VARIATION IN BENTHIC COMMUNITY STRUCTURE: THE ROLE OF THE MACROENVIRONMENT ALONG A DOWNSTREAM GRADIENT

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A Thesis Submitted to the Faculty of Baylor University in Partial Fulfillment of the Requirements for the Degree

of

Master of Science

by

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#### ABSTRACT

McKittrick Creek, a discontinuous mountain-desert stream in Guadalupe Mountains National Park, Texas, was sampled at discrete locations(pools) to test for differences among biomass, density, species diversity, equitability, and species richness in the benthic macroinvertebrate community.

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Significant differences occurred among pools for the biotic characteristics of the benthic community along the downstream gradient. Connected pools were more similar to each other than pools separated by dry reaches. The greatest biomass (700-1200 mg dry weight  $/m^2$ ) and species diversity (2.5-3.2) values occurred at the two furthest downstream pools and two furthest upstream pools, while the least biomass (150-600 mg dry weight/m<sup>2</sup>) and species diversity (2.2-2.4) values occurred at two midstream pools. Equitability (0.65-0.80) and species richness (4.0-7.6) values varied considerably among pools,

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but were generally greatest in downstream pools. Density values also varied considerably among pools  $(2500-14000 \text{ organisms/m}^2)$  with the greatest density at the furthest downstream pool.

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Variation in macroenvironmental characteristics associated with food availability was more important than substrate size and fish predation in determining the benthic community structure of McKittrick Creek. Variance in biomass and density of the benthic community was explained best by differences in quantities of coarse detritus. Pools with greater quantities of coarse detritus had less invertebrate biomass and density. Variance in species diversity and species richness values was explained best by changes in periphyton biomass. Variance in equitability values was not associated with any macroenvironmental characteristics. Although the type of food available (e.g., coarse detritus or periphyton) explained most of the variance among pools for benthic community characteristics, interaction among available food type, substrate size, and predation by fish may actually determine the benthic community structure of some pools.

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#### INTRODUCTION

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How do varying macroenvironmental characteristics, e.g., riparian vegetation density, stream gradient, along a downstream gradient affect the benthic community structure of streams? In continuous streams benthic community structure is governed to a great extent by the macroenvironmental characteristics of upstream regions, while in discontinuous streams only macroenvironmental characteristics immediately surrounding the benthic community are relevant. How macroenvironmental changes influence benthic community structure has been investigated for continuous streams (Andrews and Minshall 1979, Egglishaw and Morgan 1964, Gray et.al. 1983, Hawkins and Sedell 1981, Minshall et.al. 1983, Vannote et.al. 1980), but has not been investigated for discontinuous streams.

Upstream waters influence downstream communities. Consequently, the effects of differing macroenvironments on benthic community structure is difficult to distinguish

along a stream continuum. This is not a problem in a discontinuous stream, such as McKittrick Creek, because. other than through upstream migration of adult insects, discrete stream segments remain separated except during periods of high flow. Mountain-desert streams, which are often discontinuous, have pronounced macroenvironmental differences within a short distance along their gradients. Consequently, one would expect these streams to have more easily recognized differences in benthic community structure in response to macroenvironmental differences along their gradient than continuous streams. Discontinuous stream systems, then, provide a model for studying differences in benthic community structure that occur along a downstream gradient. As a "closed" system, these usually spring-fed streams flow at the surface for a short distance before disappearing by percolation into the substratum to resurface down-canyon.

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McKittrick Creek is such a stream. It flows discontinuously, though perenially, through McKittrick Canyon before disappearing permanently near the canyon entrance. It provided the opportunity to investigate questions about the effect of different macroenvironments along a stream continuum on benthic community structure in streams. Specifically, 1. Do significant differences occur in macrobenthic community characteristics, i.e., biomass, density, species diversity, equitability, and species richness, within a short distant along a downstream gradient in McKittrick Creek?

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2. Are the macrobenthic community characteristics of McKittrick Creek significantly correlated with any of the macroenvironmental characteristics of McKittrick Canyon?

3. Which of the following is most important in determining the macrobenthic community structure of McKittrick Creek: Food availability, substrate size composition, or predation by fish?

#### LITERATURE REVIEW

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Stream communities have been studied mainly in terms of specific interactions among two or three factors, e.g., substrate composition, current velocity, and/or food availability, at a site along a stream continuum. However, ecologists now view the stream community at a specified locale as an integral part of the entire ecosystem, which includes not only interactions at that locale, but also interactions with other ecosystems along the stream basin continuum. Fisher (1983) describes this new concept in relation to terrestrial ecosystems:

"...running water is a unidirectional, highly competent transport vector linking communities on the longitudinal gradient. The potential for an upstream community to influence those downstream through modifications of the aqueous medium far exceeds that of the terrestrial analogue which links contiguous communities through downslope winds."

#### River Continuum Concept:

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Vannote et.al. (1980) describes a conceptual stream ecosystem which integrates the physical and biological characteristics of the environment along the stream continuum with the influence that upstream communities have on downstream communities.

Stream basin morphology results from the interaction of many different variables, e.g., width, depth, gradient, flow rate, and flow volume. River systems tend towards a dynamic equilibrium among these variables by maximizing the efficiency of energy utilization (Leopold 1964). Along a longitudinal gradient, these physical variables change in a consistent and, therefore, predictable manner, i.e., streambed widens, gradient decreases, flow volume increases. The river continuum concept describes an analogous stream community which results from the dynamic equilibrium that conforms to the present physical state of a specified locale in a stream.

Accordingly, stream systems are divided into three major groups based on their size: Headwater streams (orders 1-3), mid-sized streams (orders 4-6), and large rivers (order > 6). Predictable changes in stream community structure occur along the longitudinal gradient in three broad aspects: (1) the production to respiration
ratio (P:R); (2) importance of allochthonous energy
input; (3) the dominant functional group of organisms
present, e.g., shredder vs. collector (Fig. 1).

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Production to respiration ratios change from less than 1 in headwater streams to greater than 1 in mid-sized streams. Headwater streams typically flow through high altitude forested areas. and. consequently. remain relatively well-shaded through much of the year. A lack of sunlight limits production to the extent that respiration exceeds production. Mid-sized streams typically flow through less-shaded regions and production exceeds respiration. Therefore, a change occurs from a heterotrophic to autotrophic system from headwater streams to mid-sized streams. Minshall (1978) observed that the stream's trophic state depends primarily on the degree of shading. Stream-shading usually results from riparian vegetation or steep-sloped canyon walls. The trophic state changes from autotrophic back to heterotrophic in large rivers. Although large rivers are primarily shade-free, increased turbidity and depth decrease light penetration sufficiently to allow respiration to exceed production.



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Fig. 1. Relationship between stream order and structural and functional characteristics of a stream ecosystem (adapted from Vannote et.al. 1980).

Stream benthic communities require an allochthonous source of energy when respiration exceeds production. Allochthonous organic matter, is imported, processed. exported, and/or stored along a continuum. Benthic stream communities enhance the processing of allochthonous material which alters the quantity and quality of organic matter (Cummins et.al. 1983). The allochthonous energy source in well-shaded low order streams is primarily leaf fall (coarse particulate organic matter (CPOM), > 1mm). Organismal processing or physical breakup of CPOM into fine particulate organic matter (FPOM, 50 um - 1mm) and ultrafine particulate organic matter (UPOM, 0.5 um - 50 um) occurs as CPOM progresses downstream. It is organic matter in this final form which supplies the benthos of large order rivers (>6) where an allochthonous energy source is necessary to support the benthic community. Allochthonous energy is of less importance in mid-sized streams because of autotrophy.

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According to the River Continuum Concept, if the dominant type of food changes (e.g., CPOM to FPOM and UPOM) and the trophic state of the system changes (e.g., heterotrophic to autotrophic or vice versa) then the dominant functional group of organisms (e.g., shredder or collector) should also change along the stream continuum

(Fig. 1). Cummins (1973) described basic functional groups of stream invertebrates: shredders, collectors, grazers, and predators. These are defined as:

<u>Shredders</u>: Herbivores feeding on living plant tissue and detritivores feeding on large particles (CPOM) of decomposing plant tissue. Generally food particle size is greater than 1000 microns. Feed primarily by chewing.

<u>Collectors</u>: Herbivores filter-feeding on phytoplankton and detritivores feeding on FPOM. Food particle size generally less than 1000 microns.

<u>Scrapers</u>: Herbivores feeding on periphyton. Food particle size less than 1000 microns.

<u>Predators</u>: Carnivores feeding by swallowing or piercing prey. Food particle size generally larger than 1000 microns.

Benthic invertebrates have been categorized into these functional groups, and this information has been summarized in Merritt and Cummins (1978). These are general classifications and there are many exceptions. For example, Rhyacophilidae (Trichoptera) larva generally are predaceous, however, a few Rhyacophilidae species are herbivores. Another Trichopteran, <u>Glossoma nigrior</u>, feeds primarily on periphyton in Linesville Creek, Pennsylvania, but on detritus in Augusta Creek, Michigan. Differences in feeding habits result from changes in the dominant available food type and age-specific variations within a population (Cummins, 1973).

In low-order streams, with high quantities of CPOM, shredding organisms should dominate. With increasing stream size and a change from CPOM to FPOM and UPOM, the dominant functional group changes. This change has been described in several studies (Gray et.al. 1983, Hawkins and Sedell 1981, Minshall et.al. 1983), while Hawkins et.al. (1982) found no correlation between a dominance of shredding organisms and a closed canopy typical of low order Oregon Cascade streams. This discrepancy with the River Continuum Concept was attributed to inaccurate feeding classifications of taxa, or the influence of upstream waters on downstream communities.

#### Trophic Structure of the Stream Ecosystem:

Functional groups along the stream continuum are associated with each other by their trophic relationships. The pathways of energy flow among trophic levels are well-summarized by Cummins (1964) (Fig. 2).

Generally, allochthonous energy input is of greater importance than autochthonous energy input in streams. For example, in Bear Brook, New Hampshire, autochthonous production contributed only 1 % of the total energy input, while allochthonous material contributed 99%. Other studies on rivers and streams indicate that allochthonous material is far more important as a food source than autochthonous material (Chapman and Demory 1963, Minshall 1967, Minshall 1968, Nelson and Scott 1962).

The energy budget of stream ecosystems consists of this allochthonous and autochthonous energy input, and of heat loss via respiration and material loss through stream flow as energy outputs. Because aquatic ecosystems are complex, few studies have attempted to quantify their complete energy budgets (Teal 1957, Odum 1957, Fisher and Likens 1973). The Bear Brook study by Fisher and Likens (1973) illustrates the complexity of the stream ecosystem energy budget (Fig. 3). As can be seen, allochthonous



Fig. 2. Paths of energy flow in a woodland stream ecosystem (adapted from Cummins 1964).

energy input comes in a variety of forms, e.g., CPOM, FPOM, and, is far more important than autochthonous energy input.

The maintainance of the detrital pool, which is the primary source of all sizes of particulate organic material for downstream functional feeding groups, is important in the stability of the stream ecosystem. Ecosystems with a high flow-through of energy, e.g., streams, have a low energy efficiency, which results in reduced stability or maturity (Fisher and Likens 1972), (Fig. 3). Streams reduce energy flow-through rates with retention structures such as organic debris dams (log jams or branches), which are important in the retention of organic matter (Bilby and Likens 1980, Bilby 1981). Although these "dams" are primarily found in low order streams, they may have an effect on higher order streams by controlling the rate and quantity of organic matter energy export to downstream communities. Retention devices also reduce scouring and downstream drift of invertebrates thereby allowing an increase in invertebrate standing crop which enhances organic matter processing and invertebrate productivity (Minshall et.al. 1983).





# Physical Factors Affecting Microdistribution of Benthic Organisms:

Along a stream continuum, benthic habitat characteristics are not homogeneous. Differences in macroenvironmental characteristics (e.g., increased stream size or riparian vegetation) cause changes in the microhabitat of the benthic community (e.g., changes in current velocity, substrate size and texture, sedimentation, and food availability). Differences in microhabitat characteristics cause changes in the distribution and composition of the benthic community. How these changes in the microhabitat affect the benthic community has been the subject of many investigations into benthic community dynamics (see Hynes 1970 for a comprehensive review). Although the most important microhabitat characteristics will be discussed individually, these characteristics interact to produce a benthic community structure at a specified locale in a stream.

<u>Current velocity</u>: Certain taxa select specific ranges of current velocity, while other taxa are more general in their current selection. This may be a behavioral response (to avoid being swept away), a physiological response (a need for well-oxygenated water), or an ecological response (a selection for certain prey). Chutter (1969), Rabeni and Minshall (1977), and Reice (1977) used multivariate analyses to study current velocity in the context of the complex variable it is, i.e., the relationship among substrate characteristics, food availability, and current velocity. These studies found that current velocity alone does not have a significant relationship with many aspects of the benthic community, e.g., density or composition, but instead interacts with other variables to produce a benthic .

<u>Substrate characteristics</u>: The morphology of the streambed, i.e., substrate characteristics, greatly <u>determines the composition and distribution of benthic</u> organisms. Substrate composition, which is greatly determined by the geologic and vegetational characteristics of a given region, determines the chemical and biological nature of the benthic microhabitat by affecting the availability of food, oxygen, and space for living (McClelland and Brusven 1980). Cummins (1962) suggests that "Substrate particle size may serve as a common denominator in benthic stream ecology". Hynes (1970) and Cummins and Lauff (1969) have reviewed

literature on the relationship between substrate composition and the benthic community composition. These early works describe the hypothesis of a direct relationship between the substrate composition and the benthic community structure, such that, the more complex the substratum, the more diverse the invertebrate fauna (Hynes 1970). A silty-sandy streambed is essentially a two-dimensional substrate, which provides little space for benthic organisms. However, large, loose substrata provide a three-dimensional environment which increases habitat diversity and, therefore, species diversity (Minshall and Minshall 1977, Reice 1974). Hart (1978) observed that species richness increased with increased complexity of artificial shapes, i.e., species richness was significantly higher on irregular shapes versus smooth shapes. Although studies have alluded to the importance of substrate composition, the specific effects of substrate composition on benthic community structure have been difficult to assess due to interactions among substrate composition, current velocity, and food availability (Cummins and Lauff 1969, Rabeni and Minshall 1977), (Fig. 4). Current directly influences the substrate composition, e.g., sand vs. cobblestone, while food availabilty (detritus) depends primarily on both current velocity and substrate size. Large substrate with



General relationships between environmental parameters and the microdistribution of a benthic species in a stream (adapted from Cummins and Lauft 1969), Fig. 4.

given benthic species interacts

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large interstitial spaces retains little detrital material since current, which washes-out detrital material, is greater among the substrate (Rabeni and Minshall 1977).

Cummins and Lauff (1969) suggested a "tolerance versus preference concept" when considering the microdistribution of benthic organisms. For example, environmental parameters, such as, current, temperature, or chemical factors may determine the general range of habitat which an organism will tolerate, but other parameters, such as, substrate size or food availability, may determine the range of habitat an organism will prefer. The difference between the tolerance and preference limits determines the importance of an environmental parameter.

Sedimentation: The relationship between current velocity and substrate composition is modified by the effects of sedimentation. Sediments, produced by natural erosion or man-made disturbance, fill in the interstitial substrate space. The extent of the sedimentation effect depends primarily on current velocity. High velocities reduce the "settling-out" of suspended sediments. Sedimentation reduces the availability of of interstitial spaces, which affects the composition of the benthic community. Heavily-silted streams have a lower diversity (Brusven and Prather 1974) and density of organisms (McClelland and Brusven 1980) and are more unstable which affects benthic variety and density (Chutter 1969). In an experimental study, Cummins and Lauff (1969) investigated the substrate preferences of certain organisms. Silting had a minor effect on the substrate preferences of most organisms studied, however two species, <u>Caenis</u> and <u>Perlesta</u> showed a major preference for non-silted substrates. In another study, collector organism densities were greatly reduced in stream reaches affected by sedimentation due to the damaging effects on the habitat and the filtering/feeding ability of collector organisms (Lemly 1982).

<u>Food</u> <u>availability</u>: Detritus is distributed on the substrate according to current velocity and substrate type. This distribution is greater in areas not exposed to a rapid current, such as pools or low gradient regions, and/or a substrate with sufficient interstitial spaces to retain detrital material. Food availability is important in determining density, diversity, and the composition of the benthic community. (Hawkins and Sedell 1981, Mackay and Kalff 1969, Malmqvist et.al. 1978, Minshall et.al. 1983, Vannote et.al. 1980) However, its specific effects are difficult to define because detrital distribution depends on other factors (e.g., current, substrate composition, etc.) which affect species composition. Benthic community structure was controlled by the amount of detritus present in the substrate in two studies by Egglishaw (1964, 1969). Rabeni and Minshall (1977) found that benthic insects concentrated where detritus was most abundant. Furthermore, while detritivores usually aggregate in detrital material, the effect of detritus availability can be extended to include their predators (Townsend 1980).

In summary, the preceding demonstrates a difficulty in assigning one factor as being more important than another in determining benthic invertebrate microdistribution. Although the specific lifestyle of an organism appears to correlate directly with a particular environmental factor, the correlation may result from several environmental factors working together (Townsend 1980). In general then, current velocity primarily determines substrate composition, while current velocity and substrate composition combine to affect food availability. Sedimentation, which is primarily determined by current velocity, affects substrate composition and food availability.
# Biotic Factors Affecting the Microdistribution of Benthic Invertebrates

Two primary biotic factors influence community structure: competition and predation. Competition generally represents interactions within trophic levels, while predation represents interaction between trophic levels. Competition and predation may also interact, i.e., competition may be reduced or even prevented by the presence of predators (Connell 1975). For example, when Paine (1966) removed a predaceous starfish from a rocky intertidal community, increased competition occurred among the benthos which reduced overall species richness.

<u>Competition</u>: Competition may be of two types: (1) <u>interference</u>, where direct interaction (e.g., aggressive behavior) between consumers occurs, and (2) <u>exploitation</u>, where competing individuals will consume and deplete a consumer-limiting resource (Hart 1983). Examples of limiting resources are food and space. As previously discussed food availability, substrate composition, and sedimentation affect the distribution of benthic organisms. Different species may coexist with reduced niche overlap and, therefore, competition for food and space, by developing different preference levels for environmental factors (Patrick 1975, Cummins and Lauff 1969)

Few experimental studies have analyzed the effects of competition on benthic community structure. Hart (1983) reported the occurrence of interference competition in two studies on caddisfly larvae. He showed that tunnel-dwelling larvae actively defended their homes. Larger instars usually prevailed. When large instars were removed, smaller instars occupied the tunnels. He also showed that larvae of a species of caddisfly defended their territory such that larvae were uniformly spaced on the surface of stones. This territorial defense also prevented co-occurring Baetid nymphs from utilizing the same territory. Peckarsky (1979) found that benthic organisms respond to each others presence, emmigrating towards less-colonized areas to ultimately achieve a uniform optimum density. Reice (1981) suggested that competition is relatively unimportant in determining the microdistribution of organisms in New Hope Creek, North Carolina, since morphologically and functionally similar species shared the same habitat.

Other factors such as predation pressure, food availability, and flooding combine to reduce the importance of competition in streams. These factors prevent streams from reaching an advanced state of equilibrium which would allow competition to occur. Hart (1983) felt that too little research has been done on the role of competition in streams and any suggestions that competition may be unimportant in determining benthic community structure are premature. Competition may occur on too small a scale to be detectable with present methods. Further studies on foraging behavior, habitat selection, growth, and survivorship will help determine whether or not competition plays an important role in determining benthic community structure in streams (Hart 1983).

<u>Predation</u>: Predation modifies community structure by affecting biomass, density, and species diversity of both flora and fauna. For example, herbivores grazing on algae can reduce the density of the dominant algal form which in turn may result in an increased algal diversity. A "snowball" effect follows. Increased algal diversity may increase herbivore diversity which may increase carnivore diversity (Patrick 1975). Predation studies primarily have involved the effects of vertebrate predators on invertebrate prey. In aquatic ecology the majority of research has been done on lentic (still water) ecosystems. For example, zooplankton community structure is partially determined by the presence or absence of fish predators. Brooks and Dodson (1965) found zooplankton sizes in ponds were inversely related to the abundance of fish predators, illustrating the ability for small zooplankton to avoid predation.

Whether or not vertebrate predation similarly effects lotic (running water) communities has recently been questioned. Straskraba (1965) observed a decrease in Amphipod density in stream sections with large populations of fish. Allan (1975) observed increased invertebrate densities in fish-free regions versus fish-inhabited regions of a stream. These studies suggest that fish predation does affect the benthic community of streams. However, recent experimental studies question the role of fish predation in structuring the benthic community. Jacobi (1979) found no significant differences in species composition, density, or biomass of invertebrates between stream sections containing cutthroat trout (<u>Salmo clarkii</u> <u>lewisi</u>) and a stream section without trout. Allan (1982) removed trout from a stream section and observed no

significant change in invertebrate density or composition over a four year period. Reice (1982) used basket enclosures in a stream to exclude fish and salamander predation, and found no significant differences between invertebrate communities exposed to vertebrate predation and those not exposed.

These recent studies indicate that predation may not play a major role in structuring the benthic community of streams. However, studies on prey consumption by fish indicate that fish consume many times the standing crop of benthic invertebrates. This observation is based on fish gut contents, gut clearance rate, meal size, and meal frequency. If a fish predator consumes more than the standing crop of invertebrates, then why does subsequent removal or exclusion of a fish predator not effect benthic community structure? Allan (1982) suggests that indequate sampling of the substrate may understimate the standing crop of invertebrates, prey consumption rates may be overestimated, or that underestimation of the importance of invertebrate drift may explain this discrepancy.

Allan (1983) provided several possible explanations for the role of predators in stream ecosystems:

(1) Many predator species may be "weak interactors" (Paine 1980) in the food web of the stream ecosystem. "Strong" interactors may affect a community by controlling a prey species which is competitively superior to other species in the food web. If a "weak" predator rather than a "strong" predator is removed, then predation may appear to be unimportant.

(2) Dispersal rates of invertebrates are high in streams. Space made available by past predation will be occupied rapidly.

(3) Substrate may sufficiently allow organisms to avoid predators. For example, Brusven and Rose (1981) found that sculpins (<u>Cottus rhotheus</u>) consumed more prey on a sand substrate compared to pebbles or cobbles.

(4) Many salmonids (on which most studies have been done) consume drifting insects and are considered generalist feeders. Consequently, by feeding on whatever is available in the drift, no particular taxon is preyed upon more heavily than another.

(5) It is very likely that in many streams benthic organisms have evolved in the presence of fish predation. This suggests then that stream fauna are well-adapted to co-occurring with predators and should not respond significantly to predator manipulation.

