

POPULATION DYNAMICS OF AN INVERTEBRATE
COMMUNITY AS COLLECTED BY
ARTIFICIAL SUBSTRATE IN
CHEVELON CREEK, ARIZONA

A thesis
Presented to the Graduate Faculty
Northern Arizona University

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

by
Leslie G. Brokaw
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Chapter 1

INTRODUCTION

The arid regions of the southwestern United States include a surprising variety of aquatic environments which have just recently begun to be examined. Over 5200km¹ of perennial streams exist within the State of Arizona. Hydrographic data for major drainages have been supplied over the years by various state and federal agencies. It is only recently however, that detailed ecological work has been conducted in regard to these lotic systems.

Recent examinations of stream energy budgets (Minshall, 1978) have demonstrated that desert streams, unlike streams in mesic areas, tend to be more autotrophic due in part to the reduction of the riparian canopy. Light energy can be dramatically reduced within those streams which lie within steep walled canyons. Nutrient cycling appears to be quite distinct from patterns of more mesic areas (Fisher and Minckley, 1978; Fisher and Grimm, 1979). Macroinvertebrate recolonization pathways and life cycles also appear to be finely tuned to the harsh demands of a desert lotic environment (Gray, 1979, 1980).

The limited precipitation of the area, which paradoxically results in brief periods of intense scour, high temperatures, periods

¹Estimated from D.E. Brown, N.B. Carmony and R.M. Turner, Drainage Map of Arizona Showing Perennial Streams and Some Important Wetlands, Arizona Game and Fish Department, 1977.

of drought and periods of chemical concentration, combine to create a habitat which appears, at least superficially, to be unpredictable and unstable. The climate characteristics of the desert southwest in combination with the geological substrate have resulted in numerous deep, narrow canyons which are etched upon the surface of this arid land. A number of the sedimentary formations typical of Northern Arizona resulted from sedimentation and precipitation of materials within a variously expanding and receding shallow sea. Within the region of this study lies such a formation which contains an abnormally high salt concentration.

Erosion by the study stream has exposed a salt laden water table which significantly alters water chemistry at base flow levels. The results of my research indicate that the combination of relatively high saline concentrations, restricted light availability and an incredible seasonal range of discharge have combined to favor the establishment and maintenance of an aquatic erosional insect population which is low in diversity. The insect population has, however, retained a tremendous recolonization capacity, which in effect enhances the stability of the community.

The objectives of this study were to:

- 1) Monitor selected chemical and physical parameters of the Chevelon Creek system for a 12-month period in an attempt to assess the seasonality of these parameters;
- 2) Characterize the lotic erosional macroinvertebrate community during a similar 12-month period;

- 3) Assess the interaction, if any, between seasonal chemical and physical changes and macroinvertebrate population dynamics.

Chapter 2

STUDY AREA

The massive physical barrier of central Arizona's Mogollon Rim region of the Coconino Plateau interrupts the eastward flow of moist air masses. The rain-shadow area that is created receives only slightly more annual precipitation than the southwestern Arizona deserts ($\bar{x} = 18.7\text{cm year}^{-1}$ at Winslow, Arizona). More than half of the local precipitation occurs during July, August and September as weak afternoon showers develop on the perimeter of the Southwestern Desert-Pacific Monsoon system (Green, 1964). The vegetation community for the area is Plain and Desert Grassland (Lowe, 1964).

The study area utilized was located upon the lower reaches of Chevelon Creek within a distance 1-12km south of its confluence with the Little Colorado River, approximately 20km southeast of Winslow, Arizona (Figure 1). Site 1 was located in the NE $\frac{1}{4}$ of the SW $\frac{1}{4}$ of Section 11, Township 17N, Range 17E, Navajo County, Arizona, at an elevation of 1510m. The stream bed at this site is surrounded by sheer walls of Coconino Sandstone from 15-30m high.

The stream bed lies directly upon Coconino Sandstone. Numerous potholes have been eroded by turbulent water action. Alluvial materials present generally exceed 10cm in diameter and are usually found in the pothole basins. The Site 1 sampling station was located in

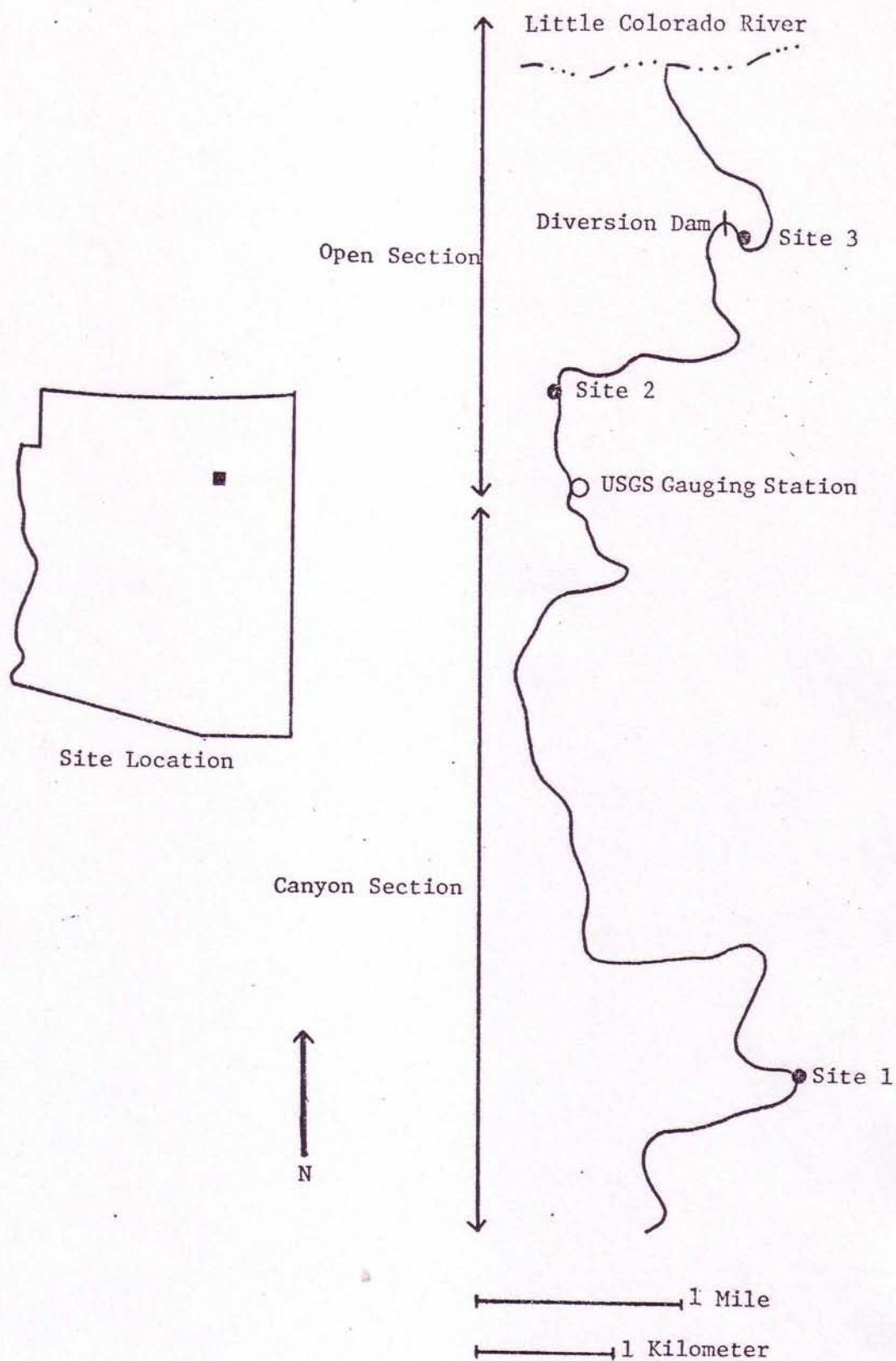


Figure 1. Map of lower Chevelon Creek, Arizona showing location of study sites.

such a pothole at a depth of 25cm at mean base flow. The pothole was located in the perennial section of the stream and at no time was isolated from stream input (PLATE I).

Site 2 was located in the SE $\frac{1}{4}$ of the NW $\frac{1}{4}$ of Section 27, Township 18N, Range 17E, Navajo County, Arizona. This site, 8.3km below Site 1, was approximately 1km below the mouth of Chevelon Canyon and was utilized as a physical and chemical comparison site because it was intermediate between Sites 1 and 3. Invertebrate samples were not collected at Site 2.

The canyon which separates Sites 1 and 2 is both deep (greater than 60m) and narrow (less than 16m). This canyon section extends for approximately 7.3km. Water tends to collect in relatively deep (13-18m) slow moving pools. Below Site 2 the stream channel is open and free from the direct influence of canyon walls.

Site 3 was located in the NW $\frac{1}{4}$ of the SW $\frac{1}{4}$ of Section 23, Township 18N, Range 17E, Navajo County, Arizona. This site was 3.5km below Site 2 and approximately 4.5km below the canyon mouth at an elevation of 1490m. In the immediate surroundings were low lying alluvial mounds capped with salt cedar (Tamarix pentandra Pall.) (PLATE II).

The streambed at Site 3 lies directly upon Moenkopi bedrock having passed over a diversionary structure located approximately 50 meters upstream. The backwater created by the diversion dam tended to collect suspended solids to the point that the stream bed below was composed primarily of shingled fragments of Moenkopi Sandstone which ranged in size from 10cm to more than 1.5m. During

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PLATE I. CHEVELON CREEK AT STUDY SITE 1.

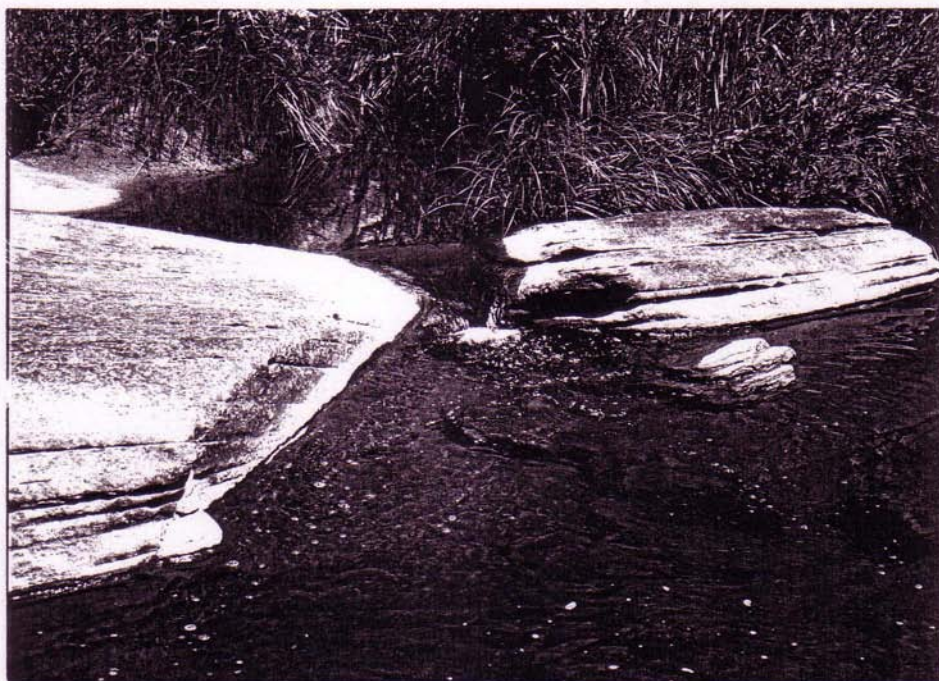


PLATE II. CHEVELON CREEK AT STUDY SITE 3.



periods of high discharge the stream bed was greatly rearranged and smaller fragments (less than 1cm) flecked off by impact were collected in the samplers.

Geological Description

Lower Chevelon Canyon lies just to the west of the Holbrook Dome (Figure 2), the largest local uplift in the Holbrook-Winslow region (Harrell and Eckel, 1939). This region of uplift is fractured to some depth allowing local recharge of the Coconino Aquifer. Moenkopi Sandstone, an impermeable stratum lies unconformably upon the Coconino Sandstone effectively preventing upward movement of the ground water at this point. The Coconino Sandstone is underlain by Supai Sandstone. The Supai Formation is relatively impermeable and contains numerous salt cells composed of various evaporites (U.S. Bureau of Reclamation, 1965). Groundwater trapped between the impermeable Moenkopi and Supai Formations is released at the point where Chevelon Canyon contacts the water table (Figure 2). The result of this contact is a multitude of seeps and wet-wall areas along the canyon that progressively increase in tonic concentration downstream. The fractured outcrop area of exposed Coconino knobs in the region is the apparent zone of recharge for the aquifer (Harrell and Eckel, 1939).

Hydrology

Chevelon Creek is a tributary of the Little Colorado River originating at the southern extreme of the Coconino Plateau flowing northeast approximately 115km until its confluence with the Little

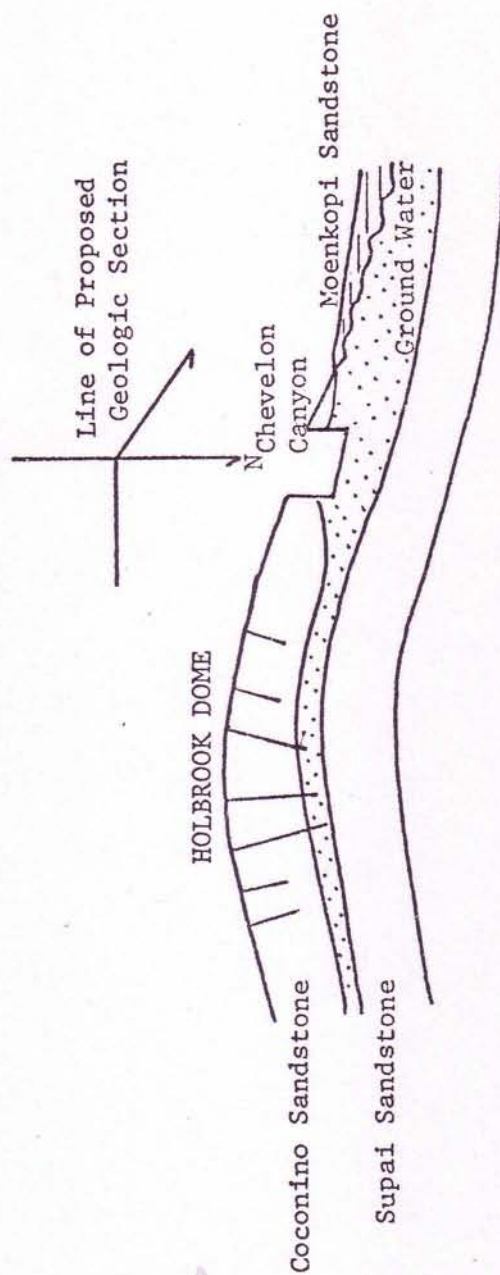


Figure 2. A proposed geologic cross-section of lower Chevelon Canyon (study area). Fissures created by local uplift in Holbrook Dome region fracture Coconino and perhaps Supai Formations allowing local recharge of aquifer. Chevelon Canyon, dissecting water table produces a series of seeps. Waved line indicates geologic unconformity.

Colorado River 18km east of Winslow, Arizona.

The waters of Chevelon Creek flow initially through Permian sediments of the central plateau region. North of Chevelon Crossing the creek enters deposits dominated by Coconino Sandstone.

Chevelon Creek drains an area of 2056km^2 (794mi^2), this area excludes 518km^2 (200mi^2) of the basin which are considered to be noncontributing. This means the excluded area does not drain directly into the surficial drainage patterns but rather serves as a closed depression contributing accumulated waters to the local groundwater supply. The major portion of Chevelon Creek is an ephemeral stream demonstrating a seasonal response to rain and snow runoff. The lower 16km of the Chevelon Creek system is perennial with registered minimal flows of less than one cubic ft sec^{-1} (CFS) several times during a 41-year record period.¹ The perennial section of the stream is sustained during periods of extended drought by springs and seeps originating in the Coconino Formation. Seasonal inputs of significant volumes of water are a result of snowmelt and rainstorms. Maximum recorded discharge of 25,300 CFS was January 19, 1952.

The Chevelon Creek system then presents two very different aspects to the observer. The first is the high discharge ephemeral second order stream (Straler, 1964) or fourth to fifth order stream (Shreve, 1966), the second is the low discharge first order perennial stream maintained during base flow by seepage from the Coconino Aquifer.

The Chevelon Creek system has a stream bifurcation ratio of

¹U.S. Geological Survey, Water Resources Division. Surface Water Records of Arizona. STORET number 09398000.

4:1 (Whitton citing Shreve, 1975). Bifurcation ratios generally range from three to five with lower ratios typically having flood hydrographs with marked discharge peaks. Higher ratios have flood hydrographs with typically low peaks sustained over a much longer period of time.

The relatively high bifurcation ratio would then correspond to a larger drainage basin such as the Chevelon Basin in which flooding, although periodic, is sustained for a period of time. This would be a somewhat different pattern from that of the typical desert wash which may flash flood and recede to previous conditions in as little as 24 hours (Fisher, 1978). Flash flooding (spate) was noted during the minimal flow period by indirect observation of debris accumulation in riparian vegetation, the swept appearance of the riparian vegetation, the refilling of evaporated potholes, the downstream movement of human refuse such as cans and bottles and the occasional absence of anchored samplers. Although secondary evidence of spate was profuse summer spates were never directly observed. These spates, I assumed, originated from very local storm events involving a small portion of the entire drainage basin. This assumption was made due to the observation that summer storms in this region, although occasionally of great intensity, are quite patchy involving a relatively small portion of the available topography.

The drainage density of the system is 0.08 and the elongation ratio is 0.61. Drainage density is derived by division of stream length (65mi) by drainage area (794mi^2). The elongation ratio is derived by the division of the diameter of a circle having the same area as the drainage basin by the longest axis of the basin. Both

figures relate length to drainage area and the ratios tend to increase with the increased size of catchment area and increased relief.

Chapter 3

MATERIALS AND METHODS

Invertebrates

Samples were collected monthly along the lower 10.5km section of Chevelon Creek above its confluence with the Little Colorado River. Two major collection sites were established. The sites selected were each considered to be a representative reach but were in part chosen for their accessibility. Over a 12-month period from July, 1979 to June, 1980 invertebrate samples were collected and pertinent physical and chemical data acquired. Physical and chemical data was augmented by previous data collected during 1977-79. Invertebrates were collected by the use of an artificial substrate composed of fourteen masonite discs separated by spacers arranged along an eyebolt. This sampler is constructed of 0.3cm tempered hardboard (masonite) cut into 7.5cm diameter plates and 2.5cm circular spacers. A total of 14 plates and 24 spacers are required for each sampler. The hardboard plates and spacers are placed on 0.625cm (0.25 inch) eyebolt so that there are eight single spaces, one double space, two triple spaces and two quadruple spaces between the plates. This sampler provides an effective surface area of 0.13m^2 . This sampler is known as a Modified Hester-Dendy Multiple Plate Sampler (Weber et al., 1973) (Figure 3).

