THE EFFECTS OF PHYSICOCHEMICAL CONDITIONS ON THE DISTRIBUTION OF BENTHIC MACROINVERTEBRATES IN ARBUCKLE RESERVOIR

Ву

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PREFACE

In the present study I attempted to determine the depth and seasonal variation in diversity and composition of benthic macro-invertebrates in Arbuckle Reservoir as measured by species diversity, variety, and equitability. I also studied the influence of physicochemical conditions on the distribution of the benthos in the reservoir.

I express appreciation to my parents and my wife for helping me through graduate school. I thank Dr. Jerry L. Wilhm for his time, effort, and support as my thesis adviser, and Drs. Troy C. Dorris and Sterling L. Burks who served as members of my advisory committee. I also thank Carl J. Ferraris for identifying the summer macroinvertebrate collection and for helping me identify the January and May samples, Nancy McClintock and James Seyfer for help in the design and analysis of the study, and Susan Durham, Michael O'Hara, David Parrish, and Jerry Wilhm III for field and laboratory assistance.

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CHAPTER I

INTRODUCTION

Considerable variation exists in species composition and abundance of benthic macroinvertebrates with depth in lakes and ponds. Individual species may aggregate at one depth range forming a characteristic concentration zone (Eggleton 1931). Dugdale (1955) found a pronounced maximum of diptera larvae in the sublittoral zone of a stratified eutrophic lake. Mundie (1955) observed a distinct zonation of species of Tanypodinae from shallow to deep water in a temperate storage reservoir. Maximum abundance of individuals and species has been shown to occur in a well defined intermediate depth zone (Eggleton 1952). Although depth preferences of many individual species have been well documented, less is known about the changes with depth of the entire invertebrate assemblage.

Seasonal variation in species composition and abundance of benthic macroinvertebrates is pronounced. Generally, biomass and numbers of individuals are at maximum in winter and minimum in summer in temperate lakes (Anderson and Hooper 1956, Hubert and Krull 1973). Numbers of species may decrease from winter to summer (Ransom and Dorris 1972), but may also be reduced in midwinter (Hubert and Krull 1973).

Differences in life history events of a species such as emergence and egg laying times cause changes in relative numbers of individuals within species and therefore in species composition and diversity of

the assemblage (Mundie 1957). Concentration zones shift to deeper water in winter and toward shallow water in summer (Eggleton 1931).

Maximum density of Chaoborus larvae shifted from the littoral to profundal zone in fall and early winter and returned in late spring (Wood 1956). A similar shift of Chaoborus larvae density was noted in Lake Beloie, U.S.S.R. (Borutsky 1939). The causes of these movements are not well defined.

Several physicochemical factors influence the temporal and spatial distribution of benthic macroinvertebrates. Oxygen content at the mud-water interface is of major importance in influencing the distribution of the benthos (Ruttner 1963, Brundin 1951). Water temperature probably alters the distribution of benthic macroinvertebrates (Lundbeck 1926 cited by Eggleton 1934, Borutsky 1939). Other possible influences are light intensity at the bottom and pH of the sediments (Hilsenhoff and Narf 1968), organic content of the sediments (Gleason 1961, McLachlan and McLachlan 1971, Wene 1940), substrate type (Beatty and Hooper 1958, Eggleton 1952), and substrate particle size (Eriksen 1964, Wene 1940). Concentration zones may be the result of an optimum interaction of edaphic and physical factors (Lundbeck 1926 cited by Dugdale 1955). More study is needed to clarify the relationships between physicochemical factors and distribution of the benthic assemblage.

The relationship between individuals and species can be calculated by the Shannon-Weaver equation (\overline{d}) . This index of diversity has been shown to be effective in reflecting changes in the composition of the benthic assemblage caused by variation of environmental conditions (Wilhm and Dorris 1966, 1968). Additional information may be obtained

by calculating evenness and variety. Galat (1974) found that evenness reflected the effect of slight differences in organic enrichment on the structure of the benthic invertebrate assemblage. Wilhm (1967) found that variety distinguished among areas of varying organic enrichment as reflected by the benthic macroinvertebrates.

The purpose of the present study is to determine (1) depth and seasonal variation in species diversity and composition of benthic macroinvertebrates in a lake and (2) the effect of physicochemical conditions on these variations.

CHAPTER II

REVIEW OF LITERATURE

Quantitative and qualitative differences exist in abundance and composition of benthic macroinvertebrates among depths in lacustrine systems. Early authors observed depth preferences of various invertebrate species (Juday 1923, and Muttkowski 1918). Juday (1921) reported that Chaoborus punctipennis larvae preferred deeper areas of Lake Mendota. Greatest densities of Hexagenia sp. were reported at 5 to 7 m (Cowell and Hudson 1969, Craven and Brown 1969b, Swanson 1967). Concentration zones were noted in several studies. Deevey (1941) classified lakes on the basis of the distribution of chironomid fauna and showed concentration zones of several species. Mundie (1957) described the concentration zones of many species of chironomid larvae in storage reservoirs. Varying depth preferences of benthic macroinvertebrates may produce changes in dominance as depth increases. Bardach et al. (1951) found molluscs and chironomids at 10 to 15 m, Chironomus plumosus and C. decorus at 15 to 25 m, and Tubifex sp. and Limnodrilus sp. below 25 m. Biomass and density tend to be lowest in deepest areas of lakes and ponds. In Lake Ashtabula Reservoir, North Dakota, numbers of individuals rose from 28% in the 0 to 3 m zone to 56% at 3 to 8 m and fell to 16% at 8 to 12 m. Biomass decreased from 53% to 37% to 9%, respectively (Peterka 1972). McLachlan and McLachlan (1971) reported that littoral faunal biomass decreased with depth.

Numbers of species and diversity generally decreased with depth in Keystone Reservoir, Oklahoma (Ransom and Dorris 1972).

Seasonal variation in benthic macroinvertebrates at a particular depth is largely due to migration of adults and distribution of eggs. Wood (1956) reported that most of the annual variation of the concentration of Chaoborus larvae in the profundal zone was due to a fall ablittoral migration and a spring adlittoral migration. Maximum density of Diptera in Lake Ashtabula was at 8 to 12 m in April, 3 to 8 m in June, and 0 to 3 m in August (Peterka 1972). Mundie (1957) observed a migration of Chaoborus flavicans to shallow water prior to emergence and egg laying. Since many insects deposit their eggs in shallow water or in association with littoral plant growth (Pennak 1953), large numbers of individuals in the littoral zone in late spring may be early instars. Large numbers of chironomid larvae (Deevey 1941) and Hexagenia nymphs (Craven and Brown 1969b) in shallow water in winter have been attributed to distribution of eggs. Subtle differences were noted in the depth preference of instars of the same chironomid species. This shift to deeper water with successive instars may account for the ablittoral fall migration (Thut 1969).

Life histories of the insects have a great influence on the fluctuations in the abundance and composition of the macrobenthos. Insect emergence in the spring and summer greatly reduces numbers and biomass and eliminates species. In the warmer climates there may be more than one emergence per year (Mundie 1957). As newly hatched larvae become large enough in early fall to be retained by a 30 mesh sieve, numbers of individuals and species begin to increase but individual biomass is lowest. Hubert and Krull (1973) reported that

greatest number and biomass occurred from November to April and smallest in July and August. Maximum variety occurred in late spring and early fall with the minimum during midwinter and midsummer periods of environmental stress. Moffett (1943) reported that change in variety of benthic macroinvertebrates during late summer was due mainly to addition of species.

In Oklahoma Craven and Brown (1969a) reported maximum abundance of benthic macroinvertebrates in January and minimum in May. They also observed peaks in both biomass and numbers of individuals of <u>Hexagenia</u> nymphs in December and May (1969b). Lowest biomass occurred in September and lowest numbers of individuals in August. In Keystone Reservoir, Oklahoma, numbers of individuals increased through winter, while number of species remained relatively constant (Ransom and Dorris 1972). Number of species decreased during spring causing a corresponding decrease in species diversity (\overline{d}).

Many characteristics of the water affect the temporal and spatial distribution of benthic macroinvertebrates. A limiting factor of major importance is the oxygen content at the mud-water interface (Ruttner 1963). Brundin (1951) stated that it is evident that the concentration of oxygen in the bottom water greatly influences the life conditions and composition of the bottom fauna in the deeper areas of lakes. Myadi (1931) concluded that the depth preference of the benthos is determined by the oxygen concentration and the benthos migrate in response to changes in oxygen tension. The distinct zonation of Tanypodinae found by Mundie (1955) was attributed to oxygen requirements of the larvae. The depth distribution of the benthic fauna altered in response to artificial reaeration of a summer stratified

reservoir (Calhoun and Hubbell 1970). Water temperature was suggested by Borutsky (1939) as the controlling factor in the annual shift of the Chaoborus concentration zone. Lundbeck (1926 cited by Eggleton 1934) also favored water temperature as the factor determining the depth distribution of chironomids. Hexagenia nymphs migrate in response to changing water temperature (Cowell and Hudson 1968). Temperature has a profound effect on the length of generation of aquatic insects (Lindeman 1942, Mundie 1957). Chironomus plumosus larval feeding is inhibited below 12°C and ceases at 5°C (Hilsenhoff 1966).