## Mountain-Desert Stream Ecoystems

The majority of research on low order streams in North America has been restricted to Rocky Mountain-Cascade streams in the West-Northwest region and the Appalachian streams of the East-Southeast region of the United States. These streams typically flow through densely forested regions and represent the low order stream described by the River Continuum Concept (Vannote et.al. 1980). However, mountain-desert streams, typical of the Southwestern United States, generally do not conform in several respects to the typical low-order stream described by the River Continuum Concept.

Deacon and Minckley (1974) provided a general description of desert lotic ecosystems. Large rivers arise in areas of high elevation and are supplied by water primarily through snow-melt or precipitation. These large, through-flowing rivers have major tributaries that also arise in high elevation regions, but percolate into the substratum or evaporate, reaching the large river only during periods of high flow or flood. Smaller streams which are found on the open desert floor are usually dry except during rain at which time they may contribute water to larger desert rivers. Desert river ecology is highly variable, however, most desert streams and rivers are subject to long periods of reduced flow followed by scouring floods. Pennak (1979) classified seven distinctive lotic systems. Desert streams were not categorized because of a lack of distinguishing characteristics. However, most desert streams experience either intermittant or discontinuous flow or both. Intermittant streams experience seasonal flow, while discontinous streams flow perenially, but have occasional dry segments where the stream flows underground. Gehlbach (1982) provided many descriptions of mountain-desert streams and rivers of the Southwestern United States.

Hynes (1970) stated that most natural streams are heterotrophic, that is, streams, which are undisturbed, are net consumers of organic matter. Autotrophic streams result from disturbance such as nutrient enrichment from human activity. Minshall (1978) observed that generalizing most streams as heterotrophic was premature. Many streams, e.g., desert streams, have had a minimal amount of research done on them. Desert streams are rarely shaded and have a potential for high rates of photosynthesis and, consequently, a net exportation of organic matter or autotrophy. Busch and Fisher's (1981) study of Sycamore Creek, Arizona suggested that this desert stream was autotrophic. However, they pointed out that it was difficult to make a generalization about the entire stream, because seasonal and daily fluctuations in production and respiration of a stream as a whole are difficult to assess.

Desert lotic ecosystems experience severe flash floods, however, few have studied the flood ecology of these ecosystems (Bane and Lind 1978, Bruns and Minckley 1980, Fisher et.al. 1982, Gray 1981, Gray and Fisher 1981). Bruns and Minckley (1980) and Bane and Lind (1978) observed the influence of severe floods on their desert stream studies. Large decreases occurred in density and biomass after the occurrence of flooding. Severe floods, i.e., floods capable of reordering the streams substrate, may occur seasonally in desert streams usually during summer or early fall rains. Harker (1953) observed that small organisms survive better during severe flooding than larger organisms. Bruns and Minckley (1980) suggested that flooding was a strong selective force for short-lived, small-bodied species in desert streams. Gray (1981) and Gray and Fisher (1981) further studied the effect of flooding on benthic community structure. Floods cause a selection against benthic organisms having dormant life stages in the substrate since these stages are

effectively removed by severe substrate scouring. Benthic organisms in desert streams generally have short life cycles. Short life cycles reduce the risk for organisms from being swept-away by floodwaters. Recolonization of the benthos by aerial migration and downstream drift is rapid after a flood. Fisher et.al. (1982) studied succession in a desert stream following a severe flood. Invertebrate dry weight biomass was reduced by 98%, but within one month invertebrate dry weight biomass was nearly 80% of the original value. Dry weight biomass in Tornillo Creek increased from near zero following a flood to 1.2  $g/m^2$  in two months (Bane and Lind 1978). This rapid ability to recolonize following floods resulted in a high secondary production (135  $g/m^2$  per year) in Sycamore Creek (Fisher and Gray 1981), much higher than the 10 g/m<sup>2</sup>per year calculated for New England streams (Fisher and Likens 1973), and the 50  $g/m^2$  per year calculated for Southeastern streams (Nelson and Scott 1962). High secondary production rates, characteristics of desert streams and their biota. (Fisher and Gray 1981) are attributed to rapid life cycles, multivoltine nature of benthic insects, and long growing seasons.

#### McKittrick Creek

Previous research on McKittrick Creek, a mountain-desert stream in Southwest Texas, has been done primarily by Lind (1969, 1971, 1979a, 1982). This provided a broad analysis of the chemical and biological characteristics of McKittrick Creek.

<u>Chemistry</u>: Water temperature generally varies from 15-25 C depending on the degree of exposure to sunlight. The water temperature is coolest where water flows from underground sources. This occurs frequently along the stream course and, therefore, even in the summer the stream temperature is often considerably cooler than the air temperature. pH values from 7.0 - 8.8, reflecting the limestone substrate of this region. The carbonate-bicarbonate buffer system is often depleted by photosynthetic processes which cause a rise in the pH and a subsequent deposition of marl. Dissolved oxygen levels range from 6.0 - 9.0 mg/l which is well-above stressful levels for benthic organisms.

<u>Flora and Fauna</u>: Riparian and aquatic macrophyte communities are diverse (Table 1). Most benthic fauna previously reported have been identified only to the generic level (Table 2). There are a few exceptions:

- 1. Three species of Dryopidae:
  - a. Helichus confluentus
  - b. H. immsi
  - c. H. triangularis a rare find.

2. Two species of Elmidae:

a. Elsianus texana

b. Heterlmis obesa - first record in Texas.

- 3. Gastropoda Physa virgata
- 4. Odonata <u>Aeshna gynacantha or dugesi</u> (<u>dugesi</u> most likely and, if so, the first report of this species in Texas).
- 5. Trichoptera Helicopsyche mexicana

The benthic fauna is more typical of Rocky Mountain streams to the north rather than the fauna of Northern Mexico. Comparisons of benthic fauna of McKittrick Creek with fauna of the Big Bend region of Texas (300 km south) support this contention. Big Bend fauna are more similar to fauna of Northern Mexico, than to fauna of McKittrick Creek (Lind 1982).

Previous benthic sampling of McKittrick has been restricted primarily to riffle areas. Estimates of the mean benthic invertebrate density of McKittrick Creek were 7000 organisms/m<sup>2</sup>, while densities as high as 20,000 organisms/m<sup>2</sup> were recorded. No benthic invertebrate biomass data have been recorded. Mean species diversity (log base 2) values ranged from 1.7 - 3.0. Diversity values were considered high for such a small stream, and reflect a stable community. Table 1. Riparian and aquatic macrophytes of McKittrick Canyon, Guadalupe Mountains National Park, Texas (after Lind 1979a).

Equisetum laevigatum (Horsetail) Adiantum capillus (Maidenhair fern) Bryum turbinatum (Turbin Moss) Hygroamblystegium irriguum (Spring Moss) Potomogeton illinoensis (Pondweed) Eleocharis montevidensis (Spike rush) Cladium jamaicense (Sawgrass) Carex microdenta (Sedge) Carex hystericina (Porcupine sedge) Juncus interior (Rush) Juncus dudleyi (Rush) Agrostis semiverticillata (Bentgrass) Leersia sp. (Cutgrass) Glyceria striata (Fowl Manna-Grass) Rorippa naturtium-aquaticum (Watercress) Aquilegia chrysantha (Columbine) Galium microphyllum (Bedstraw) Senecio sp. (Groundsel) Najas sp. (Water nymph) Spirogyra sp. Chara sp. (Stonewort) Nitella sp. (Stonewort) 

Table 2. Benthic invertebrates of McKittrick Creek, Guadalupe Mountains National Park, Texas (after Lind 1982).

Platyhelminthes Turbellaria Tricladida Planariidae Dugesia tigrina Aschelminthes Nematophora Gordioidea Gordiidae Gordius sp. Mollusca Gastropoda Basommatophora Physidae Physa sp. Arthropoda Arachnida Hydracarina Crustacea Ostracoda Cytheridae Amphipoda Talitridae Hyalella azteca Insecta Ephemeroptera Baetidae Baetis sp. Leptophlebiidae Choroterpes sp. Habrophlebia sp. Siphlonuridae Isonychia sp. Coleoptera Gyrinidae Gyrinus sp. Dytiscidae Derovatellus sp.

Dryopidae Helichus sp. Psephenidae Psephenus sp. Elmidae Hemiptera Corixidae Graptocorixa sp. Notonectidae Notonecta sp. Naucoridae Ambrysus sp. Gerridae Gerris sp. Diptera Dixidae Dixa sp. Simuliidae Simulium sp. Stratiomyidae Eulalia sp. Tabanidae Tabanus sp. Chironomidae Chironomus sp. Odonata Aeshnidae Aeshna sp. Coenagrionidae Argia sp. Lestidae Lestes sp. Trichoptera Helicopsychidae Helicopsyche sp. Hydroptilidae Agraylea sp.

Table 2. Continued.

Lepidostomatidae <u>Lepidostoma</u> sp. Limnephilidae <u>Hesperophylax</u> sp. <u>Limnephilus</u> sp. Leptoceridae <u>Athripsodes</u> sp. Philopotamidae <u>Wormaldia</u> sp. Calamoceratidae <u>Phylloicus</u> sp. Polycentropodidae Cyrnellus sp.

# STUDY AREA

# Guadalupe Mountains National Park:

This study was conducted in Guadalupe Mountains National Park (104°50' W, 31°55' N), Culberson County, Texas. The Guadalupe Mountains region of West Texas has been an area of interest for many centuries -- to the earliest known inhabitants approximately 12,000 years ago, as a landmark to the people migrating to California in the 1800's, and finally to its establishment as a national park in 1972. Scientists, as well as historians, have been interested in the Guadalupe Mountains region. Both geologically and biologically, the Guadalupe Mountains are unique, and since the preservation of the Guadalupe Mountains in 1972, research has increased (Kurtz and Goran 1978).

<u>Geologic History</u> (Brand and Jacka 1979): The Guadalupe Mountains are the result of geologic events which have occurred over the last 280 million years beginning with the Permian Period. During the early Permian Period, present-day West Texas was inundated by the sea (known as the Permian Basin). Shelf areas around a deep subbasin (Delaware Basin - approximately 2000 feet deep) allowed reef-forming organisms to grow rapidly. Behind developed reefs were shallow lagoons where carbonate, evaporite, and clastic sediments accumulated.

Reef-building continued into the middle Permian Period. Several transgressions and regressions of the sea are recorded, however, there was a tendency towards a smaller, shallower Delaware Basin. Algae, corals, bryozoans, brachiopods, and sponges were most diverse at this time. Towards the end of the middle Permian the sea in the Delaware Basin was reduced to about 1000 feet deep with a shoreline similar to the crest of the present-day Guadalupe Mountains escarpment.

In the late Permian Period the western part of the Permian Basin was uplifted, while the eastern part was pushed downward. The present-day Guadalupe Mountains were probably above sea level, while the Delaware Basin was submerged. Sedimentation began into the Delaware Basin,

and by the end of the Permian Period the Delaware Basin was filled. The Guadalupe Mountains were no more than low hills on a flat plain.

Throughout the Triassic, Jurassic, and Cretaceous Periods (225 - 65 million years ago) little change occurred in the Guadalupe Mountains region. A few Triassic and Cretaceous rocks were deposited with subsequent erosion of most of the Cretaceous rocks.

During the late Tertiary Period (25 - 2 million years ago; Miocene and Pliocene Epochs) West Texas and most of Western North America was vertically uplifted. The Delaware Basin collapsed to form the Pecos Depression - a result of dissolving rock formations by groundwater. Debris eroding from the mountains of the Western Permian Basin filled the Pecos Depression leaving the Guadalupe Mountains buried by Pliocene sands and gravels.

Finally, beginning in the early Quaternary Period (Pleistocene Epoch) erosion by the present-day Pecos River removed sediment from the Pecos Depression leaving the Guadalupe Mountains exposed.

Climate (N.P.S. data): The Guadalupe Mountains experience a variety of climatic conditions depending primarily on the degree of exposure to sunlight and elevation. The basin surrounding the mountains receives approximately 250 mm (10 in) rainfall/year. while. with increasing elevation, rainfall reaches 500-650 mm (20 -25 in) rainfall/year. The average annual rainfall at the park headquarters from 1972 - 1982 was 533 mm (21 in) with a range of 280 - 865 mm (11 - 34 in). The "rainy season" occurs from July to September when evening thunderstorms are common. Rainfall evaporates rapidly around the base of the mountains, but rain falling on the mountains seeps underground and reappears as springs in canyons or around the Guadalupe Mountain escarpment itself. At the park headquarters temperatures range from an average of 6°C  $(42^{\circ}F)$  in January to  $24^{\circ}C$   $(76^{\circ}F)$  in July. Temperatures in the mountains average  $6^{\circ}C$  (10°F) cooler. Temperatures in canyons also average cooler because of less direct sunlight.

<u>Flora and Fauna</u> (Kurtz and Goran 1978): During the last ice age (ending 10 - 15 thousand years ago) West Texas was dominated by coniferous forests, a result of the cooler, wetter climate. As the ice sheets retreated northward climatic conditions became gradually drier in

West Texas. Only in cool and damp areas, i.e., upper mountain regions, and shaded slopes has the forest of the ice age survived. Furthermore, many species of plants and animals which migrated into this region from the north during the ice age have become isolated by the wide expanse of desert which now surrounds the Guadalupe Mountains. Many of these are at the geographic limits of their range, e.g., sugar maple (<u>Acer saccharum</u>), Texas madrone (<u>Arbutus texana</u>), Rocky Mountain juniper (<u>Juniperus scopulorm</u>), and Chinquapin oak (<u>Quercus</u> <u>muhlenbergii</u>). The physical characteristics of this region coupled with fluctuations in the availability of moisture result in a variety of environments for habitation by diverse organisms.

McKittrick Canyon: McKittrick Creek flows almost completely within Guadalupe Mountains National Park, Culberson County, Texas (Fig. 5). The stream arises from two spring-fed sources, one in North McKittrick Canyon; the other in Soouth McKittrick Canyon. McKittrick Canyon and Creek are named after Felix McKittrick, a captain in the 18th Texas cavalry in the 1860's and a settler at the canyon mouth from 1869-1877. A refuge from the army, Mescalero Apache inhabited the canyon much of the 1800's. The last major battle in McKittrick Canyon between the



Fig. 5. Location of pool stations AA-E in McKittrick Creek, Guadalupe Mountains National Park, Texas.

army and the Apache occurred in 1869. (Kurtz and Goran 1978) In the early 1920's Judge J.C. Hunter settled in the region building a lodge 3.5 km from the canyon entrance. Wallace Pratt, a geologist, who believed McKittrick Canyon to be the most beautiful spot in Texas, built a seasonal home at the confluence of the North and South forks in 1930. In the 1930's Wallace Pratt described the region of the confluence of the two canyons as lush in vegetation. The stream flowed through a series of successive pools, each dammed by travertine deposits, each spilling into the next pool. However in 1945 a severe flood drastically altered the stream's appearance. Wallace Pratt said the stream was never as beautiful again (Pratt 1980). Hunter and Pratt felt the Guadalupe Mountain region should be preserved because of its unique beauty. Hunter first proposed a park in 1925, but it was not until 1966 when, with the help of Hunter and Pratt's donations of land, Congress passed legislation declaring this region a National Park. In September 1972 the Park was dedicated and opened to the public (Kurtz and Goran 1978).

South McKittrick Creek, where all sampling was done, arises approximately 10 km above the confluence of the two canyons. Today the streams are dry at this confluence but

flow again for a short distance down-canyon from the confluence before permanently percolating into the substratum about 1.5 km downstream.

South McKittrick Creek is oriented primarily North -South upstream from the confluence and East - West downstream from the confluence. The north-facing slope primarily supports a woodland dominated by gray oak (Quercus grisea complex) and alligator juniper (Juniperus deppeana), while the south-facing slope is dominated by succulent desert and desert woody vegetation. A continuum exists on the canyon floor from the confluence region towards the canyon entrance. From wet-cool Chinquapin oak (Quercus muhlenbergii) to drier-warmer adapted gray oak. Above the confluence in South McKittrick Canyon the stream terrace is dominated by deciduous woodland, i.e. sugar maple, chinquapin oak, and Texas madrone. Further upstream coniferous vegetation density increases, e.g. Pine (Pinus ponderosa), which is intermingled with bigtooth maple and gray oak (Gehlbach 1982).

Throughout its length, McKittrick Creek is shallow with alternating pools and riffles (solid line, Fig. 5) interspaced by dry reaches where the stream flows underground. Most riffles are rarely more than 15-20 cm deep, while pools vary from 15 cm to 100 cm deep with an average of about 30 cm.

Two distinctly different physiographic regions are seen in South McKittrick Canyon. The upper region is characterized by a continually narrowing canyon and steeper gradient (60 m/km). The substrate here alternates between hardened bedrock and fine gravel to cobblestone sized material; the finer material generally is located on the downstream ends of pools. The lower region widens and is characterized by a lower gradient (19 m/km). The substrate in this region is dominated by coarse gravel to cobblestone-sized substrates.

Biotically these two regions differ also. The upper region is fish-free. The only observed vertebrate predators were frogs (<u>Rana sp.</u>), and garter snakes (<u>Thamnophis cyrtopsis</u>). The lower region supports three populations of fish: Rainbow trout (<u>Salmo gairdneri</u>), yellow-belly sunfish (<u>Lepomis auritus</u>), and, although none were observed during this study, the previously reported green sunfish (<u>Lepomis cyanellus</u>) (Lind 1979a). Wallace Pratt states that originally no fish were present in McKittrick Creek. J.C. Hunter stocked the creek in the 1920's with rainbow trout and sunfish obtained from the New Mexico Department of Game and Fish, and there is some question as to whether or not some Cutthroat trout (Salmo <u>clarkii</u>) were included in the original stocking. Pratt reports that he introduced a bass population, but the stocking was not successful (Pratt 1980). Lind (1969, 1971) reported fish in the upper region at the time of his study, however, since no fish were observed in this region during this study, it appears that floods have effectively removed the fish from the upper canyon. Riparian and aquatic macrophytes, such as saw-grass (<u>Cladium</u> <u>jamaicense</u>), horsetails (<u>Equisetum laevigatum</u>), and water cress (<u>Rorippa naturtium-aquaticum</u>), increase in density from the upper region to the lower region.

## METHODS

## Experimental Design:

McKittrick Creek was sampled in the summers of 1982 and 1983. In 1982, I selected five pool stations which represent changes in the macroenvironment of McKittrick Creek along the downstream gradient. Nine or ten cores were collected from each pool on two sampling dates one week apart. Benthic organisms were removed from the core samples, and biomass, density, diversity, equitability, and richness values for invertebrates were recoreded for each pool.

In 1983, the same five pools that I sampled in 1982 and one additional pool were sampled. Ten cores were collected from each pool on two sampling dates one week apart. Again, as in 1982, the biomass, density, diversity, equitability, and richness values for invertebrates were recorded for each pool. However, in 1983, substrate size characteristics, quantities of coarse

detritus, and periphyton biomass also were recorded for each pool. I also collected rainbow trout and sunfish in 1983 to analyze their gut contents.

Data were analyzed to test for significant differences among pools for biomass, density, species diversity, equitability, and species richness values for invertebrates. A step-wise regression analysis was used to find which macroenvironmental characteristics of McKittrick Canyon were most important in explaining the variance in biomass, density, diversity, equitability, and . richness values for invertebrates in McKittrick Creek.

## Field:

Five pools (A, B, C, D, E) were sampled in 1982 (Fig. 5). In 1983, one additional pool (AB) was sampled immediately upstream from pool A. In 1982, the benthic community characteristics of pool A were markedly different from other pools. By sampling an additional pool in the same area of McKittrick Creek, I could determine whether pool A was unique or whether the benthic community characteristics of pool A were typical of this region of McKittrick Creek. Since pool A and this new pool were in the same region, pool A was renamed pool AA, and the new pool was designated pool AB. Each pool had distinguishing macroenvironmental characteristics (Tables 3 and 4). Pools AA, AB, and B are in the lower physiographic region, while pools D and E are in the upper physiographic region. Pool C is in a transitional region between the upper and lower regions. Approximately 50 m above pool C is a 3 m high waterfall which apparently is a barrier to fish movement above this pool.

Benthic Samples (1982): A coring device and hand-operated bilge pump with a hose were used to collect benthic samples. The corer was made of PVC pipe (15.2 cm inside diameter). The corer was pushed approximately 5 cm into the substrate, and substrate was removed with a scoop and stored in a jar. Each substrate type, e.g., cobblestone, gravel, was sampled proportionally. That is, if cobble-sized substrate covered 30% of the pool area, then 30% of the samples were collected from this area. In the case of a bedrock substrate, all algal and detrital material was scooped-up and stored in a jar. The pump, then, was used to collect organisms that had been dislodged and were within the corer. For each sample, approximately 4.5 1 was sieved through a 30 mesh U.S.G.S. sieve (0.6 mm opening) to collect the organisms. These organisms were added to the material already placed in the

	Pool						
Characteristic	A A	A B	В	C	D	E	
Canyon a Gradient(m/km)	19	19	42	61	6.4	64	
Canyon b Width(m)	50	50	30	10	6	6	
Orientation	N - S	N - S	N - S	N - S	NE - SW	NE - SW	
c Sunlight(hrs)	10	10	9	8	10	10	
Watershed Slope(	°) 30	30	35	40	60	60	
Pool width(m)	3	3	3	4	3	3	
Pool length(m)	14	24	22	20	1 1	11	
Pool area(m <sup>2</sup> )	32.3	74.4	71.8	80.2	34.2	29.9	
Pool volume(m <sup>3</sup> )	5.1	14.1	13.8	23.5	9.1	5.3	
Mean depth(m)	0.18	0.18	0.19	0.29	0.27	0.18	
Inlet	Yes	Yes	e No	Yes	Yes	Yes	
Dutlet	f No	Yes	Yes	e No	Yes	Yes	
Substrate	Coarse gravel/ Cobble- stone	Coarse gravel/ Cobble- stone	Fine gravel/ Coarse gravel	Coarse gravel/ Cobble- stone	Fine gravel/ Bedrock	Fine gravel/ Bedrock	

Table 3. Physical characteristics of the macroenvironment at each pool sampled in McKittrick Creek.

c = approximate hours of sunlight reaching pool during summer months.
 d = approximate slope of canyon walls adjacent to pool.

e = except during rainy periods.
f = except during high flows.

	Characteristic							
Pool	Riparian and Aquatic Vegetation	Canopy Vegetation	Fish					
A A	Surrounded by Sawgrass, and horsetail. Water- cress abundant. Algal mats visible.	Pine, Maple abundant. Pool approximately 50% shaded.	Rainbow trout					
ΑB	Approximately 50% less sawgrass and horsetail. Watercress abundant. Lower density of algae.	Pine, Maple abundant. Pool approximately 50% shaded.	Rainbow trout					
В	Sawgrass density similar to pool AB. No horsetail or watercress present.	Pine, Maple about 50% less dense than pool AA and AB. Little or no shade.	Primarily sunfish. Few trout					
с	Sparse sawgrass only.	Few trees. Canyon slope becoming too steep.	Rainbow trou					
D	Sparse sawgrass only. Little more dense than pool C.	Fewer trees than pool C.	No fish					
E	Sparse sawgrass only.	Similar to pool D.	No fish					

jar. All samples were preserved with 70% ethanol with glycerol (11.8 parts 95% EtOH : 3.3 parts distilled water : 1 part glycerol). Nine or ten samples were collected from each pool. Two series of samples were collected --June 28-30 and July 4-7, 1982. Preserved samples were brought back to the laboratory for processing.

