THE EFFECTS OF A DEEP-STORAGE RESERVOIR ON THE BENTHIC MACROINVERTEBRATE COMMUNITY OF THE GUADALUPE RIVER, TEXAS

THESIS

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TABLE OF CONTENTS

Chapter

I. INTRODUCTION 1

II. DESCRIPTION OF STUDY AREA. 4

General Description. 4
Description of Stations. 6

III. METHODS AND MATERIALS. 11

Sampling Procedures. 11
Biological Methods 11
Physicochemical Methods. 12
Statistical Methods. 13

IV. RESULTS AND DISCUSSION 22

Meteorological Conditions. 22
Physicochemical. 22
Biological 30
Statistical. 44

V. SUMMARY. 67

APPENDIX 69

I. Computer Program for Calculating $\bar{d}$, $\bar{d}$max, $\bar{d}$min, $\bar{r}$, and $\bar{f}$ 70

BIBLIOGRAPHY 72

LIST OF TABLES

Table Page

1. Monthly Rainfall in Centimeters at Canyon Dam, Texas 23
2. Mean Air Temperature, Mean Wind Velocity, and Mean Solar Illumination at Each of the Five Collecting Stations. 24
3. Mean Monthly Flow at Stations 1 and 4 in Cubic Meters per Minute 25
4. Means, Ranges, and Standard Deviations for Physicochemical Parameters at Each of the Five Collecting Stations. 27
5. Taxa Collected During the Study Period at Each of the Five Collecting Stations on the Guadalupe River, Texas. 31
6. Values of $\bar{d}$ for Accumulated Samples at Each of the Five Collecting Stations. 50
7. Values of $\bar{d}$, $\bar{r}$, Number of Individuals per Square Meter (n), and Number of Taxa (n_i) for Each Collecting Period at Each of the Five Collecting Stations. 56

LIST OF FIGURES

Figure Page

1. Map of the Study Area Showing the Five Collecting Stations 7

2. Mean Number of Taxa per Collection and the Range in Numbers of Taxa per Collection at Each of the Five Collecting Stations 42

3. Mean Density of Organisms per Collection and the Range in Density per Collection at Each of the Five Collecting Stations 43

4. Ephemeroptera: Number of Individuals per Square Meter and Number of Taxa for Each Collecting Period at Each of the Five Collecting Stations. 45

5. Trichoptera: Number of Individuals per Square Meter and Number of Taxa for Each Collecting Period at Each of the Five Collecting Stations 46

6. Coleoptera: Number of Individuals per Square Meter and Number of Taxa for Each Collecting Period at Each of the Five Collecting Stations 47

7. Diptera: Number of Individuals per Square Meter and Number of Taxa for Each Collecting Period at Each of the Five Collecting Stations 48

8. Values of $\bar{d}$ and $\bar{r}$ at Station 1 for Each Month of the Collecting Period. 51

9. Values of $\bar{d}$ and $\bar{r}$ at Station 4 for Each Month of the Collecting Period. 52

10. Values of $\bar{d}$ and $\bar{r}$ at Station 5 for Each Month of the Collecting Period. 53

11. Values of $\bar{d}$ and $\bar{r}$ at Station 2 for Each Month of the Collecting Period. 54

12. Values of $\bar{d}$ and $\bar{r}$ at Station 3 for Each Month of the Collecting Period. 55

13. Mean and Range of $\bar{d}$ and $\bar{r}$ at Each of the Five Collecting Stations. 62

CHAPTER I

INTRODUCTION

One of the most common approaches to the study of natural communities emphasizes community structure. This involves the analysis of the community as a complex assemblage of individuals belonging to different species, each with its own definite ecological requirements (Wilhm and Dorris, 1966). Some approaches to the analysis of community structure have been to determine the frequency with which species occur within a given area (Gleason, 1922; Cain, 1932), to measure the spatial distribution of species (Bartsch, 1948; Bartsch and Ingram, 1959), and species or community diversity indices (Fisher et al., 1943; Williams, 1944, 1953; Preston, 1948; Margalef, 1951, 1956; Patten, 1962; Menhinick, 1964; Pielou, 1966; Wilhm and Dorris, 1966, 1967, 1968; Wilhm, 1967, 1968a, 1968b, 1969, and 1970). Species or community diversity indices have been found to be among the simplest and most promising methods for the analysis of community structure as they permit the summarization of large amounts of information about numbers and kinds of organisms in a single numerical value (Patten, 1962) thus obviating cumbersome lists of species. Benthic macroinvertebrates make ideal subjects for such studies due to their habitat preference and low motility (Wilhm and Dorris, 1966).

The effects of artificial impoundments on streams are being increasingly investigated as more interest is generated in water quality criteria (Symons et al., 1965). Butcher (1955) and Wilhm and Dorris (1967, 1968) recommended that water quality be defined using biological rather than physicochemical standards. The presence or absence of certain benthic macroinvertebrates was used by some early investigators to monitor water quality (Kolkwitz and Marsson, 1909; Gaufin and Tarzwell, 1952, 1956; Tarzwell and Gaufin, 1953; Surber, 1953; Bartsch and Ingram, 1959). Unfortunately, closely related species may have widely divergent habits and tolerances (Thut, 1969) which may lead to confusion. In addition, the composition of communities in natural streams has been found to vary with the size of the stream, the biome through which the stream flows, and the season in which the stream is sampled (Minshall, 1969). Spence and Hynes (1971a, 1971b) have investigated the effects of an artificial impoundment on the benthic macroinvertebrates and certain fishes in a Canadian stream; however, no attempt was made to measure the diversity of these communities. Thus the effect of an impoundment on the species diversity of a community is unknown.

The object of this study was to measure the effects of Canyon Reservoir, a deep-storage impoundment, on the benthic macroinvertebrate communities of the Guadalupe River by measuring the changes in species diversity in the communities above, below, and in the reservoir for one year. With a study of this nature it was possible (1) to establish a basis for comparison to similar studies of these communities at a later date and (2) to establish a frame of reference within which one can compare other similar communities.

CHAPTER II

DESCRIPTION OF STUDY AREA

General Description

The Guadalupe River originates with the confluence of its north and south forks, near the town of Hunt in south-central Kerr County, at an altitude of about 700 m. From this point the river flows east through the Edwards Plateau region of central Texas for some 200 km. Near New Braunfels, in Comal County, the Guadalupe River flows out onto the Blackland Prairie region of Texas and, from this point, follows a generally southeastern course to the Gulf of Mexico. For the distance it flows through the Edwards Plateau, the Guadalupe River is swift-flowing and shallow with numerous riffles. Only one major tributary flows into the Guadalupe in this stretch, Johnson Creek near Ingram in Kerr County, and springs and ground seepage make up a major portion of the flow during periods of low rainfall (Rawson, 1968).

The Edwards Plateau was classified as a distinct biotic province by Blair (1950) who referred to it as the Balconian Province. The most characteristic plant association on the dry slopes in this province is a scrubby growth of <u>Juniperus</u> <u>mexicanus</u> (Mexican Juniper), <u>Quercus</u> <u>texana</u> (Texas

Oak), and Quercus virginiana (Live Oak). Along the banks of the Guadalupe River one finds Taxodium distichum (Bald Cypress), Platanus occidentalis (Sycamore), Populus deltoides (Cottonwood), and Salix sp. (Willow).

The geology of the Guadalupe River has been described by Alexander, et al. (1964). The upper reaches of the river flow through Edwards and Glen Rose limestone formations (Cretaceous). Underlying the lower end of Canyon Reservoir and extending for a few kilometers downstream is the Leona formation (Pleistocene) of sand, clays, silt, and gravel. For the rest of its course to New Braunfels the river flows through more Edwards limestone.

The only major impoundment on the Edwards Plateau stretch of the Guadalupe River is Canyon Reservoir, a joint project of the U.S. Army Corps of Engineers and the Guadalupe-Blanco River Authority (G-BRA), designed for flood control, water conservation, and recreation. The dam is located in Comal County about 200 km below the confluence of the north and south forks of the Guadalupe River. The river bed has an altitude of about 230 m at this point, the top of the conservation pool has an altitude of about 280 m, and the designed maximum level of the flood pool is about 290 m above mean sea level. Depths of up to 61 m were measured in the reservoir during the study period.

The conservation pool of the reservoir has a designed area of 3,335 ha, a shore line of about 130 km, a length of about 40 km flood pool has a designed area of 5,216 ha and a total volume of about 9.14 X 10^8 m^3. The total drainage basin emptying into the reservoir has an area of about 4,000 km^2 and includes only one large metropolitan area, Kerrville, with a population of about 14,000.

After the Guadalupe River flows onto the Blackland Prairie it changes from a swift, shallow stream to a slower, deeper stream with few riffles. The stream bed follows a meandering pattern within broad, flat river valleys (Kuehne, 1955). This pattern of flow is maintained for the next 470 km until the river empties into San Antonio Bay near Victoria, Texas.

Descriptions of Stations

The five stations sampled in this study were all located in Comal County in the Edwards Plateau region. Stations 2 and 3 were located in Canyon Reservoir, Station 1 was located in the Guadalupe River above Canyon Reservoir, and Stations 4 and 5 were located in the Guadalupe River below the reservoir (Figure 1).

Samples at Stations 2 and 3 were taken from a boat, all others were sampled by wading. To reduce the variables, Stations 1, 4, and 5 were located in riffle areas as devoid of vegetation as possible and on a substrate of gravel about 1 cm in size.

Station 1 was located on a gravel bar below the low

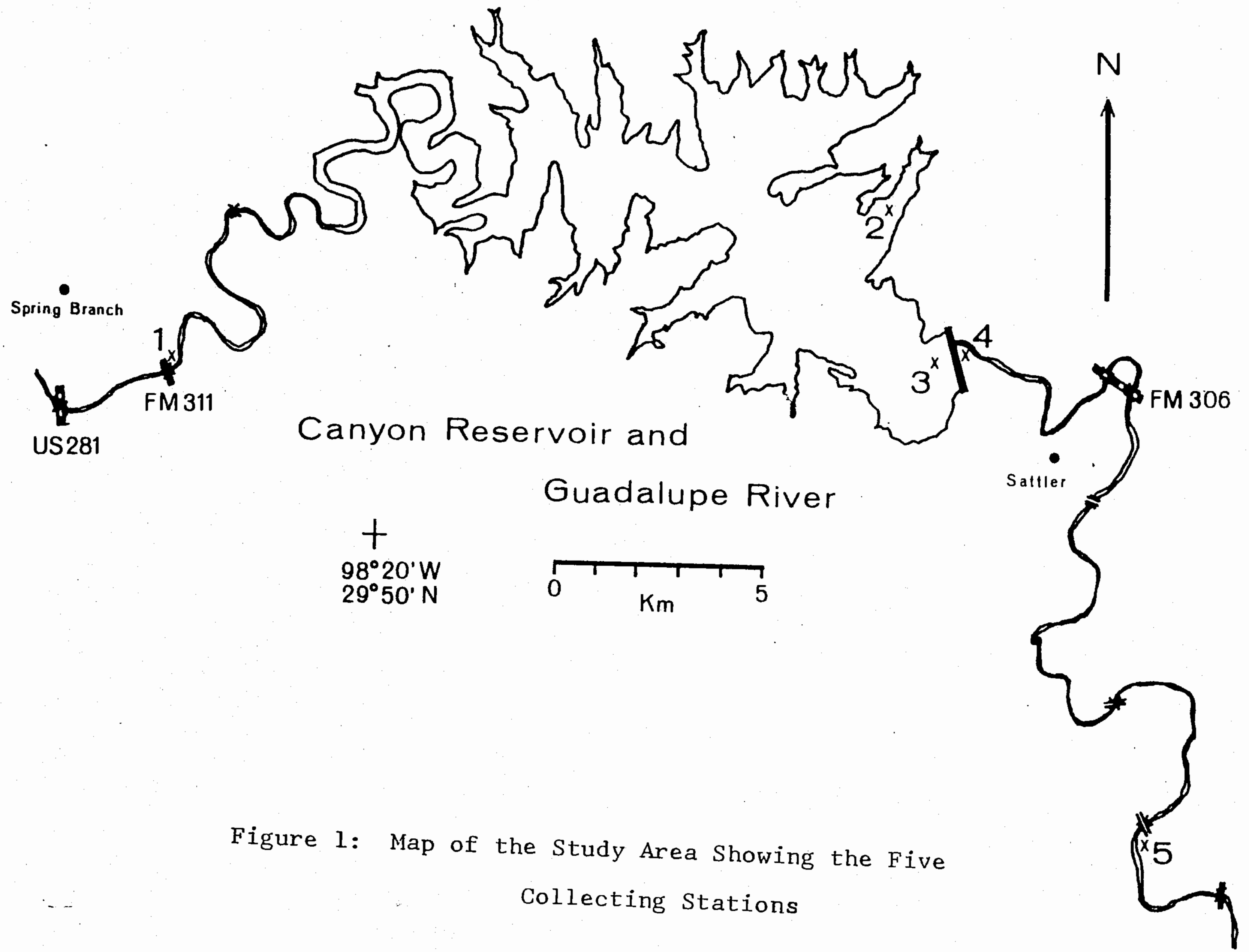

Figure 1: Map of the Study Area Showing the Five Collecting Stations

water bridge for FM 311 where the river was about 30 m wide. This station is normally about 15 km above the upper end of Canyon Reservoir and about 55 km above the dam. The substrate consisted of gravel about 1 cm in diameter mixed with a gray silt which covered a solid limestone bottom deeply sculptured by the current. No aquatic macrophytes were observed growing on this station at any time during the study period, probably because the bar was shifted continuously by the current and on several occasions removed completely. The maximum depth of the river at this point varied from 0.8 m to 2.5 m; samples were taken in depths ranging from 0.1 m to 0.5 m. The flow at this station varied more than at Stations 4 or 5 and the water was usually more turbid.

