Tony

THE INFLUENCE OF A DEEP STORAGE RESERVOIR ON THE SPECIES DIVERSITY OF BENTHIC MACROINVERTEBRATE COMMUNITIES OF THE GUADALUPE RIVER, TEXAS

by WILLARD C. YOUNG, DAVID H. KENT, and
BOBBY G. WHITESIDE

Aquatic Station, Biology Department, Southwest Texas State University, San Marcos 78666

Reprinted from THE TEXAS JOURNAL OF SCIENCE
Volume XXVII, No. 1, March, 1976

THE INFLUENCE OF A DEEP STORAGE RESERVOIR ON THE SPECIES DIVERSITY OF BENTHIC MACROINVERTEBRATE COMMUNITIES OF THE GUADALUPE RIVER, TEXAS

by WILLARD C. YOUNG, DAVID H. KENT, and
BOBBY G. WHITESIDE

Aquatic Station, Biology Department, Southwest Texas State University, San Marcos 78666

ABSTRACT

A comparison was made of the species diversity ($\bar{d}$) of the benthic macroinvertebrate communities during an annual cycle at 5 stations located in, above, and below Canyon Reservoir, a deep storage reservoir on the Guadalupe River in central Texas. New equations were derived for maximum diversity ($\bar{d}$max) and minimum diversity ($\bar{d}$min) which were utilized in calculating a new redundancy value ($\bar{r}$) which can be used for small sample sizes.

Pronounced differences were found in the structure of the faunal communities at the 5 stations as indicated by values of $\bar{d}$ and $\bar{r}$. The river above the reservoir had a community in which structural changes throughout the year resulted from the appearance and disappearance of taxa while there was no marked dominance of any one taxon. Such a condition normally exists in unpolluted shallow streams. The river immediately below the reservoir had a community with few taxa each represented by numerous individuals, a condition characteristic of communities undergoing environmental stress. Apparently this stress was created by low water temperatures and the presence of hydrogen sulfide. Further downstream the community had wide seasonal fluctuations in diversity due primarily to changes in the dominance of certain taxa. The deep reservoir station had a community influenced mostly by low temperatures, low oxygen, and high hydrogen sulfide which resulted from thermal stratification. During stratification $\bar{d}$ reached its theoretical minimum and $\bar{r}$ its theoretical maximum, indicating severe environmental stress. The station located in a shallow cove had a community structure indicating mild environmental stress. Detrimental effects of impoundment appear limited to the reservoir and the region immediately below the dam.

INTRODUCTION

The effects of artificial impoundments upon streams below the impoundments are being increasingly investigated as more interest is generated in man's influence upon water quality. Since it has been recommended that water quality be defined using biological rather than physicochemical standards (Butcher, 1955; Wilhm and Dorris, 1968), the study of the effect of im-

The Texas Journal of Science, Vol. XXVII, No. 1, March, 1976.

poundment upon community structure is a reasonable approach. One of the simplest and most promising methods of determining environmental influence on community structure has been through the development of species or community diversity indices (Fisher, *et al.,* 1943; Williams, 1944, 1953; Preston, 1948; Simpson, 1949; Margalef, 1951, 1956; Patten, 1962; Menhinick, 1964; Pileou, 1966; Wilhm and Dorris, 1966, 1968; Wilhm, 1967, 1968a, 1968b). Benthic macroinvertebrates make ideal subjects for such studies due to their habitat preference and low motility (Wilhm and Dorris, 1966). Though Spence and Hynes (1971a, 1971b) have utilized the community structure approach to investigate the effect of an artificial impoundment upon the benthic macroinvertebrates and certain fishes in a Canadian stream, community diversity indices have not been employed to determine how impoundment of water influences benthic populations.

The purpose of this study was to determine the effect of Canyon Reservoir, a deep storage impoundment formed by damming the Guadalupe River in the Edwards Plateau region of central Texas, upon the benthic macroinvertebrate communities of the Guadalupe River by measuring changes in species diversity in communities above, below, and within the reservoir through an annual cycle.