Collected samplers were disassembled and carefully cleaned in

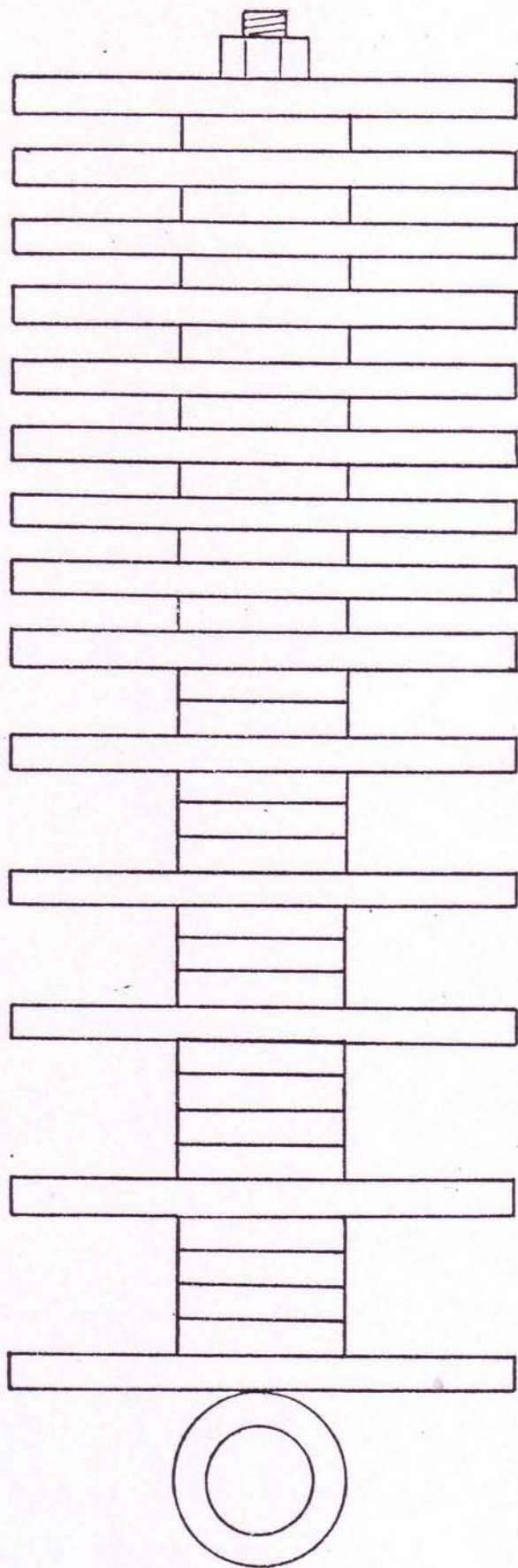


Figure 3. Illustration of an assembled modified multiple plate sampler as used in the Chevelon Creek Macroinvertebrate study; note the variation in plate spacing providing a variety of habitats.

the field using a toothbrush and a plastic wash basin. The residual fluid within the basin containing the collected invertebrates was then sieved by passage through a U.S. Standard Number 30 sieve. Retained invertebrates and debris were then flushed out of the sieve with a squirt bottle into a labeled plastic sample bag. The sieve then was carefully inspected for any remaining specimens which were manually removed and placed in the same bag. Samples were preserved in 70 percent ethyl alcohol. The cleaned sampler was reassembled and replaced into the same area it was initially withdrawn from (PLATES III, IV).

All macroinvertebrate samples were sorted and picked by hand. Sample materials were placed into a 25 x 40 x 5cm white enameled pan filled approximately one-third full of water. Groups were then separated to phylum or in the case of the insects to order. Cleaned and separated samples were labeled and stored in 50ml vials in 70 percent ethyl alcohol. Samples which contained excessively high numbers of individuals were subsampled by one of two methods. In the first method two lines were scribed upon the floor of the enameled pan which effectively divided the pan into four equal quadrants. A quadrant was selected and the invertebrates removed or the 1/4 sample was placed in a similarly delineated pan and a 1/8 sample evaluated. A second subsampling method used became necessary when at the close of the study sample size became exceedingly large. In this method the sample was drained and then placed on a balance. The gross weight of the sample was determined and a 1/100 equivalent weight was removed and evaluated. This method was considered to be valid due to the extremely low diversity of taxa with two species comprising more than

PLATE III. A DISASSEMBLED MULTIPLE PLATE SAMPLER WITH
PROCESSING PARAPHERNALIA.

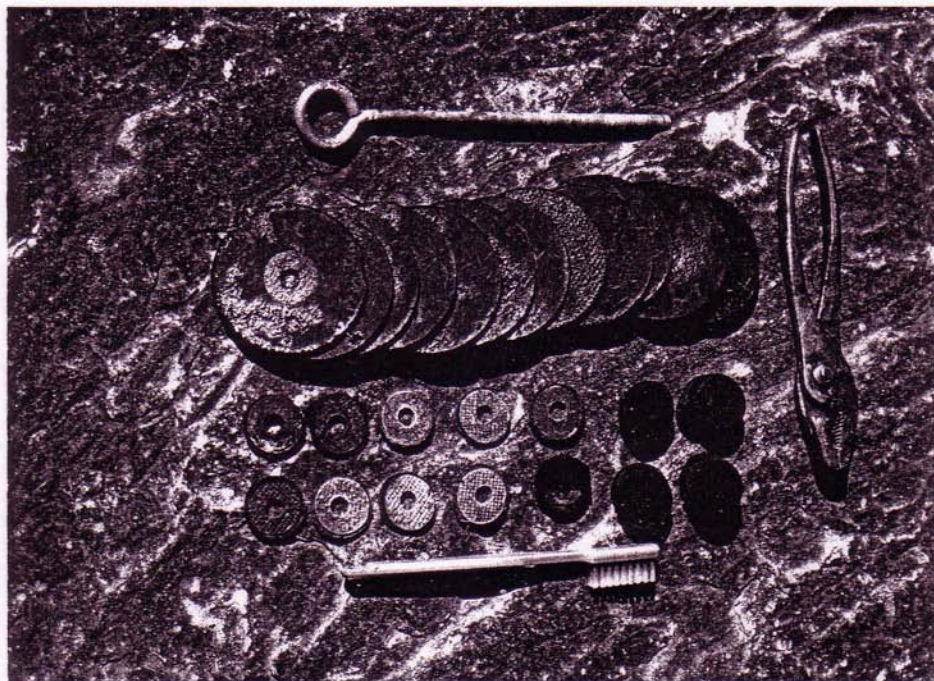
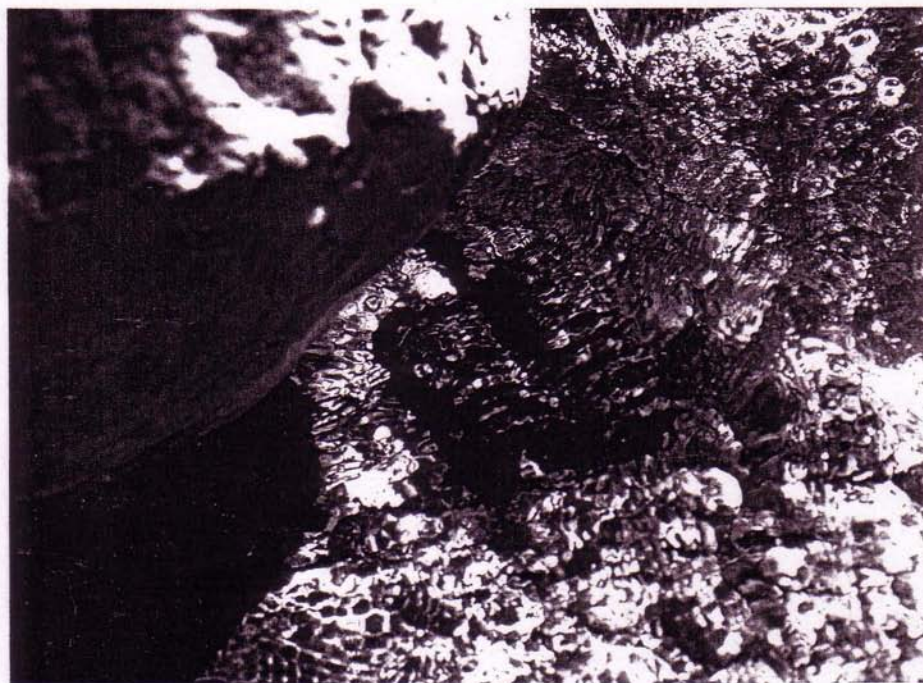


PLATE IV. A MULTIPLE PLATE SAMPLER IN SITU.



95 percent of the sample. The entire sample was examined for less common taxa.

Representative individuals were identified to genus when possible (Pennak, 1953; Usinger et al., 1959; Peterson, 1956, 1960; Borror and Delong, 1964; Merritt and Cummins, 1978).

Physico-Chemical Water Analysis

Physico-chemical data collected were temperature, pH, alkalinity, specific conductance, nitrate, phosphate, silica, sulfate, chloride and oxygen. Water temperature was recorded in degrees Celsius using a field thermometer. pH was determined utilizing a field pH meter (VWR mini pH). Alkalinity was determined by titration of a 50ml water sample to a pH of 4.3 with 0.02N H_2SO_4 . The milliliters of titrant which were used multiplied by 20 corresponded to the alkalinity of the sample. Dissolved oxygen was determined by the Winkler Azide Modification method as specified in U.S. Public Health Service Standard Methods (APHA, 1971)

Specific conductance, nutrient analysis and trace analysis were conducted in the laboratory. Water samples to be transported were filtered through 0.45um membranes and stored at 3°C until evaluation. Specific conductance was determined using a Radiometer Model CDM2c conductivity meter as per manufacturer's instructions. Water samples taken for nutrient analyses were analyzed colorimetrically using a DR-EL/2 (Hach Chemical Company) colorimeter calibrated with known standard solutions. Chloride was analyzed titrimetrically with mercuric nitrate (APHA, 1971).

For portions of this study the dissolved oxygen profile and

light extinction of selected waters were evaluated (Blinn et al., in press). Oxygen profiles were determined using a Model TDO-2 Oxygen Meter (Hydrolab Corporation). Light values were measured with an underwater photometer (Protomatic) with a spectral response peak of 580nm. An attempt was made to determine chemical oxygen demand (COD) using methods prescribed by the Environmental Protection Agency (U.S.E.P.A., 1974). The water sample was refluxed with known amounts of potassium dichromate and sulfuric acid. Dichromate that was not consumed in the reflux reaction was titrated with a known concentration of ferrous ammonium sulfate. The amount of oxidizable organic matter was directly proportional to the amount of potassium dichromate consumed.

Invertebrate samples were statistically evaluated for mean diversity (\bar{d}) as derived by the following equation:

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

Where $C = 3.321928$, a machine conversion to base 2; N = the total number of individuals present in the community; n_i = the total number of individuals in the i^{th} species. Equitability of species was determined by division of a value (S') which represented a hypothetical species number by a value (S) representing the actual number of species sampled:

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

Proportional values for representation of taxa were determined using the following formula:

$$P_i = \frac{n_i}{N}$$

Where P_i = the proportional relationship of the i^{th} taxa; n_i = number

of individuals of the i^{th} taxa and N = the total number of individuals in the community.

Discharge Data for the Chevelon Creek Drainage was provided by the 41-year record of the U.S. Geological Survey, Water Resources Division (USGS).¹

¹U.S. Geological Survey, Water Resources Division. Surface Water Records of Arizona. STORET number 09398000.

Chapter 4

RESULTS

Physical Parameters

Temperature

During 17 September 1978 to 10 June 1980 temperature ranged from 1°C to 26°C at both sites. The mean water temperature at Site 1 during the study period was 14.7°C with a standard deviation of 8.8. Mean water temperature at Site 3 was 14.9°C with a standard deviation of 8.1. The waters of Chevelon Creek demonstrated a typical seasonal pattern in regard to temperature with seasonal lows occurring in the winter months and then a gradual increase in temperature toward the seasonal summer high. Generally temperatures at Site 3 were slightly higher than those of Site 1 (Figure 4).

Discharge

The United States Geological Survey maintained a hydrological station approximately .75km upstream from Site 2 in an interrupted period from 1905-1971. Average discharge over this period was 50.3 CFS with an annual average of 30,400 acre ft year⁻¹. Recorded extremes were a low of less than 1 CFS at several times and a maximum of 25,300 CFS on 19 January 1952. Maximums observed during the period of study equaled or exceeded the historical recorded maximum and the recorded minimum of less than 1 CFS was observed (Figure 5).

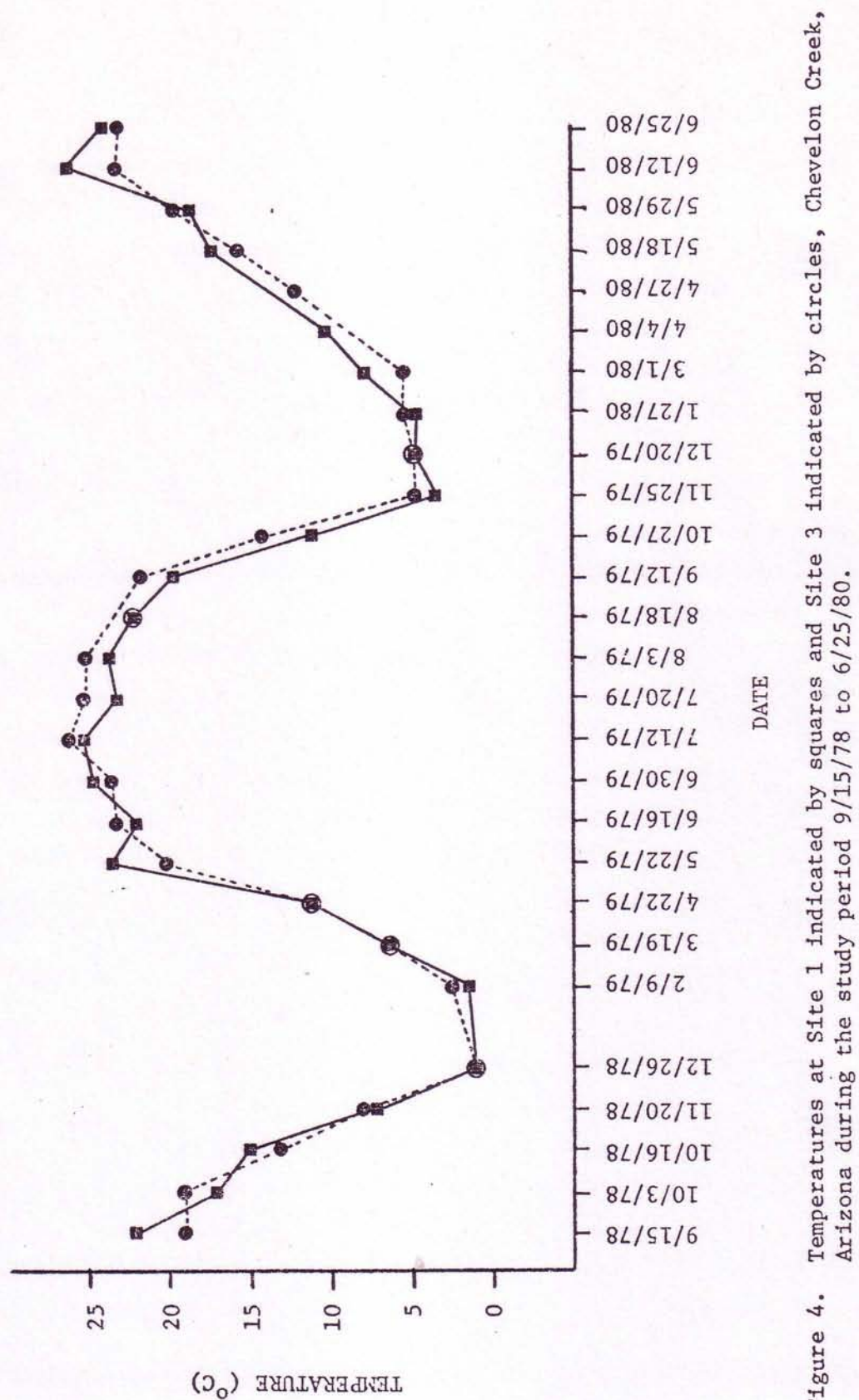


Figure 4. Temperatures at Site 1 indicated by squares and Site 3 indicated by circles, Chevelon Creek, Arizona during the study period 9/15/78 to 6/25/80.

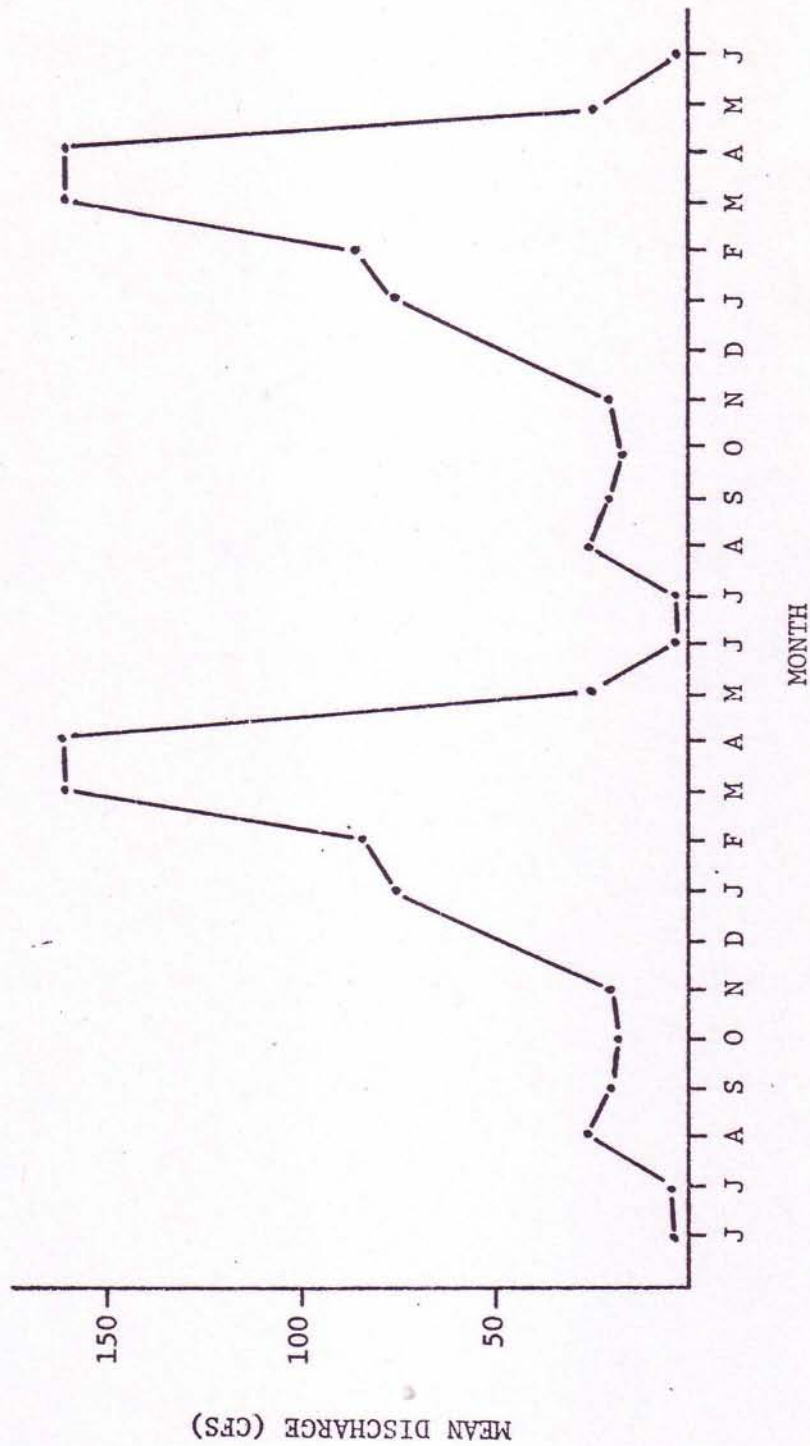


Figure 5. Mean monthly discharge of Chevelon Creek, Arizona in cubic feet per second (CFS) as calculated from the hydrologic records of the United States Geologic Survey.

