COMMUNITY STRUCTURE OF BENTHIC MACROINVERTEBRATES AND RELATED PHYSICOCHEMICAL CONDITIONS IN KEYSTONE RESERVOIR, OKLAHOMA

By

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AND RELATED PHYSICOCHEMICAL CONDITIONS

IN KEYSTONE RESERVOIR, OKLAHOMA

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PREFACE

The objectives of this study were to determine the associations and distribution of benthic macroinvertebrate species inhabiting a large impoundment, to establish relationships between physicochemical conditions and the benthic fauna, and to apply methods derived from information theory to benthic macroinvertebrate community structure.

Troy C. Dorris served as major adviser. Calvin G. Beames, L. Herbert Bruneau, William A. Drew, and Dale W. Toetz served on the advisory committee and criticized the manuscript. Jerry Wilhm assisted with data recording, and Nancy Norton wrote the computer program for species diversity calculations. Verification of invertebrate determinations were made by Walter J. Harman, Selwyn S. Roback, and Willis W. Wirth. Charles E. Dorris and David Smith helped make field collections. The assistance of all these people is appreciated.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

The number of riverine impoundments in the United States has increased rapidly during the past 20 years. The impoundments control flooding and provide water for irrigation, hydroelectric power, urban consumption, and recreation. Past studies reveal that impoundments generally differ to some degree in both physicochemical conditions and benthic fauna.

Depth, physicochemical conditions, character of the bottom deposits, and seasons influence qualitative and quantitative aspects of the bottom fauna (Eggleton, 1935). Gaufin and Tarzwell (1956) concluded that the occurrence or absence of a given species is less reliable than associations or populations of benthic invertebrates in determining the degree of pollution in streams. That conclusion is equally applicable to reservoirs and lakes. There is a need, however, for a more economical and concise method than those used in the past for reporting and comparing data on community structure in lakes and reservoirs. A more economical and concise method is used in this paper.

Analysis of community structure by methods derived from information theory was proposed by Margalef (1956). Margalef (1961) considered diversity and information to be approximately the same. It follows that large amounts of information about organisms can be briefly summarized by use of diversity indices calculated from numbers of individuals and

species in a sample (Patten, 1962). The manner in which individuals are distributed among species in a community is reflected by species diversity (d). Minimum diversity (d_{min}) exists if all individuals are of one species, and maximum diversity occurs if each individual belongs to a different species. Species diversity (d) values lie between d_{max} and d_{min}. Diversity per individual ($\bar{d}$) becomes smaller as the probability of selecting a particular species becomes a certainty and larger as the choice becomes more uncertain. Redundancy (R) reflects the same situation as $\bar{d}$ but in an inverse manner. Redundancy (R) becomes larger as the number of species decreases (less choice) and smaller as the number of species increases (more choice). Wilhm et al. (1966) give some history on the development of diversity indices for use as indicators of community structure.

Diversity indices are valid indicators of changes and differences in community structure (Patten, 1962; Mathis, 1965; Wilhm et al., 1966; Harrell, 1966). Small numbers of species and large numbers of individuals usually occur in waters receiving some type, or types, of pollutants. There is, in such cases, a large probability that an individual organism collected during sampling belongs to a species previously recognized. Redundancy (R) is high since considerable repetition of information exists. A low index of diversity is reflected by low information per individual. Non-polluted waters are characterized by larger numbers of species and smaller numbers of individuals per species. Information per individual is greater and is reflected in low redundancy values. Aquatic environments between the extremes of severe pollution and clean water have intermediate values of diversity and redundancy. Diversity indices are limited in that they indicate the presence, or

absence, and degree of pollution but give little or no indication of causal phenomena. Physicochemical determinations must be made.

Muttkowski (1918), Juday (1922), Eggleton (1931, 1935, 1952), Deevey (1941), Sublette (1957), and others have reported benthic studies in a conventional manner. Very few attempts were made to answer questions concerning life histories, benthic associations, tolerance limits, bottom preference, and other factors. In the present study, species diversity indices were used to compare areas within the same reservoir, and attempts were made to answer some questions not treated by the earlier authors.

CHAPTER II

DESCRIPTION OF AREA

General Description of Reservoir

Keystone Reservoir was formed by impounding the Arkansas River at river km 867.1, a point 3.2 km below the confluence of the Arkansas and Cimarron rivers and 32 km west of Tulsa (Fig. 1). The reservoir reached power pool level in April, 1965. The Arkansas and Cimarron rivers form the two main arms of the reservoir, and at power pool level (220.37 m MSL) the reservoir extends about 45 and 49 km up the two arms, respectively. At power pool level the reservoir has a surface area of 10,648 ha (Eley et al., 1967).

Sampling Areas

Four bays on the Cimarron arm were selected for study (Fig. 1). Bay 1, Salt Creek, is about 5 km above the confluence of the Arkansas and Cimarron rivers. Bay 2 is on the main body of the reservoir about 1 km north of Bay 1. Bay 3 is about 16 km above the confluence of the Arkansas and Cimarron rivers. Bay 4 is the lower end of House Creek about 28 km above the confluence of the Arkansas and Cimarron rivers. The bottom was a mixture of mud and sand at 1 and 3 meters in all bays, grading to soft, black ooze or deep silt at greater depths.