Station 2 was located in a cove between Parkview Estates and the Fort Sam Houston Recreation Area. Samples were taken about 20 m from the north shore and just west of a submerged gravel road which was easily seen as it entered the cove from the north and south banks. The substrate consisted of a soft, brown-black mud mixed with limestone fragments 4-5 cm in diameter. Apparently the entire bottom at this point was covered with a layer of organic detritus 2-3 cm thick. During the spring and summer the bottom supported a dense growth of <u>Najas guadalupensis</u>. Samples were taken at depths ranging from 3.0-4.5 m.

Station 3 was located over the drowned river bed, about 100 m directly out from the control tower of the dam, in the deepest part of the reservoir. The substrate varied due to the difficulty of locating exactly the same point this far out in the reservoir. Normally the substrate consisted of soft blue-black or gray clay mixed with sand, river gravel, and a few limestone cobbles 5-10 cm in diameter. Several samples showed an overlying stratum of organic detritus consisting mostly of leaves and pecan hulls. Many trees were still standing, completely submerged, along the banks of the old river bed. No living macrophytes were collected from this station. All samples were taken at depths in excess of 36 m and on one occasion a depth of 61 m was recorded.

Station 4 was located in the Guadalupe River about 100 m below the penstock of Canyon Reservoir. The substrate consisted of fine gravel or coarse sand ranging in size from 0.2-1.0 cm in diameter. Lying 3-4 cm under the gravel was a layer of fine black clay mixed with silt. During the spring a growth of filamentous green algae, Cladophora sp., appeared in patches on the bar. This algae was replaced during the summer and early fall by a growth of aerobic sulfur bacteria, Beggiatoa sp., which covered most of the bottom. During the late fall and winter the bar was completely free of aquatic macrophytes. The maximum depth of the Guadalupe River at this point was normally about 1.5 m; samples were taken in depths ranging from 0.1-0.4 m. The flow at this station was very constant except for nine days immediately after the start of this study when no water was released from Canyon Reservoir. During this time Stations 4 and 5 were completely dry.

Station 5 was located 23.7 km downstream from Canyon Reservoir, about 50 m south of one of the Hueco Springs Road bridges (98°10.6'W; 29°48.7'N). The study area was a riffle separated from the main channel by a partially submerged gravel bar about 10 m long and 2 m wide. This bar supported a growth of Typha latifolia (Cattail), Cyperus sp. (Sedge), and Salix sp. (Willow). The study area was near the east bank of the river and was about 20 m wide by 40 m long. The depth varied from about 0.7 m near the north (upstream) end to about 0.3 m at the south end. Bounding the study area on the north-east side was an extensive zone of emergent vegetation similar to that on the gravel bar previously described. The substrate consisted of coarse gravel, up to 3 cm in diameter, which covered a hard clay bottom. Apparently this study area was located in an abandoned ford since remains of a road could be seen entering the river on the west bank opposite the study area. Scattered patches of Potamogeton illinoensis (Pondweed) covered about 50% of the bottom, the remainder had no rooted macrophytes. Sampling was restricted to the patches of exposed gravel. The flow at this station was very constant except during the nine days previously mentioned when no water was released from Canyon Reservoir.

CHAPTER III

METHODS AND MATERIALS

Sampling Procedures

The five stations were sampled once each month from October 25, 1969, to October 24, 1970. Originally it was planned to combine the samples, seasonally, into sets of four for each station as was done by Wilhm and Dorris (1966). It was found, however, that two-month sets of data more readily lent themselves to critical examination than did seasonal sets of data.

Biological Methods

Bottom samples were taken at Stations 1, 4, and 5 with a Surber square foot sampler which had a net with twelve meshes per cm. Samples at Stations 2 and 3 were taken from a boat with an Ekman dredge. From October, 1969, through March, 1970, the dredge used for this purpose had a sampling area of 0.05 m^2; for the rest of the study an Ekman dredge with a sampling area of 0.02 m^2 was used and the number of samples taken at Stations 2 and 3 were adjusted accordingly.

All samples were killed and preserved in the field with 80% ethanol. The organisms were separated by hand and preserved in a solution of 70% ethanol to which had been added about 2% glycerol.

Physicochemical Methods

Meteorological conditions were measured at each station on each sampling date. The air temperature was measured with a standard centigrade mercury thermometer, wind velocity was measured with a Dwyer wind meter, and solar illumination was measured with a Tri-Lux foot-candle meter.

Sampling depths at Stations 1, 4, and 5 were measured with a meter stick while depths at Stations 2 and 3 were measured with a mechanical depth meter.

Surface water temperatures at all stations were measured with a standard centigrade mercury thermometer. The water temperatures on the bottom at Stations 2 and 3 were measured, until February, 1970, with a similar thermometer by inserting the bulb into the center of the bottom sample before it was recovered from the dredge. From February, 1970, until the end of the study, the water temperatures on the bottom at these two stations were measured with an FT3 Marine Hydrographic Thermometer.

Flow data for the Guadalupe River above and below Canyon Reservoir, and discharge from the reservoir, during the study period were obtained through the courtesy of the

Guadalupe-Blanco River Authority (G-BRA) which maintains flow-metering stations near the sampling stations. Rainfall data during the study period were also obtained from G-BRA.

Data for specific conductance, dissolved oxygen, turbidity, pH, total alkalinity, free CO_2, total dissolved solids, and planktonic chlorophyll a were obtained from Young (1971) who concurrently studied the physicochemical characteristics of Stations 1 through 4. Seasonal determinations of these parameters were made by the author at Station 5. These were found to be so nearly the same as those at Station 4 that monthly determinations of these parameters were not made.

Statistical Methods

One of the earliest diversity indices, and certainly the simplest, was calculated with this equation,

$$d = \frac{S}{N} \qquad (1)$$

where S is the number of species and N is the total number of individuals (Gleason, 1922; Williams, 1944).

The first important attempt to use such an index in the study of community structure, according to Hairston (1959), was that of Fisher, *et al.* (1943). Fisher's index

$$a = \frac{S}{\text{Log } N} \qquad (2)$$

was based upon the observation that the graph of equation 1 resembled a logarithmic curve. Other investigators have suggested that frequency distribution among species in an animal population more nearly approximates a lognormal distribution (Preston, 1948; Williams, 1953). Margalef (1951) considered the area proportional to the number of individuals and proposed as a diversity index,

$$d = \frac{S - 1}{\text{Ln } N}, \qquad (3)$$

where Ln N is the natural logarithm of N. Menhinick (1964) applied those diversity indices based upon logarithmic distributions to sweep-net samples of insects and found them unsatisfactory due to variations in sample size. To reduce the effects of sample size he proposed,

$$d = \frac{S}{N} \qquad (4)$$

One of the first diversity indices to include the numbers of individuals found in each species was proposed by Simpson (1949). This equation is,

$$d = \frac{n_i(n_i - 1)}{N(N - 1)} \qquad (5)$$

where n_i is the number of individuals in the i^{th} species and N is the total number of individuals. The values for this index range from one, if all individuals belong to the same species, to zero, if each individual belongs to a different species.

The analysis of natural communities using methods derived from information theory was first proposed by Margalef (1956). The use of these methods is based upon the assumption that diversity and information can be considered equivalent. That is, diversity can be equated with the certainty, or uncertainty, that an individual chosen at random from a community belongs to a certain species. The greater the uncertainty that such an individual belongs to a given species, the greater the diversity of the community from which it was chosen (Wilhm and Dorris, 1967). Maximum diversity occurs when all individuals are equally divided among the species present in a community. Minimum diversity occurs when all individuals present belong to the same species. Normally a natural community has a diversity which falls somewhere between these extremes. The position of the diversity between the extremes can be determined and is usually expressed as redundancy. In other words, redundancy is an expression of the dominance of one or more species and is inversely proportional to the number of species in the community (Wilhm, 1967).

The number of species (s), the number of individuals in the i^{th} species (n_i), and the total number of individuals in a community (N), are used to calculate community diversity (H), average diversity per individual ($\overline{H}$), maximum diversity (Hmax), minimum diversity (Hmin), and redundancy (R) in the following equations (Patten, 1962):

$$H = -k \sum^{s} n_i \log \frac{n_i}{N} \qquad (6)$$

$$\bar{H} = -k \sum_{i=1}^{s} \frac{n_i}{N} \log \frac{n_i}{N} \qquad (7)$$

$$Hmax = \log N! - s \log\left(\frac{N}{s}\right)! \qquad (8)$$

$$Hmin = \log N! - \log[N - (s - 1)]! \qquad (9)$$

$$R = \frac{Dmax - D}{Dmax - Dmin} \qquad (10)$$

The usefulness of H alone as a diversity index is limited due to its close correlation with sample size (Wilhm, 1967). Values for R, being unrelated to sample size, may be more useful for comparing the structures of communities with unequal numbers of organisms when used in conjunction with H. The only restriction to the use of R is that samples must be reasonably large (Patten, 1962) which means, according to Wilhm (personal communication, 1970), that values of N must be at least 100.

Wilhm (1967, 1968a, 1968b, 1969, 1970) used $\bar{H}$ as a measure of species diversity. $\bar{H}$ has been shown to be dimensionless which has enabled some investigators to insert biomass units for n_i (Wilhm, 1968a; Hannan and Dorris, 1970). In addition, as successive samples from the same community are pooled to create larger values of N, the values of $\bar{H}$ become asymptotic (Pielou, 1966; Wilhm and Dorris, 1966; Wilhm, 1968b, 1970). This characteristic enables an investigator to determine the number of samples which must be taken to achieve any desired degree of accuracy.

For this study, species diversity was calculated for each set of data using a modification of equation 7 (Wilhm, 1967). This modification consisted of changing the symbols for the parameters to indicate the use of sample values rather than known values. The resulting equation is,

$$\bar{d} = - \sum_{i=1}^{s} \frac{n_i}{n} \log_2 \frac{n_i}{n} \tag{11}$$

where the number of taxa in the sample (s), the total number of individuals in the sample (n), and the number of individuals in the i^{th} taxon (n_i), are used to calculate the average diversity per individual ($\bar{d}$).

It was also intended to use equations 6, 8, 9, and 10 (H, Hmax, Hmin, and R), with modifications similar to equation 11, as measures of species diversity. After encountering some difficulty with the use of my data in these equations, the author was advised by Dr. J. L. Wilhm, Oklahoma State University, that these equations are useful only when the total number of individuals in a sample are greater than 100. Since many of the samples in this study have fewer than 100 individuals, further attempts to use these equations were abandoned.

Since $\bar{d}$ becomes asymptotic as sample size is increased, it was possible to establish the proper sample size for each station. Ten samples were taken at each station. The data from these samples were accumulated two-at-a-time until $\bar{d}$

approached an asymptote. The number of samples required for $\bar{d}$ to approach an asymptote were taken as the proper sample size at each station (Wilhm and Dorris, 1966; Pielou, 1966; Wilhm, 1968b, 1970).

Maximum values for $\bar{d}$ are observed if all the individuals in a sample are equally divided among the taxa present in that sample, and minimum values for $\bar{d}$ are observed if each taxon in the sample, except one, contains one individual while the remaining taxon contains all the rest of the individuals in the sample. The author suggests, therefore, these alternatives to equations 6, 8, and 10.