METHODS AND MATERIALS

Study Area

Canyon Reservoir which covers 3,335 ha was formed in 1964 by a dam 35 km upstream from New Braunfels, and is the only major impoundment on the Guadalupe river in the Edwards Plateau region of central Texas. This region was classified as the Balconian Province by Blair (1950) and is characterized by limestone hills covered with a scrubby growth of *Quercus virginiana, Q. texana,* and *Juniperus mexicana.* Average rainfall in this area is 86 cm received mostly in late spring and early fall.

Five stations were sampled, 3 in the river and 2 in the reservoir. Station 1 was located immediately downstream from the highway FM 311 bridge and 15 km above the upper end of Canyon Reservoir. Station 4 was located immediately below Canyon Dam and Station 5 was established 24 km further downstream at the Hueco Springs bridge. These stations in the river were chosen for their physical similarities; all were located in riffle areas, on gravel substrate, as devoid of vegetation as possible.

Stations 2 and 3 were established within the reservoir. Station 2 was located in a shallow cove, 4 km above the dam where depth varied from 3-5 m due to changes in the level of the reservoir. The substrate of detritus supported a dense growth of *Najas quadalupensis* during the spring and summer. Station 3 was located near the dam over the inundated river bed in the deepest part of the reservoir. Bottom topography was precipitous and sampling depths ranged from 36-61 m while the substrate consisted of sand and clay mixed with detritus. No rooted macrophytes were collected at this station.

Sampling Techniques

Stations 1, 4 and 5 were sampled with a Surber square foot sampler which had a net with 12 meshes per cm. Stations 2 and 3 were sampled with an Ekman dredge. Samples were taken monthly at each station from October 1969, through October 1970. Adequate sample size was determined during the first collecting period at each station by combining samples until $\bar{d}$ approached an asymptote as described by Pielou (1966) and Wilhm (1968b). At all 5 stations, $\bar{d}$ approached an asymptote by the first 2 accumulated samples. The sample size for the remaining collections in this study were established as $0.9m^2$ at Stations 1, 4, and 5 and as $0.2m^2$ 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 original plan was to combine the samples from each station seasonally as was done by Wilhm and Dorris (1966) but it was found that 2 month sets of data were more informative.

Statistical Methods

Initially the diversity calculations for samples were made using equations for $\bar{d}$, d, dmax, dmin and R (Wilhm, 1967). After we encountered difficulty in applying the 4 latter equations to the data, Dr. Wilhm was consulted. He advised that these equations are useful only when the total number of individuals in a sample is fairly large, at least 100. Since many samples consisted of less than 100 individuals, alternatives to these equations were sought. Utilizing some of the properties of $\bar{d}$ 3 modified equations were derived.

Maximum values of $\bar{d}$ are observed if all the individuals in a sample are equally divided among the taxa present in that sample, and minimum values of $\bar{d}$ are observed if each taxon in the sample contains one individual, except one which contains all the rest of the individuals in the sample.

In a sample where the maximum value of $\bar{d}$ ($\bar{d}$max) occurs, each taxon would have the same number of individuals, or

$$n_1 = n_2 = n_3 = \ldots = n_i = \ldots = n_s = n/s$$

where s is the number of taxa in the sample, n_i is the total number of individuals in the i^{th} taxon and n is the total number of individuals in the sample. Substituting these values into the equation for $\bar{d}$ we get,

$$\bar{d}\text{max} = \log_2 s.$$

In a sample where the minimum value of $\bar{d}$ ($\bar{d}$min) occurs, (s – 1) taxa in the sample would have one individual each ($n_1 = n_2 = n_3 = \ldots = n_{s-1} = 1$), while the remaining taxon has the remaining individuals $[n_s = n - (s - 1)]$. Substituting these values for n_i into the equation for $\bar{d}$,

$$\bar{d}\text{min} = -\left[\frac{s-1}{n}\log_2\frac{1}{n}\right] - \left[\frac{n-(s-1)}{n}\log_2\frac{n-(s-1)}{n}\right].$$

The value of $\bar{d}$ relative to $\bar{d}$max and $\bar{d}$min is a measure of the dominance of one or a few taxa over the remaining taxa in the community being sampled and can be calculated as the average redundancy per individual in the community ($\bar{r}$). This equation is,

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

The values of $\bar{r}$ behave much as do those for R. As $\bar{r}$ increases, the average amount of information carried by an individual selected at random from the sample decreases, the uncertainty that such an individual belongs to a particular taxon increases, and the average diversity per individual ($\bar{d}$) decreases. The great advantage of $\bar{r}$ over R is that it can be calculated from any size sample and with much less effort.