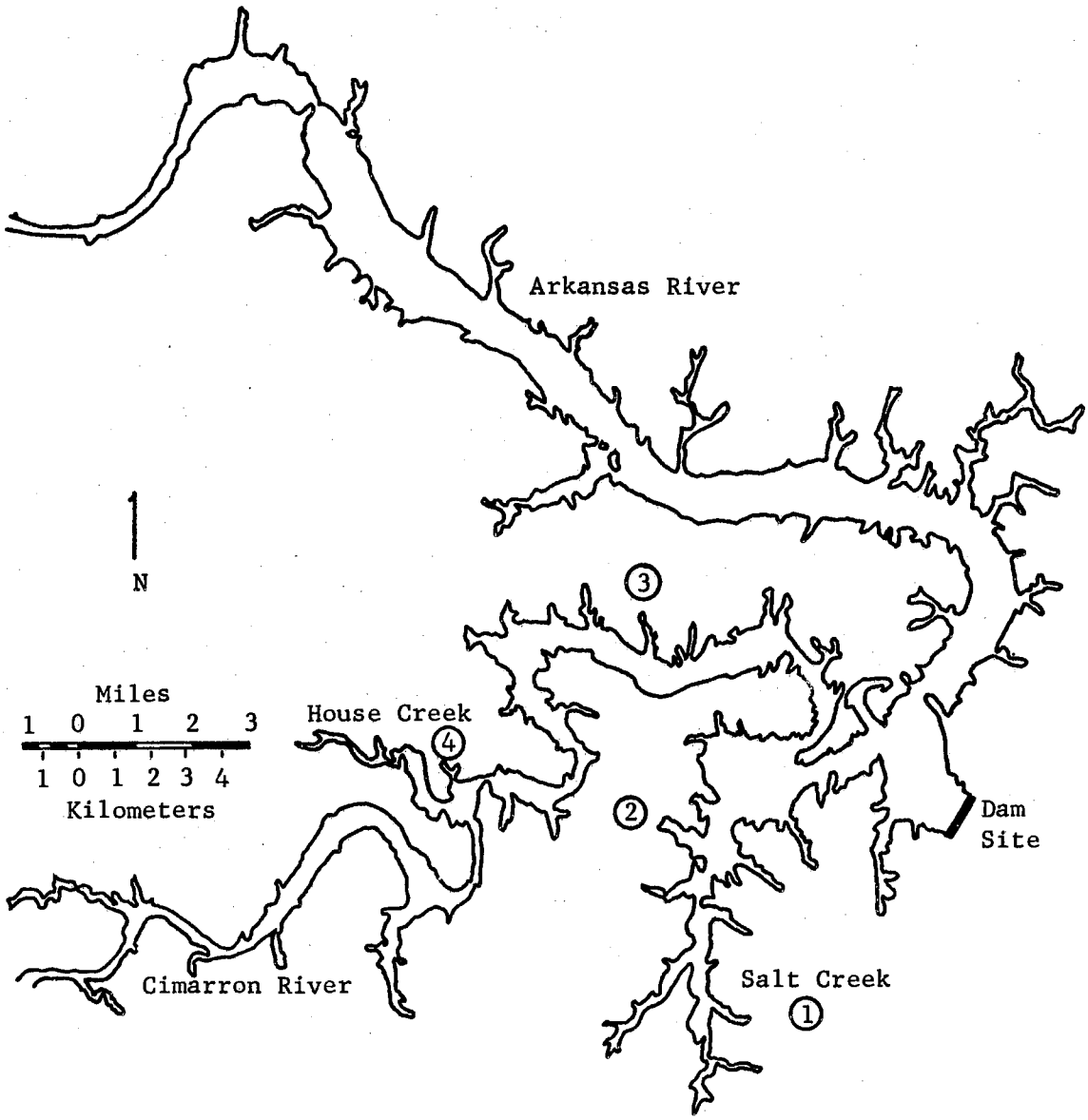

Figure 1. Keystone Reservoir, Oklahoma. Circled numbers indicate locations of bays.

CHAPTER III

PROCEDURES

Transects and Sampling Depths

Previous studies have revealed that the profundal zones of lakes and reservoirs contain very few species of benthic organisms, and the greatest diversity, regardless of physicochemical conditions, occurs in the shallower waters. This study represents the first, or one of the first, attempts at analyzing community structure of a reservoir by use of diversity indices. Therefore, four apparently different bays were selected to introduce the comparative aspect, so samples at different depths could be taken, and some information concerning the possibility of comparing reservoirs in the future could be gained. Since sampling was to be done from existing statistical populations, as opposed to populations established at random by the investigator, randomness was introduced by the methods described.

Physicochemical measurements and benthic macroinvertebrate collections were made monthly in all four bays from 4 November, 1965, to 6 October, 1966. An electronic depth indicator (Herter's Model 130) was used to establish a transect through the length of each bay on each collection date (Fig. 2). Samples were taken at odd-numbered depths from 1 through 9 meters, plus an additional sample at a greater depth. Sampling was started at every meter drop in depth, but this procedure was