Since the maximum value for $\bar{d}$ ($\bar{d}$max) occurs when the individuals in a sample are equally divided among the taxa, each taxa in such a sample would have n/s members.

$$n_1 = n_2 = n_3 = \ldots = n_s = \frac{n}{s}$$

Substituting this value for n_i into equation 11,

$$\bar{d}\text{max} = -\sum_{i=1}^{s} \frac{\frac{n}{s}}{n} \log_2 \frac{\frac{n}{s}}{n}$$

and dividing by n,

$$\bar{d}\text{max} = -\sum_{i=1}^{s} \frac{1}{s} \log_2 \frac{1}{s}$$

This equation can be further simplified to,

$$\bar{d}\text{max} = -s(\frac{1}{s}) \log_2(\frac{1}{s})$$

or:

$$\bar{d}\text{max} = -\log_2(\frac{1}{s})$$

or simply:

$$\bar{d}\text{max} = \log_2 s \tag{12}$$

The minimum value for $\bar{d}$ ($\bar{d}$min) occurs when (s - 1) taxa in the sample have one individual each while the remaining taxon has all the rest of the individuals in the sample.

$$n_1 = n_2 = n_3 = \ldots = n_{s-1} = 1$$

$$n_s = n - (s - 1)$$

Substituting these values for n_i into equation 11

$$\bar{d}\text{min} = -\sum_{i=1}^{s-1}(\frac{1}{n}\log_2\frac{1}{n}) + [-\frac{n-(s-1)}{n}\log_2\frac{n-(s-1)}{n}]$$

which may be simplified to

$$\bar{d}\text{min} = -[\frac{s-1}{n}\log_2\frac{1}{n}] - [\frac{n-(s-1)}{n}\log_2\frac{n-(s-1)}{n}] \tag{13}$$

The position of $\bar{d}$ relative to $\bar{d}$max and $\bar{d}$min is a measure of the dominance of one or more taxa in the sample. This position can be calculated with respect to the average redundancy per individual in the sample ($\bar{r}$) or the average information carried by an individual in the sample ($\bar{f}$). Equations for these functions are,

$$\bar{r} = \frac{\bar{d}\text{max} - \bar{d}}{\bar{d}\text{max} - \bar{d}\text{min}} \tag{14}$$

and,

$$\bar{f} = \frac{\bar{d} - \bar{d}min}{\bar{d}max - \bar{d}min} \tag{15}$$

The values for $\bar{r}$ behave much as do those for R. As $\bar{r}$ increases, the average amount of information carried by an individual chosen randomly from the sample decreases, the uncertainty that such an individual belongs to a particular taxon decreases, and the average diversity per individual ($\bar{d}$) decreases.

Values for $\bar{f}$ behave in inverse proportion to those for $\bar{r}$. If values for $\bar{r}$ have been calculated, the corresponding values for $\bar{f}$ can be calculated from,

$$\bar{f} = 1 - \bar{r}$$

As values for $\bar{f}$ increase, the average amount of information carried by an individual chosen at random from that sample increases, the uncertainty that such an individual belongs to a particular taxon increases, and the average diversity per individual ($\bar{d}$) increases. Both $\bar{r}$ and $\bar{f}$ vary between zero and one.

An added attraction of both $\bar{r}$ and $\bar{f}$ is that, unlike R, they may be calculated from any size sample without misleading results.

In this study $\bar{d}$, $\bar{d}max$, $\bar{d}min$, and $\bar{r}$ were calculated for each set of data using equations 11, 12, 13, and 14 respectively.

Computations were performed with an IBM 1130 data processing machine at Southwest Texas State University. The program for the computations of $\bar{d}$, $\bar{d}$max, $\bar{d}$min, $\bar{r}$, and $\bar{f}$ has been included in the Appendix (Table I).

CHAPTER IV

RESULTS AND DISCUSSION

Meteorological Conditions

During the latter half of the study period the monthly precipitation at Canyon Dam, in general, decreased to levels considerably below normal (Table I). From June through the end of the study period the only month during which the gauge at Canyon Dam received the normal amount of precipitation was September.

Air temperatures at the five stations during the study period followed a normal seasonal pattern (Table II) except for a brief warm spell during January, 1970, when a mean air temperature of 20.6° C was recorded.

Neither the mean wind velocity nor the mean solar illumination for each month during the study period followed any particular seasonal pattern (Table II).

Physicochemical

Flow in the Guadalupe River showed a general decline during the study period both above and below the reservoir (Table III). Flow below the reservoir was more constant from day-to-day than was flow above the reservoir due to

TABLE I

MONTHLY RAINFALL IN CENTIMETERS AT CANYON DAM, TEXAS*

Months		During Study	Average 1962 - 1968	Difference
1969	October	20.55	7.75	+12.80
	November	5.21	4.21	+ 1.00
	December	5.74	5.54	+ 0.20
1970	January	3.12	5.26	- 2.14
	February	7.89	5.59	+ 2.39
	March	**	**	**
	April	20.32	7.62	+12.70
	May	**	**	**
	June	2.13	7.57	- 5.44
	July	2.90	6.10	- 3.20
	August	2.34	5.26	- 2.92
	September	13.97	10.21	+ 3.76
	October	3.73	7.75	- 4.02

* Rainfall data from U.S. Army Corps of Engineers, Canyon Reservoir.

** Data not available.

TABLE II

MEAN AIR TEMPERATURE, MEAN WIND VELOCITY, AND MEAN SOLAR ILLUMINATION AT EACH OF THE FIVE COLLECTION STATIONS

	Months	Air Temperature (Centigrade)	Wind Velocity (Km/Hr)	Solar Illumination (Foot Candles)
1969	October	21.2	4.0	7550
	November	14.6	4.0	4050
	December	14.7	19.2	3700
1970	January	20.6	12.0	12000+
	February	18.0	4.0	5350
	March	17.0	8.0	8500
	April	25.6	8.0	2700
	May	26.4	4.0	10000
	June	30.6	16.0	2700
	July	31.5	16.0	4800
	August	31.5	16.0	5300
	September	22.9	0.0	5100
	October	13.5	24.0	8200

TABLE III

MEAN MONTHLY FLOW AT STATIONS ONE AND FOUR IN CUBIC METERS PER MINUTE*

Month	Station 1	Station 4
1969 October	2140.8	1125.0**
November	409.8	904.2**
December	943.8	693.0
1970 January	630.6	1282.8
February	633.6	973.8
March	1204.8	1219.8
April	703.2	1340.4
May	1094.4	648.6
June	693.0	1384.8
July	287.4	652.8
August	157.2	302.4
September	195.6	183.6
October	214.2	183.6

* Flow data from Guadalupe-Blanco River Authority.

** From October 27 through November 4 the penstock of Canyon Dam was closed and the flow at Station 4 was 0.

the controlled discharge. For nine days immediately after the start of this study, October 27 to November 4, 1969, the penstock on Canyon Dam was closed to allow general maintenance. Station 4 was completely exposed during this time as was Station 5 for the last seven days. No significant differences were noted, however, between the November collections at these stations, taken about three weeks after the penstock was reopened, and the collections made in October before the flow was interrupted.

The lowest water temperatures were recorded in January and February, 1970, and the highest water temperatures were recorded in July and August, 1970. The overall effect of the reservoir was to stabilize and lower the water temperatures at Stations 3, 4, and 5 (Table IV). Throughout the study period, the water at Station 2 was observed to be slightly warmer than the water at Station 1. This was probably due to more direct insolation of the shallow water at Station 2 which agreed with observations made by Dorris, et al. (1963) in a similar impoundment.

A similar reduction in the ranges and means of specific conductance, total alkalinity, and turbidity was observed below the reservoir (Table IV). Young (1971) attributes this to autotrophic assimilation of bicarbonates and dissolved minerals. A reduction in turbidity has also been observed in rivers below other impoundments (Symons, et al., 1964).

TABLE IV

MEANS, RANGES, AND STANDARD DEVIATIONS FOR PHYSICOCHEMICAL PARAMETERS AT EACH OF THE FIVE COLLECTING STATIONS*

Parameter	Stations 1	 2	 3	 4	 5
Water Temperature (°C)					
Mean	20.17	20.91	14.24	15.43	17.89
Standard Deviation	6.0	6.0	2.5	2.2	2.7
Range (Lower - upper)	8.0 - 29.5	14.0 - 29.7	10.7 - 17.6	12.5 - 17.7	11.5 - 26.0
Specific Conductance (uMhos/cm^3)					
Mean	521.8	358.8	437.8	429.7	450.1
Standard Deviation	40.0	24.0	21.4	13.4	18.3
Range	480 - 580	330 - 400	410 - 475	410 - 443	420 - 470
pH					
Mean	8.0	7.9	7.7	7.9	8.0
Standard Deviation	0.4	0.4	0.4	0.4	0.4
Range	7.3 - 8.4	7.2 - 8.2	7.1 - 8.3	7.4 - 8.4	7.4 - 8.4
Dissolved Oxygen (ppm)					
Mean	8.8	8.1	2.8	9.7	**
Standard Deviation	1.4	1.6	3.2	1.4	**
Range	7.1 - 10.5	5.7 - 10.5	0.0 - 7.0	7.8 - 12.5	**

TABLE IV--(Continued)

Parameter	Stations 1	2	3	4	5
Total Alkalinity (ppm)					
Mean	245.6	160.5	191.2	185.5	**
Standard Deviation	20.6	10.6	11.7	10.9	**
Range	218 - 276	143 - 173	183 - 209	172 - 204	**
Turbidity (JTU)					
Mean	77.1	18.6	27.6	15.7	**
Standard Deviation	65.9	11.7	14.8	11.0	**
Range	18 - 214	6 - 42	8 - 54	4 - 36	**
Total Dissolved Solids (ppm)					
Mean	309.7	256.7	238.7	271.3	**
Standard Deviation	28.7	42.7	55.8	40.0	**
Range	265 - 345	200 - 334	135 - 303	211 - 334	**
Chlorophyll _a_ (ppm)					
Mean	0.011	0.010	0.008	0.008	**
Standard Deviation	0.006	0.006	0.003	0.003	**
Range	0.003 - 0.018	0.003 - 0.025	0.003 - 0.013	0.003 - 0.011	**

* Data from Young (1971).

** Data not available.

Dissolved oxygen was usually higher at Station 1 than in the reservoir (Table IV) due to the reaeration action of riffle areas. In May, 1970, a thermocline was observed at Station 3 and the dissolved oxygen was rapidly depleted in the hypolimnion. From June, 1970, through the end of the study period the hypolimnion of Canyon Reservoir was anoxic. The anoxic, hypolimnetic water discharged from Canyon Reservoir was rapidly reaerated in the turbulent tailrace so that the dissolved oxygen at Station 4 was always near saturation. Due to the low temperature of the water, there was often more dissolved oxygen at Station 4 than at any other station.

The lowest pH, 7.1, was observed at Station 3 during a time when the hypolimnion was anoxic, and the highest pH, 8.4, was observed at Station 1 (Table IV). The pH at all stations usually stayed near pH 8.0 with slight fluctuations.

Total dissolved solids were highest at Station 1 throughout most of the study period (Table IV). Slight reductions were observed in the reservoir due to autotrophic assimilation in the epilimnion (Young, 1971). Station 4 had high levels of total dissolved solids during the time when the hypolimnion was anoxic.

Reid (1961) and Vollenweider (1968) found that chlorophyll a values indicated the relative abundance of phytoplanktonic organisms. In this study, the highest mean values of chlorophyll a were observed at Stations 1 and 2, and the lowest were observed at Stations 3 and 4 (Table IV).

Hydrogen sulfide was noted in the hypolimnion at Station 3 and in the tailrace as far as Station 4 from June through the end of the study period. During this time a dense growth of the sulfur bacteria Beggiatoa sp. was observed completely covering the substrate at Station 4. This hydrogen sulfide was produced by sulfur-reducing bacteria growing in the anoxic hypolimnion of Canyon Reservoir.