The character of the substrate undoubtedly has a great influence on the distribution of the benthos. Hilsenhoff (1967) concluded that none of the physical or chemical properties of the water appeared to affect Chironomus populations, but several characteristics of the mud influenced its distribution. Abundance of C. plumosus and Procladius sp. was most strongly correlated with pH of the mud (Hilsenhoff and Narf 1968). Organic content and texture of the sediments are important to the distribution of some aquatic invertebrates. As the texture of the soil became finer and correspondingly increased in organic content, abundance of chironomid larvae increased (Wene 1940). However, Hilsenhoff and Narf (1968) reported that the distribution of Procladius sp. is negatively correlated with organic content of the mud. During periods of adequate deepwater oxygenation faunal biomass in Lake Kariba, Central Africa was positively correlated with the amount of organic carbon in the profundal zone and inversely correlated with the quantity of coarse sand in the littoral (McLachlan and McLachlan 1971). greatest abundance and diversity of benthic organisms occurred in areas of sandy mud followed in order of decreasing abundance by regions of

soft, black ooze, muddy sand, clean sand, and brown, pulpy peat or gyttja (Eggleton 1952). Eriksen (1964) concluded that burrowing mayflies preferred a substrate of a certain particle size because ease of penetrance allows lower oxygen consumption. <u>Hexagenia</u> populations increased as greater depth allowed more deposition of silt (Swanson 1967).

Biotic factors may also affect the distribution of benthic macroinvertebrates. Thut (1969) stated that the distribution of two Chironomus species, two Polypedilum species, and three predatory species suggests that competition may play a role in determining the spatial distribution of the benthic fauna.

A combination of factors most likely determines the temporal and spatial arrangement of benthic organisms. Dugdale (1955) suggested that dipteran larvae may need a combination of adequate oxygen concentration and soft mud. At greater depth oxygen content decreases but organic content increases so a concentration zone may develop at the optimal interaction of these two factors. Eggleton (1952) felt that a great abundance of benthic macroinvertebrates at intermediate depths of Douglas Lake was brought about by a combination of rooted aquatic vegetation growing on a sandy mud substrate. Mundie (1957) concluded that the zonation of chironomid larvae was probably due to a combination of nature of food in the substrate and oxygen content of the water.

Variations in blood physiology have a marked effect on tolerance to low oxygen levels and hence on depth distribution of benthic organisms. Those organisms with blood pigments such as hemoglobin or erythrocruorin are better able to withstand and recover from periods

of low oxygen tension. The green or white Orthocladiinae without hemoglobin are bound to well-oxygenated environments (Brundin 1951). Mundie (1955) reported that Orthoclad larvae are intolerant to low oxygen concentration. The main functions of hemoglobin in Chironomus larvae are to enable the larvae to feed in water containing little oxygen, to act as an oxygen transport, and to increase the recovery rate from periods of anoxia (Walshe 1950). Larvae are able to feed if they are not constantly required to irrigate their tubes to absorb oxygen. Hemoglobin functions as an oxygen transport only at low oxygen concentrations (Ewer 1942). Ewer also found that no significant difference exists between Chironomus larvae with functional hemoglobin or with carboxyhemoglobin (hemoglobin rendered nonfunctional by carbon monoxide) from air saturation down to 3 mg/l. Chironomus larvae do not need hemoglobin to transport oxygen until oxygen tension falls below 1% air saturation (Leitch 1916). Hemoglobin in Tanytarsus larvae becomes functional at 25% saturation, is critical for survival at 15% saturation, and disfunctional at 5% saturation (Walshe 1947b).

Some macroinvertebrates can survive under anoxic conditions by anaerobic respiration in which internal stores on glycogen are broken down for energy leaving partially metabolized products that diffuse out or are stored until oxygen returns. Starved midge larvae in oxygen saturated water lost 0.56% of their dry weight in glycogen per day, while in oxygen-free water they lost 0.96%. Glycogen made up 13 to 14% of the dry weight of three species of Chironomus larvae that are somewhat tolerant to anoxic conditions, but only 2% of the intolerant Tanytarsus larvae (Augenfeld 1967). Recovery from anoxia begins with a short period of abnormally high oxygen consumption in

which large amounts of oxygen are absorbed to oxidize anaerobic metabolism products (Walshe 1947a). Chironomus larvae with hemoglobin can recover from anoxia in water with 7% air saturation, while larvae with carboxyhemoglobin cannot recover in water below 15% saturation (Walshe 1950). Thus, it is evident that organisms with blood pigments and glycogen stores not only have an advantage in habitats with low oxygen content but can survive under anoxic conditions as well.

Benthic macroinvertebrates may inhabit areas according to the capabilities of their respiratory metabolism. Chaoborus and Chironomus larvae were found in lakes of perennial hypolimnetic deoxygenation (Stahl 1959). The distribution of tubificid worms coincided roughly with regions of anaerobic conditions (Bardach et al. 1951). The rate of oxygen consumption of benthic organisms such as Chaoborus or the oligochaete worms that are able to adapt to low oxygen tension remains nearly constant from air saturation down to some critical point where consumption falls off linearly with ambient oxygen concentration. In organisms such as Procladius that are less tolerant to oxygen lack, consumption decreases linearly from saturation to anoxia (Berg et al. 1962). Oxygen consumption of Hexagenia recurvata was independent of oxygen content of the water from 9.75 mg/1 to 2.34 mg/1 (Morgan and Wilder 1936). Oxygen consumption of many benthic macroinvertebrates from poorly oxygenated water is much lower than that of organisms from well oxygenated water (Fox et al. 1933, 1935).

CHAPTER III

DESCRIPTION OF STUDY AREA

Arbuckle Reservoir is a multi-purpose impoundment built by the Bureau of Reclamation, United States Department of the Interior, in the Washita River Basin near Sulfur, Oklahoma. The reservoir is at the junction of Guy Sandy, Rock, and Buckhorn Creeks. The reservoir was designed for flood control, water supply, fish and wildlife habitat, and recreation. Filled in 1968, the impoundment has a maximum depth of 27.5 m in the central pool and a surface area of 950 ha at active conservation level. Drainage area of the reservoir is 32,634 ha (Gomez and Grinstead 1971) (Figure 1).

Prior to inundation the area was moderately rolling grasslands with stands of post oak and scrub oak. Soil is fine sandy loam over-laying limestone with occasional deposits of sand and gravel along the creek channels. Land in the basin is used primarily as pasture with some cropland and domestic and industrial development. More detailed information may be found in Bureau of Reclamation (1961).

Arbuckle Reservoir is a warm, monomictic reservoir which strongly stratifies during summer. The hypolimnion is virtually anoxic from June through October with water temperature ranging from 30°C at the surface to 18°C in the bottom of the central pool (Duffer and Harlin 1971). Alkalinity is 125 to 180 mg/l and the water is fairly turbid with Secchi disc reading of 1.25 to 2.5 m (Toetz 1975).

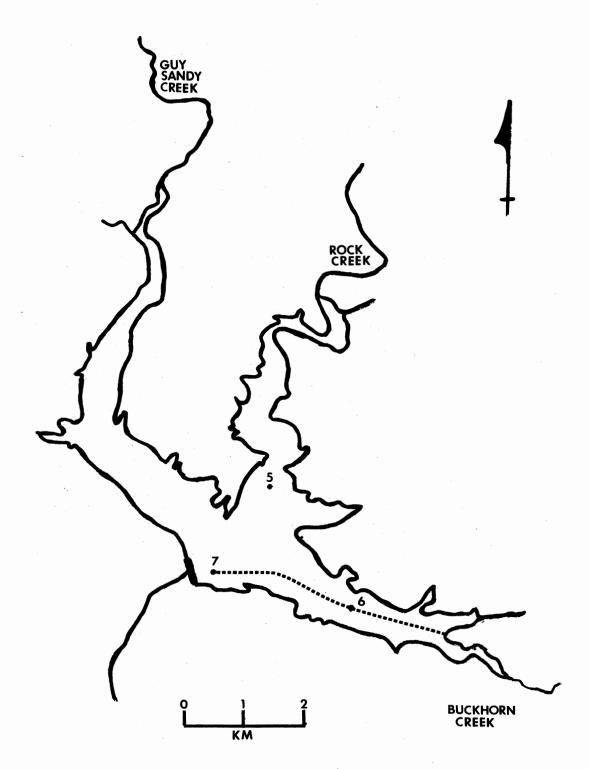


Figure 1. Arbuckle Reservoir Showing Sampling Station and $$\operatorname{Transect}$$

CHAPTER IV

MATERIALS AND METHODS

Pilot Study

Three stations were selected to measure variation in species composition and diversity of benthic macroinvertebrates with depth in July and August, 1974. Station 5 is in the Rock Creek arm of the reservoir, while Station 6 is in the Buckhorn Creek arm. Station 7 is in the central pool of the reservoir near the dam. The stations correspond to those of Duffer and Harlin (1971).