Wilhm and Dorris (1968) proposed equations for $\bar{d}$max, $\bar{d}$min, and r. These equations, however, have the same drawbacks as do those for dmax, dmin and R in that they require a fairly large sample size.

RESULTS AND DISCUSSION

Meteorological Conditions

From October 1969, through May 1970, precipitation at Canyon Dam, as measured by the United States Army Corps of Engineers, was approximately 20% above the average for those months for the previous 7 years. From June to October 1970, rainfall totaled only about 2/3 of the average amount for those months.

Air temperatures during the study period followed a normal seasonal pattern with lows of 14° C in November and December and highs of 32° C in July and August. An exception to the normal pattern was an unseasonal warm period in January 1970, when air temperatures of 21° C were recorded.

Physiochemical Conditions

Flow in the Guadalupe River, according to the Guadalupe-Blanco River Authority, declined during the latter part of the study period with a more constant day to day flow at Stations 4 and 5 than at Station 1 due to controlled discharge.

The lowest water temperatures were recorded in January and February 1970, and the highest water temperatures occurred in July and August 1970. The overall effect of impoundment was to stabilize and lower the water temperatures at Stations 3, 4, and 5. Water temperatures at Station 2 were generally slightly warmer than at Station 1, probably due to more direct insolation at Station 2.

Chemical analyses of water conducted by Young (1971) within the study area simultaneously with this study showed lower ranges and means in total alkalinity, specific conductance, and turbidity below the reservoir. Dissolved oxygen was usually higher at Station 1 than in the reservoir. A thermocline was observed at Station 3 in May 1970, and dissolved oxygen was depleted in the hypolimnion so that anoxic conditions prevailed from June 1970 until the end of the study. However, hypolimnetic water discharged from Canyon Reservoir was rapidly reaerated in the tailrace, so that dissolved oxygen at Stations 4 and 5 was near saturation. The pH at all stations remained near 8.0 except for readings of pH 7.1 while hypolimnion was anoxic at Station 3. Total dissolved solids were higher at Station 1 than at other stations. Hydrogen sulfide was noted in the hypolimnion at Station 3 and at Station 4 during the time the hypolimnion was anoxic, apparently due to the sulfur-reducing action of bacteria. During the time hydrogen sulfide was observed, dense growths of the sulfur bacteria *Beggiatoa* sp. covered the entire substrate at Station 4. The simultaneous occurrence of high dissolved oxygen concentrations and hydrogen sulfide at Station 4 when the hypolimnion was anoxic resulted from the rapid turnover of water in the tailrace. The large volume of hydrogen sulfide flowing from the hypolimnion was being oxidized at Station 4 but oxidation was not complete by the time the water reached that point.

Community Diversity

The annual variations of $\bar{d}$ and $\bar{r}$ at each station show $\bar{r}$ to vary in roughly inverse proportion to $\bar{d}$ (Fig. 1). 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 (Fig. 1). Values of $\bar{d}$ varied from 1.78 for the December-January collections to 2.18 for the February-March collections, while $\bar{r}$ varied from 0.37 to 0.38 during this same period. The number of taxa present in these 2 sets of collections changed from 6 in December-January to 9 in February-March, with no particular change in the pattern of dominance in the community (Table 1).

