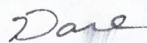March 10, 1988

Dr. Robert Behnke
Colorado State University
Dept of Fishery & Wildlife Biology
Ft. Collins, CO   80523

Dear Dr. Behnke:

Enclosed is a copy of my thesis with Dr. Fronk's, Dr. Ward's and your comments incorporated. As we discussed on the telephone, my defense is on March 22nd, at 8:30 AM in ZE444 of the Zoology Building. I really appreciate all your help and interest in my project.

Sincerely,

David Winters

DW/sb

COLORADO STATE UNIVERSITY

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR

SUPERVISION BY _____David Scott Winters_____

ENTITLED _____Seasonal relationships between the benthos, invertebrate drift and

_____brown trout predation_____

BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF

_____Master of Science_____

Committee on Graduate Work

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_____   _____
Advisor

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THESIS

Seasonal Relationships Between The Benthos, Invertebrate Drift And Brown Trout Predation

Submitted by

David S. Winters
Biology Department/Zoology Section

In partial fulfillment of the requirements
for the Degree of Masters of Science
Colorado State University
Fort Collins, Colorado

Spring 1988

ABSTRACT

SEASONAL RELATIONSHIPS BETWEEN THE BENTHOS,
INVERTEBRATE DRIFT AND BROWN TROUT PREDATION

A year round study of a foothills segment of a Rocky Mountain river was conducted to investigate the relationships between benthic macroinvertebrates, their drift patterns and the feeding habits of brown trout (*Salmo trutta*). Macroinvertebrates were collected monthly with a surber sampler. Drift was also sampled monthly, with collections made for two hour periods in each 4-hour segment of the diel cycle. Brown trout were collected seasonally with a boat electroshocking unit. Food items ingested by the trout were compared with benthic and drifting invertebrate data to determine foraging behavior.

A total of 65 taxa of benthic macroinvertebrates were collected, with only 9 being numerically abundant (Annual $\overline{x}$ >75 org./m^2). Aquatic insects comprised over 99% of the total density and number of taxa collected with ephemeropterans and dipterans accounting for more than 81% each month. Mean monthly densities of benthic macroinvertebrates were lowest during runoff and highest during autumn. Mean biomass values were also lowest during snowmelt runoff, but were highest in the spring (pre-runoff) when large mature nymphs were abundant. Diversity and equitability of benthic invertebrates were influenced substantially by life-history strategies. The highest values recorded were during runoff, when densities were low

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but individuals were evenly distributed among the taxa. The lowest values recorded were in the fall when early instars of a few taxa dominated the benthos. Functional feeding group analyses revealed that collector-gatherers dominated the benthos, while shredding invertebrates were almost non-existent.

Mean monthly drift densities were generally greater in the spring, although the highest value was recorded in January as a result of large numbers of drifting chironomid larvae. There was no significant relationship between the density of benthic macroinvertebrates and drift density. The mayfly *Baetis tricaudatus*, the black fly *Simulium arcticum* and chironomid midge larvae collectively constituted >80% of the drifting organisms. *B. tricaudatus* exhibited nocturnal maxima in drift activity 9 of the 10 months sampled. Diel patterns of chironomid and *S. arcticum* drift varied seasonally with maximum drift densities at dusk or during mid-day in different months. A mid-summer spate, with associated high turbidity, increased drift densities dramatically.

There were 4 age classes of brown trout collected during the study period. Although the 1979 (3+) year class was abundant during the fall of 1982, by the fall of 1983 no brown trout of this age class were collected. There was no significant difference between relative weight (Wr) and coefficient of condition values (K) for any of the age classes sampled, indicating no substantial change in morphometry with increase in length. Mean condition and relative weight values were lowest following snowmelt runoff, and attained maximum values in spring for the 3 youngest age classes. The oldest year class exhibited no substantial increase in condition, and remained low throughout the year.

Trout fry fed predominately on drifting aquatic and terrestrial macroinvertebrates, switching to *Brachycentrus occidentalis* larvae the following summer. The three older age classes fed predominately on *Brachycentrus* larvae, apparently plucking them from the substrate. All age classes of trout sampled fed on adult chironomids and ephemeropterans when available. Nocturnal feeding behavior was evident in summer and early fall when adult chironomids and ephemeropterans were available following sunset.

The benthic community and drift were typical of rivers in the Rocky Mountain region, with little observable impact from man-induced stress. There appears to be an ample food supply for fry and juvenile trout. However, the absence of forage fish or large available invertebrates may be limiting the size and life expectancy of the brown trout in the Arkansas River.

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Spring, 1988

ACKNOWLEDGEMENTS

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I. INTRODUCTION

A. <u>Literature Review</u>

The ecological significance of drifting benthic invertebrates within lotic ecosystems has been shown to be important in maintaining benthic populations as well as being a major food source for salmonid fish (Allan 1978a, Chaston 1969a, Elliott 1970, Müller 1954, Waters 1972). Studies have been conducted on invertebrate drift for over 50 years, although the majority of research has been done within the last two decades. While studying the importance of drifting terrestrial insects as a food source for fish, Needham (1928) also described capturing drifting aquatic invertebrates. Müller (1954) proposed that invertebrate drift was the result of crowding and food depletion, and played a key role in population dispersal. In his work, Müller also reported large numbers of drifting invertebrates, and made observations on the qualitative relationship between drift, the bottom fauna, and food consumed by fish. Müller's work and other research conducted during the 1950 – 1960 period stressed the importance of invertebrate drift and initiated subsequent studies on the mechanisms controlling drift. Waters (1962) studied the diel periodicity of drift, and observed that drift rates of several taxa of invertebrates increased at the onset of nightfall reportedly due to increased foraging activity. Waters called this pattern "behavioral drift" as opposed to drift resulting from catastrophic events (catastrophic drift), or the low densities of organisms present in the drift throughout the diel cycle (constant drift). The majority of the research conducted on the behavioral patterns of invertebrate drift has been done on nocturnally active invertebrates (e.g. *Baetis* spp.), although diurnal behavioral patterns of drift have been observed for gastropods (Marsh 1980) and the caddisfly *Oligophlebodes sigma* (Waters 1968).

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There appears to be an inverse relationship between invertebrate drift and light intensity for most taxa. As the light intensity is reduced below a critical "threshold" level, insect activity is increased. Chaston (1968) concluded that the regular occurrence of peaks in drift during the night was at least partially attributable to an endogenous element. However, the diel periodicity of drift has been primarily attributed to changing light intensity (Waters 1972). Through direct observation, Kohler (1985) found that the drift of *Baetis tricaudatus* nymphs were an active rather than passive phenomenon. His conclusion was that active drift is a component of *Baetis* food searching behavior and that nymphs enter the water column when the habitat quality falls below a threshold level. Allan *et al*. (1986) observed *Baetis* sp. movements on top of rocks in Cement Creek, Colorado. Their results indicated that *Baetis* foraging behavior on the top of rocks was greatest during the daylight hours and correlated with water temperature. Based on their direct observational studies, both Kohler (1985) and Allan *et al*. (1986) concluded that *Baetis* drift activity was not a passive phenomenon, but possibly a searching response for new food resources. Although feeding activity may be greater during the daylight hours, it may be beneficial to search for new food patches during the nocturnal hours to avoid visual predators.

The light intensity required to initiate nocturnal drift has been studied by several authors (Haney *et al*. 1983, Bishop 1969, Chaston 1968). Haney *et al*. concluded that threshold values below 30 lux were required to initiate drift in Ephemeroptera found in two rivers in New Hampshire. Laboratory studies conducted by Bishop indicated that light levels as low as 0.001 lux were needed to initiate drift. The discrepancies observed in these and other studies on the threshold levels of light initiating drift may be influenced by microhabitat features of the substrate as well as the clarity of the water. Macroinvertebrates within the interstices of the substrate are subjected to

lower light intensities than those in more exposed microhabitats. Turbidity, due to suspended particulates, also influences the amount of light reaching benthic invertebrates. The primary difficulty in establishing threshold levels of light for initiating drift is that measurements are normally conducted at the water surface, and not at the substrate where it is detected by the organisms.

Studies conducted on predator-prey relationships indicate that nocturnal increase in benthic activity and drift may be in part a predator avoidance mechanism. Allan (1978b) observed that the number of larger *Baetis bicaudatus* nymphs increased significantly in the drift during dark hours, whereas smaller nymphs exhibited a much less distinct nocturnal drift pattern. Using the electivity index of Ivlev (1961), Allan also determined that brook trout (*Salvelinus fontinalis*) in Cement Creek, Colorado, selected larger Ephemeroptera nymphs from the drift, while ignoring smaller individuals. His conclusion was that the larger *Baetis* nymphs were more active at night in order to reduce visual predation by brook trout. Ringler (1979) also concluded that there was a strong prey size selection by brown trout under laboratory conditions.

Peckarsky and Dodson (1980) studied the effects of colonization of instream cages by mayflies with and without plecopteran predators. Their conclusion was that tactile and possibly chemical stimuli resulted in an avoidance of those cages by Ephemeroptera when plecopteran predators were present. In a further study by Peckarsky (1980), she concluded that when placed in contact with a plecopteran predator, *Baetis* nymphs would enter the drift, while *Ephemerella* nymphs would "pose" with their abdomen over their thorax and head to give the appearance of being larger. Similar drift responses by *Baetis* were also observed by Corkum and Clifford (1980).

Due to the complex interactions between vertebrate and invertebrate predators and prey species, the extent of their effect on drift has not been quantified.

Catastrophic events such as spates, suspended sediment input, floods, droughts and toxicants may also influence invertebrate drift. Anderson and Lehmkuhl (1967) concluded that freshets (<2.5 cm of rainfall) resulted in a four-fold increase in the numbers and five-fold increase in biomass of drifting invertebrates. Waters (1962) also observed a large increase in the drift of the amphipod *Gammarus lacustris* and the ephemeropteran *Baetis vagans* due to heavy rain. The reduction in stream discharge has also been shown to increase drift rates (Minshall and Winger 1968, Corrarino and Brusven 1983).

The addition of pollutants may also result in increased drift rates. Crowther and Hynes (1977) concluded that concentrations of road salts (>1000 mg/l CaCl) increased the drift of all organisms found at the study area. Wallace and Hynes (1975) found that insecticides had a major effect on benthic populations, and increased drift significantly. Swain and White (1985) reported that the addition of metals reduced the nocturnal drift of ephemeropterans in the King River, Australia. They hypothesized that in the contaminated sections of the river, invertebrates spent more time searching the substrate for more favorable conditions and entered the drift less frequently.

The factors influencing catastrophic drift have been well studied and indicate that a short or long term change in environmental conditions will induce drift. However, if the invertebrates release themselves from the substrate and actively enter the drift, this may constitute an active response rather than a catastrophic dislodging.

The importance of macroinvertebrates as a food source for brown trout has been well established (Chaston 1969a, 1969b, Elliott 1970, Stauffer 1977, Jackson 1978, Campbell 1979, Alexander 1977). Elliott (1970) studied the relationship between invertebrate drift and three age classes (0+, 1+ and 2+) of brown trout in an English stream. He concluded that there was a significant correlation between invertebrate drift rates and the biomass of invertebrates in the stomachs of age 0+ and 1+ trout. Elliott also concluded that although benthic invertebrate drift was important for young fish (0+, 1+), non-drifting trichopterans comprised a greater percentage of the biomass consumed by larger (2+) trout. Tippets and Moyle (1978) found similar results for rainbow trout in the McCloud River, California. While rainbow trout fry and juveniles fed predominately on drifting benthic invertebrates, the stomachs of larger trout contained higher quantities of the caddisfly *Dicosmoecus* sp., large quantities of algae and debris indicating epibenthic feeding. Tippets and Moyle further concluded that due to low feeding efficiency, the epibenthic feeding habits of the McCloud River rainbow trout may be largely responsible for the slow growth rates of the trout observed. In laboratory tests, Chaston (1969a) observed that brown trout foraging activity was primarily nocturnal during most of the year, but daylight feeding activity predominated in summer. This increased diurnal activity during summer months was attributed to the consumption of drifting terrestrial invertebrates. Alexander and Gowing (1976) concluded that terrestrial invertebrates were an important food source for trout in small streams in Michigan, while food produced within the system was more important in the larger rivers. Based on these and other studies (Allan 1978a, Hunt 1965), it is clear that terrestrial organisms may be an important food source for brown trout when they are available.

The effects of salmonid predation on aquatic macroinvertebrate populations has been a controversial subject since Allen's (1951) classic study of the ecology of brown

trout in the Horokiwi stream, New Zealand. Allen concluded that brown trout consumed considerably more benthic invertebrates than were present in the benthos at one time. This apparent contradiction was termed *Allen's Paradox* by Hynes (1970) and has been tested and scrutinized by several authors (see review in Allan 1983). Allan (1982) studied the effects of removing brook trout from a section of Cement Creek, Colorado, on the benthic invertebrate community. Allan found no indication of increased invertebrate densities or change in species composition during the four year study. Jacobi (19769) found that removal of cutthroat trout in a Wyoming stream did not significantly alter the densities or species composition of benthic invertebrates in a Wyoming stream. Wilzbach *et al.* (1986) conducted an extensive study to elucidate the influence of habitat manipulation on the interactions between cutthroat trout and invertebrate drift in an Oregon stream. Their results indicated that as a result of increased foraging ability in manipulated stream sections with high visibility, trout growth was increased and invertebrate drift densities were reduced. They further concluded that foraging efficiency was reduced in structurally complex streams, which may limit the ability of trout to control invertebrate abundance.

Piscivorous feeding behavior by brown trout has also been documented (Stauffer 1977, Alexander and Gowing 1976, Campbell 1979 and Alexander 1977). Campbell (1979) studied the food habits and growth rates of the large piscivorous brown trout in Scottish lakes. These trout were captured in deepwater areas of the lake and were originally thought to be a separate species, commonly called ferox trout. However, Campbell determined that the ferox trout were actually large brown trout which changed their diet from primarily invertebrates to char (*Salvelinus alpinus*). As a result, the ferox trout lived to a considerably older age and attained lengths much greater than those trout which feed on invertebrates throughout their lifespan. Campbell observed that while growth was slow in the first third of life when

invertebrates were the primary food source, a critical length was reached when char were consumed and growth became rapid and large sizes were ultimately attained. Alexander (1977), who studied the North Branch of the Au Sable River in Michigan, concluded that large brown trout (> 30 cm) fed predominately on fish, mainly small brook trout. Alexander also found that if older brown trout lacked smaller trout as prey they would grow slower and fewer large "trophy" size fish would be produced.

B. Research Problem

On January 1, 1981, the Colorado Division of Wildlife implemented a 40.6 cm (16 in.) minimum size limit on all trout, with a two fish (>40 cm) per day limit, on two sections of the Arkansas River (Nehring & Anderson 1981). One section was downstream of the town of Salida, while the other was downstream of Coaldale and adjacent to the Loma Linda Campground. Electrofishing results indicated that a self-sustaining brown trout population was present in these areas, and comprised over 99% of the trout density, with rainbow and cutthroat trout also being present. Due to the size of the river and the available habitat present, it was postulated that with the implementation of these regulations the number of trout greater than 40.6 cm would increase in the next few years. Subsequent sampling in the next three years indicated that although the density of smaller brown trout (<30 cm) had increased, the number of trout greater than 30 cm had exhibited no apparent change (Nehring & Anderson 1983). The lack of response of large brown trout to the special regulations suggested that there were other factor(s) influencing the size distribution of the trout in this section of the river. Historically, mining occurred in the upper reaches of the Arkansas Valley. Nehring (1986) indicated that high heavy metal concentrations in the sexually mature trout may result in high mortality of these older age classes. His conclusion was that the cumulative stress of heavy metal toxicity, post spawning conditions and an inadequate food base may increase mortality of older brown trout.

Based on the sampling results of the Colorado Division of Wildlife, this project was developed to evaluate the relationships between the brown trout and the aquatic macroinvertebrate community in the special regulation area and to determine if the food source present is possibly limiting the size of the trout present.

C. Objectives

Quantitative information on the aquatic macroinvertebrate community in this section as well as most of the upper Arkansas River is limited to primarily two studies (La Velle 1968, Roline and Boehmke 1981). The objectives of this study centered around this lack of information and also the relationships between the brown trout and the aquatic macroinvertebrate community. The specific objectives were:

1. To quantitatively describe the benthic invertebrate community in the study site.

2. To describe the diel and seasonal drift patterns of benthic invertebrates.

3. To determine the relationships between the benthic community and invertebrate drift.

4. To describe the seasonal feeding habits of the brown trout in relation to invertebrate drift and benthic community composition.

5. To determine if the size or composition of the food base present is possibly limiting the maximum size attained by the brown trout.

II. STUDY AREA

The headwaters of the Arkansas River originate northeast of the town of Leadville near the Continental Divide in central Colorado. The river flows in a southeasterly direction, exiting the Rocky Mountains near the town of Canon City and entering the eastern plains. Upon entering Kansas, the Arkansas River has drained an area of approximately 65,000 km^2 with a main channel length of 568 km (La Velle 1968). The Arkansas River drains more than 1/4 of the total area of Colorado. Historically, the average yearly discharge recorded by the United States Geological Survey at the Parkdale station (12 km downstream of the study site) is 22.2 m^3/sec.

The Arkansas River in the study area occurs in a deep V-shaped valley comprised of metamorphic and igneous rock of Pre-Cambrian and Tertiary age (LaVelle 1968). Located in the foothills zone of the Rocky Mountains (Pennak 1977), this region receives approximately 38 cm of precipitation annually and is therefore considered semi-arid (Pennak & LaVelle 1979). The riparian vegetation consists primarily of willows (*Salix* spp.), and is restricted to the area directly adjacent to the river due to the presence of Highway 50 on the south side and railroad tracks on the north. Vegetation is sparse on the sides of the valleys, probably due to the semi-arid nature of the area, as well as the erodible nature of the soil. Stream gradient is 4.7 m/km (0.5%) at the study site (Pennak and LaVelle 1979), resulting in a series of long pools and steep riffles. The substrate is a conglomerate of sand, gravel and cobble, with large boulders interspersed.

The study site was located 3.2 kilometers upstream from the confluence with Texas Creek, at an elevation of 2133 meters (Figure 1). A representative riffle 40 meters wide was chosen adjacent to the Lone Pine Campground, and was the only site utilized for invertebrate sampling throughout the study period. Brown trout were collected directly upstream and downstream of the invertebrates sampling station.
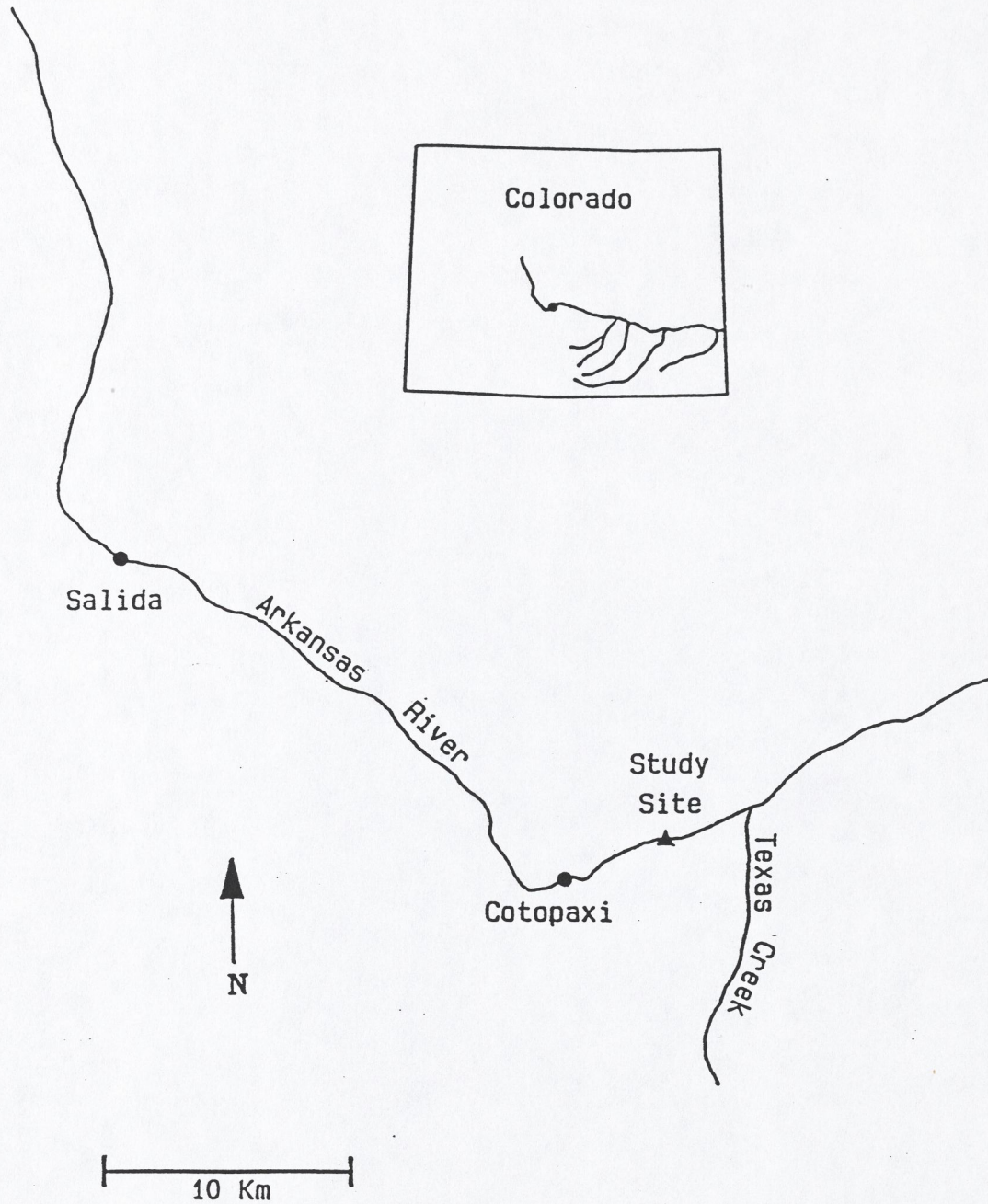
FIGURE 1: Sampling site location on the Arkansas River, Colorado.

III. MATERIALS AND METHODS

The study was conducted monthly from July 1982 through August 1983, at the predetermined study site. Samples were preserved and labeled in the field, and returned to the laboratory for processing.

A. Physico-chemical Parameters

Monthly water temperatures were recorded with a field thermometer every two hours, over a 24 hour period during drift sampling. Discharge was obtained from USGS gauging stations at Wellsville and lower Badger Creek, located upstream of the sampling site. Dissolved oxygen was determined during each sampling episode with the azide modification of the Winkler method using Hach chemicals. Hardness ($CaCO_3$) and pH were also measured monthly using a Hach field chemical kit.

Seston (>250 μm) was analyzed seasonally from the drift samples. Seston collected in the drift nets was dried at 60°C until a constant weight was attained. The samples were incinerated in a muffle furnace at 500°C for 5 hours to separate organic from inorganic fractions by loss-on-ignition. Organic and inorganic fractions are expressed as mg $\cdot$ m^{-3} $\cdot$ sec^{-1}.

B. Benthic Invertebrates

Benthic samples were collected monthly from July 1982 through August 1983, except August 1982 and June and July 1983 when high water levels precluded sampling

(Table 1). Invertebrates were collected with a Surber sampler enclosing 929 cm² and having a mesh size of 250 μm. Sampling was conducted in the same riffle during the entire study. A total of five samples were collected along a transect perpendicular to the river bank, during each sampling episode. Samples were preserved in the field with 75% ethanol and returned to the laboratory where organisms were separated from the debris, identified and enumerated. Identification was determined to the lowest practical taxonomic level using the most recent available keys (Allen and Edmunds 1965, Baumann *et al.* 1977, Edmunds *et al.* 1979, Jensen 1966, Merritt and Cummins 1984, Pennak 1978, Simpson and Bode 1979, Smith 1968, Ward 1985b, Wiggins 1978). Species counts were converted to an area basis (#/m²).

TABLE 1: Benthic, drift and trout sampling dates for the sampling site on the Arkansas River, Colorado.

	1982						1983					
	JUL 27	SEP 7	OCT 20	NOV 18	DEC 14		JAN 17	FEB 19	MAR 29	APR 16	MAY 20	AUG 30
Benthic Sampling	X	X	X	X	X		X	X	X	X	X	X
Drift Sampling	X	X	X	X	X		X	X	X	X	X	X
Fish Sampling	-	X	-	-	X		-	-	X	-	-	X

Dry weight biomass was determined for each taxon for each replicate. Organisms were dried at 60°C until a constant weight was attained. Samples were then weighed to the nearest 0.1 mg using an Ainsworth analytical balance and converted to g/m².

The Shannon-Weaver Index was used to calculate aquatic macroinvertebrate diversity. The formula is based on dominance diversity and expresses the relative importance of each species collected, not merely the relationship between total numbers of species and of individuals (Wilhm 1972). This index was utilized to determine if any perturbation was effecting the aquatic macroinvertebrate community and also for comparisons with other studies. Species diversity calculations were made using:

$$\overline{d} = \frac{C}{N} (N \log_{10} N - \sum n_i \log_{10} n_i)$$

where C = 3.321928 (converts base 10 log to base 2 [bits])
       N = total number of individuals
       n_i = total number of individuals in the ith species (Weber 1973).