Samples were taken with an Ekman dredge from 1, 5, 10, and 15 m depths at Stations 5 and 6. Six replicates were taken from each depth on 9 July and 7 August 1974. Six samples were taken from a depth of 24 m at Station 7 on both sampling dates. Samples were washed in a No. 40 U.S. Standard soil series sieve with openings of 0.420 mm and preserved in 8% formalin. Identification was to species when possible; otherwise, identification was to the lowest taxonomic unit possible.

Total number of organisms (n), number of individuals per species $(n_{\underline{i}})$, and number of species (s) were used to calculate species diversity (\overline{d}) in the following equation (Shannon and Weaver 1963):

$$\bar{d} = -\Sigma(n_i/n) \log_2(n_i/n)$$

Calculations were performed on a program described by Wilhm (1970).

Main Study

Variation in species composition and diversity with depth was measured in winter and spring. Since variation was abrupt between 1 and 5 m and since little variation existed among stations, samples were collected from more depths at one station in January and May, 1975. Four samples each were taken with an Ekman dredge from 1, 2, 4, 7, 11, 15, 19, and 24 m along a transect extending from the deepest part of the reservoir in the central pool through the Buckhorn Creek arm. Samples were washed in a No. 30 U.S. Standard soil series sieve with openings of 0.595 mm as recommended by the Environmental Protection Agency (Weber 1974). Three samples were taken from each depth during January and May to measure biomass. All samples were preserved in 8% formalin.

Temperature, dissolved oxygen concentration, and pH and organic content of the substrate were determined in January and May. Triplicate measurements of temperature and dissolved oxygen concentration were made at each depth with a Yellow Springs Instruments (YSI) model 5522 oxygen meter which was air calibrated. To obtain organic content, sediment samples were oven dried at 105°C for 24 h, ashed at 500°C for 1 h, cooled and brought to a constant weight at 105°C (Weber 1974). Sediment pH was obtained by field measurement with a Horizon Ecology 5995 probe.

Total number of organisms, number of individuals per taxon, and number of species were determined for each sample. Species diversity was estimated using the Shannon and Weaver function as defined above. Since the function does not differentiate between variety and

equitability, the following variety expression was also used (Margalef 1951):

$$d = s-1 / 1n n,$$

where s is the total number of species in the sample and n is the number of individuals. To estimate equitability, the following equation was used (Pielou 1966):

$$E = \overline{d} / \overline{d}_{max}$$

where \bar{d} is species diversity as estimated by the Shannon and Weaver function and \bar{d}_{max} is the diversity that would be obtained if all species were equally abundant. The maximum diversity is estimated by \log_2 s, when s is large. For comparisons of equitability values among depths to be meaningful, the value must be based on equal number of species (Hurlburt 1971). Number of species versus log number of individuals was plotted using individual subsamples for each depth. Number of species at 200 individuals was estimated from the curve and equitability values calculated for the number of species. Two hundred individuals were chosen because this sample size has been shown to provide maximum diversity in most freshwater benthic macroinvertebrate samples (Wilhm 1970).

Variation with depth in species diversity and variety as determined by the indices described above and in physicochemical conditions was evaluated with the following analyses of variance (AOV): Species diversity and variety:

Total			64
Depth			7
Time			1
Depth	x	Time	7
Error			48

Biomass and Physicochemical conditions:

Total	48
Depth	7
Time	1
Depth x Time	7
Error	32

Comparisons among the three indices were made by testing their fit to several models:

Linear: Index = $\beta_0 + \beta_1 X$ Quadratic: Index = $\beta_0 + \beta_1 X + \beta_2 X^2$ Cubic: Index = $\beta_0 + \beta_1 X + \beta_2 X^2 + \beta_3 X^3$,

where β_i is a rate determining coefficient and X is depth. The relationship between depth and the three indices was studied by testing the hypothesis that β_i = 0 for each coefficient above. The contribution of the various physicochemical parameters to species diversity, variety, and equitability was studied with multiple regression analysis using the model:

Index = $\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5 + \epsilon$ where: $\beta_i = \text{rate determining coefficient,}$ $X_1 = \text{Depth,}$ $X_2 = \text{Dissolved oxygen concentration,}$

 X_3 = Water temperature,

 $X_4 = pH$ of the sediments,

 X_5 = organic content of the sediments,

and ϵ is the residual (Draper and Smith 1966).

CHAPTER V

RESULTS

Physicochemical Conditions

All physicochemical parameters measured changed significantly with time (Appendix A). Dissolved oxygen content was fairly uniform over depth in January but by May a depth gradient was established (Table I). Water temperature difference between the surface and 24 m was only 1.7° C in January, but was 9.4° C in May. Water temperature averaged over depth increased during that period from 6.5 to 18.1° C. Sediment pH varied little among depths with only a slight peak at intermediate depth. Although change with time was significant, variation among depths was not. Peaks in percent organic content of the sediments were noted at 4 and 19 m in January and 2 and 24 m in May. Organic content in the upper 7 m was generally higher in May than in January.

Benthic Macroinvertebrates

Seventy-four taxa were collected in this study (Table II).

Number of species collected at any depth varied from two to 30

(Table III). Number of species decreased with depth on all sampling dates. Sharpest decrease in number of species occurred between 1 and 10 m in July and August, 1974, 2 and 11 m in January, 1975, and 4 and 11 m in May, 1975. Total number of species collected decreased from

TABLE I

PHYSICOCHEMICAL MEASUREMENTS BY DEPTH AND DATE
IN JANUARY AND MAY, 1975

Depth (m)	Oxygen (mg/1)		Temperature (°C)		pН		Organic Content (%)	
	1 Jan	9 May	1 Jan	9 May	1 Jan	9 May	1 Jan	9 May
1	13.1	9.7	7.7	21.4	7.3	7.0	0.74	5.47
2	13.0	6.5	7.0	21.4	7.4	7.1	4.84	9.23
4	12.4	6.8	6.3	21.0	7.1	7.1	6.38	6.95
7	12.2	4.0	6.1	19.0	7.4	6.9	2.49	5.97
11	12.3	5.5	6.4	18.0	7.7	7.2	3.77	1.77
15	12.3	5.3	6.0	15.6	7.2	6.7	6.63	6.12
19	11.7	3.5	6.3	16.2	7.3	7.0	7.70	7.45
24	10.7	1.5	6.0	12.0	6.2	6.8	4.26	9.06

TABLE II

BENTHIC MACROINVERTEBRATES COLLECTED IN ARBUCKLE RESERVOIR FROM JULY, 1974 TO MAY, 1975

```
Coelenterata
     Hydrozoa
          Hydra sp.
Annelida
     Hirudinea
          Unidentified species
     01igochaeta
          Dero digitata (Muller)
          Nais variabilis Piguet
          Slavinia appendiculata (d'Udekem)
          Stylaria lacustris (Linn.)
          Unidentifiable Naididae
          Aulodrilus pigueti Kowalewski
          A. pleuriseta (Piguet)
          Branchiura sowerbyi Bedd.
          Limnodrilus claparedeanus Ratzel
          L. hoffmeisteri Clap.
          L. udekemianus Clap.
          Potomothrix sp.
          Tubifex templetoni (Southern)
          T. tubifex (0.F.M.)
          Tubificid sp. A
          Tubificid sp. B
          Tubificid sp. C
          Unidentifiable tubificid with capilliform chaetae
          Unidentifiable tubificid without capilliform
            chaetae
Arthropoda
     Arachnida
          Hydracarina sp. A
          Hydracarina sp. B
     Crustacea
          Hyalella azteca (Saussure)
     Insecta
       Ephemeroptera
          Hexagenia limbata (Serville)
          H. rigida
          Brachycercus sp.
          Caenis sp.
       Odonata
          Gomphus sp.
          Libellula sp.
          Ishnura sp.
```