Chemical Parameters

General

The chemical nature of Chevelon Creek was studied over a period of 24 months, during this time a predictable pattern of chemical interaction was noted. An overriding influence upon this interaction was discharge. Mean discharge data acquired from the 41-year record of the U.S. Geological Survey demonstrated periods of sustained low flow interrupted by seasonal flooding periods. Low flow established during the late spring as surficial runoff declined and was sustained throughout the summer and early fall. This period of relative stability corresponded to a dramatic increase in specific conductance at all sites studied. Dilute waters present during high flow were concentrated from a minimum of 50umhos to as much as 3650umhos at Site 3 within a period of 90 days a percent change of 7200!

The major anions contributing to this remarkable rise in concentration showed a very close correlation with the conductance values. A linear regression analysis comparing specific conductance to Cl^- had a high positive correlation $r = 0.987$ (for $\text{SO}_4^{=}$, $r = 0.828$ and for HCO_3^- , $r = 0.898$).

pH

Throughout the period of study pH values at both sites remained similar. At Site 1 the recorded low was 5.3 and the seasonal high 8.2. The mean of 25 observations was 7.35 with a standard deviation of 0.76. At Site 3 the recorded low was 5.5 on 19 March 1979 the recorded high was 8.2 on several occasions. The mean of 27 observations was

7.4 with a standard deviation of 0.83. pH values at both sites were quite similar with the values at Station 3 (downstream) slightly exceeding those of Site 1. The lowest pH values were recorded during times of intense flood. The higher values were recorded during the summer concentration period (Figure 6).

Dissolved Oxygen

Dissolved oxygen values at Site 1 ranged from 6.2ppm to 11.4ppm. The mean of 24 observations was 8.53ppm with a standard deviation of 1.6. Oxygen concentrations at Site 3 ranged from 4.9ppm to 10.3ppm. The mean of 25 observations was 7.8ppm with a standard deviation of 1.9. Seasonal trends in oxygen levels were noted with the lowest concentrations occurring during the summer baseflow period and the highest concentrations occurring during winter months when colder water temperatures enhanced the amount of oxygen the water could hold. Oxygen levels at the two study sites were generally within 1ppm of each other. The greatest disparity between the two sites occurred on the 15 September 1979 sampling data with a difference of 4.1ppm (Figure 7).

Silica

Concentrations of silica were typically higher at Site 3 than at Site 1. Mean values for 24 observations were 5.35mg l^{-1} and 4.85mg l^{-1} respectively. The standard deviation of observed values for Site 1 was 1.33 whereas the standard deviation at Site 3 was 1.23. Observed values at Site 1 ranged from 1.2mg l^{-1} to 6.9mg l^{-1} . Observed values at Site 3 ranged from 2.4mg l^{-1} to 7.0mg l^{-1} (Figure 8).

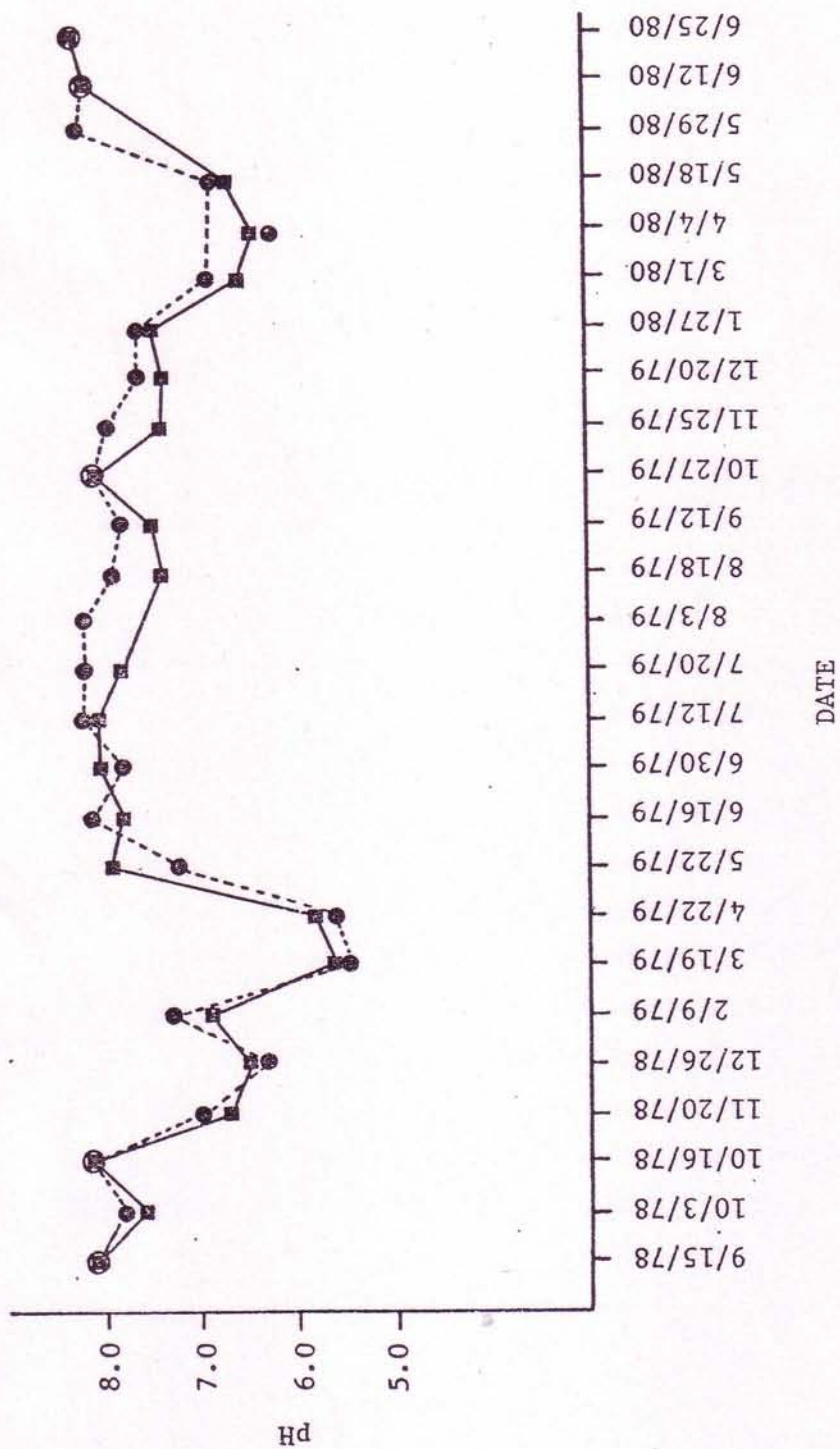


Figure 6. pH values determined at Site 1 indicated by squares and Site 3 indicated by circles, Chevelon Creek, Arizona during the study period 9/15/78 to 6/25/80.

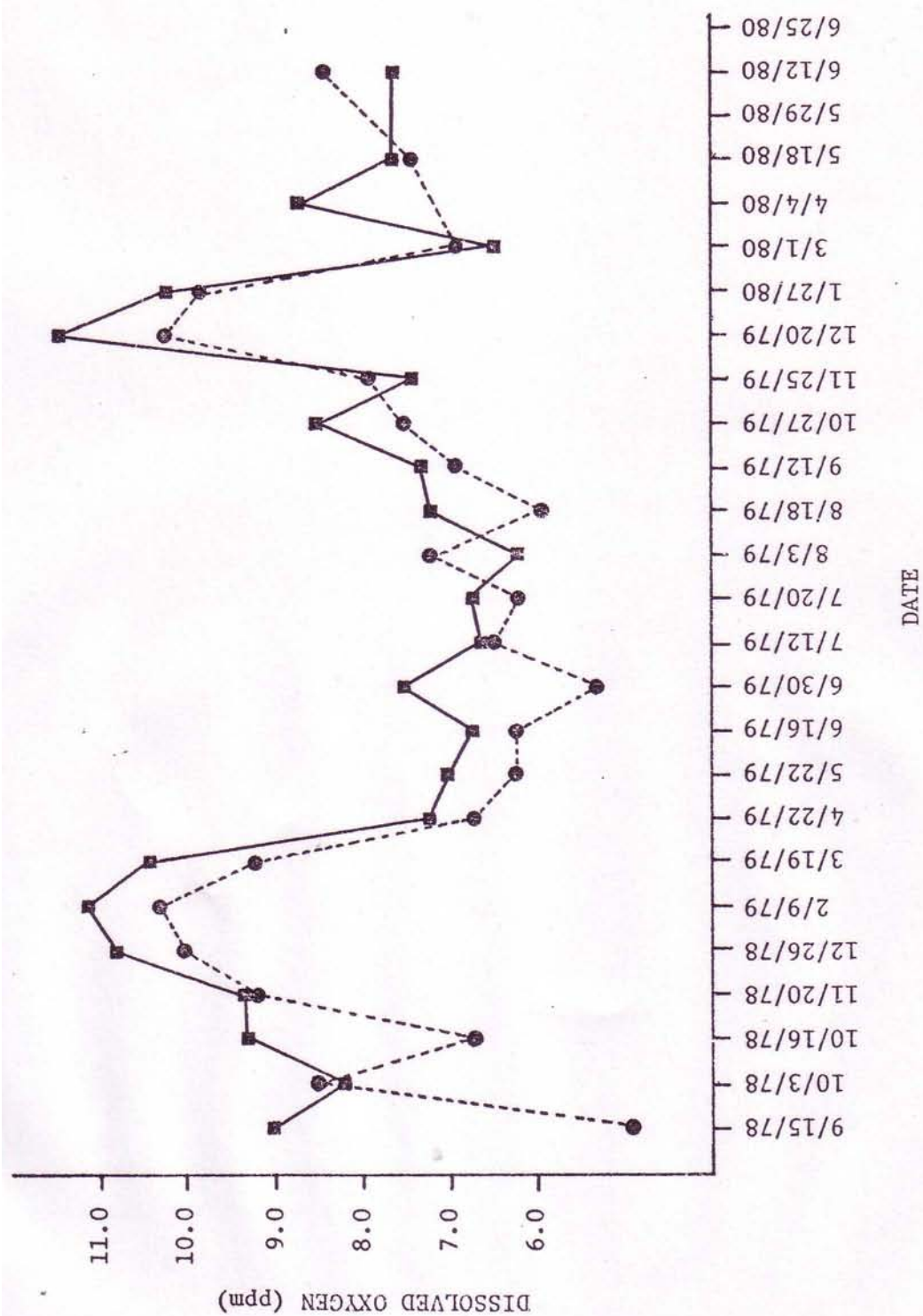


Figure 7. Dissolved oxygen concentrations in ppm at Site 1 indicated by squares and Site 3 indicated by circles, Chevelon Creek, Arizona during the period 9/15/78 to 6/12/80.

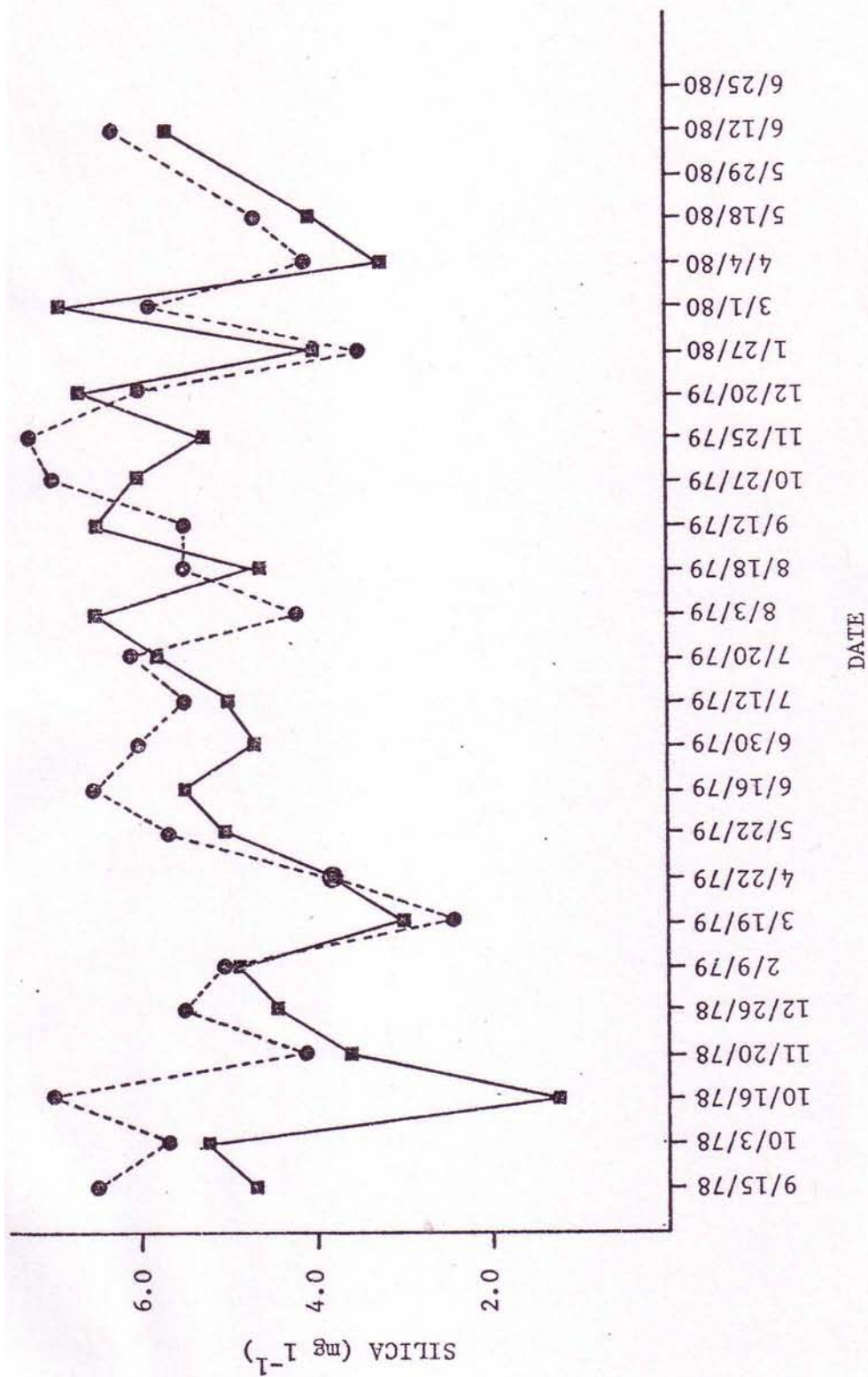


Figure 8. Silica concentrations in milligrams per liter, Chevelon Creek, Arizona. Site 1 indicated by squares, Site 3 indicated by circles for the study period 9/15/78 to 6/12/80.

Nitrate-Nitrogen

Nitrate concentrations were low and fluctuated inconsistently at both sites ranging from 0.01mg l^{-1} to 0.06mg l^{-1} . The mean values of 24 observations at Sites 1 and 3 were 0.037 (s.d. 0.057) and 0.037 (s.d. 0.059) respectively (Figure 9).

Phosphate

Phosphate-phosphorus mean concentrations at Site 1 were 0.066mg l^{-1} (s.d. 0.058). The mean value at Site 3 was 0.105mg l^{-1} (s.d. 0.08). Concentrations for both stations showed significantly higher values during the February, 1979 and 1980 sampling periods (Figure 10).

Sulfate

Sulfate (SO_4) concentrations rose and fell seasonally at the two sites. Lowest values occurred during the winter/spring flooding period and highest values occurred during the summer baseflow period. Sulfate concentrations at Site 3 were always equivalent to or greater than those at Site 1. The range of concentration for the two sites was a low of 10ppm to a high of 197ppm (Figure 11).

Alkalinity

Alkalinity at the two sites was distinctly different during the summer baseflow period and more similar during the flooding period. Alkalinity values at Site 3 always exceeded those of Site 1. The observed range of alkalinity for Site 1 was 16.5ppm to 158ppm.

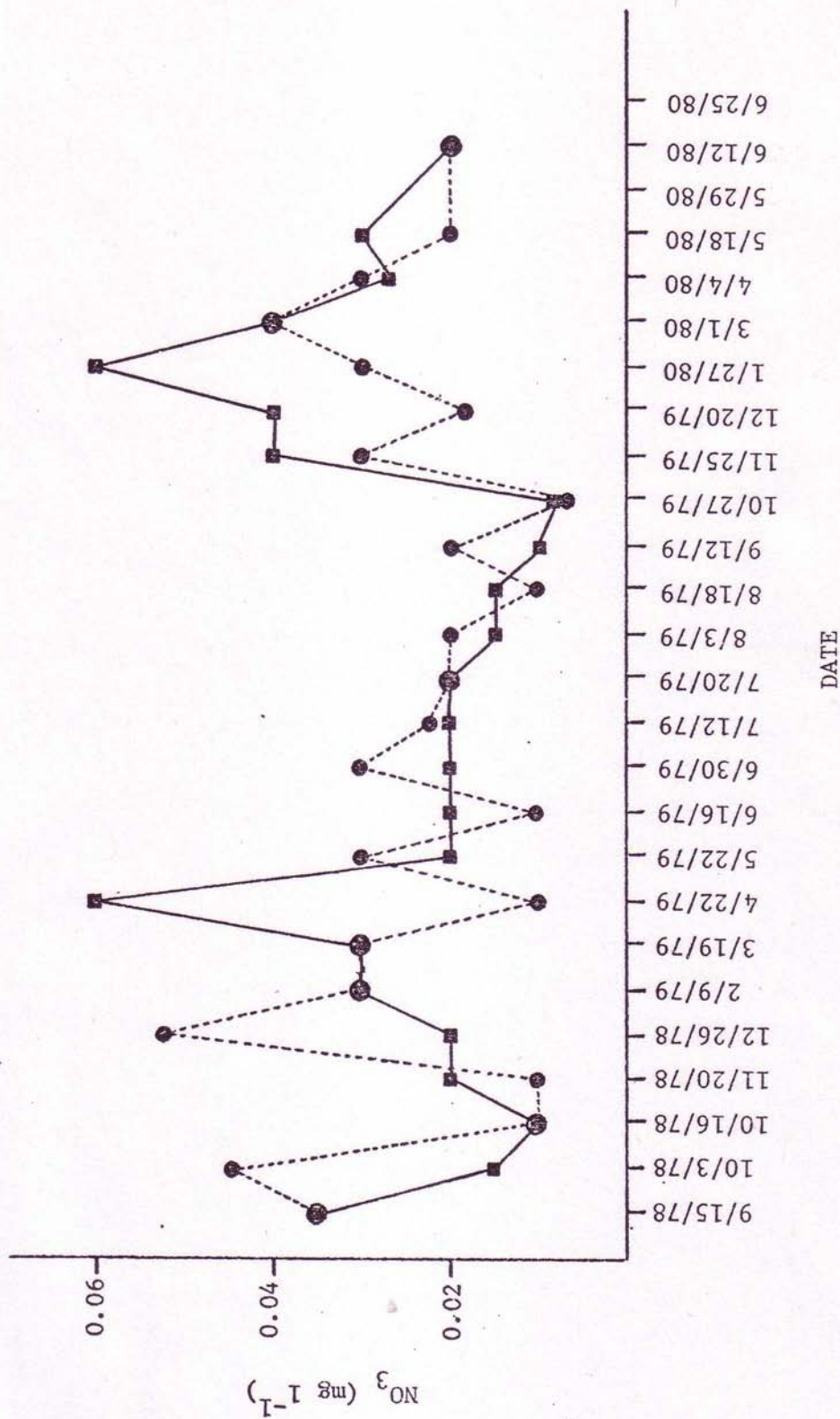


Figure 9. Nitrate-Nitrogen (NO_3) concentrations, Chevelon Creek, Arizona. Site 1 indicated by squares, Site 3 indicated by circles for the study period 9/15/78 to 6/12/80.

