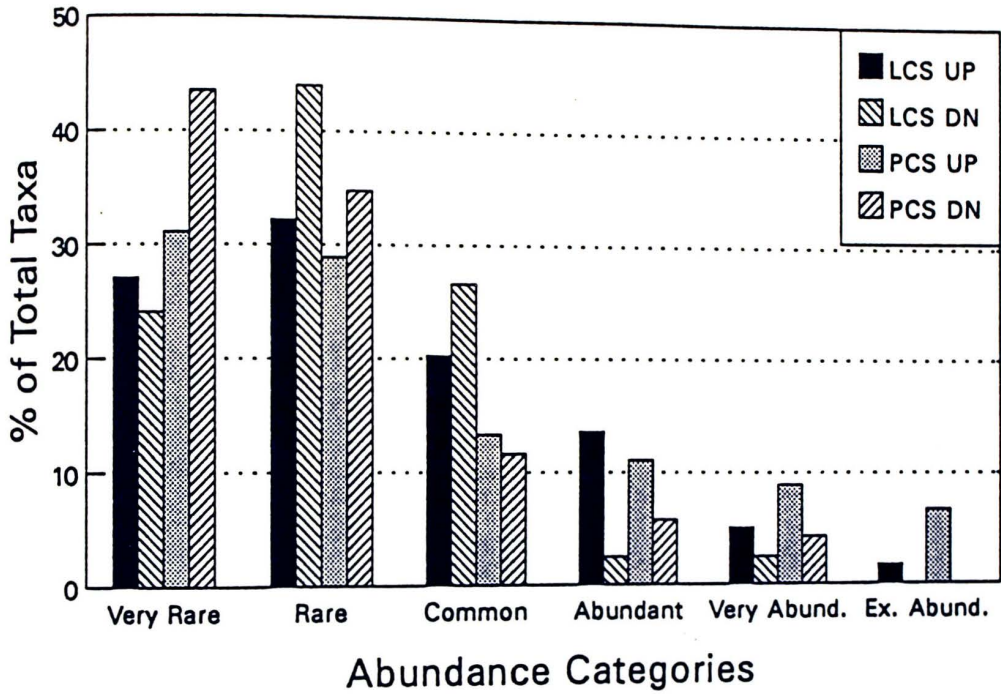


Figure 27. Rarity/abundance distribution of taxa collected based on combined samples for upstream (UP) and downstream (DN) sites of Lost Creek (LCS) and Pryor Creek Spring (PCS). Abundance categories: Very Rare < 5, Rare = 5-49, Common = 5-249, Abundant = 250-1000, Very Abundant = 1000-5000, Exceptionally Abundant > 5000 individuals.

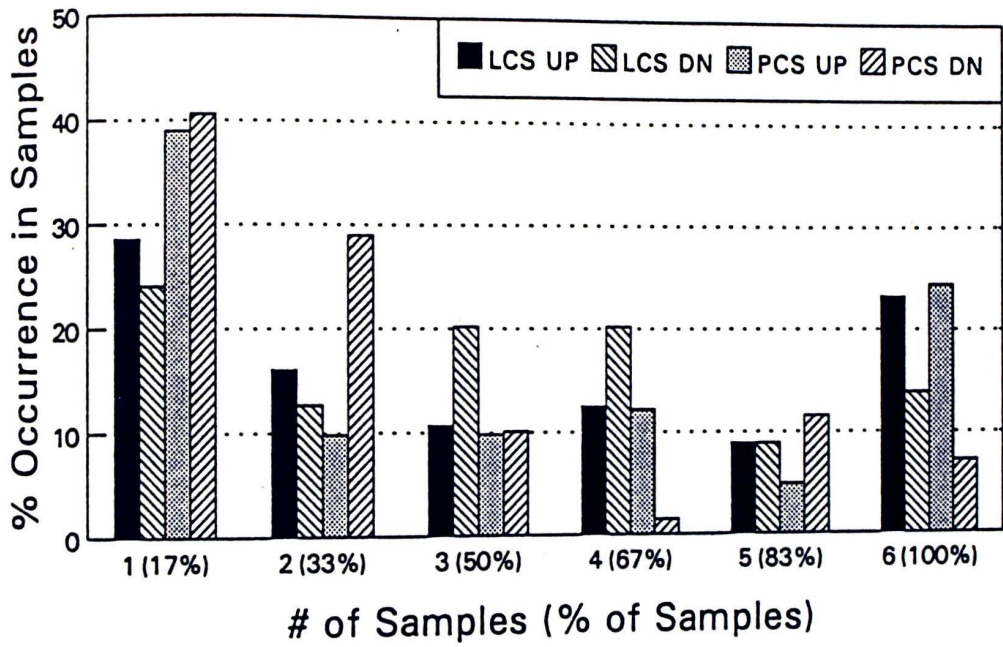


Figure 28. Number of times each taxa was found during the sampling year among the six sampling dates of the total taxa collected at the upstream (UP) and downstream (DN) sites of Lost Creek (LCS) and Pryor Creek Springs (PCS).

(40%) in PCS downstream samples, 24% were found in one sample in LCS downstream. The next greatest percentage of occurrence was in two of the samples at PCS downstream while a large percentage (40%) of LCS taxa were found in three and four samples downstream (Figure 28).

Taxa Diversity. Three diversity measures were used to compare communities: Margalef's taxa richness (R), Shannon's diversity index (H') and Pielou's evenness index (J'). All three indices for LCS were significantly ($p < 0.05$) greater downstream (Figure 29). Diversity averaged 1.74 upstream (range=1.52 to 1.93) and 2.50 downstream (range=2.20 to 2.96) with little variation between sampling dates (CV=10.0% up; =13.5% down). Evenness was lower upstream (mean=0.51; range=0.44 to 0.56) than downstream (mean=0.68; range=0.59 to 0.77), but with little change over the sampling dates (CV=9.5% up; =10.5% down). The evenness curve depicts, in essence, the variation of the nonemergent taxa since these dominate the abundance upstream and downstream. Since richness was mostly due to the emergent taxa, total richness (mean=3.63 up, =5.84 down; range=3.1 to 4.3 up, =4.7 to 6.8 down) represents the emergent group richness curves (Figures 29 and 30). The richness of the nonemergent group was low and nearly the same upstream and downstream. The emergent group downstream had less variation in diversity throughout the sampling periods than upstream (CV=11.8 up; =6.3 down).

The three indices for PCS were more confusing and only Margalef's index was significantly greater ($p < 0.05$) downstream (mean=3.7; range=2.8 to 5.4) than upstream (mean=2.38; range=2.3 to 2.6) (Figure 31). This was predominately due to the

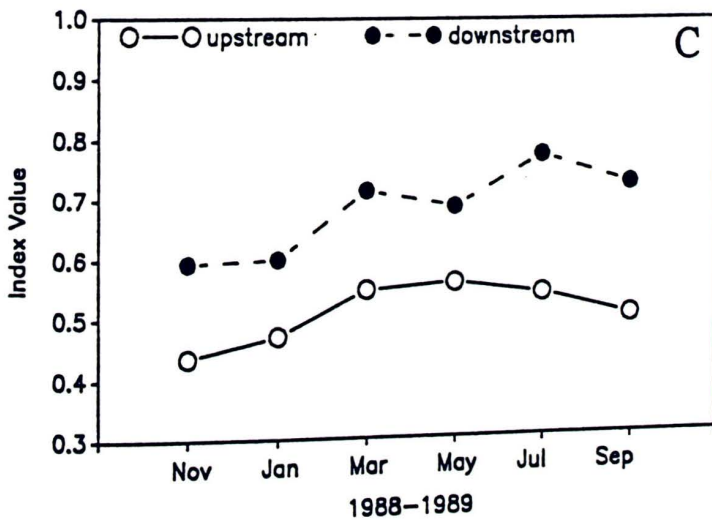
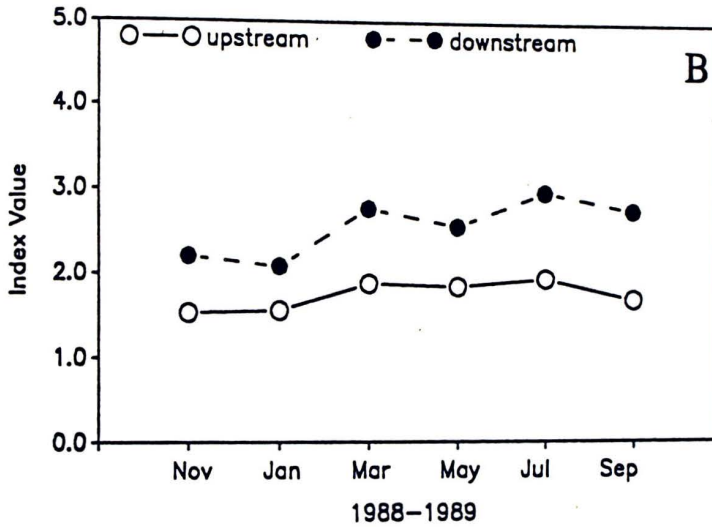
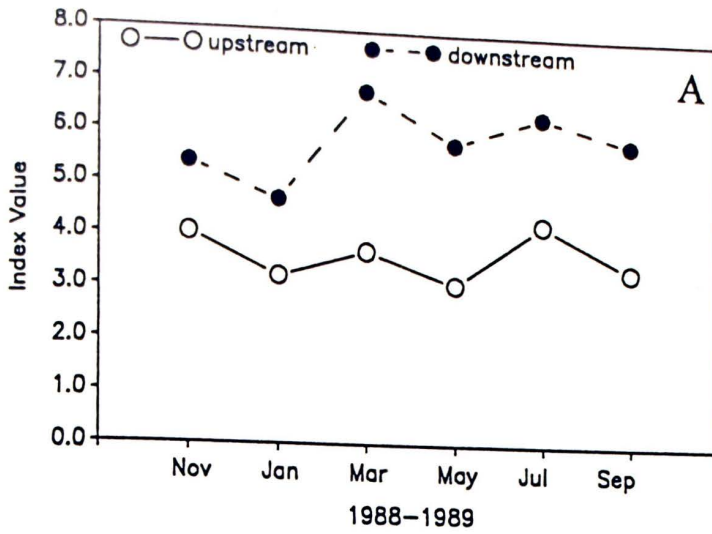


Figure 29. Richness, heterogeneity and evenness in benthic macroinvertebrate samples from upstream and downstream sites at Lost Creek Spring. A. Margalef's taxa richness index. B. Shannon-Weiner diversity index. C. Pielou's evenness index.