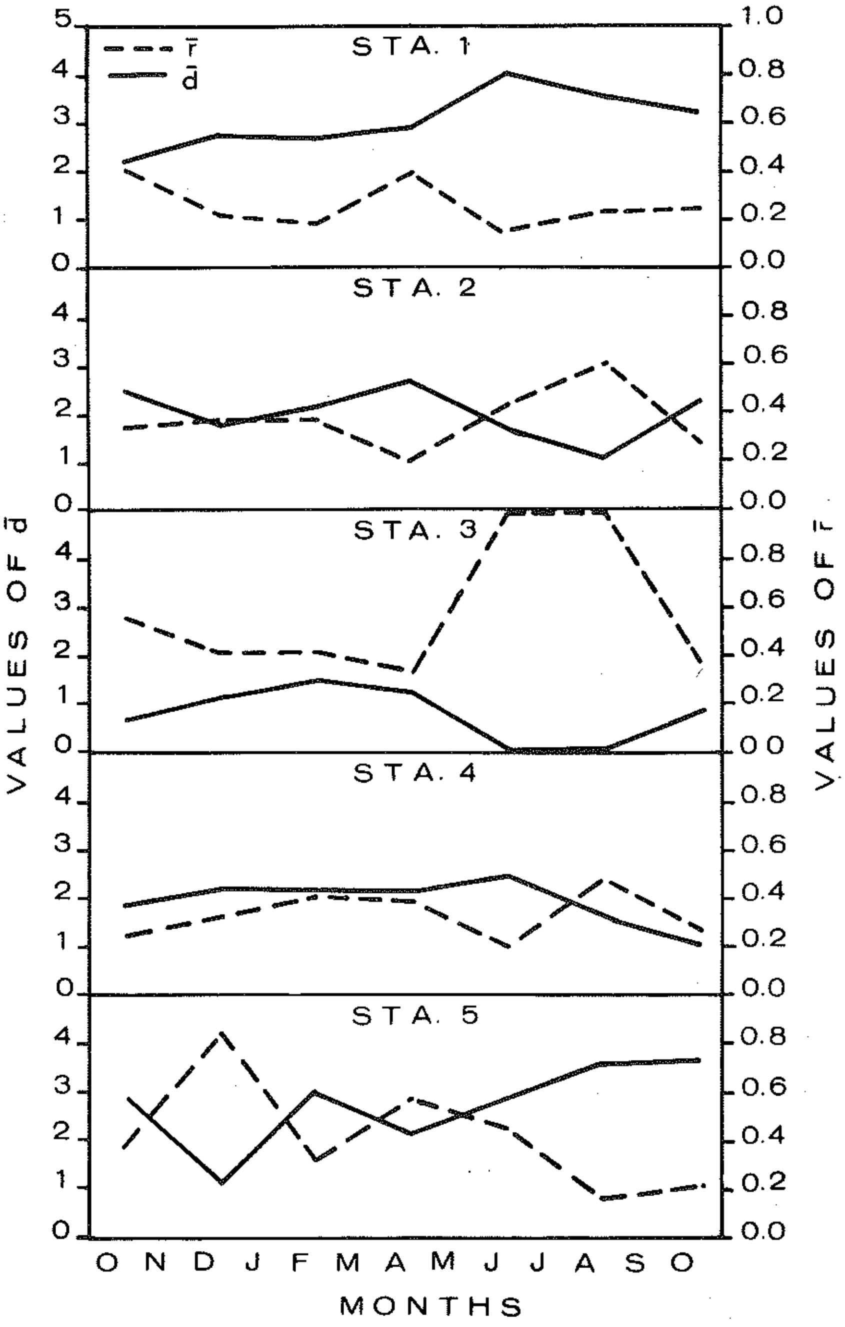

Figure 1. Values of d̄ and r̄ at each of 5 collecting stations for each 2 month collecting period.

Table 1. Number of individuals per square meter (n), and number of taxa (n_i) for each collecting period at each of the 5 collecting stations.

		Oct.– Nov.	Dec.– Jan.	Feb.– Mar.	Apr.– May	June– July	Aug.– Sept.	Oct.
Station 1	n	60	45	93	156	197	351	249
	n_i	8	9	9	21	27	23	18
Station 2	n	1940	750	673	328	329	240	493
	n_i	11	6	9	10	7	4	8
Station 3	n	170	140	367	71	42	17	25
	n_i	2	3	5	3	1	1	2
Station 4	n	49	45	60	89	13	235	229
	n_i	5	7	10	10	7	8	3
Station 5	n	243	233	158	149	149	116	215
	n_i	17	8	18	18	18	17	21

The second condition causing changes in $\bar{d}$ was illustrated by the October-November and December-January collections at Station 1 (Fig. 1). During this period $\bar{d}$ changed from 2.25 to 2.79, a change of $\bar{d}$ of roughly the same magnitude as in the previous example, while $\bar{r}$ changed from 0.41 to 0.22, a change 64 times as great as in the previous example. 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 8 to 9 (Table 1), as by a change in the pattern of dominance is clearly shown by the change in $\bar{r}$.