Biological

Eleven of the 37 taxa collected at Station 1 during this study were not collected at any other station (Table V). All of the taxa unique to Station 1 were species of insects: four Coleoptera, two Trichoptera, two undescribed species of Ephemeroptera, one Hemiptera, one Plecoptera, and one Odonata. The orders Coleoptera, Trichoptera, Odonata, and Ephemeroptera were frequently encountered in collections while the orders Hemiptera and Plecoptera were rarely collected. Notably absent from the list of organisms collected at Station 1 were gastropods, which were collected at Stations 4 and 5 below the reservoir. This absence of gastropods was due to freshets which shifted the gravel bar up and down the river, occasionally removing it altogether and exposing the limestone bedrock. Rapid repopulation of a gravel bar under these conditions can only result from drift, in which gastropods are usually absent (Anderson and Lehmkuhl, 1968; Peterka, 1969). The presence of gastropods at Stations 4 and 5 was

TABLE V

TAXA COLLECTED DURING THE STUDY PERIOD AT EACH OF THE FIVE COLLECTING STATIONS ON THE GUADALUPE RIVER, TEXAS

Taxa	Stations				
	1	2	3	4	5
Oligochaeta					
Aeolosomatidae					
Aeolosoma sp.		(+)*			
Tubificidae					
Branchiura sowerbyi	+	+	+	+	+
Lumbriculidae					
Lumbriculus sp.	+			+	+
Hirudinea					
Glossiphoniidae					
Helobdella sp.	+				+
Turbellaria					
Planariidae					
Dugesia tigrina	+			+	+
Coelenterata					
Hydridae					
Hydra sp.			+		+
Crustacea					
Astacidae					
Orconectes palmeri					

TABLE V--Continued

Taxa	Stations 1	 2	 3	 4	 5
Talitridae					
Hyalella azteca		+			+
Mollusca					
Unionidae					
Unidentified	+	+			
Sphaeriidae					
Pisidium sp.				+	+
Physidae					
Physa sp.				+	+
Planorbidae					
Gyraulus sp.				+	+
Bulimidae					
Littoridina sp.				+	+
Ephemeroptera					
Baetidae					
Baetis sp.	+	+			
Pseudocloeon sp.				+	+
Trycorythidae					
Trycorythodes sp.	+			+	+
Caenidae					
Caenis sp.	+	+			+
Leptohyphes (new species)	(+)				
Brachycercus (new species)	(+)				

TABLE V--Continued

Taxa	Stations 1	2	3	4	5
Siphlonuridae					
Isonychia sp.	+				+
Leptophlebiidae					
Thraulodes (new species)	+				+
Traverella sp.	+				+
Heptageniidae					
Stenonema sp.	+				+
Ephemeridae					
Hexagenia sp.		+			+
Odonata					
Coenagrionidae					
Argia sp.	+				+
Nehallenia sp.					(+)
Calopterygidae					
Hetaerina sp.					(+)
Gomphidae					
Erpetogomphus sp.	+				+
Libellulidae					
Erythrodiplax sp.					(+)
Leucorrhina sp.					(+)
Paltothemis sp.	(+)				

TABLE V--Continued

Taxa	Stations 1	2	3	4	5
Diptera					
Chironomidae					
Unidentified	+	+		+	+
Chironomus sp.		+	+		
Tanypodinae A		(+)			
B		(+)			
C		(+)			
Coelotanypus sp.		(+)			
Pentaneura sp.	+	+	+		
Tabanidae					
Tabanus sp.	+			+	
Simuliidae					
Simulium sp.	+			+	+
Culicidae					
Chaoborus sp.		+	+	+	
Heleidae					
Genus A		(+)			
Dasyhelea sp.					(+)
Dolichopodidae					
Genus A				(+)	
Tipulidae					
Tipula sp.				(+)	

TABLE V--Continued

Taxa	Stations				
	1	2	3	4	5
Plecoptera					
Perlidae					
Perlesta sp.	(+)				
Neoperla sp.					(+)
Trichoptera					
Hydropsychidae					
Cheumatopsyche sp.	+				+
Hydropsyche sp.					(+)
Hydroptilidae					
Hydroptila sp.	+	+			+
Leptoceridae					
Oecetis sp.					(+)
Helicopsychidae					
Helicopsyche sp.				+	+
Beraeidae					
Beraea sp.		(+)			
Philopotamidae					
Chimarra obscura	(+)				
Psychomyiidae					
Lype sp.	(+)				
Psychomyiidae Genus A		(+)			

TABLE V--*Continued*

Taxa	Stations 1	2	3	4	5
Limnephilidae					
Neophylax sp.				(+)	
Hemiptera					
Naucoridae					
Cryphocricos sp.	(+)				
Neuroptera					
Corydalidae					
Corydalus sp.	+				+
Coleoptera					
Elmidae					
Rhizelmis sp.	(+)				
Stenelmis A	+			+	+
Stenelmis B	(+)				
Hexacylloepus sp.	(+)				
Ordobrevia sp.	(+)				
Lara sp.					(+)
Dubiraphia sp.					(+)
Dryopidae					
Helichus sp.	+				+
Dryops sp.				+	+
Limnichidae					
Lutrochus sp.	+				+

TABLE V--Continued

Taxa	Stations 1	2	3	4	5
Hydrophilidae					
Berosus sp.	+				+
Lepidoptera					
Pyralidae					
Cataclysta sp.					(+)
Total Number of Taxa	37	19	5	18	42

* Parenthesis indicates taxon collected only at one station.

due to the more constant flow at these stations. Only one freshet was observed on this stretch of the Guadalupe River during the study period, and this did not result in any appreciable scouring of the stream bed.

Nineteen taxa were collected at Station 2 as compared to thirty-seven taxa collected at Station 1 (Table V). Of these, eight were collected only at this station: five Diptera, two Trichoptera, and one Oligochaeta. All of these organisms except the two Trichoptera were burrowing forms associated with the layer of organic detritus covering the substrate. Unlike any of the other stations, the faunal community at Station 2 was dominated for the entire study period by Diptera which were represented by nine species. Six of these species of Diptera were in the family Chironomidae.

The greatest paucity of taxa was observed at Station 3. During the study period only five taxa were collected at this station and from May through September, 1970, the only organism collected was _Branchiura_ _sowerbyi_, a tubificid worm. In October, 1969, and again in October, 1970, specimens of _Chaoborus_ sp. were collected at Station 3 while the hypolimnion was still anoxic and with hydrogen sulfide present near the bottom. These organisms are not considered to be highly adapted to low oxygen tensions; their presence under anoxic conditions has been observed to be due to their habit of becoming planktonic predators at night and burrowing into the substrate during the daylight hours (Woodmanse and

Grantham, 1961). This apparently accounts for their presence at Station 3 during periods of anoxia. From January through March, 1971, the most common organism in collections at Station 3 was Chironomus sp., but this organism was never collected after the reservoir stratified.

Only three taxa, out of eighteen collected, were unique to Station 4: two Diptera and one Trichoptera. No single group of organisms dominated the faunal community at this station although Diptera (especially the Chironomidae) and annelid worms (especially Lumbriculus sp.) appeared in most collections. Of more interest were the organisms which were absent. Only two taxa of Ephemeroptera were collected, compared to nine at Station 1. Two taxa of Trichoptera, represented by only three specimens, were collected at Station 4 compared to four taxa, represented by numerous specimens, at Station 1. Only two taxa of Coleoptera, represented by three specimens in one sample, were collected at Station 4 compared to eight taxa and an abundance of specimens collected at Station 1. Present at Station 4 and not at Station 1 were three taxa of Gastropods, probably because of the very constant flow below the reservoir.

Station 5 had a greater variety of organisms than Station 1 with forty-two taxa compared to thirty-seven taxa. Of these forty-two taxa, eleven were found only at this station. Twenty-one of the forty-two taxa collected at Station 5 were not collected at Station 1 despite the similarities of substrate, depth, and current between the two stations. Hyallela azteca and Hydra sp. are usually associated with rooted macrophytes rather than bare gravel; their presence in the collections probably represents drift from patches of vegetation upstream from Station 5. Considering other organisms, however, there was evidence of a difference in dominance in the faunal community between Stations 1 and 5. The dominant organisms at Station 5, as at Station 1, were Ephemeroptera larvae. At Station 1 the most common taxa collected were, in order of decreasing abundance in collections, Thraulodes sp., Tricorythodes sp., and Leptohyphes sp.. At Station 5, however, Tricorythodes sp. usually outnumbered all other organisms collected, Thraulodes sp. was present in only one collection, and Leptohyphes sp. did not occur. Three taxa of Ephemeroptera which were collected at Station 1 were not collected at Station 5, and two taxa were collected at Station 5 but not at Station 1.

Similar differences between other orders of insects occurred between Station 1 and Station 5. Two of the three Odonata taxa collected at Station 1 were also present at Station 5, along with four Odonata taxa not present at Station 1. Plecoptera were uncommon at both stations, with only Perlesta sp. occurring at Station 1 and only Neoperla sp. at Station 5. Two of the four Trichoptera taxa collected above the reservoir were present at Station 5, along with three Trichoptera taxa not found at Station 1. Of the eight taxa of Coleoptera collected at Station 1, five were also collected at Station 5 along with three additional Coleoptera taxa. The greatest differences in the Coleoptera were observed in the Elmidae. Five elmids occurred at Station 1; four were collected only at this station, while one was also collected at Stations 4 and 5. Three elmids were collected at Station 5, and two of these were found only at this station.

When the numbers of taxa collected at each station are compared (Figure 2) a definite trend can be seen. Stations 1 and 5 had almost the same mean number of taxa per collection although the greatest number of taxa in a single collection occurred at Station 1. The mean numbers of taxa at Stations 2 and 4 were also similar, but about one half as numerous as at Stations 1 and 5. The lowest mean number per collection was at Station 3 where the community was severely restricted by oxygen depletion in the hypolimnion during the warmer months. A large decline in the number of taxa along with the replacement of some taxa with other more tolerant taxa, such as occurred at Station 4 as compared to Station 1, has been reported below a similar bottom-draining reservoir in Canada (Spence and Hynes, 1971a, 1971b).

The average density per collection (Figure 3) was similar at all stations except Station 2 which supported a faunal community of much higher density throughout the study. Stations 3 and 4 went through periods of very low faunal density (Figure 3) during the warmer months when the

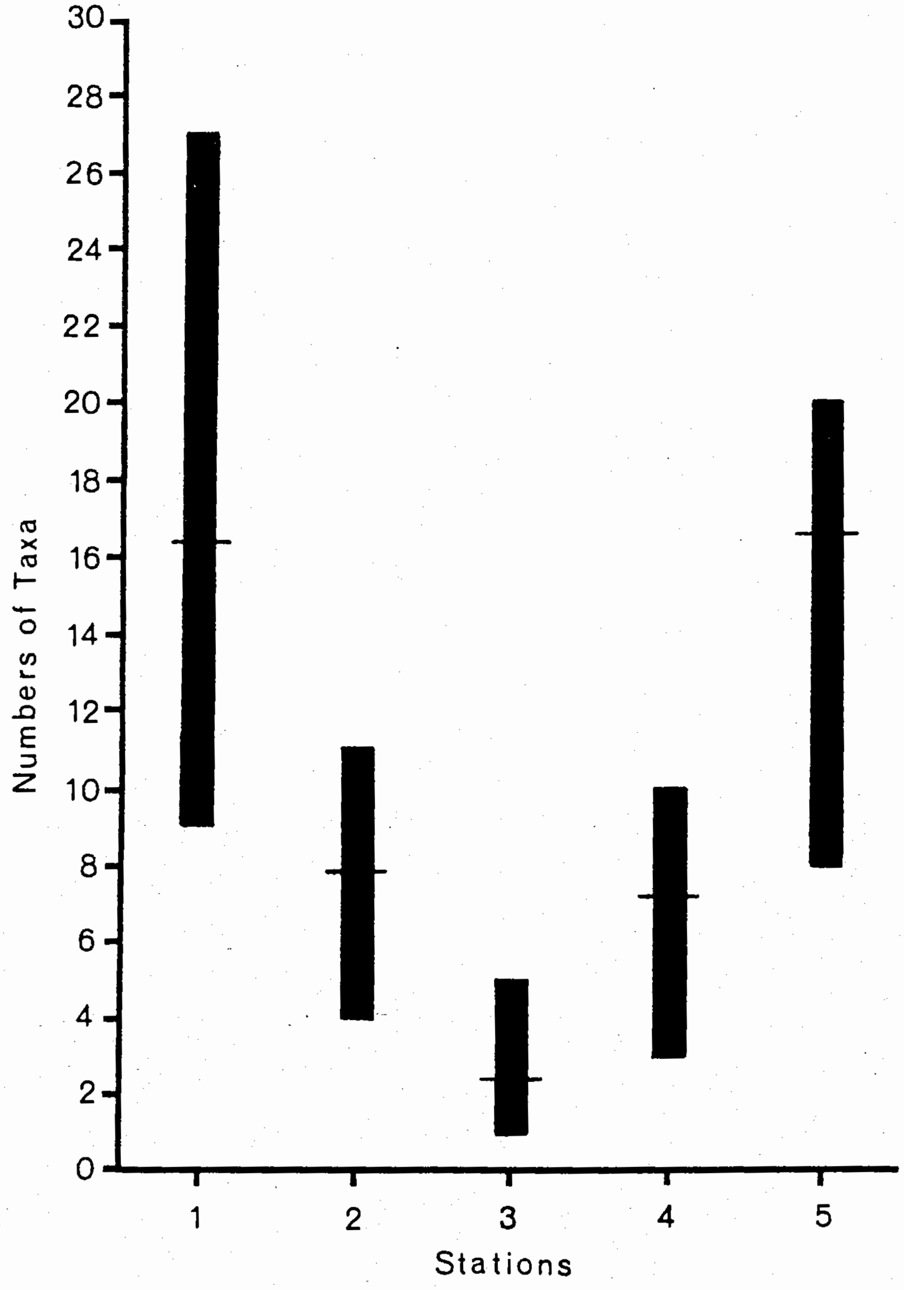

Figure 2: Mean Number of Taxa per Collection and the Range in Numbers of Taxa per Collection at Each of the Five Collecting Stations