TABLE II (Continued)

```
Megaloptera
   Sialis sp.
Coleoptera
   Dubiraphia sp.
   Stenelmis sp.
   Unidentifiable Hydroporinae
Trichoptera
   Oecetis sp.
   Unidentifiable Leptoceridae
   Polycentropus sp.
   Psychomyiid genus A (Ross)
   Neotrichia sp.
   Orthotrichia sp.
   Unidentifiable trichopteran A
Diptera
   Bezzia sp.
   Unidentifiable Ceratopogonidae
   Chaoborus punctipennis (Say)
   Clinotanypus sp.
   Coelotanypus sp.
   Procladius sp.
   Tanypus sp.
   Unidentified Pentaneurini
   Chironomus sp.
   Cryptochironomus sp.
   Dicrotendipes sp.
   Endochironomus sp.
   Glyptotendipes sp.
   Harnischia sp.
   Paralauterborniella sp.
   Polypedilum sp.
   Pseudochironomus sp.
   Stenochironomus sp.
   Stictochironomus sp.
   Tribelos sp.
   Cladotanytarsus sp.
  Micropsectra sp.
   Rheotanytarsus sp.
   Tanytarsus sp.
  Diamesa sp.
   Chironomini sp. A
  Cricotopus sp.
  Orthocladius sp.
  Psectrocladius sp.
  Trichocladius sp.
  Trissocladius sp.
  Chironomid pupae
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TABLE II (Continued)

Mollusca

Pelecypoda

Sphaerium sp.
Unidentified Unionidae

Gastropoda

Physa sp.

TABLE III

NUMBERS OF SPECIES (TOTAL IN FOUR EKMAN HAULS) BY DEPTH
AND STATION COLLECTED IN ARBUCKLE RESERVOIR

Depth	Station	9 Ju1 74	7 Aug 74	25 Jan 75	9 May 75
1	5 6 Total	16 19 29	15 14 22	- - 23	_ _ 21
2		-	. –	30	23
4		-	. -	21	24
5	5 6 Total	8 13 16	11 12 15	- - - - -	- - -
7		-	. -	17	18
10	5 6 Total	8 5 9	6 2 7	- - -	- - -
11		-	- -	10	8
15	5 6 Total	3 4 7	3 5 5	- - 8	- - 9
19				9	10
24		4	2	8	5

39 in July, to a minimum of 27 in August, 1974, and from a maximum of 49 to 37 in January and May, 1975, respectively. Density varied from 321 to 6176 individuals/m² in 1974, and from 614 to 20,689 in 1975 (Table IV). Highest density occurred at 2 m in January and 24 m in May, 1975. Smaller concentration zones were observed in summer when density was more uniform over all depths. Density tended to increase with depth on all sampling dates.

Several species had concentration zones in Arbuckle Reservoir, especially the oligochaete worm Aulodrilus pigueti and the phantom midge larva Chaoborus punctipennis (Appendix C). These species were responsible for the large densities observed in August, 1974 and May, 1975. Chaoborus punctipennis represented nearly 60% of the total density and was by far most abundant at 15 m on 7 August 1974. Aulodrilus pigueti reached over 19,000 individuals/m² at 24 m on 9 May 1975. Stylaria lacustris attained over 2300 individuals/m² at 1 m in January, 1975. Many species such as Endochironomus sp. and Hyalella azteca were only found in the upper 5 m of water. Chironomini sp. A was found only at 2 m at a density of over 4000 individuals/m2 in January, 1975, and in lesser densities at 1, 2, and 4 m in May. Coelotanypus sp., Procladius sp., and Dero digitata were more generally distributed but increased to distinct concentration zones at specific depths (e.g. 4 m on 25 January 1975 for Coelotanypus and Procladius). The most common Trichopteran, Oecetis sp. was fairly abundant in January down to 11 m and reached a maximum of 129 individuals/m² at 4 m.

Since the oligochaete worms and dipterans composed the majority of the macroinvertebrates collected, fluctuations in these groups produced

TABLE IV

DENSITY*(INDIVIDUALS/M²) OF BENTHIC MACROINVERTEBRATES BY DEPTH AND STATION COLLECTED IN ARBUCKLE RESERVOIR

Depth	Station	9 Ju1 74	7 Aug 74	25 Jan 75	9 May 75
1	5	321	909	_	• _
	5 6 X	572	666	-	-
	$\bar{\mathbf{x}}$	446	788	5112	2049
2		-	-	11580	4853
4		-	-	2910	3427
	_	• • • • •			
5	5 <u>6</u> X	1090	1006	-	
	<u>6</u>	495	458	-	_
	Х	792	7.32	· -	_
7		-	-	1288	2456
10	5	2303	3213	_	_
	5 <u>6</u> X	3091	430	_	
	$\overline{\mathbf{x}}$	2697	1822	-	-
11		-	_	1507	614
15	5	3135	6176	_	_
	6	3133	3385	_	_
	5 <u>6</u> X	3134	4780	2380	745
19		· _	-	3942	1141
24		1126	6327	1819	20689

 $[\]star \text{Values}$ are mean densities of four Ekman dredge hauls in January and May and of six hauls in July and August.

the greatest changes in composition and density of the entire assemblage. In July, 1974, the oligochaetes comprised 12.7% and the dipterans 83.9% of the total number of individuals. By August the oligochaetes had increased to 30.7% and the dipterans reduced to 67.5%. The number of species decreased by 12, mostly rarer species such as Stictochironomus sp., the Naidadae species, and the leeches.

In January, the oligochaetes comprised over 20% of the total organisms collected, but this low percentage was represented by one of the largest number of species. Stylaria lacustris and Aulodrilus pigueti were present in large numbers. The dipterans composed 69.1% of the assemblage and were represented by 23 species. Most abundant were Chaoborus punctipennis, Coelotanypus sp., Procladius sp., and an unidentifiable species of Chironomini, probably an early instar. In May, the oligochaetes comprised 69% and the dipterans 29.5% of the total. The great increase in abundance of the oligochaetes was due primarily to the tremendous growth of the population of Aulodrilus pigueti which made up 17.1% of the oligochaetes in January and 79.3% in May. The 50% reduction of dipterans probably was due to emergence. Many species of insects were greatly reduced in May.

Biomass was fairly uniform through all depths in January with peaks at 1 and 19 m (Table V). By May, biomass had increased greatly at 4 and 24 m corresponding to increased density. Variation among depths was significant in January and May (Table XIII, Appendix A). Little temporal change in biomass occurred between 11 and 19 m.

Species diversity, variety, and equitability behaved similarly over depth and time (Tables VI, VII, and VIII). Generally, all indices

TABLE V

BIOMASS* (g/M²) OF BENTHIC MACROINVERTEBRATES BY DEPTH
COLLECTED IN ARBUCKLE RESERVOIR

Depth (m)	25 Jan	9 May	
1	0.11	0.04	
2	0.11	0.13	
4	0.08	0.24	
7	0.05	0.13	
11	0.05	0.03	
15	0.08	0.08	
19	0.15	0.17	
24	0.09	0.47	

^{*}Values are means of three observations.

TABLE VI

SPECIES DIVERSITY* OF BENTHIC MACROINVERTEBRATES BY DEPTH AND STATION COLLECTED IN ARBUCKLE RESERVOIR

Depth	Station	9 Jul 74	7 Aug 74	25 Jan 75	9 May 75
1	5	3.56	3.02	_	_
	6	3.06	3.06	_	_
	Pooled	3.75	3.51	2.80	3.53
2		-	-	3.22	3.54
4		-	. - '	2.62	3.69
5	5	1.99	2.32	_	_
	6.	3.21	2.80	_	
	Pooled	2.84	2.50	-	-
7		-	· • • • • • • • • • • • • • • • • • • •	2.99	2.75
10	5	1.78	0.32	_	_
	6	0.75	0.12	_	_
	Pooled	1.24	0.31	-	-
11		-	-	2.58	1.94
15	5	1.01	0.13	_	_
	6	0.64	0.60	_	_
	Pooled	0.69	0.36	1.46	2.43
19		· · · · ·	-	1.38	2.63
24		1.15	0.48	0.79	0.43

 $[\]star Values$ are calculated from four pooled Ekman dredge hauls in January and May and from six hauls in July and August.

VARIETY* OF BENTHIC MACROINVERTEBRATES BY DEPTH AND STATION COLLECTED IN ARBUCKLE RESERVOIR

Depth	Station	9 Jul 74	7 Aug 74	25 Jan 75	9 May 75
1	5	4.41	2.46	· <u>-</u>	_
	6	4.14	2.99	_	_
	Pooled	5.99	4.11	3.58	3.94
2		-		4.19	3.70
4		- '	-	3.57	4.08
5	5	1.40	2.02	_	_
	6	3.03	2.62	-	_
	Pooled	3.50	2.63	-	-
7		-	_ '	3.35	3.27
10	5	1.39	0.82	_	_
	6	0.82	0.24	_	_
	Pooled	1.21	0.96	-	-
11			-	1.82	1.85
15	5	0.60	0.30	_	_
	6	0.66	0.65	_	_
	Pooled	0.95	0.56	1.30	1.92
19			-	1.36	1.94
24		0.80	0.15	1.36	0.53

 $[\]mbox{\tt *Values}$ are calculated from four pooled Ekman dredge hauls in January and May and from six hauls in July and August.

TABLE VIII

EQUITABILITY* OF BENTHIC MACROINVERTEBRATES BY DEPTH
AND STATION COLLECTED IN ARBUCKLE RESERVOIR