In the April-May collections at Station 1 a combination of both conditions occurred which, using $\bar{d}$ alone, might have gone undetected (Fig. 1). The number of taxa collected at this station as compared to the February-March collection increased from 9 to 21. This should have resulted in a sizeable increase in $\bar{d}$. However, the change in $\bar{d}$ was only slight, from 2.73 to 2.96. During this same period the number of individuals in a single taxon (*Thraulodes* sp., Ephemeroptera) increased to a value 10 to 20 times greater than the number of individuals in any other taxon which cancelled 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 0.19 to 0.40 (Fig. 1).

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

Both $\bar{d}$ and $\bar{r}$ reveal certain characteristics of the 3 stations located in free-flowing stretches of the river. The values of $\bar{d}$ and $\bar{r}$ at Station 1 indicate a community in which most structural changes resulted from the appearance or disappearance of taxa while the relative distribution of individuals among the taxa remained fairly constant (Fig. 1). Values of $\bar{r}$ remained less than 0.26 during the study, except for the 2 maxima already described, while $\bar{d}$ remained greater than 2.73, except for the minimum already described, and reached a maximum of 4.14 in the early summer (Fig. 1).

At Station 4, $\bar{d}$ and $\bar{r}$ remained fairly constant during the first half of the study period (Fig. 1). 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 (Fig. 1). During this time $\bar{r}$ increased from 0.21 to 0.50 for the August-September collections when the chironomid population reached a high density, and then decreased to 0.30 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 2 collecting periods than at any other time during this study, even though only 3 taxa were present in the October collection. This type of community structure, with a charcteristically low value of $\bar{d}$, is typical 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) though there was no evidence of pollution at any of the 5 stations during this study.

At Station 5, $\bar{d}$ and $\bar{r}$ fluctuated more than at the other stations (Fig. 1). 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 in the benthic 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-January collections were the result of a decrease in the number of taxa in the faunal community to about half the number collected in October-November coupled with a great increase in the number of individuals of *Tricorythodes* sp., Ephemeroptera (Fig. 1, Table 1). For the rest of the study period the numbers of taxa at this station remained constant (Table 1) and $\bar{d}$ increased as the number of individuals of *Tricorythodes* sp. decreased.

Community structure of the lake stations was also revealed by values of $\bar{d}$ and $\bar{r}$. Station 2 had an annual variation of $\bar{d}$ with maxima in the spring and fall and $\bar{r}$ followed an inverse pattern (Fig. 1). These variations 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 early spring then declined to 0.00 as all organisms other than *Branchiura sowerbyi* disappeared from the anoxic hypolimnion (Fig. 1). During this time, with only one taxon present, $\bar{r}$ reached its theoretical maximum of 1.00, 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 (Fig. 1) was caused by the presence of a single specimen of *Chaoborus* sp. which was probably not at that time an active member of the faunal community at Station 3.

Mean values of $\bar{d}$ and $\bar{r}$ also reveal community structure characteristics of the different stations. The lowest mean value of $\bar{d}$, 0.80, was observed at Station 3 (Fig. 2). This low $\bar{d}$ was the result of 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. The mean values for $\bar{d}$ of 3.12 at Station 1 and 2.73 at Station 5 (Fig. 2) on the other hand, 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 benthic 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 summer which is a critical time in the reproductive cycle of many aquatic invertebrates. The mean value of 2.03 for $\bar{d}$ at Station 2, apparently indicates environmental stress, though values of $\bar{d}$ from similar impoundments were 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 (Fig. 2). 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 (Fig. 2).