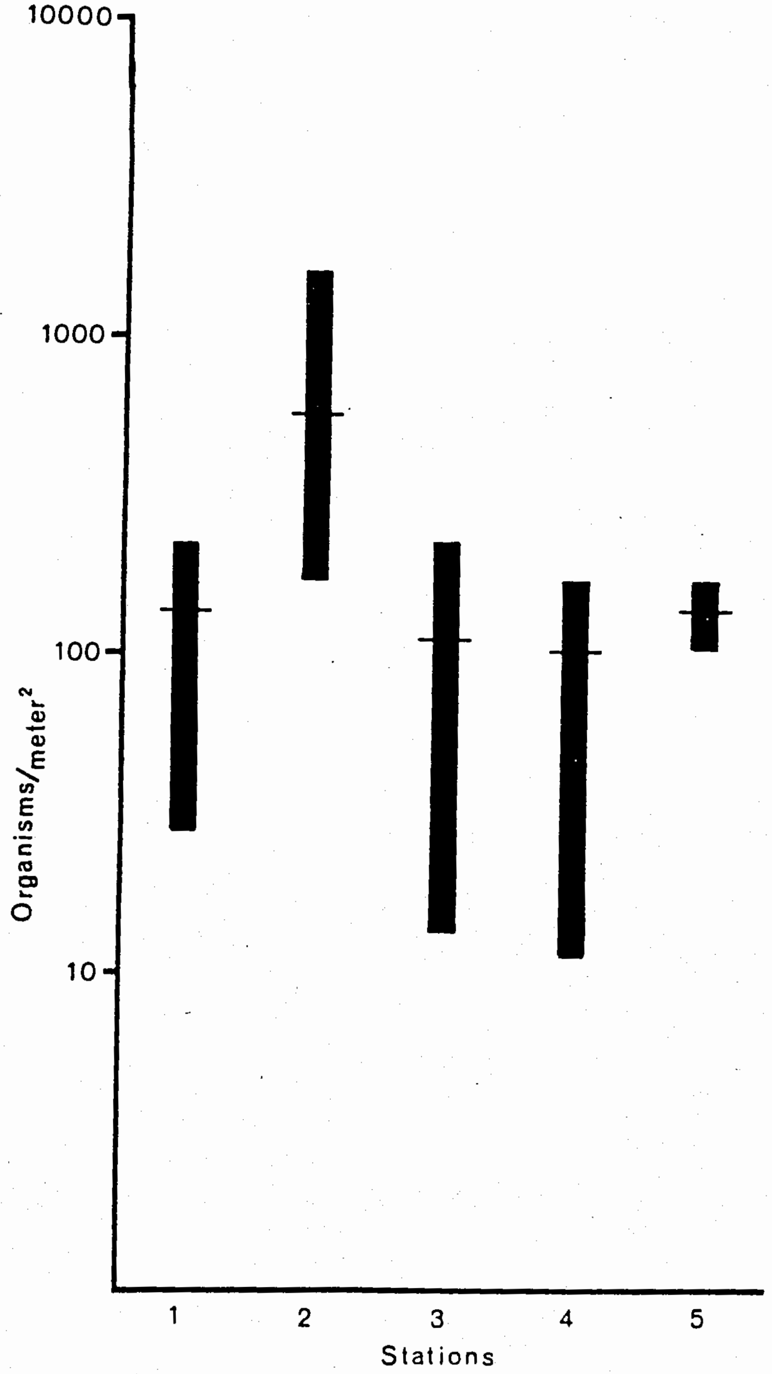

Figure 3: Mean Density of Organisms per Collection and the Range of Density per Collection at Each of the Five Collecting Stations

hypolimnion was anoxic and hydrogen sulfide was present at both stations. The great stability of environment at Station 5, as compared to the other stations, is reflected in the stability of the density of its faunal community (Figure 3).

The density of organisms and the numbers of taxa collected for the orders Ephemeroptera, Trichoptera, Coleoptera, and Diptera best show similarities and dissimilarities among the communities of the stations during the study period (Figures 4, 5, 6, and 7). With all four orders of insects, the communities with the greatest similarity were those of Stations 1 and 5. Station 2, although fairly rich in Ephemeroptera, Trichoptera, and especially Diptera, corresponded little in community structure to the lotic communities. For the entire study period, Station 2 was devoid of Coleoptera (Figure 6). The community structure at Station 4 based on these four orders was also dissimilar to the corresponding communities at the other lotic stations. In any given collection there were usually fewer Ephemeroptera, Trichoptera, and Coleoptera, and more Diptera at Station 4 than at Stations 1 or 5. Station 3 had no representatives of any of these insects except Diptera, and even these were absent when the hypolimnion was anoxic.

Statistical

At all five stations, $\bar{d}$ approached an asymptote with the first two accumulated samples and oscillated around this value during the accumulation of the remaining samples

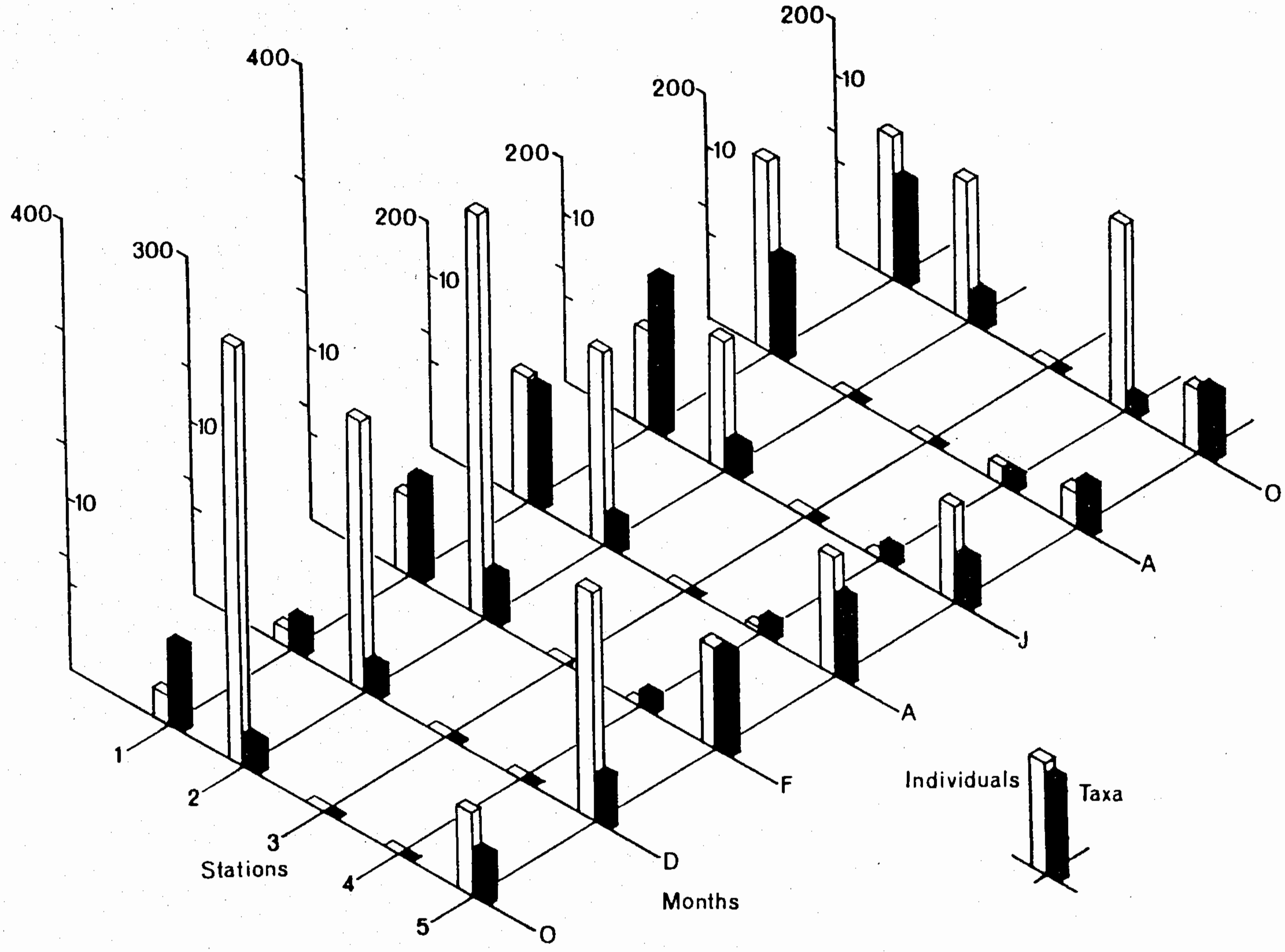

Figure 4: Ephemeroptera: Number of Individuals per Square Meter and Number of Taxa for Each Collecting Period at Each of the Five Collecting Stations

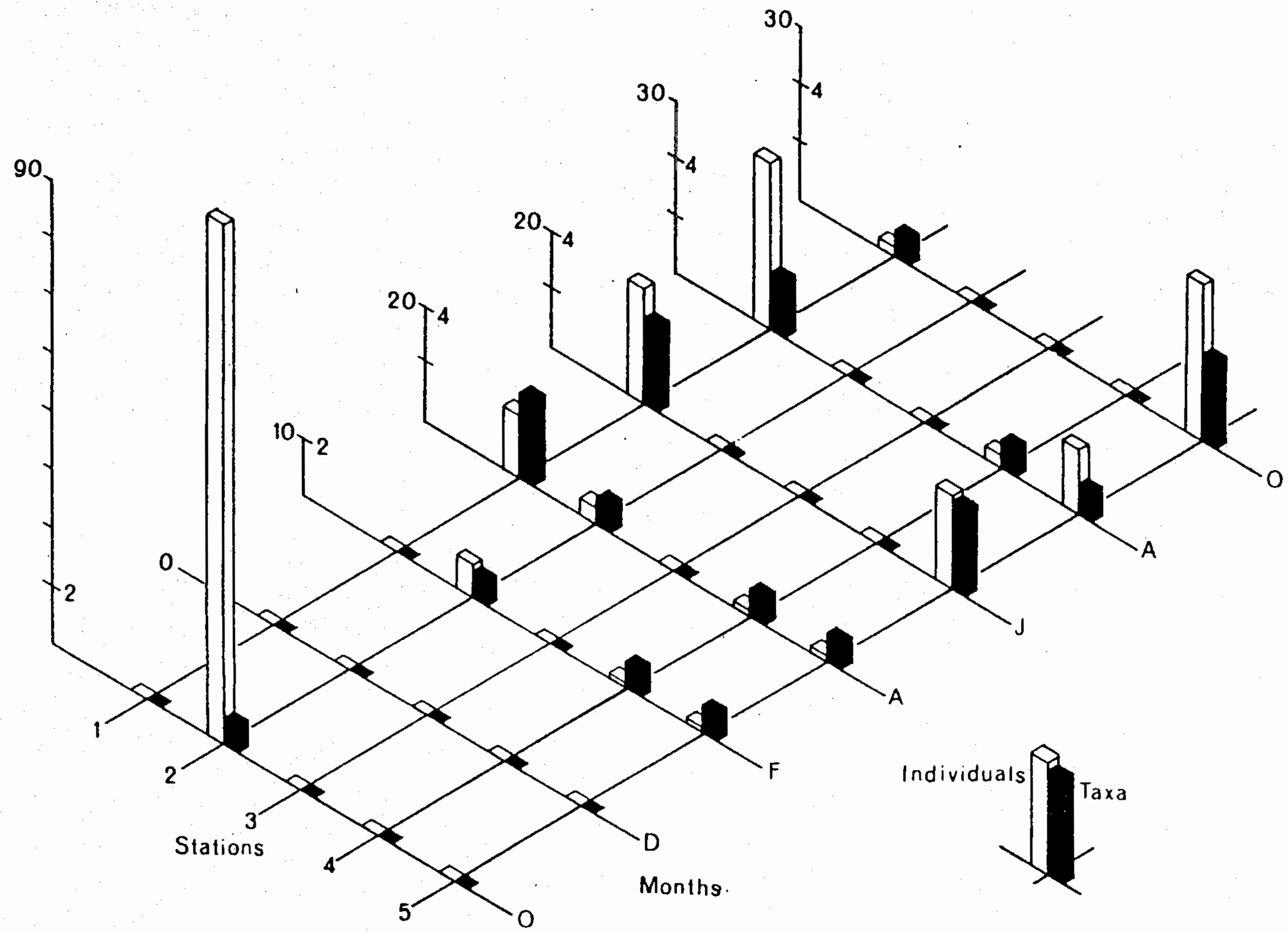

Figure 5: Trichoptera: Number of Individuals per Square Meter and Number of Taxa for Each Collecting Period at Each of the Five Collecting Stations