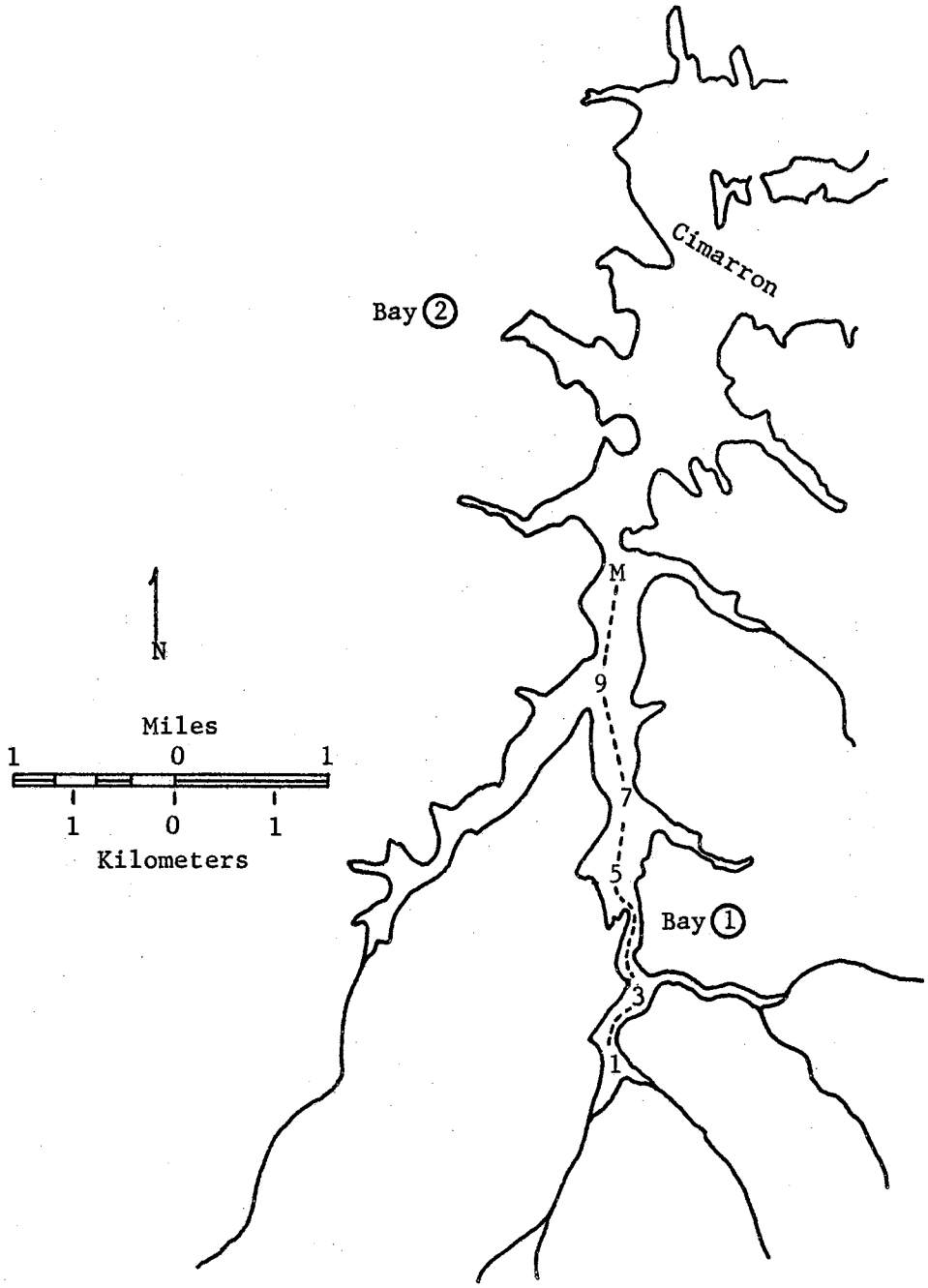

Figure 2. Bays 1 and 2. Hatched line and numbers in Bay 1 indicate sampling transect and sampling depths.

abandoned due to small variations in data between depths, to difficulty in establishing the exact depth, and to lack of time. Samples from 9 meters usually were taken on the edge of a submerged channel. A sample always was taken at the bottom of the channel.

Physicochemical Parameters

Specific conductance, converted to micromohos/cm at 25 C, and temperature were determined with a RB Solu-bridge and attached thermometer (Industrial Instruments Co.). Hydrogen ion concentration was estimated with a Hellige pH comparator. Dissolved oxygen was determined on duplicate bottom-water samples by the Alsterberg (azide) modification of the Winkler method (APHA, 1960) titrated with 0.250 N phenylarsene oxide. Transparency was determined with a 20 cm Secchi disc.

Biological

Four benthic samples were taken with a 15 cm Ekman dredge at each sampling depth and combined into a pair of double samples. Samples were washed in the field in sieves with 0.18 mm opening (80 mesh). Organisms and remaining debris were preserved in 10% formalin. Sorting and picking were done by hand, and collected organisms were preserved in 80% alcohol.

Mean monthly ash-free weight was determined for *Chaoborus punctipennis* Say larvae, and mean annual ash-free weights were determined for other species. Organisms were dried at 100 C for 3 hours and burned in a muffle furnace at 500 C for 1 hour.

Vertical migration of *Chaoborus punctipennis* larvae was investigated in August, 1966, and again in February, 1967, by vertical hauls

with nets of 0.26 mm opening. Collections were made at 2 meter intervals from 1 meter to the bottom every 3 hours for a period of 24 hours. Two Ekman dredge hauls were taken with each series of net hauls.

Species Diversity

Estimates of species diversity (d), diversity per individual ($\bar{d}$), maximum diversity (d_{max}), minimum diversity (d_{min}) and redundancy (R) were determined by equations derived from Patten (1962) (H, $\bar{H}$, m, and N were changed to d, $\bar{d}$, s and n):

$$d = \sum_{i=1}^{s} n_i \log_2 \frac{n_i}{n}$$

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

$$d_{max} = \log_2 n! - s \log_2 \left(\frac{n}{s}\right)!$$

$$d_{min} = \log_2 n! - \log_2 \left[n - (s-1)\right]!$$

$$R = \frac{d_{max} - d}{d_{max} - d_{min}}$$

where n is the total number of individuals, n_i is the number of individuals of species i, and s is the number of species per unit area. In order to define $\bar{d}$ in terms of a position the following equations were

obtained:

$$\bar{d}_{max} = \frac{d_{max}}{n}$$

$$\bar{d}_{min} = \frac{d_{min}}{n}$$

$$R = \frac{\bar{d}_{max} - \bar{d}}{\bar{d}_{max} - \bar{d}_{min}}$$

The position of $\bar{d}$ is between $\bar{d}_{max}$ and $\bar{d}_{min}$ and R remains the same.

CHAPTER IV

RESULTS AND DISCUSSION

Biological

Species Collected

A total of 25 species of benthic macroinvertebrates was collected (Table I). Twenty-four species were collected in Bay 1, 18 species in Bay 2, 16 species in Bay 3, and 13 species in Bay 4. Twelve of the 25 species were midges of the family Tendipedidae. *Polypedilum* nr. *halterale* Coq. was the only tendipedid species that did not occur in Bay 1. *Dicrotendipes* sp., *Stictochironomous* sp., and *Tendipes* sp. were not collected in Bay 2 while only *Dicrotendipes* sp. and *Pseudochironomus fulviventris* Joh. were absent from Bay 3. Five species of tendipedids did not occur in Bay 4. The ceratopogonid *Palpomyia tibialis* Meigen was taken at least once in each bay. The phantom midge *Chaoborus punctipennis* was the most abundant species collected.

Two species of oligochaetes, *Dero* sp. and *Limnodrilus hoffmeisteri* Clap., were relatively abundant in all bays. One coelenterate, one nematode, two ephemeropterans, one odonate, three trichopeterans, and one coleopteran were collected, and all were relatively scarce. The coleopteran *Berosus striatus* Say and the trichopteran *Agraylea* sp. were collected once.

Cordylophora lacustris Allman was collected 21 times in a total of

TABLE I

ANNUAL NUMBERS OF BENTHIC MACROINVERTEBRATES

Individuals/m^2

BAY	1						2						3						4					
DEPTH (Meters)	1	3	5	7	9	M*	1	3	5	7	9	M*	1	3	5	7	9	M*	1	3	5	7	9	M*
COELENTERATA																								
*Cordylophora lacustris***		P	P	P	P	P			P	P			P		P	P	P			P	P			
NEMATODA	1	1	2		1																			
OLIGOCHAETA																								
Dero sp.	72	96	370	178	265	99	65	101	80	54	73	1	6	12	8	19	23	21	4	4	3	5	2	1
Limnodrilus hoffmeisteri	2	112	104	26	105		23	248	175	45	41		26	49	19	13	11	2	59	12	4	1		
EPHEMEROPTERA																								
Caenis sp.	1	1	3				2																	
Hexagenia sp.	1		1	1			1		3		1													
ODONATA																								
Octogomphus specularis	1		1																					
TRICHOPTERA																								
Oecetis sp.					2		1													1				
Psychomyia sp.					3	6				1								4						
Agraylea sp.	1																							
COLEOPTERA																								
Berosus striatus	4																							
DIPTERA CERATOPOGONIDAE																								
Palpomyia tibialis		2			1			4	2				2		4	1	2		1					

TABLE I (Continued)