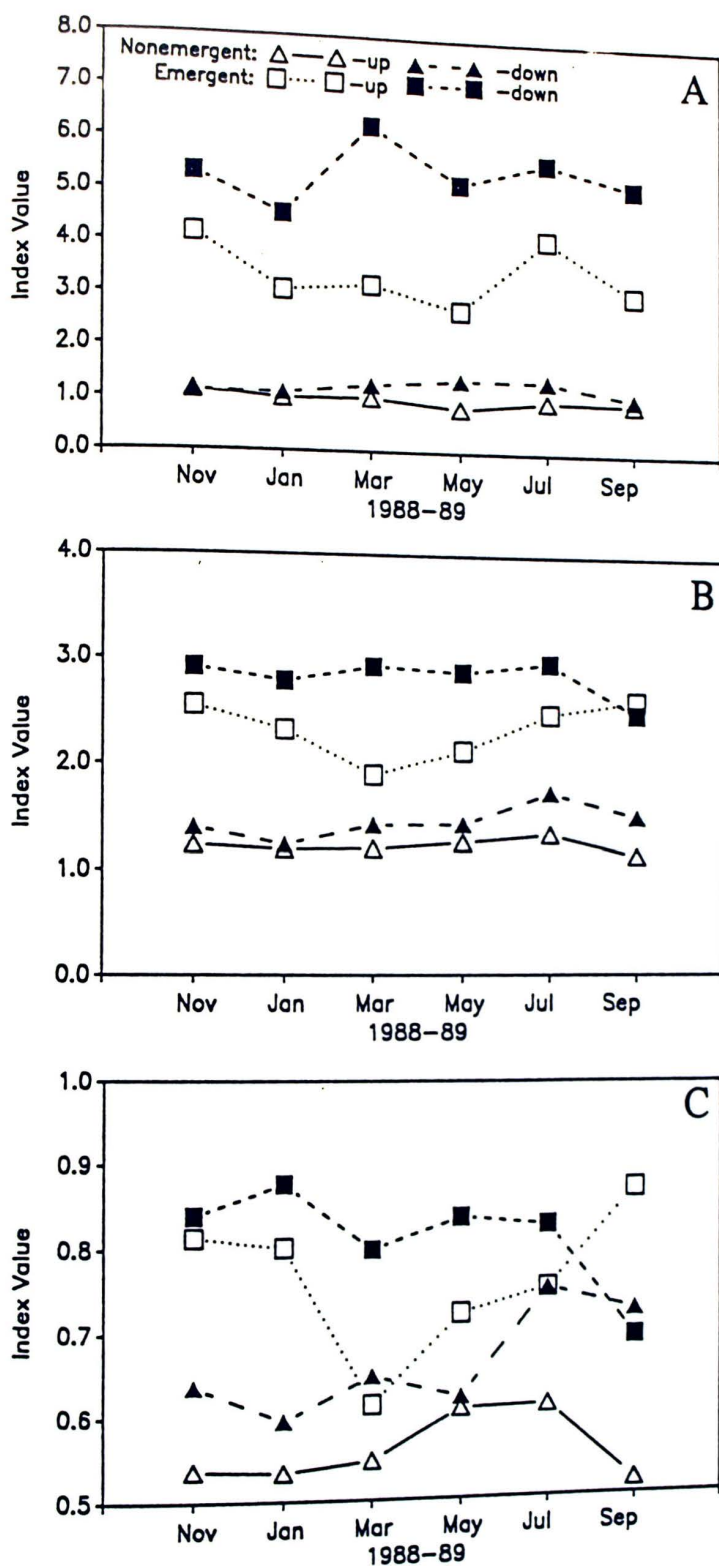


Figure 30. Richness, heterogeneity and evenness of emergent and nonemergent taxa in samples from upstream and downstream sites at Lost Creek Spring. A. Margalef's taxa richness index. B. Shannon/Weiner diversity index. C. Pielou's evenness index.

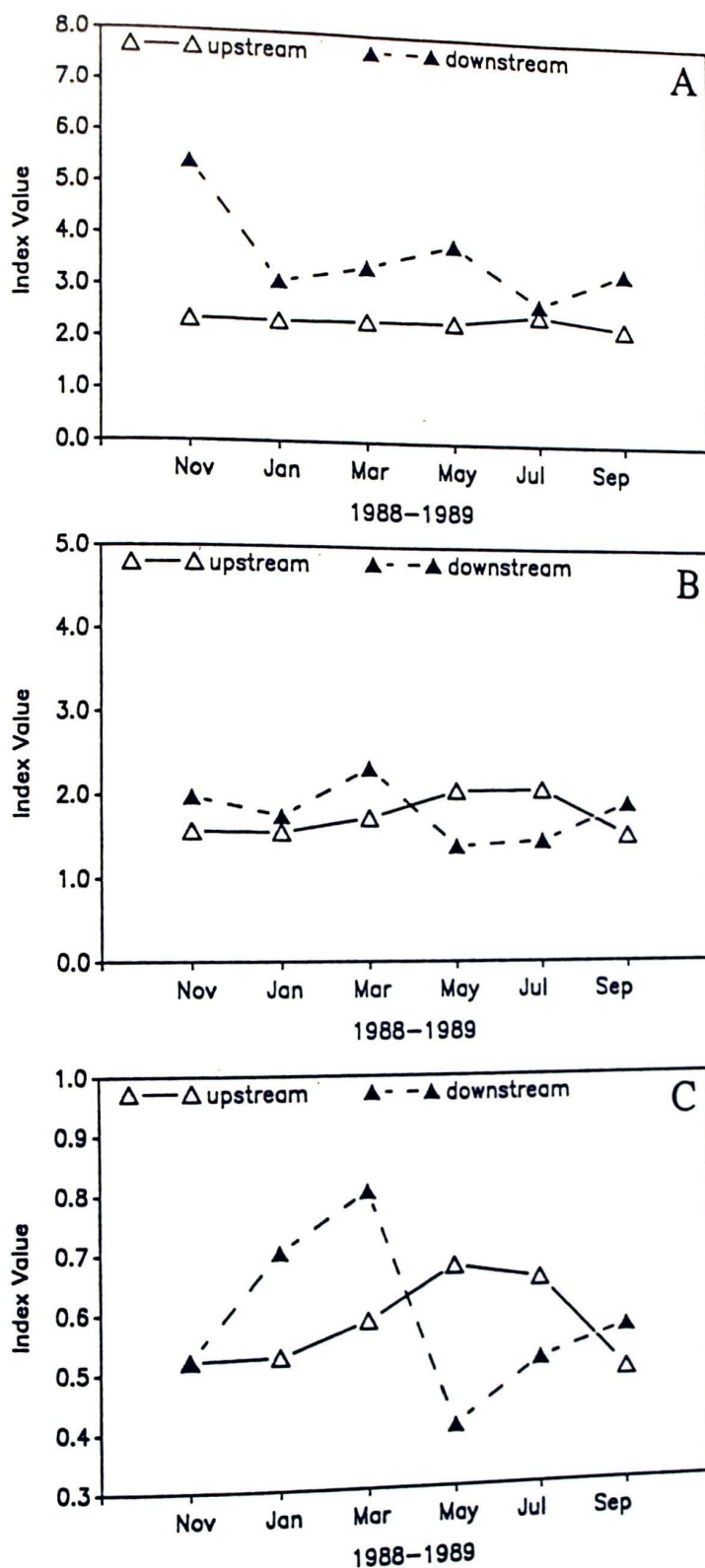


Figure 31. Richness, heterogeneity and evenness in benthic macroinvertebrate samples from upstream and downstream sites at Pryor Creek Spring. A. Margalef's taxa richness index. B. Shannon/Weiner diversity index. C. Pielou's evenness index.

nonemergent group which dominated both upstream and downstream sample density (Table 3) and had higher evenness upstream than downstream (i.e. the density of the few nonemergent taxa present downstream fluctuated 30% over the year compared to upstream which varied little [$CV=8.5\%$]) (Figure 32). Also, nonemergent richness was not significantly different ($p>0.10$) between upstream and downstream (Figure 33). Therefore, the greater nonemergent diversity upstream (mean=1.42; range=1.5 to 2.1) compared to downstream (mean=1.04; range=1.4 to 2.0) was attributable to evenness and not richness (Figure 33).

The emergent group, however, had a greater richness and evenness downstream (R, mean=3.19, range=2.3 to 4.7; J', mean=0.76, range=0.57 to 0.93) than upstream (R, mean=1.82, range= 1.5 to 2.5; J', mean=0.66, range=0.50 to 0.86) (Figure 32 and 33) yielding a greater diversity index value ($p<0.05$) downstream (mean=2.12; range=1.8 to 2.3) than upstream (mean=1.6; range=1.1 to 1.9) with less variation over time ($CV=19.4\%$ up; $=11.3\%$ down). This was surprising since variation in population size was greatest downstream due to spates. However, diversity was not greatly affected.