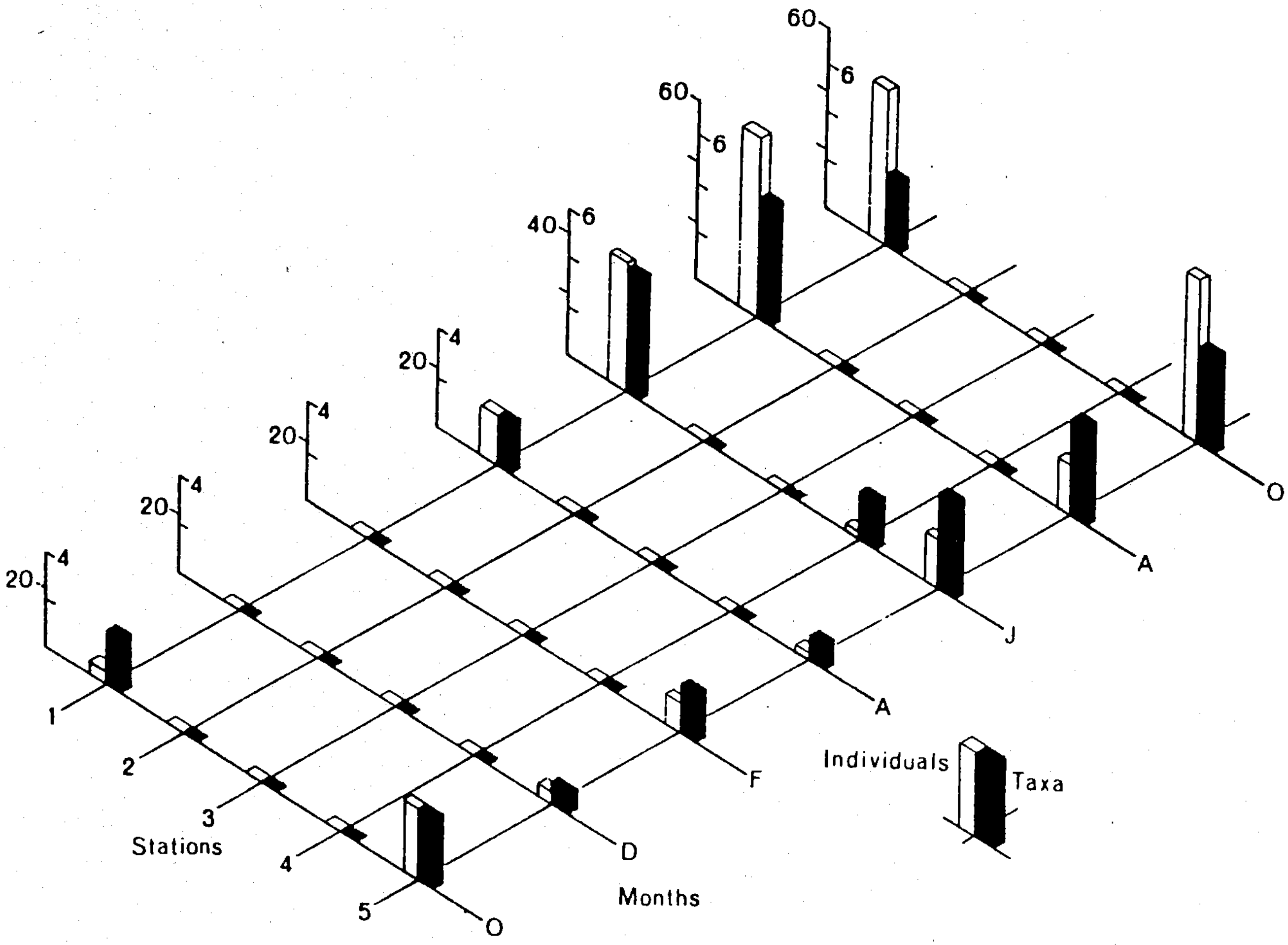

Figure 6: Coleoptera: Number of Individuals per Square Meter and Number of Taxa for Each Collecting Period at Each of the Five Collecting Stations

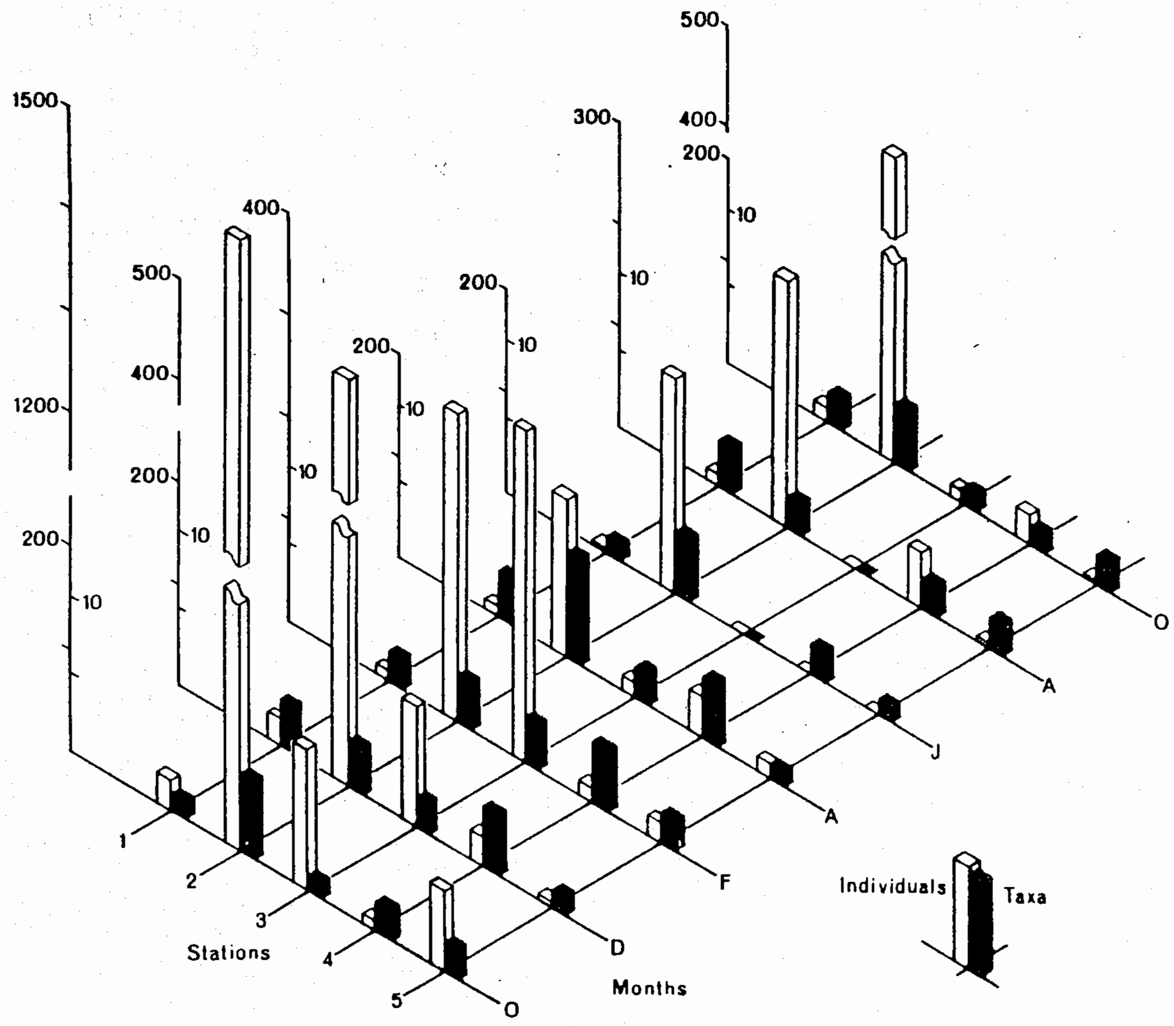

Figure 7: Diptera: Number of Individuals per Square Meter and Number of Taxa for Each Collecting Period at Each of the Five Collecting Stations

(Table VI). The sample size for the remaining collections in this study was established as 0.9 m^2 at Stations 1, 4, and 5, and 0.2 m^2 at Stations 2 and 3; in both cases the areas were in excess of the size necessary for values of $\bar{d}$ to be asymptotic.

The annual variations of $\bar{d}$ and $\bar{r}$ at each station (figures 8, 9, 10, 11, and 12) show $\bar{r}$ to vary in roughly inverse proportion to $\bar{d}$. The values of $\bar{r}$, however, are a reflection of the dominance of one or a few taxa over the other taxa in a community and should not be considered equatable with the inverse of $\bar{d}$ in all cases. Changes in $\bar{d}$ can be the result of (1) the appearance or disappearance of taxa with no change in the relative distribution of individuals among these taxa, in which case $\bar{r}$ would remain unchanged; or (2) one or more taxa establishing or losing dominance within a community without the gain or loss of any taxa, in which case $\bar{r}$ would vary in inverse proportion to $\bar{d}$. In most natural communities changes in $\bar{d}$ are a result of both factors acting more or less independently which may lead, in some instances, to apparently conflicting results.

An example of the first condition causing changes in $\bar{d}$ was illustrated by collections at Station 2 (Figure 11). Values of $\bar{d}$ varied from 1.8 for the December-January collections to 2.2 for the February-March collections while $\bar{r}$ varied from 0.372 to 0.375 during this same period (Table VII). The number of taxa present in these two sets of

TABLE VI

VALUES OF $\bar{d}$ FOR ACCUMULATED SAMPLES AT EACH OF THE FIVE COLLECTING STATIONS

	Sample Number				
Station	1	2	3	4	5
Station 1*	2.208	2.343	2.248	2.278	2.289
Station 2**	1.784	1.766	1.779	1.784	1.780
Station 3**	0.863	0.914	0.870	0.870	0.865
Station 4*	1.792	1.833	1.803	1.811	1.807
Station 5*	2.837	2.926	2.880	2.883	2.883

* Each sample represents 0.18 m^2.

** Each sample represents 0.10 m^2.

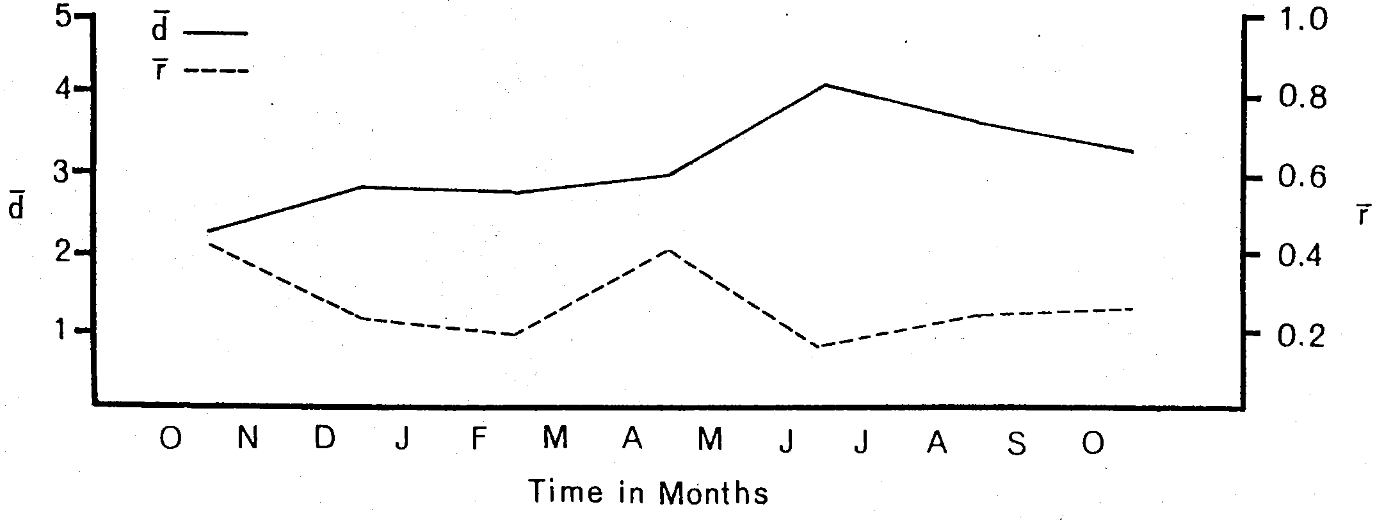

Figure 8: Values of $\bar{d}$ and $\bar{r}$ at Station 1 for Each Month of the Collecting Period