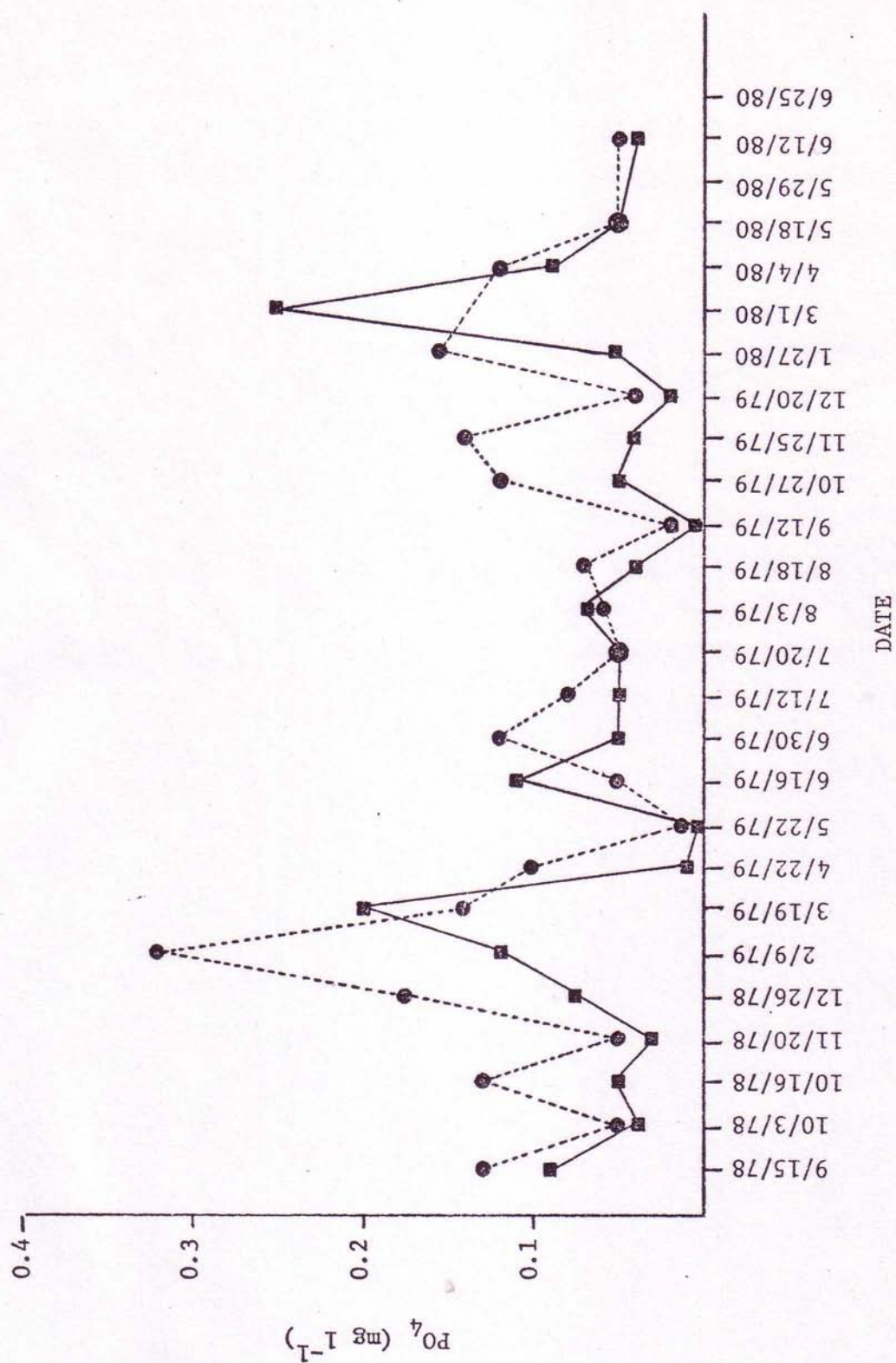


Figure 10. Phosphate-phosphorus (PO_4) concentrations, Chevelon Creek, Arizona. Site 1 indicated by squares, Site 3 indicated by circles for the study period 9/15/78 to 6/12/80.

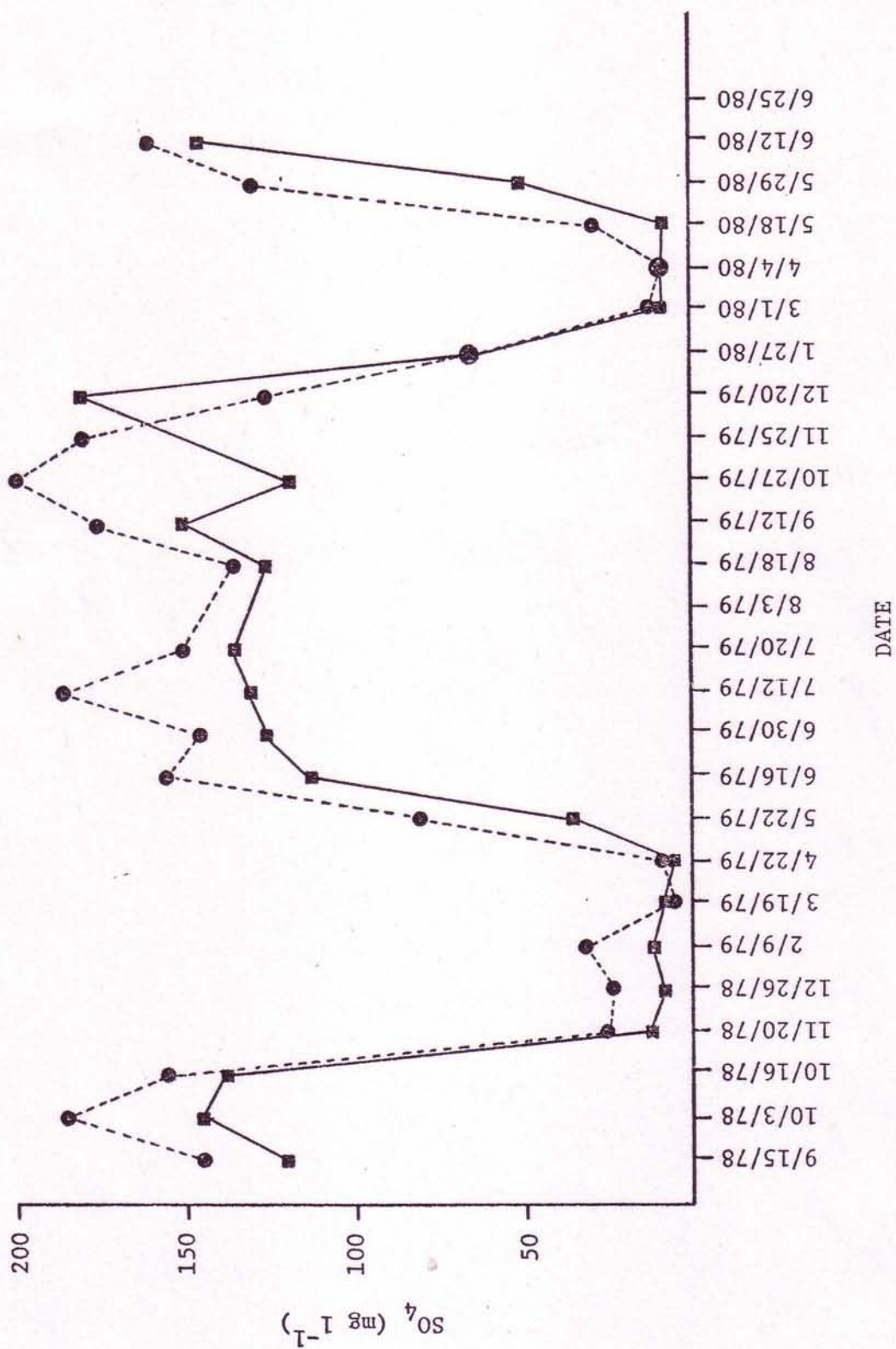


Figure 11. Sulfate concentrations in Mg l^{-1} at Site 1 indicated by squares and Site 3 indicated by circles, Chevelon Creek, Arizona during the study period 9/15/78 to 6/12/80.

The recorded range for Site 3 was 18ppm to 214ppm. During the baseflow period there was generally a 50ppm difference between sites. This variance was not observed during the flooding period (Figure 12).

Chloride

Chloride values for the Chevelon Creek system generally exceeded those for sulfate. There exists within the system a distinct concentration gradient from relatively dilute upstream waters to relatively concentrated downstream waters. Chloride concentrations at the upstream site ranged from 5ppm to 138ppm. The mean of 23 observations was 69.4ppm (s.d. 47.7). Chloride values for Site 3 were always higher than those of Site 1. Site 3 values ranged from 20ppm to 1127ppm. The mean of 27 observations was 610.8ppm (s.d. 444.7). During the summer baseflow period the concentration difference between the two sites was nearly 1000ppm (Figure 13).

Specific Conductance

Specific conductance values reflected the ionic concentration gradient of SO_4^- , HCO_3^- and Cl^- . Conductance values at Site 3 always exceeded those of Site 1. During the baseflow period conductance values varied between sites as much as $2900 \mu\text{mhos cm}^{-1}$. Conductance values were similar during winter/spring flooding. Values for Site 1 ranged from $32 \mu\text{mhos cm}^{-1}$ to $970 \mu\text{mhos cm}^{-1}$. Site 3 values ranged from $62 \mu\text{mhos cm}^{-1}$ to $3800 \mu\text{mhos cm}^{-1}$ (Figure 14). The recorded high, low and mean values were compared for HCO_3^- , SO_4^- , Cl^- and specific conductance for Sites 1 and 3 (Figure 15).

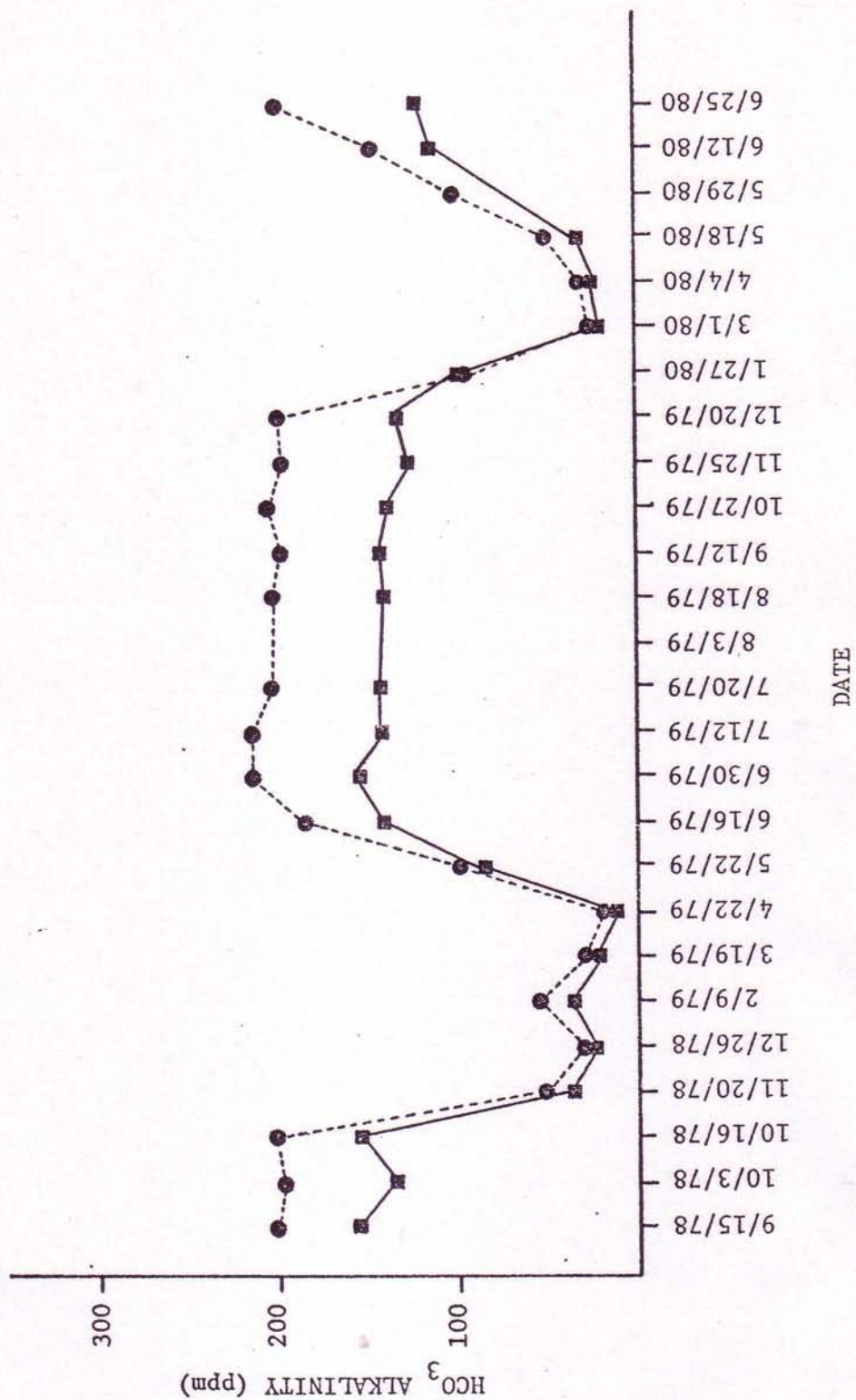


Figure 12. Bicarbonate alkalinity (HCO_3^-) in ppm at Site 1 indicated by squares and Site 2 indicated by circles during the study period 9/15/78 to 6/25/80.

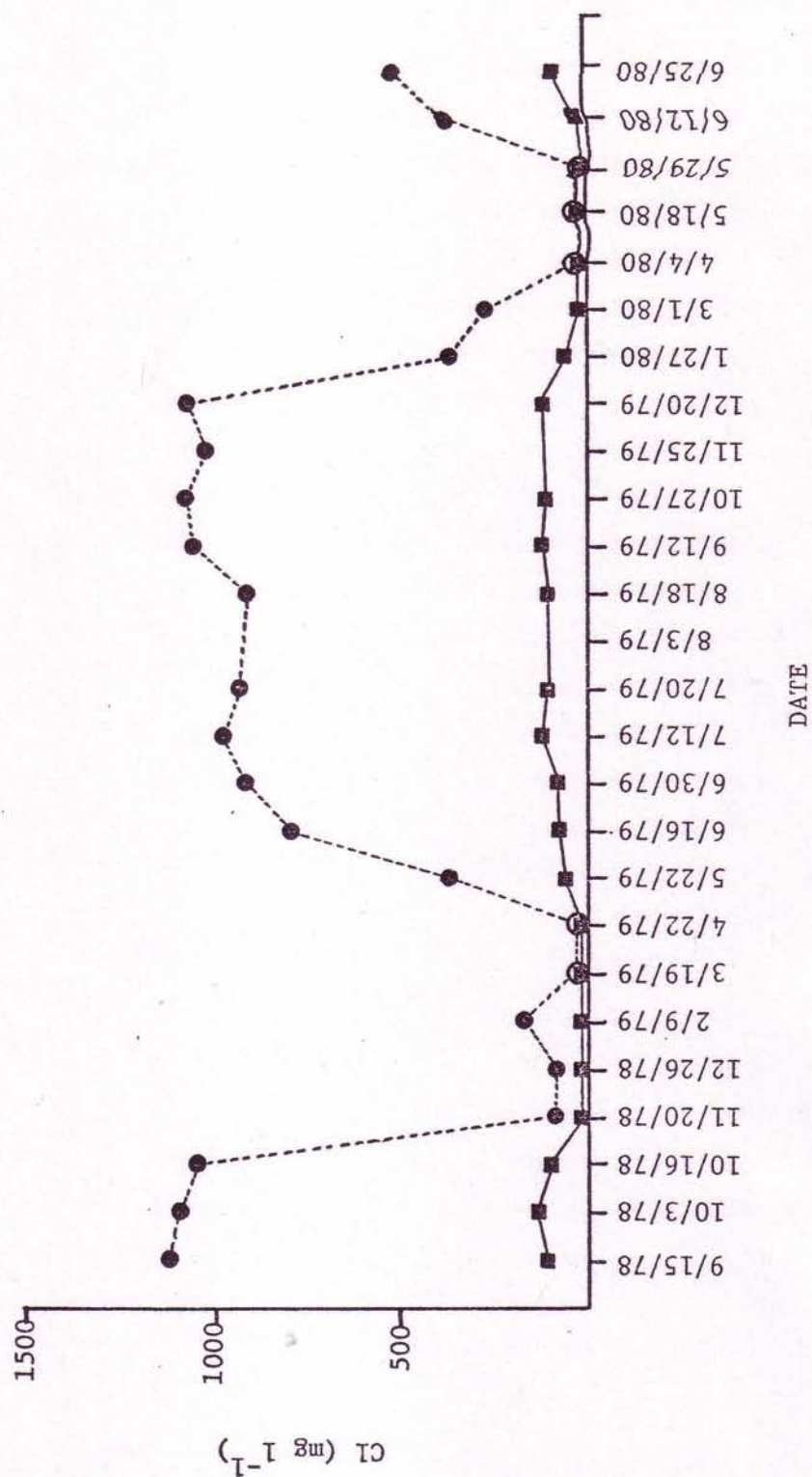


Figure 13. Chloride concentrations in milligrams per liter at Site 1 indicated by squares and Site 3 indicated by circles at Chevelon Creek, Arizona during the period 9/15/78 to 6/25/80.