Longitudinal zonation. Definite zones of habitation existed for many of the taxa. As mentioned above, the stoneflies, mayflies, odonates, and beetles were found downstream but were nearly absent upstream. A few of the taxa of the other orders were captured often enough to determine an upstream or downstream preference. Several of the trichopterans, *Molanna blenda* (100%), *Lepidostoma griseum* (88%), *Diplectrona modesta* (65%), *Glossossoma nigrior* (70%), *Ochrotrichia eliaga* (98%), and *Goera*

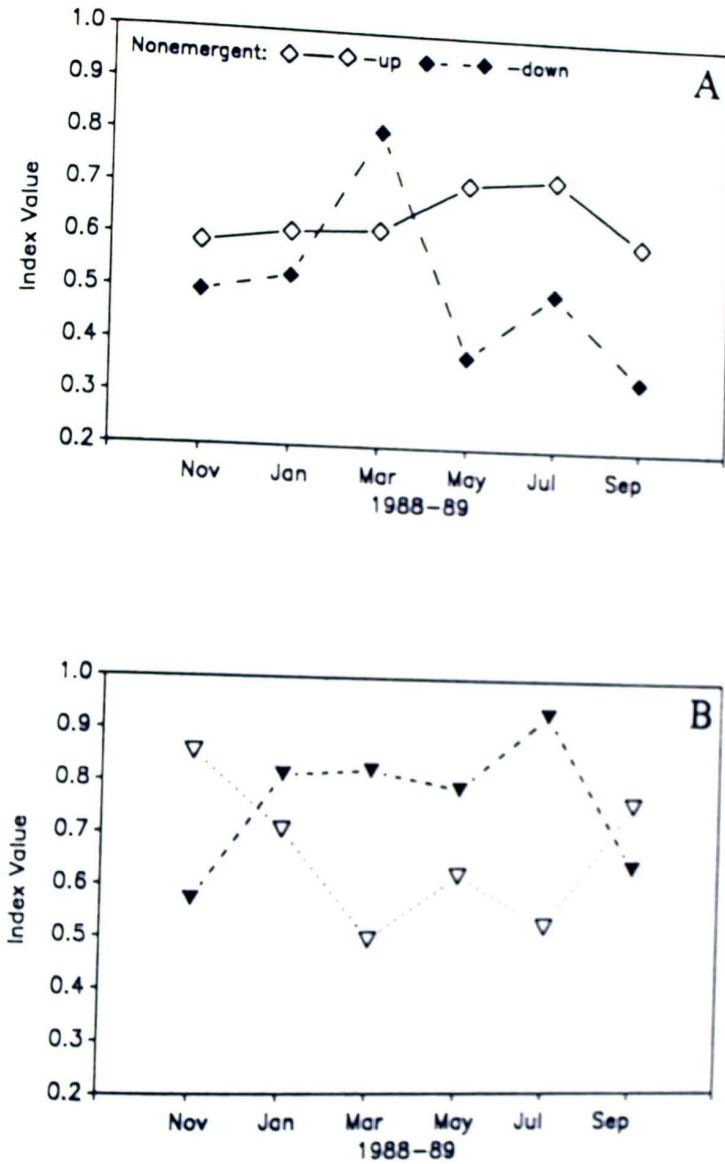


Figure 32. Pielou's evenness of benthic macroinvertebrates from upstream and downstream sites of Pryor Creek Spring. A. nonemergent taxa. B. emergent taxa.

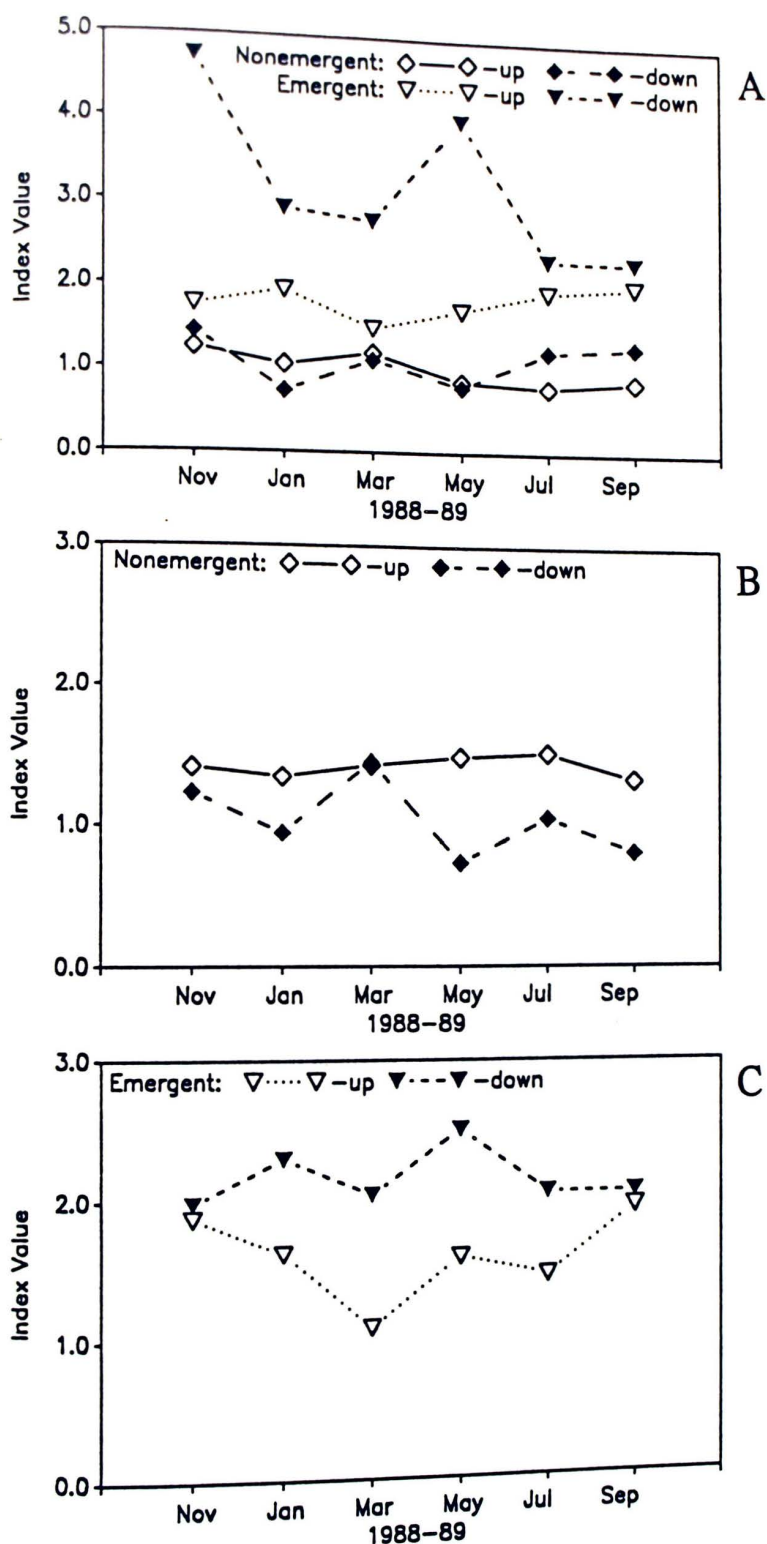


Figure 33. Richness, heterogeneity and evenness in benthic macroinvertebrate samples from upstream and downstream sites at Pryor Creek Spring. A. Emergent and nonemergent, Margalef's taxa richness index. B. Shannon-Weiner diversity index of nonemergent taxa. C. Shannon-Weiner diversity of emergent taxa.

calcarata (83%) were mostly limited to upstream sites at LCS. At PCS, *Oxyethira* sp. was totally (100%) limited to the upstream sites. *Glossossoma nigrior* was found about equally upstream (55%) and downstream (45%). *Diplectrona modesta* and *Rhyacophila* sp. occurred only at the downstream sites at PCS. *Cheumatopsyche oxa*, *Chimarra* sp., *Triaenodes* sp., *Polycentropus* spp., and *Agapetus avitus* inhabited only the downstream sites at LCS.

Of the chironomids, *Dicrotendipes* sp., *Paratendipes* sp., and *Chaetocladius* sp. were found mostly upstream (95-100%) at LCS and PCS. *Parametriocnemus* spp., *Tvetenia* sp., and *Rheotanytarsus* sp. were primarily upstream dwellers at LCS (78-98%) but were found mostly downstream at PCS (84-100%). The reverse was true for *Natarsia* sp. (94% LCS down, 91% PCS up). *Stempellinella* sp. was almost entirely (93%) a downstream dweller at LCS. *Helleniella* sp. was only found downstream at PCS, while *Micropsectra* spp. was found mostly (93%) upstream.

In both springbrooks, the black fly, *Simulium* sp., was entirely limited to the downstream sites while the miniscus fly, *Dixa* sp., was limited to upstream sites. Of the nonemergent taxa, the gastropod, *Physella* sp., was abundant at LCS and PCS upstream sites yet was found not at all downstream at LCS and in small numbers at PCS. *Lirceus fontinalis* was found 98% of the time upstream at LCS. Primarily upstream dwellers at both LCS and PCS were the planarian, *Phagocata gracilis* (88% at both), the water mite, Hydracarina (96% LCS, 80% PCS), and the amphipod, *Crangonyx* sp. (81% LCS, 99% PCS).

Functional Feeding Groups. Collectors-gatherers were the most dominant functional feeding group (ffg) at both LCS and PCS, upstream and downstream (73% LCS, 60% PCS). While the collectors-gatherers remained the largest percentage of the abundance downstream, this group decreased by 82% at LCS and by 11% at PCS from upstream to downstream. Most groups increased substantially from upstream to downstream: collectors-filterers by 295% at LCS and 262% at PCS, shredders by 583% at LCS and 300% at PCS; scrapers by 154% at LCS and 18% at PCS, omnivores increased by 160% at LCS downstream, but staying the same in abundance at PCS. Some ffg's had different distributions with predators remaining about the same up and downstream in abundance at both springs, herbivores decreasing by 16 times downstream at LCS (no herbivores present at PCS), and scavengers increasing by 28% at LCS downstream and decreasing by 21% at PCS downstream (Figure 34 and 36).

Shredders would be expected to be the most prevalent group in these two headwater streams (Cummins et al 1975). Shredders are defined by Merritt and Cummins (1984) as chewers of CPOM while collectors-gatherers are sediment feeders of FPOM. Gammarids were observed on dead leaves that were stripped of all tissues except for the leaf venation. If gammarids were considered as shredders and not collectors-gatherers, the percentage of shredders would increase to 14% at LCS upstream (from 0.6%) and increase to 35% from 4% at LCS downstream. At PCS the number of shredders would increase to 49% from 0.2% upstream and to 48% from 0.8% downstream (Figure 35 and 37).

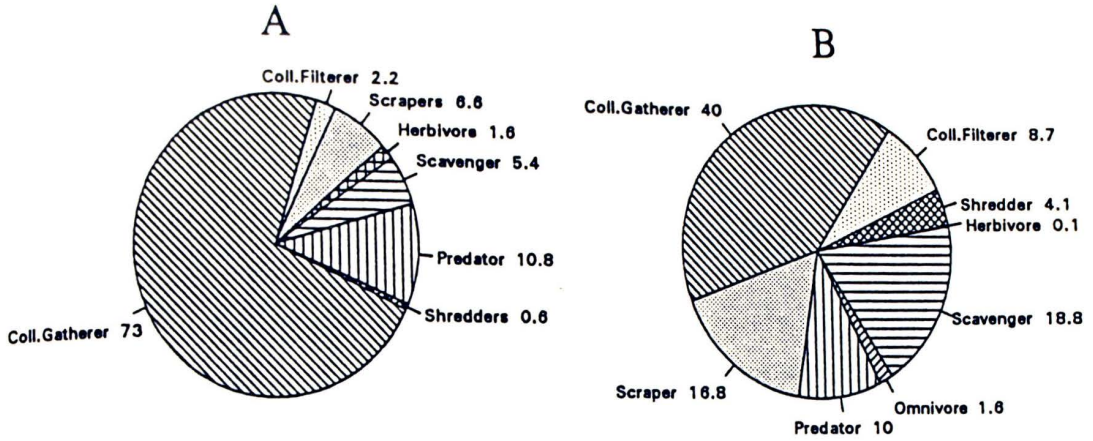


Figure 34. Percent representation of functional feeding groups in all macroinvertebrate samples from Lost Creek Spring, November 1988 to September 1989, with gammarids considered as collectors-gatherers. A. Upstream sites. B. Downstream sites.