The Shannon-Weaver Index formula was applied to the combined samples for each month.

Equitability, a component of overall diversity was used to evaluate the relationship between the calculated $\overline{d}$ and an expected $\overline{d}$ that conforms to MacArthur's broken stick model of abundance values (Weber 1973). Equitability calculations were computed using:

$$e = \frac{s'}{s}$$

where s = number of taxa in the sample, and
       s' = the derived number of species calculated from a table based on MacArthur's broken stock model (Lloyd & Ghelardi 1964).

Each taxon was assigned to one or a combination of five functional groups described by Cummins & Klug (1979). These functional groups were scrapers, shredders, collector-gatherers, collector-filterers and predators. The specific functional feeding group designations of the taxa collected were established from Merritt & Cummins (1984). This analysis was conducted for comparisons with other

rivers in Colorado (Ward *et al*. 1986) and the River Continuum Concept (Vannote et al. 1980).

C. Invertebrate Drift

Invertebrate drift was sampled on the same dates as the benthic samples (Table 1). The drift nets were 1 meter in length, with an opening of 0.14 m^2 and mesh diameter of 250 μm. Three nets were positioned from the left bank to midstream along the same transect that benthic samples were collected. The nets were positioned by sliding metal rings attached to the nets over steel rods driven into the substrate. An additional net was positioned directly above each submerged net to capture invertebrates drifting in the upper water column and surface drift. Because moonlight may suppress nighttime drift (Waters 1962), samples were collected when the moon was in no more than the first 1/4 phase. Samples were collected for two hours in each 4-hour segment of the diel cycle. Net setting schedules commenced at sunset. Water velocity through each net was measured during each two hour set with a Price AA current velocity meter. Drift samples were preserved in 75% ethanol and returned to the laboratory where organisms were sorted from the debris, identified and enumerated. Drift densities (organisms $\cdot$ m^{-3} $\cdot$ sec^{-1}) were calculated for seasonal and diel comparisons.

Regression analysis (Snedecor & Cochran 1967, Elliott 1971) was utilized to determine if there was a statistically significant relationship between the density of aquatic macroinvertebrates and invertebrate drift densities throughout the sampling period. Statistical analysis was performed on transformed [$\log_{10}$ (n+1)] values. This transformation normalizes the data allowing the use of methods associated with a normal distribution.

To further quantify the relationship between the benthos and drift, the Percent Similarity index (Whittaker 1975) was calculated. This index incorporates the relationship between the number of taxa as well as the percent composition of each taxon collected. Percent similarity calculations were made using:

$$PS = 2 \sum \min (n_a \text{ or } n_b)/(N_a + N_b)$$

where n_a and n_b = importance values of a given species in samples A and B

N_a and N_b = total importance values of all species in samples A and B

D. Fish Sampling

Brown trout were collected seasonally from September 1982 through August 1983 (Table 1). Although the summer sampling episode was intended to be in June, extremely high water conditions delayed sampling to August when water levels had receded. Sampling was conducted both upstream and downstream of the benthic invertebrate sampling site with a boat electroshocker, utilizing a mobile electrode unit as used by the Colorado Division of Wildlife in larger rivers (Nehring and Anderson 1981). The electrode is thrown away from the boat in areas of suitable trout habitat and rapidly retrieved to the boat. By using direct current (DC) the fish were attracted to the electrode and followed it to the boat. The trout were then netted and placed immediately in a live well in the boat.

An effort was made during the first sampling period to collect trout every four hours, corresponding to the drift sampling schedule. However, due to low trout densities and the extensive amount of time and manpower needed to coordinate both efforts, this schedule was abandoned on the first sampling episode (7 September 1982), and 40 trout were collected the next morning following the drift net collections.

During the subsequent seasonal sampling periods, 20 brown trout were collected prior to nightfall and 20 the following morning to determine diel feeding patterns.

Length (mm) and weight (g) were measured for each fish for condition analysis using the relative weight (Wr) formula developed by Wege and Anderson (1978). This index compares the actual weight (W) to a standard weight (W_S) for fish of the same length using:

$$Wr = \frac{W}{W_S} \times 100.$$

Where W = actual weight of the fish captured
Ws = standard weight

The standard weight formula for brown trout (log W = -4.883 + 2.976 log TL) was derived from an extensive summary of length-weight data in Carlander (1969). This particular measure of condition was utilized because it recognizes that most fish become more robust as they grow, which is not taken into account in the coefficient of condition (K). Relative weight analysis was calculated for each age class of trout for each sampling period for comparison between ages as well as seasonally. For comparative purposes, the coefficient of condition was also calculated for each age group. The coefficient of condition was calculated using:

$$K = \frac{W}{L^3}$$

Where K = coefficient of condition

W = weight (grams)

L = length (millimeters)

Scales were extracted from each trout between the dorsal and lateral line on the left side for age determination. Scales were wet-mounted on microscope slides and aged utilizing a Bausch & Lomb Tri-Simplex Projector. The procedures used for age determination are reviewed by Jearld (1983). The aging system follows the numerical

classification   (e.g. a O+ designation represents a brown trout in the first year following egg hatching).

Brown trout foregut contents were removed with a modification of the stomach pump described by Seaburg (1957). This pump utilizes a small pressurized water tank commonly used for pesticide spraying, with a small diameter surgical tubing attached to the nozzle. Water was forced into the trouts foregut and contents were flushed into a 250 μm sieve. All brown trout were released following gut content removal. Each stomach sample was labeled and preserved in 75% ethanol. Prior to the study, 15 brown trout were stomach pumped, and then sacrificed to determine the efficiency of the stomach pump. Results indicated that the vast majority (>98%) of organisms in the foregut were removed by the pump. Stomach contents were preserved in 75% ethanol and returned to the laboratory where invertebrates were identified to the lowest possible taxonomic level using available keys.

Each food item extracted from the foregut was identified, enumerated, and then dried at 60°C to determine biomass and relative importance for each age group of trout. To determine brown trout feeding preference, Ivlev's (1961) electivity index was utilized for selectivity of organisms from the drift or benthos. Electivity calculations were made using:

$$E = (r_i - p_i)/(r_i + p_i)$$

where r_i = percentage by number of a taxa in the stomach and

p_i = the percentage by number in the environment (drift or benthos)

This index was also used to determine if there was any diel variation in food selection.

IV. RESULTS AND DISCUSSION

A. Physico-chemical Parameters

Perhaps the most important variable influencing aquatic macroinvertebrate composition and life-history phenomenon in unpolluted streams is temperature (Hynes 1970, Ward 1985a, Ward and Stanford 1982). Mean water temperature values recorded during the sampling period (Table 2) depicted a pattern commonly found in unregulated lotic ecosystems in the Rocky Mountain region (Canton *et al.* 1984, Ward 1984a, Zimmerman and Ward, 1984). Mean temperatures ranged from 0°C in December, to 17.9°C in July. The considerable diel fluctuations in temperature recorded, especially in spring and summer, were similar to those recorded in an unregulated section of the South Platte River, Colorado (Zimmerman and Ward 1984). Diel fluctuations were also recorded in mid winter. This was probably the result of the absence of ice cover, allowing solar radiation to elevate water temperatures during the day.

Discharge also followed a pattern common in stream systems in the Rocky Mountain region, with maximum discharge occurring during the summer months as a result of snowmelt runoff, and minimum values recorded in spring prior to runoff (Canton *et al.* 1984, Zimmerman and Ward, 1984). Stream discharge for the Arkansas River was 10% above normal during the 1982 water year and 60% above normal for the 1983 water year (Ugland *et al.* 1983). Precipitation was 63% above normal in the fall of 1982, and was again higher than normal the following spring. Increased precipitation, combined with unusually cool weather conditions resulted in higher than

normal snow pack in the Arkansas River drainage during the study period. Unusually warm air temperatures in June, combined with rain storms resulted in a rapid snowmelt, and a dramatic increase in discharge in mid June. Discharge remained considerably higher than normal in July and August of 1983 and decreased to historical median values in September.

TABLE 2: Physico-chemical results for the sampling site on the Arkansas River, Colorado.

PARAMETER	1982					1983					
	JUL	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	AUG
Mean Daily Temp. (°C)[a]	17.9	15.0	6.0	2.2	0	1.2	2.8	5.0	7.2	8.7	16.3
Temperature Range[a]	17-19	14-16	4-8	1-4	0	0-3	2-4	4-7	6-10	7-11	15-19
Discharge (m^3/sec)	29.0	19.3	17.1	20.1	18.2	16.4	17.0	11.1	7.6	8.9	25.3
Dissolved O_2 (mg/l)	8	10	10	10	10	10	11	10	10	9	8
D.O. (% Saturation)	110	129	104	94	87	91	106	102	107	101	105
pH	--	--	--	--	--	7.4	7.4	7.7	8.0	7.9	8.0
Hardness (mg/l as $CaCO_3$)	86	120	120	359	137	86	120	171	154	137	120

a Diel ranges recorded during drift sampling.

Dissolved oxygen values exhibited little change through the study, ranging from 8.0 mg/l in July and August to 11.0 mg/l in February (Table 2). The solubility of oxygen is inversely proportional to water temperature (Wetzel 1975), and the lower values recorded in the summer are probably due primarily to the relatively high stream temperatures. Dissolved oxygen levels are comparable to values recorded by La Bounty *et al*. (1975) and Roline and Boehmke (1981) in other foothills sections of the

Arkansas River. Recorded levels of dissolved oxygen approached or were above saturation throughout the sampling period. Physical aeration as a result of turbulence is probably the most important source of oxygen in running waters (Hynes 1970). The supersaturated values recorded for most of the months were probably the result of instream photosynthesis and the turbulent nature of the stream where the samples were taken. The three months when the river was not supersaturated (November – January) also corresponded to the lowest mean temperature values. During this time, the river exhibited the highest capacity to retain oxygen. However, the turbulence present during this time period was apparently not great enough to result in saturated levels.

Values for pH were determined from January – August 1983 (Table 2). The values were all in the basic range and were slightly higher than those found by LaVelle (1968) near the study site. La Bounty *et al*. (1975) and Roline and Boehmke (1981) also recorded pH values that were slightly basic throughout the foothills and montane region of the Arkansas River.

Hardness (mg/l as $CaCO_3$) ranged from 85.5 to 359.1 during the study period (Table 2). These values were higher than values recorded from the headwaters of the Arkansas River near the town of Leadville (Roline and Boehmke 1981). There were no apparent seasonal trends, and values were in the moderately hard to very hard range (U.S. EPA 1976). The values were also within the suggested range for rearing salmonid fishes (Piper *et al*. 1982).

Organic and inorganic seston transport was greatest during the snowmelt runoff sampling period in August (Figure 2). In fact, there was a significant correlation between inorganic seston transport and total discharge throughout the year (r = 0.98,

p < 0.05). There was also a significant correlation between organic seston transport and discharge (r = 0.91, p < 0.05). Milner *et al*. (1981) and Farnworth *et al*. (1979) in their reviews of sediment dynamics and its relationship to aquatic biota concluded that sediment transport is primarily a function of discharge and the shear forces associated with various discharge levels. La Velle (1968) found that greater than 70% of the suspended sediment in the Arkansas River was less than the 250 μm mesh diameter of the drift nets used for this study. Based on LaVelle's results, it appears that seston transport quantified by the drift nets adequately estimated the larger size fraction, but total seston transport was obviously underestimated.
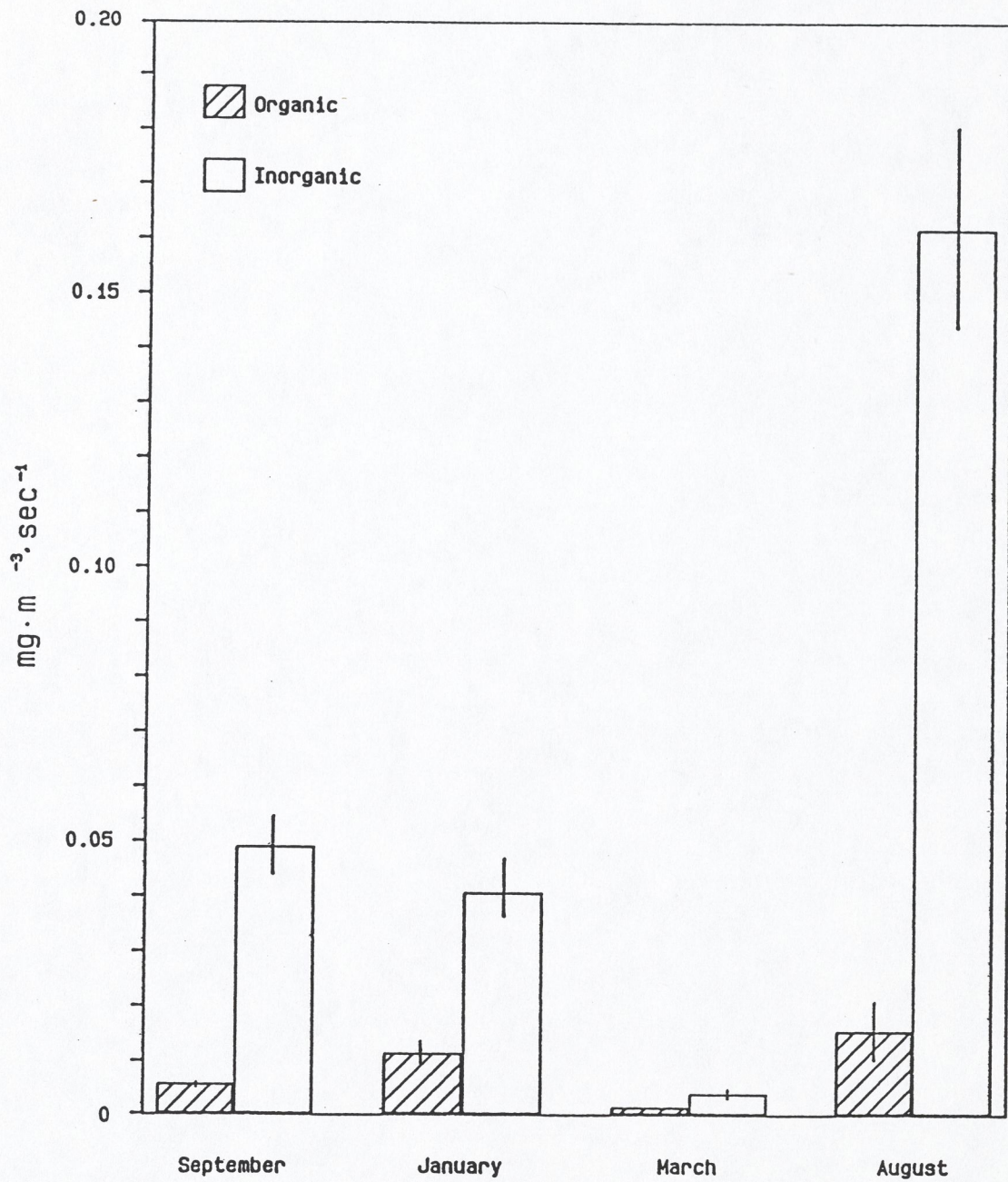
FIGURE 2: Seasonal seston transport (>250 μm) at the study site on the Arkansas River, Colorado. Vertical bars indicate $\pm$ one standard error.

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B.   Benthic Invertebrates

A total of 65 taxa of benthic macroinvertebrates were collected during the study period (Table 3), although only 9 were numerically abundant (annual $\overline{x} > 75$ org./m^2) (Appendix Tables A-1, A-2). Aquatic insects comprised more than 99% of the densities of benthic macroinvertebrates collected during the study (Table 4), with ephemeropterans and dipterans collectively contributing more than 81% each month. These values were similar to those found by Ward (1976) in an unregulated section of the South Platte River in Colorado, and by Ward et al. 1986 in rivers in the same elevational range as the study site. Lavelle (1968) also found a similar composition in the benthic community throughout the upper mainstem of the Arkansas River. Non-insect taxa such as *Hyallela azteca* and *Sperchon* sp. were incidental in the benthos throughout the sampling period.

Although aquatic insects comprised the majority of the biomass (Table 5), the relative importance of each order differed considerably from the density. Plecoptera and Trichoptera comprised a considerably higher percentage of the biomass throughout most of the study period. This discrepancy was due to the greater body size of plecopterans and trichopterans, compared with ephemeropterans and dipterans.

Mean monthly density values ranged from 1059 org/m^2 in July 1982 to 7317 org/m^2 in August 1983 (Figure 3). Values were generally higher in late summer and fall (August - October) while the lowest values were observed in July and November. Mean monthly biomass values ranged from 0.43 g/m^2 in July to 2.9 g/m^2 in April (Figure 4). Although biomass fluctuated somewhat, values were relatively low in late summer through early winter, increasing substantially in late winter through spring. The apparent inverse relationship between density and biomass appears to be a

TABLE 3: Aquatic macroinvertebrates collected from the benthos, drift samples and trout stomach samples at the study site on the Arkansas River, Colorado.

INSECTA

Ephemeroptera

Ameletus sp.
 Baetis tricaudatus
 Ephemerella inermis
 Epeorus longimanus
 Rhithrogena hageni
 Rhithrogena undulata
Tricorythodes minutus

Plecoptera

Capnia sp.
 Isogenoides zionensis
 Isoperla sobria
 Triznaka signata
 Claassenia sabulosa
 Hesperoperla pacifica
 Paraleuctra sp.
 Pteronarcella badia
 Taenionema nigripenne

Trichoptera

**Helicopsyche borealis*
 Hydropsyche cockerelli
 Hydropsyche occidentalis
 Hydropsyche oslari
 Brachycentrus occidentalis
 Coluptila sp.
 Glossosoma sp.
 Leucotrichia sp.
 Lepidostoma sp.
 Psychomyia flavida
 Rhyacophila acropedes
 Rhyacophila angelita
 Rhyacophila coloradensis
Neothremma sp.

Coleoptera

*Dyticidae
Haliplus sp.
 Optioservus sp.
 Oreodytes sp.
 Zaitzevia parvula

Diptera

Antocha sp.
 Atherix pachypus
 Bibiocephala sp.
 Chelifera sp.
 Wiedemannia sp.
 Hexatoma sp.
 Hemerodromia sp.
 Tipula sp.
 Palpomyia complex
 Simulium arcticum
 Cardiocladius sp.
 Constempelina sp.
 Diamesa sp. A
 Diamesa sp. B
 Eukiefferiella
 Micropsectra sp.
 Orthocladius-Cricotopus group
 Pagastia sp.
 Phaenopsectra sp.
 Parametriocnemus sp.
 Thienemannimyia sp.
 Protanyderus margarita

COLLEMBOLA
 Podura sp.

CRUSTACEA
 Amphipoda
  Hyalella azteca

 *Cladocera
 *Copepoda
 *Ostracoda

HYDRACARINA
 Sperchon sp.

OLIGOCHAETA
 Tubificidae

NEMATODA

* Collected only in drift samples
** Collected only in trout stomach samples

TABLE 4: Benthic macroinvertebrate percent composition by density, collected at the study site on the Arkansas River, Colorado.

| | 1982 | | | | | 1983 | | | | | | Total |
	J*	S	O	N	D	J	F	M	A	M	A	Avg.
Plecoptera	0.8	1.0	4.0	6.0	4.0	2.0	1.0	2.0	3.0	6.0	0.4	3.0
Ephemeroptera	24.0	9.0	27.0	35.0	47.0	31.0	35.0	34.0	45.0	76.0	47.0	37.0
Trichoptera	11.0	9.0	9.0	6.0	4.0	2.0	2.0	3.0	11.0	3.0	14.0	7.0
Diptera	57.0	79.0	59.0	53.0	45.0	64.0	62.0	62.0	39.0	15.0	38.0	52.0
Coleoptera	6.0	0.1	0.3	0.1	0.0	0.1	0.2	0.2	0.2	0.3	0.6	0.8
Amphipoda	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hydracarina	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.1
Oligochaeta	0.2	0.0	0.1	0.2	0.0	**	0.0	0.0	0.2	0.3	0.0	0.1
Nematoda	0.0	0.0	0.2	0.0	0.3	0.0	0.0	0.0	0.4	0.0	0.0	0.1

* denotes July
** indicates density <0.1%

TABLE 5: Benthic macroinvertebrate percent composition by biomass, collected at the study site on the Arkansas River, Colorado.

| | 1982 | | | | | 1983 | | | | | | Total |
	J*	S	O	N	D	J	F	M	A	M	A	Avg.
Plecoptera	0.3	6.0	22.0	55.0	50.0	56.0	33.0	38.0	44.0	27.0	31.0	33.0
Ephemeroptera	45.0	19.0	5.0	5.0	6.0	7.0	3.0	5.0	19.0	45.0	15.0	16.0
Trichoptera	7.0	7.0	57.0	25.0	16.0	8.0	5.0	10.0	22.0	9.0	17.0	18.0
Diptera	26.0	69.0	13.0	15.0	27.0	28.0	59.0	47.0	15.0	17.0	37.0	32.0
Coleoptera	4.0	**	0.4	0.1	0.0	1.0	**	0.3	0.4	0.2	0.6	0.6
Amphipoda	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hydracarina	**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**	**	0.0	0.0
Oligochaeta	8.0	0.0	**	**	0.0	**	0.0	0.0	**	2.0	0.0	0.9
Nematoda	0.0	0.0	3.0	0.2	0.0	0.0	0.0	0.0	**	0.0	0.0	0.3

* denotes July
** indicates biomass <0.1 mg
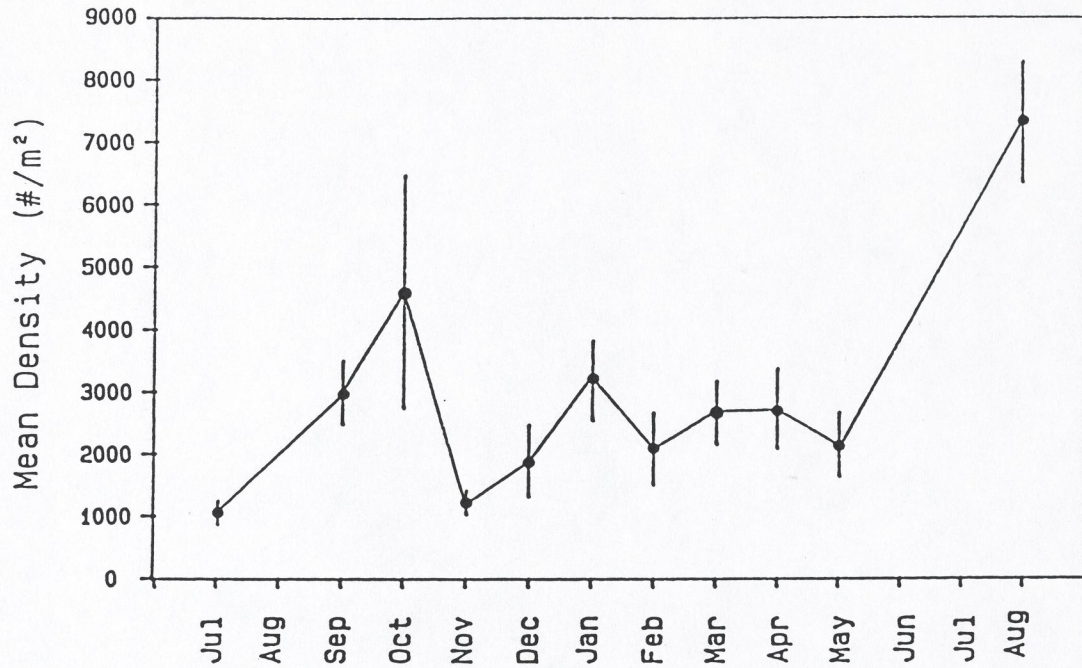
FIGURE 3: Mean density values of benthic macroinvertebrates collected at the study site on the Arkansas River, Colorado. Vertical bars indicate ± one standard error.
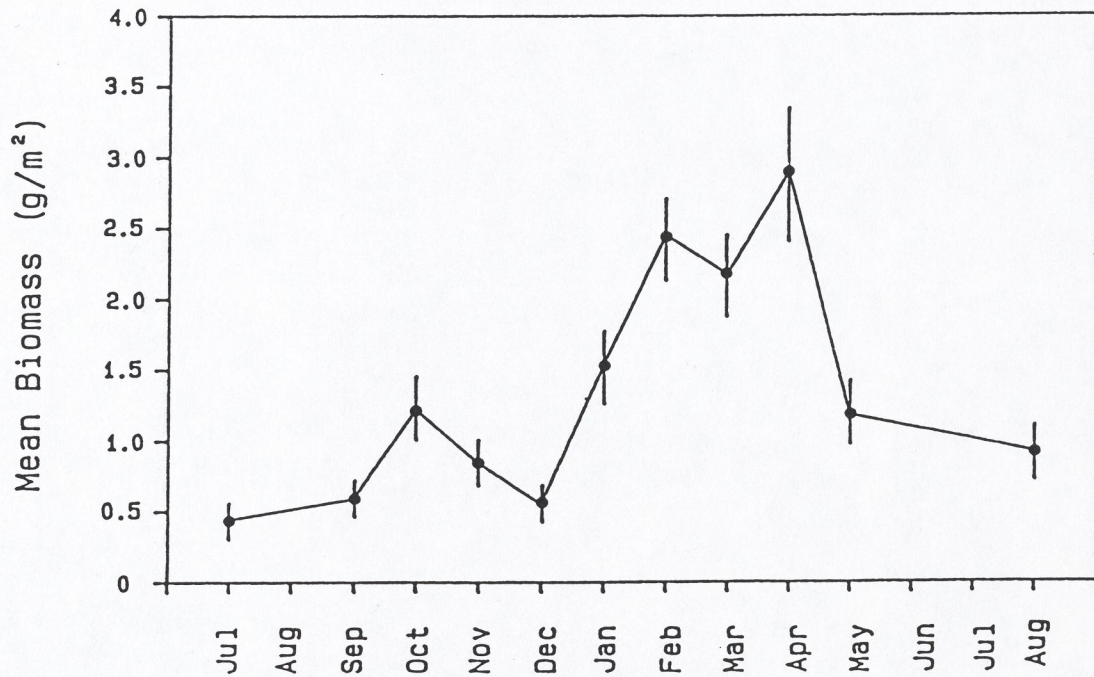
FIGURE 4: Mean biomass values of benthic macroinvertebrates collected at the study site on the Arkansas River, Colorado. Vertical bars indicate ± one standard error.

result of seasonal life-history strategies. The high density and low biomass values recorded in late summer and fall are the result of the hatching of many aquatic insects resulting in large numbers of early instars. Early instars of *Baetis tricaudatus* and *Parametriocnemus* sp. were present throughout this time period, and comprised a high percentage of the density. Hynes (1970) states that autumn is a period of hatching of the eggs of species which will grow during the winter, and is thus a period of increasing, often maximum numbers. To avoid the harsh environmental conditions during snowmelt runoff, it would appear to be more beneficial for benthic macroinvertebrates to be in a diapausing egg stage or an adult stage. The low total density and biomass during July, and subsequent increase in the number of early instars in the late summer and fall indicates that large numbers of aquatic insects are hatching during this period. The relatively low density values observed in November were the result of a decline in the numbers of all major groups of aquatic insects. Stream discharge had increased 7.0 m³/sec., 2 days prior to the sampling period (Ugland *et al*. 1983). Although elevated levels of turbidity were not apparent, the sudden increase in discharge may have catastrophically displaced many benthic invertebrates. Hynes found that losses caused by predation and environmental factors such as floods may decrease total density during this time of year. Although there was a negative trend in density during November, the chironomid *Diamesa* sp. increased more than two-fold (Appendix Table A-1). Elgmork and Saether (1970) found this genus only in the headwater reaches of a Colorado mountain stream. Their conclusion was that this genus was restricted to coldwater reaches of their study stream. Herrmann *et al*. (1987) found that *Diamesa leona* emerged from November through April near the study site, with the main emergence period being from November through February. The increased abundance of *Diamesa* in November indicates that they may be present as active larvae only when stream temperatures are reduced in fall and winter. The subsequent increase in density and biomass during

mid-winter was due to an overall increase in the numbers of ephemeropterans and *Diamesa*. Benthic densities of *Diamesa* increased from 207 org/m^2 in November to 1657 org/m^2 in January. These results indicate that a considerable number of *Diamesa* larvae hatched from eggs during these months. The increase in total Ephemeroptera density from 415 org/m^2 in November to 1022 org/m2 in January may be a result of extended hatching of *Baetis tricaudatus*.