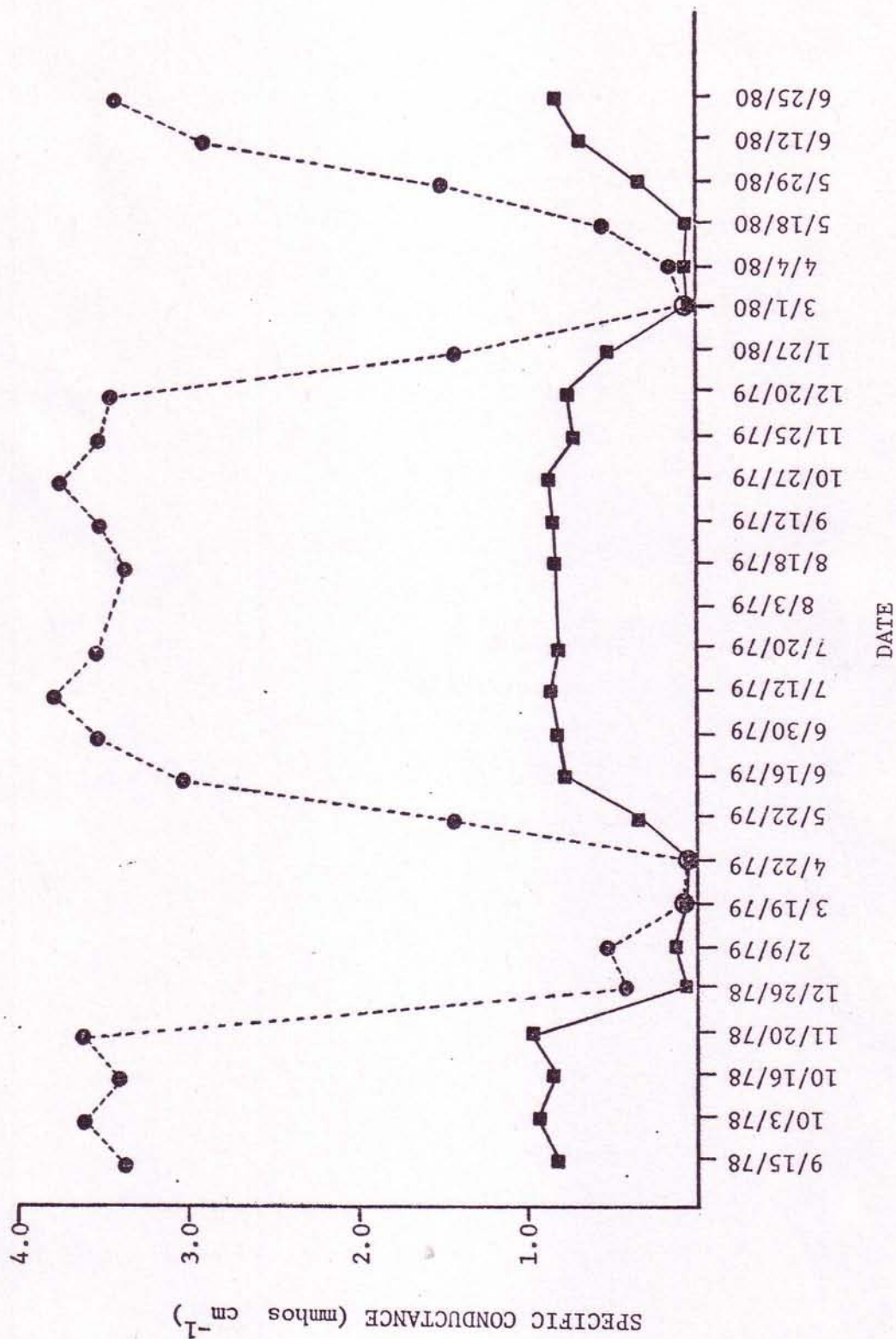


Figure 14. Specific conductance in mmhos cm^{-1} at Site 1 indicated by squares and Site 3 indicated by circles, Chevelon Creek, Arizona during the study period 9/15/78 to 6/25/80.

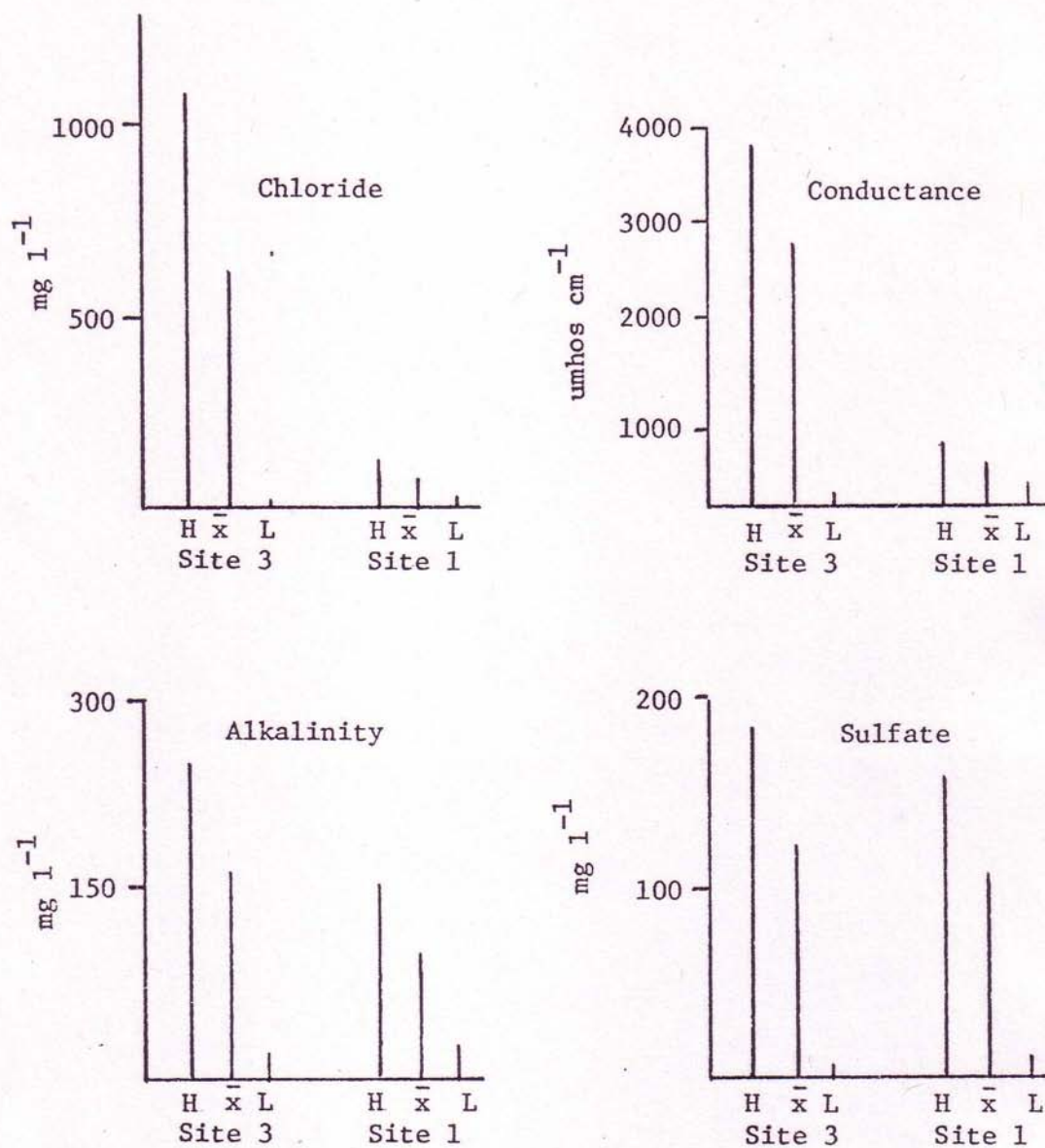


Figure 15. A comparison of observed high (H), low (L) and mean (\bar{x}) values for chloride, alkalinity, sulfate and specific conductance at Sites 1 and 3 Chevelon Creek, Arizona.

Invertebrates

Taxa

During the 12-month period when invertebrate collections were made (July 1979 to June 1980), 18 different taxa were collected using the multiple plate sampling device (Table 1). Of these 18 taxa only seven were common to both sites. The majority of the individuals collected were from the insect orders Diptera, Trichoptera and Ephemeroptera. Of these three orders, the dipterans were most abundant in both species richness and absolute numbers. Several taxa were represented by a single collection (Plumatella sp., Ferrissia sp. and Argia sp.). Other taxa could be considered rare in that although collected several times, few were collected when compared to those more common. These "rare" taxa were the megalopteran Corydalus sp., the elmid Microcyllloepus sp., the stratiomyid Eulalia sp. and the anthomyids of the genus Limmophora. By far the most common invertebrates were in the genera Simulium and Calopsectra (Diptera). Of the 55 individual collections made Simulium sp. was present in 54 and Calopsectra sp. in 53. This constitutes a genus presence of 98 percent for Simulium sp. and 96 percent for Calopsectra sp. Individual numbers ranged from 8 to more than 190,000 per m².

For the blackfly (Simulium) populations the variation in total numbers between Site 1 and Site 3 ranged from 207/m² in the 27 October 1979 sample to as much as 8262/m² in the 20 December 1979 sample. The midge (Calopsectra) population total variance ranged from a minimum of 40/m² in the 20 December 1979 collections to more

Table 1. List of Taxa Collected from June 1979 to June 1980 Using a Multiple Plate Sampling Device at Two Sites on Chevelon Creek, Arizona.

Taxa	Site 1	Site 3
Insecta		
Diptera		
<u>Simulium vittatum</u>	*	*
<u>Calopsectra</u> sp.	*	*
<u>Pentanura</u> sp.	*	*
<u>Limmophora exsurida</u>	-	*
<u>Limmophora aequifrons</u>	-	*
<u>Eulalia</u> sp.	-	*
Trichoptera		
<u>Hydropsyche</u> sp.	*	*
Ephemeroptera		
<u>Baetis</u> sp.	*	*
<u>Baetodes</u> sp.	*	-
Odonata		
<u>Argia</u> sp.	*	-
Neuroptera		
<u>Corydalis</u> sp.	-	*
Coleoptera		
<u>Microcylloepus</u> sp.	*	*
Lepidoptera		
<u>Parargyractia</u> sp.	-	*
Crustacea		
<u>Cambarus</u> sp.	*	-
Arachnida		
<u>Acari</u> sp.	*	-

Table 1. (continued)

Taxa	Site 1	Site 3
Mollusca		
Gastropoda		
<u>Physa</u> sp.	-	*
<u>Ferrissia</u> sp.	*	-
Bryazoa		
<u>Plumatella</u> sp.	*	*

* Denotes presence

- Denotes absence

than $192,000/m^2$ in the 10 June 1980 collections. At no time during the 12-month study period did the midge population at the upstream site (Site 1) exceed the population of the downstream site (Site 2) (Figure 16). The numbers of the blackfly population alternated from upstream dominance in the period 12 August to 27 October 1979 to downstream dominance during the period 27 October 1979 to 27 January 1980 (Figure 17).

Statistical Evaluation

Diversity values were calculated for those aggregate collections which exceeded 100 individuals. Diversity values for collections containing less than 100 individuals must be viewed with extreme caution as even a minor numerical fluctuation will inordinately skew values. At Site 1 \bar{d} ranged from 0.23 on 2 October 1979 to 1.09 on 10 June 1980. Diversity values were generally lower than 1.0 with average of 0.61 (s.d. 0.35). Diversity values at Site 3 ranged from 0.18 on 10 June 1980 to 1.11 on 2 October 1979 (Table 2).

Equitability at Site 1 ranged from 0.16 on 27 October 1979 to 0.62 on 10 June 1980. The average equitability was 0.32 (s.d. 0.17). Equitability at Site 3 ranged from 0.09 on 10 June 1980 to 0.54 on 27 October 1979. The seasonal average was 0.29 (s.d. 0.16).

When individual species numbers were compared to total numbers within the collective sample a proportion of taxa was determined. I found that at both Sites 1 and 3 Simulium sp. and Calopsectra sp. (Diptera) were predominant at most times of the year. At Site 1 Simulium sp. remained dominant throughout the entire study period with proportional representation ranging from 74.7 percent on 6 June 1980

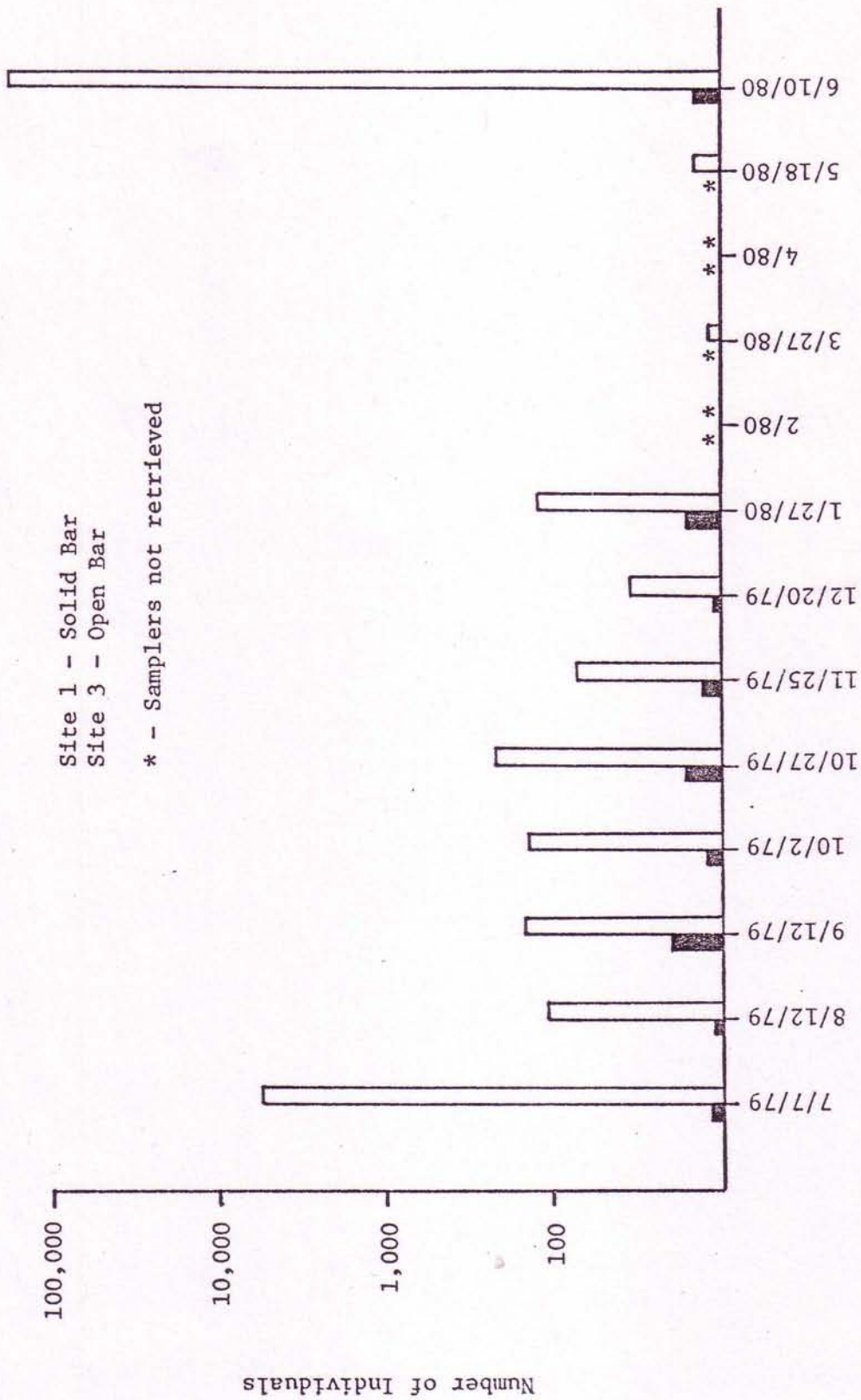


Figure 16. Plot of mean populations of Calopsectra sp. at Chevelon Creek, Arizona, 1979 to 1980.

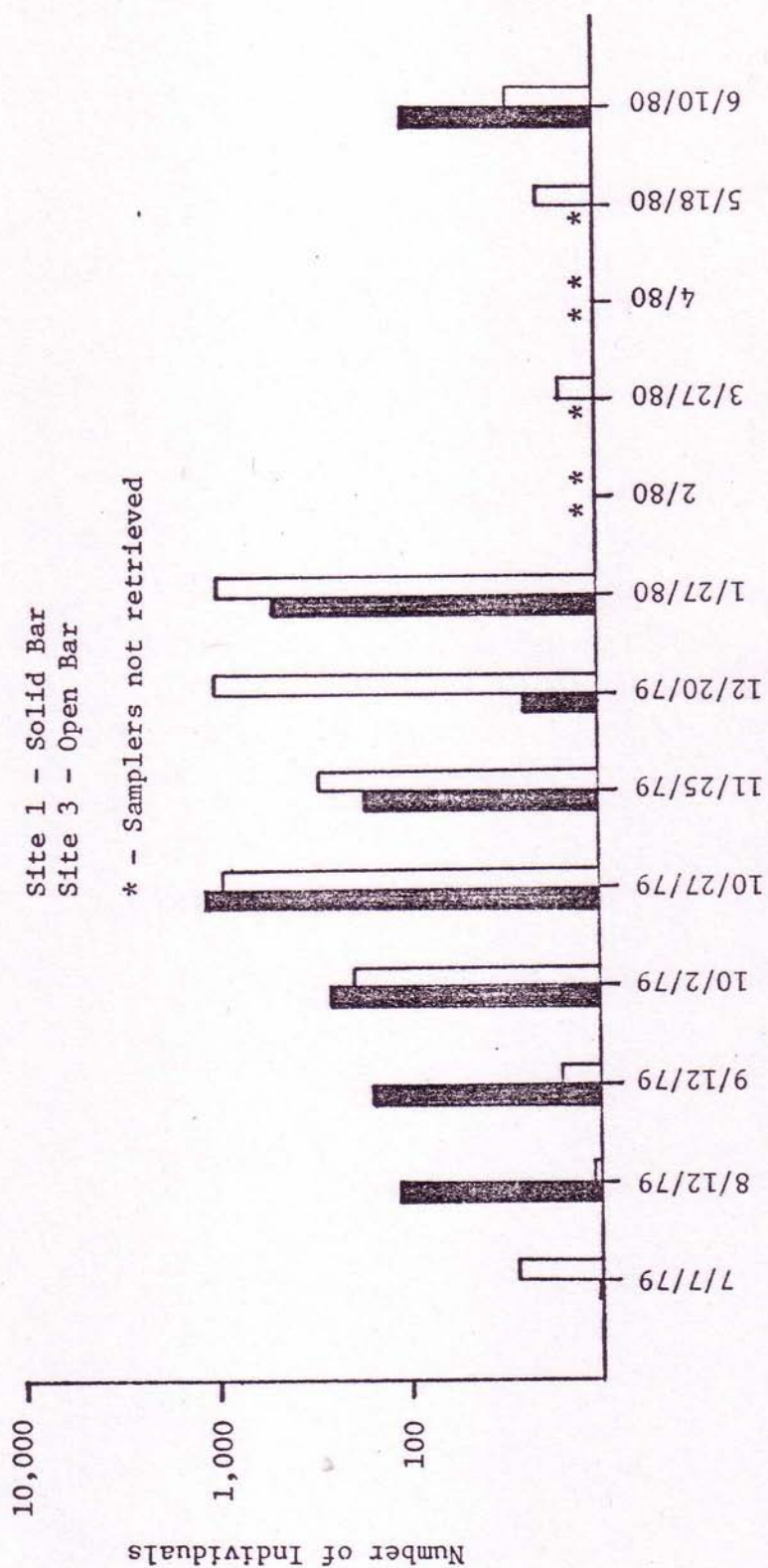


Figure 17. Plot of mean populations of Simulium sp. at Chevelon Creek, Arizona, 1979 to 1980.

Table 2. Showing \bar{d} and Equitability for Collections Exceeding 100 Individuals.