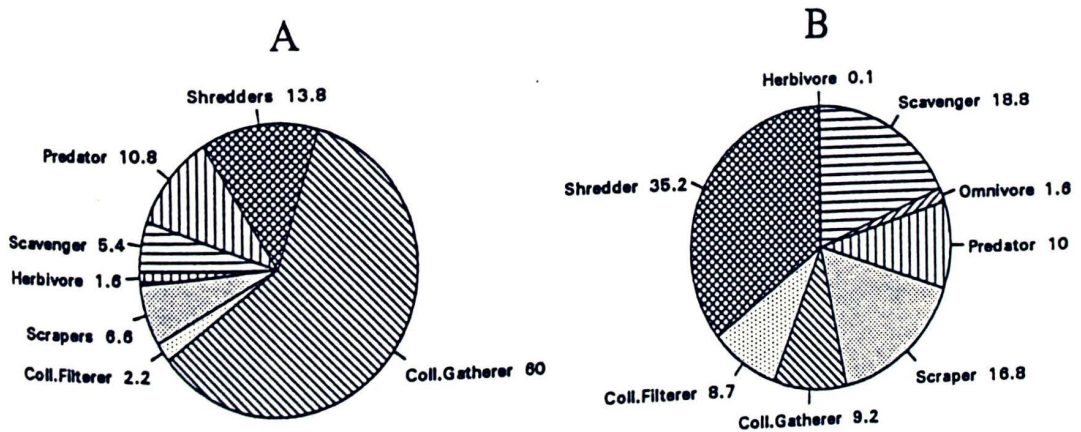


Figure 35. Percent representation of functional feeding groups in all macroinvertebrate samples from Lost Creek Spring, November 1988 to September 1989, with gammarids considered as shredders. A. Upstream sites. B. Downstream sites.

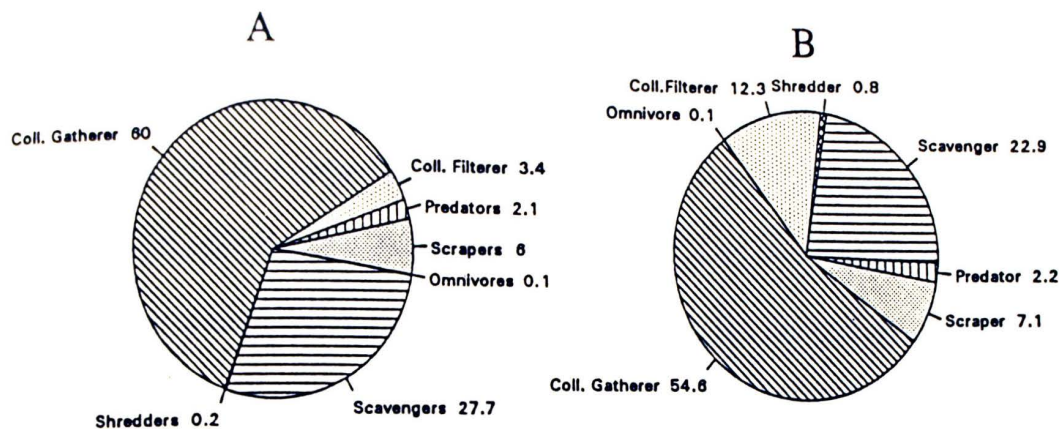


Figure 36. Percent representation of functional feeding groups in all macroinvertebrate samples from Pryor Creek Spring, November 1988 to September 1989, with gammarids considered as collectors-gatherers. A. Upstream sites. B. Downstream sites.

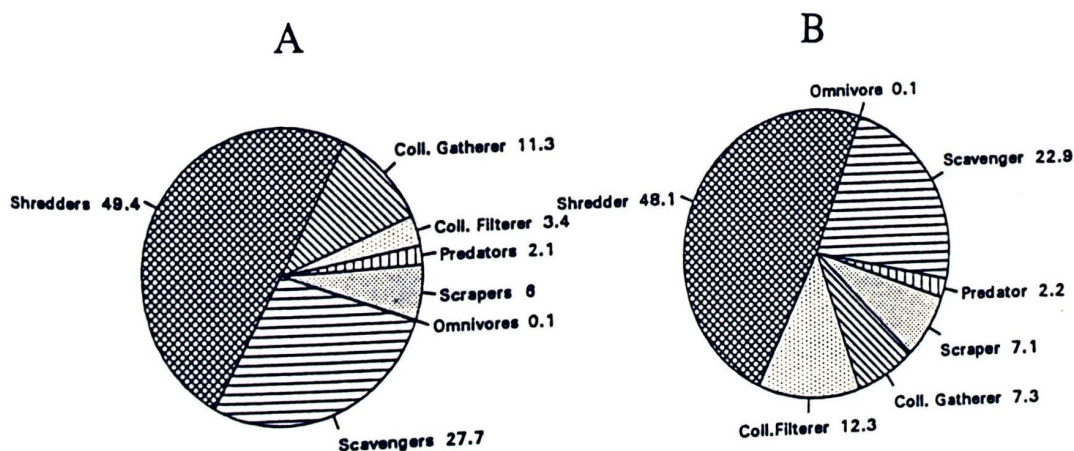


Figure 37. Percent representation of functional feeding groups in all macroinvertebrate samples from Pryor Creek Spring, November 1988 to September 1989, with gammarids considered as shredders. A. Upstream sites. B. Downstream sites.

Physicochemical Data

Chemistry and Nutrient Data. Over the duration of this one-year study, variation in dissolved oxygen, pH and temperature was very slight for both upstream and downstream sites in both springbrooks. Variations of these three parameters were not correlated for upstream and downstream sites for LCS. A small stream flowing along road 235 into a large pool above the downstream sites may have created an interruption in the continuum between upstream and downstream. PCS appeared to be a continuous spring from source to mouth since variations in the D.O., pH, and temperature were correlated upstream and downstream. In PCS, the wet-weather stream that joined the springbrook between the upper and lower sites flowed only during wet weather.

Higher dissolved oxygen levels downstream were due to increased turbulence and mixing of atmospheric oxygen into the water as the stream flowed down gradient over rough substrate. However, oxygen was plausibly not a limiting factor throughout the springbrook. All levels of oxygen were above the levels considered the minimum concentration for good fish populations (> 5.0 ppm, EPA 1976) and are likely a level sufficient to sustain most macroinvertebrates. In addition, the presence of gammarid amphipods at both upstream sites indicates that oxygen was in sufficient amounts for these cool-adapted invertebrates. Pennak (1978) states "an abundance of dissolved oxygen appears to be an environmental necessity" to most species of amphipods.

The pH levels were never below 5.0, a level which stresses aquatic life (EPA 1976). Lower pH levels at the sources were likely caused by naturally higher dissolved

CO₂. The pH increased as water moved downstream as dissolved carbon dioxide was consumed by photosynthesis of algae and lost via diffusion into the atmosphere.

At PCS, temperature was very similar between upstream and downstream sites. Longitudinal difference in the faunal assemblage was unlikely due to this factor. Monthly temperature variation was greater at LCS downstream (7%) than upstream (3%), but was still slight. The greater temperature variation at LCS downstream sites may be due to the occurrence of more pools in this springbrook between upstream and downstream sites. The longer residency time of water may result in a greater impact of ambient temperature variations on this water.

Substrate and Discharge. Differences in chemical factors between upstream and downstream were slight, but physical dissimilarities (substratum and discharge) were significantly different. More exposed cobble and gravel were found downstream at both streams apparently due to the periodic increases in discharge that washed away the lighter sand and silt. No such increases in discharge occurred at the upstream sites and therefore the substrate was compacted with sand and silt filling the interstitial space between the gravel and cobble.

The occurrence of increases in downstream discharge that moved the substrate (spates) appeared to be the greatest single difference between the upstream and downstream reaches especially at PCS. During the course of this study, these high flow events were never measured at PCS and measured only once at LCS, the displacement of substrate that these spates caused was visually apparent.

Macroinvertebrate Analysis

Similar to other spring studies, this study found a significant increase in aquatic macroinvertebrate taxa diversity only a short distance downstream from the spring source. Upstream in the springbrooks, a few taxa comprised a large percentage of the abundance with most other taxa being represented by only a few individuals. Comparatively, downstream taxa diversity increased significantly with abundances more evenly distributed among the taxa.

Similarity. Using similarity analysis based on the presence or absence of shared taxa (Jaccard's), the three upstream sites were more similar to each other than they were to the downstream sites at both springs. Likewise, the three downstream sites were more similar to each other than they were to the upstream sites. There were many more insect taxa present downstream than upstream which caused the dissimilarity between the macroinvertebrate community of the downstream reach compared to that of the upstream reach.

When calculating similarities of sites at PCS, Morisita's index did not reveal distinct upstream and downstream clusters as it did for LCS. This was initially unexpected because of the significant increase (87%) in the number of taxa occurring downstream. Morisita's index is not sensitive to rare or uncommon taxa in the presence of very abundant taxa and so essentially ignores the many uncommon taxa. Therefore, clustering is based primarily on the more abundant taxa (*G. pseudolimnaeus*, *G. minus*, *Oligochaeta*) which, in general, were present in abundance at all six sampling sites. The result is a sequential clustering of sites based primarily on the most abundant taxa.

Habitat Preference and Availability. At PCS, *G. pseudolimnaeus* and *G. minus* dominated (57%) the upstream sites. *Gammarus pseudolimnaeus* was the most dominant gammarid (71%) at site 1 which had a slow velocity and a predominantly sand substrate (80%). *Gammarus minus* was dominant (83%) at site 2 which had a moderate flow and a coarse gravel substrate with little sand. Both species were equally dominant at site 3 which consisted of equal parts of coarse gravel and sand. The density of *G. pseudolimnaeus* dropped off significantly downstream and *G. minus* became the most dominant gammarid (71%) where the substrate consisted of primarily gravel and cobble.