Although total densities were generally lower during late winter and early spring, biomass was greatest during the spring (Figures 3 and 4). Hynes (1970) indicates that in the absence of winter plecopterans, the biomass in early spring increases as renewed growth occurs in individuals which have overwintered. This was apparent during the late winter and spring when water temperatures began to increase. The density and biomass of ephemeropterans continued to increase through the spring attaining densities of 1622 org/m^2 and biomass of 0.6 g/m^2 in May. The decrease in density and biomass in late spring, was apparently the result of the emergence of several taxa of aquatic insects. During the April sampling period, the trichopteran *Brachycentrus occidentalis* was observed forming clusters of pupal cases on the surface of rocks. During this period, densities were 258 org/m^2 and biomass 0.3 g/m^2 for this species (Appendix Tables A-1, A-2). Subsequent sampling in May resulted in decreased densities of 30 org/m^2 and biomass of 0.1 g/m^2. Based on results from the April and May sampling period, the majority of these trichopterans emerge in mid-April to mid-May when mean daily water temperatures exceed a mean value of 7°C. These results were similar to the pupation and emergence periods of the same species described by Krueger and Cook (1984) for a Minnesota stream. Winget (1984) found similar results for *B. occidentalis* in the Huntington River, Utah. Winget concluded that the pupation and subsequent emergence of *B. occidentalis* prior to snowmelt runoff was a strategy to avoid high water velocities and sediment scouring. Pupae of

Glossosoma sp. were also collected in the mid-May samples, which was approximately a month later than a peak in densities of *Glossosoma intermedium* pupae found by Krueger and Cook. Pupae of *Simulium arcticum* were collected from March through May. A decrease in *Simulium* larvae from 553 org/m^2 in February to 4 org/m^2 in May was observed indicating emergence during this time period. The plecopteran *Isogenoides zionensis* also exhibited a decrease in density in May. Adult *Isogenoides* were observed during May and June on riparian vegetation at the study site. Krueger and Cook (1981) studied the life cycles of plecopterans in Minnesota, and concluded that emergence of *Isogenoides olivaceous* occurred during May. Fuller and Stewart (1977) also found that *Isogenoides zionensis* emerged in the upper Gunnison River, Colorado in late May. The chironomid *Diamesa* sp. also exhibited a considerable decrease from 650 org/m^2 in April to 2 org/m^2 in May. No diamesan chironomids were collected the following August (Appendix Table A-1). The decline in densities of *Diamesa* in spring and absence in late summer may be the result of a fast seasonal life cycle to avoid high water temperatures as active larvae. The majority of the summer and fall seasons are apparently spent in the egg stage.

The general seasonal trends observed, followed the seasonal cycle described by Hynes (1970). It appears that many insects (e.g. *Brachycentrus occidentalis* and *Isogenoides zionensis*) emerge in late spring and summer prior to or during snowmelt run-off. In late summer and fall, high densities and low biomass are the result of the hatching of insects. During late fall and early winter densities generally decrease, probably due to mortality, but biomass increases as the insects grow. Although densities increased somewhat in spring, biomass increased dramatically as water temperatures increased and insects growth rates increased.

Diversity and equitability values exhibited no apparent seasonal trends throughout the sampling period, although the two indices exhibited similar fluctuations (Figures 5 and 6). Diversity values ranged from 3.29 in November to 2.28 in August with a mean value of 2.81. Wilhm (1970) evaluated diversity levels from numerous authors based on a variety of unpolluted and polluted streams. The values calculated at the study site were all above the values recorded by Wilhm in streams receiving pollution and most were in the range of clean water streams. Environmental stress inherent in many mountain stream systems has been shown to reduce diversity index levels where pollution is not apparent (Winget and Mangum 1979). The wide ranges of diversity and equitability values observed appear to be the result of life-history and environmental phenomenon. During July 1982 when snowmelt run-off was receding, densities were low (1059 org/m^2) but numbers were quite evenly distributed among the taxa. This even distribution resulted in the second highest diversity (3.23) and equitability (0.62) values calculated for the study period. However, in August 1983 when densities were highest (7317 org/m^2), diversity (2.28) and equitability (0.26) were the lowest. These low values were primarily a result of high densities (3277 org/m^2) of early instar *Baetis tricaudatus* which had recently hatched. Low values observed in January and March were primarily due to relatively high densities of the chironomid *Diamesa* sp.

Mean diversity values from a metal stressed section of the Arkansas River near the town of Leadville never exceeded 1.90 (Roline and Boehmke, 1981). They also found that diversity values from sites located just downstream of two major sources of heavy metals in the Arkansas River were even further suppressed, with values of approximately 1.37 and 1.25. Using their results for comparison, it does not appear that the aquatic macroinvertebrate community at the study site is suppressed to an
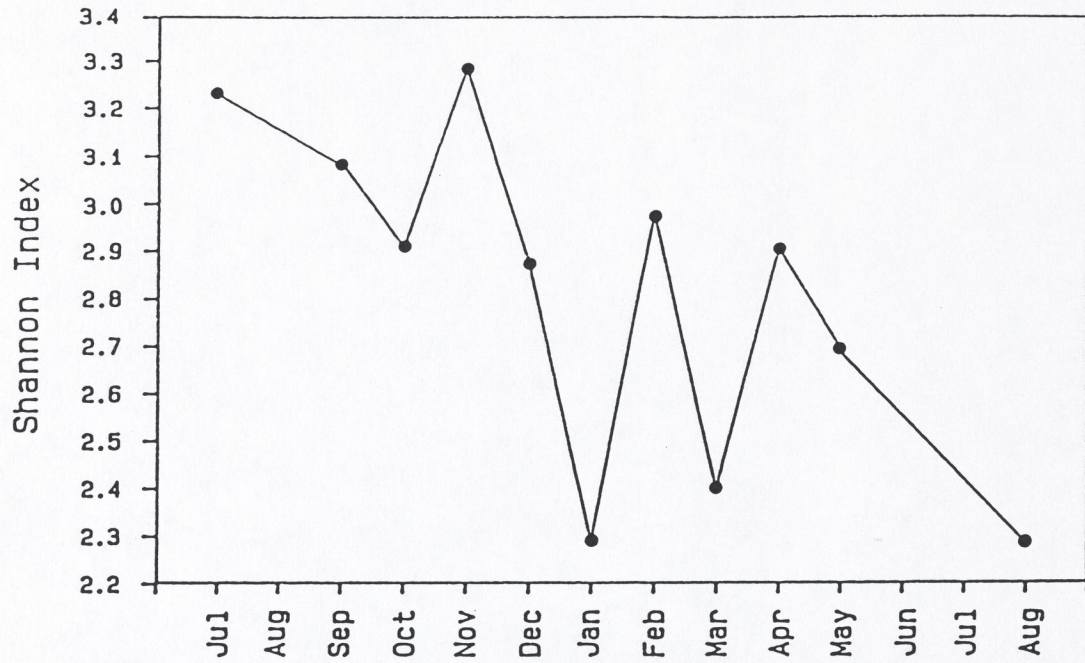
FIGURE 5:   Shannon-Weaver diversity values of benthic macroinvertebrates collected at the study site on the Arkansas River, Colorado.
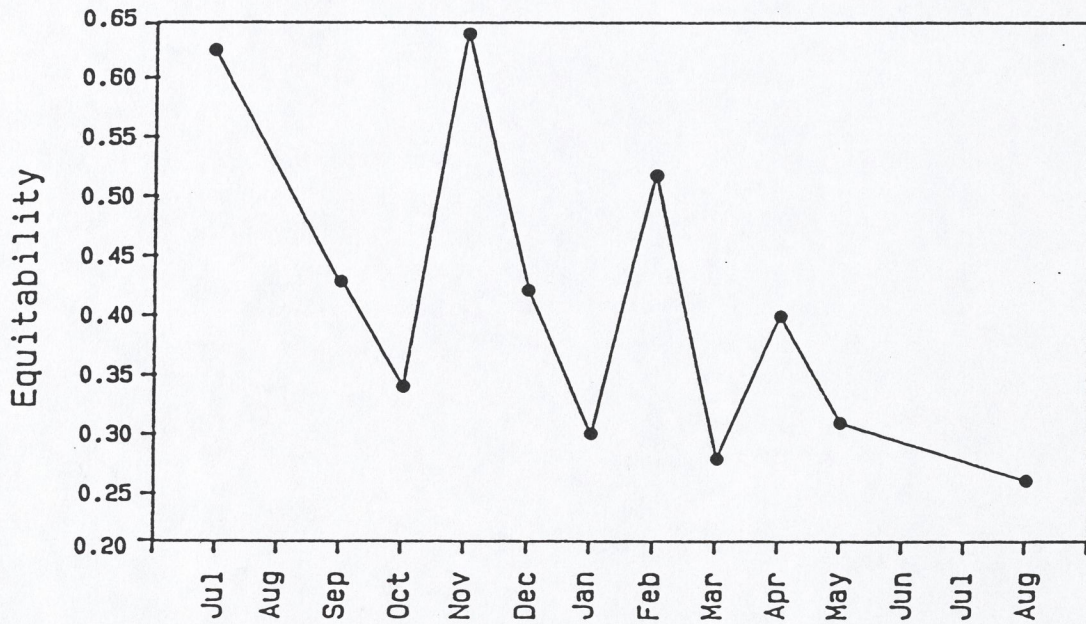
FIGURE 6:   Equitability values of benthic macroinvertebrates collected at the study site on the Arkansas River, Colorado.

appreciable degree by heavy metal contamination or other environmental stresses. Although the use of diversity indices has been widely used to monitor the effects of pollution on aquatic macroinvertebrate populations, it appears that life-history strategies and environmental stress as a result of snow melt runoff may influence values on a seasonal basis in the Arkansas River.

Functional feeding group analysis revealed that collector-gatherers dominated the fauna in terms of density throughout the year (Figure 7). Shredders were numerically insignificant and are not shown on the figure. The relative importance of scrapers and collector-filterers varied seasonally as the abundance of individual taxa changed, while the percentage of predators remained low throughout the sampling period. In describing the River Continuum Concept, Vannote *et al.* (1980) hypothesized that medium sized streams (orders 4-6) would be dominated by collectors and grazers, with shredders and predators comprising a small percentage of the composition. The reduced importance of shredders in the medium-sized streams compared to headwater reaches is attributable to a decline in the relative importance of coarse particulate organic matter (CPOM, particle size >1mm). The increased numbers of collectors is apparently the result of a food base dominated by fine particulate organic matter (FPOM, particle size <1mm) which is partly supplied by upstream processing of CPOM. The increased percentage of scrapers at the study site is probably the result of increased primary production as a result of decreased canopy and increased light available for photosynthesis. Lavelle (1968) studied primary production in the upper Arkansas River, and concluded that net productivity varied widely near my study site, averaging 14.7 g O_2/m^2/day, with the highest levels during June. The net primary productivity values recorded by La Velle near the study site correspond to the positive P/R values (>1.0) which would be expected in mid-size streams according to the River Continuum Concept.

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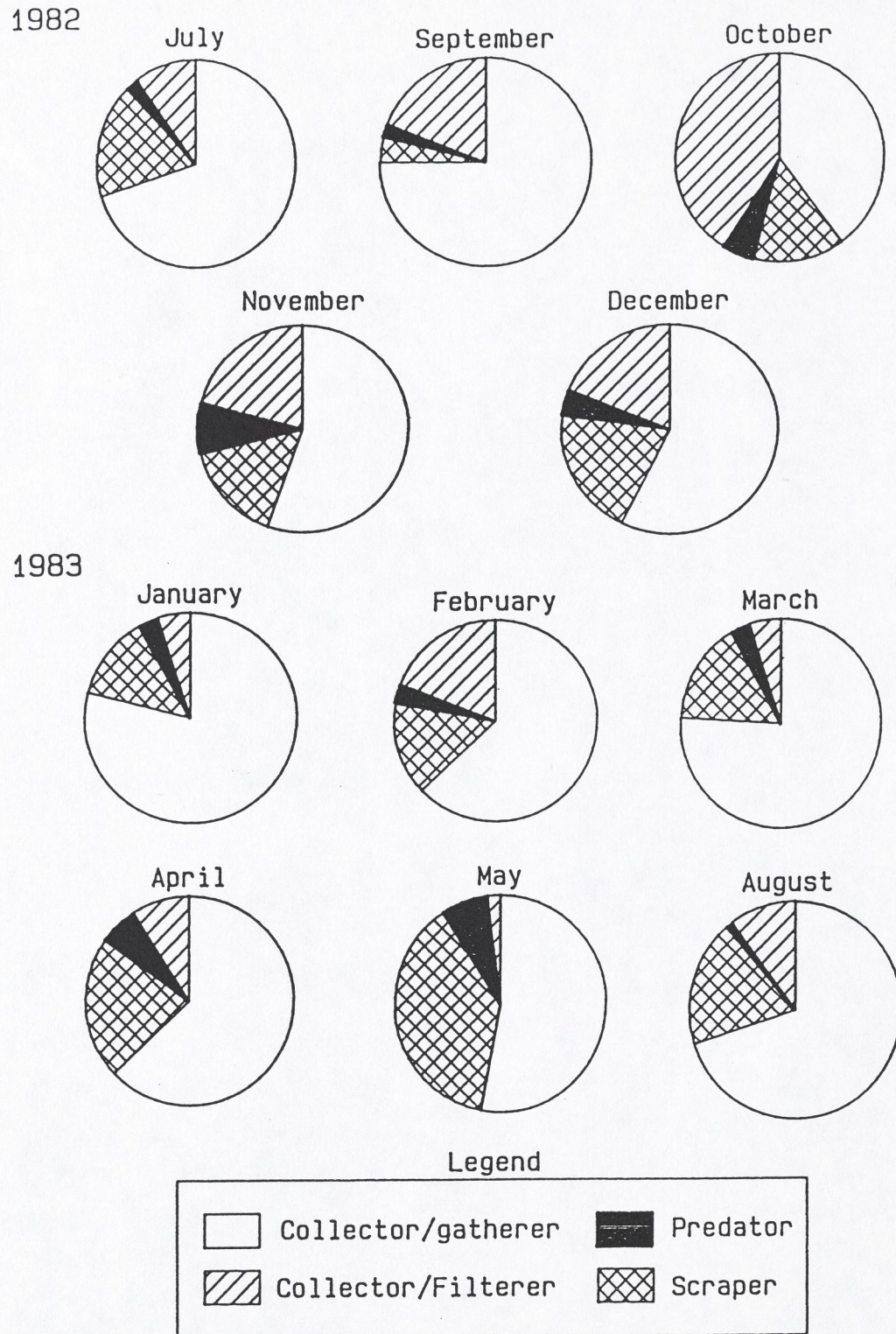
FIGURE 7:   Relative abundance of functional feeding groups collected at the study
            site on the Arkansas River, Colorado.

C.   Invertebrate Drift

A total of 40 taxa of aquatic macroinvertebrates were collected in the drift samples during the sampling year (Appendix Table A-5). Aquatic insects dominated, comprising 75% of the total taxa collected.

Ten invertebrate taxa collected in the drift were not present in the benthic samples (Table 3). Although no additional orders of aquatic insects were collected in the drift nets, 3 types of crustaceans (Cladocera, Ostracoda and Copepoda) were captured which were absent from the benthic samples. Each of the seven genera of aquatic insects found exclusively in the drift nets were collected only once during the sampling period and were probably rare in the study area. The three taxa of crustaceans collected only in the drift nets were relatively more common. The most abundant, the Ostracoda, are common in lotic systems (Pennak 1978), but riffles may not be the preferred habitat. Hynes (1970) indicated that although Copepoda and Cladocera may inhabit mostly lentic ecosystems, individuals may be found in low velocity areas of rivers. The absence of these crustaceans in the benthic samples and relatively low frequency of occurrence in the drift indicates that these small crustaceans may inhabit areas of low water velocities in the pool and backwater areas upstream of the study site, and were occasionally swept into the current where they drift downstream.

Two Ephemeroptera genera (*Baetis tricaudatus* and *Rhithrogena hageni*) were present in drift samples each month (Appendix Table A-5). Baetidae are generally considered good swimmers and inhabit fast flowing streams in the Rocky Mountain area (Edmunds, et al. 1979). However, *Rhithrogena hageni* is dorso-ventrally flattened, and resides in the low velocity boundary layer around rocks in riffle habitat (Hynes 1970). Stewart and Szczytko (1983) found that although *Rhithrogena* was present in

drift collections in the Dolores and Gunnison Rivers in Colorado, their densities were considerably less than *Baetis tricaudatus*, as was true in the present study. Their results also showed higher drift densities of *Rhithrogena* in rivers with higher benthic densities, indicating that the drift of this ephemeropteran may be density dependent.

Simulium arcticum and chironomids were also collected in drift nets during all the sampling months (Appendix Table A-5). *Simulium* spp. are commonly found in the drift (Rutter and Poe 1978, Kroger 1974) and occasionally at high densities (Wotton, *et al*. 1979). Larvae occasionally release themselves from the substrate due to lack of food, suitable substrate or competition for space and drift downstream on silken threads to suitable sites (Peterson 1984). The abundance of *Simulium arcticum* in the benthos and their propensity to drift probably resulted in their presence throughout the sampling year in the drift samples. Chironomidae were also present in the drift samples throughout the year.

Chironomids, *Simulium arcticum* and *Baetis tricaudatus* comprised over 80% of drifting individuals throughout the sampling period (Figure 8). Plecopterans, trichopterans as well as other ephemeropterans and dipterans, although abundant in the benthos, comprised only a small portion of the drift. *Simulium arcticum* comprised a relatively high percentage of the drift in late summer to mid-winter and comprised a much lesser percentage in the spring and summer following pupation and emergence. The drift density of *Baetis tricaudatus* was relatively constant throughout the sampling period, while the drift density of chironomid larvae fluctuated considerably. During the winter and spring months, relatively high densities of the chironomid *Diamesa* sp. A entered the drift. Waters (1972) concluded that there may be increased feeding activity prior to pupation as the mature larvae move to preferred bottom types, or
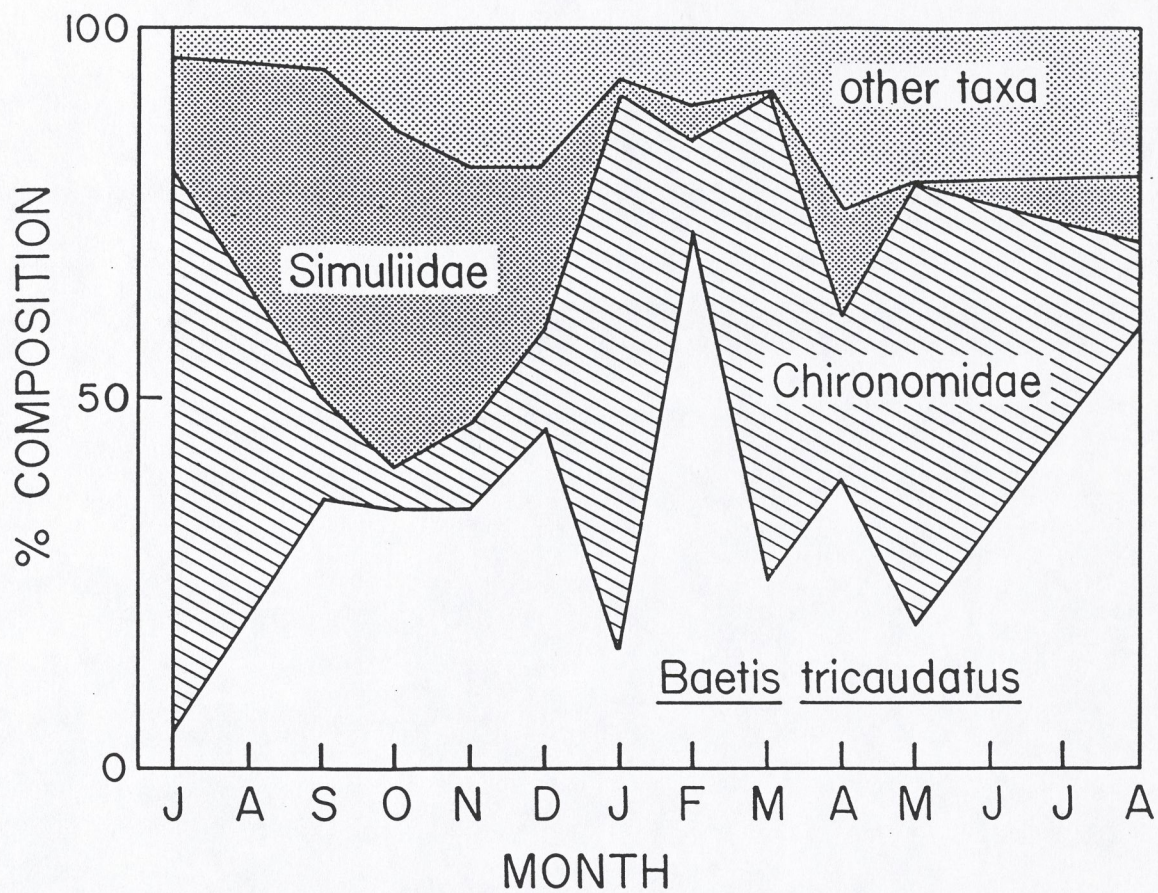
FIGURE 8: Percentage composition of drifting benthic macroinvertebrates at the study site on the Arkansas River, Colorado.

areas of suitable current velocities. Waters also found that an increase in population density of a particular taxon may place the greatest intensity of population pressure upon available living space. Consequently, an increase in intra-specific competition may occur, and result in increased activity and drift. The relatively high percentage of *Baetis tricaudatus* throughout the sampling period may be a result of the high densities in the benthos as well as the propensity of these Ephemeroptera to enter the drift.