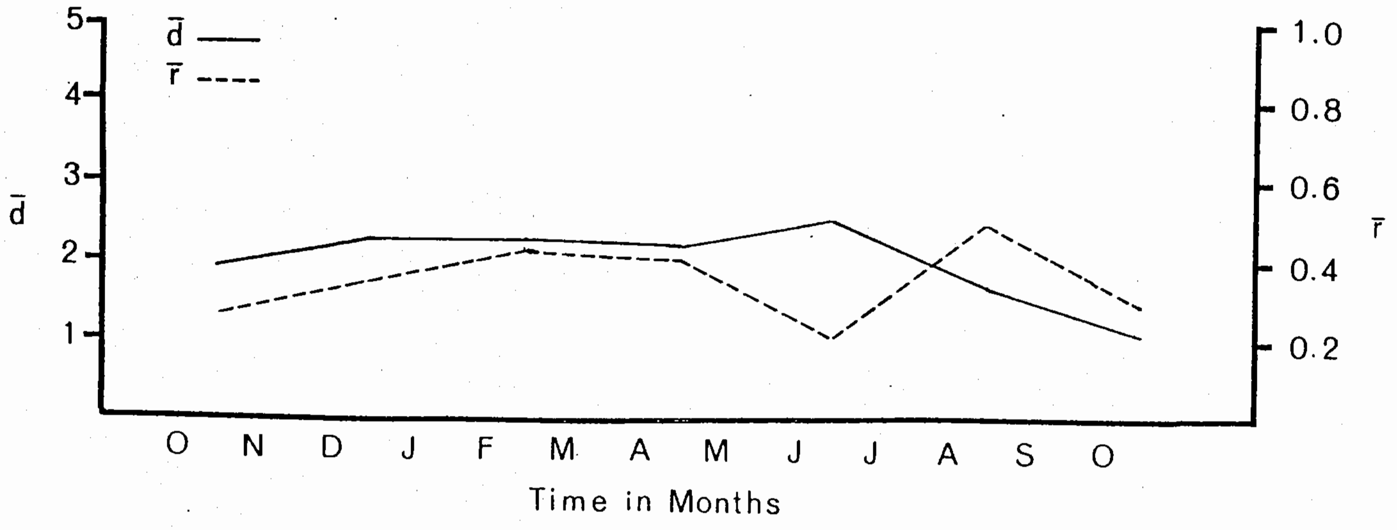

Figure 9: Values of $\bar{d}$ and $\bar{r}$ at Station 4 for Each Month of the Collecting Period

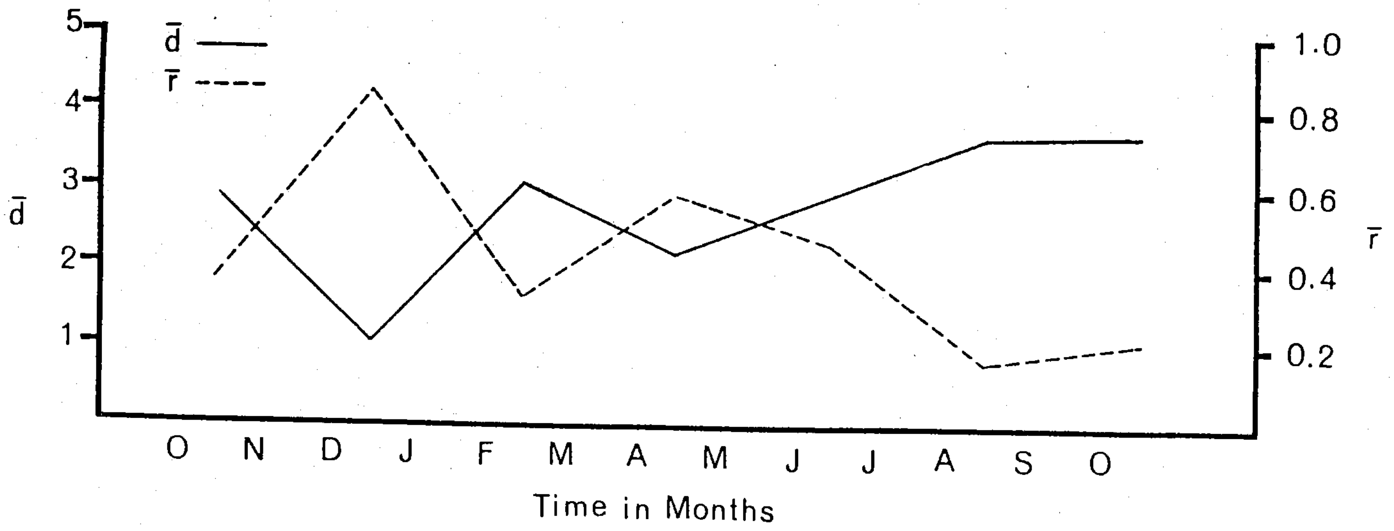

Figure 10: Values of $\overline{d}$ and $\overline{r}$ at Station 5 for Each Month of the Collecting Period

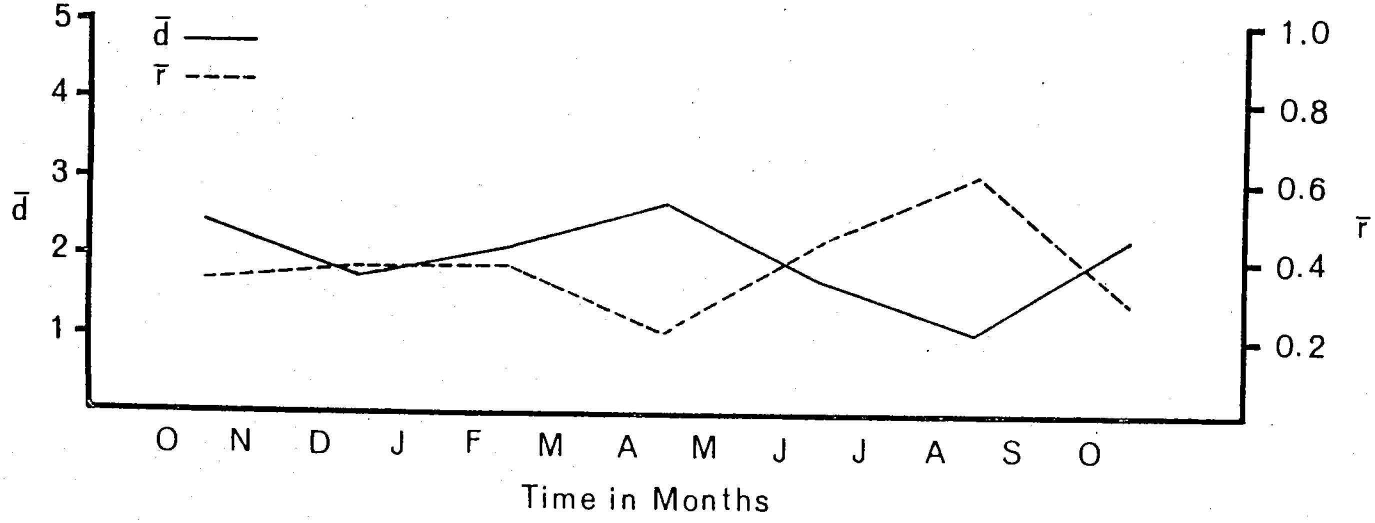

Figure 11: Values of $\bar{d}$ and $\bar{r}$ at Station 2 for Each Month of the Collecting Period

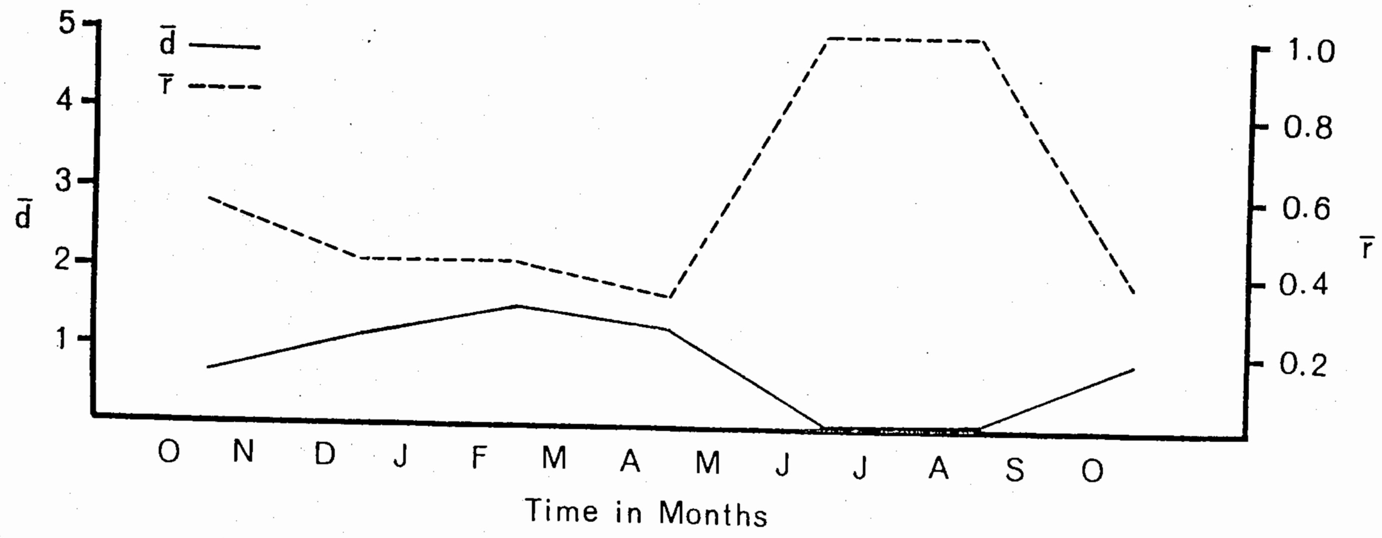

Figure 12: Values of $\bar{d}$ and $\bar{r}$ at Station 3 for Each Month of the Collecting Period

TABLE VII

VALUES OF $\bar{d}$, $\bar{r}$, NUMBER OF INDIVIDUALS PER SQUARE METER (n), AND NUMBER OF TAXA (n_i) FOR EACH COLLECTING PERIOD AT EACH OF THE FIVE COLLECTING STATIONS

		October November	December January	February March	April May	June July	August September	October
Station 1	$\bar{d}$	2.248	2.790	2.733	2.957	4.141	3.513	3.284
	$\bar{r}$	0.408	0.216	0.188	0.399	0.157	0.244	0.263
	n	60	45	93	156	197	351	249
	n_i	8	9	9	21	27	23	18
Station 2	$\bar{d}$	2.415	1.785	2.176	2.733	1.777	1.077	2.275
	$\bar{r}$	0.339	0.372	0.375	0.210	0.444	0.513	0.300
	n	1940	750	673	328	329	240	493
	n_i	11	6	9	10	7	4	8

TABLE VII--(Continued)

		October November	December January	February March	April May	June July	August September	October
Station 3	$\bar{d}$	0.672	1.149	1.542	1.287	0.000	0.000	0.918
	$\bar{r}$	0.569	0.416	0.418	0.330	1.000	1.000	0.382
	n	170	140	367	71	42	17	25
	n_i	2	3	5	3	1	1	2
tation 4	$\bar{d}$	1.934	2.263	2.247	2.160	2.550	1.694	1.155
	$\bar{r}$	0.259	0.344	0.423	0.401	0.211	0.498	0.299
	n	49	45	60	89	13	235	229
	n_i	5	7	10	10	7	8	3
tation 5	$\bar{d}$	2.925	1.007	3.050	2.158	2.815	3.650	3.704
	$\bar{r}$	0.364	0.844	0.325	0.580	0.456	0.161	0.207
	n	243	233	158	149	149	116	215
	n_i	17	8	18	13	18	17	21

collections changed from six in December and January to nine in February and March, with no particular change in the pattern of dominance in the community (Table VII).

The second condition causing changes in $\bar{d}$ was illustrated by the October-November and December-January collections at Station 1 (Figure 8). During this period $\bar{d}$ changed from 2.5 to 2.8, a change of $\bar{d}$ smaller than the change in the last example, while $\bar{r}$ changed from 0.408 to 0.216, a change in $\bar{r}$ about 64 times as great as in the last example (Table VII). In this case the change in $\bar{d}$ was caused not so much by a change in the number of taxa in the collections, which increased from eight to nine (Table VII), as it was by a change in the pattern of dominance in the community.

In the April-May collections at Station 1 a combination of both conditions occurred which, using $\bar{d}$ alone, might have gone undetected (Figure 8). The number of taxa collected at this station increased from nine in the previous sampling period to twenty-one. This should have resulted in a sizeable increase in $\bar{d}$. During this same period the number of individuals in a single taxon (<u>Thraulodes</u> sp., Ephemeroptera) increased to a value ten to twenty times greater than the number of individuals in any other taxon which canceled any significant increase in $\bar{d}$. The appearance of this one taxon as dominant in the community shows clearly as an increase of $\bar{r}$ from 0.188 to 0.399 (Table IV).

In short, while $\bar{d}$ is insensitive to the number of individuals in a sample and thus allows one to compare the species diversities of communities differing widely in their numbers of individuals, $\bar{r}$ is equally insensitive to the number of taxa in a sample and thus allows one to compare the dominance patterns of communities differing widely in their numbers of taxa.

The values of $\bar{d}$ and $\bar{r}$ at Station 1 indicated a community in which most structural changes were the appearance or disappearance of taxa while the relative distribution of individuals among the taxa remained fairly constant (Figure 8). Values of $\bar{r}$ remained less than 0.26 during the study, except for the two maxima already described, while $\bar{d}$ remained greater than 2.70, except for the minimum already described, and reached a maximum of 4.14 in the early summer (Table VII).