In LCS, tremendous numbers of the isopod *Lirceus fontinalis* were found at both site 1 and 3 (24,438 and 18,771/m², respectively). In Minckley's (1963) study of Doe Run Spring, the isopod *Caecidotea* (formerly *Asellus*) was found in even greater densities (63,990/m²). In that spring, the primary habitat was in the aquatic moss *Fissidens*. For comparison, he also took separate samples from substrate without vegetation and found *Caecidotea* densities of only 1400/m² indicating a habitat preference for a vegetated substrate. In LCS, the aquatic moss *Amblystegium tenax* probably would have held as dense a *Lirceus* population as was found for *Caecidotea* in Minckley's study if the samples consisted entirely of the moss. A relatively smaller population of *L. fontinalis* (7,210/m²) was found in the samples from site 2 which consisted mainly of coarse sand and little of the aquatic moss. At LCS site 2, *Gammarus pseudolimnaeus* was found in greater densities (5,324/m²) than sites 1 (1,570/m²) and 3 (1,877/m²). It may have a substrate preference for sand.

The gastropod *Physella* also had different population densities at each of the upstream sites at LCS. There was a greater number of *Physella* at site 1 (1,649/m²) yet few at site 2 (272/m²). It was absent from site 3 and none was present in the downstream samples. Because of the thinness of its shell, it is easily crushed by tumbling of rocks during spates so it is usually found in quiet backwaters of streams. Its ability to surface breathe may be a reason for its success at site 1 where dissolved oxygen levels may have been inadequate for other snails. This hypothesis is substantiated by the absence at site 1 of the pleurocerid gastropod *Goniobasis*, a thick-shelled non-surface breathing snail, while it was found at sites 2 and 3 and all downstream sites. It requires greater levels of dissolved oxygen and is not easily crushed during high flow events.

At LCS and PCS upstream, there were very few stonefly, mayfly and caddisfly taxa. These aquatic insect orders are characteristic of cool streams (Anderson and Wallace 1984). In upstream PCS samples, only the caddisflies *Glossossoma nigrior* and *Oxeythira* were present in large numbers. *Glossossoma nigrior* lives on top of rocks scraping periphyton and *Oxeythira* lives on vascular hydrophytes (probably filamentous algae) as piercer-herbivores. At upstream LCS, the invertebrate situation was similar. Few stoneflies or mayflies were found in any of these three sites. Among the caddisflies, only periphyton scrapers dwelling on top of rocks such as *Glossossoma nigrior* and *Goera calcarata*, and clingers and climbers associated with vascular hydrophytes, such as *Lepidostoma grisea* and *Ochrotrichia eliaga*, were present. Isopods and amphipods are positively thigmotactic and negatively phototactic. Their preferred

habitat is under rocks and within mosses and organic matter where, as detritivores, they consume decaying organic matter. Many of the caddisflies that were found only in the upstream sites are typical inhabitants of springs and other cool lotic environments. These caddisflies included *Glossosoma nigrior*, *Diplectrona modesta*, *Goera calcarata*, *Lepidostoma grisea*, and *Molanna blenda*. These taxa along with many of the chironomid genera limited to the upstream sites were probably able to exist along with the dense crustacean population because they inhabit different niches. Their densities were great in some of the upstream samples; *Ochrotrichia eliaga* comprised 43% (2,640/m²) of the insect density in March, and at PCS, *Micropsectra* comprised 50% (9,298/m²) of the July insect sample density. It appears that the insect taxa which inhabited a niche among the dense populations of nonemergent invertebrates were able to achieve large densities because they did not compete for available resources and their populations were not depleted by washouts.

Interstitial Spaces. The reduction of interstitial spaces due to the unsorted, compact nature of the substrate in the upstream reaches of both springs may limit the diversity of aquatic insects in these reaches. In such a situation, the insects could not easily escape predation by moving into the substrate. In addition, less interstitial niche space is available to provide habitat and food (Williams 1984). Williams and Hynes (1974) state that "the number of animals occurring on the surface of a stream seem almost insignificant compared with those found beneath it". Therefore it is clear that interstices in the substrate represent a critical habitat within a stream.

Spates. In this study the isopod *Lirceus*, the gastropods *Physella*, the amphipod *Crangonyx*, the flatworm *Phagocata*, and water mites (Hydracarina) were mostly or entirely limited to the upstream sites where spates did not occur. Although amphipods were found at PCS downstream, the numbers fluctuated greatly. The density of amphipods in lower PCS was greatly reduced following the spates that occurred in March and July, yet their numbers had apparently recovered by the September sampling. At LCS, oligochaetes and gammarids had a decrease in population in March and July but their numbers had increased by May and September.

The downstream emergent macroinvertebrate population was strongly affected by the spates at PCS, while spates appeared to have no affect on the emergent population at LCS downstream. Several taxa were found in samples for the first time or in greater densities in May and September following the March and July spates. For example, simuliids (blackflies) were not present upstream at LCS and PCS. However, they were found downstream in both streams only after the March and July spates. There was a large population present in May and September at LCS and in September at PCS suggesting that the increase in discharge and concurrent disturbance of substrate may have opened up patches for colonization. Simuliids, in general, are recognized as opportunistic colonizers; poor competitors with recruitment throughout the year allowing them to rapidly colonize disturbed areas (Hemphill and Cooper 1983, Hynes 1970). Several other genera found at the downstream sites could also be considered opportunistic colonizers.

Other spring studies have noted similar changes in faunal assemblages due to flooding. In Doe Run Spring in Kentucky, Minckley (1963) noted that after flooding invertebrate diversity increased as the normally numerically dominant amphipods and isopods became less important in the community. During periods of modal discharge, the fauna was dominated by *Caecidotea* and *Gammarus*. Five kilometers downstream, the assemblage of invertebrates was comprised mainly of Ephemeroptera, Plecoptera, Trichoptera and Diptera, including simuliids, with an average invertebrate density of 3,064/m². This downstream site was noted to fluctuate in velocity and depth. Dudley (1953) noted a much different faunal assemblage in four Colorado springbrooks. Two springbrooks were dominated by the fingernail clam *Pisidium*, the snail *Physa*, the amphipod *Hyallorella*, and chironomid midge larvae. Densities averaged 2,145 invertebrates/m² at one spring, and 4,656 individuals/m² at the second. The other two springbrooks were much more diverse, the communities including mayflies, stoneflies, beetles, caddisflies, and dense populations of simuliids. Invertebrate densities in these two springbrooks averaged 1,106 and 1,845/m². Dudley mentioned that flooding and shifting of substrate occurred in the latter two springbrooks and did not occur in the two aforementioned springs. *Hyallorella* and the flatworm *Dugesia* were absent from the two springbrooks impacted by flooding while *Pisidium* and *Physa* were present in much lower densities compared to the unimpacted springbrooks.

In both the Minckley and Dudley investigations, the presence of simuliids at the sites with greater diversity suggests that these areas experienced washouts that allowed species of blackflies to colonize and probably provide similar opportunity to other taxa.

From their report, it appears that increases in discharge had a profound effect on faunal assemblages.

Rapid increases in discharge sorts the substrate material, opening up interstitial spaces which are important habitation sites for many species of invertebrates including Ephemeroptera, Plecoptera, Trichoptera (EPT). At LCS these three groups were found upstream and downstream, however, there were many more species of each order found downstream. At PCS upstream there were few insects other than chironomids. EPT were found almost exclusively downstream. By moving into the substrate, the so called hyporheic zone, these insects can escape the scouring effects of spates. Clifford (1982) found that many insects moved into the substrate during a spate. According to Williams and Hynes (1974), the long, slender and flexible bodies of larval dipterans, beetles and many EPT species is advantageous for slithering through the narrow interstices of the substrate. They postulate that the slender body form of these groups enables them to find food deposits in interstitial areas, escape predation and follow receding water of drying streams into the hyporheic zone. This may preadapt them to using the hyporheic zone to escape the scouring effect of spates (Clifford 1982, Gray and Fisher 1981, Williams 1981, 1984, Resh et al. 1988).

While many species of insects appear to have adapted to flooding, amphipods, flatworms, isopods and some genera of gastropods are unable to burrow into the substrate and are easily washed from the substrate during increases in discharge (Chandler 1966, Marchant 1981, Ailee 1929). Amphipods and isopods appear to have compensated for being washed downstream by being positively rheophilic, resulting in

oriented upstream migration (Minckley 1964). Culver (1971) postulated that although amphipods are easily washed out, "the release of young [from the marsupium] before flooding is an alternative strategy to evolving ability to withstand current."

Recolonization. Downstream drift, upstream migration, vertical migration through the substrate, and aerial migration and oviposition by females are the means by which recolonization occurs (Williams and Hynes 1976). Drift has been found to be a major source for recolonization (Williams 1981). Drift is a means by which arthropods, especially nonemergent invertebrates, can emigrate to downstream habitats (Waters 1972, Waters and Hokenstrom 1980). Drift was especially important at PCS downstream. Oligochaetes and amphipods quickly recolonized this area after the spates in March and July. A study of macroinvertebrate drift in these two springs (Gillis and Hamilton 1989) found a 24-hour drift density (24-HDD=estimated number of individuals drifting within 100 m³ of water averaged over a 24-hour period) of 1,485 individuals/100 m³ of water in September 1989 at PCS. The amphipod *Gammarus pseudolimnaeus* comprised 98% of this density. This large number of drifting individuals is higher than 24-hour drift densities reported for much larger rivers (Waters and Hokenstrom 1980).

At both LCS and PCS, the reach above the wet-weather creek which was not disturbed by spates provided recolonizers to the disturbed sites below the wet-weather creek. At LCS upstream, there were very few amphipods sampled (15% of the population) yet they represented 49% of the overall population downstream. The small population upstream did not appear to be large enough to supply the recolonization of

the downstream reach after spates had occurred. However, the stream reach between the upstream and downstream sites and above the wet weather creek was visually noted to have a large population of gammarids. From this area, drifting individuals could support recolonization of the downstream reach.