Mean drift densities ranged from 0.13 org $\cdot$ m^{-3} $\cdot$ sec^{-1} in September to 2.02 org $\cdot$ m^{-3} $\cdot$ sec^{-1} in January, with a mean rate of 0.53 org $\cdot$ m^{-3} $\cdot$ sec^{-1} throughout the year (Figure 9). Although drift densities were generally lower in fall and higher in winter and spring, the low densities recorded were apparently influenced by life history and environmental factors. The relatively high drift densities recorded in January were the result of large numbers of the chironomid larvae *Diamesa* sp. A entering the drift. These cold stenotherms may have been active prior to pupation and inadvertently entered the drift as a result of increased foraging activity. Invertebrate drift was also relatively high in February. However, chironomid densities were considerably lower than the previous month, while *Baetis tricaudatus* dominated the drift. Although there were numerous adult chironomids present, and larvae were observed in the benthos during February, the decrease in larval *Diamesa* in the drift may be a result of inactivity or some environmental phenomenon. The second highest drift density, which was observed in August was the result of a catastrophic event which occurred during the 1030 sampling period. The river became turbid during that time period as a result of upstream road construction or a spate. Total invertebrate drift density for that time period exhibited a 7 fold increase over the other 5 sampling intervals during that month. Several other studies have indicated that increased suspended sediments and turbidity increase the drift rates of aquatic
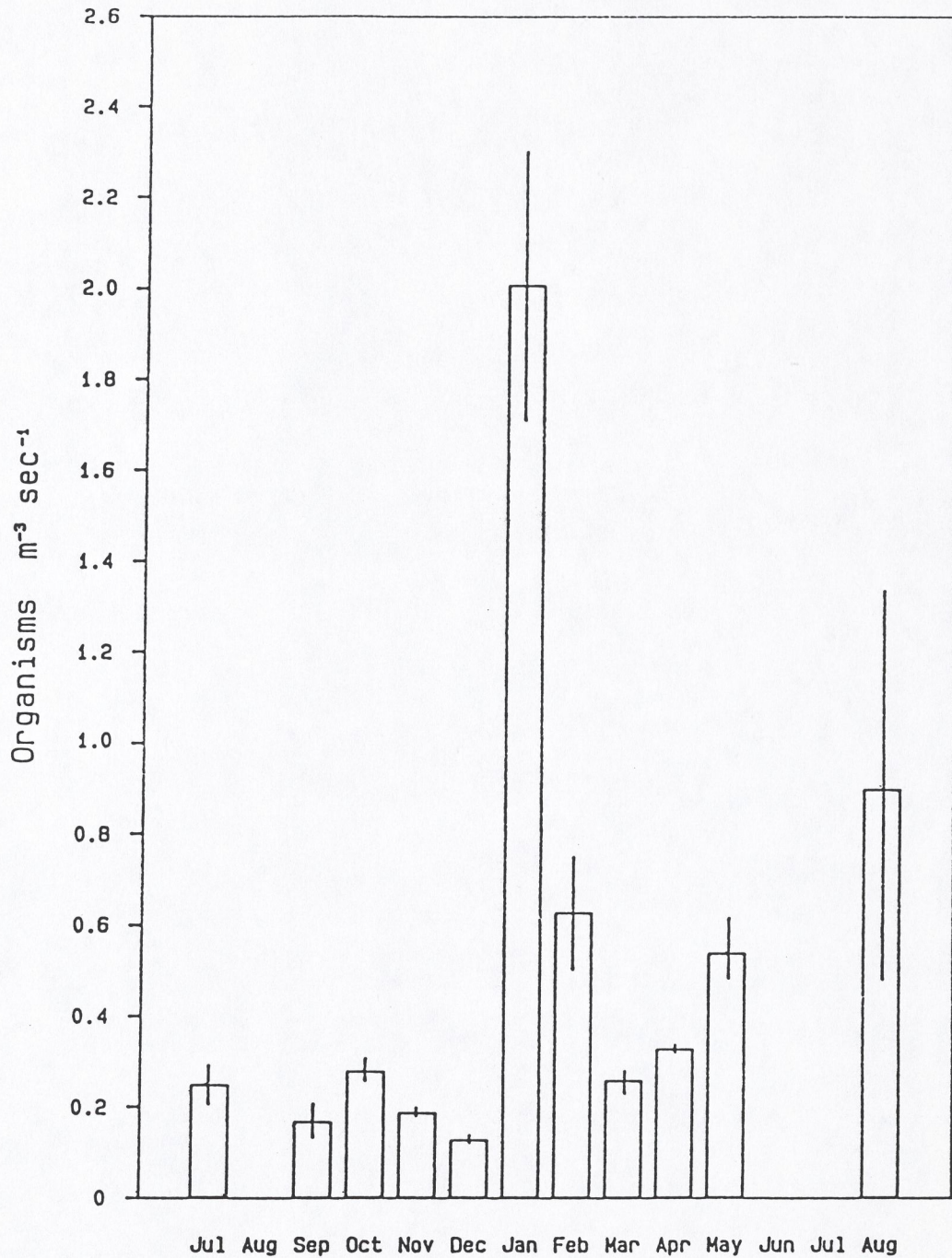
FIGURE 9: Mean drift densities for benthic macroinvertebrates at the study site on the Arkansas River, Colorado. Vertical bars indicate ± one standard error.

macroinvertebrates (Ciborowski *et al.* 1977, Rosenberg and Wiens 1975). These studies reported a direct relationship between suspended sediment concentration and invertebrate drift. Cummins (1972) described a simplified model in which aquatic invertebrates, when faced with adverse environmental conditions enter the drift. Although an increased sediment load has been shown to increase invertebrate drift, whether this phenomenon initiates an active entry into the current or catastrophically sweeping individuals off the substrate has not been determined.

There was a negative relationship between mean daily temperature and drift densities, but the correlation was not statistically significant ($r = -0.41$, $p > 0.05$). Although mean daily temperatures exhibited a typical seasonal pattern for unregulated streams in the Rocky Mountain region, cooling in winter and subsequent warming during the following spring, no apparent trends in mean drift densities were apparent.

No significance ($r = -0.07$, $p > 0.05$) was found between stream discharge measured on the drift sampling dates and mean drift density. Many stream insects in the Rocky Mountain Region time their emergence and ovipositing strategies following runoff. However, this life history strategy apparently did not influence mean drift densities at the study site.

There was no significance ($r = 0.48$, $p > 0.05$) between benthic density and invertebrate drift densities. Although the drift density of certain individual taxa may be related to population density (e.g. *Diamesa*), the influence of behavioral drift (e.g. *Baetis tricaudatus*) and life history strategies of individual taxa appear to mask any relationships at the community level.

Percentage similarity (ps) values between benthic densities and drift densities ranged from 29% in May 1983 to 85% in January 1983 with a mean value of 61% (Figure 10). Similarity has not previously been used to correlate drift-benthic relationships, although they have been used in benthic studies and drift studies to correlate faunal similarity between sites (Chadwick, *et al*. 1986, Canton and Chadwick 1985, Ward 1986, Wilzbach *et al*. 1986). The results indicate a high variability between months with no apparent trends. As previously discussed, there was also considerable variability between benthic composition (Appendix Table A-1 and A-2) and drift composition (Figure 8) throughout the year. When the ps index was applied to these highly variable parameters, the results exhibited no apparent trends. In May when the ps value was lowest, chironomids comprised 55% of the total drift while only contributing 13% of the benthic density, and two ephemeropterans, *Ephemerella inermis* and *Rhithrogena hageni* comprised 65% of the benthos while only comprising 8% of the drift. Although there were several other minor discrepancies between the composition of the drift and the benthos during this month, the differences between these three taxa probably resulted in the low ps value calculated.

The high ps value calculated for January was the result of the dominance of the *Baetis tricaudatus* and chironomid larvae in the benthos as well as the drift. None of the other taxa collected, comprised more than 4% of the benthic or drift density. Although there were 10 taxa collected in the drift that were not collected in the benthic samples, their relative importance is apparently too low to influence the relatively high ps value for that particular month.

1.   Behavioral Drift Patterns

Drift densities for *Baetis tricaudatus* were highest following sunset for nine of the ten months in which diel comparisons could be made (Figure 11). No trends were
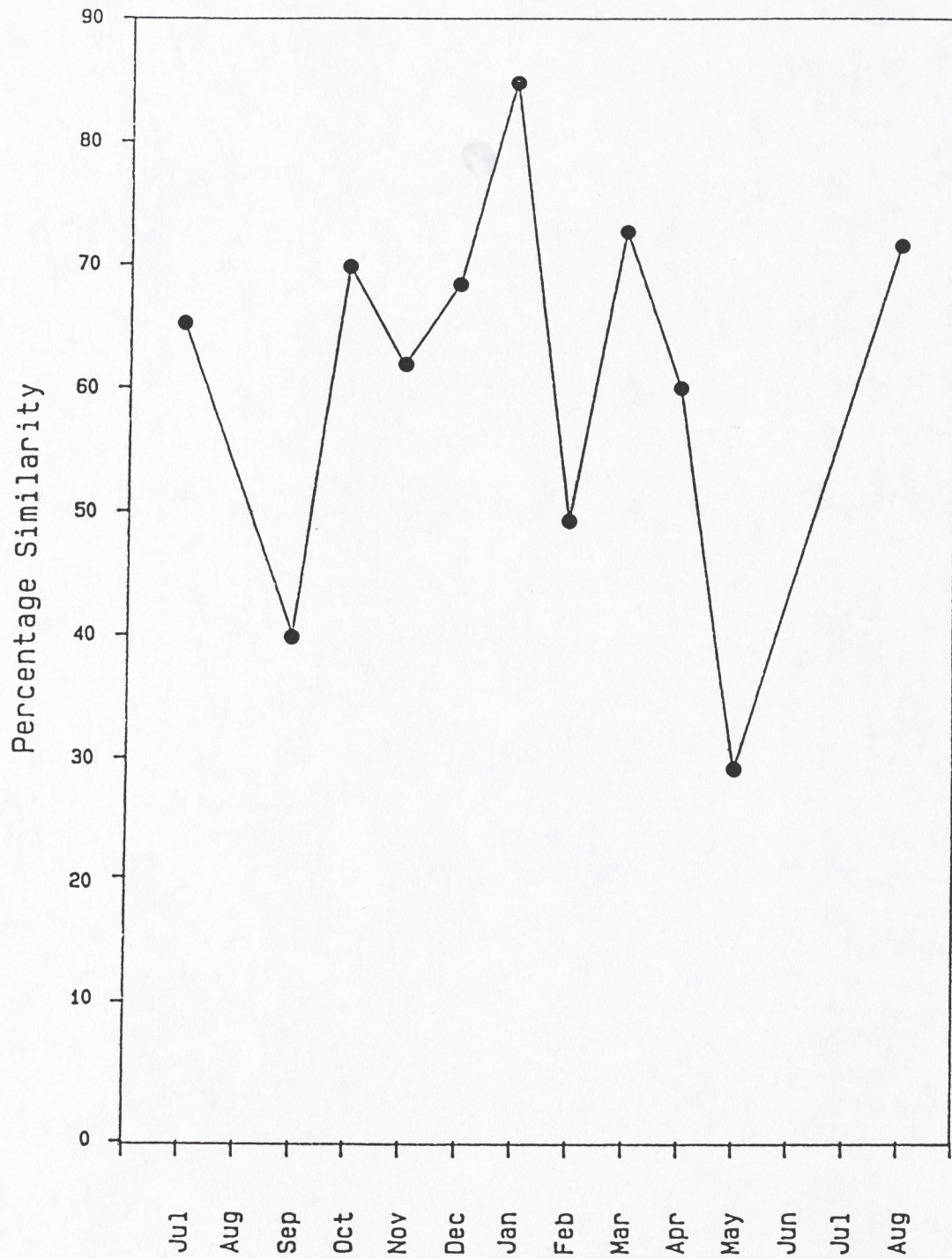
FIGURE 10: Percentage similarity (ps) for benthic densities and drift densities of benthic macroinvertebrates at the study site on the Arkansas River, Colorado.

apparent during July when snowmelt runoff was occurring and in December due to limited sampling as a result of frazil ice formation in the early morning hours. These results indicate a behavioral type drift pattern throughout the year which is not influenced by seasonal or environmental conditions. Similar behavioral drift patterns have been found by several authors (Chaston 1969b, Elliott 1967, Holt and Waters 1967, Stewart and Szczytko 1983), and their results indicate that there are several factors influencing this phenomenon. Waters (1972) in his review of invertebrate drift indicated that light intensity, acting as an exogenous stimulus, was the primary factor governing behavioral drift patterns. However, more recent studies have shown that food abundance and feeding behavior influence the active entry of invertebrates into the drift (Kohler 1985) as well as avoidance of invertebrate or vertebrate predators (Peckarsky 1980, Allan 1978b). The nocturnal maxima of *B. tricaudatus* is probably a result of a combination of increased feeding and food patch searching behavior during the dark hours as well as predator avoidance, as fish and invertebrate predators are present throughout the year. Wiley and Kohler (1984) also determined that behavioral drift is a composite phenomenon resulting from a number of independent, and to some extent unknown causes. The fact that there was no apparent seasonal relationship between benthic densities and drift densities of *B. tricaudatus* larvae further demonstrates that behavioral drift for this species is probably not a result of crowding and intraspecific competition, but probably related to general foraging behavior and predator avoidance.

During the August sampling period, there was a six-fold increase of *B. tricaudatus* drift densities during the middle of the day (Figure 11). This was apparently a catastrophic or behavioral response to a sudden increase in suspended sediment load caused from road construction or a spate upstream of the sampling site. Several studies have indicated that increased sediment loads or turbidity will initiate

FIGURE 11: Diel drift densities for *Baetis tricaudatus*. The horizontal bar represents the nocturnal hours, with SS and SR corresponding to sunset and sunrise, respectively.

drift in aquatic macroinvertebrates (Farnworth *et al*. 1979, Luedtke and Brusven 1976, Brooker and Hemsworth 1978). However, whether this actually causes the larvae to loose their grasp and catastrophically enter the drift or actively enter the drift due to the adverse environmental conditions created by the increased suspended sediment load has not been determined. Spates, which result in increased turbidity levels in the Arkansas River are common throughout the spring and summer (LaVelle 1968, and pers. observation). Although the effects on the aquatic macroinvertebrate community due to this sudden increase in suspended sediment has not been determined, a considerable amount of displacement of the benthic community must occur.

Chironomidae exhibited none of the nocturnal maxima of drift that was apparent with *B. tricaudatus* larvae (Figure 12). Conversely, chironomid drift was generally greatest during daylight hours, especially in late winter (January, March) and spring (April and May). Ferrington (1984) addressed the problem of analyzing chironomid drift results to determine behavioral information. His results indicated that detailed taxonomic study of this diverse family is necessary to determine behavioral patterns of drift as well as sampling with small diameter net mesh openings (200 μm or less) to sample early instars. During summer and fall, members of the subfamily Orthocladiinae dominated the benthos and were represented by several genera, while during the winter and spring, diamesans dominated the benthos (Appendix Table A-1). Different behavioral activities in the benthos and drift by several different genera during the summer and fall months may have masked any behavioral patterns of drift at the species level as addressed by Ferrington. However, during the winter and spring *Diamesa* dominated the chironomid benthic densities and drift, indicating a density related drift phenomenon.

FIGURE 12: Diel drift densities for Chironomidae. The horizontal bar represents the nocturnal hours, with SS and SR corresponding to sunset and sunrise, respectively.

The observed trend for diurnal drift for chironomids in winter and spring may be related to increased temperatures (Table 2). The increased drift densities during the daylight hours, especially during midday (January, March) and at sunset (April, May) may be a result of increased foraging behavior prior to pupation and subsequent drift. Whether this phenomenon is due to competitive interaction due to foraging behavior (Wiley and Kohler 1984), searching behavior (Kohler 1985) or catastrophic entry into the drift while foraging could only be determined by controlled experiments with the winter active *Diamesa* larvae.

Chironomid drift densities exhibited an approximate six-fold increase during the period of high turbidity at mid-day in August (Figure 12). This phenomenon was apparently the result of an active or catastrophic entry into the current as a result of the undesirable conditions initiated by the increased suspended sediment load during that period. Farnworth *et al.* (1979) in their review of the effects of sedimentation on aquatic macroinvertebrates concluded that increased sediment loads often deplete benthic invertebrate populations, often through increased drift. The increased drift densities apparently result in mass relocation of invertebrates, and may cause a reduction in benthic densities at the study site.

There were no consistent behavioral drift patterns observed for *Simulium arcticum* (Figure 13). Peaks in drift were observed during the nocturnal phase (September and October) as well as during the diurnal phase (November and July). *Simulium* drift densities exhibited no increase corresponding to diel temperature changes in April and May prior to emergence. *Simulium* larvae pupated primarily in late winter (late February-March) and emerged in March and April (Appendix Table A-2). These findings would indicate that the *Simulium* larvae would become more active in mid-winter (January and February) prior to pupation, and be more prevalent in the
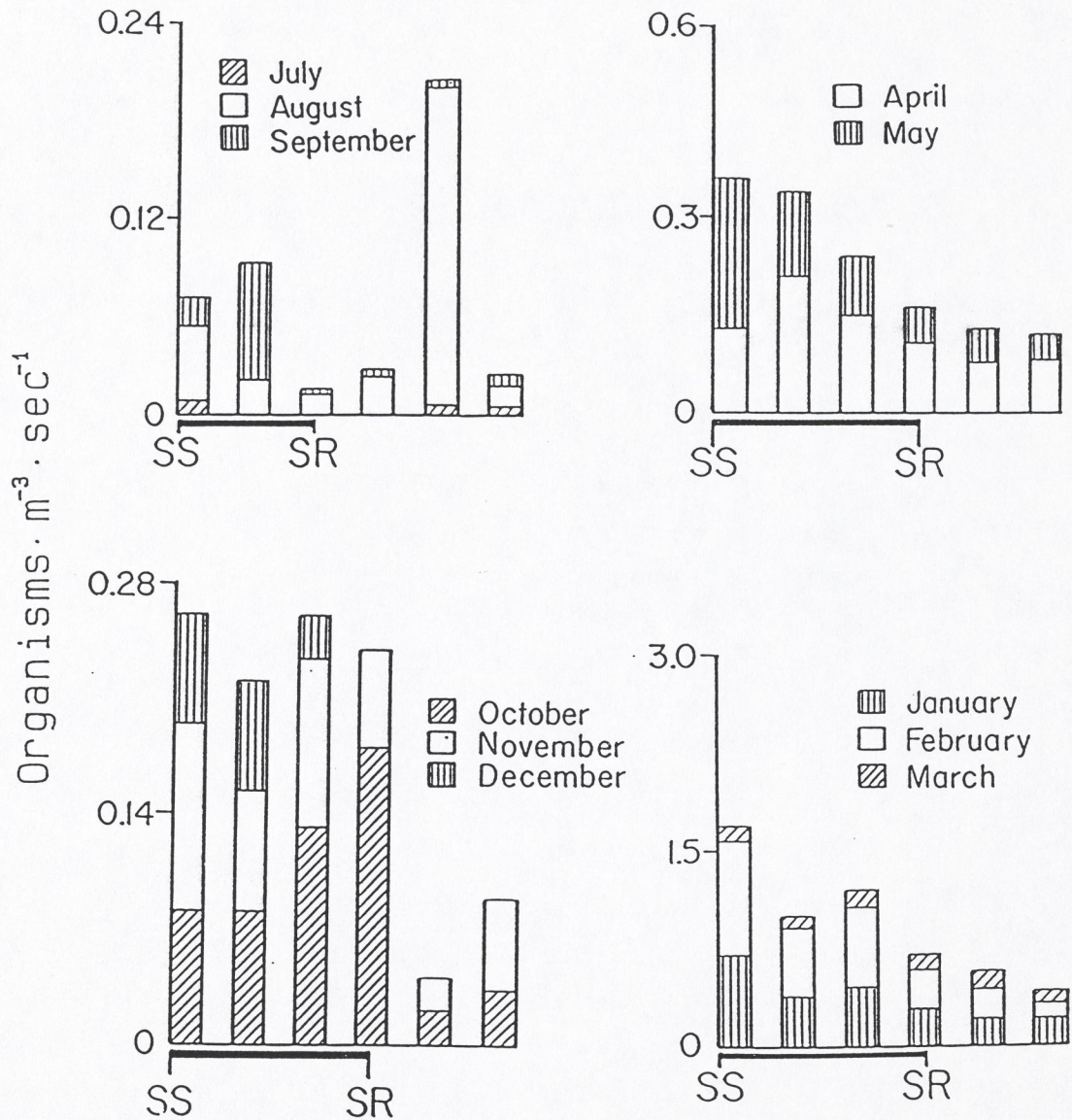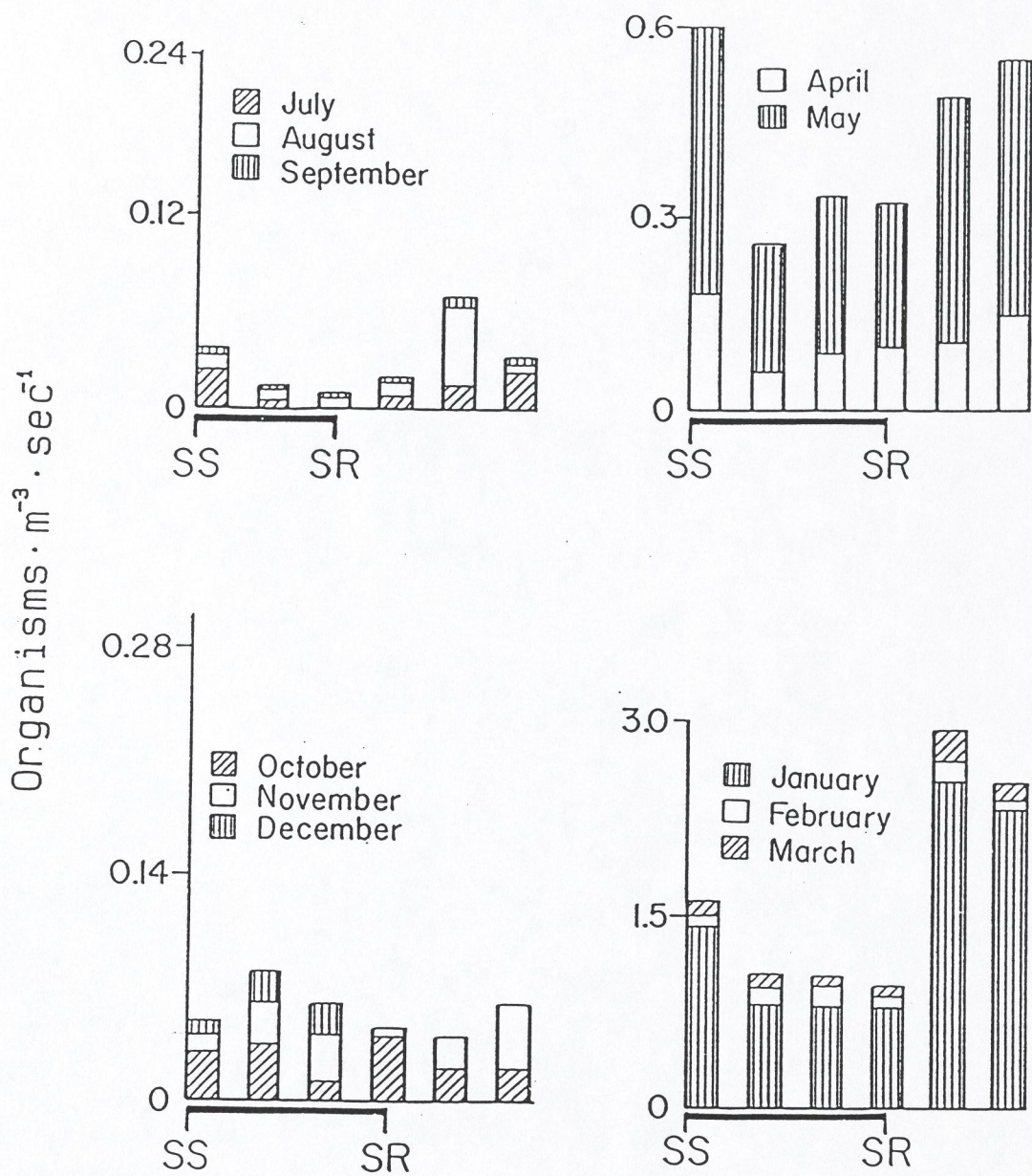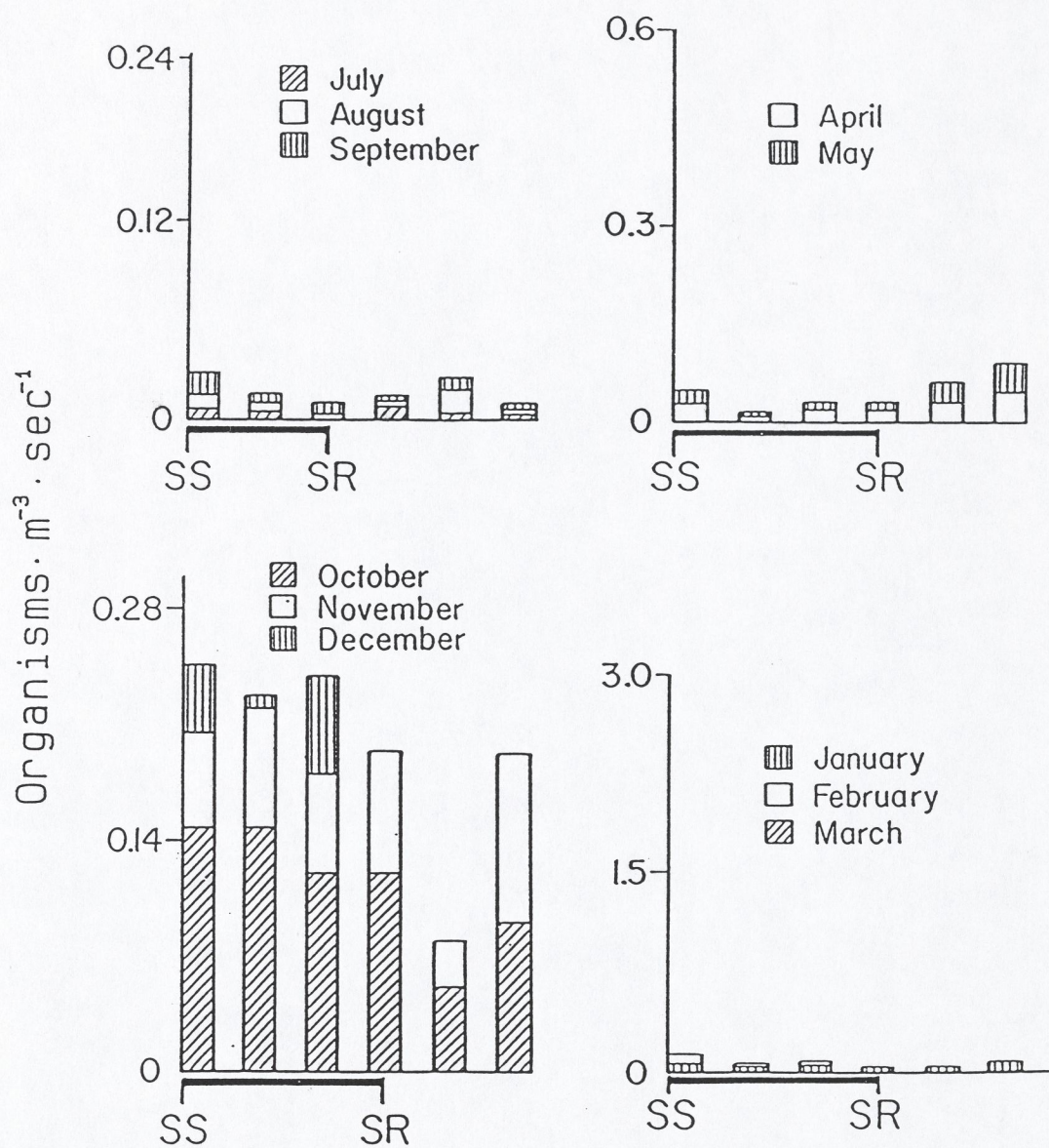
FIGURE 13: Diel drift densities for *Simulium arcticum*. The horizontal bars represents the nocturnal hours, with SS and SR corresponding to sunset and sunrise, respectively.

drift. However, no relationship was apparent, with drift being the lowest in January through March. Si*mulium arcticum* drift is apparently not related to pre-pupation activity in the study area. This phenomenon may be related to their ability to attach to the substrate and reduce catastrophic entry in the drift.