Date	Site 1 \bar{d}	e	Site 3 \bar{d}	e
7/20/79	*	*	0.36	0.18
8/12/79	0.88	0.41	0.60	0.37
9/12/79	1.06	0.49	0.61	0.25
10/2/79	0.23	0.19	1.11	0.46
10/27/79	0.26	0.16	0.94	0.54
11/25/79	0.47	0.23	0.73	0.18
12/20/79	0.44	0.18	0.56	0.15
1/27/80	0.44	0.18	0.56	0.23
2/80	-	-	-	-
3/80	-	-	-	-
4/27/80	-	-	*	*
5/18/80	-	-	0.80	0.49
6/10/80	1.09	0.62	0.18	0.09

* less than 100 individuals in collection

- no data

to 96.9 percent on 2 October 1979. The midge genus Calopsectra ranged from a seasonal low of 0.7 percent on 12 August 1979 to a seasonal high of 17.2 percent on 6 June 1980. Proportional values determined for the two predominant species at Site 3 were quite different from those of Site 1. Proportional representation of Simulium sp. ranged seasonally from 0.5 percent on 20 July 1979 to 95.2 percent on 20 December 1979. Values for Calopsectra sp. ranged from 4.5 percent on 20 December 1979 to 98.3 percent on 10 June 1980 (Table 3).

Table 3. Proportional Representation of Various Taxa at Two Sites on Chevelon Creek, Arizona, 7/20/79 to 6/10/80 as Collected by Multiple Plate Sampler.

	Site 1		%		Site 3		%
7/20/79				<u>Simulium</u>	48		0.5
				<u>Calopsectra</u>	8656		95.0
				<u>Hydropsyche</u>	160		1.8
				<u>Baetis</u>	48		0.5
				<u>Physa</u>	176		1.9
				TOTAL	9088		
8/12/79	<u>Simulium</u>	106	79	<u>Simulium</u>	3		2.2
	<u>Calopsectra</u>	1	0.7	<u>Calopsectra</u>	120		90.0
	<u>Pentaneura</u>	1	0.7	<u>Elmidae</u>	1		0.7
	<u>Baetis</u>	25	18.7	<u>Physa</u>	10		7.5
	TOTAL	134		TOTAL	134		
9/12/79	<u>Simulium</u>	666	77.1	<u>Simulium</u>	59		7.8
	<u>Calopsectra</u>	103	11.9	<u>Calopsectra</u>	675		89.4
	<u>Chironomidae</u>	1	0.1	<u>Chironomidae</u>	3		0.4
	<u>Hydropsyche</u>	9	1.0	<u>Pentaneura</u>	1		0.1
	<u>Baetis</u>	84	9.7	<u>Baetis</u>	7		0.9
	<u>Baetodes</u>	1	0.1	<u>Argia</u>	1		0.1
	TOTAL	864		<u>Physa</u>	8		1.0
				<u>Corydalus</u>	1		0.1
				TOTAL	755		
10/2/79	<u>Simulium</u>	1367	96.9	<u>Simulium</u>	838		56.7
	<u>Calopsectra</u>	28	2.0	<u>Calopsectra</u>	618		41.8
	<u>Baetis</u>	16	1.1	<u>Hydropsyche</u>	9		0.6
	TOTAL	1411		<u>Baetis</u>	11		0.7
				<u>Physa</u>	3		0.2
				TOTAL	1479		
10/27/79	<u>Simulium</u>	3051	96.3	<u>Simulium</u>	2956		67.6
	<u>Calopsectra</u>	80	2.5	<u>Calopsectra</u>	1396		31.9
	<u>Baetis</u>	35	1.1	<u>Hydropsyche</u>	8		0.2
	<u>Elmidae</u>	2	-	<u>Baetis</u>	6		0.1
	TOTAL	3168		<u>Physa</u>	8		0.2
				TOTAL	4374		

Table 3. (continued)

		Site 1	%		Site 3	%
11/25/79	<u>Simulium</u>	951	93.1	<u>Simulium</u>	1531	84.3
	<u>Calopsectra</u>	39	3.8	<u>Calopsectra</u>	259	14.3
	<u>Hydropsyche</u>	13	1.3	<u>Limnophora</u>	2	0.1
	<u>Baetis</u>	17	1.7	<u>Stratimyidae</u>	1	0.1
	<u>Ferrissia</u>	1	0.1	<u>Hydropsyche</u>	13	0.7
	TOTAL	1021		<u>Plecoptera</u>	1	0.1
				<u>Physa</u>	4	0.2
				<u>Corydalus</u>	1	0.1
				<u>Elmidae</u>	3	0.2
				<u>Lepidoptera</u>	1	0.1
				<u>Ferrissia</u>	1	0.1
				TOTAL	1817	
12/20/79	<u>Simulium</u>	162	93.6	<u>Simulium</u>	3385	95.2
	<u>Calopsectra</u>	2	1.2	<u>Calopsectra</u>	160	4.5
	<u>Chironomidae</u>	4	2.3	<u>Chironomidae</u>	2	0.1
	<u>Baetis</u>	5	2.9	<u>Physa</u>	6	0.2
	TOTAL	173		<u>Lepidoptera</u>	1	-
				TOTAL	3554	
1/27/80	<u>Simulium</u>	2109	93.8	<u>Simulium</u>	3615	90.0
	<u>Calopsectra</u>	72	3.2	<u>Calopsectra</u>	339	8.4
	<u>Chironomidae</u>	31	1.4	<u>Chironomidae</u>	26	0.6
	<u>Hydropsyche</u>	5	0.2	<u>Hydropsyche</u>	18	0.4
	<u>Elmidae</u>	1	-	<u>Physa</u>	18	0.4
	<u>Baetis</u>	29	1.3	TOTAL	4016	
	TOTAL	2247				
5/18/80	NO DATA			<u>Simulium</u>	112	10.2
				<u>Calopsectra</u>	52	4.7
				<u>Hydropsyche</u>	7	0.6
				<u>Baetis</u>	925	84.4
				TOTAL	1096	

Table 3. (continued)

		Site 1	%			Site 3	%
6/10/80	<u>Simulium</u>	230	74.7	<u>Simulium</u>	1032	1.3	
	<u>Calopsectra</u>	53	17.2	<u>Calopsectra</u>	77056	98.3	
	<u>Baetis</u>	22	7.1	<u>Pentaneura</u>	162	0.2	
	<u>Cambarus</u>	3	1.0	<u>Limnophora</u>	5	-	
	<u>TOTAL</u>	308		<u>Baetis</u>	125	0.2	
				<u>TOTAL</u>	78380		

Chapter 5

DISCUSSION

Geological Factors

The major portion of Chevelon Creek originates in the Coconino Sandstone Formation which lies variously exposed along the northern edge of the Mogollon Rim. The Coconino Sandstone, of Permian age, is a result of aeolian deposits. It is noted for its crossbedded appearance and porosity (Koval, 1976; Harrel and Eckel, 1937). This formation is largely a deposit of variably cemented, fine grained wind blown sands exhibiting crossbedding and extensive jointing. The thickness of the Coconino Formation varies from 200 to 900 feet. It is the principle water bearing rock of the region. Recharge of the Coconino Aquifer occurs at higher elevation along the Mogollon Rim. The groundwater follows the northeasterly dip of the formation. Artesian conditions resulting from confinement by overlying impermeable formations are present in the Coconino in most places outside of the recharge area (USDI-USBR 1965).

Following the dip of the Coconino Formation toward the northeast, Chevelon Creek flows through an extensive section of Kaibab Limestone, a marine deposit of late Permian age. The fine-grained nature of this limestone tends to encourage runoff rather than groundwater retention. The Coconino Sandstone is again exposed for the last 15km of the stream's course the overlying Kaibab Formation having been

eroded away. It is this portion of the Coconino Formation which sustains baseflow of lower Chevelon Creek during periods of drought. The region for recharge of this portion of the aquifer is not the upstream exposure of the Mogollon Rim area but rather the region of the Holbrook Dome to the east. The Holbrook Dome is the largest local uplift in the Winslow-Holbrook region. It is located to the southwest of Holbrook, Arizona and directly to the east of the study area. The southern portion of the anticline is much steeper than that of the north, dipping southward as much as 45° . The axis of the anticline extends 45° to the northwest. The Coconino Formation is widely exposed near the crest of the anticline. Toward the crest of the dome a great number of open fissures and crevices occur, an apparent result of the uplifting motion. Individual fissures range in size from a few meters to more than 3 kilometers and extend downward in excess of 100 meters. Water entering these fissures proceeds downward until the local groundwater level is reached. The entire aquifer is maintained above the Supai Formation of late Pennsylvanian Age. This tightly grained formation functions as an aquatard (Koval, 1976) and contains a considerable amount of salt, evaporitic remains of a shallow sea (Harell and Eckel, 1937).

It is my belief that the uplifting process which created the Holbrook Dome fractured not only the Coconino Formation but also the underlying Supai Formation. Exposed evaporites thus dissolve into the existing groundwater and are witnessed on the surface as saline springs and seeps. The saline concentration gradient which is found in Chevelon Creek is a result of the increasing influence of these seeps in a downstream direction. The canyon section which separates

Sites 1 and 3 is characterized by wet-wall seeps as high as 1.5 meters above the water level, evidence of even more productive springs below the water level is noted by bubbling and turbulence. The discharge of this multitude of springs and seeps does show a seasonality in that greatest discharge is always noted following the winter/spring flooding period with decreasing discharge as baseflow is approached. There is then evidence that a portion of flood waters effectively enter the ground water system diluting the saline system. This would explain why there is a lag period between flooding and the recording of the highest saline concentrations toward the end of the baseflow period.

Water Chemistry

The Chevelon Creek system is quite unusual in that it presents two very distinct physical and chemical regimes. The winter/spring flooding period has waters which favorably compare to other regional streams. Ionic concentrations are low, specific conductance is low, temperatures are low and dissolved oxygen concentrations are high. If this condition persisted throughout the entire 12-month period, Chevelon Creek would not be notable. When flooding does subside however, another distinct physico-chemical regime is established. Due to decreased surficial flow, the influence of the saline seeps increases. A sharp seasonal increase in anionic constituents corresponding to the seasonal discharge decline is evident (Figures 4, 5, 11, 12, 13, 14). The concentrated waters persist throughout the dry season until discharge increases in the late fall or early winter. During the concentration period a clear chemical gradient is established with water becoming increasingly concentrated with downstream

progression. Within a relatively short distance (15km) waters change from dilute to concentrations approaching 10 percent sea water. Such predictability of concentration periods and concentration gradient both spatially and temporally is unique to aquatic investigations published to date.

As would be expected, temperature and discharge are closely correlated. The warmest temperatures recorded correspond to the periods of lowest flow and cold temperatures correspond roughly to periods of high flow. The coldest temperatures however, occur independently of discharge. In 1978 the low corresponded to the flood period but in 1979 the low preceded the flood period.

Certain chemical factors are noticeably influenced by the discharge regime. Dissolved oxygen concentrations were higher at both sites with increased discharge and decreased temperature, but the yearly high in 1980 corresponded to the end of the baseflow period when water temperatures were low but productivity was high. Generally dissolved oxygen was in higher concentration at Site 1 (Figure 7). This may be attributed to the higher concentration of autotrophs at this site and the increasing respirational demands of downstream waters, particularly the canyon section. Organic nutrient concentrations (Figures 9, 10) were also affected by discharge. As discharge increased due to increased surficial flow nitrate and phosphate concentrations experienced their yearly peaks. This may be attributable to the fact that, unlike streams of more mesic areas where allochthonous input and subsequent leaching occurs year-round throughout the entire drainage basin, allochthonous material in arid drainage basin collects in the dry stream bed for a significant portion of the year. When surficial

drainage increases this accumulated material is picked up and swept downstream. A characteristic peak of nutrient concentration follows this initial flushing period (Fisher and Minckley, 1978; Fisher and Grimm, 1979; Blinn et al., 1981). As detrital materials collect in the dry stream beds, slow degradation releases nutrients forming in effect a nutrient bank which is only drawn upon when discharge increases.

Silica concentrations were also related to discharge (Figure 10). The lowest silica concentrations were found to occur toward the end of baseflow due to an increasing demand of the diatom community as population concentrations reached their maximum. Silica concentrations remain low due to the diluting effect of flood waters.

pH was also correlated to discharge (Figure 6), with seasonal lows corresponding to periods of most turbulent discharge activity. During the latter part of the baseflow period increased community respiration results in increased CO_2 input. This activity causes a mass shift of the H_2CO_3 , HCO_3^- , $\text{CO}_3^{=}$ constituents to the right resulting in a slightly lower pH.

Unlike many desert streams wherein sulphate is often the major anionic constituent (Johnson, 1968), Chevelon Creek is essentially a sodium chloride system. As the diluting influence of surficial waters declines, the anionic concentration increases. Concentrations of chloride (Figure 13), at Site 3 ranged from $900\text{--}1100\text{mg l}^{-1}$ during baseflow, a figure which was nearly ten times higher than values determined for Site 1 during the same period. Sodium concentrations during a similar period were 685mg l^{-1} at Site 3 compared to 88mg l^{-1} at Site 1 (Dames and Moore, 1977). In comparison, sulfate concentrations (Figure 11) during a similar period ranged from 185mg l^{-1} at

Site 3 to 25mg l^{-1} at Site 1. Concentrations of other major ions were more uniform throughout the 10.5km study section but all showed similar downstream increases in concentration.

During the winter/spring flooding periods specific conductance and major ionic constituent concentrations were considerably reduced and relatively homogeneous throughout the study section. Specific conductance during this dilution period was reduced to less than 0.5mmhos cm^{-1} . While total alkalinity was reduced from summer values of greater than 210mg l^{-1} to less than 20mg l^{-1} .

The evaluation of the chemical oxygen demand (COD) of Chevelon waters was not successful. It was hoped that a careful analysis of organic materials present in the samples would show a variation in the fine particulate organic material (FPOM) and coarse particulate organic material (CPOM) ratios.

Macroinvertebrates

Sampling Techniques

The use of artificial sampling devices is questioned by some limnologists who feel that quantitative analysis must be made by sampling existing natural substrates. The traditional device utilized in these procedures is the Surber sampler (APHA, 1971). For quantitative sampling this device is the most commonly used. The Surber can only be used in flowing water having depths no greater than 18 inches and ideally no more than 12 inches. The reliability of this device is affected by how well the frame is seated upon the substrate, the amount of backwash developed in the collecting net, the care and patience of the individual using the device, the depth to which the

substrate is disturbed, the degree to which the substrate is cleared of colonizing organisms and the drift of organisms from upstream areas (Chutter, 1972).

The precision of the Surber device is questionable. EPA investigators comparing sampling device efficiency on a Southeastern United States trout stream found that the coefficient of variation (standard deviation x 100/mean) ranged from 11 percent to greater than 100 percent (Weber et al., 1973). A similar comparison on a stream in New Zealand produced like results (Allen, 1951). A major failing of the Surber method is that results are not comparable to other studies due to variation in substrate and method. An additional problem created by the use of the Surber in a small stream such as Chevelon is that it is essentially a destructive technique in which the substrate is disturbed and cleaned. Replicate samples, required to reduce variation, can effectively alter an entire study site. Subsequent samples would then be questionable as to whether the sampling technique was determining the resultant community.

It was then for these reasons that the multiple plate sampling device was chosen (Hester, 1962; Fullner, 1971). Advantages of an artificial substrate are that the confounding effects of substrate variations are reduced, a higher level of precision is achieved and quantitatively comparable data is obtained (Weber et al., 1973; Beak et al., 1973). Disadvantages of the use of artificial substrates are that long exposure times are required, anchorage and maintenance are difficult, samplers are visible and vulnerable to vandalism, natural substrate community interactions are not evaluated (Cummins et al., 1964) and the samplers are selective. It must be noted

however, that no existing device currently used in limnological macro-invertebrate inventories is not selective.

The multiple-plate sampling device is recommended by the EPA and the U.S. Geological Survey Water Resources Division (USGS). The amount of time the sampler is incubated is recommended to be 4-6 weeks. Cover and Harrel (1978) found that a four-week colonization period was adequate for maximum mean diversity to be achieved. The same authors also recommended that a minimum of three sampling devices be used at each site.

The sampling devices utilized in this study conform to the specification of the EPA and USGS. These samplers vary from those specified by the American Public Health Association in that there are two spaces separated by four spacers, two spaces separated by three spacers and one space separated by two spacers (Figure 3). It was observed in a study I conducted in Bright Angel Creek, Arizona, that there is a definite preference on the part of certain species for either larger or smaller spaces. Spatial preference was not noted in the Chevelon Creek study perhaps due to the low comparative numbers of taxa which may in effect indicate a decreased spatial competition.

The major advantage of the MPS device is that if it is used by other investigators quantitative data will be comparable. This has not been the case with other sampling devices. For a more detailed discussion of the effectiveness of this sampler see Meier et al., 1979; Cover et al., 1978; Beak et al., 1973; and Mason et al., 1973.

Macroinvertebrates Population Dynamics

Because they are the two major biotic components of the macroinvertebrate community, this discussion will be primarily concerned with the population dynamics of the blackfly Simulium vittatum and the midge Calopsectra sp. A seasonal evaluation of macroinvertebrates in Chevelon Creek showed that there was low species diversity and low community equitability at both sample sites (Table 3). It was found that when mean diversity was lowest at Site 1 (2 October 1979) it was highest at Site 3. Accordingly when mean diversity was highest at Site 1 (10 June 1980) it was lowest at Site 3. Equitability figures showed a similar inverse relationship with the Site 1 low of 27 October 1979 corresponding to the Site 3 high and the Site 1 high of 10 June 1980 corresponding to the Site 3 low. Although this inverse relationship could be coincidental with the relatively small number of data points a coincidence is improbable. If the percent composition of the collective samples is determined (Table 3) and the resultant values plotted for the three most common species, another interesting relationship is discovered (Figure 18). At Site 1 Simulium remained the dominant component throughout the 12-month study period. Calopsectra is common but proportionally subordinate to Simulium. When the proportional representation is plotted for Site 3 a very different pattern is noted. The proportional representation of the two most common components oscillates. When Simulium is most common Calopsectra is rare whereas when Calopsectra is common Simulium is rare. The high numbers of one species appear to exclude the other species. Absolute numbers between the sites were roughly