Benthic Samples (1983): Samples were collected in an identical manner to the 1982 samples except for the method for selecting sampling points within each pool. Each pool was mapped on a grid. Coordinates were selected using a standard random numbers table. The sampling location, according to these coordinates, was found in the pool and a sample was collected from this location. Ten samples, collected from each pool during July 4-5, 1983 and during July 9-10, 1983, were preserved and brought back to the laboratory for processing.

#### Collection of Substrate for Periphyton Analysis

(1983): Ten grid points were selected in each pool from a random numbers table (see above). Substrate was scooped from each location designated by coordinates selected from the random numbers table, was allowed to dry in the sun for 4-6 hr, and was brought back to the laboratory for periphyton analysis. <u>Collection of Fish (1983)</u>: Rainbow trout were collected from pools AA, AB, and C, and yellow-belly sunfish were collected from pool B. Length, weight, and sex were recorded. Scales were removed to determine the age of each fish. Fish guts were removed from each place and placed in 10% formalin immediately after capture.

#### Laboratory:

<u>Processing of Benthic Samples</u>: Each sample was washed through 10 and 30 mesh U.S.G.S. soil sieves (2 mm and 0.6 mm openings, respectively), and the two subsamples then were separated with sugar flotation (Lind 1979b). In 1982, the substrate was discarded after removal of organisms. In 1983, after removal of organisms, the substrate from each sample was placed in a pan, dried at 100°C for 48 hr and stored. Organisms were usually identified to the generic level (Ward and Whipple 1959, Wiggins 1977).

Removal of Allochthonous Material From Substrate (1983): Substrate was rinsed to remove coarse particulate allochthonous material (particles > 0.5 mm). This allochthonous material was dried in an oven at  $100^{\circ}$ C for 48 hours and then weighed. After removal of allochthonous material substrate was placed in a pan and dried at  $100^{\circ}$ C for 48 hr.

Processing of Substrate From Benthic Samples (1983): Dried substrate was sieved through a series of five U.S.G.S. sieves using a Tyler shaker. Mesh sizes 4, 10, 20, 40, and 60 were used (4.75 mm, 2 mm, 0.85 mm, 0.425 mm, 0.25 mm respectively). Substrate held by the 4.75 mm sieve was hand-sorted into substrate > 16 mm and substrate < 16 mm. Substrate which passed through all sieves (< 0.25 mm) was also collected. Each substrate size class was then weighed.

<u>Processing of Substrate for Periphyton Analysis</u> (1983): An aliquot from each sample was ground into particles < 5 mm in diameter. Five to ten g subsamples of ground substrate were weighed for analysis. The Walkley-Black method (Jackson, 1958) was used to determine g organic matter/g substrate (Appendix A). Four replicate measurements were determined for each sample from each pool. <u>Processing of Fish Guts</u>: All material was removed from each gut, and prey items were separated from algal and detrital material using a dissecting scope. Organisms were identified to the lowest taxonomic level possible. Approximate lengths were recorded for benthic invertebrates present in the gut.

#### Data Analyses:

<u>Analysis of Benthic Organisms</u>: The length and the dry weight (100°C for 48 hr) of each organism were measured and a length/weight relationship for each major taxon was determined using linear regression analysis (Dixon and Brown 1981) (Appendix B). A mean biomass for each pool for taxa was calculated using these regression equations (Appendix C, Table C-1). Rare individuals were weighed to obtain a mean biomass for each pool. Mean Shannon-Weaver (1949) diversity (log base two), mean equitability, and mean species richness values were calculated using numbers of individuals per taxon per sample.

I compared differences between sampling periods for each biotic characteristic with a group t-test (Dixon and Brown 1981) (Appendix B). An analysis of variance (ANOVA)

was used to compare pools for biomass, density, species diversity, equitability, and species richness (Dixon and Brown 1981) (Appendix B). A comparison of means test was used to determine which pool differences were significant. An ANOVA was used to compare mean lengths of common taxa among pools (common = when combined, organisms comprised > 60% of the total density of invertebrates in each pool). Group t-tests also was used to test for significant differences between 1982 and 1983 for each biotic characteristic for each pool. Results were considered significant at the 0.95 level of confidence.

<u>Substrate Analysis (1983)</u>: Substrate was classified by size, using size-frequency plots, according to the methods of Morgans (1956). The size classifications of Cummins (1962) (Table 5) were used. Weights of substrate size classes were expressed as a cumulative percent of the total weight(g) of the substrate in a given sample, and the cumulative percent was plotted against a Phi scale. A Phi scale is the conversion of substrate particle size into whole integers, where Phi is defined as the negative log (base 2) of the particle size(mm). Two statistics were obtained from size-frequency plots: (1) the median Phi unit by weight, and (2) the quartile spread (the number of Phi units between the 25% and 75% particle size
levels). The quartile spread describes the uniformity of substrate particle size. An ANOVA was used to determine significant differences (p < 0.05) for mean Phi values and mean quartile spreads among pools.

Table 5. Substrate particle size (after Cummins 1962).

Substrate Type	Minimum Size (mm)	Phi Scale
Boulder	256	-8
Cobble	64	- 6
Pebble	16	- 4
Gravel	2	- 1
Very Coarse Sand	1	0
Coarse Sand	0.5	- 1
Medium Sand	0.25	2
Fine Sand	0.125	3
Very Fine Sand	0.0625	4
Silt	0.0039	5-8
Clay	0.0039	9

<u>Analysis of Allochthonous Organic Material (1983)</u>: Allochthonous material (Coarse Particulate Organic Matter - CPOM) for each sample was expressed as g dry weight  $CPOM/m^2$ . An ANOVA was used to determine significant differences (p < 0.05) for mean CPOM among pools.

<u>Periphyton Analysis (1983)</u>: Measurements of g organic matter/g substrate were expressed as g periphyton/m<sup>2</sup> for each pool. An ANOVA was used to determine significant differences (p < 0.05) for mean periphyton biomass among pools. Fish Feeding Analysis (1983): A Shannon-Weaver diversity index (H') was calculated for benthic and terrestrial invertebrates present in fish guts. A linear food selection index also was calculated for benthic invertebrates present in the gut (Strauss 1979). This index indicates an avoidance or preference for specific prey items available to the predator. No values were calculated for terrestrial invertebrates since no information on their abundance in the environment was known. A Wilcoxon signed-rank test was used to determine if the mean lengths of individuals of various taxa in fish guts were significantly larger than the mean lengths of the individuals of the same taxa in the benthos. Results were considered significant at the 0.95 confidence level for the Wilcoxon signed-rank test.

Multivariate Analysis of Environmental Data (1983):

A step-wise regression analysis (Dixon and Brown 1981) (Appendix B) was used to determine the relative importance of independent macroenvironmental variables in controlling variance in each dependent biotic variable -- biomass, density, species diversity, equitability, and species richness. Regression equations containing the most important macroenvironmental variables that describe these biotic characteristics were obtained. A minimum F-statistic of 4.0 was necessary before an independent variable could be included in the regression equation.

## RESULTS

<u>Identification of Benthos</u>: Representatives of five phyla were collected from the benthos of McKittrick Creek (Table 6). Arthropoda, class Insecta, comprised the greatest density of benthic invertebrates. Most of the 55 taxa collected were identified to genus.

<u>Benthic Community Structure(1982)</u>: The greatest biomass values (560-970 mg/m<sup>2</sup>) occurred at downstream pool AA and upstream pools D and E, while the least biomass values (170-280 mg/m<sup>2</sup>) occurred at pools B and C (Tables 7 and 8). Density values for organisms were greatest at pool AA (7300-9140 organisms/m<sup>2</sup>) and lowest (2000-3500 organisms/m<sup>2</sup>) at pools B and C. The density values for organisms were not significantly different between pools D and E (4000-5200 organisms/m<sup>2</sup>).

Table 6. Taxonomic List of Invertebrates collected from McKittrick Creek, Guadalupe Mountains National Park, Texas (1982 and 1983). (\* indicates taxa collected independently of core samples and are not considered in analysis of the benthic community).

Platyhelminthes

Turbellaria Tricladida Planariidae <u>Dugesia tigrina</u>

Aschelminthes

Nematophora Gordioidea Gordiidae <u>Gordius</u> sp.

Mollusca

```
Gastropoda
Basommatophora
Physidae
<u>Physa</u> sp.
Pelecypoda
Heterodonta
Spaeriidae
<u>Pisidium</u> sp.
```

Annelida

Oligochaeta

Arthropoda

Arachnida Hydracarina

```
Crustacea
   Ostracoda
      Cytheridae
   Amphipoda
      Talitridae
         Hyalella azteca
Insecta
   Ephemeroptera
      Baetidae
         Baetis sp.
      Leptophlebiidae
         Choroterpes sp.
      Caenidae
         Caenis sp.
   Coleoptera
      Dytiscidae
         Derovatellus sp.
        *Acilius sp.
        *Laccophilus sp.
        *Tropisternus sp.
      Hydrophilidae
         Helochares sp.
         Hydrochus sp.
      Dryopidae
         Helichus sp.
      Elmidae
         Elsianus sp.
         Stenelmis sp.
      Gyrinidae
        *Gyrinus sp.
      Hydraenidae
        *Hydraena sp.
   Hemiptera
      Corixidae
        *Graptocorixa sp.
      Notonectidae
        *Notonecta sp.
      Naucoridae
         Ambrysus sp.
      Gerridae
         Gerris
      Veliidae
         Microvelia sp.
        *Rhagovelia sp.
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Table 6. Continued.

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Table 6. Continued.
      Diptera
         Empididae
         Ceratopogonidae
         Diptera A
         Dixidae
            Dixa sp.
         Simuliidae
            Simulium sp.
         Stratiomyidae
            Eulalia sp.
         Tabanidae
            Tabanus sp.
        *Syrphidae
         Chironomidae
            Orthocladinae
            Tanypodinae
            Chironomini
      Odonata
         Aeshnidae
            Aeshna sp.
         Coenagrionidae
            Argia sp.
         Lestidae
            Archilestes sp.
         Libellulidae
            Paltothemis sp.
      Trichoptera
         Helicopsychidae
            Helicopsyche sp.
         Odontoceridae
            Marilia sp.
         Hydropsychidae
            Hydropsyche sp.
         Hydroptilidae
            Oxyethira sp.
            Hydroptila sp.
            Mayatrichia sp.
         Lepidostomatidae
            Lepidostoma sp.
         Limnephilidae
           *Hesperophylax sp.
           *Limnephilus sp.
         Philopotamidae
            Wormaldia sp.
         Calamoceratidae
           *Phylloicus sp.
         Polycentropodidae
            Polycentropus sp.
```

			POOL		
Taxon	A A	В	C	D	E
Baetis Choroterpes Caenis Oxyethira Hydroptila Mayatrichia Helicopsyche Lepicostoma Wormaldia Marilia Trichop. Pupae Argia Archilestes Anisoptera	12.0(121) 73.9(444) 8.7(77) 69.7(1020) 7.8(88)  6.8(49) 0.8(6)  3.0(16) 22.4(38) 27.0(93) 	50.1(244) 19.1(110) 1.1(12) 0.7(18)   0.1(6) 3.3(20) 4.0(6) 53.7(55) 12.6(12)	18.0(164) 0.4(12)  0.4(6) 0.6(18)  4.6(18) 7.1(12) 5.9(18)  0.4(12)	45.2(238) 5.6(67) 3.0(18)  0.5(6)  1.6(104) 29.2(49) 10.7(30) 72.3(67) 11.0(18) 0.2(12)	62.9(280) 12.7(55) 1.4(6) 0.4(6) 0.6(12) 1.0(6)  0.3(12) 5.2(30) 12.7(30) 38.3(43) 8.8(18) 0.9(18)
Elmidae Larvae Dytiscidae Lar. <u>Helichus</u> Elsianus Stenelmis Helochares	27.6(49) 4.6(55)   	4.8(61) 2.7(35)   	10.0(61) 0.4(6)   4.6(6)	87.1(420) 0.1(6)  100.6(37) 0.4(12) 	41.5(822) 1.7(24) 281.7(40)  1.5(24) 
Derovatellus Ambrysus Tanypodinae Chironomini Ortnocladinae Ceratopogonidae Tabanus Eulalia Diptera A Diptera Pupae Hydracarina Physa Dugesia sp. Oligochaetae Ostracoda	 23.0(740) 32.8(855) 23.0(334) 7.0(109) 18.5(5)  24.7(192) 6.3(33) 2.6(82) (12) 5.8(38) 1.4(22) 125.5(1294)	5.5(6) 15.9(378) 25.4(634) 0.2(6) 16.7(298) 2.9(12) 0.1(6) 2.0(49) 4.3(134) 0.1(6) (12) 	 27.3(701) 36.7(1176) 1.2(24) 6.1(152) 12.1(6)  4.0(49) 3.7(104) 0.7(18) (24) 7.6(24) 	2.2(12) 2.3(12) 26.2(981) 30.5(914)  36.1(451) 69.5(12) 17.6(347) 8.3(116)  (30) 1.2(6) 	3.8(24) 21.0(152) 25.0(780) 38.1(1042) 0.7(24) 38.3(701) 2.6(6) 15.0(12) 43.9(781) 2.8(61) 0.9(12) (6) 3.5(30) 23.6(6) 
n. azteca	130.9(1519)	2.4(18)	10.0(202)	0.4(37)	0.5(0)
Mean (+ S.D.) Total Biomass	672.0 <u>+</u> 271.9	225.4 + 237.9	170.3 + 64.7	565.5 <u>+</u> 428.2	682.5 + 619.1
Mean (+ S.D.) Total Density	7292.0 + 2644.0	2016.0 + 1580.0	2875.0 + 1256.0	4002.0 <u>+</u> 2368.0	5068.0 <u>+</u> 1449.0

Table 7. Mean dry weight biomass-mg/m<sup>2</sup>(mean density of organisms/m<sup>2</sup>) for each taxon per pool for June 28-30, 1982.

			Pool		
Taxon	A A	В	С	D	E
Baatie	11 2/188)	81 0/1122)	21 8/221)	56 3/310)	16 2/2861
Chopotoppos	70 8(658)	12 0(1452)	7 6(10)	16 1(286)	40.2(200)
Caepis	5 9(110)	1 2(67)	0 2(24)	2 0(40)	0 11(6)
Orvethina	116 1(1864)	1.5(01)	1. 4(18)	0.5(6)	0.4(0)
Hydroncila	4 2(47)	0 6(24)	0.1(6)	0 4(12)	2 1 ( 27 )
Mavatrichia	0.3(8)	0.2(6)		1.4(49)	1 7 (55)
Marilia		5.4(24)		15,9(30)	18.6(55)
Helicopsyche	8.0(49)				
Wormaldia		4,4(6)		0.1(6)	2.3(73)
Polycentropus	0.7(6)				
Lepidostoma	0.9(24)			0.5(24)	0.2(6)
Trichop, Pupae	8.3(16)	2.1(6)		8.9(12)	3.8(6)
Argia	74.5(164)	36.6(55)	9.9(6)	36.2(93)	35.6(55)
Archilestes	3.3(8)			8.5(12)	19.6(24)
Anisoptera		1.1(18)	8.9(12)	2.6(43)	0.3(18)
Elmidae Larvae	7.6(23)	13.8(146)	15.1(110)	43.5(506)	73.5(725)
Dytiscidae Lar.	0.8(55)	2.4(43)	0.9(24)	0.4(12)	0.7(24)
Helichus			37.8(6)	308.9(55)	530.1(104)
Elsianus				18.8(6)	14.5(6)
Stenelmis				3.0(24)	1.9(18)
Helochares				0.1(6)	·
Derovatellus		0.3(6)		13.0(73)	9.0(37)
Ambrysus				6.6(24)	9.2(73)
Tanypodinae	30.3(995)	24.0(835)	40.4(1084)	) 32.7(1103)	32.5(1072)
Chironomini	45.4(1104)	20.7(628)	18.6(707)	33.9(1036)	20.4(755)
Orthocladinae	75.3(1003)		0.7(12)		0.5(6)
Ceratopogonidae	9.9(157)	18.5(396)	14.0(219)	21.1(408)	21.0(280)
Tabanus	16.2(16)		13.0(12)	3.2(6)	8.2(6)
Eulalia				0.2(6)	37.5(24)
Diptera A	43.2(298)	11.3(104)	19.3(323)	45.9(823)	31.7(615)
Empididae			0.2(6)		0.0(12)
Simuliidae				0.4(6)	
Diptera Pupae	4.2(78)	2.7(58)	6.6(104)	2.0(37)	0.0(0)
Hydracarina	1.3(39)	0.2(12)		0.4(18)	1.3(18)
Physa	(24)	(0)	(0)	(12)	(24)
Dugesia sp.	14.4(55)	2.4(18)	11.0(18)	(-3(43)	19.7(110)
Oligochaetae	0.9(10)	0.2(12)	2.1(10)	3.7(12)	0.1(0)
Ostracoda	93.4(760)	2 5(20)	11 2/506V	10 0/1001	6 2/61)
M. azteca	140.9(1378)	3.5(30)	44.7(506)	12.3(122)	0.2(01)
Mean (+ S.D.)	792.2 +	250.6 +	276.2 +	707.8 +	965.5 +
Total Biomass	184.9	104.7	152.7	592.4	768.9
Mean (+ S.D.)	9140.0 +	3070.0 +	3497.0 +	5178.0 +	4849.0 +
Total Density	3930.0	969.0	943.0	2779.0	1939.0

Table 8. Mean dry weight biomass-mg/m<sup>2</sup>(mean density of organisms/m<sup>2</sup>) for each taxon per pool for July 4-7, 1982.

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Differences occurred among pools for the taxa contributing most to the biomass for each sampling period (Tables 9 and 10). Amphipoda and Ostracoda contributed 30-40% to the biomass at pool AA, while at pools D and E Amphipoda contributed less than 2% to the biomass and Ostracoda were not collected. Adult Coleoptera were not present at pools AA, B, and C, but contributed 33-65% to the biomass at pools D and E. Diptera were also a major contributor to the biomass (15-35%) of pools AA, D, and E. Ephemeroptera (30-40%) and Diptera (30%) contributed the most to the biomass of pool B, while Ephemeroptera (11%), Amphipoda (11-16%), and Diptera (40-53%) were the greatest contributors to the biomass of pool C.

Amphipoda (15-20%), Ostracoda (8-18%), Diptera (31-40%), and Trichoptera (17-22%) were the greatest contributors to the density at pool AA (Tables 9 and 10). Diptera (67-75%) and Ephemeroptera (18-21%) were the greatest contributors to the density of pool B, while Diptera (57-77%) contributed the most to the density of pools C, D, and E.

Differences in total biomass among pools could not be attributed solely to differences in the mean lengths of taxa among pools. (Tables 11 and 12). <u>Baetis</u>, Choroterpes, Argia, Hyllala azteca, Ceratopogonidae,

Table 9. Percent contribution to mean biomass (mean density) by major taxonomic groups per pool for June 28-30, 1982.

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			Pool		
Taxonomic Group	АА	В	U	Q	L
Ephemeroptera	14.0(8.8)	31.7(18.2)	10.7(6.1)	9.5(8.1)	10.7(6.9)
Trichoptera	16.4(16.7)	3.6(3.0)	7.5(1.9)	7.4(4.7)	3.0(1.9)
Odonata	. 4.0(1.3)	29.9(3.3)	3.7(1.0)	14.7(2.4)	7.0(1.6)
Coleoptera Larvae	4.8(1.4)	3.4(4.5)	6.1(2.3)	15.3(10.6)	6.3(16.7)
Coleoptera Adult	4.	2.4(0.3)	2.7(0.2)	18.1(1.5)	42.1(1.9)
Hemiptera	1	1	1	0.4(0.3)	3.1(3.0)
Diptera	20.1(31.3)	29.9(75.2)	53.4(76.9)	33.1(70.5)	23.6(69.3)
Hydracarina	0.4(1.1)	0.1(0.3)	0.4(0.6)		0.1(0.2)
Amphipoda	20.6(20.8)	1.1(0.9)	11.0(9.1)	1.5(0.9)	0.1(0.1)
Ostracoda	18.6(17.7)	1	-	:	-
Tricladida	0.9(0.5)	l I	4.4(0.8)	0.2(0.2)	0.5(0.6)
01 i gochaetae	0.2(0.3)	1		1	3.5(0.1)

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Table 10. Percent contribution to mean biomass (mean density) by major taxonomic groups per pool for July 4-7, 1982.

			Pool		
laxonomic Group	АА	В	C	D	ы
Sphemeroptera	11.2(10.5)	39.2(21.4)	10.8(8.7)	10.8(11.0)	6.4(10.8)
Trichoptera	17.5(22.0)	5.1(2.1)	.1.7(1.2)	4.1(2:7)	3.0(4.8)
Odonata	9.8(1.9)	15.0(2.4)	6.8(0.5)	6.7(2.8)	5.8(2.0)
Coleoptera Larva	ae 1.1(0.9)	6.5(6.5)	5.8(3.8)	6.1(10.0)	7.7(15.2)
Coleoptera Adul	t	0.1(0.2)	13.7(0.2)	48.6(3.2)	57.5(4.9)
lemiptera	1	1	1	0.9(0.5)	1.0(1.5)
Diptera	28.8(40.0)	30.8(67.1)	40.4(70.9)	19.9(66.8)	15.8(57.0)
Hydracarina	0.2(0.4)	0.1(0.4)	1	.0.1(0.3)	0.1(0.4)
Amphipoda	18.7(15.1)	1.4(1.0)	16.2(14.5)	1.7(2.4)	0.6(1.3)
Ostracoda	11.8(8.3)	4	1	1	1
<b><i>Tricladida</i></b>	1.8(0.6)	1.0(0.6)	4.0(0.5)	1.0(0.8)	0.5(2.3)
Oligochaetae	0.1(0.2)	0.1(0.4)	0.8(0.5)	0.5(0.2)	[1

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			Pool		
Taxon	ΔΔ				 c
Baetis	2.4	3.6	2.8	3.8	4.2
Choroterpes	4.6	3.8	3.0	1.9	4.4
Caenis	2.1	2.0		2.8	4.3
Oxyethira	2.2	1.8	2.5		2.8
Hydroptila	2.4		1.3		2.3
Mayatrichia				1.8	2.0
Wormaldia		1.5		3.5	3.3
Marilia	7.0	5.0	5.7	5.8	5.3
Trichop. Pupae	6.4	7.5	7.5	6.4	5.7
Argia	5.0	7.7	4.3	6.8	6.7
Archilestes				8.8	10.7
Anisoptera		7.0	1.5	1.4	1.4
Elmidae Larvae	5.4	3.9	3.9	4.9	3.3
Dytiscidae Lar.	3.8	3.3	4.0	2.8	3.5
Helichus					7.4
Elsianus		'		5.8	
Stenelmis				1.8	2.2
Helochares			4.5		
Derovatellus		2.0		2.1	2.4
Ambrysus				2.9 .	2.3
Tanypodinae	3.6	3.7	3.7	3.1	3.5
Chironomini	4.6	4.1	3.9	3.8	3.3
Orthocladinae	4.3	3.5	3.8		2.9
Ceratopogonidae	5.3	4.6	4.4	6.5	5.4
Tabanus	18.0	14.0	14.5	13.0	7.0
Eulalia		1.5			4.6
Diptera A	5.2	3.9	4.3	3.5	4.1
Diptera Pupae	3.9	2.8	2.7	2.7	2.7
Hyallela azteca	2.7	3.0	2.1	2.5	2.3

Table 11. Mean length (mm) of each taxon per pool for June 28-30, 1982.