Drift densities for *Simulium arcticum* was four times higher during the mid-day, high suspended sediment period in August than the next previous sampling period (Figure 13). There is apparently an avoidance mechanism of the unfavorable conditions created by the sudden influx of suspended sediment during this time period.

D. Age, Growth and Condition of Brown Trout

Four age classes of brown trout were sampled during the 1982-1983 sampling period (Figure 14). Several studies have documented the growth rates of brown trout throughout an annual cycle (Lorz 1974, Schuck 1943, Mortensen 1982, and Allen 1951). Their general observations were that brown trout growth was either extremely limited or non-existent during periods of low water temperature. Trout sampling was too limited in this study to detect periods of accelerated growth. The 1979 (3+) year class was collected during the fall, winter and spring sampling periods (Figure 14). However, there were no 1978 (4+) brown trout collected in any of the sampling periods. Nehring and Anderson (1984) found that although age 2+ and 3+ trout are common in the study area, age 4+ fish are relatively rare. Nehring and Anderson also found that only 4% of the trout captured in 1982 and 0% of the trout collected in 1981 were from this age group, indicating an extremely high mortality of these older trout. Several other studies have shown increased mortality in brown trout in the fourth year of life. Nehring and Anderson (1983) found that 4+ brown trout comprised only 0.7% of the brown trout in the upper Cache La Poudre River, while no brown trout of this age were captured from the South Platte River near Deckers,
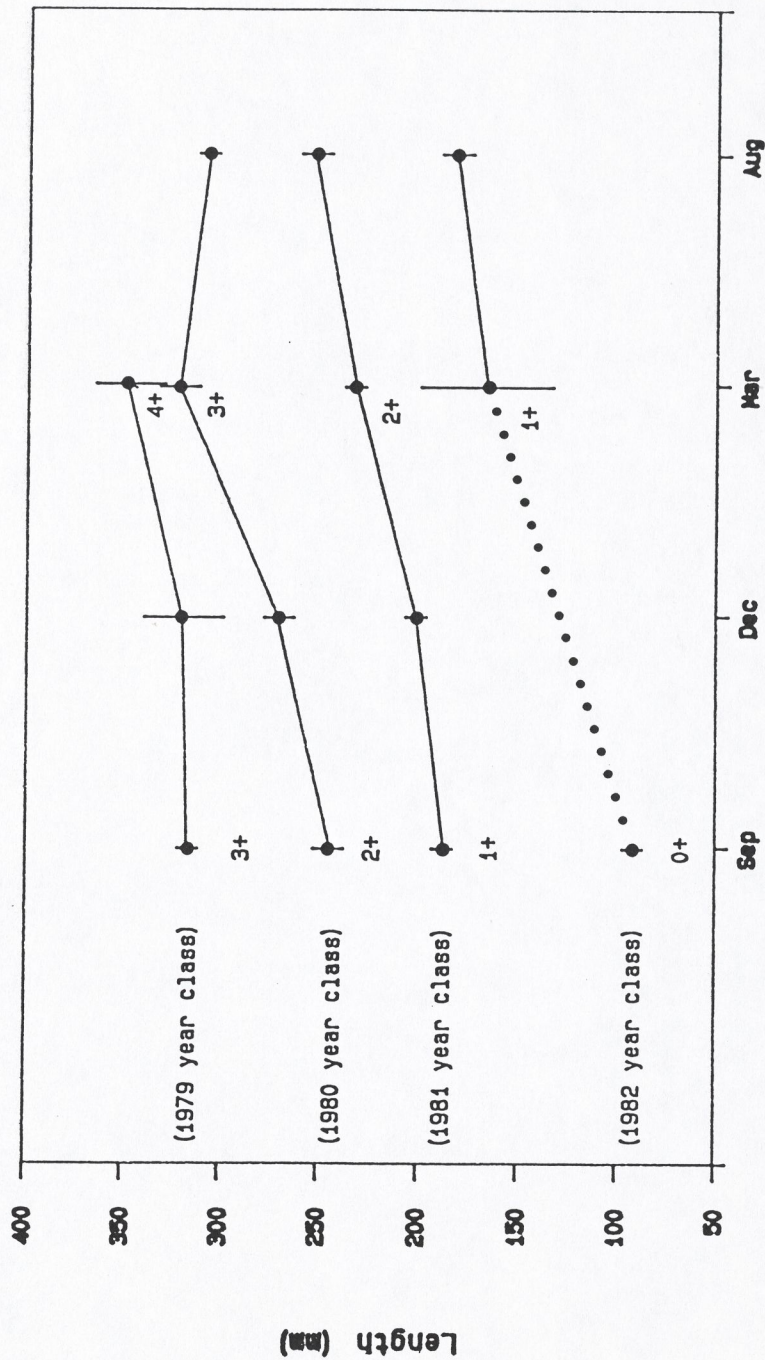
FIGURE 14: Mean lengths of the four age classes of brown trout collected at the study site on the Arkansas River, Colorado (vertical bars represent 95% C.I.).

Colorado. Schuck (1943) found that survival from hatching to the 3+ age was approximately 1%, while survival to 4+ was only 0.31%. It should be noted that Schuck excluded fisherman harvest in his calculations.

The 1980 (2+) age class comprised a considerably higher percentage of the total trout collected during the pre-spawning sampling periods in September 1982 and August 1983. During September and August, the 1979 age class comprised 42% and 25% respectively, while during the post spawning sampling period in December and in March they comprised only 10% and 8% respectively. During the study, there was a special effort to collect larger fish for analysis. The declining number of older trout following spawning indicates that there may be high mortality of post spawning trout in the study area. This high mortality of age 4+ brown trout is apparently not related to fishing pressure as very few brown trout reach the legal size of 40.6 cm.

Mean coefficient of condition factors (K) and relative weight (Wr) values are presented in Figure 15 for the four age classes of brown trout sampled. There was a close correlation between K and Wr for each of the year classes of brown trout observed, which was significant in each instance ($r \geq 0.99$, $p < 0.05$). The major criticisms of the coefficient of condition analysis is that it does not take into consideration that many fish species become more robust as they grow (Wege and Anderson 1978). As a result, K values tend to be greater in larger fish than smaller ones and comparisons between different year classes are not possible. This does not appear to be true for trout in the study area. The extremely close correlation between Wr and K values indicate that the brown trout in the study area are not becoming significantly more robust or plump as they mature. Based on these results, it would appear that the coefficient of correlation or relative weight are adequate in comparing conditions between different size classes of brown trout in the Arkansas River.
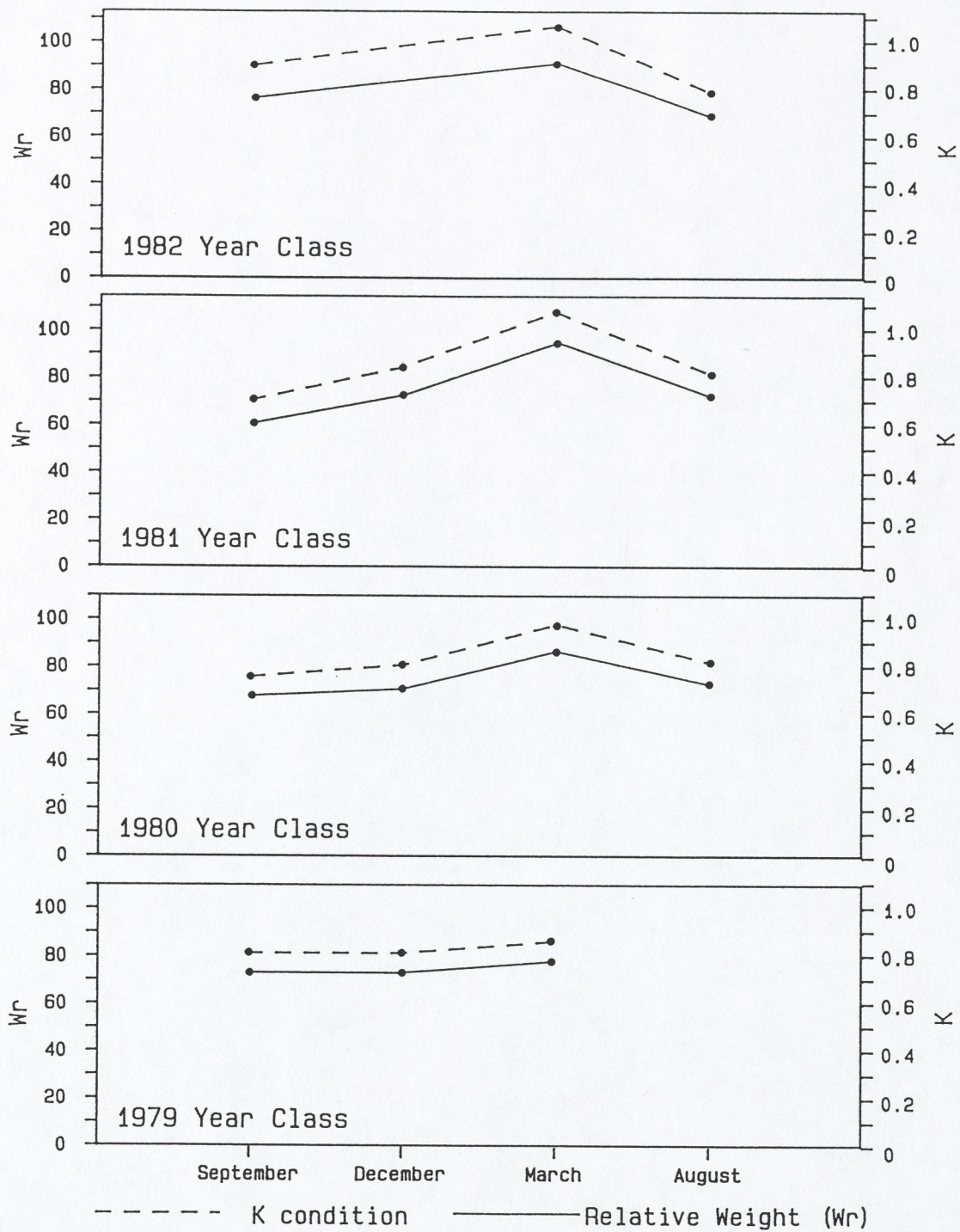
FIGURE 15: Mean condition (K) and relative weight (Wr) for the brown trout collected at the study site on the Arkansas River, Colorado.

There was a trend for both K and Wr values to increase from the first sampling period in September to March for the three youngest year classes (Figure 15). However, the oldest year class (1979) remained relatively constant throughout the sampling period. The K and Wr values for all the trout sampled the following August were considerably lower than the previous March.

The condition values calculated indicate that the brown trout in the Arkansas River study area are generally in poor condition. Allen (1951) found that mean condition never fell below 1.0 for brown trout collected throughout the year in the Horokiwi stream, New Zealand. Lorz (1974) studied several brown trout streams in Oregon. His conclusion was that the trout he sampled were in better condition in the fall of the year, and tributaries where brown trout exhibited lower conditions (all greater than 0.93) were the result of possible overpopulation. Reimers (1957) studied the effects of starvation on brown trout and the resultant loss of condition. His conclusion was that brown trout could survive for extended periods of time (six or seven months) without food in colder seasons. However, during warmer times of the year when metabolism was higher, mortality was considerably higher when the trout were held without food. Reimers also found that while brown trout could survive during winter months at conditions of between 0.8 and 0.6, mortality generally occurred when condition was less than 0.6.

The general increase in condition of the 1980-82 year classes seems to follow the trends observed by Reimers (1957). As the macroinvertebrate density data indicated, benthic macroinvertebrates were least abundant in the summer months when water temperatures and the trouts metabolic rates are highest. The lowest conditions observed in the late summer may be a result of increased metabolism during the snowmelt runoff period when food is less abundant and discharge is high. During the

fall, winter and spring, flows are more stabilized and food is more abundant. Although low winter temperatures probably impede weight gain, the lack of ice cover in the study area during the sampling period may result in a variable temperature regime. As a result, trout foraging may increase during short periods of relatively higher water temperatures during the winter. The inability of the 1979 year class to improve condition between any of the sampling periods may indicate an inability of the trout to effectively utilize the food source present. Reimers found that brown trout starved at an average of 16.4°C (mean monthly values) exhibited 32% mortality after 60 days and 56% mortality at 90 days. The initial mean K value of the trout at the study site was 0.81 in September, while the condition of the 1979 year class collected in March was 0.86. Reimers also found that mortality was reduced significantly (10%) once water temperatures began to recede. It appears to be beneficial for brown trout to gain as much energy reserves as possible prior to snowmelt runoff conditions food sources are diminished and visibility is reduced through increased turbidity. Although the younger brown trout appear to be capable of utilizing the available food sources to gain adequate conditions for the harsh spring conditions, the older (4+) year class may not be capable of storing adequate reserves of fat tissue to sustain them through the harsh spring and summer periods. Post spawning mortality may also account for mortality in the 3+ year class trout. Nehring and Anderson (1982, 1983) found very few brown trout >30cm at the study site during their March sampling episodes.

E. Brown Trout Foraging

1. 1982 Year Class

The diet of the 1982 year class of brown trout was comprised almost entirely of ephemeropterans and chironomids during September and March, indicating a drift feeding behavior during these sampling periods (Figure 16). In the following August

however, *Brachycentrus occidentalis* larvae dominated the organisms ingested by this year class.

The drift feeding behavior of young salmonids has been well documented (Tippets & Moyle 1978, Jonsson & Graven 1985, Elliott 1970, Griffith 1974, Skinner 1985 and Dauble, *et al*. 1980). The general conclusion from these studies was, that it is more energetically beneficial for young trout to feed on smaller drifting organisms than to incorporate a searching behavior for larger non-drifting organisms. Skinner (1985) found that small trout may have to expend an excessive amount of energy capturing, handling and ingesting large food items. Bannon and Ringler (1986) found that there was a direct relationship between mouth-gape size and the food ingested by brown trout. Similar results were found for the atherinid fish, *Xenomelaniris venezuelae* by Unger and Lewis (1983) in Argentina. These studies concluded that prey handling time, as a result of the physical size of the mouth, limits the size of the prey ingested. As a result, smaller individuals ingested significantly smaller taxa and individuals than did larger fish. Although there were considerably larger taxa of benthic invertebrates present at the study site during September and March, it appears that it is energetically more productive for small trout to feed on the more abundant drifting invertebrates.

The abundance of *Brachycentrus occidentalis* larvae ingested by the 1982 year class the following August may be a size related phenomenon. During August, early instar *Brachycentrus* larvae were relatively abundant in the drift (Figures 17 and 18). Dill (1983) determined that flexibility is an important adaption of the foraging behavior of fishes. The presence of larval trichopterans in the drift may have afforded the smaller brown trout with a food source which was of a more optimal size than the smaller ephemeropteran and chironomid larvae present at that time.

FIGURE 16: Percentage composition by numbers and weight of food organisms of the 1982 year class of brown trout.

1982
Year Class

% Numbers   % Weight
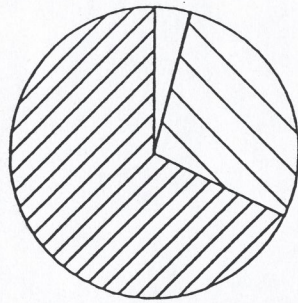
September
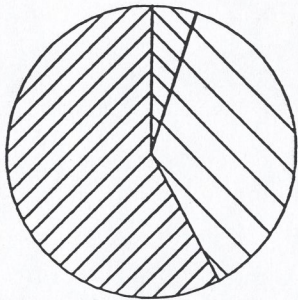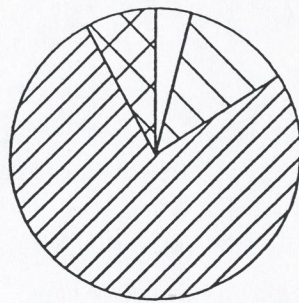
March
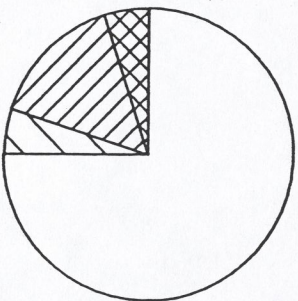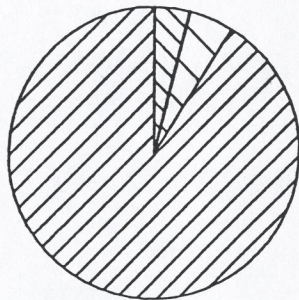
August
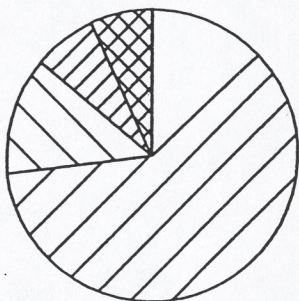
Legend

☐ Trichoptera		◺ Diptera	
Trichoptera cases		Terrestrial	
Ephemeroptera		Unidentified	
Plecoptera			

The relative abundance by weight of food organisms ingested was generally a reflection of the densities consumed (Figure 16). Ephemeropterans (primarily *Baetis tricaudatus*) dominated the weight of organisms ingested in the September and March samples, while *Brachycentrus* larvae and especially their cases dominated the weight in the August samples. It would not appear energetically beneficial to ingest a food particle which is comprised primarily of inert materials. However, Davis & Warren (1971) found that *Brachycentrus* larvae contained a considerably higher caloric value than ephemeropterans or chironomid larvae. Based on their results, and the relative abundance of *Brachycentrus* larvae by weight, more energy is gained even after the weight of the cases is taken into consideration.

a. Electivity

The results of the electivity analysis (Figure 19) further illustrates the optimal handling size theory observed by several authors (Bannon and Ringler 1986, Unger and Lewis 1983, Browman and Marcotte 1986). There was a strong positive correlation between the head capsule width of *Baetis tricaudatus* and electivity for both the nocturnal sampling periods (r = 0.72) and the diurnal sampling periods (r = 0.92). Allan (1978) also found that brown trout as well as brook trout selected larger *Baetis bicaudatus* nymphs from the drift. Conversely, the 1982 year class avoided larger *Brachycentrus* larvae and selected the early instars which were abundant in the drift during August. There was a strong negative correlation (r = -0.65) for the nocturnal sampling periods as well as the diurnal sampling period (r = -0.64) between headcapsule width and electivity for *Brachycentrus* larvae. This apparent contradiction in size related predation is probably associated with the drift feeding nature of the small brown trout present. During September and March, when *Baetis* nymphs were relatively large compared to August, they comprised a high proportion of the diet and thus influenced electivity. However, in August when only early instar
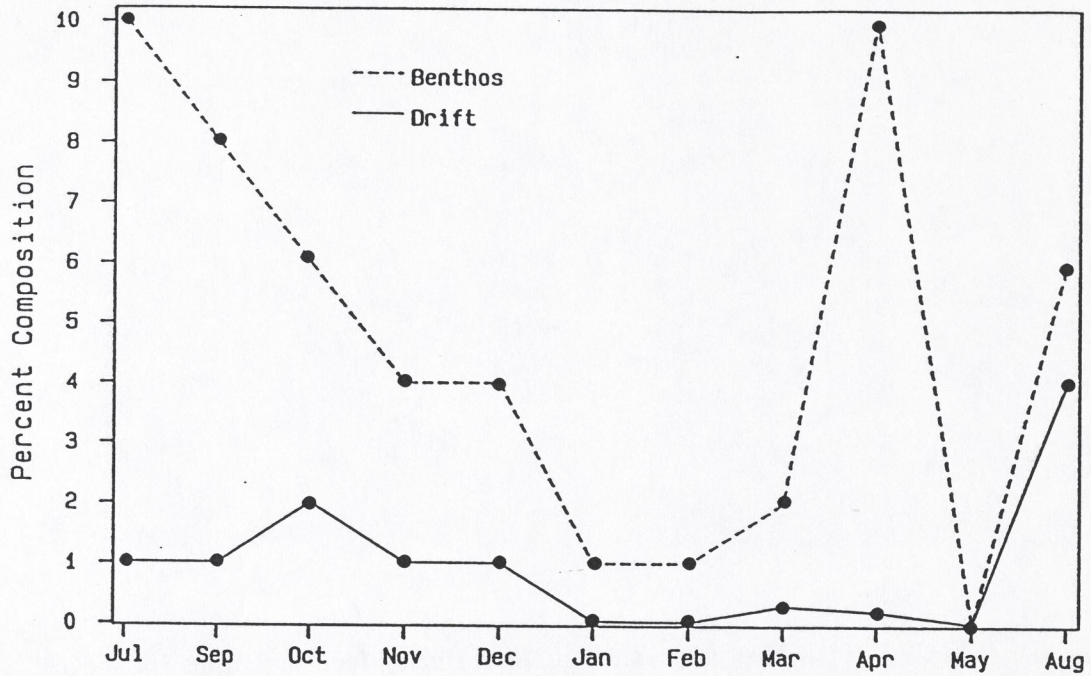
FIGURE 17: Percentage composition of *Brachycentrus occidentalis* in the drift and the benthos collected at the study site on the Arkansas River, Colorado.
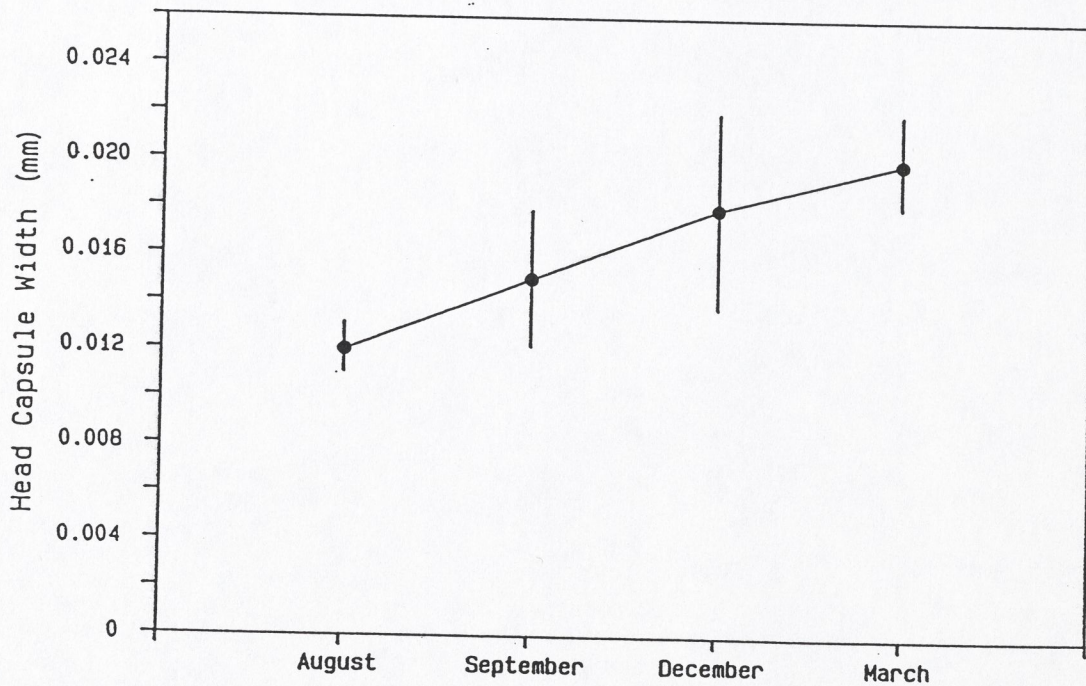
FIGURE 18: Mean headcapsule widths of *Brachycentrus occidentalis* larvae collected seasonally. Vertical bars indicate ± one standard error.