Depth	Station	9 Jul 74	7 Aug 74	25 Jan 75	9 May 75
1	5	0.78	0.78	-	_
	6	0.68	0.74	_	-
	Pooled	0.80	0.83	0.67	0.78
2		-	-	0.76	0.82
4		-		0.64	0.82
5	5	0.62	0.65	_	_
	6	0.72	0.73	_	_
	Pooled	0.77	0.68	-	-
7		-	, -	0.68	0.67
10	5	0.60	0.16	_	_
	6	0.32	0.10	-	_
	Pooled	0.46	0.16	-	-
11		-	-	0.77	0.53
15	5	0.47	0.10	_	
	6	0.30	0.28	_	_
	Pooled	0.30	0.21	0.49	0.70
19		-	_	0.49	0.78
24		0.50	0.48	0.26	0.21

^{*}Values are calculated from four pooled Ekman dredge hauls in January and May and from six hauls in July and August.

decreased with depth although there were isolated high values from deeper water. These decreases were sharp from surface to 10 m and then slight to 24 m in July and August, 1974. Decreases in January and May were linear. Spatial variation in species diversity and variety was significant on all dates (Tables XIV and XV, Appendix A). No measure of variation was possible for equitability due to its method of calculation. Temporal variation was more evident in the species diversity and variety values. Values for all indices were lowest in July and August, 1974, and highest in January and May, 1975, with minimum in August and maximum in May.

The method used for equalizing sample size for the calculation of equitability values worked especially well in the shallower depths. However, correlation coefficients for each sample (Table XVIII, Appendix A) show that the number of species versus log number of individuals relationship was not as effective in the samples from deeper water where an insufficient number of species were available on which to calculate a line. For example, on 7 August 1974, all subsamples at 24 m contained the same number of species and no relationship between species and number of individuals existed.

The relationship between depth and the various indices was tested for fit to several models (Tables XIX and XX, Appendix B). At the 0.05 significance level, diversity and variety fit the linear model in January and May, 1975, but in July and August, 1974, appeared to fit a higher order model. Partial sums of squares values and R^2 values reinforce these conclusions. (Tables XXI and XXII, Appendix B). The July, 1974 species diversity data very nearly fits a quadratic model ($\alpha = .05$). In August, the quadratic model has a good fit. In January

and May, only the linear depth term in the first order model is highly significant. The same is true for variety. It can be seen for both indices that in July, January, and May adding terms does not greatly increase the R^2 values. In August the change in R^2 value after adding the depth-squared term is large. Since lack of fit test cannot be done for the equitability values, only partial sums of squares and R^2 values can be used (Table XXIII, Appendix B). In July and August both linear and quadratic terms are significant and there is a large increase in R^2 as the quadratic term is added to the model. In January and May only linear terms are significant and there is no great increase in R^2 as terms are added.

Effects of Physicochemical Conditions
on Species Diversity, Variety,
and Equitability

Few physicochemical parameters appeared to have any effect on the information indices in January and May (Table XXIV, Appendix B). In January, depth had a significant effect ($\alpha = .10$) on species diversity and variety indices and sediment pH was significant in the equitability and species diversity models. In May, water temperature and sediment pH were significant in the species diversity model and depth and water temperature in the equitability model. The variety model was unaffected by any physicochemical parameter.

CHAPTER VI

DISCUSSION

Number of species decreased with depth on all sampling dates, with the minimum occurring in August, 1974, and the maximum in January, 1975. This condition is generally found in temperate, northern hemisphere lakes. Abundance of benthic macroinvertebrates was greatest in shallow water and deepest areas. Peaks in number of individuals in deep water usually coincided with increases in populations of certain species such as Aulodrilus pigueti at 24 m on 9 May 1975 and Chaoborus punctipennis at 15 m on 7 August 1974. C. punctipennis has been well documented as a deep water species (Juday 1921, Eggleton 1932). In Lake Texoma, Oklahoma, Sublette (1957) found depth distributions for C. punctipennis and Oecetis sp. similar to those found in Arbuckle Reservoir.

Seasonal variation of benthic macroinvertebrates in Arbuckle Reservoir differed slightly from that found in other regional lakes. Although abundance was lowest in summer as is generally found, the winter and spring samples were anomalous. Due to an enormous population of <u>Aulodrilus pigueti</u> in May, the greatest abundance occurred on this date. Maximum abundance occurred in midwinter in Keystone Reservoir, Oklahoma (Ransom and Dorris 1972), Lake Texoma (Sublette 1957), and Boomer Lake, Oklahoma (Craven and Brown 1969a), and in

other temperate lakes. Seasonal variation in number of species was similar to that found in these regional lakes.

Biomass of benthic macroinvertebrates was greatest in shallow and deepest areas of the reservoir and roughly coincided with density of the organisms. Peterka (1972) found greatest biomass in the upper 3 m of Lake Ashtabula Reservoir, North Dakota, and least in deepest water. High biomass in May in Arbuckle Reservoir in deeper water was due to large numbers of Aulodrilus pigueti.

Information indices generally were lowest in August and highest in January and May. Values for all indices were highest in shallow water and lowest in deepest areas. Reduction in these indices was primarily due to loss of rare species and increased density of common species. Ransom and Dorris (1972) also observed that species diversity decreased with depth and reached a minimum in late summer. Maximum variety occurred in late spring in Arbuckle Reservoir which concurs with observations made by Hubert and Krull (1973) in Oakwood Bottoms Greentree Reservoir, Illinois. Equitability generally decreased with depth as only a few species dominated the deeper strata.

The modeling procedures were useful in showing that the rate of change of variation with depth in benthic macroinvertebrates changes with time. The lack of fit tests, R² values, and partial sums of squares show that species diversity, variety, and equitability decreased linearly with depth in January and May, 1975. For July, 1974, however, lack of fit tests for species diversity and variety are inconclusive. Partial sum of squares values indicate that the transition for these indices was being made from a linear model to a quadratic model. By August, 1974, the transition had been made and

species diversity and variety of benthic macroinvertebrates decreased sharply in the first 10 m and then leveled off. Partial sums of squares and R^2 values indicate that equitability values fit a second order model in July and this pattern intensified by August. It is likely that transition to a second order model fit for all indices was aided by the increasing severity of physicochemical conditions.