			Pool		
laxon	AA	В	C	D	E
Postic	2 0	2 1	0 6		2 2
Chapat	2.0	3.1	2.0	4.0	3.3
Choroterpes	4.1	3.5	4.3	3.1	2.5
Caenis	2.2	1.7	1.4	2.3	2.5
Oxyethira	2.5		2.7	3.0	
Hydroptila	2.8	1.7	1.3	1.4	2.2
Mayatrichia	2.0	1.8		1.5	2.6
Wormaldia		9.0		3.0	3.4
Marilia		4.9	4.8	6.4	4.4
Trichop. Pupae	6.0	6.5		7.3	7.5
Argia	6.3	7.2	12.0	6.3	7.6
Archilestes	6.3			10.5	10.5
Anisoptera		2.0	9.3	2.8	1.3
Elmidae Larvae	5.4	3.6	5.0	3.6	3.9
Dytiscidae Lar.	1.6	3.4	2.7	2.6	2.6
Helichus			7.0	6.7	6.7
Elsianus				6.0	5.3
Stenelmis				2.0	2.0
Helochares				2.0	
Derovatellus		2.0		2.2	2.1
Ambrysus				2.8	2.5
Tanypodinae	3.5	3.3	3.6	3.1	3.2
Chironomini	4.6	3.6	3.2	3.7	3.4
Orthocladinae	4.8		4.3		5.5
Ceratopogonidae	5.4	4.6	5.7	4.8	5.8
Tabanus	10.0		15.3	14.0	13.0
Eulalia				2.0	4.9
Diptera A	5 7	5 8	4 5	3.9	4.2
Dintera Punae	2 6	2 7	2 6	2 4	2 3
Hvallela aztena	2.0	2 2	2.3	2 4	2.3
allera allera					

Table 12. Mean length (mm) of each taxon per pool for July 4-7, 1982.

Orthocladinae, Tanypodinae, and Chironomini comprised > 60% of the total density of invertebrates of each pool. <u>Baetis</u> were significantly larger (F-ratio = 3.01, p < 0.01) in upstream pools (D and E). Chironomini were significantly larger (F-ratio = 3.65, p < 0.01) in downstream pools (AA and B). No other taxa from the above group were consistently larger or smaller (p > 0.05) in upstream or downstream regions.

The mean species diversity (H') and its richness component (S) had a trend among pools similar to that of biomass (Table 13). Pools A, D, and E had similar diversity and richness values, while pools B and C, which were similar to each other, were significantly less. Insignificant differences occurred among pools for equitability (J) values (Table 13). Values ranged from 0.73 to 0.80 for each sampling period.

No significant differences occurred between sampling periods for any biotic characteristics measured except for species richness values at pool D (Tables 14-18). However, significant variation occurred among pools for biomass, density, diversity, and richness values for invertebrates for each sampling periods (Table 19). Equitability was not significantly different among pools for either sampling period. Pool AA had significantly

Table 13. Mea (J) sam	n ( <u>+</u> S.D.) , and spect pling perio	species d les richne od in 1982	iversity ( ss (S) val	H'), equita ues for ea	ability ch
			Pool		
Characteristi	c A A	В	С	D	E
<u>June</u> 28-30, 1	982				
Diversity (H')	2.78 <u>+</u> 0.53	2.35 <u>+</u> 0.56	2.13 <u>+</u> 0.55	2.69 <u>+</u> 0.38	2.88 <u>+</u> 0.22
Equitability (J)	0.75 <u>+</u> 0.08	0.80 <u>+</u> 0.08	0.73 <u>+</u> 0.08	0.77 <u>+</u> 0.06	0.77 <u>+</u> 0.05
Species Richness (S)	5.86 <u>+</u> 1.24	4.51 <u>+</u> 1.59	4.17 <u>+</u> 1.18	5.59 <u>+</u> 1.36	6.39 <u>+</u> 1.42
July 4-7, 198	2				
Diversity (H')	3.18 <u>+</u> 0.21	2.65 <u>+</u> 0.50	2.45 <u>+</u> 0.47	2.91 <u>+</u> 0.25	2.86 <u>+</u> 0.49
Equitability (J)	0.79 <u>+</u> 0.05	0.77 <u>+</u> 0.08	0.75 <u>+</u> 0.10	0.76 <u>+</u> 0.06	0.78 <u>+</u> 0.05
Species Richness (S)	6.68 <u>+</u> 1.06	5.73 <u>+</u> 1.47	4.94 <u>+</u> 1.14	7.18 <u>+</u> 1.06	6.16 <u>+</u> 1.82

Table	14. Resu tota 1982 for ** =	<pre>lts of gro l biomass with mear July 4-7, p &lt; 0.01;</pre>	oup t-tes of pools n total b 1982. ( ; *** = p	ts compar: AA-E for iomass of * = p < 0. < 0.001).	ing mean June 28-30, pools AA-E .05;
Pool	Sample	Size M	lean S	t. Dev.	I-Statistic
A A	1 0 7	7 <sup>1</sup> 6 8	44.22 39.26	242.32 254.57	0.45
В	9 9	25	50.64 25.42	104.72 237.85	0.29
С	9 9	21 11	76.23 70.32	152.71 64.71	1.92
D	9 9	7 C 5 C	07.84 65.25	592.42 428.17	0.59
E	9 9	96 68	65.49 82.47	768.94 619.14	0.86

		*		
Table	<pre>15. Results of     total dens:     for June 28     of organis;     1982. (* =     *** = p &lt; 0</pre>	group t-tes ity of organ 3-30, 1982 w ms of pools = p < 0.05; 0.001).	ts compari isms of po ith mean t AA-E for 3 ** = p < 0	ing mean ools AA-E total density July 4-7, 0.01;
Pool	Sample Size	Mean	St. Dev.	T-statistic
AA	1 O 7	7291.60 9140.00	2663.54 3930.43	-1.16
В	9 9	2016.22 3070.11	1580.41 969.20	-1.71
С	9 9	2875.33 3496.67	1256.22 942.77	-1.19
D	9 9	4002.00 5178.00	2368.00 2778.80	-0.87
E	9 9	5061.89 4849.11	1449.44 1938.79	0.26

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Table	<pre>16. Results of    species div    28-30, 1982    of pools AA    p &lt; 0.05; *</pre>	group t-t. ersity of with mean -E for Jun * = p < 0	ests compar pools AA-E n species di ly 4-7, 1982 .01; *** = p	ing mean for June iversity 2. (* = p < 0.001).
Pool	Sample Size	Mean	St. Dev.	T-statistic
A A	1 0 7	2.77 3.18	0.53	-1.92
В	9 9	2.35	0.56 0.50	-1.18
С	9 9	2.13 2.45	0.55 0.48	-1.30
D	9 9	2.69	0.38 0.25	-1.48
Е	9 9	2.87 2.85	0.22 0.52	0.11
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1				

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Table	<pre>17. Results of equitabilit 1982 with m for July 4- p &lt; 0.01; *</pre>	<pre>group t-tes y of pools ean equital 7, 1982. ** = p &lt; 0</pre>	AA-E for bility of (* = p < 0 .001).	ing mean June 28-30, pools AA-E .05; ** =
Pool	Sample Size	Mean	St. Dev.	T-statisti
AA	1 O 7	0.75 0.79	0.08 0.05	-1.31
В	9 9	0.80	0.08	0.88
С	9 9	0.73 0.75	0.08	-0.34
D	9 9	0.77 0.76	0.06	0.59
Е	9 9	0.77	0.05	-0.47

Table	18. Results of species ri 28-30, 198 pools AA-E 0.05; ** =	group t-tests comp chness of pools AA- 2 with mean species for July 4-7, 1982 p < 0.01; *** = p	paring mean -E for June s richness of 2. (* = p < < 0.001).
Pool	Sample Size	Mean St. Dev	v. T-statistic
A A	1 0 7	5.86 1.24 6.68 1.06	-1.43
в.	9 9	4.51 1.59 5.73 1.47	-1.70
С	9 9	4.17 1.18 4.94 1.14	-1.42
D	9 9	5.59 1.36 7.18 1.06	-2.75
Е	9 9	6.39 1.42 6.16 1.82	0.30

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Table 19. ANOVA for biotic characteristics of the macrobenthic community of McKittrick Creek for June 28-30, 1982 (I) and July 4-7, 1982 (II). ECM = equality of cell means; E = error; SS = sums of squares; df = degrees of freedom; MS = mean square. (\* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.001).

Biotic Characteristic	Sampling Period	Source of Variance	SS	df	MS	F-Ratio
Biomass	I	ECM	2242828.50	4	560707.13	4.04**
		E	5684801:50	41	138653.69	
	II	ECM	3602768.00	4	900692.00	4.27**
		E	8017033.50	38	210974.56	
Density	I	ECM	********	4	********	10.40***
		E	********	41	3857025.25	
	II	ECM	********	24	********	8.31***
		E	********	38	5241009.00	
Diversity	I	ECM	1.81	4	0.45	44.36**
		E	4.26	41	0.10	
	II	ECM	1.10	4	0.28	3.28*
		E	3.19	38	0.08	
Equitability	I	ECM	0.02	4	0.01	1.20
		E	0.21	41	0.01	
	II	ECM	0.01	24	0.00	0.57
		E	0.18	38	0.00	
Species	I	ECM	31.63	4	7.92	4.25**
Richness		E	76.39	41	1.86	
and a table and	II	ECM	26.19	4	6.55	3.56*
		E	69.99	38	1.84	

\*\*\*\* = values > 10.000.000

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greater invertebrate biomass, density, diversity, and richness values than nearby pools B and C (Tables 20-24). Although pools D and E were farther upstream from pool AA than pools B and C, no significant differences occurred among pools AA, D, and E for invertebrate biomass, diversity, equitability, and richness values. Pool AA had significantly greater invertebrate density values than each other pool.

Benthic Community Structure (1983): Generally, downstream pools AA and AB had the greatest biomass values  $(1000-1200 \text{ mg dry weight/m}^2)$ , while upstream pools C, D, and E had the next greatest biomass values (550-1050 mg dry weight/m<sup>2</sup>). Pool B had the least biomass values  $(220 \text{ mg dry weight/m}^2)$  (Tables 25 and 26). Downstream pool AA had the greatest density values for invertebrates for each sampling period (11700-13850 organisms/m<sup>2</sup>). Pools C, AB, and E had similar densities values  $(8300-10700 \text{ organisms/m}^2)$ . Lesser density values occurred in pools D (5400-6600 organisms/m<sup>2</sup>) and B  $(2700-3000 \text{ organisms/m}^2)$  (Tables 25 and 26).

Different taxa contributed the most to biomass in each pool (Tables 27 and 28). Amphipoda contributed 8-35% to the biomass of pools AA, AB, and C, but contributed

Table	20.	Com poo 4-7 ***	ls ;	ris AA 198 P	on -E 2. <	0	of (*	m = 01	e J )	an un P	is ie <	f 2 0	08.	r 05	t 30 5;	,	ta 1 * *	9	83	pi 2 p	a	as 1 0	s Ji	01	of y ;		
						J	in	e -	2	8-	30	5,	-	1 9	98	2					-	 	-				
Pool		A A				В			-		(	2	-			-		-	D		-	 	-		E		
AA B C D E	0 -2 -0 0	.00 .61 .93 .62	* *		0 -0 1 2		00 31 34 50	*	-		0 2 2	.0.2	0252	* * *	*	-		00		57			-	0		00	
							Ju	 1 y	-	 4 -	7	,	1	98	82	-					-	 	-				
Pool		AA				B			-		(	0				-			D -		-	 	-		E		
AA B C D E	0 - 2 - 2 - 0 0	.00 .34 .23 .36 .75	*		0023		0012	* *	-		0 1 3	. 0	0098	*	*			0		00	)			(	).(	00	

Table	21. Comparis organism 1982 and ** = p <	on of means of pool July 4-7 0.01; **	ans for t s AA-E f , 1982. t* = p <	otal densi or June 28 (* = p < 0 0.001).	lty of 3-30, 0.05;
		June 28	3-30, 198	2	
P001	A A 	в	C	D	E
A A B C D E	0.00 -5.85*** -4.89*** -3.65*** -2.47**	0.00 0.93 2.14* 3.29**	0.00 1.22 2.36*	0.00 1.14	0.00
		July 1	-7, 1982		
Pool	A A	B	С	D	E
A A B C D E	0.00 -5.26*** -4.89*** -3.43** -3.72***	0.00 0.40 1.95 1.65	0.00 1.56 1.25	0.00	0.00

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Table	22. Compar of pool 4-7, 19 *** = 1	ison of me ls AA-E fo 982. (* = p < 0.001)	ans for s p < 0.05;	pecies div -30, 1982 ** = p <	ersity and July 0.01;
		June 2	8-30, 198	2	
Pool	A A	В	С	Ď	E
AA B C D E	0.00 -2.18* -3.23** -0.63 0.28	0.00 -1.02 1.51 2.40*	0.00 2.53 3.42**	0.00 0.89	0.00
		July	4-7, 1982		
Pool	A A	В	с	D	E
A A B C D E	0.00 -2.34* -3.31** -1.08 -1.37	0.00 -1.03 1.35 1.04	0.00 2.38* 2.08*	0.00 -0.31	0.00

Table	23. C 0 4 *	ompar1 of pool -7, 19 ** = p	son of me s AA-E fo 82. (* = < 0.001)	eans for me or June 28 p < 0.05;	ean equita -30, 1982 ** = p <	and July 0.01;
			June 2	8-30, 1982	2	
Pool	A	A	B	C	D	Е
AA B C D E	0. 1. -0. 0. 0.	00 54 55 73 62	0.00 -2.04* 0.79 -0.89	0.00 1.25 1.15	0.00	0.00
Pool	 A		July B	4-7, 1982 C	D	E
A A B C D E	0. -0. -1. -0. -0.	00 70 29 98 27	0.00 -0.63 -0.30 0.46	0.00 0.33 1.09	0.00 0.76	0.00

Table	24. Compari of pool 4-7, 19 *** = p	son of mea s AA-E for 82. (* = p < 0.001).	ns for me June 28- o < 0.05;	ean specie 30, 1982 ** = p <	s richness and July 0.01;
		June 28	-30, 1982	2	
Pool	A A	В	C	D	E
AA B C D E	0.00 -2.14* -2.69* -0.42 0.85	0.00 -0.54 1.69 2.92**	0.00 2.22* 3.45**	0.00 1.23	0.00
		July 4	-7, 1982		
Pool	A A	В	С	D	E
A A B C D E	0.00 -1.39 -2.55* 0.72 -0.77	0.00 -1.24 2.26* 0.66	0.00 3.50** 1.90	0.00	0.00

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			Po	01		
Taxon	A A	AB	В	С	D	E
Baetis Choroterpes Caenis Oxyethira Hydroptila Mayatrichia Helicopsycha	74.0(806) 99.3(543) 8.4(115) 12.3(241) 13.7(192) 37.3(230)	49.8(296) 51.7(356) 9.7(115) 1.8(44) 	14.9(110) 23.9(143) 2.1(17) 	54.1(406) 41.2(220) 1.0(6) 1.2(33) 0.6(17) 1.1(33)	30.1(269) 28.6(159) 5.1(33) 0.2(6) 0.7(11) 0.8(33)	43.1(455) 11.5(71) 0.9(17) 0.4(6) 0.9(33) 0.5(22)
Lepidostoma Polycentropus Wormaldia	6.4(28) 0.3(6)	7.4(44) 0.5(6)		6.4(6)	0.2(6)	0.2(6)
Marilia Trich. Pupae <u>Argia</u> <u>Archilestes</u> Anisoptera Elmidae Larvae Dytiscidae Lar	10.6(44) 10.4(17) 148.5(269)  0.1(6) 3.1(28) . 0.5(17)	9.0(28) 8.1(11) 205.7(258) 11.3(17) 0.1(6) 	2.2(33) 9.3(38)  0.4(17) 13.4(49) 0.1(6)	3.3(17) 22.8(44) 14.5(11) 41.3(38) 22.4(143) 0.1(11)	21.5(71) 82.9(93) 12.7(6) 0.1(11) 29.5(570)	13.6(116) 2.1(11) 42.1(66) 13.4(11) 0.1(6) 22.2(367) 0.2(11)
Helichus Elsianus Stenelmis Derovatelius Hydrocnus Ambrysus	1.7(11)			2.3(11) 2.3(12)	462.0(82) 75.9(22) 1.2(11) 3.1(17) 70.0(11)	267.6(44)  2.3(11) 44.0(71)
Gernidae Tänypodinae Chironomini Ortnocladinae Ceratopogonidae Tabanus Eulalia	1.4(6) 25.8(940) 46.2(1815) 18.5(642) 9.3(274) 70.3(11)	23.9(888) 27.0(1201) 9.2(395) 6.1(175) 17.5(11)	20.6(669) 19.2(899) 1.7(44) 15.7(592) 24.2(17)	40.1(1190) 61.6(4035) 9.8(192) 18.2(658) 77.9(17)	22.1(960) 56.5(2593) 22.1(702) 83.7(28)	19.1(948) 66.5(3426) 0.4(11) 36.7(1008) 57.8(22) 0.1(6)
Diptera A Diptera B Simuliidae Diptera Pupae Hydracarina Physa Pisidium	1.6(22) 8.4(44)  1.4(77) 5.5(126) (126) (17)	0.3(6) 0.3(17) 0.1(6) 1.8(60) 13.4(104) (384) (66)	0.3(6) 7.1(220) (44)	4.4(17) 0.2(6) 6.3(356) 0.7(27) (6)	1.3(49) 0.3(5) 2.5(143) 0.5(22) 	18.5(389) 14.9(548) 0.1(27) (11)
Dugesia sp. Gordius Oligochaetae Ostracoda 31 H. azetca 14	50.9(269)  31.0(39) 60.6(3350) 27.7(1393)	99.6(351)  20.8(82) 152.5(1398) 204.4(2001)	1.6(17) 61.4(11) 4.6(66)	12.1(99) 2.3(22) 170.2(2977)	27.0(82) (6) 0.22(17) 	6.4(44) (6) 1.9(17) N (11) 22.6(493)
Mean (+ S.D.) Total Biomass Mean (+ S.D.) Total Density N = biomass < 3	1185.0 <u>+</u> 745.8 11704.0 <u>+</u> 5435.0 0.05 mg/m <sup>2</sup>	$\begin{array}{c} 979.1 \\ 804.5 \\ 8495.0 \\ 7074.0 \end{array}$	222.8 + 244.3 2998.0 + 1632.0	613.3 + 389.7 10698.0 + 4923.0	6557.0 <u>+</u> 2512.0	710.0 + 488.3 8291.0 + 4434.0

Table 25. Mean dry weight biomass-mg/m<sup>2</sup>(mean density of organisms/m<sup>2</sup>) for each taxon per pool for July 4-5, 1983. .

Table	26.	Mean dry	weight biomass-mg/m <sup>2</sup> (mean density of organisms/m <sup>2</sup> )
		for each	taxon per pool for July 9-10, 1983.

	des series and		P	001		
Taxon	A A	A B	В	C	D	E
Raptig	29 1(416)	53 3(526)	23.9(186)	44.2(461)	12 9/148)	14 0/115
Cherry	13 3/553	25.5(220)	B E (77)	0.0/77)	12.9(140)	14.0(11)
Lnoroterpes	13.2(55)	25.0(241)	0.5(77)	9.0(77)	12.0(88)	32.1(219
Caenis	20.8(192)	5.4(115)	2.9(66)	2.1(28)	0.5(33)	3.2(37)
Oxyethira	24.4(537)	2.6(66)		1.3(44)		
Hydroptila	1.0(22)	0.1(6)	0.2(6)	0.5(11)	0.7(17)	0.6(17)
Mavatrichia	0.1(6)		0.1(6)		0.4(22)	0.7(28)
Heliconsyche	42 5(225)	32,1(77)				
Legidostoma	27 4(82)	26 0/40)				
Polycostoona	21.4(02)	50.3(437				
rorycentropus		200				
wormaldia						
Marilia	2.9(6)	2.9(6)	4.6(44)		1.3(33)	6.0(50)
Trion. Pupae	1.9(6)					
Argia	120.3(159)	208.1(280)	31.0(55)	56.8(44)	44.9(88)	25.9(55)
Archilestes	2.9(6)				5.7(6)	6.2(17)
Anisontera			20.4(34)	16.3(44)		0.3(17)
Elmidaa lamua-			2 1/201	20 1/225	15 5/262	20 5/710
Dimiuae Larvae			2.1(30)	20.1(225)	13.5(203)	30.5(113
Dytiscillae Lar	. 1.7(22)		1.0(0)	0.1(11)	0.4(6)	0.3(17)
Helichus		33.1(6)		56.2(11)	162.6(33)	169.9(33)
Elsianus					20.9(6)	18.7(6)
Stenelmis						3.2(33)
Derovatellus					9,9(44)	12.6(33)
Hydrochus						9.2(6)
Ambrugue					1 3/11)	17 6(03)
Knorysus		0.01161			1.51117	11.01937
nemiptera A	* * * * *	0.2(10)				
Gerridae	2.3(0)					
Microvelia						2.5(6)
Tanypodinae	57.6(1754)	25.4(674)	23.8(718)	32.5(1102)	15.0(565)	27.8(120
Chironomini	108.2(3514)	49.3(1316)	19.8(642)	47.9(3174)	54.3(2566)	78.7(351
Ortnocladinae	29.8(746)	15.4(624)	0.4(17)	7.6(181)	0.5(22)	1.7(55)
Ceratopogonida	e14.0(411)	2,2(115)	7,1(302)	14,9(603)	35.6(855)	65.6(251
Tabaana	61 0/111	66 2(11)	38 2/61		108 11/11/1	8 1/61
Laballus	01.01117	00.3(11)	20.3107		100.4(44)	0.1107
Eulalia	0.1(6)					
Dixa	1.6(11)					
Diptera A	1.2(11)		0.5(11)	11.5(71)	0.1(6)	30.8(625
Diptera B	0.2(0)			0.2(0)		
Simullidae						
Diptera Pupae	22.612081	10.0(115)	11.5/3071	6.413291	4.4(148)	16.0(565
Hudrananina	11 2/1271	12 0(121)	0 1(6)	0 7(11)	1 0/27	1 0(22)
nyur acar ina	11.6(131)	(2001)	0.1(0)	0.1(11)	1.0(21)	1.91221
rnysa	(121)	(350)	(00)	(55)	(0)	
PISICIUM	(27)	(44)				
Dugesia sp.	46.6(258)	52.6(400)	0.5(11)	8.6(60)	8.4(55)	13.2(44)
Gordius						(6)
Oligocnaetae	46.7(17)	3.0(28)	30.8(17)	0.5(17)	0.7(11)	2.0(22)
Ostracoda 3	73.4(3471)	395.8(3679)			0.6(6)	
H aztana	20 0(1404)	134 1(1701	3 4177)	179 7 (4112)	15 5(262)	36 4/600
n. acceda	30.0(1404)	134+111721		112-114112)	13.5(205)	50.41009
Mann /+ C D \	1155 3 -	1168 4 6	221 1	E16 0 -	531.3 .	625 6
mean (= 5.0.)	100.3 *	1100.4 -	221.1 +	510.0 +	231.2 -	033.0 .
lotal Blomass	657.8	1237.2	. 230.5	282.9	361.7	205.
Mean (+ s.n. v	12852 0 +	10592 0 .	2692 0 +	10674 0 +	5372 0 +	10706 0 .
	13053.0 -	10720 -	2092.0 4	10014.0 -	2002	5070
			1400.0			

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Table 27. Percent contribution to mean biomass (mean density) by major taxonomic groups per pool for July 4-5, 1983.