FIGURE 19: Electivity values of the primary food organisms for the 1982 year class of brown trout.

1982 Year Class

September

March

Electivity

August

Baetis
tricaudatus

Rhithrogena
hageni

Brachycentrus
occidentalis

Chironomidae
larvae

Simulium
arcticum

Chironomidae
adult

Ephemeroptera
adult

Terrestrial

⊠ Benthos - Day   ⊠ Drift - Day

▨ Benthos - Night   ▨ Drift - Night
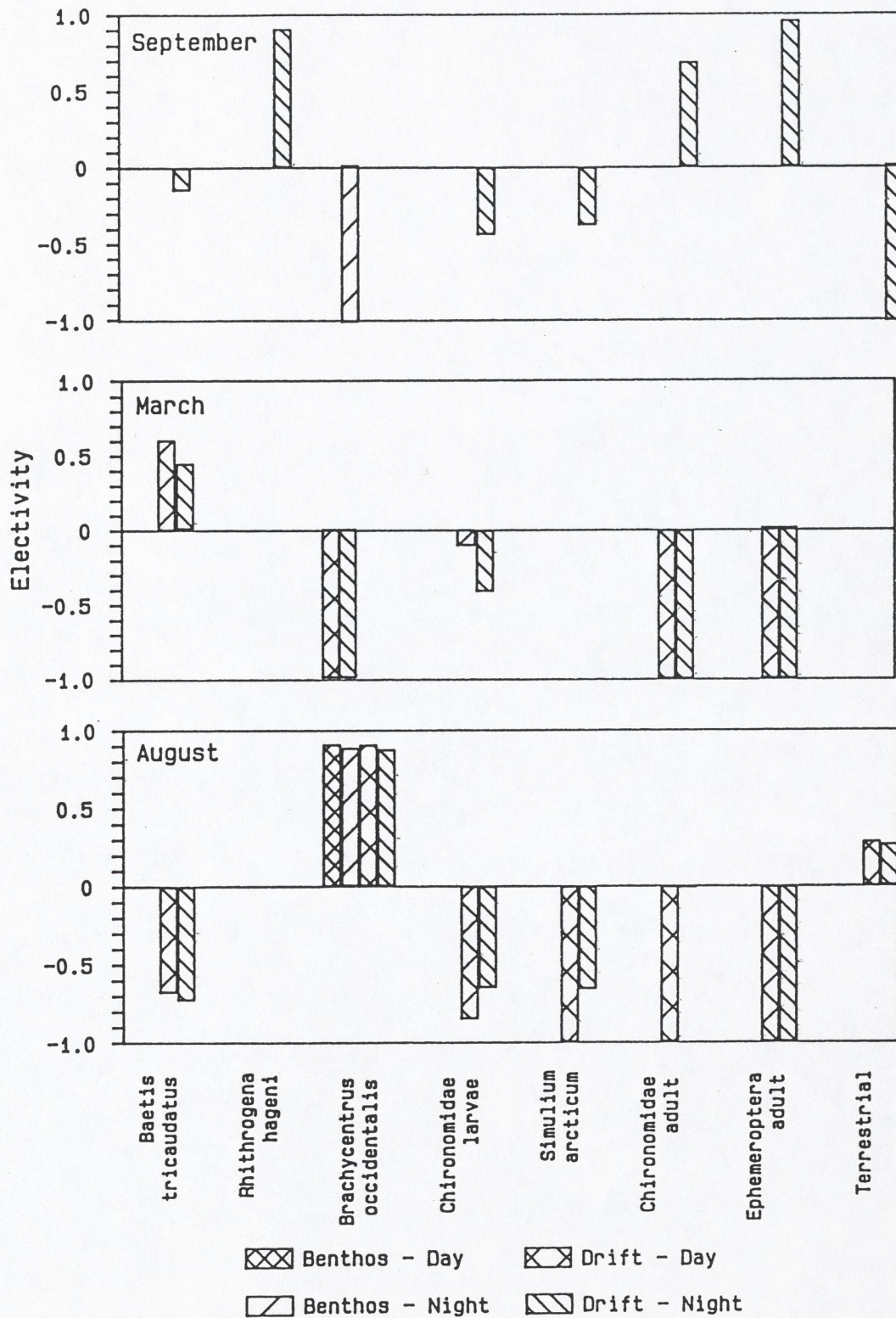
Baetis were available, *Brachycentrus* were the largest prey item consistently available in the drift. As a result, the 1982 year class elected to consume primarily the drifting *Brachycentrus* larvae. The lack of the larger *Brachycentrus* larvae in the stomach contents during the September and March sampling period further indicates that they were feeding on drifting organisms during the August as well as the previous sampling periods.

The electivity results for the remainder of the taxa analyzed exhibit various trends due to their seasonal availability (e.g. terrestrial arthropods and adult ephemeropterans) and their abundance in the drift. *Rhithrogena hageni* was strongly selected in September while constituting a relatively small percentage (<10%) of the drift and food consumed during the other two sampling months. Although chironomid and *Simulium arcticum* larvae were numerically abundant in the drift, they comprised a small percentage of the food intake throughout the year, resulting in negative electivity values. Adult ephemeropterans and chironomids were a major component of the diet in September, resulting in high electivity values. The general foraging behavior observed in September may be a result of the lack of an optimum sized prey to concentrate on. In March, when *Baetis* larvae were the dominant prey item and in August when *Brachycentrus* dominated the diet, there was very little positive selection for any other organisms. However, in September when both *Brachycentrus* and *Baetis* were apparently not of an optimal size or unavailable, a general drift feeding strategy was observed. Bannon and Ringler (1986) found that although optimal size prey was rare in a New York stream, size selective predation did occur. Terrestrial organisms were the only other positively selected food source other than *Baetis* and *Brachycentrus* in August.

2.   1981 Year Class

The diet of the 1981 year class of brown trout sampled was dominated by *Brachycentrus* larvae, although dipterans (primarily chironomids) and *Baetis tricaudatus* were also a relatively important component of the food organisms ingested (Figure 20). These observations indicated that a dissimilar foraging behavior was being utilized by the larger 1981 year class when compared to the 1982 year class.

Werner and Hall (1974) found that when prey abundance is low, prey of different sizes are ingested as they are encountered. They also found that as the abundance of a prey item is increased, size classes or prey species which aren't of an optimal size are precluded from being ingested and only preferred organisms are eaten. This prey "switching" may have occurred between the young of the year and yearling trout in the Arkansas River.   In August, the yearling trout were apparently selecting the optimal size *Brachycentrus* larval (Figure 18).   Once the yearling brown trout have imprinted on this larger food source, they appeared to maintain this foraging behavior throughout the following year. Drift densities of *Brachycentrus* larvae were relatively low when compared to their abundance in the benthos throughout the majority of the year (Figure 17).   This trend indicates that although the 1981 year class may be feeding on early instar *Brachycentrus* larvae in the drift during August, they were most likely plucking the larvae from the surfaces of the rocks the remainder of the year. Terrestrial arthropods (primarily Formicidae) were also prevalent in the stomach contents, comprising a higher percentage of the contents than the 1982 year class. Cada *et al*. (1986) also found that terrestrial arthropods (primarily Formicidae) comprised a considerably higher percentage of the organisms ingested by 1+ and older rainbow and brown trout in southern Appalachian streams. Their conclusion was that the reliance of both species of trout on terrestrial organisms for a substantial part of their diets in summer and autumn may have been related to the low density of

FIGURE 20:   Percentage composition by numbers and weight of food organisms of the 1981 year class of brown trout.

1981
Year Class

% Numbers   % Weight

September

December

March

August

Legend

☐ Trichoptera		▨ Diptera	
▨ Trichoptera cases		▨ Terrestrial	
▨ Ephemeroptera			
▨ Plecoptera			
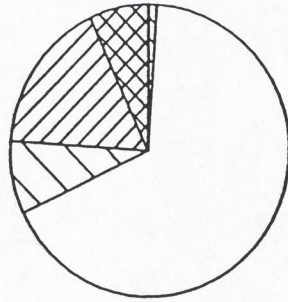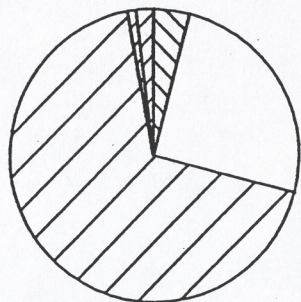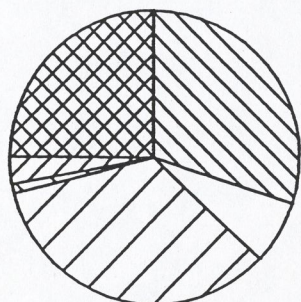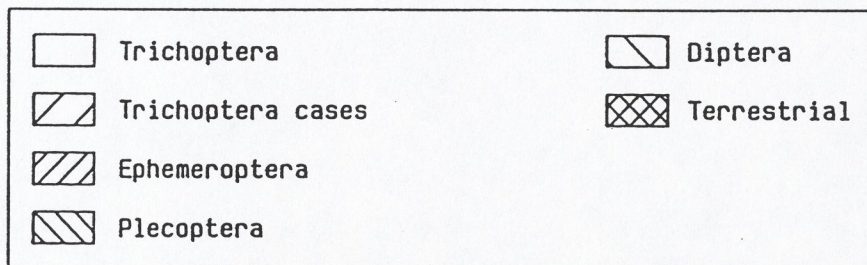
aquatic invertebrate drift at that time of year. The authors also indicated that low benthic invertebrate production may limit the drift available as food.

Trichopteran cases dominated the weight of the ingested material throughout the year (Figure 20). However, the biomass of *Brachycentrus* larvae by far exceeded that of any of the other food organisms ingested during these sampling periods. The biomass of ingested material from the August sampling period was more evenly distributed between terrestrial organisms, plecopterans and *Brachycentrus* cases.

a.   Electivity

Electivity values for the two ephemeropterans analyzed (*Baetis tricaudatus* and *Rhithrogena hageni*) exhibited similar trends to the 1982 year class (Figure 21). There was a positive selection for *Baetis* larvae in March, while the brown trout did not select them in any of the other sampling periods. There was a strong preference for *Rhithrogena hageni* during the September sampling period, while this species contributed a small percentage (<10%) of the diet and drift in the following sampling periods. The electivity values for *Baetis* were considerably lower for this age class than the 1982 year class, indicating a lower selection for this taxon.

Electivity values for *Brachycentrus occidentalis* larvae were considerably different from the 1982 year class (Figure 21). There was a strong preference for *Brachycentrus* larvae in all of the sampling periods. These results indicate that the 1981 year class is actively searching for the *Brachycentrus* larvae. Due to the extremely low drift rates of the larvae in all the months except August, it is apparent that the trout are plucking them from the top of rocks. Due to the similar proportion relative abundance of *Brachycentrus* in the benthos and drift for the August sampling period, it was not apparent whether the trout were selecting the

FIGURE 21: Electivity values of the primary food organisms for the 1981 year class of brown trout.

1981 Year Class
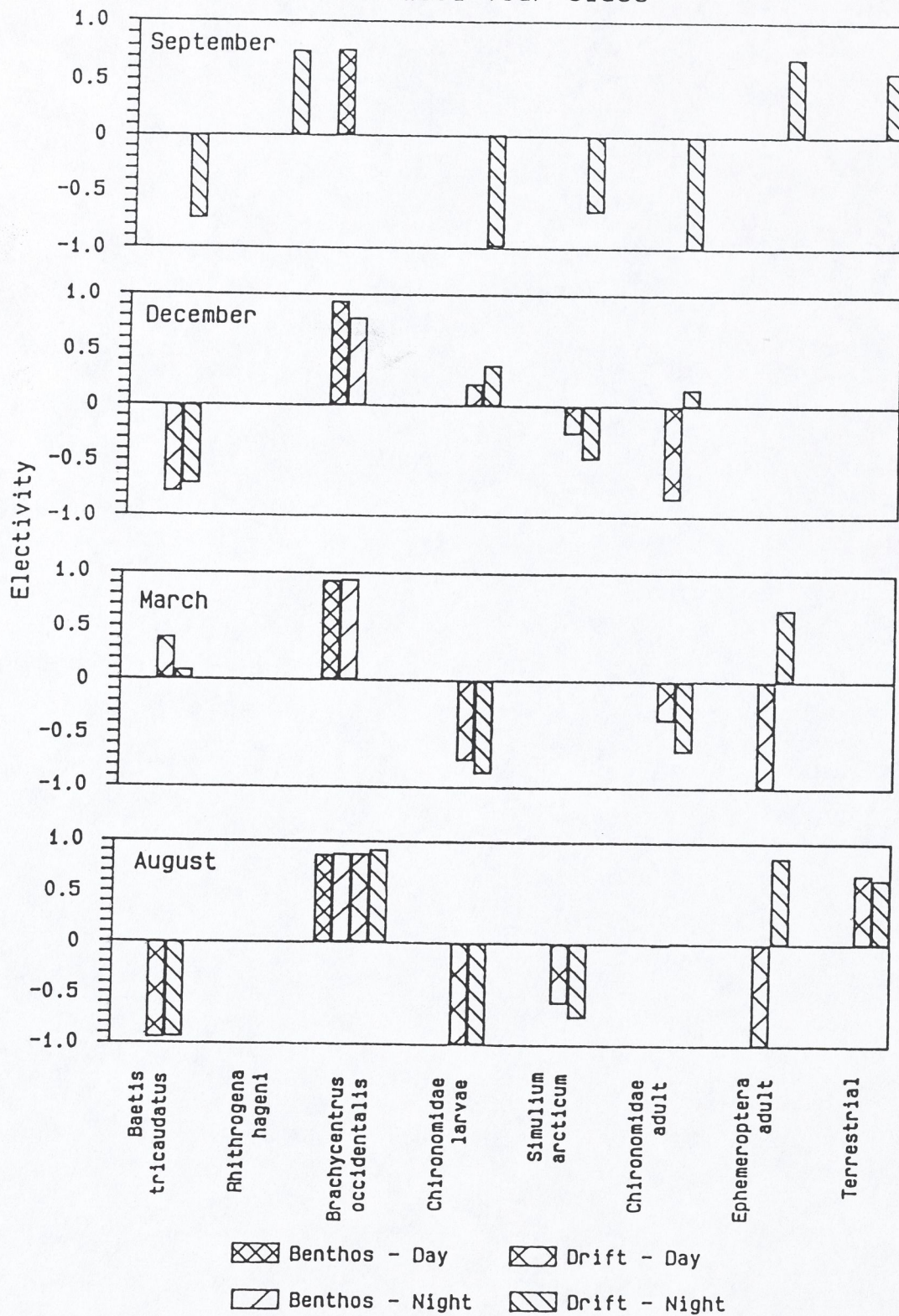
early instars from the drift or plucking them from the substrate. The importance of epibenthic feeding behavior is apparent for this age class, and has been documented by several other researchers (Allen 1951, Elliott 1970, Tippets and Moyle 1978, Elliott 1972 and Newman 1987). Newman found that prediction models were not capable of determining whether brown trout were selecting invertebrates from the drift or benthos. His results were especially confusing when low drift organisms, in this case trichopterans were encountered in the diet. During the August sampling period, electivity values give no indication of whether the brown trout were foraging on drifting *Brachycentrus* or picking them off the substrate.

Chironomid and *Simulium arcticum* larvae were generally ignored, except during the December sampling period (Figure 21). During this period, the large chironomid *Diamesa* was abundant in the drift, and was the dominant chironomid in the trout stomach contents. In March, chironomid larvae comprised a small proportion of the diet and drift (<10%) and were not included in the electivity analysis.

There were varying degrees of electivity for adult chironomids and ephemeropterans, with no strong electivity for adult chironomids during any sampling period. Herrmann *et al.* (1987) found that *Diamesa leona* emerged throughout the winter months near the study site. Due to the brachypterous nature of these chironomids, they may be vulnerable to trout predation during the winter months. There was a noticeably higher electivity for adult chironomids in the nocturnally sampled trout while there was a strong negative electivity for the diurnally sampled trout during December. Due to the low water temperatures recorded for this period, and frazil ice present shortly following midnight, it is doubtful that the trout were feeding on them during the night. Rather, foraging probably occurred the previous afternoon. Numerous adult dipterans were observed on the water and collected in

drift samples the previous afternoon. Reimers (1957) concluded that it took from 43 to 70 hours to digest food organisms at 0°C. Digestion was probably not adequate to observe any appreciable difference in food habits during the 12 hours separating the two sampling periods, given the low water temperature and resulting low rate of metabolism.

Electivity values were quite high for adult ephemeropterans for the nocturnally sampled trout, although there were no adults found in any of the trout collected during the day. There are several studies which have indicated that adult Ephemeroptera oviposit prior to or during the night to avoid predation and increase the chances of reproductive success (Boerger and Clifford, 1975, Edmunds *et al*. 1979, Friesen *et al*. 1980). During this period of diminished light intensity, the brown trout are foraging on the vulnerable adults as they oviposit or are dying on the water surface following ovipositing. Although emerging adult ephemeropterans were collected in the drift nets during the daylight hours in March and August, it appears that they are more susceptible during the ovipositing stage than the emergence stage, which occurs during the daylight hours.

There was a strong selection for terrestrial arthropods in September and August when they were available to the trout (Figure 21). Hymenoptera (Formicidae) accounted for the highest percentage of these food items, and were common along the stream banks.

3. <u>1980 Year Class</u>

The diet of the 1980 year class of brown trout was dominated by *Brachycentrus* larvae during the September, December and March sampling periods (Figure 22). These findings were even more apparent than the two younger year classes present, as

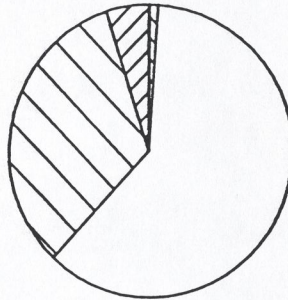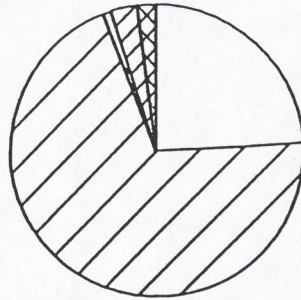**FIGURE 22:** Percentage composition by numbers and weight of food organisms of the 1980 year class of brown trout.
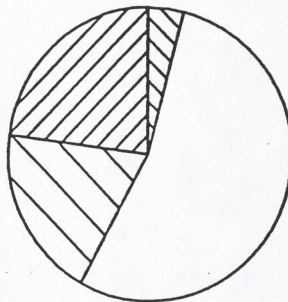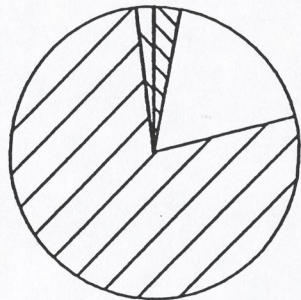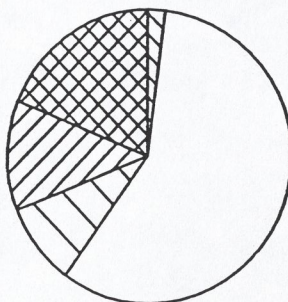
1980
Year Class

% Numbers % Weight

September

December

March

August

Legend

Trichoptera   Diptera

Trichoptera cases   Terrestrial

Ephemeroptera   Fish

Plecoptera
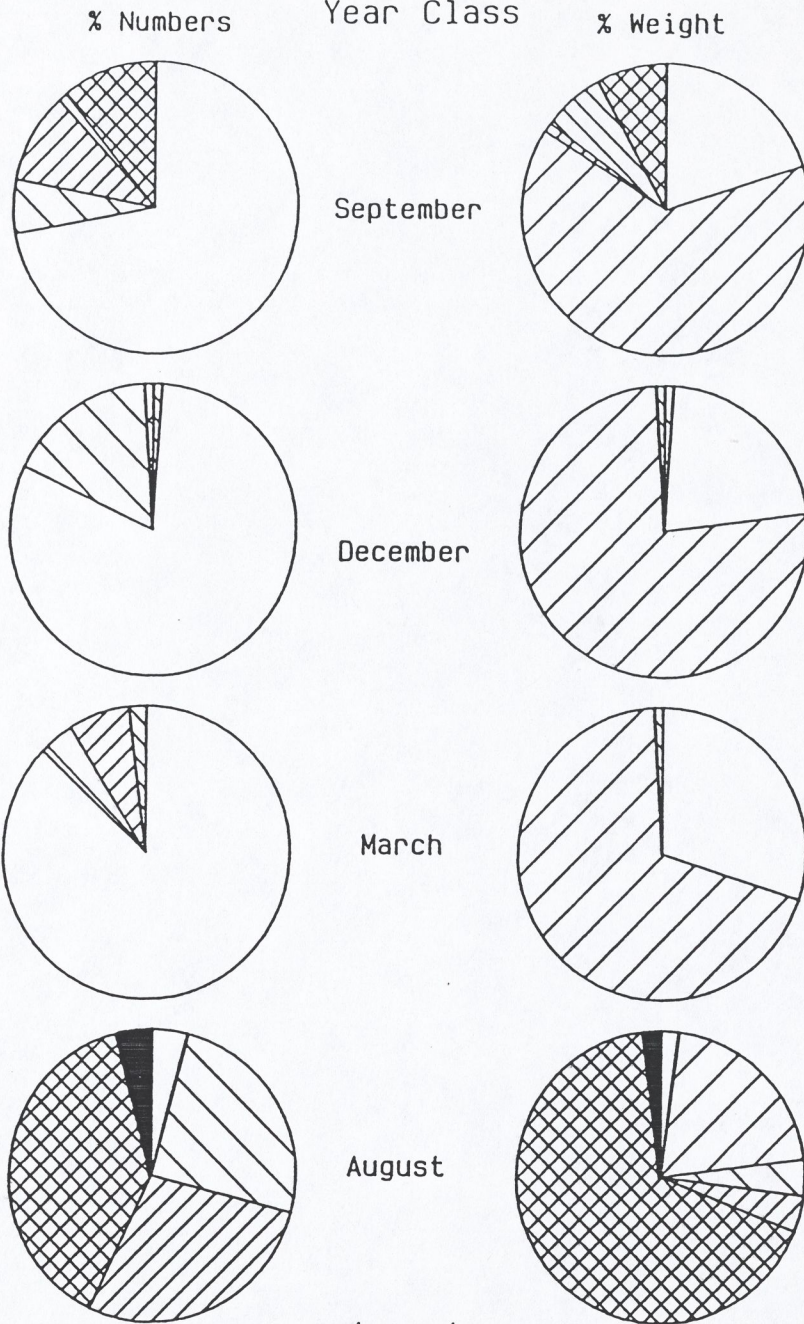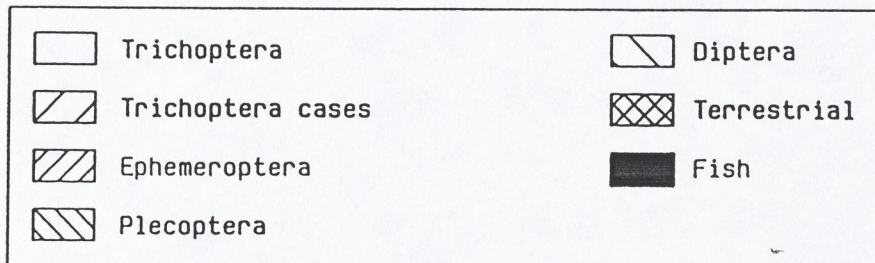
Brachycentrus larvae comprised no less than 70% of the organisms in the diet of the 1980 year class during these periods. Elliott (1970) found similar results for brown trout in an English stream. His results indicated that 2+ age and older trout fed predominately on limnephilid trichopterans. Elliott also found that drift feeding, although not as important in older trout, persists throughout their life span. Dipterans and ephemeropterans were present in the stomach contents during all the sampling periods indicating that they were still an important food source, although only occasionally consumed. Terrestrial arthropods comprised the highest percentage of the ingested organisms during August, and were also preyed upon during the September sampling period. The relatively low numbers of *Brachycentrus* larvae found in the 1980 year class in August indicates that this year class was generally feeding opportunistically on other drifting organisms, including dipterans, ephemeropterans and terrestrial invertebrates. However, in the months when *Brachycentrus* larvae were probably larger than the drifting organisms, they selected the non-drifting *Brachycentrus*.