Aerial recolonization usually occurs in the spring and autumn months; the peak emergence and mating periods for aquatic insects. After disturbance of the substrate in the fall, rapid recolonization by the emergent species appears to have occurred at the downstream sites of PCS. Several genera were found for the first time in samples following spates. Some of these taxa could be considered opportunistic colonizers (Hemphill and Cooper 1983) or fugitive species (Huston 1979). These taxa can rapidly colonize recently disturbed habitat especially if disturbance occurs during or slightly before the period when females are available to lay eggs. *Glossossoma nigrior* and *Dolophilodes distinctus*, caddisfly species that emerge throughout the year, would be especially well adapted to such a strategy.

In LCS downstream where the density of emergent individuals fluctuated very little, vertical migration from the hyporheic zone and downstream drift within the water column may have been important in the recovery of benthic macroinvertebrate populations following spates. There was not a significant loss of density even during the January spate which occurred at LCS downstream. Recovery by vertical migration from the substrate is more important during times of the year when emerging adults are not available to recolonize the stream (Gray and Fisher 1981) and may have been most important at LCS downstream.

Disturbance and Competition. Lengthy periods between episodes of disturbances can lower diversity when species begin to compete for limited resources; some are outcompeted and ultimately eliminated from the community (Connell 1978). This may be occurring at LCS and PCS, especially at PCS where the stream size is small. Without an occasional washout where isopods and amphipods are removed or reduced in number, these crustaceans may dominate the resources by sheer numbers of individuals. There were many amphipods drifting in the water column at PCS (Gillis and Hamilton 1989) and any habitat made available after spates could be rapidly colonized by these crustaceans.

Stability. Species diversity indices (e.g. Shannon-Weiner) give ratios of the relationship of the number of species to their importance values (usually their density) (Odum 1971). These indices are used in stream ecology studies as a measure of the degree of stress response. If a community is comprised of numerous rare species and only a few abundant species, the diversity will be fairly high indicating an unstressed community. In a stressed community, diversity is low and consists of a few rare species and a few very abundant species that are adapted to the conditions (Odum 1971).

Diversity contributes to overall community stability. Stability is ensured by the existence of many species (Patrick 1970). In a diverse community, the food web is complex and productivity is maintained even when disturbance occurs. Stability is indicated when the number of individuals remain similar over time although the species assemblage may (Patrick 1970). As a species fluctuates in number through emergence

or changes in trophic relationships during difficult life stages, another species is there to take its place (Patrick 1970).

According to these hypotheses relating stability to community diversity, PCS appears to have a less stable community than LCS. The PCS community varied greatly over time in density at both upstream (61%) and downstream (81%) compared to LCS up (15%) and down (30%). However, this was mainly due to changes in the nonemergent taxa, which apparently were unable to maintain their place during flooding downstream. At both LCS and PCS upstream reaches, taxa richness was lower than downstream. The emergent densities upstream fluctuated more than emergent invertebrate densities downstream even though the upstream taxa were not affected by spates. It appears that once the upstream insect taxa emerged, there were not other taxa available to take their place.

Differences Between the Springs. Comparison of the macroinvertebrates of these two springs reveals a number of fundamental differences in the communities. Comparatively, PCS was less rich in taxa than LCS. There were more rare and very rare taxa present and taxa were captured less frequently than in LCS. This may be due to the smaller size of PCS compared to LCS. Also, PCS does not appear to be as old a stream as LCS since the complexity of aquatic macroinvertebrate community is less developed as indicated by lower richness and diversity. Alternatively, human manipulation at PCS may have damaged the original community and because of this the community is only in the beginning stages of development. Evidence of a springhouse over the source and a pipe that carries away some water indicates possible significant

human intervention at this spring. Hynes (1970) states that "the longer a locality has been in the same condition the richer is its biotic community and the more stable it is". The absence of certain species, such as *Molanna*, *Lepidostoma*, and *Goera* found at LCS and typically of some other springs in the region, indicates that PCS might be younger or in a state of recovery following significant disturbance.

Spring Limited Taxa. Most spring surveys indicate that species richness is low at the source but increases longitudinally downstream (cf. Sloan 1956, Ward and Dufford 1979). This study supports those findings. There were several taxa in which 80-100% of the population was only found upstream (LCS=15 taxa, PCS=14 taxa). Although diversity is low in a spring, this habitat supports a group of taxa that are adapted to the cool headwater environment and are usually not found in other aquatic habitats. Therefore, springs contribute to overall species diversity of these groups (Erman and Erman 1990). Rather than having a stressed community, as might be suggested by the low richness and diversity, a spring has a unique community confined by minimally varying physicochemical parameters. The spring communities are often isolated from other such communities, providing a novel opportunity for allopatric speciation.

Functional Feeding Groups. An analysis of functional feeding groups demonstrates the trophic relations between individual groups which are actually part of a complex food web. Grazers consume algal and bacterial growth on rocks and plants, autochthonous energy sources unavailable to other aquatic organisms. Shredders consume coarse particulate organic matter (CPOM), primarily dead plant matter such

as leaves from allochthonous sources, an energy resource otherwise unavailable to the stream community. Only 40% of the CPOM is actually digested and the remainder is voided as feces. These feces are a major contribution to the fine particulate organic matter (FPOM). The available nutrients in the FPOM are fixed by the collectors-filterers and collectors-gatherers. All of these feeding groups are eaten by the invertebrate predators in the invertebrate community, thus completing the consuming portion of the food web. All feeding groups could be referred to as "fish food" since they are consumed by fish and other vertebrate predators (Cummins 1974).

In the river continuum model (Vannote et al. 1980), streams have been classified into headwater streams, mid-order streams, and rivers. In this model, headwater streams are dominated by "shredders" due to the large amount of nutrients which arrive as unprocessed (CPOM) leaves and stems from the surrounding terrestrial environment (Iversen 1988). Collectors-gatherers and predators are expected in these communities. The streams are often shaded so that little or no algae growth is available for scrapers. The particle sizes of organic matter are larger than that be used by most collectors-filterers so they are absent or rare.

The mid-order streams (orders 4-6) are nutrient rich according to this model. They receive the leakage of nutrients from upstream, mostly as FPOM, which is utilized by collectors-filterers and collectors-gatherers. These streams tend to be autotrophic with more sunlight reaching the stream, resulting in greater opportunity for growth of photosynthetic organisms allowing grazers to exist. Shredders are fewer in number since

the allochthonous input of CPOM is far less important relative to the size of the stream (Cummins 1974, Minshall et al 1985).

In both upstream and downstream sites of Lost Creek and Pryor Creek springs, the most well represented functional feeding group was the collectors-gatherers, consisting mostly of amphipods and isopods. The river continuum model predicts that headwater streams should be dominated by shredders. While amphipods are often considered to be collectors-gatherers, they are also very important shredders in these systems. As they are collecting fungi and bacteria on the surface of the decaying leaves, they shred the underlying plant tissue leaving behind only the vascular tissue. During functional feeding group analysis, when the amphipods were taken out of the collectors-gatherers group and designated as shredders, the percentages of shredders changed substantially, especially at PCS. Following this adjustment, the shredders were nearly equal in number at upstream and downstream communities in PCS (approx. 48% both up and down). Following the reclassification of the amphipod trophic relationships from collector-gatherers to shredders, the percent representation by collectors-gatherers was reduced to 11.2% upstream and 7.3% downstream. At LCS upstream, the reclassification of amphipods to the shredders group had a less significant effect; the shredders increased to 13.8% from 0.6% of the population. Downstream, *Gammarus pseudolimnaeus* was the dominant invertebrate and reclassification changed the abundance of shredders from 4.1% to 35.2%.

CHAPTER 6

SUMMARY

Quantitative and qualitative investigations of benthic macroinvertebrate faunas and the physicochemical environments of two temperate springs, Lost Creek Spring and Pryor Creek Spring, were conducted from September 1988 to September 1989. The relatively pristine springs are located within Land Between The Lakes in northwest Middle Tennessee. Springs are becoming increasingly threatened as land practices cause contamination of groundwater. They may be the most sensitive aquatic ecosystems in this region because of their unique spring limited fauna.

In both springs, upstream sites close to the sources were compared to downstream sites located, in both cases, below a confluence with wet weather creeks. These wet weather creeks caused large increases in downstream discharge during storm events causing spates. These changes in discharge were noted by physical displacement of emergence traps which were in the springs throughout the study period. During these spates, habitat was altered as substrate and organic matter were shifted. The substrate was sorted by tumbling, washing away the sand and silt and exposing gravel and cobble. Spates did not occur at the upstream sites; therefore, substrates were compacted with sand filling the interstitial spaces.

Physicochemical analysis demonstrated little difference between the upstream and downstream sites at PCS with slight variations in all parameters. The spring appeared to be a continuum from source to mouth with all variations correlated within the upstream and downstream reaches. LCS did not appear to be a continuous spring from source to mouth because variations in parameters at the upstream reach and downstream

reach did not correlate. However, variations among all parameters were slight with little difference between upstream and downstream.

The mean density of macroinvertebrates was 40,182 individuals/m² at LCS and 57,310 individuals/m² at PCS. Of the macroinvertebrates collected, over 74% at LCS and 73% at PCS were upstream. Most of those individuals (86%) were noninsect invertebrates such as amphipods, isopods, flatworms, and gastropods. These taxa are unable to burrow into the substrate and are easily washed away during spates (Chandler 1966, Marchant 1981, Ailee 1929). The population of amphipods at PCS downstream was strongly affected by spates and fluctuated greatly. At LCS downstream, the two dominant taxa, Oligochaeta and *Gammarus*, alternately dominated the habitat. As one population decreased in density the other increased, causing the combined noninsect population density to remain constant. The oligochaete population decreased in March, and the gammarid population decreased in July, coinciding with the occurrence of spates.

Of the 90 taxa identified from LCS and the 80 taxa identified from PCS, most were insects (86% at LCS, 80% at PCS). Richness of insect taxa increased significantly downstream (over 43% at LCS and 87% at PCS). Insect diversity varied less downstream than upstream. This was surprising since the upstream sites were not affected by spates. It appears that as the insect taxa emerged from the upstream sites, there were few other insects present to take their place. The isopod and amphipod populations probably limited diversity due to their extremely high densities. The insect taxa that were present inhabited very different niches compared to the amphipods and

isopods. The lack of interstitial space upstream was probably another limitation to insect diversity since many insect taxa burrow into the substrate escaping predation, seeking food and habitat.

During spates at the downstream sites, the noninsect taxa, which may dominate the upstream habitat by excluding or restricting less competitive species, were washed out. Insects were able to escape spates by moving into the hyporheic zone. These insects could then recolonize the newly opened patches of habitat. Aerial recolonization by poor competitors such as *Simulium* could also occur on these newly opened patches further increasing diversity.