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			Poo	01		
Taxonomic Group	AA	AB	В	U	D	ω
Ephemeroptera	15.3(12.7)	11.4(9.5)	18.4(9.1)	15.7(5.9)	6.0(7.0)	7.8(6.6)
Trichoptera	7.7(6.6)	7.3(2.7)	1.0(1.1)	2.0(1.0)	2.2(2.1)	2.5(2.4)
Odonata	12.5(2.4)	22.4(0.4)	4.4(1.9)	12.8(0.9)	8.9(1.7)	7.9(2.5)
Coleoptera						
Larvae	0.3(0.4)	1	6.1(1.8)	3.7(1.4)	2.8(8.7)	3.1(4.6)
Coleoptera						
Adult	0.1(0.1)	1	1	0.4(0.1)	54.2(2.0)	38.0(0.7)
Hemiptera	0.1(0.1)	0.1(0.9)	11	1	6.5(0.2)	6.2(0.9)
Diptera	15.3(33.1)	8.8(34.3)	39.8(82.8)	35.6(60.7)	17.6(68.5)	30.2(76.8
Hydracarina	0.5(0.1)	1.4(1.3)	1	0.1(0.3)	0.1(0.3)	N (0.3)
Amphipoda	10.8(12.1)	20.9(24.9)	2.1(2.2)	27.8(27.9)	2.8(7.9)	3.2(5.5)
Ostracoda	30.4(29.0)	15.6(17.4)	1	1	1	N (0.1)
Tricladida	4.3(2.3)	10.2(4.5)	0.7(0.6)	2.0(0.9)	2.6(1.3)	0.9(0.5)
01 i gochaetae	2.6(0.3)	.2.1(1.0)	27.6(0.4)	0.4(0.2)	N (0.3)	0.3(0.2)

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Table 28. Percent contribution to mean biomass (mean density) by major taxonomic groups per pool for July 9-10, 1983.

			Pod	01		
Taxonomic Group	AA	AB	В	U	Q	ы
Ephemeroptera	5.5(4.8)	7.2(8.7)	16.0(12.5)	10.7(5.3)	4.9(5.0)	7.8(3.5)
Trichoptera	8:7(6.4)	6.4(2.0)	.2.2(2.1)	0.3(0.5)	0.5(1.3)	1.1(1.0)
Odonata	10.7(1.2)	17.8(0.3)	23.2(3.4)	14.2(0.8)	9.5(1.8)	5.2(0.9)
Coleoptera						
Larvae	0.2(0.2)	1	1.4(1.7)	3.9(2.1)	3.0(5.0)	4.8(6.8)
Coleoptera						
Adult	1	2.8(0.1)	I t	10.9(0.1)	36.2(1.5)	33.6(1.1)
Hemiptera	0.3(N)	N (0.2)	1		0.3(0.2)	3.1(0.9)
Diptera	25.7(48.6)	14.5(28.0)	41.5(71.6)	23.4(51.5)	40.9(78.4)	36.0(79.3
Hydracarina	1.0(1.0)	1.1(1.2)	0.1(0.2)	0.7(0:1)	0.2(0.5)	0.3(0.3)
Amphipoda	7.8(10.2)	11.5(16.9)	1.5(2.9)	34.8(38:7)	2.9(4.9)	5.7(5.7)
Ostracoda	32.3(25.3)	33.9(36.1)	1	1	0.1(0.1)	1
Tricladida	4.0(1.9)	4.5(3.9)	0.2(0.4)	0.2(0.6)	1.6(1.0)	2.1(0.4)
01 i gochaetae	4.0(0.1)	0.3(0.3)	13.9(0.7)	0.1(0.2)	0.1(0.2)	0.3(0.2)

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1-6% to the biomass of each other pool. Ostracoda contributed 15-35% to the biomass of pools AA and AB, while contributing less than 0.1% to the biomass in other pools. Adult Coleoptera contributed less than 3% to the biomass of downstream pools AA, AB, and B, up to 10% of the biomass of pool C, and 33-55% to the biomass of pools D and E. Diptera were important contributors to the biomass of each pool (10-42%).

Amphipoda (10-25%), Ostracoda (17-36%), and Diptera (28-49%) were the greatest contributors to density in pools AA and AB (Tables 27 and 28). Amphipoda (28-39%) and Diptera (51-61%) contributed the most to the density in pool C, while Diptera alone (69-83%) contributed the most to the density in pools B, D, and E.

Differences in mean total biomass among pools could not be attributed solely to differences in mean lengths of organisms of various taxa among pools. (Tables 29 and 30). <u>Baetis</u>, <u>Choroterpes</u>, <u>Argia</u>, <u>Hyallela azteca</u>, Ceratopogonidae, Orthocladinae, Tanypodinae, Chironomini, again comprised > 60 % of the total density of invertebrates for each pool. <u>Baetis</u> was significantly larger (F-ratio = 2.76, p < 0.05) in upstream pools than in downstream pools. Chironomini and Tanypodinae were significantly larger (F-ratio = 4.65 and 4.74

Taxon	Pool						
	AA	AB	В	С	D	E	
Baetis	2.6	3.1	3.6	2.5	3.5	2.5	
Choroternes	4.7	4.3	4.4	5.3	4.6	4.8	
Caenis	2.2	2.2	3 4	4.3	3.9	2.4	
Orvethira	2.1	1.8		1.8	1.5	2.8	
Hydroptila	2.3			1.7	1.6	1.5	
Mavatrichia				1 7	1 1	1 3	
Helicopeyche	3 6	4 0					
Lapidostoma	2.0	1 2					
Polycoptpopule	5-5	4.5		8 5			
Wonnaldia	0.0	4.0		0.5	2 8	2.0	
wormaidia	E 1	6 E	2 9	1 8	5.0	2.0	
Thickor Busso	5.9	6.0	5.0	4.0	5.2	4.5	
irichop. rupae	5.0	6.0	2 0	6 1	6 2	4.0	
Argia	1.0	0.1	3.9	11 9	12 0	0.5	
Archilestes	1 5	9.0	1 5	11.0	13.0	10.5	
Anisoptera	1.5	3.0	1.5	0.3	1.3	1.3	
Elmidae Larvae	5.1		0.0	4.0	2.0	3.0	
Dytiscidae Lar.	2.3		3.3	1.1		1.9	
Helichus					6.9	6.7	
Elsianus					6.0		
Stenelmis					2.0		
Derovatellus	2.3			2.3	2.0	2.1	
Ambrysus					6.1	3.1	
Tanypodinae	3.2	2.9	3.1	3.5	2.6	2.5	
Chironomini	3.2	3.0	3.4	2.5	2.9	2.8	
Orthocladinae	2.8	2.1	3.2	3.9		3.0	
Ceratopogonidae	4.0	4.2	3.5	3.3	3.5	3.8	
Tabanus	12.0	15.0	10.0	14.8	14.8	12.9	
Eulalia						1.8	
Diptera A	6.1	2.6	4.5	8.5	3.1	4.2	
Diptera Pupae	2.5	2.3	2.2	2.2	2.2	2.1	
H. azteca	2.5	1.9	2.8	1.6	1.8	1.7	

## Table 29. Mean length (mm) of each taxon per pool for July 4-5, 1983.

Taxon	Pool							
	A A	AB	В	C	D	E		
Baetis	2.3	2.5	2.7	2.4	2.9	2.8		
Choroterpes	5.5	3.6	2.6	3.9	4.6	4.2		
Caenis	2.9	1.9	2.0	1.1	1.1	2.2		
Oxyethira	2.0	1.8		1.5	·			
Hydroptila	2.0	0.8	1.5	2.0	1.8	1.9		
Mayatrichia	1.0		1.3		1.2	1.3		
Helicopsyche	3.5	4.8						
Lepidostoma	4.5	3.6						
Polycentropus	6.0							
Wormaldia								
Marilia	8.0	8.0	4.7		2.5	3.5		
Trichop, Pupae	5.3							
Argia	6.1	6.0	5.6	10.4	5.4	5.5		
Archilestes	7.0				11.0	10.2		
Anisoptera			3.3	3.9		1.2		
Elmidae Larvae			3.6	3.9	2.7	3.1		
Dytiscidae Lar.	2.2		5.5		2.3	2.4		
Helichus		7.0		6.0	6.3	7.1		
Elsianus					5.5	6.0		
Stenelmis						2.0		
Derovatellus					2.1	2.5		
Ambrysus					2.4	2.8		
Tanypodinae	3.4	3.6	3.5	3.3	2.7	2.8		
Chironomini	3.6	3.3	3.5	2.3	2.9	3.1		
Orthocladinae	3.2	2.5	2.6	3.6	2.5	2.6		
Ceratonogonidae	3.6	3.7	3.2	3.3	3.9	3.4		
Tabanus	25.0	11.0	23.0		15.2	12.5		
Fulalia	3.0		23.0					
Dintera A	5.5		3.8	6.9	2.4	3.7		
Distara Pusse	2 7	2 7	2.3	1 9	2 5	2.4		
H aztoca	1 0	1 0	1.6	1 6	1 9	1 8		
n. azueca	1.9	1.7	1.0	1.0				

Table 30. Mean length (mm) of each taxon per pool for July 9-10, 1983.

respectively, p < 0.001) in downstream pools than in upstream pools. All other individuals of the above taxa were not consistently significantly larger or smaller in upstream or downstream regions.

Greatest species diversity (H') values occurred in downstream pools AA and AB (H' = 2.85-3.2) (Table 31). Similar species diversity values occurred for all other pools. Values of H' ranged from 2.48 at pool C to 2.74 at pool D. Equitability (J) values fluctuated among pools (Table 31). Greatest equitability values occurred at pools AB and D (J = 0.78-0.80), while most values ranged from 0.66 to 0.72 for all other pools. Downstream pools AA and AB had the greatest species richness (S) values (S = 6.9-7.6), while pools B and C had the least species richness values (S = 4.5-5.1) (Table 31). Species richness values for pools D and E ranged from 5.6 to 6.6.

No significant differences occurred between sampling periods for any biotic characteristics measured except for the biomass of pool D (Tables 32-36), however, significant differences occurred among pools for biomass, density, species diversity, and species richness values for invertebrates for each sampling period (Table 37). As in 1982, differences in equitability values among pools were not significant for either sampling period. No
			F	001		
Characteristi	C AA	АВ	В	С	D	E
July 4-5, 198	3					
Diversity (H')	2.98 <u>+</u> 0.55	3.20 <u>+</u> 0.45	2.40 <u>+</u> 0.35	2.39 <u>+</u> 0.19	2.74 <u>+</u> 0.47	2.50 <u>+</u> 0.45
Equitability (J)	0.72 <u>+</u> 0.13	0.80 <u>+</u> 0.12	0.78 <u>+</u> 0.10	0.66 <u>+</u> 0.06	0.72 <u>+</u> 0.10	0.67 <u>+</u> 0.09
Species Richness (S)	7.41 <u>+</u> 0.66	7.59 <u>+</u> 1.04	4.53 <u>+</u> 0.93	5.06 <u>+</u> 0.93	6.60 <u>+</u> 1.57	5.89 <u>+</u> 1.15
July 9-10, 19	83					
(H')	2.86 <u>+</u> 0.38	3.10 <u>+</u> 0.42	2.58 <u>+</u> 0.33	2.38 <u>+</u> 0.25	2.43 <u>+</u> 0.61	2.66 <u>+</u> 0.27
Equitability (J)	0.70 <u>+</u> 0.08	0.79 <u>+</u> 0.12	0.80 <u>+</u> 0.07	0.68 <u>+</u> 0.07	0.69 <u>+</u> 0.15	0.77 <u>+</u> 0.07
Species Richness (S)	6.93 + 1.17	7.10 + 0.86	5.28 + 1.17	4.73 + 0.79	5.56 + 1.41	5.82 + 1.20

	total biom 1983 with a for July 9 p < 0.01;	ass of pool mean total -10, 1983. *** = p < 0	<pre>LS AA-E for biomass of (* = p &lt; ).001).</pre>	July 4-5, pools AA-E 0.05; ** =
Pool	Sample Size	Mean	St. Dev.	T-statistic
A A	10 10	1191.3 1151.2	745.8 657.8	0.11
AB	1 0 1 0	979.1 1168.3	804.5 1237.1	-0.41
В	1 0 1 0	222.8 221.1	244.3 230.5	0.02
C	1 0 1 0	615.5 516.9	389.7 282.9	0.65
D	1 0 1 0	1071.2 540.8	534.2 361.7	2.61*
E	1 0 1 0	710.0	488.3	0.42

t-tests comparing mean

lable 33.	total densi 1983 with m for July 9- p < 0.01; *	group t-tests compar ty of pools AA-E for ean total density of 10, 1983. (* = p < ** = p < 0.001).	<pre>ing mean July 4-5, pools AA-E 0.05; ** =</pre>
Pool	Sample Size	Mean St. Dev.	T-statistic
A A	10 10	11620.2 5434.8 13847.8 5593.2	-0.90
ΑB	1 0 1 0	8482.0 7073.6 10590.7 10738.9	-0.52
В	1 0 1 0	2993.9 1631.7 2685.0 1466.0	0.45
C	1 0 1 0	10840.1 4772.1 10674.3 4942.8	0.08
D	1 0 1 0	6552.6 2512.1 5367.5 3091.9	0.94
E	10 10	8288.9 4433.9 10690.6 5977.7	-1.02

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Table	34. Resu: spec 4-5, pool: p < 0	lts of gr ies diver 1983 wit s AA-E fo D.05; **	oup t-test sity of po h mean spe r July 9-1 = p < 0.01	cs compari pols AA-E cies dive 0, 1983. ; *** = p	ing mean for July ersity of (* = p < 0.001)
Pool	Sample	e Size	Mean S	St. Dev.	T-statist
A A	1 ( 1 (	) )	2.97 2.92	0.55 0.44	0.25
AB	1 ( 1 (	0	3.20 3.10	0.45 0.42	0.50
В	1(	0	2.40 2.58	0.34 0.33	-1.20
С	11	0	2.39 2.38	0.19 0.25	0.06
D	1 (	0	2.74 2.43	0.47 0.61	1.30
Ε	1	2	2.50 .	0.45	-0.98

Table 35.	<pre>Results of g: equitability 1983 with mea for July 9-10 p &lt; 0.01; **</pre>	roup t-test of pools A an equitabi 0, 1983. ( * = p < 0.0	A-E for a lity of p * = p < 0 01).	ing mean July 4-5, Dools AA-E D.05; ** =
Pool	Sample Size	Mean S	t. Dev.	T-statistic
АА	10 10	0.72 0.70	0.13 0.08	0.41
AB	1 0 1 0	0.80 0.79	0.12	0.13
В	1 O 1 O	0.78 0.80	0.10 0.07	-0.65
С	1 0 1 0	0.66	0.06	-0.61
D	10 10	0.72 0.69	0.10 0.15	0.44 -
E	10 10	0.67 0.70	0.09 0.07	-1.07

Table	36.	R e S j 1 9 A J * 1	es pe 98-	ul ci E =	t e wf p	s it or	orh	f J O	ch me ul	r n y 1	ol es n ;	1 p s s - *	p 1 *	t- of 0,	- t	e p e 1	st oc 98 P	sl r 33 <	s i	с 0	A.		E Star	r s = )	i: f		Br c <	m J P	e u o o	ar 1 y 0 l	1 . s 05	;	-5	,
Pool		Sar	n p	1 e	-	Si	- - -	e i				1e	- a		-	-		St.				eı			-	T -	- 5	t -	I a I		s	- t	ic	
A A				10	)						76		49	13					0		61	6 7							1	. 1	3			
ΑB				10	)						7		5 1	9					1	•	8	4							1	. 1	4			
В				10	)						2		52	3					0	•	9:	32						-	1	. 6	53			
C				10	)						52		0 7	6 3					000		9:	39							0	. 8	36			
D				10	)	-					6 4		65	0					1	•	5	7							1	. 5	55			
Е				10	)						n tu		8	9					1	•	1 :	5							0	• 1	4			

Table 37. A	NON f M	ICH	fo	r	ri	i c	t k	ic Cr	ee	k	ar f	a	ct	er	11	s t y	4-	-5	,	1	98	he 3	(	na I)	C r	n	be	en J	th ul	l i	c of	c -	10	n m ) ,	u	nit 198
(	II)		E	C	М	-	е	qu	al	1	ty	4	of	C	e	11	r	ne	ar	15	;	Ε		e	rr	0	r		SS	5		S	un	15	0	of
S	qua	re	s;		dſ		•	de	gr	e	es	4	of	f	r	ee	do	D m	;	M.	S	=	m	ea	n	'n	qu	a	re	е.						
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Biotic			Sa	m	pl	ir	g		So	u	rc	e	0	f																						
characteris	tic		P	e	ri	00	1		٧	a	r i	ar	ne	e			SS	5				C	f				N	15					F-	r	a	tio
																							-		• •	-	•	• •		• •		• •		• •		
Biomass					1					1	EC	М		6	53	40	11	14	. 0	0		5	0		12	6	80	3	4.	. 7	5		3	3.	9	**
											E			*	*	* *	* 1	* *	**	*		54			3	2	43	31	3	. 8	8					
					II					1	EC	М		7	2	08	91	15	. 5	0		5			14	4	11	19	5	. 1	3		3	3.	7	7**
											Ε				*	* *	* 1	* *	* *	*		54			3	8	29	92	4.	. 0	0					
Density					I					1	EC	M			*	* *	* *	• *	* *	*		5			* *	*	*		*	* *	*				4	5 * *
											E				*	* *	* 1	**	* *	*		54			* *	*	* 1	* *	*	• •	*					S. 1.
					II					1	EC	M		*	*	* *	* 1	* *	* *	*		5			* *	*	* 1	• *	* 1	* *	*		14		6	5**
											E			*	*	* *	* *	*	* *	*		54			* *	*	* *	* *	* 1	• *	*					
versit	y				I					1	EC	м						5	. 5	5		5							1	. 1	1		6	5.	20	**
	-										Ε							9	. 6	7		54							0	. 1	8					
					II					1	EC	М						3	. 9	9		5							0	. 8	0		1	١.	8	3**
											Ε							8	. 9	2		54							0	. 1	7					
Equitabil	ity				1					- 1	EC	м						0	. 1	5		5							0	. 0	3		10	2.	9	6*
											Ε							0	. 5	5		54							0	. 0	1					
					II					1	EC	М						0	. 1	4		5							0	. 0	3		2	2.	91	8*
											E							0	. 5	2		54							0	. 0	1					
Species					I					1	EC	М						17	. 4	3		5						1	5	. 4	9		13	3.	1	9**
Richnes	S										Ξ						6	53	. 4	0		54							1.	. 1	7.					
					II					1	EC	М					1	+3	. 9	5		5							8	. 7	9		7	1.	1	1 * *
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\*\*\*\*\*\* = value > 10,000,000.00

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significant differences occurred between adjacent downstream pools AA and AB for any biotic characteristics (Tables 38-42). Pools AA and AB had significantly greater invertebrate biomass, species diversity, and species richness values than nearby pools B and C. In 1982, pool AA had a significantly greater invertebrate density value than pools B and C, but in 1983, invertebrate density values at pool C were not significantly different from pool AA. No significant differences occurred among pools AA, AB, and E for invertebrate biomass, density, and equitability values. Pool D, which was similar to pool AA in 1982, was significantly different, in 1983, from pool AA for all biotic characteristics except equitability.

Benthic Community Structure (1982 vs. 1983): Pool AA had the greatest year to year variation in the biotic characteristics. Biomass, density and species richness values increased significantly in 1983 (Tables 43-47). Pool C had significant increases in biomass and density values, but had a significant decrease in equitability values. Pool E had an increase in density values for invertebrates, but had a significant decrease in density and equitability values. Pools B and D were unchanged for their biotic characteristics from 1982 to 1983.