At Station 4, $\bar{d}$ and $\bar{r}$ remained fairly constant during the first half of the study period (Figure 9). When the hypolimnion in Canyon Reservoir became anoxic and hydrogen sulfide began to appear in the hypolimnetic water released from the dam, $\bar{d}$ decreased from a maximum of 2.55 in early summer to 1.16 in October (Figure 9; Table VII). During this time $\bar{r}$ increased from 0.211 to 0.498 for the August-September collections when the chironomid population reached a high density, and then decreased to 0.299 for the October collection as other taxa tolerant of the hydrogen sulfide in the water increased in numbers. The density of organisms at

Station 4 was much greater during the last two collecting periods than at any other time during this study, even though only three taxa were present in the October collection. This type of community structure, with a characteristically low value of $\bar{d}$, is symptomatic of communities undergoing environmental stress. The few taxa tolerant of the altered environment, with reduced competition, may reach unusually high population densities. The low value of $\bar{d}$, 1.16, for the October, 1970, collection at this station was within the range of values of $\bar{d}$ observed for streams receiving industrial or domestic wastes (Wilhm, 1969, 1970) even though there was never any evidence of pollution at any of the five stations during this study.

At Station 5, $\bar{d}$ and $\bar{r}$ had much greater ranges than at the other stations (Figure 10). At this station, $\bar{r}$ appeared to behave in inverse proportion to $\bar{d}$ throughout most of the study period. This behavior of $\bar{r}$ was caused by changes in the dominance pattern of the faunal community. These changes in the dominance pattern were also major factors influencing $\bar{d}$ at this station. The low $\bar{d}$ and the high $\bar{r}$ observed in December and January were the result of a decrease in the number of taxa in the faunal community to about half the number collected in October and November coupled with a great increase in the number of individuals of <u>Tricorythodes</u> sp., Ephemeroptera (Table VII). For the rest of the study period the numbers of taxa at this station remained very constant (Table VII) and $\bar{d}$ increased as the number of individuals of *Tricorythodes* sp. decreased.

Station 2 had an annual variation of $\bar{d}$ with maxima in the spring and fall (Figure 11). These did not correspond well with maxima at the other stations but did correspond with maxima of chlorophyll *a* observed by Young (1971) at this same station and attributed by him to mixing of nutrients into the water caused by the spring and fall overturns of the reservoir.

At Station 3 the maximum $\bar{d}$ occurred in the early spring then declined to 0.00 as all organisms other than *Branchiura sowerbyi* disappeared from the anoxic hypolimnion (Figure 12). During this time, with only one taxon present, $\bar{r}$ reached its theoretical maximum of 1.000, indicating the complete dominance of the faunal community by one taxon. The increase of $\bar{d}$ and the accompanying decrease of $\bar{r}$ for the October collection (Figure 12) was caused by the presence of a single specimen of *Chaoborus* sp. which, as has already been mentioned, was probably not at that time an active member of the faunal community at Station 3.

The lowest mean value of $\bar{d}$, 0.80, was observed at Station 3 (Figure 13). This low $\bar{d}$ was symptomatic of the severe environmental stress experienced by the faunal community at Station 3 during the warmest months while the hypolimnion was both anoxic and suffused with hydrogen sulfide. Similar low values of $\bar{d}$ have also been observed

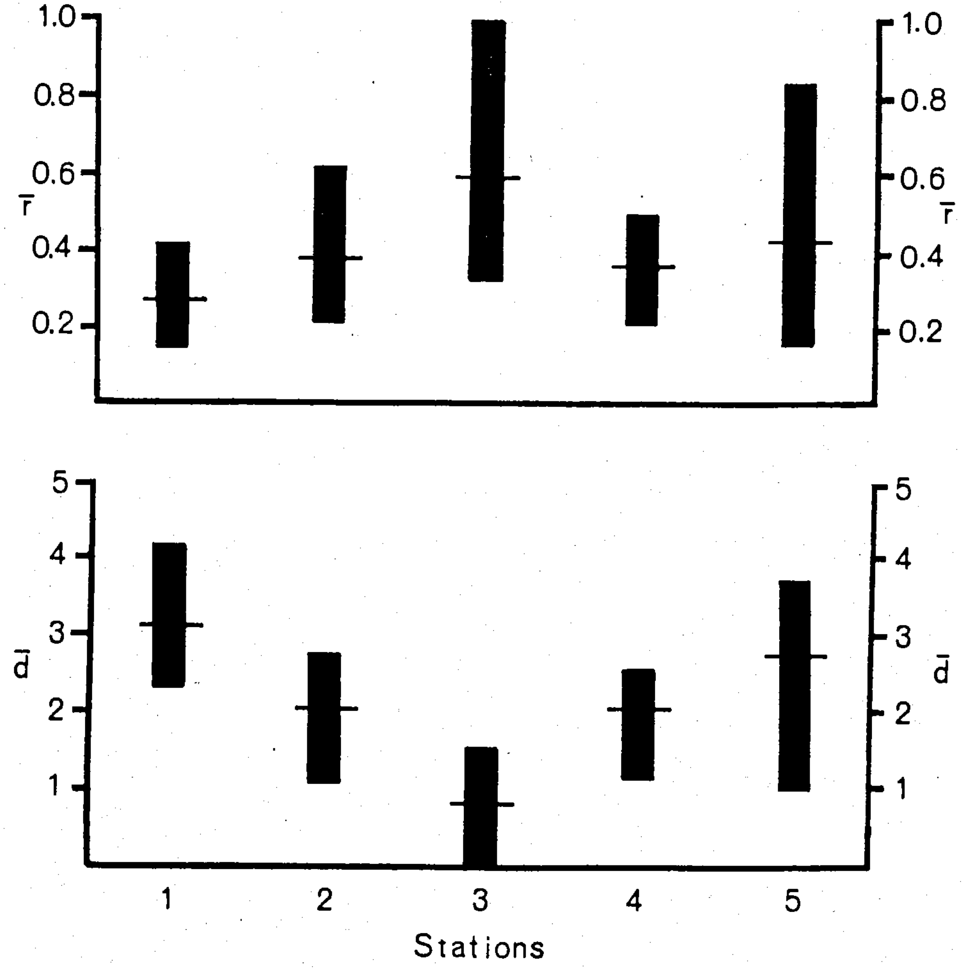

Figure 13: Mean and Range of $\bar{d}$ and $\bar{r}$ at Each of the Five Collecting Stations

in aquatic environments experiencing severe pollution (Wilhm, 1969, 1970) but, as has already been mentioned, no evidence of pollution was ever observed at any of the five collecting stations. The mean values for $\bar{d}$ of 3.12 at Station 1 and 2.73 at Station 5 (Figure 13) were similar to values for $\bar{d}$ reported from clean, nonpolluted streams in other parts of the country (Wilhm, 1969). The mean value of 2.01 for $\bar{d}$ at Station 4 indicated the faunal community at this station was experiencing some environmental stress though not so severe as that experienced at Station 3. This stress on the community at Station 4 resulted from the presence of hydrogen sulfide in the water and possibly from the lower water temperature during the warmest months which are a critical time in the reproductive cycle of many aquatic invertebrates. The mean value of 2.03 for $\bar{d}$ at Station 2, although similar to the mean value for $\bar{d}$ at Station 4, may or may not have indicated environmental stress as values of $\bar{d}$ from similar impoundments was unavailable for comparison.

The lowest mean value of $\bar{r}$, 0.27, occurred at Station 1 where the smallest range of $\bar{r}$ was also observed (Figure 13). This was due to the stability of the benthic macroinvertebrate community at this station. The highest mean value of 0.59 for $\bar{r}$ was observed at Station 3 due to the instability of this community. There were no significant differences among the mean values for $\bar{r}$ at Stations 2, 4, and 5 (Figure 13).

Similarities between Station 1 and Station 5 were apparent in the mean numbers of taxa present at both stations (Figure 2), in the mean numbers of organisms per m^2 (Figure 3), in the fluctuations of the populations of certain insects (figures 4, 5, 6, and 7), and in the mean values of $\overline{d}$ at both stations (Figure 13). The dissimilarities between Stations 1 and 5 are apparent in the faunal composition of each community (Table V), the variations of $\overline{d}$ (figures 8 and 10), the more constant number of taxa present at Station 5 (Table VII), and the mean values and ranges of values of $\overline{r}$ (Figure 13).

Station 1 was an established climax community of benthic macroinvertebrates adapted to conditions of high summer temperatures and great variations of flow. The occasional scouring of this station by freshets did not significantly effect the community structure because this community had become adapted to such occurrences through the elimination of any members which could not burrow into the substrate for protection or be carried along with the drift to other suitable habitats. Particularly affected by these freshets were the gastropods which were absent from this community. Values of $\overline{r}$ were lower at Station 1 than at Station 5 because of a more efficient utilization of niches which limited populations of individual taxa through more rigorous competition.

Station 5 represented an environment not more than five years old with a correspondingly young community of benthic macroinvertebrates. The original macroinvertebrate community in this stretch of the Guadalupe River was probably very similar to the community found at Station 1. With the filling of Canyon Reservoir, however, the flow was stabilized (Table III), almost completely eliminating scouring of the stream bed, and the average water temperature was reduced (Table IV) with the greatest reduction coming during the warmest months, a critical time in the reproductive cycle of many aquatic invertebrates. The high values of $\bar{d}$ indicate successful reorganization of the benthic macroinvertebrate community to fill the new set of niches made available by the change in environment, but the high values of $\bar{r}$ and the wide ranges of values of $\bar{d}$ and $\bar{r}$ probably indicate a community still involved in secondary succession.

The benthic macroinvertebrate community at Station 4 had to cope with hydrogen sulfide and an even greater reduction in temperature in the hypolimnetic water released from Canyon Reservoir during the warm months than did the faunal community at Station 5. The resulting environmental stress caused a decline in the number of taxa at Station 4 similar to a reduction in the number of taxa of benthic macroinvertebrates below a bottom draining reservoir in Canada reported by Spence and Hynes (1971a). This environmental stress was also indicated by a reduction of $\bar{d}$ to a value similar to values of $\bar{d}$ recorded for streams undergoing environmental stress from industrial or domestic pollution, although no such pollution was ever in evidence.

The construction and subsequent filling of Canyon Reservoir on the Guadalupe River has resulted in sizeable changes in the benthic macroinvertebrate communities in the reservoir and in the Guadalupe River below the reservoir. The changes of the benthic macroinvertebrate community within the reservoir came from the adaptation of the existing lotic faunal community to a lentic environment. The changes of the benthic macroinvertebrate community in the Guadalupe River below the reservoir were a result of a reduction of the water temperature during the warm months, the elimination of scouring by freshets, and, in the stretch of river immediately below the reservoir, the presence of hydrogen sulfide in the water. Except for the stretch of river just below the reservoir, the diversity of the faunal community below the reservoir was almost as high as the diversity of similar stretches of the river above the reservoir. In the Guadalupe River just below Canyon Reservoir, and in the deepest parts of Canyon Reservoir, there was evidence of severe environmental stress occurring during the warmest months of the year.

CHAPTER V

SUMMARY

A biological survey was undertaken to determine the effects of Canyon Reservoir, a bottom-draining deep-storage impoundment, on the benthic macroinvertebrate community of the Guadalupe River. Community structure was analyzed using two diversity indices, $\bar{d}$, which has frequently been used to analyze communities in polluted streams, and $\bar{r}$, an index proposed by the author. Both proved to be effective in analyzing the structure of natural aquatic communities.

Collections of organisms were made once a month at five stations located above, below, and in Canyon Reservoir from October, 1969, to October, 1970. These collections were combined into two-month sets for statistical analysis.

From May through October, 1970, Canyon Reservoir was stratified and for most of this time the hypolimnion was anoxic. During most of this time only one species, *Branchiura sowerbyi*, was collected from the deep collecting station in the reservoir. Diversity maxima were observed in the shallow benthic macroinvertebrate community in Canyon Reservoir in the spring and fall at the same time that maxima were observed for planktonic chlorophyll *a*. These were times when maximum mixing of nutrients and dissolved oxygen occurred in Canyon Reservoir.

Below Canyon Reservoir there was a reduction in water temperature, a reduction in the scouring effects of freshets, and the occurrence of hydrogen sulfide in the water as a result of anaerobic reduction of sulfates by thio-bacteria in the hypolimnion of the reservoir during the warmer months.

Although there was considerable change in the faunal composition of the benthic macroinvertebrate community below the reservoir as compared to the benthic macroinvertebrate community above the reservoir, the diversity of the benthic macroinvertebrate community 23.7 km below the reservoir was as high as the diversity of a similar community above the reservoir. Immediately below the dam, however, there was a considerable reduction in the diversity of the benthic macroinvertebrate community due to the reduced water temperature combined with the occurrence of hydrogen sulfide in the water during the warmest months.

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