BAY	1						2						3						4					
	Individuals/m^2																							
DEPTH (Meters)	1	3	5	7	9	M*	1	3	5	7	9	M*	1	3	5	7	9	M*	1	3	5	7	9	M*
CULICIDAE																								
Chaoborus punctipennis	5	286	396	342	301	539	37	223	262	211	262	1,324	13	71	530	912	591	1,500	23	516	1,543	2,496	2,512	642
TENDIPEDIDAE																								
Calopsectra group A R.	32	31	33	7	50	4	36	9	7	2	8		34	26	11	2	8	2	7	5	2			1
Cryptochironomus sp.	153	49	28	20	18	2	116	14	12	7	6		13	43	13	14	5	2	20	1		1		
Dicrotendipes sp.	7	3	4	1	8																			
Glyptotendipes nr. lobiferus	73	54	8	16	4	1	2	6	15	3	2		3	1	1	5	3		3	6	7	2	2	
Harnischia nr. arbortiva	41	29	28	29	9	7	68	16	15	8	9		9	5	19	15	12	2	4	4	5	2		
Polypedilum nr. halterale							65	3	3	2	4		62	14	9	3	8	5	78	2	1	6		
Procladius poss. bellus	4	22	76	18	17	9	32	112	131	66	88		20	32	110	113	27	12	12	29	17	6		
Pseudochironomus fulviventris	27	5	2	9		1			1															
Stictochironomus sp.	10	8	10	2									1											
Tendipes nr. attenuatus	15	18	17	12	6		15	10	15	10	1		3	11	2									
Tendipes plumosus	29	51	40	31	16	7	49	30	52	34	13	2	16	23	16	9	5	1	5	6	7	2	4	1
Tendipes sp.	8	19	12	19	9	12											2							

*Depths greater than 9 meters

**Not included in diversity indices determinations

1,232 dredge samples and was taken from all four bays. This unique colonial hydroid coelenterate generally has been found in inland waters of relatively high salt content (Hutchinson, 1967). It occurs in east coast estuaries and has been taken in rivers and streams in the eastern half of the U.S. (Pennak, 1953; Isom et al., 1962; Davis, 1957). There is one published record of earlier collections in Oklahoma (Blair, 1964).

Many common aquatic species such as most mayflies and dragonflies, molluscs, megalopterans, most annelids, tabanids, stratiomyids, and most coleopterans and hemipterans were absent from the reservoir. Sublette (1957) collected a total of 87 species of macroscopic benthic invertebrates from Lake Texoma (Denison Reservoir), Oklahoma. Comparison between the two reservoirs is not possible since Sublette (1955) did not measure conductivity.

Seasonal Changes in Numbers of Benthic Organisms

There was a significant increase in numbers of individuals each month from November to February or March in all four bays (Table II). Increases in Bay 1 were due to significant increases in numbers of both species of annelid worms and slight increases in tendipedid species. The total annelid worms in Bay 2 was 126 per m^2 in November and 327 per m^2 in February. The increase in Bay 2 from February to March was due to *Chaoborus punctipennis*. *C. punctipennis* larvae increased from November to February only in Bay 4, and increases in Bay 4 were due almost entirely to increases in this species. Aquatic annelids reproduce during the winter months, but development is prolonged by low temperature. Severe stagnation also prolongs development and greatly

TABLE II

TOTAL NUMBERS AND BIOMASS OF BENTHIC MACROINVERTEBRATES AND RELATIVE NUMERICAL ABUNDANCE AND BIOMASS OF *Chaoborus punctipennis* (PER M^2 BY MONTH)

BAY	1						2					
	Total Benthic Macroinvertebrates		*Chaoborus punctipennis* Included in Total				Total Benthic Macroinvertebrates		*Chaoborus punctipennis* Included in Total			
	Individuals	Ash-Free Weight	Individuals		Ash-Free Wt.		Individuals	Ash-Free Weight	Individuals		Ash-Free Wt.	
MONTH	No.	Mg.	No.	%	Mg.	%	No.	Mg.	No.	%	Mg.	%
Nov.	135	51	7	5	0.7	1	288	76	134	47	13	17
Dec.	561	149	111	20	12	8	463	110	129	28	14	13
Jan.	688	226	66	10	7	3	447	140	97	22	10	7
Feb.	1,281	343	29	2	3	1	790	238	97	12	10	4
Mar.	1,147	312	70	6	8	3	1,586	357	952	60	102	29
Apr.	901	264	201	22	28	11	784	274	152	19	21	8
May	548	92	4	1	0.5	1	344	132	9	3	1	1
June	214	35	149	70	14	40	719	110	610	85	56	51
July	775	70	762	98	64	91	716	85	633	88	53	62
Aug.	2,206	251	1,971	89	190	76	1,307	149	1,072	82	103	69
Sept.	672	91	524	78	43	47	576	80	359	62	29	36
Oct.	192	33	86	45	8	24	345	51	232	67	23	45

TABLE II (Continued)

BAY	3						4					
	Total Benthic Macroinvertebrates		*Chaoborus punctipennis* Included in Total				Total Benthic Macroinvertebrates		*Chaoborus punctipennis* Included in Total			
	Individuals	Ash-Free Weight	Individuals		Ash-Free Wt.		Individuals	Ash-Free Weight	Individuals		Ash-Free Wt.	
MONTH	No.	Mg.	No.	%	Mg.	%	No.	Mg.	No.	%	Mg.	%
Nov.	177	23	106	60	11	48	402	49	370	92	37	76
Dec.	404	66	250	62	27	41	696	84	657	94	72	86
Jan.	386	85	230	60	23	27	---*	--*	---*	--*	--*	--*
Feb.	---*	--*	---*	--*	--*	--*	1,699	189	1,655	97	173	92
Mar.	397	127	160	40	17	13	1,162	177	1,040	90	111	63
Apr.	312	80	156	50	22	28	461	70	402	87	66	94
May	230	47	7	3	0.8	2	121	24	34	28	4	17
June	297	41	110	37	10	24	393	59	319	81	29	49
July	1,912	170	1,840	96	154	91	2,127	185	2,107	99	176	95
Aug.	2,240	224	2,166	97	209	93	2,528	243	2,466	98	237	98
Sept.	883	101	691	78	56	55	2,238	185	2,184	98	178	96
Oct.	1,003	145	789	79	77	53	2,681	265	2,633	98	257	97

*No sample taken because of ice cover

reduces the percentage of hatch. Cold temperature extends the development time of C. punctipennis eggs, and severe summer stagnation prevents hatching (Eggleton, 1931). Therefore, increases in numbers of segmented worms and Chaoborus larvae during the winter months were not unexpected. A second increase in late summer or early fall was due mostly to increases of C. punctipennis larvae. Large numbers of earlier instars appeared in the bottom mud in August.