A A (*	-E for July = p < 0.05	y 4-5, 1983 5; ** = p <	and July 0.01; **	9-10, 198 ** = p <`0.	3. 001).
		July 4-5,	1983		
A A	A B	В	C	D	E
0.00 -0.83 -3.80*** -2.26* -0.47 -1.89	0.00 -2.97** -1.43 0.36 -1.06	0.00 1.54 3.33** 1.91	0.00 1.79 0.37	0.00 -1.42	0.00
		July 9-10,	1983		
A A	AB	В	с	D	E
0.00 0.05 -3.38** -2.31* -2.24*	0.00 -3.42** -2.35* -2.29*	0.00 1.07 1.13	0.00	0.00	
	AA (* AA 0.00 -0.83 -3.80*** -2.26* -0.47 -1.89 	AA-E for July (* = p < 0.03) AA AB 0.00 -0.83 0.00 -3.80*** -2.97** -2.26* -1.43 -0.47 0.36 -1.89 -1.06 AA AB 0.00 0.05 0.00 -3.38** -3.42** -2.31* -2.35* -2.24* -2.29* -1.88 -1.93	AA-E for July 4-5, 1983 (* = p < 0.05; ** = p < July 4-5, AA AB B 0.00 -0.83 0.00 -3.80*** -2.97** 0.00 -2.26* -1.43 1.54 -0.47 0.36 3.33** -1.89 -1.06 1.91 July 9-10, AA AB B 0.00 0.05 0.00 -3.38** -3.42** 0.00 -2.31* -2.35* 1.07 -2.24* -2.29* 1.13 -1.88 -1.93 1.50	AA-E for July 4-5, 1983 and July (* = p < 0.05; ** = p < 0.01; ** July 4-5, 1983 AA AB B C 0.00 -0.83 0.00 -3.80*** -2.97** 0.00 -2.26* -1.43 1.54 0.00 -0.47 0.36 3.33** 1.79 -1.89 -1.06 1.91 0.37 July 9-10, 1983 AA AB B C 0.00 0.05 0.00 -3.38** -3.42** 0.00 -2.21* -2.35* 1.07 0.00 -2.24* -2.29* 1.13 0.06 -1.88 -1.93 1.50 0.43	AA-E for July 4-5, 1983 and July 9-10, 198 (* = p < 0.05; ** = p < 0.01; *** = p < 0. July 4-5, 1983 AA AB B C D 0.00 -0.83 0.00 -3.80*** -2.97** 0.00 -2.26* -1.43 1.54 0.00 -0.47 0.36 3.33** 1.79 0.00 -1.89 -1.06 1.91 0.37 -1.42 July 9-10, 1983 AA AB B C D 0.00 0.05 0.00 -3.38** -3.42** 0.00 -2.21* -2.35* 1.07 0.00 -2.24* -2.29* 1.13 0.06 0.00 -1.88 -1.93 1.50 0.43 0.37

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Table	39. Compar of poc (* = p	bls AA-E fo < 0.05;	neans for t or July 4-5 ** = p < 0.	otal dens 5, 1983 an 01; *** p	ity of org d July 9-1 < 0.001).	anisms 0, 1983.
			July 4-5,	1983		
P001	A A	AB	В	C	D	E
AA AB C D E	0.00 -1.50 -4.13*** -0.37 -2.43* -1.59	0.00 -2.63* 1.13 -0.92 -0.09	0.00 3.76*** 1.70 2.53*	0.00 -2.05* -1.22	0.00 0.83	0.00
			July 9-10	, 1983		
Pool	A A	AB	В	C	D	E
AA AB B C D E	0.00 -1.21 -4.14*** -1.18 -3.14** -1.17	0.00 -2.93** •0.03 -1.94 0.04	0.00 2.96** 0.99 22.97**	0.00 -1.97 0.01	0.00 1.97	0.00

Table	40. Compa AA-E (* =	rison of me for July 4- p < 0.05; *	ans for s 5, 1983 a * = p < 0	pecies di nd July 9 .01; ***	versity of -10, 1983. = p < 0.001	pools ).
			July 4-5,	1983		
Pool	A A	AB	В	С	D	E
AA	0.00					
AB	1.20	0.00				
В	-3.04**	-4.24***	0.00			
С	-3.09**	-4.30***	-0.06	0.00		
D	-1.22	-2.45*	1.82	1.87	0.00	
E	-2.49*	-3.69***	0.55	0.61	-1.26	0.00
			July 9-10	, 1983		
Pool	A A	A B	В	С	D	E
AA	0.00					
AB	1.02	0.00				
В	-1.85	-2.88**	0.00			
C	-2.95**	-3.97***	-1.09	0.00		
D	-2.70**	-3.72***	-0.84	0.25	0.00	
E	-1.40	-2.42*	0.46	1.55	1.30	0.00

Table	41. Comp pool (* =	arison of s AA-E for p < 0.05;	means for July 4-5, ** = p < 1	equitabili 1983 and 0.01; ***	ty of pool July 9-10, = p < 0.00	s 1983. 1).
			July 4-5,	1983		
Pool	A A	A B	В	C	D	E
AA	0.00					
AB	1.80	0.00				
В	1.35	-0.45	0.00			
С	-1.20	-3.00**	-2.55*	0.00		
D	-0.03	-1.83	-1.38	1.17	0.00	
Ε	-1.02	-2.82**	-2.37*	0.18	-0.99	0.00
			July 9-10,	1983		
Pool	A A	A B	В	с	D	E
AA	0.00					
AB	2.11*	0.00				
В	2.42*	0.30	0.00			
C	-0.37	-2.48*	-2.79**	0.00		
D	-0.14	-2.25*	-2.56*	0.23	0.00	
	0 30	-1 81	-2 12*	0.67	0.44	0.00

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Table	42. Compar AA-E f (* = J	or July 4- <pre></pre>	ans for sp 5, 1983 an * = $p < 0$ .	ecies ric 1d July 9- 01; *** =	nness of p 10, 1983. p < 0.001	).
		J	uly 4-5, 1	983		
Pool	A A	A B	B	C	D	E
AA	0.00					
AB	0.36	0.00				
В	-5.95***	-6.31***	0.00			
С	-4.86***	-5.23***	1.08	0.00		
D	-1.69	-2.05*	4.26***	3.18**	0.00	
E	-3.14**	-3.50***	2.81**	1.73	-1.45	0.00
		J	uly 9-10,	1983		
Pool	A A	J A B	uly 9-10, B	1983 C	D	E
Pool	A A 0 . 00	A B	uly 9-10, B	1983 C	D	E
Pool AA AB	AA 0.00 0.35	AB 0.00	uly 9-10, B	1983 C	D	E
Pool AA AB B	AA 0.00 0.35 -3.32**	AB 0.00 -3.66***	uly 9-10, B 0.00	1983 C	D	E
AA AB B C	A A 0.00 0.35 -3.32** -4.43***	AB 0.00 -3.66*** -4.78***	uly 9-10, B 0.00 -1.12	1983 C	D	E
AA AB B C D	A A 0.00 0.35 -3.32** -4.43*** -2.76**	AB 0.00 -3.66*** -4.78*** -3.10**	0.00 -1.12 0.56	0.00 1.67	D 0.00	E

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Table	43. Resultotal total with summe toget ** =	ts of gro biomass mean tota r 1983. her for e p < 0.01	oup t-test of pools al biomass (All samp each year) ; *** = p	s compari AA-E for of pools les have . (* = p < 0.001).	ng mean summer 1982 AA-E for been lumped < 0.05;
 D1					
P001	Sample	Size r	iean S	t. Dev.	T-statistic
AA	17 20	72 117	21.59 73.23	241.06 684.69	-2.76**
В	18 20	23	38.03 21.96	178.75 231.15	0.24
С	1 8 2 0	22	23.28	126.15 335.34	-4.08***
D	1 8 2 0	63 80	36.55 02.66	506.77 525.78	-0.99
E	18 20	82	23.98	692.71 384.23	0.82

ladie 44.	total dens summer 198 organisms (All samp) each year) *** = p <	group t-tes sity of organ 2 with mean of pools AA- es have been . (* = p < 0.001).	total dens total dens for summ lumped to 0.05; ** =	ng mean ols AA-E for ity of er 1983. gether for p < 0.01;
Pool S	Sample Size	Mean	St. Dev.	T-statistic
A A	17 20	8052.71 12778.50	3265.42 5514.00	-2.94**
В	18. 20	2543.17 2789.45	1382.54 1513.15	-0.52
С	18 20	3186.00 10757.20	1123.87 4729.38	-6.94***
D	13 20	4589.89 5960.00	2576.69 2808.38	-1.56
Е	18 20	4955.50 9464.75	1664.19 5288.14	-3.46***

Table	45.	Res spe 198 AA- bee p <	ul cie 2 v E f n 1	ts es vit for Lum	of di h s ipe	g ve me um d **	rc an me tc	ou si er og	p ty sp 1 et	t 9 h <	-t of 83 er 0	es es	st 50 50	s ol di (A r ;	c v v l v l v l e *	ei a *	mp AA s s ch	a - - - -	r i E ty p y e F	f f lea	g of esr<	m 	esph.	ar 00 av (*	nm ol e	e! s = )	
								-								- :				-			-		-		
Pool	Sa	ampl	e :	512	e			M	ea	.n				St	••		De	v	•	-	T -	S	t	a t	1	S	tic
AA		1 2	7 0					2 2	.9	4					000	•	47						-	0.	0	4	
В		1 2	8 0					2 2	.5	9					000	•	54 34							0.	1	0	
С		1 2	8 0					22	.2	8					000	•	4721						-	1.	2	7	
D		1 2	8 0					2 2	.7	4					00	•	50							0.	9	1	
Е		1 2	8 0					2 2	.8	6					000	•	38 37							2.	.2	9	×
								-		-						-		-		-			-		-		

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Table	46.	Results equitab with me summer togethe ** = p	of gro ility o an equi 1983. r for o < 0.01	<pre>bup t-tes of pools itability (All sam each year ; *** = p</pre>	ts comparin AA-E for su of pools A ples have b ). (* = p < 0.001).	ng mean nmmer 1982 A-E for Seen lumped < 0.05;
Pool	Sa	mple Si	ze	Mean	St. Dev.	T-statistic
AA		17 20		0.77 0.71	0.07 0.11	1.96
В		18 20		0.78 0.79	0.08	-0.28
С		18 20		0.74 0.67	0.09 0.07	2.58**
D		18		0.77	0.05	1.88

0.70

0.78

0.69

0.13

0.05

0.08

20

18

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Table 47	Results of g species rich 1982 with me AA-E for sum been lumped p < 0.05; **	roup t-tests ness of pool an species r mmer 1983. ( together for = p < 0.01;	<pre>comparing s AA-E for ichness of All samples each year) *** = p &lt;</pre>	mean summer pools s have ). (* = 0.001).
Pool	Sample Size	Mean S	t. Dev. T-	statistic
AA	17 20	6.20 7.15	1.21 0.99	-2.65**
В	18 20	5.12 4.90	1.61 1.07	0.49
С	18 20	4.55 4.89	1.16 0.85	-1.17
D	18 20	6.39 6.08	1.44	0.64
E	18 20	6.27 5.85	1.59 1.14	0.94

<u>Substrate Size Characteristics</u>: Significant differences in mean particle size and size distribution occurred among pools (Table 48). Mean particle sizes (Phi) ranged from -4.45 to -4.79 for pools AA, AB, and C, and from -3.50 to -3.75 for pools B, D, and E (Table 49). The mean quartile spread (Phi) ranged from 1.31 to 1.32 for pools AA, AB, and C, and from 1.67 to 2.07 for pools B, D, and E. No significant differences occurred among downstream pool B and upstream pools D and E for mean particle size and mean quartile spread (Table 50). Also, no significant differences occurred among pools AA, AB, and C for mean particle size and mean quartile spread.

## Coarse Particulate Organic Matter (CPOM):

Significant differences in mean CPOM occurred among pools (Table 48), with the greatest CPOM occurring in pool B  $(234 \text{ g/m}^2)$  (Table 49). Pools C, D, and E had similar quantities of CPOM (95-115  $\text{g/m}^2$ ), while pools AA and AB had the least CPOM (20-30  $\text{g/m}^2$ ). No significant differences occurred among pools AA, AB, C, and D for quantities of CPOM (Table 51). Pool B had significantly greater quantities of CPOM than the other pools. Pool E had significantly greater quantities of CPOM than the other pools AA and AB and AB, significantly lesser quantity of CPOM than pool B, and was not significantly different from pools C and D.

Table 48. ANOVA of pool characteristics of McKittrick for 1983.

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ECM = equality of cell means; E = error; SS = sums of squares; df = degrees of freedom; MS = mean square. (\* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.001).

harantoristins	Source of Variance	55	ЧF	SW	Fratio
			10		
lean Substrate	ECM	33.73	5	6.75	8.13***
article Size	ы	11 .06	109	0.83	•
Juartile Spread	ECM	9.83	5	1.97	10.45***
	ы	20.50	109	0.19	
POM	ECM	587989.44	5	117597.89	***6h.T
	ы	1789691.63	114	15699.05	
eriphyton	ECM	6656.65	5	1331.33	0.71
Jiomass	ы	101410.80	54	1877.98	

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Mean (+ S.D.) substrate characteristics of each pool of McKittrick Creek. Table 49.

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(Ph1)       (g/m <sup>-</sup> )       Blomass(g/m <sup>-</sup> ) $-4.8 \pm 0.4$ $1.3 \pm 0.3$ $20.7 \pm 25.1$ $103.0 \pm 54$ $-4.8 \pm 0.4$ $1.3 \pm 0.5$ $30.3 \pm 80.2$ $121.9 \pm 63$ $-4.8 \pm 0.4$ $1.7 \pm 0.5$ $30.3 \pm 80.2$ $121.9 \pm 63$ $-3.8 \pm 1.2$ $1.7 \pm 0.5$ $234.4 \pm 195.2$ $92.5 \pm 30$	Particle Size Quartile Spread CPOM Periphyton (Phi) (Phi) Biomass(g/m <sup>2</sup> ) Biomass(g/m <sup>2</sup> )	Biomass(g/m <sup>2</sup> ) 103.0 ± 54.6 121.9 ± 63.7 92.5 ± 30.8 90.8 ± 32.1 95.3 ± 37.5	$\begin{array}{c} CPOM\\ (g/m^2)\\ g/m^2)\\ 20.7 \pm 25.1\\ 30.3 \pm 80.2\\ 234.4 \pm 195.2\\ 96.9 \pm 120.9\\ 96.9 \pm 150.7\end{array}$	Quartile Spread (Phi) $1.3 \pm 0.3$ $1.7 \pm 0.5$ $1.7 \pm 0.5$ $1.3 \pm 0.4$ $1.9 \pm 0.5$	<pre>Particle Size     (Phi)     -4.8 ± 0.4     -4.8 ± 0.4     -3.8 ± 1.2     -4.5 ± 1.0     -3.6 ± 1.1</pre>
$-4.5 \pm 1.0$ $1.3 \pm 0.4$ $96.9 \pm 120.9$ $90.8 \pm 32$ $-3.6 \pm 1.1$ $1.9 \pm 0.5$ $96.9 \pm 150.7$ $95.3 \pm 37$	$-4.8 \pm 0.4$ $1.3 \pm 0.3$ $20.7 \pm 25.1$ $103.0 \pm 54.6$ $-4.8 \pm 0.4$ $1.3 \pm 0.5$ $30.3 \pm 80.2$ $121.9 \pm 63.7$ $-3.8 \pm 1.2$ $1.7 \pm 0.5$ $234.4 \pm 195.2$ $92.5 \pm 30.8$ $-4.5 \pm 1.0$ $1.3 \pm 0.4$ $96.9 \pm 120.9$ $90.8 \pm 32.1$ $-3.6 \pm 1.1$ $1.9 \pm 0.5$ $96.9 \pm 120.9$ $90.8 \pm 32.1$	96.2 + 29.5	113.8 + 108.3	2.1 ± 0.6	-3.5 + 1.1

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	50. Compari substra (* = p	te uniform < 0.05; **	ins for sub ity in McK = p < 0.0	littrick Cr 1; *** = p	eek in 19 < 0.001)	83.
		Mean Su	ibstrate Pa	rticle Siz	e	
2001	 ۵ ۵	Δ.R.	 B	с	 D	
AA	0.00					
AB	0.02	0.00				
В	-3.34**	-3.36**	0.00			
С	-1.15	-1.17	2.16	0.00		
D	-4.19***	-4.20***	-0.79	-2.98**	0.00	
E	-4.27***	-4.28***	-1.10	-3.11**	-0.26	0.00
			atasta Uni			
		Sut	strate Uni	formity		
Pool	A A	Sut AB	strate Uni B	formity	 D	E
2001 AA	A A	Sut AB	strate Uni B	formity	D	E
001 AA AB	A A 0.00 0.07	AB 0.00	B	formity	D	E
A A B	AA 0.00 0.07 2.55*	AB 0.00 2.49*	B 0.00	formity	D	E
A A A B B C	AA 0.00 0.07 2.55* -0.03	AB 0.00 2.49* -0.09	0.00 -2.55*	formity C	D	E
A A A B B C D	AA 0.00 0.07 2.55* -0.03 3.91***	AB 0.00 2.49* -0.09 3.84***	0.00 -2.55* 1.30	C 0.00 3.89***	D 0.00	E

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Table 51.	Comparis and peri (* = p <	son of mea phyton bi 0.05; **	ns for coar omass for M = p < 0.01	se partic cKittrick ; *** = p	ulate orga Creek in < 0.001).	nic matte 1983.
		Coarse P	articulate	Organic M	atter	
P001	A A	AB	В'	C	D	E
AA B C D E	0.00 0:24 5.39*** 1.92 1.92 2.35*	0.00 5.15*** 1.68 1.68 2.11*	0.00 -3.47*** -3.47*** -3.04**	0.00 0.00 0.43	0.00 0.43	0.00
		P	eriphyton B	iomass		
Pool	A A	AB	В	С	D	E
AA AB B C D	0.00 0.97 -0.54 -0.63 -0.40	0.00 -1.52 -1.60 -1.38	0.00 -0.08 0.14	0.00		
E	-0.34	-1.32	0.20	0.29	0.06	0.00

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<u>Periphyton Biomass</u>: Significant differences did not occur among pools for mean periphyton biomass (Table 48 and 51). Biomass values ranged from 90-125 g/m<sup>2</sup> (Table 49).

Fish Feeding Analysis: A high diversity was found in fish guts, which indicates that trout and sunfish were euryphagous (Table 52). No clear trends were found to indicate whether fish were feeding primarily on aquatic or terrestrial organisms (Table 52). Fish were feeding opportunistically and not necessarily on the most abundant prev as indicated by the linear food selectivity index (Table 53). Organisms, which were common in the benthos. were not necessarily common common prey items. The more negative the food selectivity index the more a particular prey type was avoided, not found, or not captured. The more positive the value the more a particular prey type was consumed. Most index values were around zero suggesting non-selective feeding. Mean lengths of benthic organisms in fish guts of trout collected from pool AB were significantly greater than the mean lengths of the same benthic organisms in the benthos of pool AB (Tables 54 and 55). No significant differences occurred between the mean lengths of benthic organisms in fish guts and mean lengths of the same benthic organisms in the benthos

Characteristics of fish and diversity of gut contents collected from McKittrick Creek in summer of 1983. (F = female; M = male; RT = rainbow trout; YS = yellow-belly sunfish). Table 52.

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PoollFishSexAge(yr)Length(mm)Weight(gm)% Benthic% TerrestrialAARTF1.0178< 10097.03.0AARTF1.5178< 10090.790.7AARTF1.5170< 10094.054.0AARTF1.5170< 10090.790.7AARTF1.5170< 10094.0100.0ABRTF1.5170< 10084.016.0ABRTF1.25180< 10084.016.0ABRTF2.0230< 10084.016.0ABRTF2.0230< 10084.016.0ABRTF2.0230< 10086.713.3ABRTM1.25240< 10086.713.3ABYSM2.5110< 10086.713.3BYSM2.5110< 10066.733.3BYSF2.22133< 10066.733.3BYSF2.25133< 10066.733.5BYSF2.25133< 10066.733.5BYSF2.25133< 10066.733.5CRTM1.0133< 10066.537.5<				Characte	eristic		6u	t Contents	
AA         RT         F         1.0         178         < 100	Pool	Fish	Sex	Age(yr)	Length(mm)	Weight(gm)	# Benthic	# Terrestrial	•н
AA         RT         F         1:5         178         < 100         46:0         54:0           AA         RT         F         1:5         170         < 100	AA	RT	EL.	1.0	178	< 100	0.79	3.0	2.44
AA         RT         M         1.25         170         < 100         9.3         90.7           AA         RT         F         1.5         160         < 100	AA	RT	EL.	1:5	178	< 100	46.0	54:0	2:62
AA       RT       F       1:5       160       < 100	AA	RT	Σ	1.25	170	< 100	9.3	90.7	2.05
AA         RT         F         1.5         170         < 100         84.0         16.0           AB         RT         F         1.25         180         < 100	AA	RT	E.	1:5	160	< 100	0.06	10:0	3:26
AB       RT       F       1.25       180       < 100       65.0       35.0         AB       RT       F       2.0       230       < 100       64.0       56.0       56.0         AB       RT       F       2.0       195       < 100       65.0       56.0       56.0         AB       RT       F       2.0       195       < 100       65.0       56.0       56.0         AB       RT       M       1.25       240       < 100       66.7       13.3       54.2         B       YS       H       2.5       133       < 100       53.3       46.7       13.3         B       YS       F       2.25       133       < 100       53.3       46.7       33.3         B       YS       F       2.255       110       < 100       53.3       46.7       33.3         B       YS       F       2.255       100       < 100       53.3       46.7       33.3         C       RT       M       1.0       13.3       < 100       65.5       544.5       544.5         C       RT       M       2.255       35.25       33.2       54.5 </td <td>AA</td> <td>RT</td> <td>Ŀ</td> <td>1.5</td> <td>170</td> <td>&lt; 100</td> <td>84.0</td> <td>16:0</td> <td>3.43</td>	AA	RT	Ŀ	1.5	170	< 100	84.0	16:0	3.43
AB         RT         F         1.25         180         < 100         65.0         35.0           AB         RT         F         2.0         230         < 100				+					
AB         RT         F         2.0         230         < 100         44.0         56.0           AB         RT         F         2.0         195         < 100	AB	RT	Ŀ	1.25	180	< 100	65.0	35.0	4.43
AB         RT         F         2.0         195         < 100         86.7         13.3           AB         RT         M         1.25         240         < 100         45.8         54.2           B         YS         M         2.5         133         < 100         45.8         54.2           B         YS         M         2.5         133         < 100         53.3         46.7           B         YS         F         2.5         110         < 100         53.3         46.7           B         YS         F         2.55         110         < 100         53.3         46.7           B         YS         F         2.255         110         < 100         53.3         46.7           B         YS         F         2.255         100         < 100         53.3         37.5           B         YS         F         2.255         100         < 100         61.8         33.2           C         RT         M         1.0         133         < 100         61.8         33.2           C         RT         M         2.0         230         < 100         61.8         33.2 <td>AB</td> <td>RT</td> <td>H</td> <td>2.0</td> <td>230</td> <td>&lt; 100</td> <td>44.0</td> <td>56.0</td> <td>3.74</td>	AB	RT	H	2.0	230	< 100	44.0	56.0	3.74
AB         RT         M         1.25         240         < 100         45.8         54.2           B         YS         H         2.5         133         < 100	AB	RT	H	2.0	195	< 100	86.7	13.3	2.67
B       YS       M       2.5       133       <	AB	RT	Σ	1.25	240	< 100	45.8	54.2	4.11
B       YS       H       2.5       133       <							•		-
B       YS       F       2.5       115       < 100	В	YS	M	2.5	133	< 100	53.3	46.7	2.37
B       YS       M       2.5       110       < 100	В	YS	EL.	2.5	115	< 100	20.0	80.0	1.77
B       YS       F       2.25       100       < 100	В	YS	Ψ	2:5	110	< 100	66.7	33.3	3.69
B       Y.S       F       2.25       95       < 100	В	YS	EL.	2.25	100	< 100	70.6	29.4	3.45
C       RT       M       1.0       133       < 100	В	YS	E.	2.25	56.	< 100	62.5	37.5	3.33
C       RT       M       1.0       133       < 100		•							
C     RT     F     1.5     250     100     45.5     54.5       C     RT     F     2.0     230     < 100	C	RT	Σ	1.0	133	< 100	61.8	38.2	2.70
C         RT         F         2.0         230         < 100         6.5         93.5           C         RT         M         2.25         255         100         22.0         78.0           C         RT         M         2.20         200         < 100	С	RT	£1.	1.5	250	100	45.5	54.5	3.52
C RT M 2:25 255 100 22.0 78.0 C RT M 2.0 200 <100 13.6 86.4	C	RT	ſ.	2.0	230	< 100	6.5	93.5	1.69
C RT M 2.0 200 < 100 13.6 86.4	C	RT	Ψ	2:25	255	100	22.0	78.0	3.16
	С	RT	Σ	2.0	200	< 100	13.6	86.4	2.15

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Table 53.	Mean percent density (mean food selectivity value) of benthic
	organisms in guts of fish from pools AA, AB, B, and C. Linear
	food selection indices only calculated if organism was
	present in the gut. (Pools AA, AB, and $C = trout;$
	pool B = sunfish).