A comparison of the free-flowing river stations, Stations 1, 4 and 5, show each to be distinctly different. Station 1 and Station 5 were similar in the mean value of $\bar{d}$ at both stations (Fig. 2), but dissimilar in the variations of $\bar{d}$ (Fig. 1), the more constant number of taxa present at Station 5 (Table 1) and mean values and ranges of values of $\bar{r}$ (Fig. 2). 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 freshests did not significantly affect the community structure because this community had become adapted to such occurrences through the elimination of any organisms which could not burrow into the substrate

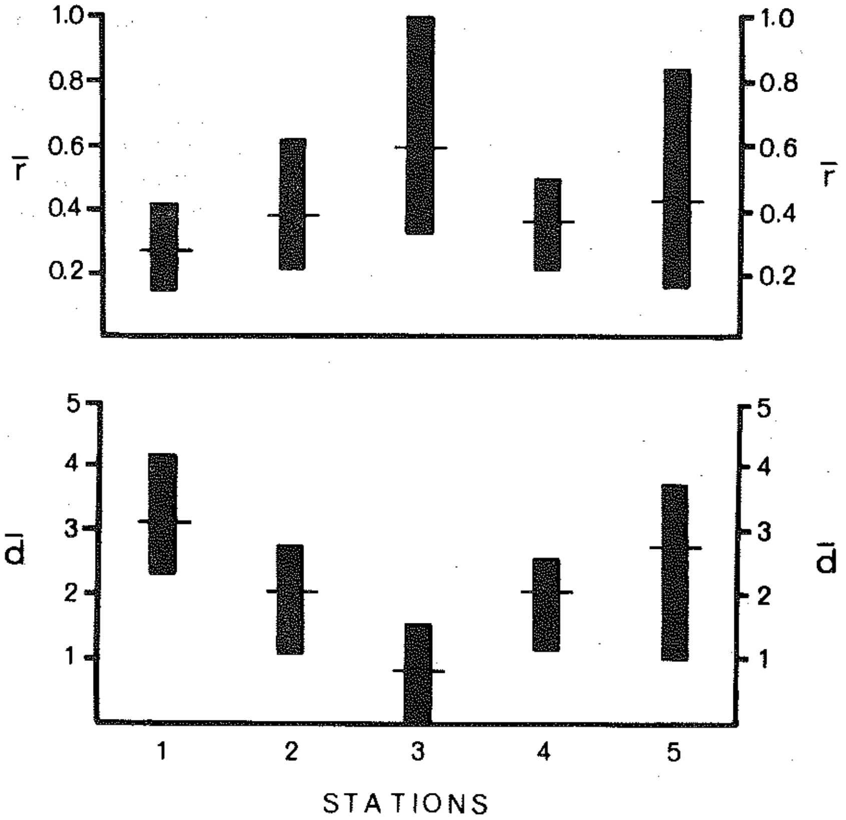

Figure 2. Means and ranges of d̄ and r̄ at each of 5 collecting stations. Horizontal line represents the mean and vertical bar represents the observed range.

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 r̄ were lower at Station 1 than at Station 5 which may have resulted from more efficient utilization of niches which limited populations of individual taxa through more rigorous competitions.

Station 5 represented an environment not more than 5 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, almost completely eliminating scouring of the stream bed. The mean water temperature at Station 5 was also lower (mean 17.9° C) and more stable (range 11.5 – 26.0° C) than at Station 1 (mean 20.2° C, range 8.0 – 29.5° C) and the greatest reduction in temperature occurred during the warmer months which is 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 changes in the environment, but the high values of $\bar{r}$ and the wide ranges of values of $\bar{d}$ and $\bar{r}$ (Fig. 2) possibly indicate a community still involved in secondary succession.

The benthic macroinvertebrate community at Station 4 was influenced by the hydrogen sulfide and low temperatures in the hypolimnetic water released from Canyon Reservoir during the warm months more than the community at Station 5. As a result of the environmental stress created by these factors, Station 4 was distinctly different from either Station 1 or 5. Spence and Hynes (1971a) reported that similar environmental stress caused a decline in the number of taxa of benthic macroinvertebrates below a bottom draining reservoir in Canada.