Biomass and Numbers of Individuals

Total biomass as ash-free weight in Bay 1 was 343 mg per m^2 for a total of 1,281 individuals in February, while in August it was 251 mg per m^2 for 2,206 individuals (Table II). Mean ash-free weight per individual in February was 0.27 mg and 0.11 mg in August. This difference was largely due to the difference in weight of the dominant species. The mean weight per individual of Limnodrilus hoffmeisteri was about six times greater than that of Chaoborus punctipennis larvae. C. punctipennis larvae dominated both numbers and biomass in Bays 1 and 2 during the summer and early fall. They comprised the largest percentage of numbers in Bay 3 the entire year but dominated the biomass only during the summer and early fall. C. punctipennis larvae dominated both numbers and biomass at all times in Bay 4.

Chaoborus punctipennis

Vertical migration behavior, especially during summer and fall, makes C. punctipennis larvae readily available to fish predators, and this was the dominant benthic species in the reservoir. Juday (1922) determined that protein and fat comprised 76% of the larval dry weight of C. punctipennis, and he considered these larvae to be excellent

fish-food. Carter (1967) found the greatest concentrations of fishes near Bays 3 and 4 in the summer and fall, while concentration was greatest near the common junction of the Arkansas and Cimarron rivers during the spring and winter months. A few dredge samples were taken each month near the common junction, and C. punctipennis larvae were the only benthic organisms collected.

The shallower depths in Bays 1 and 2 were not dominated by Chaoborus punctipennis larvae (Table III). C. punctipennis larvae comprised the greatest percentage of individuals from 5 m through the maximum depth in Bay 3 and all depths except 1 m in Bay 4. A consistently high percentage of C. punctipennis larvae and scarcity of other species in Bay 4 was probably due to a bottom of deep silt, high turbidity, and high conductivity.

Physicochemical

pH and Temperature

Observed differences in pH (Table IV) and temperature (Fig. 3) among bays proved to be insignificant. Small variations were due to differences in sampling dates. Slightly lower pH values were observed in the deeper water especially during the late spring and summer months.

Transparency

Secchi disc transparency was lowest in Bay 4 and highest in Bay 2 at all times (Fig. 4). Cimarron water was always turbid, but turbidity decreased between Bay 4 and the junction of the two rivers. At no time could the Secchi disc be observed below 0.75 m in Bay 4 and generally was less than 0.50 m. Low transparency in Bay 4 probably contributed

TABLE III

RELATIVE NUMERICAL ABUNDANCE OF *Chaoborus punctipennis* BY DEPTH*

BAY	Individuals Per M^2											
	1			2			3			4		
Depth (m)	Total Benthics	*Chaoborus punctipennis* Total	*Chaoborus punctipennis* %	Total Benthics	*Chaoborus punctipennis* Total	*Chaoborus punctipennis* %	Total Benthics	*Chaoborus punctipennis* Total	*Chaoborus punctipennis* %	Total Benthics	*Chaoborus punctipennis* Total	*Chaoborus punctipennis* %
1	489	5	1	489	36	7	210	13	6	154	23	15
3	952	462	49	765	215	28	274	70	26	571	412	72
5	1,096	382	35	733	254	35	723	518	72	1,564	1,509	96
7	685	330	48	427	203	48	1,088	892	82	2,470	2,441	99
9	786	290	37	485	253	52	688	587	85	2,466	2,457	99
M	653	522	80	1,282	1,277	99	1,513	1,467	97	631	628	99

*Rounded to nearest whole number

TABLE IV

MEAN MONTHLY pH BY DEPTH FOR ALL BAYS COMBINED

Month	DEPTH 1	3	5	7	9	M
Nov.	8.1	8.2	8.1	8.0	8.0	8.0
Dec.	8.1	8.1	8.1	8.1	8.1	7.8
Jan.	8.2	8.1	8.1	8.1	8.2	7.6
Feb.	8.2	8.2	8.2	8.3	8.3	7.8
Mar.	8.4	8.3	8.3	8.3	8.3	7.8
Apr.	8.3	8.3	8.3	8.3	8.3	8.1
May	8.3	8.1	7.9	8.2	7.7	7.7
June	8.1	7.9	7.5	7.6	7.5	7.3
July	8.4	7.6	7.5	7.4	7.2	7.2
Aug.	8.2	7.8	7.7	7.8	7.5	7.3
Sept.	8.4	7.9	7.9	7.9	7.8	7.6
Oct.	8.4	8.3	8.3	8.2	8.2	8.1