According to the modeling procedures that included the physico-chemical data, stratification was not sufficiently distinct by May to influence the structure of the benthic assemblage. In the absence of the stressful condition of summer, species diversity and equitability in January were influenced only by depth and sediment pH. By May, water temperature had begun to be influential and sediment pH was still a significant factor. The more severe summer physicochemical conditions undoubtedly affected the benthic macroinvertebrate assemblage to a greater extent. The pattern of temperature and oxygen stratification is remarkably similar to the second order decrease with depth in summer of the species diversity, variety, and equitability models discussed earlier.

Peaks in density tended to coincide with peaks in percent organic content of the sediments as well as peaks in biomass. Although part of the organic content of the sediments was due to the organisms, part of it was due to detritus since changes in organic content did not always coincide with changes in density or biomass of these organisms. However, certain species, such as <u>Aulodrilus pigueti</u> and Chironomini sp. A, were usually found in areas of high organic content which suggests a relationship. Since <u>A</u>. <u>pigueti</u> and probably Chironomini sp. A are detritivores, they would benefit from the high organic

content. McLachlan and McLachlan (1971) reported faunal biomass was positively correlated with the amount of organic carbon in the sediments. Wene (1940) found a significant correlation between organic content and abundance of chironomid larvae. Species of Chironomini such as Chironomus decorus (Gleason 1961) and Chironomus plumosus (Hilsenhoff and Narf 1968) have been positively correlated with organic content of the sediments.

Blood pigments, such as hemoglobin and erythrocruorin, appeared to enable several species to withstand low oxygen conditions. Chapman (1969) states that among the insects only those species of the Chironomus group such as Chironomus sp. (Leitch 1916, Ewer 1942, Walshe 1947a), Endochironomus sp. (Mundie 1957), Stictochironomus sp. and Micropsectra sp. (Brundin 1951), and Tanytarsus sp. (Walshe 1947b) have respiratory pigments. These genera, when compared to Orthocladiinae, were able to inhabit depths containing much less dissolved oxygen. Members of the subfamily Orthocladiinae found in Arbuckle were confined to the upper 1 or 2 m and disappeared as summer progressed. Most species possessing respiratory pigments were present on all dates and at all depths. Other invertebrates which have tracheae, gills, and other respiratory adaptations were generally not found in the poorly oxygenated areas. However, the insects most abundant in the deeper areas of the reservoir on all dates, Chaoborus punctipennis, Coelotanypus sp., and Procladius sp. do not have respiratory pigments. Among the oligochaetes, only the Tubificidae have erythrocruorin (Pennak 1953). Species of this family are well represented in the poorly oxygenated areas of Arbuckle Reservoir, notably Aulodrilus pigueti. Stylaria lacustris, a naidid, was not able to survive except

in the well oxygenated surface waters. <u>Dero digitata</u>, another naidid, was able to live at all depths in January and May, but was not present in July and August. Specimens of <u>Dero digitata</u> from deeper samples possessed larger gills than those collected from shallower areas, which may have accounted for the species' ability to inhabit deeper water with less oxygen content.

CHAPTER VII

SUMMARY

A study of the temporal and spatial variation of benthic macroinvertebrates, and the effect of physicochemical conditions on those
variations was conducted in July and August, 1974, and January and May,
1975 in Arbuckle Reservoir, Oklahoma. Six samples were taken with an
Ekman dredge from each of four depths at two stations on 9 July and
7 August 1974. Six samples were also taken from 24 m in the central
pool on these dates. Four samples were taken from each of eight depths
on a single transect on 25 January and 9 May 1975. Three samples were
also taken from each depth on these latter dates for biomass. Triplicate measures of dissolved oxygen, water temperature, sediment pH, and
sediment organic content were also taken in January and May.

Benthic macroinvertebrates were identified to lowest possible taxonomic unit. Species diversity, variety, and equitability were calculated for each sample and pooled to provide values for each depth. Comparisons among the three indices were made by testing their fit to linear, quadratic, and cubic models. The effects of the various physicochemical parameters on the information indices were studied with multiple regression techniques.

Seventy-four taxa were collected on the four sampling dates.

Number of species decreased with depth on all dates and was lowest in August and highest in January. Density tended to increase with depth

with occasional peaks or concentration zones. Spatial patterns in density were greatly influenced by fluctuations in abundance of certain common species. No temporal pattern was discernable.

Species diversity, variety, and equitability decreased with depth on all sampling dates and were lowest in August and highest in January and May. Reduction in these indices was due primarily to loss of rare species and increased density of common species. Variety was the least sensitive to spatial variation in benthic macroinvertebrates, and all were equally sensitive to temporal variation.

Species diversity and variety nearly fit a quadratic decrease with depth in July and fit the quadratic model by August. Equitability fit the quadratic model in July and the fit was better by August. All three indices decreased linearly with depth in January and May.

Few measured physicochemical conditions influenced the distribution of the benthic macroinvertebrate assemblage in January and May. In January, with the absence of the stressful environmental conditions of summer, sediment pH had a significant effect on variation in species diversity and equitability with depth. In May, water temperature was significant in the species diversity and equitability models, and sediment pH was still a factor in the species diversity model. It appeared that sediment organic content was influential in the distribution of two common species.

Species that possess respiratory pigments generally were able to inhabit areas with lower oxygen content, whereas the Orthocladiinae, with no such pigments were confined to oxygen-rich environments. There were, however, abundant species that were tolerant of the low oxygen tension that do not have respiratory pigments. The tubificid

oligochaete worms and members of the <u>Chironomus</u> group of dipterans, which possess the pigments, have been well documented as tolerant of low oxygen environments.

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APPENDIX A

STATISTICAL RESULTS

TABLE IX

ANALYSIS OF VARIANCE OF DISSOLVED OXYGEN MEASUREMENTS FROM ARBUCKLE RESERVOIR

Source	d.f.	F Value	Prob > F
Total	47		
Time	1	14352.4	< .005
Depth	7	380.117	< .005
Depth x Time	7	121.644	< .005
Error	32		

TABLE X

ANALYSIS OF VARIANCE OF WATER TEMPERATURE MEASUREMENTS FROM ARBUCKLE RESERVOIR

Source	d.f.	F Value	Prob > F
Total	47		
Time	1	52687.7	< .005
Depth	7	696.108	< .005
Depth x Time	7	437.527	< .005
Error	32		

TABLE XI

ANALYSIS OF VARIANCE OF SEDIMENT PH MEASUREMENTS
FROM ARBUCKLE RESERVOIR

Source	d.f.	F Value	Prob > F
Total	47		
Time	1	51.2712	< .005
Depth	7	1.7409	> .05
Depth x Time	7	50.6126	< .005
Error	32		

TABLE XII

ANALYSIS OF VARIANCE OF SEDIMENT PERCENT ORGANIC CONTENT MEASUREMENTS FROM ARBUCKLE RESERVOIR