During the August sampling period, a single longnose dace (*Rhinichthys cataractae*) was found in a trout stomach. Several studies have found that adult brown trout are highly piscivorous in the presence of an available forage fish (Stauffer 1977, Alexander 1977 and Campbell 1979). While the lower Arkansas River in the plains zone exhibits a higher diversity of cyprinid fishes which would appear to be good forage for brown trout, the Arkansas River in the foothills and montane zones are almost devoid of these small fish species (Loeffler, *et al*. 1982, and unpublished CDOW electroshocking results). The only cyprinid fish species available in the study area is the longnose dace, which would appear to be ideal for trout forage based on its size. However, they apparently are quite cryptic (Trautman 1957) and may not be readily available for trout consumption. Juvenile catostomids are also

present at the study area, but apparently are not utilized extensively as a food source. As a result, the older, larger trout must feed almost exclusively on invertebrates throughout their adult life span. Campbell (1979) found that to attain the large size characteristic of the ferox trout in Scottish lakes, the trout had to switch from an invertebrate diet to a forage of char (*Salvelinus alpinus*). Alexander (1977) found that 75% of the diet of large brown trout in the summer and 80% of the diet in the winter was comprised of fish in a Michigan River. It appears that although there are some longnose dace as well as young white suckers (*Catostomus commersoni*) and longnose suckers (*Catostomus catostomus*) in the study area, they were unavailable as forage for the 1980 year class of brown trout.

The biomass of ingested material in the fall, winter and spring was dominated by *Brachycentrus* larvae and their cases (Figure 22). This trend was even more prevalent than the 1981 and 1982 year class. However, in August terrestrial arthropods dominated the foregut contents. There was a strong positive relationship (r = 0.89) between trout age class length and the percentage of terrestrial organisms in the diet during the month of August, indicating an increased selection for terrestrial organisms as the trout increase in length during the summer months when they are available. Terrestrial arthropods appear to be of a more optimal size for the larger trout during those months when *Brachycentrus* larvae are too small to be selected.

a. Electivity

The results of the electivity analysis for the 1980 age class are presented in Figure 23. There was generally a negative electivity of *Baetis tricaudatus* larvae throughout the year, although individuals were consumed in all months sampled. There was again a positive selection for *Rhithrogena hageni* larvae in September, although to a lesser extent than the previous two age classes. These results indicate

FIGURE 23:   Electivity values of the primary food organisms for the 1980 year class of brown trout.

1980 Year Class
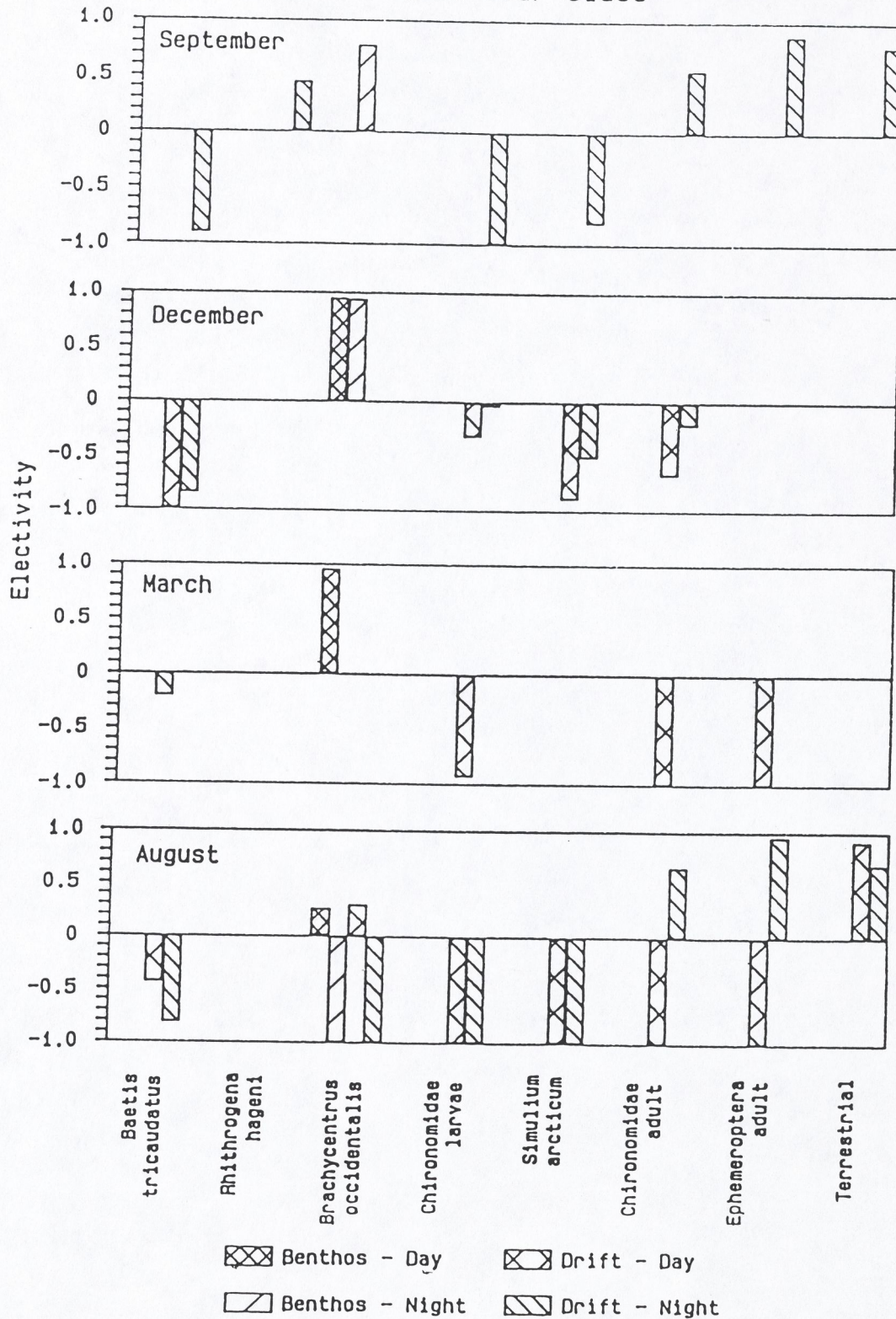
that these two drifting ephemeropterans comprise a smaller proportion of the diet of the 1980 age class as compared to the 1982 and 1981 age classes. The avoidance of these two organisms may again be a size related phenomenon or due to their smaller size, they may not be in sufficient numbers to initiate a feeding response. There was a strong positive correlation (r = 0.97) between *Brachycentrus* head capsule width and electivity for this age class of trout sampled during the day, as well as those sampled during the night (r = 0.86) during the sampling period. This contrast to the smaller 1982 age class indicates that the 1980 age class of brown trout are preferentially feeding on relatively larger *Brachycentrus* larvae throughout most of the year, and avoiding the smaller larvae present in the summer months. In August, there is some feeding on *Brachycentrus* larvae during the day. However, at night when visibility is probably inadequate to detect them at the substrate level, they are rejected.

There was an almost total rejection of chironomid and *Simulium arcticum* larvae by the 1980 year class. During the December sampling period however, there was some predation occurring on *Diamesa* and *Simulium* larvae, but was small when compared to the numbers present in the drift. The electivity results for the December sampling period indicates that when the relatively small *Simulium* and Chironomidae larvae are within a detectable distance for the waiting trout, they may be periodically ingested.

Adult chironomids and ephemeropterans were again consumed primarily during the nocturnal hours while being rejected or were unavailable during the day during the summer and autumn sampling periods. These results further document the nocturnal surface feeding behavior of the brown trout during periods when adults are present. There was a slight negative electivity for adult chironomids in December, with trout

sampled at night exhibiting a more positive selection. However, the low metabolism of the trout during this time period precludes any diel comparisons of food habits.

Surface drifting terrestrial arthropods (primarily Formicidae) were also selected during the September and August sampling periods when they were available. During these months, terrestrial arthropods were present throughout the diel cycle and were apparently consumed during the night as well as the day. The surface feeding nature of this age class as well as the 1981 year class during the night indicates that there is enough light to sufficiently see organisms or at least a silhouette.

4.   1979 Year Class

The diet of the oldest brown trout sampled, the 1979 year class, was dominated by *Brachycentrus* larvae throughout the sampling period (Figure 24). Ephemeropterans were uncommon in the stomach contents, and plecopterans rare. The absence of this age class during the August sampling episode, precludes any comparisons.

The absence of fish in the foregut contents throughout the year further illustrates the unavailability of forage fish for the larger brown trout. Campbell (1979) found that brown trout in Scottish lochs which did not switch to a diet of char were shorter lived, and grew less than those fish which did. Alexander (1977) studied the feeding behavior of large brown trout in the Au Sable River, Michigan. He concluded that the diet of the large trout studied was comprised of 82% fish in the summer, of which 61% were small brook trout. His conclusion was that the brown trout population is probably detrimental to the brook trout population. However, Alexander also concluded that if the older brown trout did not have the brook trout to prey upon, they would probably grow more slowly and fewer "trophy" size fish would be produced.

FIGURE 24: Percentage composition by number and weight of food organisms of the 1979 year class of brown trout.

1979
Year Class

% Numbers   % Weight
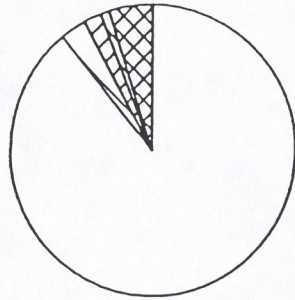
September

December

March

Legend

☐ Trichoptera		◹ Diptera	
◩ Trichoptera cases		⊠ Terrestrial	
⊘ Ephemeroptera			
⊘ Plecoptera			
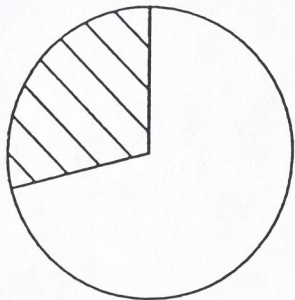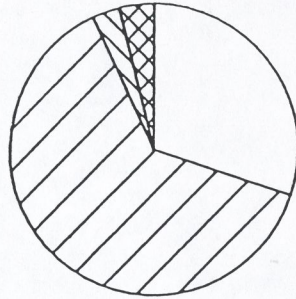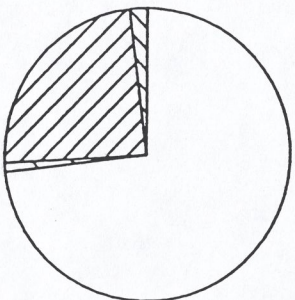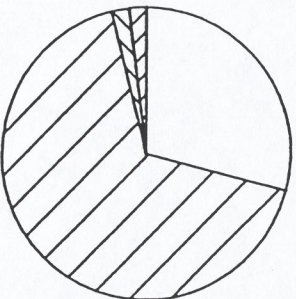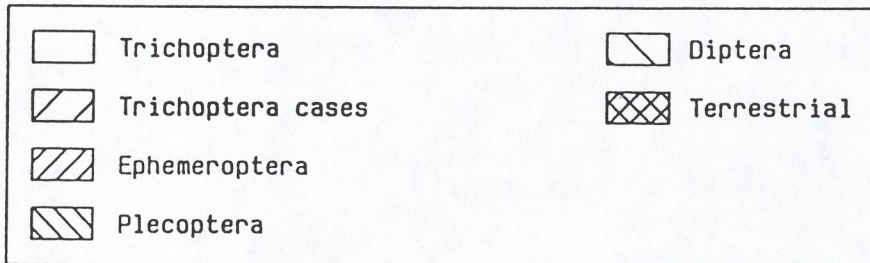
The percentage composition by weight of the ingested material was dominated by *Brachycentrus* larvae and especially their cases (Figure 24). Terrestrial arthropods, dipterans and ephemeropterans contributed only a small percentage of the biomass ingested, even less so than any of the younger year classes. With no less than 63% of the weight comprised of inert *Brachycentrus* cases during any of the sampling periods, it would appear that this age class was attaining only a marginal amount of nutrition from the food sources they are ingesting.

Allen (1969) concluded that if a fish is unable to compensate for growth by taking larger food organisms, a relatively greater amount of energy will be expended in feeding. The energy expenditure associated with searching behavior could result in asymptotic growth. Allen also suggested that the need for larger food organisms is commonly met by feeding on small fish and large benthic invertebrates. The increasing importance of epibenthic feeding on *Brachycentrus occidentalis* larvae as the fish become older at the study site is apparent by the dominance of this organism in the stomach samples. Stauffer (1977) concluded that the epibenthic feeding behavior of brown trout in the main stem of the Au Sable River in Michigan was a result of a depauperate invertebrate community resulting from overgrazing. Stauffer concluded that as a result of the active foraging on the benthos in the main stem and a resultant increased energy expenditure, growth was significantly slower than in the South Branch, where benthic densities were approximately 4 times higher. Tippets and Moyle (1978) also concluded that the epibenthic feeding habits of the McCloud River rainbow trout may be responsible for their slow growth rates.

a. Electivity

Results of the electivity analysis for the 1979 year class are presented in Figure 25. *Baetis tricaudatus* larvae were negatively elected in all months sampled during the

night, while there was a positive selection during the day in March. These results indicate that although predation was occurring on the *Baetis* larvae during the day, they were apparently rejected during the nighttime. *Baetis* larvae comprised over twice the percentage abundance of organisms in the drift during the nocturnal hours as during the diurnal hours (28.8% and 11.6% respectively) during the March sampling period. If abundance of prey were the only mechanism controlling the feeding preference of these brown trout, it would be energetically more productive to prey on *Baetis* larvae during the night. However, it appears that visibility may be an overriding factor. Although it has been shown for all the age classes of trout sampled that night feeding on surface drifting organisms is occurring during the summer months, there is probably sufficient illumination to see at least silhouettes against the lighter night sky. When the trout is looking toward the substrate at night however, the background probably appears very dark if not black, and silhouettes are probably extremely hard to detect. In all the year classes of trout sampled in March, there was a higher electivity for *Baetis* during the daylight hours than during the night. These findings would concur with Allan's (1978b) theory that larger *Baetis* larvae drift at night to avoid predation from trout. *Rhithrogena hageni* was generally rejected during the September sampling period, although a few individuals were found in the stomach contents. There was a considerably higher electivity for *Rhithrogena* larvae for all the age classes of trout sampled than the *Baetis* larvae during the nighttime in September (Figures 19, 21, 23, 25). The preference for *Rhithrogena* and apparent avoidance of *Baetis* may be due to behavioral adaptions of the two invertebrates. *Rhithrogena hageni* is dorsoventrally flattened, and comprised low densities in the drift. Upon entering the drift, the *Rhithrogena* larvae are swept downstream for possibly long distances and may be highly visible to trout. Conversely, *Baetis* larvae are adept at swimming (Edmunds *et al.* 1979) and may enter the drift for short periods of time, making them more difficult to detect.

FIGURE 25: Electivity values of the primary food organisms for the 1979 year class of brown trout.

1979 Year Class

Electivity

September

December

March

Baetis
tricaudatus

Rhithrogena
hageni

Brachycentrus
occidentalis

Chironomidae
larvae

Simulium
arcticum

chironomidae
adult

ephemeroptera
adult

terrestrial

⊠ Benthos – Day   ⊠ Drift – Day

▧ Benthos – Night   ▨ Drift – Night
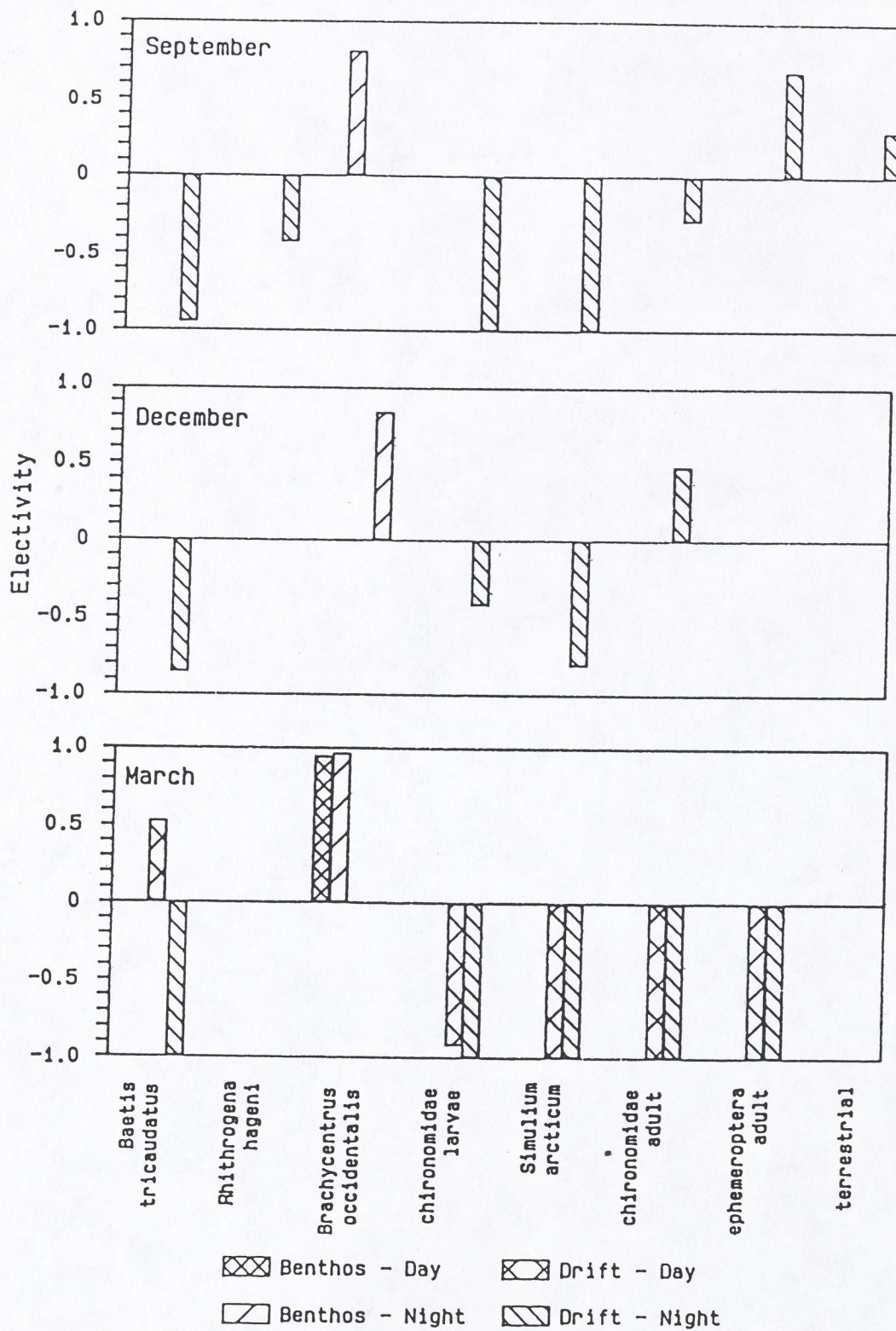
Several authors have observed the swimming ability of baetiid ephemeropterans (Corkum and Clifford 1980, Corkum 1978 and Ciborowski 1983). Ciborowski determined that live *Baetis tricaudatus* nymphs were able to settle out of the drift more quickly than dead nymphs. Corkum and Cliffor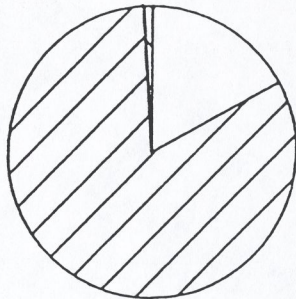d found that *Baetis tricaudatus* actively entered the drift, and larger nymphs were able to reattach themselves to the substrate more quickly than immature nymphs. The last consideration for the electivity of *Rhithrogena* nymphs to *Baetis* nymphs is the size or robustness of the organism. It would appear that the robust, dorso-ventrally flattened body of the *Rhithrogena* nymphs would be more visible under low light conditions than the slender fusiform shape of the *Baetis* nymphs. Electivity values were higher during the day for *Baetis* of all the age classes in which night and day trout samples were collected (Figures 19, 21, 23, 25).

Brachycentrus larvae were again the most selected prey item during the sampling period (Figure 25). There was very little evidence based on electivity values whether the trout collected during sampling period were feeding on the *Brachycentrus* larvae during the day or night. Examination of the cases of the *Brachycentrus* larvae indicated that digestion may take a considerable amount of time. The cases appeared to collapse or flatten as the larvae were being digested, but remained intact in all the stomach samples examined. Due to the extended time needed to digest the *Brachycentrus* larvae, diel comparisons were not conclusive.

Chironomid and *Simulium arcticum* larvae were generally ignored throughout the sampling period, although there was some foraging on them in December. These results indicate that these relatively small larvae, although abundant in the drift are of a size which is too small to be accepted as a food source with any regularity, and are only occasionally ingested.

Ephemeroptera and chironomid adults exhibited various degrees of electivity by the larger brown trout throughout the sampling year. There was a positive selection for chironomid adults in December, while they were generally avoided the rest of the year. There was also a positive selection for adult ephemeropterans in September and an avoidance in March when they were present. This may have been a result of the abundance and vulnerability of *Diamesa* adults during the mid-winter months (Herrmann *et al.* 1987). The 1979 year class exhibited a positive electivity for terrestrial arthropods during the September sampling period. The preceding year classes of brown trout exhibited a similar trend to the 1979 year class in September (Figure 23) indicating that the adult trout as well as the juveniles and fry were generally feeding on surface drift during the September sampling period during the night. There was some drift feeding occurring during the December sampling period, but due to the low water temperatures and subsequent low digestion rates, any diel feeding behavior could not be distinguished.

SUMMARY AND CONCLUSIONS

The Arkansas River at the study area appears to be typical of unregulated rivers in the Colorado Rocky Mountain region, in terms of the physico-chemical properties measured. Discharge attained maximum values during the summer months in both 1982 and 1983, with minimum values recorded prior to snowmelt runoff in the spring of 1983. Mean daily temperature values also exhibited seasonal trends, with maximum values recorded during summer months, and minimum values during midwinter. Suspended inorganic and organic matter transport (seston) is primarily flow driven at the study site. The high correlation between discharge and seston transport indicates that noticeably higher quantities of inorganic as well as organic matter are transported during the snowmelt runoff period.

Benthic macroinvertebrates exhibited trends which are generally found in unregulated river systems in the Rocky Mountain region. Aquatic insects dominated the benthic densities, while non-insect groups were poorly represented throughout the sampling period. Dipterans and ephemeropterans dominated benthic densities, while benthic biomass values were more evenly distributed between the 4 main orders of insects collected (Ephemeroptera, Diptera, Trichoptera and Plecoptera).

Benthic densities were lowest during snowmelt runoff, although an unexplainable reduction in densities occurred in November. Densities increased following runoff as hatching resulted in numerous early instars of several taxa being collected. Benthic

densities remained fairly constant throughout the winter and spring months, with a decrease from the April to May sampling period as several taxa began emerging. Benthic biomass trends were more dramatic, with biomass remaining comparatively low in summer and fall, and increasing during the winter and spring months. The dramatic decrease in biomass from April to May can be attributed primarily to the emergence of several taxa of benthic invertebrates (e.g. *Simulium arcticum* and *Brachycentrus occidentalis*). It would appear that at least some aquatic macroinvertebrates in the Arkansas River emerge during the late spring, when discharge is relatively stable and water temperatures are increasing. Emergence during this time of the year may be an evolutionary strategy to avoid the harsh conditions associated with snowmelt runoff.

Diversity and equitability values fluctuated greatly due to life history and environmental phenomenon. The lowest values were attained in January and August, when one taxon dominated the benthos. The highest values were recorded when densities were low, but individuals were evenly distributed among the species. It is apparent that the Shannon-Weaver Index and Equitability results were not an adequate measure in discerning the effects of catastrophic events such snowmelt runoff where the densities of all taxa were low but individuals were evenly distributed among the species. Conversely, when the benthic densities were not evenly distributed, due to the presence of high densities of early instar invertebrates, the values recorded were indicative of environmental stress.