Thus, the construction and subsequent filling of Canyon Reservoir on the Guadalupe River has resulted in appreciable changes in the benthic macroinvertebrate communities in the reservoir and in the Guadalupe River below the reservoir. However, evidence that the quality of water released from the reservoir has been only temporarily lowered is shown by the high species diversity at Station 5. Although the community at that station is dissimilar to that at Station 1 due to altered environmental conditions, the high species diversity indicates the stream has largely recovered from adverse environmental effects resulting from impoundment. Detrimental effects of impoundment appear limited to the impoundment itself and the river stretch immediately below the dam.

ACKNOWLEDGMENTS

The authors wish to thank Dr. J. L. Wilhm, Oklahoma State University, for his advice concerning species diversity indices. Aid rendered by the Computer Center of Southwest Texas State University is gratefully acknowledged.

LITERATURE CITED

Blair, W. F., 1950–The biotic provinces of Texas. *Tex. Jour. Sci.* 2: 93-117.

Butcher, R. W., 1955–Relation between the biology and the polluted condition of the Trent. *Verhandl. Int. Ver. Limnol.* 12: 823-827.

Fisher, R. A., A. S. Corbet, and C. B. Williams, 1943–The relation between the number of individuals in a random sample of an animal population. *Jour. Anim. Ecol.* 12: 42-58.

Margalef, R., 1951–Diversidad de especies en las comunidades naturales. *Pub. Inst. Biol.*

Apl. (Barcelona) 9: 5-27.

———, 1956–Informacion y diversidad especifica en las comunidades de organismos. *Invest. Pesq.* 3: 99-106.

Menhinick, E. F., 1964–A comparison of some species-individuals diversity indices applied to samples of field insects. *Ecology* 45: 859-861.

Patten, B. C., 1962–Species diversity in net phytoplankton of Raritan Bay. *Jour. Marine Res.* 20: 57-75.

Pileou, E. C., 1966– The measurement of diversity in different types of biological collections. *Jour. Theor. Biol.* 13: 131-144.

Preston, F. W., 1948–The commonness, and rarity, of species. *Ecology* 29: 254-283.

Simpson, E. H., 1949–Measurement of diversity. *Nature* 163: 688.

Spence, J. A. and H. B. N. Hynes, 1971a–Differences in benthos upstream and downstream of an impoundment. *Jour. Fish. Res. Board Canada* 28: 35-43.

——— and ———, 1971b–Differences in fish populations upstream and downstream of a mainstream impoundment. *Jour. Fish. Res. Board Canada* 28: 45-46.

Wilhm, J. L. 1967–Comparison of some diversity indices applied to populations of benthic macroinvertebrates in a stream receiving organic wastes. *Jour. Water Pol. Cont. Fed.* 39: 1673-1683.

———, 1968a–Use of biomass units in Shannon's formula. *Ecology* 49: 153-156.

———, 1968b–Use of a statistical technique for recommending sample size in collecting benthic macroinvertebrate populations. *Proc. Okla. Acad. Sci.* 47: 159-161.

———, 1969–Community diversity. The stream ecosystem. *Inst. of Water Res., Michigan State Univ. Tech. Rep.* No. 7: 8-13.

———, 1970–Range of diversity index in benthic macroinvertebrate populations. *Jour. Water. Pol. Cont. Fed.* 42: 221-224.

——— and T. C. Dorris, 1966–Species diversity of benthic macroinvertebrates in a stream receiving domestic and oil refinery effluents. *Amer. Midl. Nat.* 76: 427-449.

——— and ———, 1968–Biological parameters of water quality. *Bioscience* 18: 477-481.

Williams, C. B., 1944–Some applications of the log-arithmetic series and the index of diversity to ecological problems. *Jour. Ecol.* 32: 1-44.

———, 1953–The relative abundance of different species in a wild animal population. *Jour. Anim. Ecol.* 22: 14-31.

Young, W. J., 1971–The influence of impoundment and thermal stratification in Canyon Reservoir on the physicochemical limnology and chlorophyll a of the Guadalupe River, Texas. Unpublished M. A. Thesis, Southwest Texas State University, San Marcos.