				Po	001			
Organism		AA		AB		В		С
Baetis	4.6	(-0.01)	4.0	(0.01)	7.7	(0.03)	1.6	(-0.03)
Choroterpes	0.5	(-0.02)		'				
Caenis			0.2	(-0.01)				
Oxyethira	0.9	(-0.02)	0.2	(-0.01)				
Hydroptila	0.1	(-0.01)						
Marilia	× .				2.5	(0.01)	0.4	(0.00)
Helicopsyche	1.8	(0.00)	3.6	(0.03)				
Argia	0.4	(-0.01)	1.8	(-0.01)			6.4	(0.06)
Paltothemis							1.0	(0.01)
Helichus			0.6	(0.01)				
Derovatellus			0.4	(0.01)			0.7	(0.01)
Dytscidae Larvae	0.4	(0.00)						
Chironomini	4.1	(-0.17)	1.1	(-0.12)	5.4	(-0.22)	0.4	(-0.34)
Orthocladinae .	2.0	(-0.03)	1.1	(-0.04)				
Tanvpodinae	1.4	(-0.09)			4.5	(-0.20)		
Ceratopogonidae	6.4	(0.04)	0.5	(-0.02)	5.9	(-0.11)	1.3	(-0.05)
Tabanus	0.1	(0.00)	0.2	(0.00)	0.8	(0.01)		
Hydracarina	0.5	(-0.01)	0.4	(-0.01)				
Physa	8.3	(0.07)	19.3	(0.16)	3.5	(0.02)	2.7	(0.03)
Ostracoda	4.6	(-0.22)	8.7	(0.18)	2.0	(0.02)		
H. azteca	22.2	(0.11)	4.5	(-0.15)	0.8	(-0.02)	16.9	(-0.16)

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Mean lengths (mm) of benthic invertebrates in the guts of fish collected from McKittrick Creek (mean lengths (mm) of benthic invertebrates in benthos of pools). Table 54.

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		1004		
Taxon	AA	AB	В	C
Baetis	3.7(2.5)	4.3(2.7)	4.5(3.0)	6.3(2.4)
Choroterpes	3:3(4.8)			
Caenis		3.0(2.1)		1
Oxyethira	2.0(2.0)	2.0(1.8)		
Hydroptila	2.0(2.3)		r t t	1
Marilia		1	3.0(4.3)	5.0(4.8)
Argia	13.5(6.7)	8.1(6.0)		10.8(8.3)
Helichus		6.5(7.0)		
Derovatellus	1	4.3(N)		2.3(2.3)
Dytiscidae Larvae	5.0(2.2)	-+-	[ [	[ 1 1
Chironomini	2.8(3.5)	3.9(3.2)	3.1(3.4)	2.0(2.4)
Orthocladinae	3.5(3.0)	4.0(2.3)	444	111
Tanypodinae	3.5(3.3)	1 1 1	4.1(3.3)	
Ceratopogonidae	3.2(3.8)	4.3(4.0)	3.5(3.4)	5.8(3.3)
Tabanus	8.0(18.5)	25.0(13.0)	16.0(13.4)	1
H. azteca	2.2(2.2)	2.7(1.9)	2.3(2.1)	2.2(1.6)

Table 55.	Results of Wilcoxon signed rank test comparing mean lengths of benthic organisms in fish guts with mean lengths of the same benthic organisms in pools. (T+ = signed rank statistic; * = p < 0.05).	
Pool	Sample Size T+ statistic	
A A	10 27.0	
AB	10 52.0*	
В	7 20.0	
С	6 18.0	

of pools AA, B, and C.

Macroenvironmental Characteristics Determining the Benthic Community Structure: Twelve macroenvironmental variables were used in the step-wise regression analysis (Table 56). A correlation matrix of dependent and independent variables was produced by this regression analysis (Appendix C. Table C-2). Independent variables primarily associated with food availability explained the greatest percent of the variance in biomass, density, species diversity, and species richness (Table 57). A negative correlation with CPOM was most important in explaining variation in biomass  $(R^2 = 0.9166)$  and density  $(R^2 = 0.7159)$ , while the quantity of periphyton was most important in explaining variation in species diversity ( $R^2 = 0.9616$ ) and species richness ( $R^2 =$ 0.7219). No independent macroenvironmental characteristics were important in explaining variance in equitability. Macroenvironmental characteristics associated with substrate characteristics were also important in explaining variance in species richness (Table 57).

Table 56. Macroenvironmental characteristics of McKittrick Creek used in stepwise regression analysis.

Coarse particulate organic matter (CPOM > 0.5 mm, gm/m<sup>2</sup>) Periphyton biomass (gm/m<sup>2</sup>) Mean substrate particle size (Phi) Substrate uniformity (Phi) Pool area (m<sup>2</sup>) Pool volume (m<sup>3</sup>) Mean pool depth (m) Riparian vegetation (% shoreline with macrophyte growth) Canopy (% of pool shaded by woodland vegetation) Sunlight (Mid-summer hours/day) Canyon width (m) Stream gradient (m/km) Table 57. Independent macroenvironmental characteristics explaining variance in dependent biotic characteristics of the macrobenthic community of McKittrick Creek.

Biotic Characteristic	Variance Explained by:	Cumulative R-square	Regression equation
Biomass	CPOM (x) Sunlight (x <sub>2</sub> ) Riparian (x <sub>3</sub> )	0.9166 0.9785 0.9974	$y = -87.57 - 4.16(x_1) + 117.80(x_2) - 2.33(x_3)$
Density	CPOM (x <sub>1</sub> )	0.7159	$y = 12439.55 - 39.32(x_1)$
Diversity	Periphyton (x1)	0.9616	$y = 0.30 + 0.02(x_1)$
Equitability	No variables impo	rtant	
Species Richness	Periphyton (x) Pool Area (x <sub>2</sub> ) Substrate Uniformity (x <sub>3</sub> )	0.7219 0.9416 0.9969	$y = 5.91 + 0.80(x_1) - 0.30(x_2) - 0.21(x_3)$

## DISCUSSION

Benthic community structure in streams is governed both by the microenvironment surrounding the community and the macroenvironment. Macroenvironmental characteristics to a great extent govern downstream benthic community structure in continuous streams, while in discontinuous streams only the macroenvironmental characteristics immediately surrounding the community are relevant. Predictable and discernable spatial variation in benthic community structure results from variation in macroenvironmental characteristics along the downstream gradient (Allan 1975, Gray et.al. 1983, Minshall et.al. 1983). In continuous streams recognition of structural changes requires long distances because upstream waters influence downstream communities. On the other hand, discontinuous streams, such as McKittrick Creek, are comprised of discrete segments, and, since upstream waters do not appear to influence downstream communities, distinct differences in benthic community structure should

occur within short distances along the downstream gradient.

Consequently, one may investigate questions about the role of macroenvironmental variation along a downstream gradient on the benthic community structure of streams. Lacking the influence of upstream waters and because obvious macroenvironmental differences occur along the downstream gradient of McKittrick Creek, I expected pools (see Fig. 5) in discrete stream segments to differ for one or more benthic community characteristics, i.e., density, biomass, species diversity, equitability, and species richness. Pools within a continuous segment, e.g., D and E, should not be significantly different for these benthic community characteristics.

Allochthonous material (detritus), an important food source for stream communities, is provided by riparian vegetation, and greater densities and biomass of benthic invertebrates have been found where detritus was concentrated (Rabeni and Minshall 1977, Egglishaw 1964, 1969). Minshall (1968) concluded that the cause of less invertebrate density, biomass, and diversity in streams was the lack of riparian vegetation. Since vegetation densities increase along the downstream gradient of McKittrick Creek, I expected to find increasing invertebrate densities, biomasses, and diversities along this gradient.

Substrate size in pools appeared to vary along the downstream gradient of McKittrick Canyon. Cummins (1962) suggested that substrate size may serve as the common denominator in benthic stream ecology. Smaller-sized substrates support less density, biomass, and diversity of invertebrates than larger-sized substrates (Hynes 1970). Also, large, loose substrates provide a three-dimensional environment which increases habitat diversity and, therefore, species diversity (Reice 1974). Because substrate size varied among pools, I expected to find less density, biomass, and diversity in pools with a small-sized substrate.

Predation should be considered in evaluating community structure. Established fish populations inhabit downstream pools of McKittrick Creek. Allan (1975) found a greater density of invertebrates in regions of a stream without fish than in regions with fish. But, recent studies indicate that predation may not structure the benthic community of streams (Allan 1982, 1983, Jacobi 1979, Reice 1982). These studies were done on continuous streams where upstream waters influence downstream communities by providing a continuous source of invertebrates for recolonization of downstream regions. Because fish populations in McKitrrick Creek are effectively isolated by dry stream reaches, food resources for trout and sunfish must come from within each discrete stream segment. Also, replacement of benthic prey lost to predation by fish must come from within this discrete stream segment or from aerial sources. Invertebrate drift, which is an important means for invertebrate recolonization of downstream communities in continuous streams. I expected, then, that benthic communities subjected to predation pressures should have less density, biomass, and diversity values than benthic communities not subjected to predation pressures.

To summarize my hypotheses, the greatest density, biomass, and diversity of benthic invertebrates in McKittick Creek should occur where food availability and substrate size and complexity are greatest. Also, regions of McKittrick Creek, which are subjected to predation by fish should have less density, biomass, and diversity of invertebrates than comparable fish-free regions.

To test these hypotheses, McKittrick Creek was first sampled in summer of 1982. Significant differences occurred for benthic community characteristics within a short distance along the downstream gradient as long as these benthic communities were separated by dry reaches. Pools D and E, which were not separated, were not significantly different for any benthic community characteristics. Two trends were apparent in the benthic structure of McKittrick Creek. First, the greatest density, biomass, and species diversity values consistently occurred at downstream pool AA. Second, a distinct shift occurred in the taxa contributing the most to the biomass of downstream pools AA, B, and C and to the biomass of upstream pools D and E (Fig. 6). Adult Coleoptera, which contributed little to biomass in the downstream pools contributed greatly to the biomass of the upstream poools. Amphipoda contributed greatly to the biomass at downstream pools AA and C, but contributed little to all other pools, and Ostracoda, which contributed greatly to the biomass of pool AA contributed nothing to the biomass of the other pools.

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According to my 1982 data, the greatest density, biomass, and species diversity values for invertebrates were in the canyon region with the greatest vegetation


Fig. 6. Percent contribution to total biomass of each pool by Amphipoda, Ostracoda, and adult Coleoptera in summer 1982; density. However, I had expected to find a continuous increase in values of density, biomass, and diversity for invertebrates along the downstream gradient. Upstream regions with the least riparian vegetation density had similar biomass and diversity values as downstream pool AA. Pool B, which had a greater density of riparian vegetation than upstream pools D and E, had significantly less density, biomass, and diversity values for invertebrates. Also, pool C, which had a similar density of riparian vegetation as pools D and E, also had significantly less density, biomass, and diversity values of invertebrates.

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The effect of small-sized substrate on benthic community structure was not expected. Upstream pools D and E, had a smaller-sized substrate than pool AA, but had a similar invertebrate biomass and diversity values as pool AA.

The results of the effects oof fish predators on the benthic community were not consistent. Pools B and C, which had fish, had significantly less density, biomass, and diversity values for invertebrates than pools without fish, but pool AA, which also had fish, had similar invertebrate biomass and diversity values as pools without fish and significantly greater density value than pools without fish. However, which taxa were contributing the most to total biomass was affected. Thus, predation by fish, while not necessarily affecting total biomass, probably were affecting species composition by removing vulnerable prey.

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The 1982 data revealed that differences did occur along the downstream gradient of McKittrick Creek. However, my original predictions about the benthic community structure of this discontinuous stream were not completely supported. This was probably because the interaction of factors, e.g., food availability, substrate size, and predation by fish, was more complex than I perceived. After the 1982 study, high density, biomass, and species diversity values for invertebrates occurred with abundant food, large substrate, and fish predators (e.g., pool AA). Decreased food and fish predation resulted in less density, biomass, and diversity values for invertebrates (e.g., pools B and C). If the fish predator was absent, the food supply was low, and substrate size was small, greater biomass and diversity values for invertebrates once again were recorded (e.g., pools D and E). Density values may be reduced at pools D and E because less space is available among the small-sized substrate. To test this new hypothesis based

on 1982 observations, sampling designed for multivariate analysis was done.

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In 1983, significant differences again occurred among pools for benthic community characteristics as long as these pools were separated by dry reaches. Adjacent pools AA and AB, and D and E were similar to each other respectively. As in 1982, two trends were apparent. First, the greatest biomass, and diversity values for invertebrates were recorded at the furthest downstream pools, that is, pool AA and the newly sampled pool AB, and upstream pools D. and E. Density values, which had previously been greatest at pool AA, were now similar among pools AA, AB, and C. Second, species composition again differed between downstream and upstream pools (Fig. 7). Adult Coleoptera which contributed little to the biomass of downstream pools AA, AB, B, and C, contributed greatly to the biomass of upstream pools D and E. Also, Amphipoda, which contributed greatly to the biomass of pools AA, AB, and C, contributed little to the biomass of each other pool. Ostracoda, which contributed greatly to the biomass at pools AA and AB, contributed little to the biomass of each other pool.





The information obtained from fish gut analysis and the multivariate analysis contradicted several of my a priori predictions about the importance of food availability, substrate size, and predation by fish in determining the benthic community structure of McKittrick Creek. First, variation in biomass and density values was explained best by macroenvironmental characteristics associated with food availability. A negative high correlation with the quantity of coarse detritus explained the majority of variance in biomass and density values among pools. This conflicts with published literature observing that an increase in detritus causes an increase in biomass and density values for invertebrates. Minshall (1968) concluded that the cause of reduced invertebrate density and diversity values in a stream was the lack of riparian vegetation. In a comparison of substrate types as related to the benthos, Mackay and Kalff (1969) found that detritus as a substrate type had a greater density of invertebrates than stone substrates (e.g., sand, gravel, and cobblestone). Rabeni and Minshall (1977) concluded that detritus availability was of primary importance to aquatic insect microdistribution in streams, with more insects found where detritus was concentrated. Egglishaw (1964, 1969) also found greater density and diversity values for invertebrates in concentrated detritus.

By comparing my findings in McKittrick Creek with the findings of other researchers, I formulated hypotheses to explain the occurrence of a negative correlation of coarse detritus with the biomass and density of invertebrates. The dominant source of coarse detritus in McKittrick Creek is maple leaves (Acer saccharum). Kaushik and Hynes (1971) studied the decomposition of leaves in streams, and found that maple leaves decomposed rapidly compared to other species (e.g., beech, alder, and oak). Furthermore, in feeding experiments, Gammarus sp. preferred maple leaves over other leaves. Petersen and Cummins (1974) determined that 80 to 90% of a maple leaf decomposed within 120 days. What is left after this period resembled fine detritus. The greatest period of input of coarse detritus (leaves) into McKittrick Creek is in autumn. Consequently, 80-90% of this leaf fall in the stream should be decomposed by early to late spring.

Cummins and Klug (1979) found that shredding organisms increased in abundance from autumn through spring, while scraper organisms became dominant during the summer. This dominance of scrapers in the summer correlated with the highest seasonal P:R ratio and warmest temperatures. The abundance of shredders corresponds with the seasonal increase of allochthonous input (Anderson and Cummins 1979). Shredders were the dominant functional group only where coarse detritus was greatest (Malmquist et.al. 1978). Young (1978) observed that in streams having a small shredder fauna and a short detritus residence time, leaves were not as important as other food types.

Therefore, in McKittrick Creek shredders should be most abundant in the winter and spring when coarse detritus is the most abundant food source. Few shredders. e.g., Marilia sp. and Lepidostoma sp., were present during the summer of either 1982 or 1983 (Table 58). However, samples collected in spring and winter have vielded the Trichoptera shredders Limnephilus sp., Hesperophylax sp., and Phylloicus sp. These three taxa were not collected during the summer months although empty cases of various shredder taxa were commonly found in benthic samples. The majority of taxa collected during this study were primarily fine detritus feeders; either scrapers or filterers (Table 59). Breakdown of coarse detritus during the winter months would yield fine detritus for fine detritus feeders in the summer. Enhanced breakdown of detritus by shredders is important in providing a supply of food for fine detritus feeders (Short and Maslin 1977, Short et.al. 1980).

Table 58. Percent of the total density of organisms in each pool contributed by each functional group of benthic invertebrates.

		Summer	1982			
	Pool					
Functional Group	AA	AB	В	С	D	E
Collector/Scrapers Predators Shredders Collector/Filterers	70.6 16.0 0.3 13.1		54.4 44.4 0.9 0.3	60.3 39.4 0.3 0.0	54.2 43.0 1.3 1.5	57.5 40.4 1.1 1.0
		Summer	1983			
	Pool					
Functional Group	A A	AB	В	С	D	E
Collector/Scrapers Predators Shredders Collector/Filterers	55.6 16.5 0.6 27.3	57.7 14.1 0.7 27.5	50.6 47.9 1.5	81.2 12.0 0.1	68.8 30.2 0.9	62.5 36.3 1.1

Table 59. Functional groups of organisms collected from McKittrick Creek. (Classifications according Merritt and Cummins 1978).

Functional Group							
Collector/ Scrapers*	Predator	Shredder	Collector/ Filterer				
Baetis Choroterpes Caenis Oxyethira Hydroptila Mayatrichia Helicopsyche Helichus Elsianus Stenelmis H. azteca Helochares Hydraena Dixa Eulalia Dugesia Elmidae Larvae Chironomini Orthocladinae Syrphidae Oligochaete	Argia Archilestes Aeshna Paltothemis Derovatellus Acilius Laccophilus Gyrinus Tropisternus Notonecta Graptocorixa Ambrysus Tabanus Hydracarina Tanypodinae Ceratopogonida Empididae	Marilia Lepidostoma Phylloicus Hesperophylax Limnophilus Hydrochus	Wormaldia Polycentropus Simuliidae Pisidium Ostracoda				

Coarse detritus present in the pools during the summer was probably from windblown whole leaf litter from the arid canyon slopes. Wallace et.al. (1982) found that streams with greatly reduced densities of shredders had a significant decrease in the decomposition rate of maple leaves. They concluded that reduction in detrital processing rates leads to an accumulation of organic matter. This accumulation would be particularly great in a stream which can not readily export organic matter, e.g., a discontinuous stream like McKittrick Creek. Others have also concluded that the rate of disappearance of leaf packs in streams is correlated with the abundance of invertebrate shredders (Petersen and Cummins 1974, Sedell 1975, Anderson and Grafius 1975).

Without shredders to process newly acquired coarse detritus, detritus accumulation may actually stress the benthic community. Because little flow occurs out of the pools of McKittrick Creek, leaf litter falling into the stream will, for the most part, be retained in the . receiving pool. Detritus settling to the bottom of these pools will fill interstitial spaces in the substrate. Rabeni and Minshall (1977) showed that small substrates retain detritus more readily than large substrates in a continuous stream. This retention by small substrates is

a direct result of less current moving among the interstitial spaces. In pools, however, with little current flow, detritus should be retained well among all sizes of substrate. The filling in of interstitial spaces reduces habitat space which will reduce biomass and density of invertebrates. Barber and Kevern (1973) also found reduced invertebrate biomass and density values where high quantities of detritus was present. They made two suggestions for this apparent discrepancy. First, high quantities of detritus may form compact aggregates. Material on the inside of these aggregates would be unavailable to benthic invertebrates since the available surface area per weight of available food is decreased. Compact aggregates will not form when lower quantities of detritus are available, making detrital particles accessible to invertebrates. Secondly, with high organic matter concentrations and its associated microbial flora, oxygen concentrations in the interstitial spaces may be reduced below tolerance levels for many benthic invertebrates. Reduced oxygen concentrations could be enhanced in pools where little mixing of the substrate by current occurs.

Substrate size alone was not important as a determinant of biomass and density values for benthic invertebrates of McKittrick Creek. However, as previously mentioned, when detritus accumulates on the bottom of pools the interstitial spaces of the substrate will be filled. This accumulation compounds the negative effects of increased quantities of coarse detritus in streams, and may be an increasingly important factor if fish predation is considered in conjunction with coarse detritus concentrations and substrate size.

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Fish, potentially important determinants of benthic community structure in McKittrick Creek, appear to have had little effect on the biomass and density of the invertebrate community of most pools. This was consistent with the recent literature which suggests that fish are relatively unimportant potential predators on benthos. Jacobi (1979) found no significant differences in invertebrate species composition, density, or biomass between stream sections containing cutthroat trout (<u>Salmo</u> <u>clarkii lewisi</u>) and a stream section without trout. Allan (1982) removed trout from a stream section and observed no significant change in invertebrate density or composition over a four year period. Reice (1982) used basket enclosures in a stream to exclude fish and salamanders.

No significant differences occurred between invertebrate communities exposed such to vertebrate predators and those not exposed. Except for pool B. fish-free pools did not have consistently greater invertebrate biomass or density values than pools with fish in McKittrick Creek. Pool B had significantly lower biomass and density values than the other pools. While this has been explained by the negative correlation with coarse detritus, predation by fish as a determinant of benthic community structure of this pool or any other pool may not be ruled out since fish predation could not be included in the regression analysis. Pools AA, AB, and C, which also had fish, had a significantly larger substrate size than pool B. Interstitial space provides benthic invertebrates with a refuge from fish predation. Rainbow trout, which are visual predators (Johannes and Larkin 1961), forage near areas where invertebrates have refuge (e.g., vegetation, or rock) and will feed on prey which appear on the periphery of this refuge. While trout will consume large quantities of indigestible algae and detritus to obtain prey (Tippets and Moyle 1978), a rock substrate provides benthos with a safe refuge. At pool B the high concentrations of coarse detritus may fill the little refuge available among the interstitial substrate spaces. Consequently, a combination of high concentrations of

coarse detritus, coupled with a small-sized substrate, may enhance the importance of fish in determining the distribution of invertebrates in pool B.