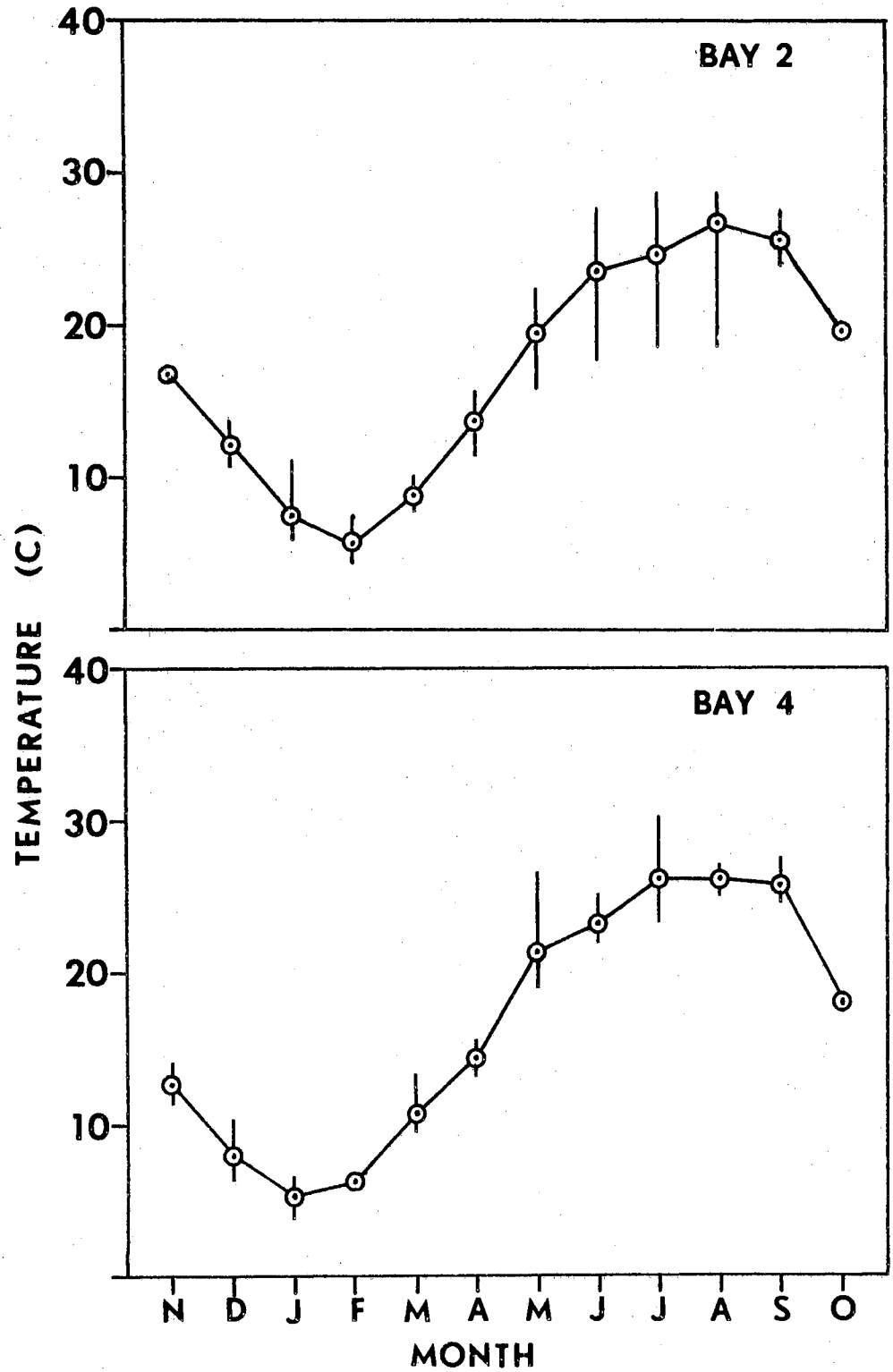

Figure 3. Mean Monthly Variations in Temperature in Bays 2 and 4. Vertical lines indicate range. Maximum temperature was recorded at 1 m and minimum temperature at maximum depth unless otherwise indicated.

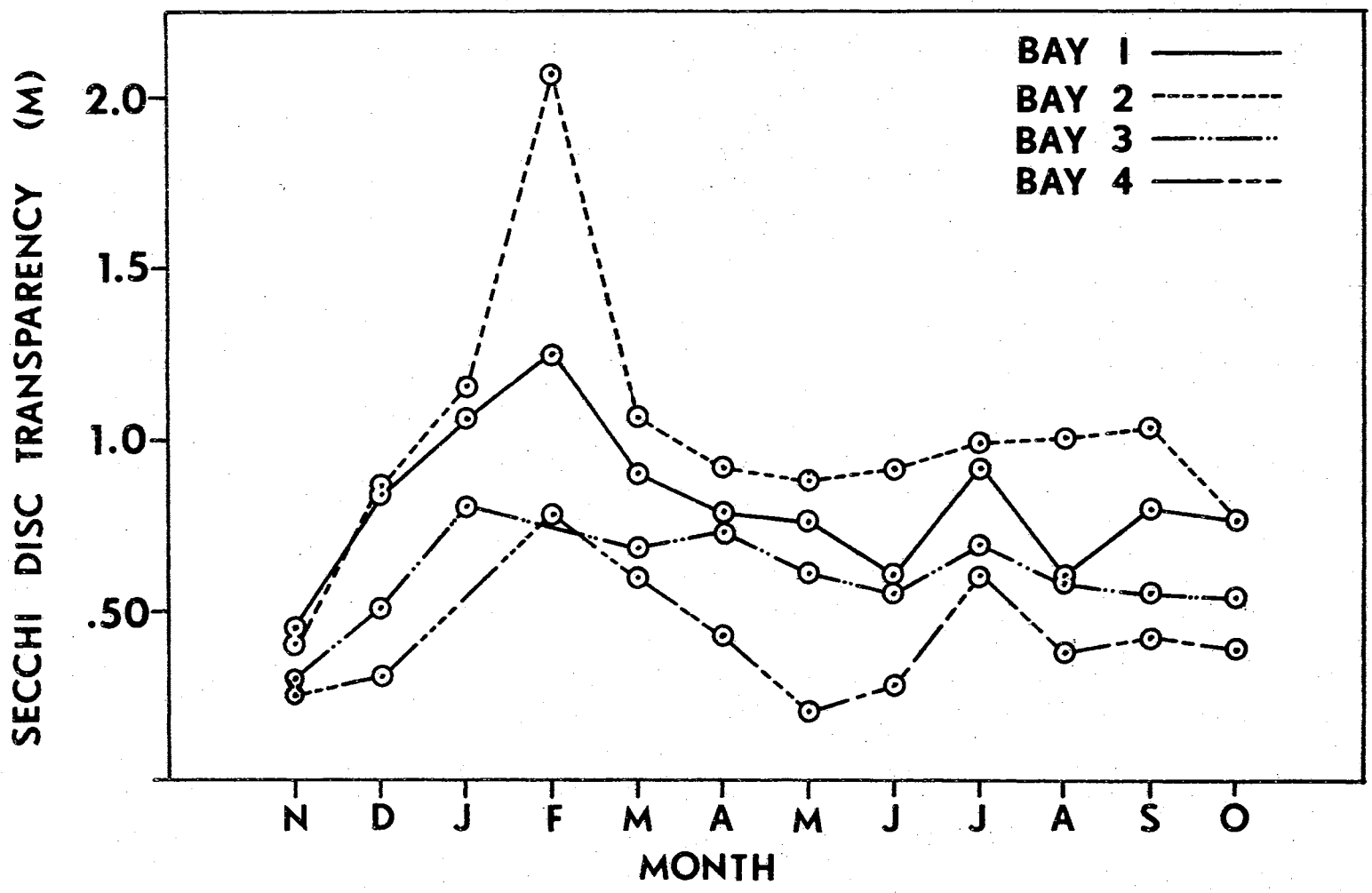

Figure 4. Mean Monthly Secchi Disc Measurements

to low primary productivity and to the small numbers of detritus feeders. Secchi disc transparency in Bays 1 and 2 was always significantly greater than in Bays 3 and 4.

Dissolved Oxygen and Conductivity

The deeper waters of all bays were devoid of dissolved oxygen during the summer months and contained only small concentrations during the remainder of the year (Fig. 5). Local thunderstorms and resulting runoff temporarily upset stratification and increased dissolved oxygen in Bay 3 just prior to sampling in June and September.