At PCS, diversity was lower than at LCS. PCS was a smaller spring yet the density of the downstream noninsect population was greater than three times that found at LCS during some sampling periods. It appears that competition for available habitat was more intense at PCS; the drift densities at upper PCS were 15 times greater than drift densities at upper LCS. The absence of certain species typical of springs in this region indicates that PCS may be a younger spring than LCS or in a state of recovery from human manipulation. According to some concepts of diversity and stability (cf. Patrick 1970), PCS downstream had a less stable community than LCS. At PCS downstream, macroinvertebrate density and richness fluctuated significantly ($p < 0.05$) throughout the sampling year. While at LCS downstream, macroinvertebrate sample density and richness were not significantly different ($p > 0.10$). The number of species remained similar throughout the sampling period while the types of species changed, identifying LCS downstream as a stable community.

The absence of spates may be the most important factor limiting diversity. Disturbance may increase diversity by rearranging the substrate, thus creating new patches of habitat. Disturbance also may limit the abundances of certain competitive species allowing less competitive species to become established.

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Appendices

Appendix I. Substrate composition (as % of total) in LCS and PCS

LCS	Site	1	2	3	4	5	6
small cobble		5	5	5	35	10	10
very coarse gravel		20	5	55	50	10	50
coarse gravel		45		25	10	30	20
medium gravel		25	15	10	5	30	
fine to very fine gravel		5	10	5		10	10
very coarse, coarse fine and very fine sand			65			10	10
PCS	Site	1	2	3	4	5	6
small cobble		5		5	15		
very coarse gravel			5	5	25	20	60
coarse gravel		5	40	20	35	30	15
medium gravel		5	25	5	15	30	15
fine and very fine gravel		5	25	10	10	20	10
very coarse, coarse, fine and very fine sand		80	5	55			

Classification of stream substrate channel materials by particle size from Lane (1947) reprinted in Platts (1983):

small cobble = 128-64 mm
 very coarse gravel = 64-32 mm
 coarse gravel = 32-16 mm
 medium gravel = 16-8 mm

fine gravel = 8-4 mm
 very fine gravel = 4-2 mm
 very coarse sand = 2-1 mm
 coarse sand = 1.0-.5 mm

Appendix II. Taxa list for Lost Creek Spring and Pryor Creek Spring

TAXON	Lost Creek Spring		Pryor Creek Spring	
	UP	DN	UP	DN
Planariidae				
<u>Phagocata</u>	X	X	X	X
Oligochaeta				
Sphaeriidae				
<u>Sphaerium</u>	X	X	X	X
Physidae				
<u>Physella</u>	X		X	X
Pleuroceridae				
<u>Goniobasis</u>	X	X	X	X
Gammaridae				
<u>Crangonyx</u>	X	X	X	X
<u>Gammarus pseudolimnaeus</u>	X	X	X	X
<u>Stygobromus</u>				
Asellidae				
<u>Lirceus fontinalis</u>	X	X	X	X
<u>Caecidotea</u> sp. 1	X	X	X	
<u>Caecidotea</u> sp. 2		X	X	
<u>Orconectes</u>	X	X	X	X
Hydracarina				
Capniidae		X		X
<u>Allocapnia</u>				X
Chloroperlidae	X	X		
<u>Alloperla</u>				X
Leuctridae		X		
<u>Leuctra</u>				X
Nemouridae	X	X		
<u>Amphinemura</u>				X
Perlidae		X		
<u>Acroneuria</u>				X
Baetidae	X	X		X
<u>Baetis</u>		X		
<u>Pseudocloeon</u>				X
Heptageniidae		X		
<u>Stenacron</u>				X
Sialidae	X	X		
<u>Sialis</u>			X	X
Glossosomatidae	X	X		
<u>Glossosoma nigrior</u>				X
Hydropsychidae	X	X		
<u>Diplectrona modesta</u>				X
Hydroptilidae	X	X		
<u>Ochrotrichia</u>			X	X
Limnephilidae	X	X		
<u>Pycnopsyche</u>				

Appendix II, continued

TAXON	Lost Creek Spring		Pryor Creek Spring	
	UP	DN	UP	DN
Ceratopogonidae				
<u>Bezzia</u>	X	X	X	X
<u>Palpomyia</u>	X	X	X	X
Empididae				
<u>Hemerodromia</u>	X	X	X	X
Simuliidae				
<u>Simulium</u>		X		X
Tabanidae				
<u>Tabanus</u>		X	X	X
Tipulidae				
<u>Limnophila</u>	X	X	X	X
<u>Pedicia</u>	X	X	X	X
<u>Tipula</u>	X	X	X	X
Chironomidae				
Undet. pupae				
Chironominae				
<u>Dicerotendipes</u>	X		X	X
<u>Micropsectra</u>	X	X	X	X
<u>Paratendipes</u>	X		X	X
<u>Polypedilum</u>	X	X		X
<u>Rheotanytarsus</u>	X	X		X
<u>Tribelos</u>				X
Orthoclaadiinae				
<u>Chaetocladius</u>	X	X	X	X
<u>Corynoneura</u>	X	X	X	X
<u>Cricotopus/Orthocladus</u>	X	X		X
<u>Heleniella</u>		X		X
<u>Krenosmittia</u>	X	X	X	X
<u>Parametrioctenemus</u>	X	X	X	X
<u>Thienemaniella</u>	X	X		
<u>Tvetenia</u>				X
Tanypodinae				
<u>Natarsia</u>	X	X		X
<u>Rheopelopia</u>	X		X	X
<u>Trissopelopia</u>		X		
Undet. Diptera				

Appendix III. Taxa list for Lost Creek Spring with month of collection and abundance rating.

TAXON	UP	DN	COLLECT. DATE-UP	ABUND. UP	COLLECT. DATE-DN	ABUND. DN
Planariidae						
<u>Phagocata</u>	X	X	ALL YR	VA	ALL YR	C
Oligochaeta	X	X	ALL YR	VA	ALL YR	VA
Sphaeriidae						
<u>Sphaerium</u>	X	X	9a,11,1,5,7,9	C	11,1,5,7	C
Physidae						
<u>Physella</u>	X		ALL YR	A		
Pleuroceridae						
<u>Goniobasis</u>	X	X	9A,10,11,1,7,9	R	ALL YR	C
Gammaridae						
<u>Crangonyx</u>	X	X	ALL YR	A	11,3,5,7,9	C
<u>Gammarus pseudolimnaeus</u>	X	X	ALL YR	VA	ALL YR	VA
<u>Stygobromus</u>	X	X	9A,10,11,3	R	ALL YR	C
Asellidae						
<u>Lirceus fontinalis</u>	X	X	ALL YR	EA	11,3,5,7,9	A
<u>Caecidotea</u> sp. 1	X	X	10	VR	1	VR
<u>Caecidotea</u> sp. 2		X			3,7	R
Cambaridae						
<u>Orconectes</u>	X	X	3	VR	1,3,5,7	R
Hydracarina	X	X	ALL YR	A	11,5,9	R
Capniidae		X			1,3	R
<u>Allocapnia</u>						
Chloroperlidae						
<u>Alloperla</u>	X	X	5	VR	1,3,9	R
Leuctridae					1,3,5,7,9	C
<u>Leuctra</u>		X				
Nemouridae					3,7,9	R
<u>Amphinemura</u>	X	X	7	VR		
Perlodidae					11	VR
<u>Clasperia</u>		X			1,3,7	R
<u>Isoperla</u>		X				
Perlidae					11,5,7,9	R
<u>Acroneuria</u>		X				
Baetidae					ALL YR	A
<u>Baetis</u>	X	X	9A,10,1,3,5,7	R	3,5	R
<u>Pseudocloeon</u>		X				
Ephemerellidae					11,3	R
<u>Dannella</u>		X			11,3,5,7,9	R
Heptageniidae					11,3,5,7	C
<u>Heptagenia</u>		X				
<u>Stenacron</u>					3,5,9	R
Gomphidae						
<u>Gomphus</u>		X			11	VR
Calopterygidae					9	C
<u>Calopteryx</u>		X				
<u>Hetaerina</u>					7	VR
Corydalidae						
<u>Nigronia</u>	X	X	10,7	R		

Appendix III, continued

TAXON	UP	DN	COLLECT. DATE-UP	ABUND. UP	COLLECT. DATE-DN	ABUND. DN
Sialidae						
<u>Sialis</u>	X	X	9A,10,11,1,7,9	C	11,1,5,7,9,	C
Glossosomatidae		X			11,1,3,5,7	C
<u>Agapetus avitus</u>	X	X	ALL YR	A	ALL YR	C
<u>Glossosoma nigrior</u>						
Hydropsychidae		X			5,7,9	C
<u>Cheumatopsyche oxa</u>	X	X	10,11,1,3,7,9	C	11,1,3,9	R
<u>Diplectrona modesta</u>						
Hydroptilidae	X	X	1,3,5,9	A	3	R
<u>Ochrotrichia</u>						
Limnephilidae	X	X	9A,10,11,3,5,7,9	C	11,7,9	R
<u>Goera calcarata</u>	X	X	7	VR	11,1	R
<u>Pycnopsyche</u>						
Leptoceridae		X			1	VR
<u>Triaenodes</u>						
Lepidostomatidae	X	X	9A,1,3,7,9	C	3	R
<u>Lepidostoma</u>						
Molannidae	X		9A,11	VR		
<u>Molanna blenda</u>					3,5,7,9	C
Philopotamidae		X				
<u>Chimarra</u>					ALL YR	C
Polycentropodidae		X				
<u>Polycentropus</u>					9	VR
Psychomyiidae	X	X	9A,11	VR		
<u>Lype diversa</u>					1,3,7,9	R
Psephenidae		X			7	VR
<u>Psephenus herricki</u>						
Elmidae		X				
<u>Microcylloepus</u>						
Ceratopogonidae	X		7	VR	11,3,9	R
<u>Alluaudomyia</u>	X	X	10,11,1,3	R	9	VR
<u>Bezzia</u>	X	X	5	VR		
<u>Palpomyia</u>						
Dixidae	X		9A,10,3,9	R		
<u>Dixa</u>						
Empididae	X		1	VR	5,7,9	R
<u>Clinocera</u>	X	X	9A,10,11,3,7	R		
<u>Hemerodromia</u>	X		1,5			
Muscidae					3,5,7,9	C
Simuliidae		X			5	VR
<u>Simulium</u>						
Tabanidae		X			1,7	VR
<u>Tabanus</u>					11,3	R
Tipulidae		X		R	5	VR
<u>Antocha</u>	X	X	9A,10,11	VR	11,3,7	R
<u>Limnophila</u>	X	X	9A,10,7	R		
<u>Pedicia</u>	X	X	9A,10,11,1			
<u>Tipula</u>						