Previously, I predicted that species diversity values should be greatest in regions of McKittrick Creek with the most food availability (i.e., CPOM, FPOM, UPOM, and periphyton), and where the greatest substrate complexity occurs. And, as predicted, the greatest species diversity values were recorded in downstream pools AA and AB. Variance in species diversity values was best explained by a positive correlation with periphtyon biomass, and variance in species richness values, the component of species diversity that significantly differed among pools, was also best explained by a positive correlation with periphyton biomass. This association of periphyton biomass with species diversity and richness values was not surprising. Because increased concentrations of coarse detritus were negatively correlated with biomass and density, periphyton as a food source was increasingly important for the summer benthic community. Another important food source, which may determine species diversity and richness, is fine detritus (< 0.5 mm). Unfortunately, concentrations of fine detritus were not measured. However, many fine detritus feeders were

collected (Tables 58 and 59), which suggests that fine detritus is an important food source for the summer benthic community.

Increasing shade by riparian trees occurs in downstream regions of McKittrick Creek and might be expected to reduce periphyton production. However, no significant differences occurred among pools for periphyton biomass. Studies have shown that periphyton production depends on available sunlight and on sufficient substrate surface area for periphyton attachment (Patrick 1975). Periphyton production in McKittrick Creek, then, may be determined by a combination of available sunlight and substrate size. Pools D and E, which were not shaded by vegetation, had a significantly smaller substrate than pools AA and AB which were shaded by vegetation. A reduction in periphyton production on the rock substrate may also result from the shading effects of accumulating coarse detritus, as well as, by dense riparian vegetation. This may also explain why pool B had low species diversity and species richness.

A small amount of the variance in species richness was explained by a positive correlation with substrate uniformity. Previous studies also have associated large-sized substrates with increased species richness (Allan 1975, Reice 1980, Mackay and Kalff 1969, Minshall 1968). De March (1976) observed that species richness was greater in coarse substrates, but declined as interstitial spaces were filled in by sediment and detritus. A small amount of the variance in species richness also was explained by a negative correlation with quantities of coarse detritus. Quantities of coarse detritus were also negatively correlated with substrate size. Therefore, as coarse detritus fills the little interstitial (habitat) space available in a small particle-sized substrate, decreased species richness should occur.

Surprisingly, fish populations did not appear to consistently influence biomass or density of benthic invertebrates as I had expected. Pools AA, AB, and C, which had fish, did not always have a significantly different biomass and density than pools D and E which had no fish. However, as already discussed, biomass and density at pool B may be influenced by a fish predator in conjunction with quantities of coarse detritus and substrate size. While not affecting total biomass or density in most pools, fish apparently influenced the composition of the benthic community. Larvae of Coleoptera were collected from all pools. However, Adult Coleoptera, which were common in pools without fish, were rarely collected from pools with fish. Adult Coleoptera, e.g., <u>Helichus</u> sp. and <u>Derovatellus</u> sp., were found in the guts of several fish. However, without analyzing more fish guts it is difficult to say how fish are influencing the composition of the benthic community.

Fish in McKittrick Creek were difficult to classify as strictly generalist or selective feeders. Most food selectivity values were near zero. This indicates random feeding. Also, a high species diversity of invertebrates was found in fish guts. While some fish fed primarily on aquatic invertebrates, others fed primarily on terrestrial invertebrates. These data would indicate that fish in McKittrick Creek were general feeders. On the other hand, Amphipoda and Chironomidae were abundant in the benthos, yet contributed little to the diet of fish, while adult Coleoptera, which were rare in the benthos, were found in fish guts. These data suggest that fish in McKittrick Creek were selective feeders.

Fish, in addition to having the potential to affect biomass, density, and species composition, may also influence benthic community structure in two other ways. First, fish may control the size composition of the benthos. While, trout reportedly select large organisms as prey more often than small organisms (Bisson 1978,

Tippets and Moyle 1978, Ware 1972), this was not generally true for benthic prey obtained from the guts of fish from McKittrick Creek. The mean lengths of benthic invertebrates in the guts of fish collected from pools AA, B, and C were not significantly larger than the mean lengths of benthic invertebrates collected from the benthos. Only at pool AB were the mean lengths of benthic prey in fish guts significantly larger than the mean lengths of benthic invertebrates collected from the benthos. Some fish consumed algal and leaf material suggesting that fish in McKittrick Creek will ingest vegetation to obtain the organisms using it as a refuge. If fish consumed vegetation to obtain prey, then no preference for larger benthic invertebrates should be found since both large and small prey should be found in this vegetation. Second, fish may determine benthic community structure by controlling competition among benthic prey. Murdoch (1969) suggested that a predator may stabilize community structure by feeding on the most abundant prey which minimizes competition for food resources by the prey. Studies involving intertidal organisms and plants have suggested that competition for food resources rarely occurs because either predation or physical extremes prevent high population densities of particular taxa from occurring (Connell 1975). Trout are

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reported to selectively feed on the most abundant prey (Bryan and Larkin 1972). However, as mentioned previously, certain taxa, e.g., Amphipoda and Chironomidae, which were abundant in the benthos were not abundant in fish guts. This suggests that fish may not be important in minimizing competition in these prey populations. However, too little is known about the ecology of the fish in McKittrick Creek to rule out their importance in minimizing competition. It is interesting that the benthos around pools AA and AB, which have established fish populations, was sampled by Lind in 1969 and 1971 (Lind 1979a). Little change appears to have occurred in the benthic community since that study. This suggests that fish are an integral part of the normal functioning of the McKittrick Creek ecosystem.

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I have made many observations about the role of fish in the McKittrick Creek ecosystem. However, the small number of fish collected and the fact that guts were only sampled once makes it difficult to make any broad conclusions about the role of fish in this stream. In light of recent research which suggests that fish are an unimportant determinant of the benthic community structure of continuous streams, it is important that further research on fish is done in McKittrick Creek to determine if fish indeed are unimportant in determining the benthic community structure.

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Several conclusions about the benthic community structure of discontinuous streams in general and McKittrick Creek in particular may be drawn from this study. First, differences in benthic community structure occur along the downstream gradient of McKittrick Creek. Pools, separated by dry stream reaches, differ from each other, while connected pools did not differ from each other. Clearly, then, discontinous streams allow study of the effects of variation in macroenvironmental characteristics on benthic community structure because the influence of upstream waters on downstream communities has been removed. Second, this study also shows the difficulty of naming one factor as more important than another in determining benthic community structure. While food availability appears to ultimately determine the benthic community structure of McKittrick Creek, other factors must be considered simultaneously. For example, was the negative correlation of coarse detritus with biomass and density of invertebrates (pool B) the result of a reduction in refuge space for predator avoidance, or the result of reduced oxygen concentrations from organic matter decomposition? Finally, the benthic community

structure of McKittrick Creek probably changes seasonally. This change would be a function of the type of food available. Herbivores and fine detritus feeders were dominant in the summer when periphyton production was greatest and fragmented coarse detritus was probably most abundant. Shredder taxa, which are present at other times of the year, are probably most abundant during autumn and winter during leaf fall.

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#### SUMMARY

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Significant changes occured in the macrobenthic community structure of McKittrick Creek along its downstream gradient. Biomass and density values produced the greatest variability among pools. Significant differences in species diversity values also occurred among pools. Fluctuations in species diversity values were primarily a result of fluctuations in species richness and not equitability.

Differences in macrobenthic community structure were associated with variance in macroenvironmental characteristics primarily associated with food availability. Specifically:

1. Variance in biomass and density was negatively correlated with coarse detritus biomass.

2. Variance in species diversity was positively correlated with periphyton biomass.

3. Species richness was positively correlated with peiphyton biomass, substrate particle size, and substrate uniformity.

The effects of predation by fish are difficult to address primarily because only a small number of fish were analyzed. However, general trends were apparent in the fish samples. Specifically:

1. Total biomass and total density of benthic organisms in pools were generally unaffected by fish predation.

2. Fish were feeding opportunistically.

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3. Fish were not necessarily feeding on the most abundant prey.

4. Fish may influence the composition of the benthic community.

APPENDICES

APPENDIX A

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WALKLEY-BLACK METHOD OF ORGANIC MATTER ANALYSIS

### APPENDIX A

Walkley-Black Method of Organic Matter Analysis (from Jackson 1958)

Reagents:

1. Standard 1 N Potassium Dichromate: Weigh exactly 49.04 gm  $K_2Cr_2O_7$ . Dissolve in distilled water, and dilute to 1 liter.

2. Standard 1 N Ferrous Sulfate: Weigh 278.0 gm  $\text{FeSO}_4$ . 7  $\text{H}_2\text{OO}$ . Dissolve in distilled water with 15 ml concentrated Sulfuric Acid. Dilute to 1 liter.

3. Indicator - 0.3% solution of Barium Diphenylamine Sulfonate (modification after Maciolek 1962): Weigh 0.15 gm Barium Diphenylamine Sulfonate and dissolve in 50 ml warm distilled water.

#### Procedure:

Place ground substrate in Erlenmeyer flask. Pipette

exactly 10 ml of 1 N Potassium Dichromate solution onto sample. Swirl, then add 20 ml concentrated Sulfuric Acid and mix for 1 minute. Let stand 20-30 minutes. Run standardization blank in the same way. Dilute solution to 300-400 ml with distilled water. Add 10 ml 85% ortho-Phosporic Acid, 0.2 g Sodium Fluoride, and 5-10 drops of indicator. Titrate with ferrous sulfate solution. Color shifts from reddish to violet to blue before a 1 drop endpoint which changes the color to a brilliant green.

Calculation of Percent Organic Matter (% O.M.):

 $% 0.M. = 10[1 - (T/S)] \times Factor$ 

- T = sample titration ml ferrous sulfate
   solution
- S = blank titration ml ferrous sulfate
   solution

Factor =  $(N \text{ Fe}^2)(12/4000)(1.72/0.77)(100/\text{Sample weight})$ 

N Fe<sup>2</sup> = 
$$\frac{(\# \text{ ml } K_2 \text{Cr}_2 \text{O}_7)(\text{Normality } K_2 \text{Cr}_2 \text{O}_7)}{\text{ml blank titration}}$$

(12/4000) = meq of Carbon 1.72 = factor for organic matter from Carbon 0.77 = percent recovery of organic matter

# APPENDIX B

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STATISTICAL ANALYSES

## APPENDIX B

## Statistical Analyses:

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<u>Group t-test</u>: A group t-test is a statistical test which tests the null hypothesis that the means of two independent samples are not significantly different from each other. The assumption that both samples came at random from normal populations with equal variances should be met. However, the t-test is considered a very robust test. If not all these theoretical assumptions are met, especially if the sample sizes are equal or nearly equal, the results of t-test analyses may be depended on (Zar 1974).

The t-test equation for testing the null hypothesis concerning the differences between two means is:

$$t = \sqrt{\frac{(N_1 - 1)s_1^2 + (N_2 - 1)s_2^2}{(N_1 + N_2 - 2)}} \left(\frac{\frac{1}{N_1} + \frac{1}{N_2}}{\frac{1}{N_1} + \frac{1}{N_2}}\right)$$

where  $(X_1 - X_2)$  is the difference between the two means;  $N_1$  and  $N_2$  are the sample sizes for each population;  $s_1$  and  $s_2$  are the sample variances for each population. The above equation is used if the sample variances are assumed to be equal. The following is an example of a BMDP statistical computer program for group t-test analysis (Dixon and Brown 1981): /PROBLEM TITLE = 'BIOMASS OF POOL AA'. /INPUT VARIABLES ARE 2. FORMAT IS '(I2,F10.3)'. /VARIABLE NAMES ARE A, B. GROUPING IS A.

/GROUP CODES(1) = 1,2. NAMES(1) = WEEKI, WEEKII. /TEST TITLE = 'BIOMASS WEEK I VS. BIOMASS WEEK II'. /END. DATA

Analysis of Variance: When more than two populations are sampled a multisample analysis is used, which statistically compares the means of all populations. The null hypothesis is that the means of all populations are equal. The alternate hypothesis is that at least one mean comparison between a pair of populations was significant. However, which population comparison was significant is not given by an analysis of variance. Analysis of variance assumes that all populations have a normal distribution, all population variances are equal, and that all sample sizes are equal. However, as with a group t-test, the analysis of variance is a very robust test,

and, as long as sample sizes are equal or nearly equal, a considerable heterogeneity of population variances is allowed (Zar 1974).

Analysis of variance partitions the total variation present in a data set into separate components. Each component is associated with an identifiable source of variation, e.g., mean of population one, mean of population two, etc.,. One component represents variation attributed to uncontrolled factors and random errors associated with response measurements (Bhattacharyya and Johnson 1977).

If the result of an analysis of variance is significant, i.e., the means of all populations are not equal, then a follow-up test is used for between population comparisons. The group t-test previously described is inappropriate for such analyses. Instead, a multi-comparison test is used for such analyses. The t-test used for a multiple comparison of group means was:

$$t = \frac{(\bar{x}_1 - \bar{x}_2)/(1/N_1 + 1/N_2)^{\frac{1}{2}}}{ESS/(N - G)^{\frac{1}{2}}}$$

where  $X_1 - X_2$  is the difference between means of populations 1 and 2;  $N_1$  and  $N_2$  are the sample sizes of populations 1 and 2; ESS is the error sums of squares for the analysis of variance; N - G is the degrees of freedom where N is the sample size and G is the number of groups (Dixon and Brown 1981).

An example of a BMDP statistical computer program for an analysis of variance used in this analysis was: /PROBLEM TITLE IS 'ANOVA OF BIOTA OF MCKITTRICK CREEK'. /INPUT VARIABLES ARE 2. FORMAT IS '(I2,F10.3)'. /VARIABLE NAMES ARE POOL, BIOTA. GROUPING IS POOL. /GROUP CODES(1) = 1, 2, 3, 4, 5. NAMES(1) ARE POOL1, POOL2, POOL3, POOL4, POOL5. /DESIGN TITLE IS 'ANOVA BETWEEN POOLS OF MCKITTRICK CREEK'. DEPENDENT IS BIOTA. /PRINT MININUM. MAXIMUM. MEAN. CORRELATION. /END. DATA

<u>Regression</u> <u>analysis</u> Regression analysis determines the relationship between a dependent variable and one or more independent variables. In such a case the magnitude of the dependent variable is a function of the magnitude of the independent variables. Regression analyses may be "simple", where the relationship is between only two variables, or "multiple", where the relationship is between a dependent variable and two or more independent variables.

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A simple linear regression, e.g., the relationship between the weight of <u>Baetis</u> and the length of <u>Baetis</u>, is represented by the equation  $Y = \alpha + \beta X$  -- the equation for a straight line. Data are unlikely to be found in a straight line, so simple linear regression analysis finds the "best-fitting" line through the data. The "best-fitting" line is defined as that which results in the smallest value for the sum of squares (least squares) of the deviations from the line for all values. For example, if Y represents the data point and Y the point on the line vertically above or below Y, then the deviation from the regression line is described as (Y - Y). The "best-fitting" line is the minimum value obtained from the equation:

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$$\sum_{i=1}^{n} (\mathbf{Y}_i - \hat{\mathbf{Y}}_i)^2$$

where n equals the number of data points comprising a sample (Zar 1974).

The following is an example of a BMDP statistical computer program for a simple linear regression (Dixon and Brown 1981): /PROBLEM TITLE IS 'LENGTH VS. WEIGHT IN BAETIS'. /INPUT VARIABLES ARE 2. CASES ARE 16. FORMAT IS '(2F5.2)'. /VARIABLE ADD = 2. NAMES ARE LENGTH, WEIGHT, ALENGTH, BWEIGHT. /TRANSFORMATION ALENGTH = LOG(LENGTH). BWEIGHT = LOG(WEIGHT). /PRINT CORRELATION: /PLOT PROBABILITY. RESIDUALS. /REGRESSION TITLE IS 'LENGTH/WEIGHT RELATIONSHIP IN BAETIS'. DEPENDENT IS BWEIGHT. INDEPENDENT IS ALENGTH. /END. DATA

The multiple regression equation has no theoretical limit on the number of independent variables which may influence the dependent variable. The general equation for a multiple regression is:

 $Y = \alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_m X_m \quad \text{where m is the last} \\ \text{independent variable.}$ 

All independent variables included in a multiple regression equation do not necessarily have a significant effect on the magnitude of the dependent variable. In order to find the "best" regression model a step-wise regression analysis may be used. This analysis adds or removes independent variables one at a time to check if the new combination of independent variables produces a "better-fitting" line than the previous combination of independent variables.

The following is an example of a BMDP statistical computer program for a step-wise regression analysis (Dixon and Brown 1981):

/PROBLEM TITLE IS 'DENSITY VS. MACROENVIROMENT'.
/INPUT VARIABLES ARE 10.
FORMAT IS '(A3, 9F7.2)'.
FILE IS 'MACRO.DAT'. (DATAFILE)
/VARIABLE NAMES ARE ID, DENSITY, SUBSTRATE, CPOM,
GRADIENT,
CANWIDTH, CANSLOPE, CANOPY, RIPARIAN, XDEPTH.
LABEL IS 1.
/REGRESS DEPENDENT IS DENSITY.
/PRINT CORRELATION. FRATIO.
/PLOT VARIABLE. RESIDUAL. NORMAL. DNORM.
/END.
APPENDIX C

TABLES

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## APPENDIX C

Table C-1. Regression equations for lenght/weight relationships for common taxa of McKittrick Creek. Lengths(X) and weights(Y) were log transformed. (Lengths are entered in millimeters; weights are expressed as 100 x weight in milligrams). (For all F-ratios, p < 0.001).</p>

Taxon	R	egr	ession	n	equa	ti	on		R-s	qu	ar	е	F-	ra	at	i¢
											**	• .•	• • •		•••	-
Baetis	Log(Y)	*	-0.18	+	2.4	81	Log	(X).	1	э.	53		10	3.	. 9	2
Choroterpes	Log(Y)		-0.30	+	2.2	22[	Log	(X)	]	Ο.	61		7	2.	. 2	9
Argia	Log(Y)		-0.02	+	2.2	2[	Log	(X)	]	ο.	71		10	9.	. 3	4
Wormaldia	Log(Y)		-1.42	+	3.4	4[	Log	(X)	]	ο.	77		2	27 .	. 0	5
Oxytheria	Log(Y)	-	0.18	+	1.5	3[	Log	(X)	]	Ο.	48		1	18.	. 5	4
Mayatrichia	Log(Y)	-	0.18	+	1.5	30	Log	(X)	]	0.	48		4	18.	. 5	4
Hydroptila	Log(Y)		0.18	+	1.5	30	Log	(X)	]	Ο.	48		2	18.	. 5	4
Elmidae Larvae	Log(Y)	=	-0.82	+	2.6	50	Log	(X)	]	Ο.	63		5	55	. 9	3
Ceratopoganidae	Log(Y)		-0.53	+	1.7	1[	Log	(X)	]	Э.	58		L	10	. 8	2
Diptera A	Log(Y)	-	-0.65	+	2.2	2[	LOG	(X)	]	Ο.	82		18	86.	. 6	1
Tanypodinae	Log(Y)		-0.44	+	1.7	2[	Log	(X)	1	ο.	62		8	32.	. 5	3
Orthocladinae	Log(Y)		-0.24	+	1.5	9[	Log	(X)	]	ο.	71		7	5.	. 3	2
Chironomini	Log(Y)		-0.37	+	1.4	71	Log	(X)	1	0.	60		6	9.	. 6	5
Eulalia	Log(Y)		-0.57	+	3.6	21	Log	(X)	1	0.	76		2	: 4 .	. 7	4
Hvallela azteca	Log(Y)	-	0.29	+	1.8	81	Log	(X)	1	0.	51			8.	. 4	3

Table C-2. Correlation matrix of dependent biotic characteristics and independent macroenvironmental characteristics of McKittrick Creek.

		1	2	3	4	5	6	7	8	9
Biomass	(1)	1.00								
Density	(2)	0:73	1.00							
Diversity	(3)	0.82	0.41	1.00						
Equitability	(4)	-0.07	-0.49	0.50	1.00					
Richness	(5)	0.94	0.52	0.94	0.26	1.00				
Substrate Siz	e(6)	-0.62	-0.66	+0.65	-0.05	-0.55	1.00			
Substrate							2.4.2.2			
Uniformity	(7)	-0.39	-0.47	-0.43	-0.02	-0.30	0.94	1.00		
CPOM Biomass	(8)	-0.96	-0.85	-0.70	0.25	-0.82	0.68	0.47	1.00	
Periohyton										
Biomass	(9)	0.71	0.34	0.96	0.57	0.85	-0.62	-0.42	-0.64	1.00
Gradient	(10)	-0.57	-0.30	-0.84	-0.55	-0.71	0.77	0.67	0.44	-0.76
Canvon Width	(11)	0.53	0.27	0.82	0.56	0.67	-0.77	-0.67	-0.40	0.73
Sunlight	(12)	0.62	0.10	0.65	0.33	0.77	0.09	0.35	-0 41	0.54
Canvon Slope	(12)	-0.22	-0.23	+0.50	-0.41	-0.20	0.33	0.35	0.41	-2.48
Pool Area	(14)	-0 38	-0.21	-0.06	0.33	-0 35	-0.28	-0 56	0.20	1 1 2
Pool Volume	(15)	-0.38	-0.06	-0 32	-0.11	-0 50	-0.31	-0.54	0.17	-0.14
Mean Denth	(16)	-0.24	-0.05	-0.60	-0.66	-0.50	0.12	-0.08	0.05	-0 51
Canony Cover	(17)	0.64	0.00	0.00	0.50	0.50	-0.70	-0.00	-0.65	0.91
Rinarian	1111	0.00	0.30	0.90	0.50	0.13	0.19	-0.05	0.54	0.01
Density	(18)	0 32	0 05	0 62	0.55	0 #7	-0.64	-0 54	-0.16	0.51
		0.52							0.10	
										•
		10	11	12	13	14	15	16	17	
Cradient	(10)	1 00								
Grautent	(10)	-1.00	1 00							
Canyon widen	1121	-1.00	1.00	1 00						
Sunlight Class	1121	-0.33	0.30	1.00	1 00					
Canyon Stope	(13)	0.05	-0.07	0.21	1.00					
POOL Area	(14)	-0.17	0.20	-0.71	-0.50	1.00				
POOL VOLUME	(15)	0.13	-0.11	-0.85	-0.34	0.90	1.00	1 00		
mean Depth	(10)	0.03	-0.03	-0.59	0.34	0.22	0.00	1.00		
Canopy Cover	(17)	-0.99	0.98	0.41	-0.80	0.09	-0.19	-0.03	1.00	
Hiparian										
Density	(18)	-0.93	0.94	0.17	-0.88	0.22	-0.07	-0.54	0.89	

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