The general composition of functional feeding groups were similar to those found in studies conducted in other mid-size streams and rivers (Ward *et al.* 1986, Canton and Chadwick 1983). The absence of shredders, such as the large plecopteran *Pteronarcys californica,* is attributable to the paucity of riparian vegetation

throughout much of the upper Arkansas River valley resulting in a limited food supply for those invertebrates utilizing CPOM as a food source. The high densities of collector-gatherers, such as the ephemeropterans *Baetis tricaudatus* and *Ephemerella inermis* and the chironomids *Parametriocnemus* sp. and *Diamesa* sp., indicate that upstream processing of CPOM has resulted in an invertebrate food base comprised essentially of FPOM at the study site. Collector-filterers comprised up to 41% of the total composition in October and only 2% during May. These changes were primarily the result of the emergence of *Simulium arcticum* and *Brachycentrus occidentalis* during the April - May period.

Macroinvertebrate drift was also dominated by aquatic insects, with *Baetis tricaudatus, Simulium arcticum* and chironomids collectively comprising more than 80% of the organisms collected during any sampling period. Three types of crustaceans (Copepoda, Ostracoda and Cladocera) were collected in the drift nets. The presence of these crustaceans in the drift samples and absence in the benthic samples indicates that they are not inhabiting the riffle areas, but probably low water velocity areas near the banks, and occasionally enter the drift.

Drift densities were generally higher in winter and spring, with the highest densities recorded in January. The January maxima was the result of a large number of the chironomid *Diamesa* sp. A entering the drift, possibly as a result of an increase in activity prior to pupation. During the August sampling period, a sudden influx of sediment from an upstream disturbance resulted in a 7 fold increase in drift densities. Conditions where the suspended seston load is increased dramatically may have only a short term impact on the aquatic macroinvertebrates community. During extended periods of high suspended seston transport during snowmelt runoff, benthic

macroinvertebrates may have evolved life history strategies to avoid the harsh conditions (Ward 1984, Winget 1984).

There was no significant relationship between invertebrate drift densities and water temperature, discharge or benthic densities, although a sudden increase in suspended seston in August apparently increased drift dramatically. The elevated densities of drifting benthic invertebrates as a result of increased seston transport may result in displacement of benthic invertebrates. Percentage similarity (ps) was utilized to compare densities of benthic invertebrates and drifting invertebrates. The results were highly variable and further indicate that there is little relationship between the benthos and drift at the community level in the Arkansas River.

Baetis tricaudatus drift patterns exhibited nocturnal maxima and diurnal suppression throughout the sampling period. This trend indicates that these ephemeropterans are active, even during periods of low water temperatures. Chironomidae larvae exhibited no apparent diel drift patterns, although diurnal drift densities were generally greater in winter and spring. This phenomenon may be related to increased water temperatures, and a resultant increase in activity. *Simulium arcticum* exhibited no apparent diel drift patterns, with maximum densities during late fall, and relatively low values recorded the remainder of the sampling period.

Brown trout age structure exhibited trends similar to those previously observed by the Colorado Division of Wildlife. There was high mortality between the 3+ and 4+ age classes, a trend also observed in many other river systems in Colorado (Nehring and Anderson 1983), and by Fredenberg (1985) in the Bighorn River, Montana. Fredenberg attributed the high mortality of older brown trout to a lack of prey of an

adequately large size. Condition analysis revealed that the three youngest year classes increase in condition from the early fall periods through the following spring. However, there was a considerable decrease in condition from the pre-runoff sampling period in March, to the post-runoff period the following August. The oldest year class remained at approximately the same level of condition through the sampling period. It would appear, that the snowmelt runoff period during the summer months may be the most limiting period of the year for the first three year classes of brown trout in the study area. During this portion of the year, the benthic community is reduced, discharge is elevated considerably, suspended sediment is increased and metabolism is increased due to an increase in water temperature. Following runoff, the conditions are reversed, with benthic populations and drift increasing, visibility improving and discharge stabilizing. However, the rigors of spawning may have reduced or eliminated any of the beneficial effects of the increased environmental conditions during the fall and resulted in the lack of increased condition observed for the oldest age class sampled in December. The inability of the 1979 year class to exhibit growth prior to runoff may be a factor in this high mortality in the study area. It would appear that the three youngest year classes of brown trout were able to utilize the available food, and reach a condition level sufficient to survive the runoff period. The lack of any observable increase in condition of the oldest year class following runoff indicates that they may not be able to gain sufficient energy reserves to survive the harsh conditions during the post spawning, and following snowmelt period.

There was an apparent size selective foraging behavior associated with each of the age classes of brown trout collected at the study site. The youngest year class sampled (1982) fed predominantly on smaller drifting organisms, with no epibenthic feeding apparent. The three successive year classes, however, became more dependant

on the low drift *Brachycentrus occidentalis* larvae throughout most of the year. During the late summer sampling period, when early instar *Brachycentrus* larvae were present, the 1982 year class fed mostly on them, while they became successively less important in the following year classes. During this late summer period, terrestrial arthropods became more important for the 1981 and 1980 year classes, and a more opportunistic feeding behavior was observed. The oldest year class sampled (1979) fed predominantly on *Brachycentrus occidentalis* larvae during all the periods they were sampled, with the majority of the ingested material being inert cases. Although there are some forage fish present at the study site (e.g. catostomid fry and *Rhinichthys cataractae*) they are either undetectable by the larger trout or are too few in numbers to be utilized as a food source by the brown trout at the study area.

Following the fry stage, the brown trout rely heavily on *Brachycentrus occidentalis* larvae as a major source of their nutritional intake. Although the caloric content of these trichopterans is relatively high, the inert cases ingested with these invertebrates results in the bulk of food intake having no nutritional value. Although the available literature indicates that brown trout should *switch* to a larger, more energetically beneficial prey during the 3+ age class, the lack or unavailability of adequately large forage items result in the epibenthic feeding behavior observed for this age class. It would appear that during the first three years of life, the brown trout are able to thrive on a diet of aquatic macroinvertebrates, while the following year classes are unable to sustain themselves on this food source and eventually perish.

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APPENDIX

SUPPLEMENTAL DATA AND RESULTS

TABLE A-1: Benthic macroinvertebrate densities ($\#/m^2$) by taxa, collected from the Arkansas River, Colorado 1982-1983.

TAXA	1982				
	Jul	Sep	Oct	Nov	Dec
INSECTA					
Ephemeroptera	263	258	1474	415	884
Baetis tricaudatus	71	204	968	263	536
Ephemerella inermis	151	37	327	84	260
Rhithrogena hageni	41	17	179	69	88
Plecoptera	8	30	232	71	69
Isogenoides zionensis	--	13	17	30	9
Isoperla sobria	6	11	58	37	17
Triznaka signata	--	--	99	--	15
Claassenia sabulosa	--	6	45	4	28
Paraleuctra sp.	--	--	9	--	--
Pteronarcella badia	2	--	--	--	--
Taenionema nigripenne	--	--	4	--	--
Trichoptera	116	252	447	68	72
Brachycentrus occidentalis	110	230	323	45	32
Coluptila sp.	--	2	17	4	6
Glossosoma sp.	2	--	6	2	4
Hydropsyche occidentalis	4	4	65	2	2
Hydropsyche oslari	--	--	13	2	11
Hydropsyche sp.	--	13	15	11	4
Leucotrichia sp.	--	2	--	2	4
Psychomyia flavida	--	--	6	--	--
Rhyacophila angelita	--	--	2	--	--
Rhyacophila coloradensis	--	--	--	--	9
Diptera	615	2324	2384	620	850
Atherix pachypus	4	6	--	2	6
Bibiocephala grandis	--	4	--	--	2
Chelifera sp.	--	2	4	11	--
Cardiocladius sp.	2	--	--	--	--
Diamesa sp. A	--	45	93	207	463
Eukiefferiella sp.	157	247	24	82	15
Hexatoma sp.	--	--	4	--	--
Hemerodromia sp.	--	--	2	--	2
Micropsectra sp.	32	2	4	13	6
Orthocladius-Cricotopus grp	2	540	628	96	58
Palpomyia complex	6	2	4	--	--

TABLE A-1:   Continued

TAXA	1982				
	Jul	Sep	Oct	Nov	Dec
Pagastia sp.	--	--	--	--	4
Parametriocnemus sp.	245	839	--	--	--
Protanyderus margarita	2	--	4	--	--
Simulium arcticum	105	555	1560	202	293
Wiedemannia sp.	--	--	--	9	--
Chironomidae pupae	58	80	56	2	--
Coleoptera	69	4	17	--	--
Optioservus sp.	29	4	17	--	--
Zaitzevia parvula	6	--	--	--	--
HYDRACARINA					
Sperchon sp.	4	--	--	--	--
OLIGOCHAETA	2	--	6	4	--
CRUSTACEA					
Amphipoda					
Hyalella azteca	2	--	--	--	--
NEMATODA	--	--	9	--	--
TOTAL	1,080	2,869	4,603	1,179	1,879

TABLE A-1: Continued

TAXA	1983					
	Jan	Feb	Mar	Apr	May	Aug
INSECTA						
Ephemeroptera	1023	717	921	1368	1622	3475
Baetis tricaudatus	790	512	497	693	237	3277
Ephemerella inermis	108	108	297	549	852	11
Epeorus longimanus	--	--	--	4	6	--
Rhithrogena hageni	125	97	127	122	527	187
Plecoptera	80	60	49	101	125	32
Isogenoides zionensis	47	17	17	18	2	4
Isoperla sobria	30	43	15	72	105	9
Triznaka signata	--	--	9	--	--	9
Claassenia sabulosa	2	--	6	11	17	11
Hesperoperla pacifica	--	--	2	--	--	--
Trichoptera	110	45	73	341	62	999
Brachycentrus occidentalis	80	13	41	258	4	321
Coluptila sp.	11	4	4	14	2	2
Glossosoma sp.	13	4	2	--	4	--
Hydropsyche cockerelli	15	--	4	7	2	--
Hydropsyche occidentalis	--	--	13	--	30	41
Hydropsyche oslari	--	2	--	--	--	--
Hydropsyche sp.	--	17	--	36	--	465
Leucotrichia sp.	--	--	2	18	4	127
Lepidostoma sp.	--	2	4	--	--	--
Psychomyia flavida	--	2	2	4	8	30
Rhyacophila acropedes	--	--	--	4	--	--
Rhyacophila coloradensis	2	--	--	--	4	13
Glossosoma pupae	--	--	--	--	2	--
Diptera	2053	1257	1640	872	284	2817
Atherix pachypus	2	2	--	4	9	9
Chelifera sp.	2	--	--	54	4	4
Cardiocladius sp.	--	--	--	--	47	--
Constempelina sp.	--	--	--	--	--	43
Diamesa sp. A	1661	230	1255	650	2	--
Diamesa sp. B	--	155	--	--	2	--
Eukiefferiella sp.	153	174	--	7	62	474
Hemerodromia sp.	--	--	2	--	--	--
Micropsectra sp.	--	--	2	4	4	--

TABLE A-1: Continued

TAXA	1983					
	Jan	Feb	Mar	Apr	May	Aug
Orthocladius–Cricotopus grp	82	67	26	58	6	454
Palpomyia complex	--	--	4	--	--	2
Parametriocnemus sp.	--	26	9	872	284	1681
Protanyderus margarita	--	--	--	--	--	2
Simulium arcticum	127	553	86	36	4	39
Thienemannimyia sp.	19	--	--	11	--	--
Tipula sp.	--	4	6	--	--	--
Chironomidae pupae	6	45	6	32	9	105
Simulium pupae	--	--	243	18	2	4
Coleoptera	4	4	6	7	6	4
Optioservus sp.	4	2	6	7	6	4
Oreodytes sp.	--	2	--	--	--	--
HYDRACARINA						
Sperchon sp.	--	--	--	4	2	--
OLIGOCHAETA	2	--	--	7	6	--
NEMATODA	--	--	--	11	--	--
TOTAL	3,272	2,083	1,640	2,710	2,109	7,328

TABLE A-2: Benthic macroinvertebrate biomass (gms/m^2 dry weight) by taxa, collected from the Arkansas River, Colorado 1982-1983.

TAXA	1982				
	Jul	Sep	Oct	Nov	Dec
INSECTA					
Ephemeroptera	0.2019	0.0658	0.0558	0.0441	0.0338
Baetis tricaudatus	0.0370	0.0260	0.0284	0.0323	0.0198
Ephemerella inermis	0.1296	0.0303	0.0052	0.0056	0.0056
Rhithrogena hageni	0.0353	0.0095	0.0222	0.0062	0.0084
Plecoptera	0.0014	0.0197	0.2627	0.4588	0.2755
Isogenoides zionensis	--	0.0090	0.1102	0.4156	0.1007
Isoperla sobria	0.0010	0.0047	0.0073	0.0073	0.0022
Triznaka signata	--	--	0.0024	--	0.0013
Claassenia sabulosa	--	0.0060	0.1403	0.0359	0.1713
Paraleuctra sp.	--	--	0.0019	--	--
Pteronarcella badia	0.0004	--	--	--	--
Taenionema nigripenne	--	--	0.0006	--	--
Trichoptera	0.0753	0.0230	0.6926	0.2127	0.0897
Brachycentrus occidentalis	0.0512	0.0172	0.6215	0.1894	0.0768
Coluptila sp.	--	--	0.0002	--	0.0002
Glossosoma sp.	0.0056	--	0.0011	0.0080	0.0011
Hydropsyche occidentalis	0.0185	0.0034	0.0605	0.0080	0.0015
Hydropsyche oslari	--	--	0.0067	0.0049	0.0077
Hydropsyche sp.	--	0.0024	0.0002	0.0024	0.0009
Psychomyia flavida	--	--	0.0022	--	--
Rhyacophila angelita	--	--	0.0002	--	--
Rhyacophila coloradensis	--	--	--	--	0.0015
Diptera	0.1154	0.2570	0.1628	0.1260	0.1463
Atherix pachypus	0.0200	0.0144	--	0.0062	0.0174
Bibiocephala sp.	--	0.0047	--	--	0.0054
Chelifera sp.	--	0.0002	0.0002	0.0045	--
Diamesa sp. A	--	0.0022	0.0043	0.0486	0.0809
Eukiefferiella sp.	0.0194	0.0460	0.0030	--	0.0026
Hexatoma sp.	--	--	0.0037	--	--
Hemerodromia sp.	--	--	0.0004	--	0.0002
Micropsectra sp.	0.0022	--	--	--	--
Orthocladius-Cricotopus group	0.0006	0.0629	0.0872	0.0202	0.0028
Palpomyia complex	0.0006	--	--	--	--
Pagastia sp.	--	--	--	--	0.0002

TABLE A-2: Continued

TAXA	1982				
	Jul	Sep	Oct	Nov	Dec
Parametriocnemus sp.	0.0237	0.0765	--	--	--
Protanyderus margarita	--	--	0.0043	--	--
Simulium arcticum	0.0392	0.0353	0.0461	0.0351	0.0368
Wiedemannia sp.	--	--	--	0.0049	--
Chironomidae pupae	0.0097	0.0148	0.0136	0.0065	--
Coleoptera	0.0186	--	0.0043	--	--
Optioservus sp.	0.0119	--	0.0043	--	--
Zaitzevia parvula	0.0067	--	--	--	--
OLIGOCHAETA	0.0346	--	0.0002	--	--
CRUSTACEA					
Amphipoda					
Hyalella azteca	0.0015	--	--	--	--
NEMATODA	--	--	0.0388	--	--
TOTAL	0.4487	0.3655	1.2172	0.8416	0.5453

TABLE A-2: Continued

TAXA	1983					
	Jan	Feb	Mar	Apr	May	Aug
INSECTA						
Ephemeroptera	0.1276	0.0378	0.1113	0.2728	0.5978	0.1338
Baetis tricaudatus	0.1020	0.0211	0.0790	0.1881	0.1171	0.1151
Ephemerella inermis	0.0043	0.0075	0.0196	0.0592	0.2984	0.0026
Epeorus longimanus	--	--	--	--	0.0017	--
Rhithrogena hageni	0.0213	0.0092	0.0127	0.0255	0.1806	0.0161
Plecoptera	1.0682	0.3800	0.8153	0.6430	0.3554	0.2802
Isogenoides zionensis	1.0609	0.3697	0.7515	0.5572	0.0204	0.1313
Isoperla sobria	0.0071	0.0103	0.0073	0.0747	0.2470	0.0026
Triznaka signata	--	--	0.0034	--	--	0.0004
Claassenia sabulosa	0.0002	--	0.0359	0.0111	0.0880	0.1459
Hesperoperla pacifica	--	--	0.0172	--	--	--
Trichoptera	0.1545	0.0648	0.2098	0.3222	0.1220	0.1490
Brachycentrus occidentalis	0.1263	0.0609	0.1868	0.2799	0.0017	0.0552
Coluptila sp.	--	--	--	0.0007	0.0002	--
Glossosoma sp.	0.0101	0.0009	0.0006	--	0.0006	--
Hydropsyche cockerelli	0.0170	--	0.0108	0.0197	0.0062	--
Hydropsyche occidentalis	--	--	0.0095	--	0.1119	0.0613
Hydropsyche oslari	--	0.0004	--	--	--	--
Hydropsyche sp.	--	0.0024	--	0.0147	--	0.0202
Leucotrichia sp.	--	--	0.0017	0.0018	0.0004	0.0043
Lepidostoma sp.	--	0.0002	0.0004	--	--	--
Psychomyia flavida	--	--	--	--	0.0004	0.0069
Rhyacophila acropedes	--	--	--	0.0054	--	--
Rhyacophila coloradensis	0.0011	--	--	--	0.0004	0.0011
Glossosoma pupae	--	--	--	--	0.0002	--
Diptera	0.5453	0.8511	1.0260	0.2125	0.2221	0.3290
Atherix pachypus	0.0034	0.0198	--	0.0072	0.0758	0.0060
Chelifera sp.	0.0019	--	--	0.0294	0.0006	--
Cardiocladius sp.	--	--	--	--	0.0039	--
Constempelina sp.	--	--	--	--	--	0.0004
Diamesa sp. A	0.4433	0.1808	0.1119	0.1020	--	--
Diamesa sp. B	--	0.0071	--	--	0.0009	--
Eukiefferiella sp.	0.0355	0.0050	--	--	0.1217	0.0889
Hemerodromia sp.	--	--	0.0026	--	--	--
Micropsectra sp.	--	--	--	--	0.0004	--

TABLE A-2: Continued

TAXA	1983					
	Jan	Feb	Mar	Apr	May	Aug
Orthocladius-						
Cricotopus group	0.0069	0.0013	0.0006	0.0158	0.0011	0.0385
Palpomyia complex	--	--	--	--	--	0.0009
Parametriocnemus sp.	--	0.0006	--	--	0.0105	0.1530
Protanyderus margarita	--	--	--	--	--	0.0155
Simulium arcticum	0.0508	0.4220	0.0198	0.0230	0.0019	0.0045
Thienemannimyia sp.	0.0024	--	--	0.0011	--	--
Tipula sp.	--	0.2001	0.3863	--	--	--
Chironomidae pupae	0.0011	0.0144	0.0019	0.0140	0.0049	0.0159
Simulium pupae	--	--	0.5029	0.0200	0.0004	0.0058
Coleoptera	0.0215	0.0002	0.0067	0.0061	0.0028	0.0058
Optioservus sp.	0.0215	--	0.0067	0.0061	0.0028	0.0058
Oreodytes sp.	--	0.0002	--	--	--	--
OLIGOCHAETA	--	--	--	--	0.0243	--
NEMATODA	--	--	--	0.0004	--	--
TOTAL	1.9171	1.3339	2.1091	1.4570	1.3244	0.8978

TABLE A-3: Frequency of occurrence of benthic macroinvertebrates captured in drift nets, at the study site on the Arkansas River, Colorado.

Taxa	1982					1983						%†
	Jul	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Aug	
INSECTA												
Ephemeroptera												
*Ameletus sp.	–	–	–	x	–	–	–	–	–	–	–	9
Baetis tricaudatus	x	x	x	x	x	x	x	x	x	x	x	100
Epeorus longimanus	–	–	–	–	–	–	–	–	–	x	x	9
Ephemerella inermis	x	–	x	x	x	x	x	x	x	x	–	82
Rhithrogena hageni	x	x	x	x	x	x	x	x	x	x	–	100
*Tricorythodes minutus	–	–	x	–	–	–	–	–	–	–	–	9
Ephemeroptera Adult	–	x	–	–	–	–	–	x	–	x	x	36
Plecoptera												
*Capnia sp.	–	–	–	x	–	–	–	–	–	–	–	9
Claassenia sabulosa	–	x	x	x	x	–	–	–	–	–	–	45
Hesperoperla pacifica	–	–	x	–	x	–	–	x	–	–	–	45
Isogenoides zionensis	–	x	–	–	–	–	–	x	–	–	–	27
Isoperla sobria	–	x	–	–	–	x	x	x	x	x	–	55
Paraleuctra sp.	–	x	x	x	x	x	x	x	x	x	x	91
Pteronarcella badia	–	–	–	–	–	–	–	–	–	–	–	0
Taenionema nigripenne	–	–	–	–	–	–	–	–	–	–	–	0
Triznaka signata	–	–	x	–	–	x	–	–	–	–	–	18
Trichoptera												
Brachycentrus occidentalis	x	x	x	x	x	x	x	x	x	–	x	91
Coluptila sp.	–	x	x	–	x	x	x	x	x	x	–	73
Glossosoma sp.	–	–	x	x	x	x	x	x	x	–	–	73
Hydropsyche sp.	–	x	x	x	x	x	x	x	–	–	x	73
Lepidostoma sp.	–	–	–	–	–	x	x	–	–	–	x	18
Leucotrichia sp.	x	x	x	x	x	x	x	x	x	–	x	91
*Neothremma sp.	–	–	–	x	–	–	–	–	–	–	–	9
Psychomyia flavida	–	x	–	x	–	–	–	x	x	x	x	55
Rhyacophila acropedes	–	–	–	–	–	–	–	–	–	–	–	0
Rhyacophila angelita	–	–	–	–	–	–	–	–	–	–	–	0
Rhyacophila coloradensis	x	x	–	x	–	x	–	x	x	x	x	73
Trichoptera Adult	–	x	–	–	–	–	–	–	–	x	–	18

TABLE A-3: Continued

Taxa	1982					1983						%†
	Jul	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Aug	
Diptera												
*Antocha sp.	-	-	-	-	-	x	-	-	-	-	-	9
Atherix pachypus	-	x	-	-	x	x	x	-	-	-	x	45
Bibiocephala sp.	-	x	-	-	-	-	-	-	-	-	-	9
Chelifera sp.	-	-	-	x	-	-	-	-	-	x	-	18
Hemerodromia sp.	-	-	-	-	-	-	-	-	-	-	-	0
Hexatoma sp.	-	-	x	-	-	-	-	-	-	-	x	18
Palpomyia complex	-	-	-	-	-	-	-	-	-	-	-	0
Protanyderus marg.	-	-	-	-	-	-	-	-	-	-	-	0
Simulium arcticum	-	-	-	-	-	-	-	-	-	-	-	0
Simulium pupae	x	x	x	x	x	x	x	x	x	x	x	100
Simulium adult	-	-	-	x	-	-	-	x	-	x	-	27
Tipula sp.	-	x	x	x	x	x	x	x	x	-	x	82
Wiedemannia sp.	-	-	-	-	-	-	-	-	-	-	-	0
Chironomidae pupa	x	x	x	x	x	x	x	x	x	x	x	100
Chironomidae larvae	x	x	x	x	x	x	x	x	x	x	x	100
Chironomidae adult	x	x	x	x	x	x	x	x	x	x	x	100
Coleoptera												
*Haliplus sp.	-	-	-	x	-	-	-	-	-	-	-	9
Optioservus sp.	x	x	x	x	x	x	x	-	x	x	x	91
Oreodytes sp.	-	-	-	-	-	-	-	-	-	-	-	0
Zaitzevia parvula	-	-	-	-	-	-	-	-	-	-	-	0
*Dyticidae	-	-	-	-	-	x	-	-	-	-	-	9
HYDRACARINA												
Sperchon sp.	-	x	x	x	x	x	x	-	x	-	x	73
COLLEMBOLA												
*Podura sp.	-	x	-	x	-	-	x	x	x	x	x	64
CRUSTACEA												
Amphipoda												
Hyalella azteca	x	x	x	x	x	x	-	x	-	-	x	73
*Cladocera	-	-	-	x	-	-	-	-	-	-	x	18
*Ostracoda	-	x	-	x	-	x	x	x	x	-	x	64

TABLE A-3:   Continued

| Taxa | 1982 | | | | | 1983 | | | | | | † |
	Jul	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Aug	
*Copepoda	-	-	x	-	-	x	x	x	-	-	x	45
OLIGOCHAETA	x	-	-	x	x	x	-	-	x	x	-	55
NEMATODA	-	x	x	x	x	x	x	-	x	x	x	82
Total Number of Taxa	11	23	22	27	20	26	21	19	22	16	22	

† = Frequency of Occurence
* = Taxa not collected in Benthic sample
x = Taxa collected during that month