Conductivity at the bottom usually increased from the shallowest to the maximum depth in all bays (Table V). Maximum conductivity occurred in all bays during the winter months. Consistently lower conductivity occurred at the Bay 1 maximum depth than at that depth in the other three bays.

Rivers and streams in the southern Great Plains drain large semi-arid basins and carry large amounts of dissolved solids. The Cimarron River transported a high concentration of dissolved solids, mostly sodium chloride, into Keystone Reservoir. Lighter, less-salty water from the Arkansas River overlaid this salt-heavy water producing stable chemical stratification in all months. Stratification varied seasonally as mineralization of the Cimarron varied (Eley et al., 1967). During summer, superimposed thermal stratification prevented mixing below 8 m. Spring and summer rainfall reduced conductivity. Heavy Cimarron water produced density currents which flowed through the reservoir, resulting in low dissolved oxygen in the deeper water of Bay 2 and high conductivity in the deeper waters of all bays during the winter.

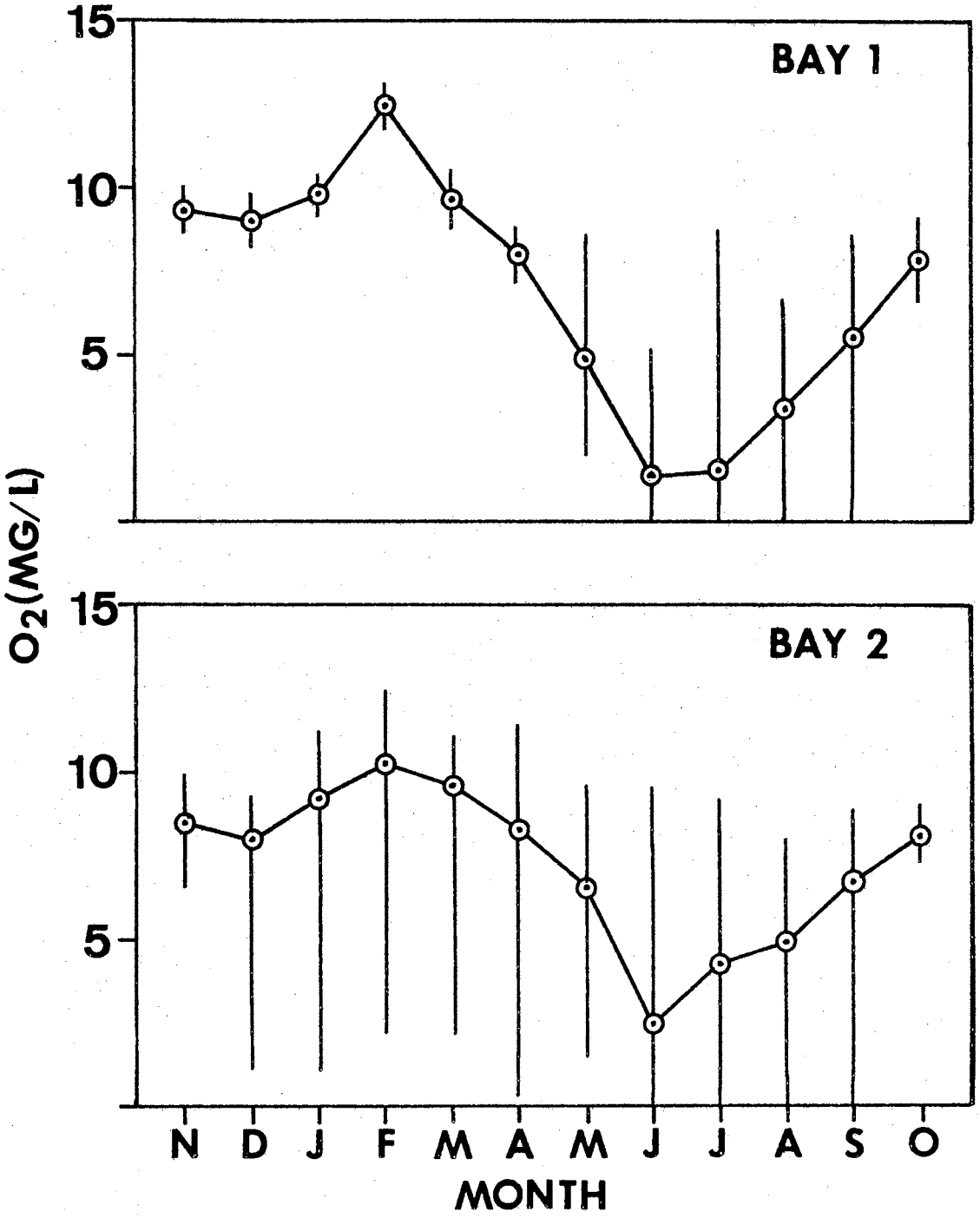

Figure 5. Mean Monthly Dissolved Oxygen on Bottom in Bays 1 and 2. Vertical lines indicate range. Maximum O_2 occurred at 1 m and minimum O_2 at maximum depth in all months.