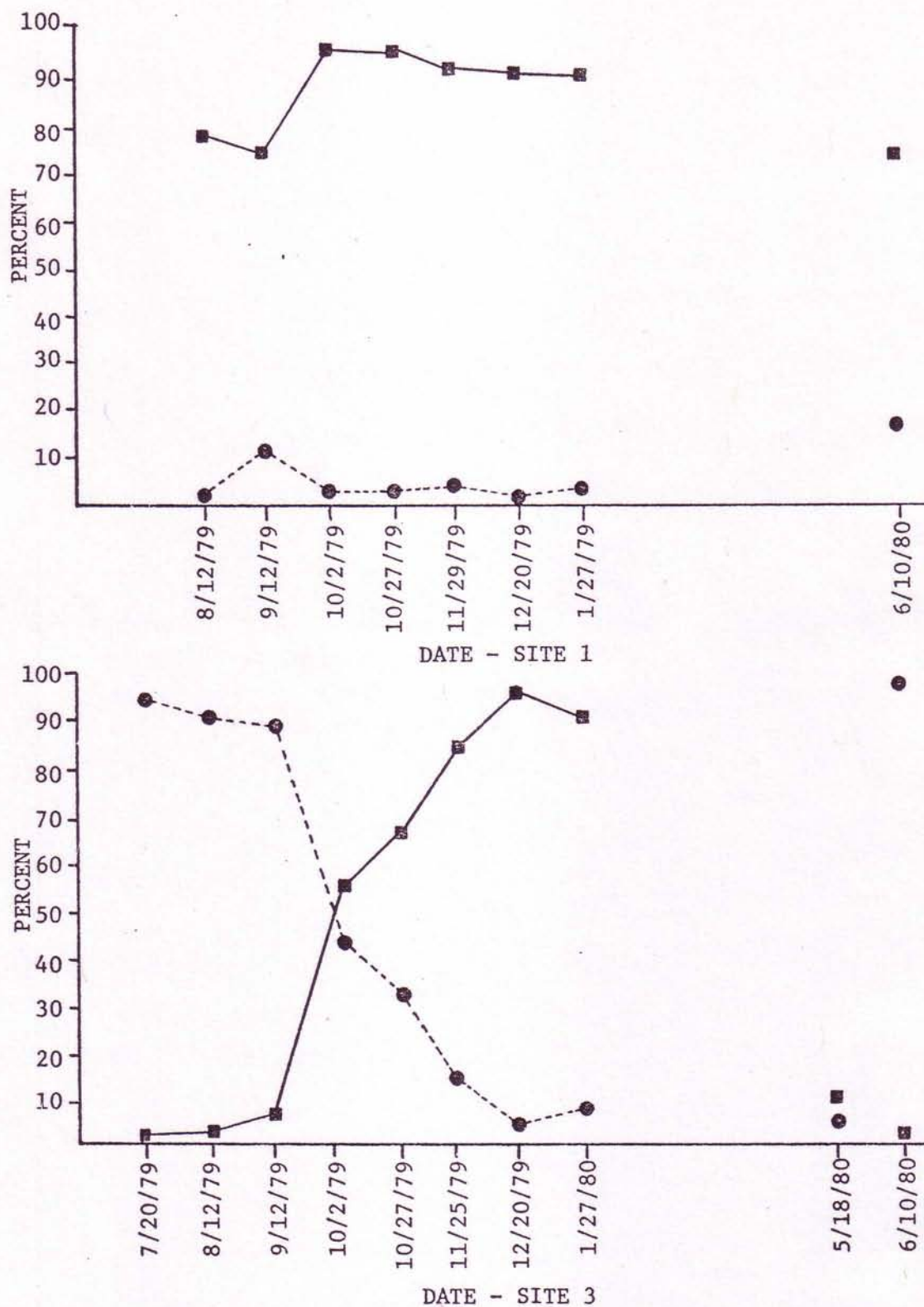


Figure 18. The proportional relationships of two taxa: Simulium indicated by squares, Calopsectra indicated by circles, at Sites 1 and 3, Chevelon Creek, Arizona as collected by multiple plate sampler from 7/20/79 to 6/10/80.

comparable for numerous dates (Table 3). The collections were made using equivalent devices, the depth of each sample was the same, the current velocity over each sampler was roughly equivalent (61.5cm sec^{-1} at Site 1 versus 91.5cm sec^{-1} at Site 3), temperature, dissolved oxygen and pH were similar, major differences in water chemistry were ionic concentration and specific conductance. Maitland (1960) found that the most important physico-chemical factors connected with the distribution of the Simuliidae are stability of substrate, local current velocity and amount of solids present in the water. The current regimes to which samplers were exposed at Sites 1 and 3 were a mean of 61.5cm sec^{-1} and a mean of 91.5cm sec^{-1} respectively. Maitland determined that Simuliidae have a definite current requirement, ranging from $43\text{--}122\text{cm sec}^{-1}$. Other investigators found current requirements of $30\text{--}60\text{cm sec}^{-1}$ (Wu, 1931) and $30\text{--}150\text{cm sec}^{-1}$ (Zahar, 1951). Local current velocities are well within the favorable range so current effects may be of minor importance. In another investigation into the relocation behavior of blackflies, researchers found the species investigated (Prosimulium mixtum and Cnephia dacotema) both preferred specific current velocities but did not increase relocation behavior when exposed to varying depth ($2\text{--}30\text{cm}$) and temperature ($2\text{--}30^{\circ}\text{C}$) (Gersabeck, 1979).

The relative tolerance of the two species to ionic concentration appears to play no role in the population dynamics, since the rise and fall of proportional representation of both groups does not correspond with the seasonal ionic progression.

Macroinvertebrates may be placed in four trophic categories determined by feeding habits and food particle size (Cummins, 1974).

Shredders utilize particles larger than 1mm and exist primarily upon filamentous algae, living vascular plant material or allochthonous material such as leaves. The scraper component utilizes particles less than 1mm which are acquired by scraping them from the substrates. Collectors gather particles from the water which are less than 1mm in size. Predators feed on prey larger than 1mm by piercing or swallowing them. Insect taxa collected from Chevelon Creek by MPS are trophically classified in Table 4.

Food availability is a major factor in the population dynamics of the macroinvertebrate community (Anderson and Cummins, 1979; Gray, 1980). Following ecological disturbance Gray found that the collector component was the most resilient due to increased input of fine particulate organic matter and the facultative trophic shift of predators to a detritivoric habit due to low prey availability. The shredder component lags behind development of the other three trophic groups perhaps due to the absence of filamentous algae and allochthonous material as a result of scour (Gray, 1980).

Both Simulium sp. and Calopsectra sp. are filter feeders, straining bacteria, diatoms and organic debris out of the water. Ehrman and Chouteau (1979) demonstrated that filter feeding blackfly populations were highly sensitive to levels of fine particulate organic material ($FPOM < 10^3 \mu m$). Blackflies were significantly more abundant below a FPOM source than above whereas other benthic macroinvertebrates showed no response. In their study a series of fens (marshes) served as catch basins for the coarse particulate organic matter (CPOM) component. The shredder component of the macroinvertebrate community depends largely upon CPOM as an energy source. With

Table 4. The Habitat and Trophic Relationships of Insect Taxa Collected from June 1979 to June 1980 in Chevelon Creek, Arizona Utilizing Multiple Plate Sampling Devices (After Merritt, 1978)

Taxa	Habitat	Trophic Relationship
Diptera		
<u>Simulium</u> sp.	lotic, erosional	collectors, scrapers
<u>Calopsectra</u> sp.	lotic, erosional	collectors, filterers
<u>Pentaneura</u> sp.	lotic, erosional	predator, engulfer
<u>Limnophora</u> sp.	lotic, erosional	predator of simuliidae
<u>Eulalia</u> sp.	lentic, emergent	
Trichoptera		
<u>Hydropsyche</u> sp.	lotic, erosional	collectors, filterers
Ephemeroptera		
<u>Baetis</u> sp.	lotic, erosional	collectors, scrapers
<u>Baetodes</u> sp.	lotic, erosional	scrapers
Odonata		
<u>Argia</u> sp.	lotic, erosional	predator, engulfer
Megaloptera		
<u>Corydalus</u> sp.	lotic, erosional, depositional	predator, engulfer
Coleoptera		
<u>Microcylloepus</u> sp.	lotic, erosional	unknown

Table 4. (continued)

Taxa	Habitat	Trophic Relationship
Lepidoptera		
<u>Parargyractis</u> sp.	lotic, erosional	scraper

elimination of CPOM by the catchment area the shredder component was also eliminated. With reduced spatial competition the FPOM feeders increased in number. Vannote (1980) has demonstrated that in the majority of lotic systems the CPOM/FPOM ratio decreases in a downstream direction. It is possible that the deep waters (13-18m) of the canyon section which separates the two study sites act as a CPOM sink. The shredder component is in low proportion at both study sites, representing at no time more than two percent of the total community perhaps due to the limited riparian vegetation. CPOM that is available due to leaf drop may collect in the canyon area and slowly degrade to FPOM which is then available for the collectors below. Further investigation is necessary to determine the role of CPOM and FPOM in population dynamics in this system.

Another factor which may be regulating population dynamics is the relative abundance of case building materials for Calopsectra. Calopsectra sp. is a tube dwelling collector which constructs a case of fine sand or silt grains. Hydra-like projections on one end of the case serve as support for the food collecting net which the animal spins. If tube building materials were absent the animals ability to acquire food would be severely limited to the detriment of the population (Figure 19).

Case building materials are in low supply at Site 1 due to the scouring action of spate on the bedrock. Throughout the entire year the bedrock substrate is smooth and clean of most, if not all, case building materials. This may explain the predominance of the other collector component throughout the year. The population peak of Calopsectra corresponds to a period when receding flood waters

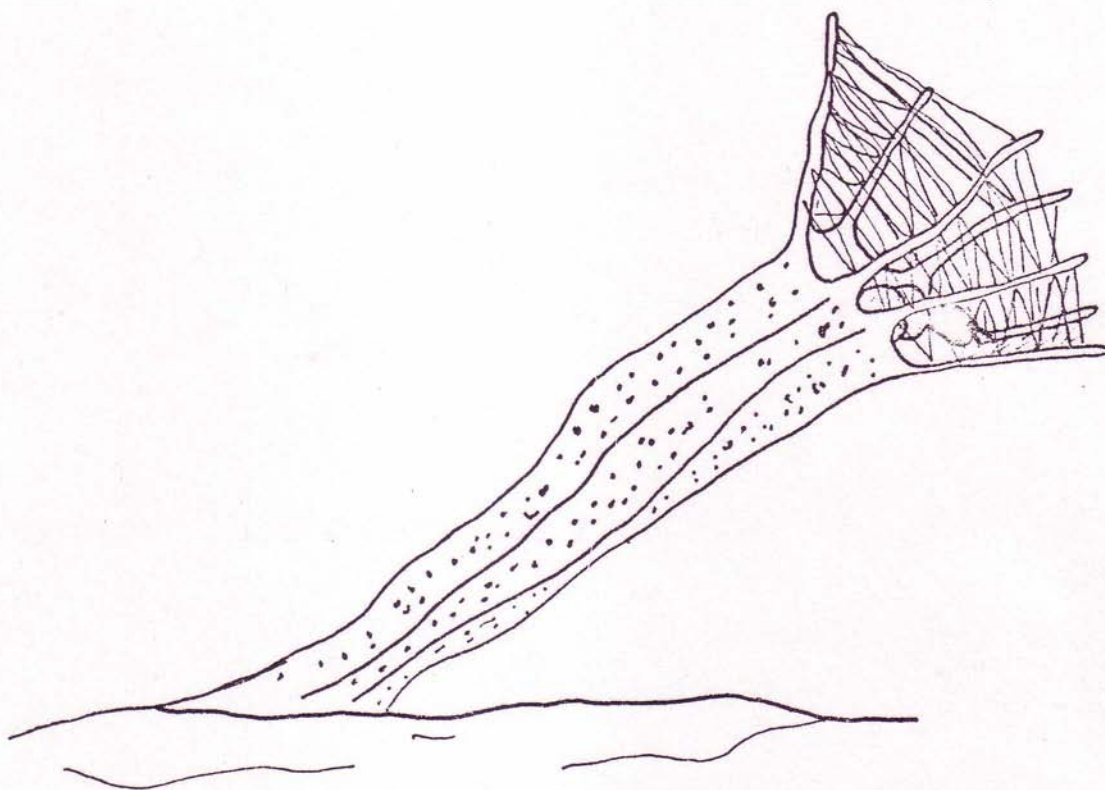


Figure 19. Illustration of Calopsectra sp. as observed in Chevelon Creek, Arizona. Note the granular case composition and the food gathering net.

are depositing case-building materials eroded from the canyon section. As case material becomes available the population peaks to the exclusion of the blackflies. During the winter/spring scour period the case material is unavailable and the midge population is low.

A third factor which may be affecting collector population dynamics is a seasonal progression of diatom blooms. The increase in population of Simulium vittatum at Site 3 in the fall corresponds to a shift of diatom populations. Over a period of two years it was observed that a well-defined sequential succession of phytoplankton occurred (Figures 20, 21). Thalassiosira pseudonanna first appeared during early May immediately following the reduction in discharge when specific conductance was $1.2 \text{ mmhos cm}^{-1}$. This species was quickly replaced by Chaetoceros muelleri when specific conductance of the water was $2.0 \text{ mmhos cm}^{-1}$. Chaetoceros muelleri was in turn replaced by Rhizosolenia minima at the beginning of September. Each successive diatom species commonly attained greater cell densities than the preceding species with R. minima reaching a density of $8.9 \times 10^3 \text{ cell l}^{-1}$. Rhizosolenia minima remained the dominant until temperatures were reduced ($<10^\circ\text{C}$) or winter flooding occurred. This same temporal sequence was qualitatively observed for four years and quantitatively analyzed over a two-year period. (Blinn et al., in press).

The operating mechanisms involved in this successional pattern are complex. Factors related to the succession are specific conductance, light intensity, divisional rates and residence time in the canyon section. It is interesting to note that the mean cell diameter of Thalassiosira pseudonanna ($\bar{x} = 4.5 \mu\text{m}$) is significantly smaller than

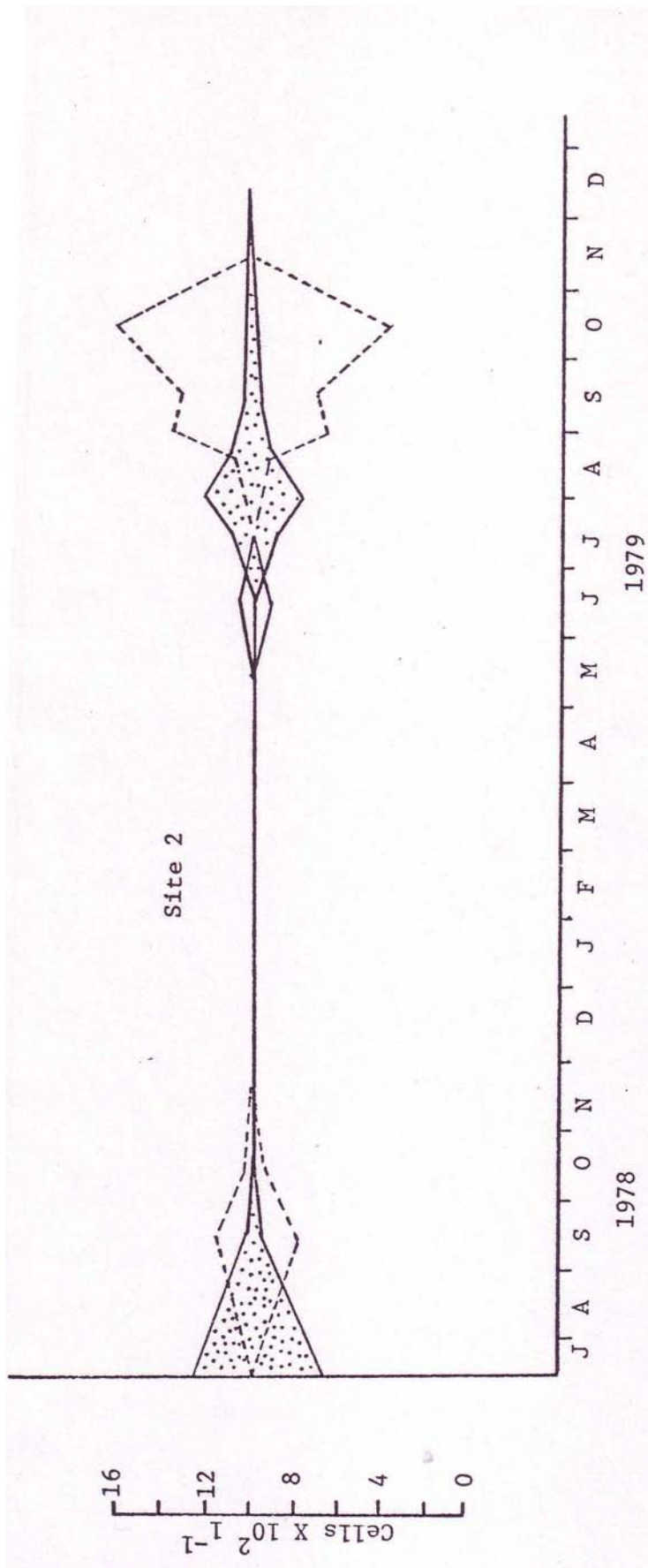


Figure 20. Seasonal population dynamics of three diatom species at Site 2, Chevelon Creek, Arizona. *Chaetoceros muelleri*, stippled; *Rhizosolenia minima*, dashed open line; *Thalassiosira pseudonanna*, solid open line.

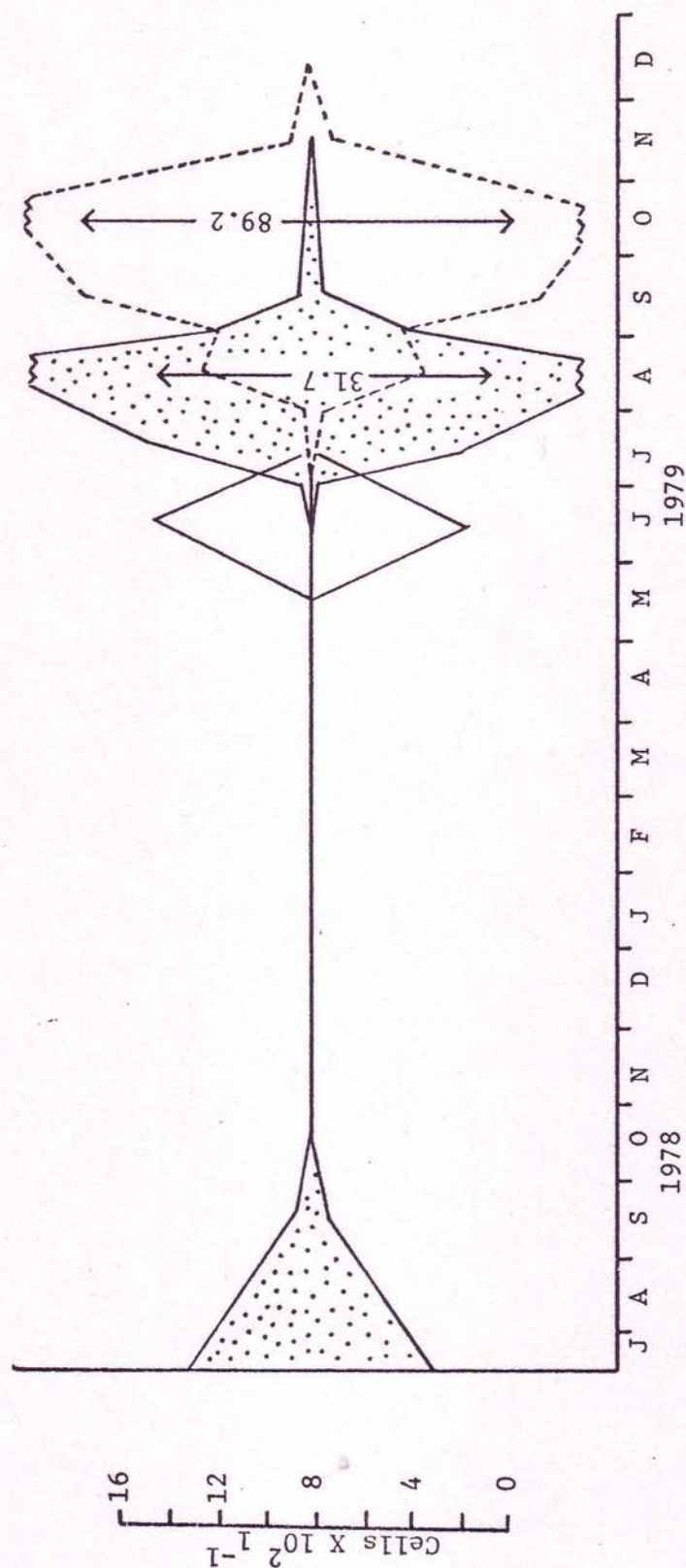


Figure 21. Seasonal population dynamics of three diatom species at Site 3, Chevelon Creek, Arizona. *Chaetoceros muelleri*, stippled; *Rhizosolenia minima*, dashed open line; *Thalassiosira pseudonana*, solid open line.