Source	d.f.	F Value	Prob > F
Total	47		
Time	1	141.780	< .005
Depth	7	69.856	< .005
Depth x Time	7	36.929	< .005
Error			

TABLE XIII

ANALYSIS OF VARIANCE OF BIOMASS MEASUREMENTS
FROM ARBUCKLE RESERVOIR

Source	d.f.	F Value	Prob > F
Total	47		
Time	1	6.2602	.01 < p < .05
Depth	7	3.4430	< .01
Depth x Time	7	2.9002	.01 < p < .05
Error	32		

TABLE XIV

ANALYSIS OF VARIANCE OF SPECIES DIVERSITY VALUES FROM ARBUCKLE RESERVOIR IN JULY AND AUGUST, 1974

Source	d.f.	F Value	Prob > F
Total	95		
Reps	5	0.2991	> .05
Time	1 .	6.6282	.01 < p < .05
Station	1	1.9348	> .05
Depth	3	34.3256	< .01
Time x Station	1	0.0301	> .05
Time x Depth	3	6.2560	< .01
Station x Depth	3	3.7302	$.01$
Time x Depth x Stat	ion 3	1.8610	> .05
Error	75		

TABLE XV

ANALYSIS OF VARIANCE OF SPECIES DIVERSITY VALUES FROM ARBUCKLE RESERVOIR IN IN JANUARY AND MAY, 1975

Source	d.f.		F Value	Prob > F
Total	63			
Time	1		3.715	> .05
Depth	7		19.270	< .01
Depth x Time	7		2.680	.01 < p < .05
Error	48	•		

TABLE XVI

ANALYSIS OF VARIANCE OF VARIETY VALUES
FROM ARUBCKLE RESERVOIR IN
JULY AND AUGUST, 1974

Source	d.f.	F Value	Prob > F
Total	95		
Reps	5	0.4899	> .05
Time	1	4.6769	$.01$
Station	1	3.5325	> .05
Depth	3 3	26.513	< .01
Time x Station	1	0.0378	> .05
Time x Depth	3	3.9151	$.01$
Station x Depth	3	3.6113	$.01$
Time x Station x Depth	n 3	0.3921	> .05
Error	75	,	

TABLE XVII

ANALYSIS OF VARIANCE OF VARIETY VALUES FROM ARBUCKLE RESERVOIR IN JANUARY AND MAY, 1975

Source	d.f.	F Value	Prob > F
Total	63		
Time	1	0.7250	> .05
Depth	7	16.455	< .01
Depth x Time	7	1.7620	> .05
Error	48		

TABLE XVIII

CORRELATION COEFFICIENTS AND SLOPES FOR SPECIES VERSUS LOG NUMBER OF INDIVIDUALS CURVES FOR EQUITABILITY CALCULATIONS BY DEPTH AND STATION

Depth	Station	9 Jul	. 74	7 Aug	74	25 Ja	n 75	9 May	75
(m)		r*	m*	r .	m	r	m	r	m
1	5	0.944	5.11	0.920	3.29	_	_	· -	_
	6	0.920	5.83	0.841	4.16	_		- ,	-
	Pooled	0.902	5.93	0.906	4.61	0.983	5.20	0.930	7.11
2		-	- ' ,	_	-	0.850	6.24	0.900	4.82
4		- .	-	· -	<u> </u>	0.890	4.46	0.900	7.26
5	5	0.893	2.31	0.868	2.68	-	_	-	-
	6	0.955	5.10	0.801	3.01	-	-	-	
	Pooled	0.643	2.58	0.858	2.84	_	-	-	_
7		_	-		· _	0.940	6.32	0.770	4.35
10	5	0.890	1.44	0.652	1.28	-	-	_ '	-
	6	0.479	0.419	0.658	0.325	-	-	-	-
	Pooled	0.730	1.06	0.793	0.953	-	-	-	- ,
11		-	-	_	· -	0.698	1.57	0.840	3.04
15	5	0.869	0.651	0.536	0.647	-	-	-	-
	6	0.603	0.566	0.849	0.893	-	_		-,
	Pooled	0.861	0.790	0.441	0.521	0.972	2.15	0.990	1.94
19		-	-	-	-	0.360	1.07	0.960	1.76
24		0.797	0.948	0.000	0.000	0.774	2.65	0.630	0.33

^{*}r is the correlation coefficient and m is the slope.

APPENDIX B

MODELING RESULTS

TABLE XIX

LACK OF FIT CALCULATIONS FOR SPECIES
DIVERSITY VERSUS DEPTH MODELS

Mode1	Date	Source	d.f.	F Value	Prob > F
Linear	9 Jul 74	L.O.F.* P.E.*	2 55	3.9838	<.01
	7 Aug 74	L.O.F. P.E.	2 55	31.834	<.01
	25 Jan 75	L.O.F. P.E.	6 24	1.9557	>.05
	9 May 75	L.O.F. P.E.	6 24	2.3203	>.05
Quadr.	9 Jul 74	L.O.F. P.E.	1 55	6.5688	.01< p < .05
	7 Aug 74	L.O.F. P.E.	1 55	28.844	<.01
	25 Jan 75	L.O.F. P.E.	5 24	2.0102	>.05
	9 May 75	L.O.F. P.E.	5 24	2.7446	.01 < p < .05
Cubic	9 Jul 74	L.O.F. P.E.	0 55	· · -	-
	7 Aug 74	L.O.F. P.E.	0 55	-	
	25 Jan 75	L.O.F. P.E.	4 24	2.4286	>.05
	9 May 75	L.O.F.	4	3.3163	.01 < p < .05

^{*}L.O.F. is lack of fit and P.E. is pure error.

TABLE XX

LACK OF FIT CALCULATIONS FOR VARIETY VERSUS DEPTH MODELS

Model	Date	Source	d.f.	F Value	Prob > F
Linear	9 Jul 74	L.O.F.* P.E.*	2 55	3.0418	>.05
	7 Aug 74	L.O.F. P.E.	2 55	17.592	<.01
	25 Jan 75	L.O.F. P.E.	6 24	2.0319	>.05
	9 May 75	L.O.F. P.E.	6 24	1.7409	>.05
Quadr.	9 Jul 74	L.O.F. P.E.	1 55	4.0049	>.05
	7 Aug 74	L.O.F. P.E.	1 55	19.194	<.01
	25 Jan 75	L.O.F. P.E.	5 24	1.8007	>.05
	9 May 75	L.O.F. P.E.	5 24	2.0720	>.05
Cubic	9 Jul 74	L.O.F. P.E.	0 55	-	-
	7 Aug 74	L.O.F. P.E.	0 55	-	_ '
	25 Jan 75	L.O.F. P.E.	4 24	2.2396	>.05
	9 May 75	L.O.F. P.E.	4 24	2.5659	>.05

^{*}L.O.F. is lack of fit and P.E. is pure error.

TABLE XXI

B VALUES, F VALUES FROM PARTIAL SUM OF SQUARES,
AND R² VALUES FOR SPECIES DIVERSITY
VERSUS DEPTH MODELS

R ² 0.1761 0.1944 0.2532
0.1944
0.2532
0.2532
0.4136
0.5857
0.6068
0.6758
0.6911
0.6941
0.6049
0.6070
0.6118

^{*}DEPTH is the linear term, DEP2 is the second order term, and DEP3 is the third order term.

TABLE XXII

B VALUES, F VALUES FROM PARTIAL SUMS OF SQUARES,
AND R² VALUES FOR VARIETY
VERSUS DEPTH MODELS

Date	Mode1	Source	B Value	F Value	Prob> F	R ²
9 Ju1 74	Linear	DEPTH*	-0.0608	24.9625	0.0001	0.3243
J.	Quadr.	DEPTH	-0.1109	7.9836	0.0067	0.3473
		DEP 2	0.0022	1.7968	0.1860	
	Cubic	DEPTH	0.0053	0.0024	0.9610	0.3640
		DEP 2	-0.0105	0.8846	0.3515	
•		DEP3	0.0003	1.3119	0.2575	
7 Aug 74	Linear	DEPTH	-0.0811	41.2797	0.0001	0.4425
	Quadr.	DEPTH	-0.1997	28.2413	0.0001	0.5414
		DEP 2	0.0051	10.9905	0.0017	
	Cubic	DEPTH	-0.1501	2.0350	0.1599	0.5437
		DEP 2	-0.0003	0.0008	0.9783	
		DEP3	0.0001	0.2550	0.6158	
25 Jan 75	Linear	DEPTH	-0.1030	60.1269	0.0001	0.6671
	Quadr.	DEPTH	-0.1846	13.3874	0.0010	0.6964
		DEP 2	0.0034	2.8013	0.1049	
	Cubic	DEPTH	-0.2094	2.3486	0.1366	0.6969
		DEP 2	0.0060	0.2035	0.6554	
		DEP3	-0.0001	0.0383	0.8462	
9 May 75	Linear	DEPTH	-0.1089	36,8932	0.0001	0.5515
	Quadr.	DEPTH	-0.1274	3.1962	0.0843	0.5526
		DEP2	0.0008	0.0720	0.7904	
	Cubic	DEPTH	-0.0777	0.1624	0.6900	0.5539
		DEP2	-0.0044	0.0544	0.8173	
		DEP3	0.0001	0.0772	0.7830	

^{*}DEPTH is the linear term, DEP2 is the second order term, and DEP3 is the third order term.

TABLE XXIII

B VALUES, F VALUES FROM PARTIAL SUMS OF SQUARES,
AND R² VALUES FOR EQUITABILITY
VERSUS DEPTH MODELS

			<i>,</i> .		. *	
Date	Model	Source	B Value	F Value	Prob F	R ²
9 Ju1 74	Linear	DEPTH*	-0.0200	13.9123	0.0033	0.5584
	Quadr.	DEPTH DEP 2	-0.0526 0.0015	15.3646 6.6052	0.0029	0.7341
	Cubic	DEPTH DEP2 DEP3	-0.0027 -0.0040 0.0001	0.0064 1.3188 2.5471	0.9382 0.2804 0.1450	0.7927
7 Aug 74	Linear	DEPTH	-0.0276	8.4295	0.0144	0.4338
	Quadr.	DEPTH DEP2	-0.1044 0.0035	39.1678 23.7246	0.0001 0.0007	0.8321
	Cubic	DEPTH DEP2 DEP3	-0.0582 -0.0016 0.0001	1.7153 0.1169 1.2551	0.2227 0.7403 0.2916	0.8527
25 Jan 75	Linear	DEPTH	-0.0173	14.7206	0.0086	0.71.04
	Quadr.	DEPTH DEP 2	0.0122 -0.0012	0.7874 4.9460	0.4155 0.0757	0.8544
	Cubic	DEPTH DEP2 DEP3	0.0140 -0.0014 0.0001	0.1185 0.1302 0.0025	0.7480 0.7364 0.9627	0.8545
9 May 75	Linear	DEPTH	-0.0173	5.7488	0.0535	0.4893
	Quadr.	DEPTH DEP 2	0.0073 -0.0010	0.0646 0.7840	0.8094 0.4165	0.5585
	Cubic	DEPTH DEP2 DEP3	-0.1076 0.0108 -0.0003	3.3197 3.5862 4.4080	0.1425 0.1312 0.1037	0.7900

^{*}DEPTH is the linear term, DEP2 is the second order term, and DEP3 is the third order term.

TABLE XXIV

B VALUES AND F VALUES FROM PARTIAL SUMS OF SQUARES FOR INDICES VERSUS PHYSICOCHEMICAL PARAMETERS

Index	Date	Source	B Value	F Value	Prob > F
₫	25 Jan	DEPTH*	-0.0959	11.1117	0.0026
_	25 0411	OXYCON	-0.6289	2.0628	0.1629
		TEMP	0.2011	0.5222	0.4764
		SEDPH	0.9206	7.7361	0.0099
		SEDORG	-0.0333	0.4592	0.5040
		SEDORG	-0.0555	0.4392	0.3040
	9 May	DEPTH	0.0682	0.7742	0.3870
	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	OXYCON	-0.0845	0.7778	0.3859
		TEMP	0.5550	6.4869	0.0171
		SEDPH	-2.1058	3.1062	0.0897
		SEDORG	0.0559	0.9602	0.3362
		, ,			
d	25 Jan	DEPTH	-0.1153	8.8498	0.0063
		OXYCON	-0.6005	1.0363	0.3181
		TEMP	0.6294	2.8172	0.1052
		SEDPH	0.3128	0.4922	0.4892
		SEDORG	0.0126	0.0361	0.8508
	9 May	DEPTH	-0.0412	0.1794	0.6754
		OXYCON	-0.1123	0.8705	0.3594
		TEMP	0.3062	1.2527	0.2733
		SEDPH	-1.7600	1.3760	0.2514
		SEDORG	0.0992	1.9191	0.1777
_					
E	25 Jan	DEPTH	-0.0172	4.2532	0.1753