TAXON	UP	DN	COLLECT. DATE-UP	ABUND. UP	COLLECT. DATE-DN	ABUND. DN
Undet. Diptera		X				
Chironomidae						
Undet. pupae	X	X			3,7	R
Chironominae			9A,10,11,3,5,7	C		
<u>Demicryptochironomus</u>		X			11,3,5,9	R
<u>Dicrotendipes</u>	X					
<u>Micropsectra</u>	X	X	1,3,5	C	11,3,7	R
<u>Microtendipes</u>	X	X	ALL YR	C		
<u>Paralauterborniella</u>	X	X	9A,11,3	R	ALL YR	C
<u>Paratendipes</u>		X			11,1,3,5	C
<u>Polypedilum</u>	X	X	9A,10,1,3,5,7	C	11	VR
<u>Rheotanytarsus</u>	X	X	9A,10,3,7,9	R		
<u>Stempellinella</u>	X	X	ALL YR	A	5,7,9	R
<u>Tanytarsus</u>	X	X	9A,10,11,7,9	R	11,1,7,9	C
<u>Tribelos</u>		X	7	VR	11,5,7,9	C
Orthoclaadiinae					11,1,3,5,7	R
<u>Chaetocladius</u>	X	X			11	VR
<u>Corynoneura</u>	X	X	9A,10,5,7,9	C	5,9	VR
<u>Cricotopus/Orthocladus</u>	X	X	11,5	R	1,5,9	R
<u>Eukiefferiella</u>	X		9A,10,7,9	R	3,5	VR
<u>Heleniella</u>	X	X	5	R		
<u>Heterotrissocladius</u>	X		9A,3,9	R	3,7,9	R
<u>Krenosmittia</u>		X	9A,10	VR		
<u>Limnophyes</u>	X				11	VR
<u>Metriocnemus</u>	X	X	10	VR		
<u>Parachaetocladius</u>		X	9A,7,9	R	11	VR
<u>Parametriocnemus</u>	X	X			1	VR
<u>Pseudorthocladus</u>		X	ALL YR	A	3,5,7,9	R
<u>Stilocladius</u>		X			3,7,9	R
<u>Thienemaniella</u>	X	X	ALL YR	C	3	VR
<u>Tvetenia</u>	X	X	ALL YR	A	ALL YR	C
Tanypodinae					1,3,5	R
<u>Natarsia</u>	X	X	11	VR	11,1,7,9	R
<u>Rheopelopia</u>	X	X	9A,10,11,1,3,7,9	R	3,5,7,9	R
<u>Trissopelopia</u>	X	X	9A,10,11,3,5,7,9	C	ALL YR	C
<u>Zavreliomyia</u>	X	X	11	VR	11,3,7,9	R

(9A=Sep 1988; 10=Oct 1988; 11=Nov 1988; 1=Jan 1989; 3=Mar 1989; 5=May 1989; 7=July 1989; 9=Sep 1989.
 EA=exceptionally abundant = > 5000 specimens; VA=very abundant = 1000-5000 specimens; A=abundant = 250-999
 specimens; C=common = 50-249 specimens; R=rare = 5-49 specimens; VR=very rare = < 5 specimens.)

Appendix IV. Taxa list for Pryor Creek Spring with month of collection and abundance rating.

TAXON	UP	DN	COLLECT. DATE-UP	ABUND. UP	COLLECT. DATE-DN	ABUND. DN
Planariidae	X	X	ALL YR	A	11,1,3,7,9	R
<u>Phagocata</u>	X	X	ALL YR	EA	ALL YR	VA
Oligochaeta						
Sphaeriidae	X	X	ALL YR	VA	11,7,9	R
<u>Sphaerium</u>						
Physidae	X	X	ALL YR	VA	11,5,9	R
<u>Physella</u>						
Pleuroceridae	X	X	11	VR	11,5	R
<u>Goniobasis</u>						
Planorbidae	X	X	9	VR	11,7	R
<u>Helisoma</u>						
Gammaridae	X	X	10,11,3,5,7,9	A	9	VR
<u>Crangonyx</u>	X	X	ALL YR	EA	ALL YR	VA
<u>Gammarus pseudolimnaeus</u>	X	X	ALL YR	EA	ALL YR	VA
<u>Gammarus minus</u>	X	X	10,3	R	11,9	R
<u>Stygobromus</u>						
Asellidae	X	X	11,1	VR	ALL YR 11,9	R VR
<u>Lirceus fontinalis</u>		X				
<u>Caecidotea</u> sp. 1	X		3	VR		
<u>Caecidotea</u> sp. 2						
Cambaridae	X		1	VR		
<u>Cambarus</u>	X		11	VR	ALL YR	C
<u>Orconectes</u>	X	X	ALL YR	A		
Hydracarina					1,3	R
Capniidae		X				
<u>Allocapnia</u>					11,3	VR
Chloroperlidae		X				
<u>Alloperla</u>					5	VR
Leuctridae		X				
<u>Leuctra</u>					11,1	R
Nemouridae		X				
<u>Amphinemura</u>					11	VR
Perlidae		X				
<u>Acroneuria</u>					11,9	R
Baetidae		X			5	R
<u>Baetis</u>		X				
<u>Pseudocloeon</u>					1	VR
Heptageniidae		X				
<u>Stenacron</u>						
Corixidae			10	R		
<u>Tricocorixa</u>	X					

Appendix IV, continued

TAXON	UP	DN	COLLECT. DATE-UP	ABUND. UP	COLLECT. DATE-DN	ABUND. DN
Sialidae		X			11,7	
<u>Sialis</u>						
Glossosomatidae	X	X	ALL YR	A	11,1,5,7,9	A
<u>Glossosoma nigrior</u>						
Hydropsychidae		X			11,1,9	A
<u>Diplectrona modesta</u>						
Hydroptilidae		X			3	VR
<u>Ochrotrichia</u>	X		7	R		
<u>Oxeythira</u>						
Limnephilidae	X	X	11,1,7,9	R	11,1,3	R
<u>Pycnopsyche</u>						
Philopotamidae	X		7	VR		
<u>Dolophilodes distinctus</u>						
Rhyacophilidae		X			1	R
<u>Rhyacophila</u>						
Dytiscidae		X			11,7	VR
<u>Hydroporus</u>						
Elmidae		X			11	VR
<u>Dubiraphia</u>						
Dryopidae		X			11	VR
<u>Pelonomis</u>						
Ceratopogonidae		X			7	VR
<u>Atrichopogon</u>	X	X	9A,10,11,1,3	C	11,1,3,9	C
<u>Bezzia</u>	X	X	9A,10,11,1,3	R	3	VR
<u>Palpomyia</u>						
Empididae	X	X	9A,9	R	5,9	R
<u>Hemerodromia</u>	X	X	1	VR	1,5	VR
Ephydriidae					5,9	C
Simuliidae		X			11	VR
<u>Simulium</u>		X				
Sciomyzidae					5	VR
Tabanidae	X	X	10,5	VR		
<u>Tabanus</u>	X		10	VR		
<u>Chrysops</u>					11	VR
Stratiomyidae		X				
<u>Allognosta</u>					1	VR
Tipulidae		X			9	R
<u>Hexatoma</u>	X	X	10,11,1	VR	11,1	R
<u>Limnophila</u>		X			11,1	R
<u>Pedicia</u>	X	X	9			9R
<u>Tipula</u>	X	X	3			
Undet. Diptera						

TAXON	UP	DN	COLLECT. DATE-UP	ABUND. UP	COLLECT. DATE-DN	ABUND. DN
Chironomidae						
Undet. pupae	X	X	1,5,7,9			
Chironominae				C	11,1,3,5,9	R
<u>Chironomus</u>	X		5			
<u>Dicrotendipes</u>	X	X	3,5,7,9	R		
<u>Micropsectra</u>	X	X	ALL YR	C	5	
<u>Paratendipes</u>	X	X	ALL YR	VA	11,1,5,7,9	VR
<u>Polypedilum</u>	X	X	9A,10,1,5,7,9	A	3,5	C
<u>Rheotanytarsus</u>		X		C	11,1,3,5,9	VR
<u>Stenochironomus</u>		X			11,5,9	C
<u>Stictochironomus</u>	X		5,7		11	A
<u>Tribelos</u>		X		R		VR
Orthoclaadiinae					11	VR
<u>Chaetocladius</u>	X	X	9A,10,5,7,9	VA	5,9	C
<u>Corynoneura</u>	X	X	10,11	R	1,3,5	R
<u>Cricotopus/Orthocladus</u>	X	X	3,7	R	5,9	R
<u>Diplocladius</u>		X			11,5	R
<u>Georthocladus</u>		X			11	VR
<u>Gymnometriocnemus</u>		X			11	VR
<u>Heleniella</u>		X			11,3,9	C
<u>Krenosmittia</u>		X			5	VR
<u>Parametriocnemus</u>	X	X	9A,10,3,5,7,9	C	11,3,5,7,9	A
<u>Psilometriocnemus</u>		X			7	VR
<u>Thienemaniella</u>	X	X	9A,10,11,1,5,7,9	C	11,1,5,7,9	R
<u>Tvetenia</u>	X	X	9A,10,7	R	11,1,5,7,9	C
<u>Zalutschia</u>		X			11	VR
Tanypodinae						
<u>Acrotanypus</u>	X		10	R		
<u>Natarsia</u>	X	X	9A,10,5,7,9	R	5	VR
<u>Rheopelopia</u>		X			11	VR
<u>Trissopelopia</u>	X		10	VR		
Diamesinae						
<u>Diamesa</u>		X			11,5	R
<u>Potthastia</u>		X			5	VR

(9A=Sep 1988; 10=Oct 1988; 11=Nov 1988; 1=Jan 1989; 3=Mar 1989; 5=May 1989; 7=July 1989; 9=Sep 1989.
 EA=exceptionally abundant = > 5000 specimens; VA=very abundant = 1000-5000 specimens; A=abundant = 250-999
 specimens; C=common = 50-249 specimens; VR=very rare = < 5 specimens.)