Chaetoceros muelleri (\bar{x} = 7-12um) which in turn smaller than Rhizosolenia minima (\bar{x} = apical valve diameter 4-7um, perivalvar distance 15-40um). The temporal oscillations of the macroinvertebrate compound at Site 3 may be due to the relative size of available phytoplankton and the ability or inability to collect food of that size. Calopsectra sp. may be more efficient at collecting small diatoms (T. pseudonanna) whereas Simulium sp. is more effective in collecting larger ones (R. minima). The maintenance of proportional dominance at Site 1 by Simulium sp. may also be food size affected. The predominant diatom at this location throughout the year is the centric Stephanodiscus invisitatus (\bar{x} = 8-10um). In his investigation concerning the recolonization and trophic habits of invertebrates in Sycamore Creek, Arizona Gray (1980) found that the tube building, net spinning chironomid component such as Calopsectra sp. subsists almost exclusively upon diatoms. Gut analysis indicated diatoms form approximately 89 percent of the total diet. Gut analysis of Simulium sp., however, indicates a facultative shift between collecting and scraping. Diet components were 60 percent diatoms, 38 percent detritus and two percent filamentous algae. Perhaps the more refined ability of Calopsectra sp. to collect diatoms provides a distinct advantage as phytoplankton becomes more common in the water column. If this is indeed the case then there is a clear interaction within the Chevelon system between light intensity, specific conductance, phytoplankton residence time and the population dynamics of the macroinvertebrate community. In a study conducted on several English streams Hansford (1978) found that blackfly abundance was closely correlated with phytoplankton concentrations. Population peaks of Simuliidae were

predictable by determining Chlorophyll a concentrations.

Statistical Evaluation

Diversity indices during the entire study were exceedingly low at both sampling sites. Diversity indices are a statistical tool for measuring the quality of an environment and the effect of environmental stress upon a community. The use and significance of diversity indices is based upon the observed phenomenon that undisturbed, organically enriched and chemically stable communities have relatively large numbers of species with the absolute numbers of no single species overwhelming any other. Many forms of environmental stress tend to affect the biological community to the disadvantage of one component or to the advantage of another. The apparent result is the reduction or enhancement of species numbers in relation to the hypothetical stable community. (There are naturally occurring extreme environments in which the diversity of the macroinvertebrate community may be low, examples would be the profundal fauna of a deep lake or the blackfly dominated communities of torrential streams (Weber et al., 1973). There are essentially two factors affecting species diversity, the absolute number of species present and the distribution or proportion of individuals present within the species. In this thesis mean diversity is that value derived in the Shannon-Weaver function as modified by Lloyd et al. (1968).

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

Where $C = 3.321928$, a function which converts base 10 to base two;

N = the total number of individuals present in the community;

n_i = the total number of individuals in the i^{th} species. Mean

diversity is thus affected by both community richness and by species proportion, mean diversity numbers may range from zero to 3.321928 log N. Recalling that two components affect the diversity function an effort has been made to evaluate that portion due to the inequitable distribution of individuals among species. The \bar{d} as calculated is compared to a hypothetical \bar{d} based upon a population in which all species are equally abundant. It has been observed that in nature equitability of species is unusual if not unlikely. The term "equitability" was proposed by Lloyd and Ghelardi (1964) which compared \bar{d} with a maximum \bar{d} based upon the distribution within MacArthur's broken-stick model (MacArthur, 1957). Lloyd and Ghelardi developed a table which compared the number of species (s) within a given sample to the anticipated number of species (s') as conforms to MacArthur's model (Table 4). The proposed measure of equitability is:

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

Where s = the number of taxa present in the sample, and s' = the value as determined from the table. To determine an e value for a given \bar{d} the higher tabular \bar{d} as listed in the table is divided into the corresponding whole number and the resulting quotient multiplied by the \bar{d} , this number is then divided by the number of taxa present within the sample. Equitability ranges from 0 to 1 in the vast majority of cases.

It has been noted that in unpolluted waters, \bar{d} is generally between 3.0 and 4.0, whereas in polluted waters \bar{d} is generally less than 1.0. Equitability provides a much more discriminating evaluation of water degradation. U.S. Environmental Protection Agency findings

Table 5. The Diversity of Species, \bar{d} , Characteristic of MacArthur's Model for Various Numbers of Hypothetical Species, s' (Lloyd, 1964).

s'	\bar{d}	s'	\bar{d}
1	0.0000	47	4.9787
2	0.8113	48	5.0084
3	1.2997	49	5.0375
4	1.6556	50	5.0661
5	1.9374	51	5.0941
6	2.1712	52	5.1215
7	2.3714	53	5.1485
8	2.5465	54	5.1749
9	2.7022	55	5.2009
10	2.8425	56	5.2264
11	2.9701	57	5.2515
12	3.0872	58	5.2761
13	3.1954	59	5.3004
14	3.2960	60	5.3242
15	3.3899	61	5.3476
16	3.4780	62	5.3707
17	3.5611	63	5.3934
18	3.6395	64	5.4157
19	3.7139	65	5.4378
20	3.7846	66	5.4594
21	3.8520	67	5.4808
22	3.9163	68	5.5018
23	3.9779	69	5.5226
24	4.0869	70	5.5430
25	4.0937	71	5.5632
26	4.1482	72	5.5830
27	4.2008	73	5.6027
28	4.2515	74	5.6220
29	4.3004	75	5.6411
30	4.3478	76	5.6599
31	4.3936	77	5.6785
32	4.4381	78	5.6969
33	4.4812	79	5.7150
34	4.5230	80	5.7329
35	4.5637	81	5.7506
36	4.6032	82	5.7681
37	4.6417	83	5.7853
38	4.6792	84	5.8024
39	4.7157	85	5.8192
40	4.7513	86	5.8359
41	4.7861	87	5.8524
42	4.8200	88	5.8687
43	4.8532	89	5.8848
44	4.8856	90	5.9007
45	4.9173	91	5.9164
46	4.9483	92	5.9320

Table 5. (continued)

s'	\bar{d}	s'	\bar{d}
93	5.9474	180	6.8918
94	5.9627	182	6.9076
95	5.9778	184	6.9233
96	5.9927	186	6.9388
97	6.0075	188	6.9541
98	6.0221	190	6.9693
99	6.0366	192	6.9843
100	6.0510	194	6.9992
102	6.0792	196	7.0139
104	6.1069	198	7.0284
106	6.1341	200	7.0429
108	6.1608	205	7.0783
110	6.1870	210	7.1128
112	6.2128	215	7.1466
114	6.2380	220	7.1796
116	6.2629	225	7.2118
118	6.2873	230	7.2434
120	6.3113	235	7.2743
122	6.3350	240	7.3045
124	6.3582	245	7.3341
126	6.3811	250	7.3631
128	6.4036	255	7.3915
130	6.4258	260	7.4194
132	6.4476	265	7.4468
134	6.4691	270	7.4736
136	6.4903	275	7.5000
138	6.5112	280	7.5259
140	6.5318	285	7.5513
142	6.5521	290	7.5763
144	6.5721	295	7.6008
146	6.5919	300	7.6250
148	6.6114	310	7.6721
150	6.6306	320	7.7177
152	6.6495	330	7.7620
154	6.6683	340	7.8049
156	6.6867	350	7.8465
158	6.7050	360	7.8870
160	6.7230	370	7.9264
162	6.7408	380	7.9648
164	6.7584	390	8.0022
166	6.7757	400	8.0386
168	6.7929	410	8.0741
170	6.8099	420	8.1087
172	6.8266	430	8.1426
174	6.8432	440	8.1757
176	6.8596	450	8.2080
178	6.8758	460	8.2396

Table 5. (continued)

s'	\bar{d}
470	8.2706
480	8.3009
490	8.3305
500	8.3596
550	8.4968
600	8.6220
650	8.7373
700	8.8440
750	8.9434
800	9.0363
850	9.1236
900	9.2060
950	9.2839
1000	9.3578

show that non-polluted waters never demonstrate equitability values of less than 0.5 whereas even slight levels of eutrophication or other forms of environmental stress reduce equitability to below 0.5 and generally range from 0.0 to 0.3 (Weber et al., 1973).

The mean diversity of a community is often taken to indicate the relative stress a community is subjected to (Weber, 1973). It has been stated that as diversity decreases the stability of the community also decreases (Colinvaux, 1973). The Chevelon Creek invertebrate community is indeed subject to a great deal of environmental stress. Flow regimes range from 1 CFS to 23000 CFS. Salinity increases temporally and spatially. Macon (1975) in an evaluation of the mixohaline waters of the Tees Estuary of Great Britain found that numbers of taxa declined as salinity increased from a freshwater base and likewise declined with dilution from a sea water base. Freshwater organisms maintain a physiological solution more concentrate than the surrounding medium. Minor fluctuations in the salinity of the medium have little effect upon viability. When external concentrations exceed the physiological concentration dehydration occurs and death is rapid (Beadle, 1957). Chevelon residents must then be tolerant of salinity fluctuations, a quality which few freshwater invertebrates possess. Chevelon Creek presents itself as an island available for colonization but one which is geographically isolated and one whose environmental demands are severe. The result is a low mean diversity and wild oscillations in population numbers. I feel however, that rather than indicating instability these fluctuations lend themselves to the overall stability of the community. Residents are super-opportunists ready to numerically capitalize upon fluctuating conditions. The

physiological lability of these invertebrates lends itself to the stability of this impoverished community. The tremendous recolonization potential of certain components is demonstrated by the Calopsectra genus during the 18 May to 10 June 1980 period wherein, in a period of 23 days the population increased from 130 individuals per m^2 of sampling surface to nearly 200,000 individuals per m^2 of sampling surface a Δ percent of 153,700! Gray (1980) has witnessed chironomid generation times as short as 9 days from egg to adult. It is interesting to note that another common genera in Chevelon Creek also has an abbreviated generation time. Baetis quilleri of Sycamore Creek has been shown to have a generation time of 9-11 days. The three most common genera are multivoltine and exhibit no dormant period. These tremendous and continuous reproductive capacities enhance the viability and persistence of these genera within a highly stressed system.

Chapter 6

SUMMARY

Chevelon Creek presents an unusual if not a unique lotic system. Two distinct physical-chemical periods occur on a seasonal basis. Both the autotrophic and heterotrophic communities respond in number and composition to these seasonal fluctuations. Diversity of taxa in the macroinvertebrate community is low and equitability values are correspondingly low. Two dipteran genera represent the major invertebrate component. There is apparent competitive exclusion (spatial/trophic) between these two species. At no times were equivalent proportions sustained for more than one month. At the upstream Site 1, Simulium vittatum maintained a proportional dominance over Calopsectra sp. for the entire 12 months of the study. Proportional dominance at the downstream Site 3 oscillated predictably (Figure 18). Factors affecting this oscillation may variously be FPOM availability, variation in food size and/or availability of case building materials for the tube dwelling Calopsectra sp. Further investigation is necessary to determine which of these factors is having the most profound effect. Chevelon Creek may be typical of many desert streams where steep-walled canyons restrict insolation impoverishing the autotrophic community (Blinn et al., 1981). The trophic habit of FPOM collector predominated the sample community (Table 5). The shredder component was notably absent although the physical nature of the multiple plate sampling device is such that vegetative material is commonly entrapped between the plates. The sample

community appears to be typical of desert streams (Gray, 1980). Numerically the collector component maintains dominance due in this case to osmotic tolerance, rapid generation time and strong colonizing ability. In his study of Sycamore Creek, Gray found a similar pre-dominance. Representatives of other trophic habit lagged behind the colonization of collectors but if conditions stabilized the number of representatives of slower developing taxa increased. Within the Chevelon system, stability is not achieved due to the meteorological, physical and chemical conditions. Macroinvertebrates of the lotic erosional habit remain in a constant state of perturbation which has paradoxically become the communities' constant state.

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Appendix Table 1. Physico-Chemical Data for Chevelon Creek, Arizona 15 September 1978 to 12 June 1980.
Site 1.*

Dates	NO ₃	PO ₄	Si	O ₂	pH	HCO ₃	SO ₄	CL	Sp Cond	T
15 Sept 78	0.03	0.09	4.75	9.0	8.1	158	120	125	0.810	22
03 Oct 78	0.02	0.04	5.25	8.2	7.6	138	145	137	0.910	17
16 Oct 78	0.01	0.05	1.2	9.3	8.1	154	138	105	0.830	15
20 Nov 78	0.02	0.03	3.6	9.3	6.7	37	5	25	0.097	7
26 Dec 78	0.02	0.08	4.4	10.8	6.4	26	8	8	0.066	1
09 Feb 79	0.03	0.12	4.9	11.1	6.9	38	11	15	0.100	2
19 Mar 79	0.03	0.20	3.0	10.4	5.6	23	7	8	0.056	6
22 Apr 79	0.06	0.01	3.8	7.2	5.8	17	4	13	0.032	11
22 May 79	0.02	0.01	5.0	7.0	7.9	87	35	35	0.340	24
16 June 79	0.02	0.11	5.5	6.7	7.8	141	112	90	0.780	22
30 June 79	0.02	0.05	4.7	7.5	8.0	154	125	95	0.800	24
12 July 79	0.02	0.05	5.0	6.6	8.0	142	130	125	0.840	25
20 July 79	0.01	0.05	5.8	6.7	7.8	142	135	105	0.800	23
03 Aug 79	0.02	0.07	6.5	6.2	-	-	-	-	0.780	24

Appendix Table 1. (continued)

Dates	NO ₃	PO ₄	Si	O ₂	pH	HCO ₃	SO ₄	CL	Sp Cond	T
18 Aug 79	0.02	0.04	4.6	7.2	7.3	140	126	105	0.820	22
12 Sept 79	0.01	0.01	6.5	7.3	7.4	144	150	127	0.820	20
27 Oct 79	0.01	0.05	6.0	8.5	8.0	140	118	115	0.870	11
25 Nov 79	0.04	0.04	5.3	10.5	7.4	128	-	-	0.700	4
20 Dec 79	0.04	0.02	6.7	11/4	7.3	136	160	115	0.760	5
27 Jan 80	0.06	0.05	4.0	10.2	7.4	101	65	65	0.500	5
01 Mar 80	0.04	0.25	5.9	9.7	6.5	20	11	14	0.060	8
04 Apr 80	0.03	0.09	3.2	8.7	6.3	26	8	38	0.053	10
18 May 80	0.03	0.05	4.1	7.6	6.7	32	7	5	0.008	17
29 May 80	-	-	-	-	-	-	50	35	0.320	18
12 June 80	0.02	0.04	5.7	7.6	8.1	116	145	92.5	0.690	26
25 June 80	-	-	-	-	8.2	126	-	-	0.830	24

* Temperature recorded in degrees Celsius, specific conductance in millimhos cm⁻¹, all others in mg l⁻¹ (ppm.)

Appendix Table 2. Physico-Chemical Data for Chevelon Creek, Arizona 15 September 1978 to 12 June 1980.
Site 3.*

Dates	NO ₃	PO ₄	Si	O ₂	pH	HCO ₃	SO ₄	CL	Sp Cond	T
15 Sept 78	0.03	0.13	6.5	5.9	8.1	201	145	1127	3.400	19
03 Oct 78	0.05	0.05	5.8	8.5	7.8	198	185	1100	3.650	19
16 Oct 78	0.01	0.13	7.0	6.7	8.1	202	155	1050	3.440	13
20 Nov 78	0.01	0.05	4.1	9.2	7.0	52	25	99	0.365	8
26 Dec 78	0.12	0.17	5.5	10.0	6.3	30	24	90	0.420	1
09 Feb 79	0.03	0.32	5.0	10.3	7.3	55	32	175	0.550	2
19 Mar 79	0.03	0.14	2.4	9.2	5.5	26	6	15	0.109	6
22 Apr 79	0.01	0.10	3.8	6.7	5.6	18	5	20	0.062	11
22 May 79	0.08	0.01	5.7	6.2	7.2	99	80	375	1.480	20
16 June 79	0.01	0.05	6.5	6.2	8.1	186	155	800	3.080	23
30 June 79	0.03	0.12	6.0	5.3	7.8	214	145	915	3.550	24
12 July 79	0.02	0.08	5.5	6.5	8.2	214	185	990	3.800	26
20 July 79	0.02	0.05	6.1	6.2	8.2	204	150	945	3.550	25
03 Aug 79	0.02	0.06	4.3	7.2	8.2	-	-	-	3.800	25
18 Aug 79	0.01	0.07	5.5	5.9	7.9	204	135	920	3.390	22

Appendix Table 2. (continued)

Dates	NO ₃	PO ₄	Si	O ₂	pH	HCO ₃	SO ₄	CL	Sp Cond	T
12 Sept 79	0.02	0.02	5.5	6.9	7.9	198	175	1060	3.510	22
27 Oct 79	0.01	0.12	7.0	7.5	8.0	206	197	1088	3.750	14
25 Nov 79	0.03	0.14	7.3	10.0	7.9	198	178	1038	3.520	5
20 Dec 79	0.02	0.04	6.0	10.2	7.6	202	125	1095	3.450	5
27 Jan 80	0.08	0.16	3.5	9.8	7.5	98	65	370	1.410	5
19 Mar 80	0.04	0.35	5.9	9.3	6.9	21	12	290	0.090	8
04 Apr 80	0.03	0.12	4.1	8.7	6.2	30	8	37	0.164	10
27 Apr 80	0.02	0.05	3.8	8.3	6.4	22	12	30	0.150	12
18 May 80	0.02	0.05	4.8	7.4	6.8	50	28	130	0.550	16
29 May 80	-	-	-	-	-	-	50	383	1.500	20
12 June 80	0.02	0.05	6.3	8.4	8.1	149	160	768	2.900	23
25 June 80	-	-	-	-	8.2	202	-	-	3.400	23

* Temperature recorded in degrees Celsius, specific conductance in millimhos cm⁻¹, all others in mg l⁻¹.

Appendix Table 3. Comparison of Light Energy Striking Surface Waters of Chevelon Creek in Shaded and Lighted Portions of the Canyon Section and Open Stream Channel (Site 3) with Corresponding Net Primary production. Light Values Equal the Mean of at Least 10 Measurements Taken Between 1000 and 1400 h. during each day.

DATE	CANYON SECTION				SITE 3 (DIRECT LIGHT)	
	INDIRECT LIGHT (SHADED)	NET PRIMARY PRODUCTION	DIRECT LIGHT	NET PRIMARY PRODUCTION	DIRECT LIGHT	NET PRIMARY PRODUCTION
5/18/80	750 ft-c 0.049 g cal/cm ² min		7100 ft-c 0.462 g cal/cm ² min		7350 ft-c 0.478 g cal/cm ² min	
5/29/80	720 ft-c 0.047 g cal/cm ² min		6900 ft-c 0.449 g cal/cm ² min	7.0 mgC/m ³ /hr	7200 ft-c 0.463 g cal/cm ² min	13.4 mgC/m ³ /hr
6/12/80	735 ft-c 0.048 g cal/cm ² min	2.2 mgC/m ³ /hr	7150 ft-c 0.464 g cal/cm ² min	2.8 mgC/m ³ /hr	7500 ft-c 0.488 g cal/cm ² min	8.2 mgC/m ³ /hr