		OXYCON	-9.1178	0.8569	0.4523
		TEMP	0.0149	0.0341	0.8705
		SEDPH	0.2935	9.3069	0.0927
		SEDORG	-0.0021	0.0225	0.8945
	0 Mass	DEDUII	0.0760	12 2112	0 0691
	9 May	DEPTH	0.0769	13.2112	0.0681
		OXYCON	0.0105	0.1628	0.7257
		TEMP	0.2601	19.1325	0.0485
		SEDPH	-0.9430	8.3640	0.1017
		SEDORG	-0.0054	0.1209	0.7612

^{*}DEPTH is depth, OXYCON is dissolved oxygen concentration, TEMP is water temperature, SEDPH is sediment pH, and SEDORG percent sediment organic content.

APPENDIX C

DENSITY DATA

TABLE XXV

DENSITY (INDIVIDUALS/M²) OF BENTHIC MACROINVERTEBRATES
BY SPECIES, STATION, AND DEPTH IN ARBUCKLE RESERVOIR
ON 9 JULY 1974

Depth	1	Sta 5	tion 5	15	1	Stat 5	ion 6 10	15	Station 7
Hirudinea	7				-				
Stylaria sp.	7								
Naididae									7
Aulodrilus pigueti			50			50		294	768
A. pleuriseta				22					50
Branchiura sowerbyi		36	36		7				
Limnodrilus hoff.	7								
Potomothrix sp.				72					
Tubif. w/cap. ch.	7*		22*		7*				
Tubif. w/o cap. ch.1	100*				14*			114*	
<u>Hyalella</u> <u>azteca</u>	29				208				
Hexagenia sp.						7			
Brachycercus sp.						7			
Caenis sp.	7		*,						
<u>Ishnura</u> sp.	7				14				
Sialis sp.	7		7						
Leptoceridae					29	43			
Polycentropus sp.	50								
Campanif. Trichopt.					14				
Ceratopogonidae	7		:						
Chaoborus punctipen.	7	538	1212	940	7	43	2819	2654	265

TABLE XXV (Continued)

		Stat	ion 5			Stai		Station 7	
Depth:	1	5	10	15	1	5	10	15	24
Coelotanypus sp.		144	265		29	172	29	64	,
Procladius sp.	29	50	29		22	. 29	64	7	
Tanypus sp.		272	646			22	165		
Pentaneurini					7				
Chironomus sp.			36		,	7	14		
Cryptochironomus sp	. 7	7,			7	22			
Dicrotendipes sp.					7				
Endochironomus sp.					36				
Glyptotendipes sp.			*		7				
Polypedilum sp.						14			
Pseudochironomus sp	. 22								
Stenochironomus sp.		7							
Stictochironomus sp	. 7								
Chironomini sp. A					7	22			
Chironomini sp. B					7				
Micropsectra sp.	7				7	57			
Tanytarsus sp.		29			122				
Psectrocladius sp.					7				
Chironomid pupae		7*							36*
Unionidae					7				
Physa sp.		7							

^{*}These values were included in density totals but were not used in determining total number of species or species diversity, variety, or equitability since they are unidentifiable, immature forms and probably do not represent different species.

TABLE XXVI

DENSITY (INDIVIDUALS/M²) OF BENTHIC MACROINVERTEBRATES
BY SPECIES, STATION, AND DEPTH IN ARBUCKLE RESERVOIR
ON 7 AUGUST 1974

			tion 5				ation		Station 7
Depth:	1	5	10	15	1	5	10	15	24
<u>Aulodrilus</u> pigueti						7		179	5674
Branchiura sowerbyi	136	7			186	7	7	7	
Limnodrilus hoff.	22								
Tubifex templetoni	57		· 7	43				136	
Tubificid sp. A	86*								
Tubif. w/cap. ch.	7*								
Tubif. w/o cap. ch.	186				115			43	7
Hyalella azteca	22								
Hexagenia limbata		22							
Gomphus sp.						7			
Sialis sp.					7				
Dubiraphia sp.	200								
Leptoceridae						14			
Polycentropus sp.	57				50				
Chaoborus punctipen.		194	3063	6076	7	108	423	3006	646
Coelotanypus sp.	14	165	122	57	43	100		14	
Procladius sp.	7	115			14	43			
Tanypus sp.		438	7		108	115			
Pentaneurini	29	7			14				
Chironomus sp.		7	7			14			

TABLE XXVI (Continued)

		Stat	ion 5			Stat	ion 6		Station 7
Depth:	1	5	10	15	1	5	10	15	24
Cryptochironomus sp.	22				22				
Dicrotendipes sp.	7					7			
Harnischia sp.	7	22		,		7			
Paralauterborn. sp.					14				
Polypedilum sp.			, i		14				
Pseudochironomus sp.	7								
Tanytarsus sp.	43	22			29	29			
Orthocaldius sp.					29				
Unionidae		7	7		14				

^{*}See footnote on TABLE XXV.

TABLE XXVII

DENSITY (INDIVIDUALS/M²) OF BENTHIC MACROINVERTEBRATES
BY SPECIES AND DEPTH IN ARBUCKLE RESERVOIR
ON 25 JANUARY 1975

				Dep	oth (m)			
	1	2	4	7	11	15	19	24
Hydra sp.		269		22		32	11	11
Hirudinea				43			•	
Dero digitata	75	75		32	97	11.	22	64
Nais variabilis	97							
Slavina appendiculata	43							
Stylaria lacustris	2379	1420	32	11				
Aulodrilus pigueti		452	86	64			430	43
Branchiura sowerbyi			22					
Limnodrilus clapare.							11	
Tubifex templetoni		32						
Tubifex tubifex		108	22					
Tubif. w/cap. ch.	64*	75*	11*	,			118*	
Tubif. w/o cap. ch.	54*	194*		11*	,		43*	
Hyalella azteca	807	43		11		•		
Hydracarina sp. A								11
Hydracarina sp. B		11						
Hexagenia limbata		97	22				32	
H. rigida	11	75						
Caenis sp.	75	11	11					
<u>Dubiraphia</u> sp.	11	11						
Stenelmis sp.		22			<i>2</i>	•		

TABLE XXVII (Continued)

				. De	epth (m))		
	1	2	4	7	11	15	19	24
Hydroporinae		11						
Oecetis sp.	86	43	129	97	86	11		
Psychomyiid genus A.		43						
Neotrichia sp.			11					
Orthotrichia sp.				11				
Bezzia sp.	11	32	11					
Chaoborus punctipen.			22	11	323	1690	2777	1615
Clinotanypus sp.				11			•	
Coelotanypus sp.	11	753	829	398	172	140	22	
Procladius sp.	54	527	1152	377	560	334	140	32
Tanypus sp.			11					
Chironomus sp.		226	258	75	172	151	336	32
Cryptochironomus sp.	75	172		22	32			
Dicrotendipes sp.	161	54	11					
Endochironomus sp.	11							
Paralauterborn. sp.	54	151						
Polypedilum sp.		43	22	35				
Stictochironomus sp.					22			
Tribelos sp.		11						
Chironomini sp. A		4198						
Cladotanytarsus sp.	215	990	32					
Micropsectra sp.			11					

TABLE XXVII (Continued)

· ·											
	Depth (m)										
	1	2	4	7	11	15	19	24			
Rheotanytarsus sp.	237			:							
Tanytarsus sp.	355	527	11	35	32						
Orthocladius sp.	118										
Psectrocladius sp.					11						
Trichocladius sp.	11										
Trissocladius sp.	75	140									
Sphaerium sp.	22	764	183	22		11					
Physa sp.			•					11			

^{*}See footnote on TABLE XXV.

TABLE XXVIII

DENSITY (INDIVIDUALS/M²) OF BENTHIC MACROINVERTEBRATES
BY SPECIES AND DEPTH IN ARBUCKLE RESERVOIR
ON 9 MAY 1975

	Depth (m)										
	1	2	4	7	11	15	19	24			
Hirudinea				11							
Dero digitata	86	140	86	22	280	151	204	1098			
Slavina appendiculata	<u>.</u> 11										
Stylaria lacustris	280	215		32	11			•			
Aulodrilus pigueti		22	108	11	11	258	75	19,20			
Branchiura sowerbyi				43		11					
Limnodrilus clapare.				21			54				
L. <u>hoffmeisteri</u>	32			43			11				
Tubifex templetoni		43	22	,							
T. tubifex	•	108	22	108							
Tubif. w/cap. ch.	97*	409*	194*	366*	54*	11*		22			
Tubif. w/o cap. ch.	194*	215*	151*	151*	75*	22*		43			
Hexagenia limbata		11	64	64			11				
Libellula sp.	11	11									
<u>Sialis</u> sp.		32	32								
Dubiraphia sp.	11	43	22	11							
Oecetis sp.			32		11						
Psychomyiid genus A	22	11									
Bezzia sp.	54	32	32								
Chaoborus punctipen.			161	97	32	22	151	97			
Coelotanypus sp.	11	441	506	506		32	129				

TABLE XXVIII (Continued)

	Depth (m) 1 2 4 7 11 15 19 24										
	1	2	4	7	11	15	19	24			
Procladius sp.	54	301	614	775	97	151	409	204			
Chironomus sp.	409	377	248	86		43	64	11			
Cryptochironomus sp.	64		22		11	11					
Dicrotendipes sp.				11							
<u>Harnischia</u> sp.	43	172	291	43			11				
Polypedilum sp.	215	301	323	,	32						
Stenochironomus sp.			11	11							
Stichtochironomus sp.	22										
Cladotanytarsus sp.	76	1119	54								
Micropsectra sp.	22	11	11								
Rheotanytarsus sp.			11								
Tanytarsus sp.	183	43	54	32		22					
Diamesa sp.	97	280	54								
Chironomini sp. A.	11	118	194								
Cricotopus sp.	22							ì			
Trissocladius sp.		54									
Chironomid pupae	22*	226*	108*	11*		11*	22*	11*			
Sphaerium sp.		118									

^{*}See footnote on TABLE XXV.

VTTA

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Master of Science

Thesis: THE EFFECTS OF PHYSICOCHEMICAL CONDITIONS ON THE DISTRIBUTION

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