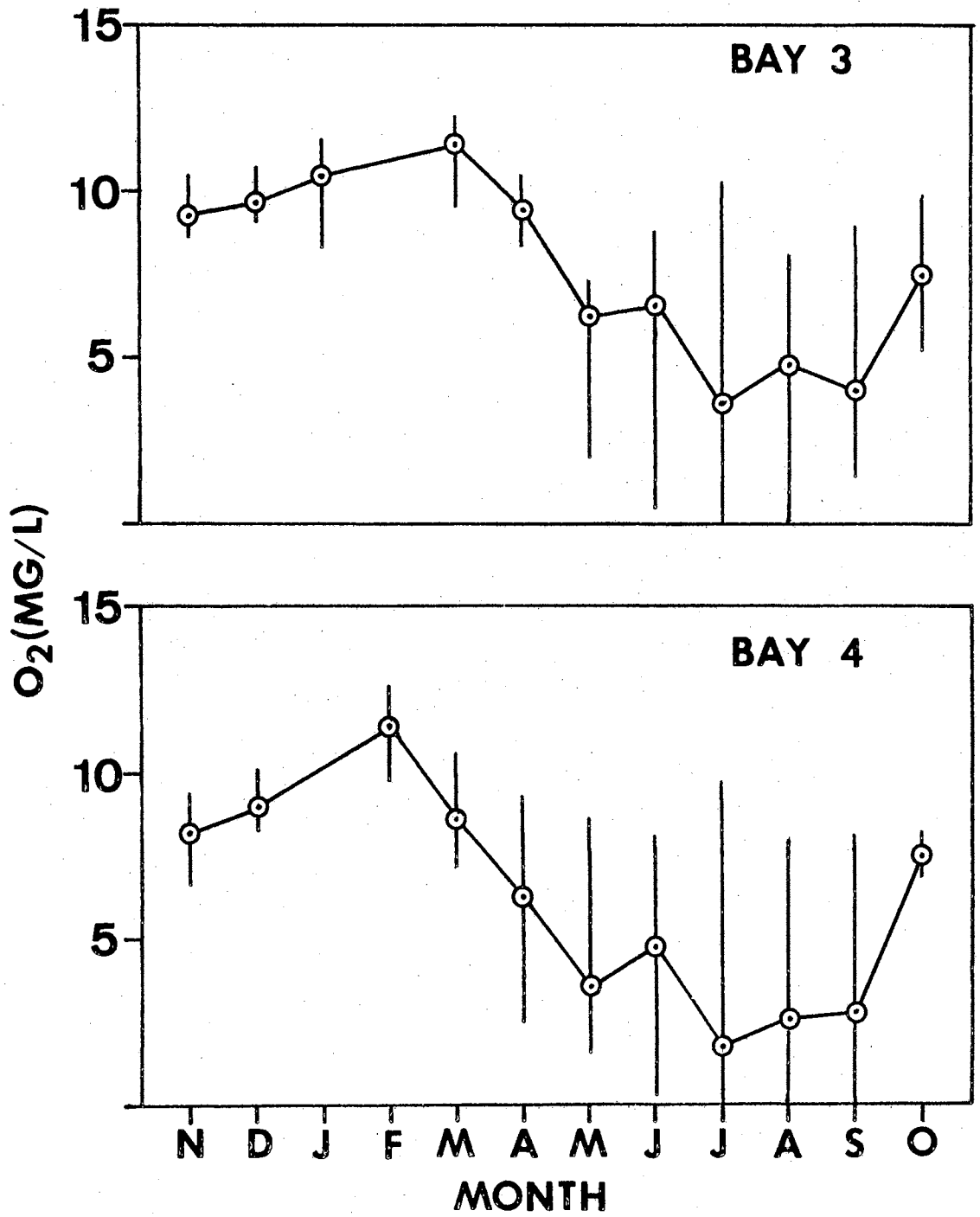

Figure 5 (Continued)

TABLE V

RANGE OF SPECIFIC CONDUCTANCE VALUES (MICROMHOS/CM) BY MONTH

BAY	1		2		3		4	
Month	1 m	14 m	1 m	17 m	1 m	15 m	1 m	11 m
Nov.	1,600	1,450	1,250	4,700	1,350	3,200	1,420	8,200
Dec.	1,550	1,700	1,740	4,800	1,650	2,600	1,500	6,000
Jan.	1,800	2,300	2,200	4,900	2,000	8,000	-----*	-----*
Feb.	2,200	2,350	2,300	8,500	-----*	-----*	2,200	11,000
Mar.	2,600	7,000	3,200	8,400	2,750	6,300	2,500	6,600
Apr.	2,800	3,000	2,650	6,400	2,950	7,000	3,400	6,000
May	2,700	2,900	2,800	4,400	3,000	4,100	1,500	3,800
June	2,750	2,900	2,900	3,600	2,700	3,600	1,800	3,400
July	2,750	2,850	2,600	3,600	2,450	4,400	2,150	2,950
Aug.	2,550	3,200	2,350	2,700	2,400	3,000	1,500	2,100
Sept.	2,500	2,500	2,250	2,400	2,400	4,750	1,950	2,500
Oct.	2,350	2,350	2,150	2,200	2,200	2,400	2,600	2,650

*No samples taken because of ice cover

A highway causeway across the lower end of Bay 1 with a narrow opening into the main reservoir probably prevented the salt-heavy Cimarron water from entering Bay 1. This resulted in consistently lower conductivity and higher winter dissolved oxygen concentration in this bay. Cimarron water was well oxygenated from top to bottom during the winter months in Bays 3 and 4, but most of the dissolved oxygen disappeared by the time the Cimarron water reached the stagnated bottom waters of the main body of the reservoir (Fig. 5).

Selective withdrawal is an important tool in the management of water quality of reservoirs. Water with excessive dissolved salts may be released at times when it is needed for power or navigation, but not for municipal or irrigation use (Brooks, 1964). In July and August, 1966, the U.S. Corps of Engineers released extra water from Keystone Reservoir to maintain power pool levels in downstream reservoirs. Water was released through sluice gates near the bottom of the dam to drain off the stagnant hypolimnion. Hypolimnitic water was at first mixed with epilimnitic water released through tainter gates, but by August anoxic bottom water composed the total discharge. Specific conductance of the hypolimnion decreased from 7,000 to 3,000 micromhos between July 22 and August 2, and the temperature of the hypolimnion increased from 16 to 21 C. Dissolved oxygen increased from 0 to 5 mg/L between August 2 and September 1 (Eley et al., 1967).

Species Diversity by Month

Monthly species diversity, diversity per individual, and redundancy were calculated for each bay from both numbers of individuals and biomass. Annual indices by depth were also calculated for each bay from

both individual numbers and biomass. Since ($\bar{d}$) and R numbers were smaller, they were easier to use in evaluating community structure. Therefore, d, d_{max}, and d_{min} values are included in an appendix for reference only.

In general $\bar{d}$ was high and R was low in Bays 1 and 2 from November through April (Figs. 6, 7). There were monthly increases in numbers of individuals during the winter, while the number of species remained comparatively high, with some fluctuation, in both bays (Fig. 8). This consistently high number of species resulted in high $\bar{d}$ numbers, which is an indication of good water quality in Bays 1 and 2 during the winter months. The physical and chemical data from depths 1 through 9 meters in both bays support this contention. Increases in numbers of individuals in Bays 1 and 2 were due to increases in annelid worms and tendipedid larvae from month to month during the winter. During the late spring and summer $\bar{d}$ declined while R increased in Bays 1 and 2. Numbers of individuals declined during this same period due to an earlier emergence of Chaoborus punctipennis, a later emergence of tendipedid larvae, and a decrease in numbers of annelid worms. However, the reason for a decline in $\bar{d}$ and an increase in R from winter through the spring and summer was a steady decrease in the number of species from 20 in February to 4 in July in Bay 1 and 13 in March to 7 in July in Bay 2. After July $\bar{d}$ decreased and R increased in Bay 1 due to increases in numbers of species. Eggs from the early emerging Chaoborus punctipennis adults were beginning to hatch and resulted in an increase in numbers of individuals collected after July. There was a slight drop in number of species between September and October in Bay 1, but there was a large decrease in numbers of individuals from August through

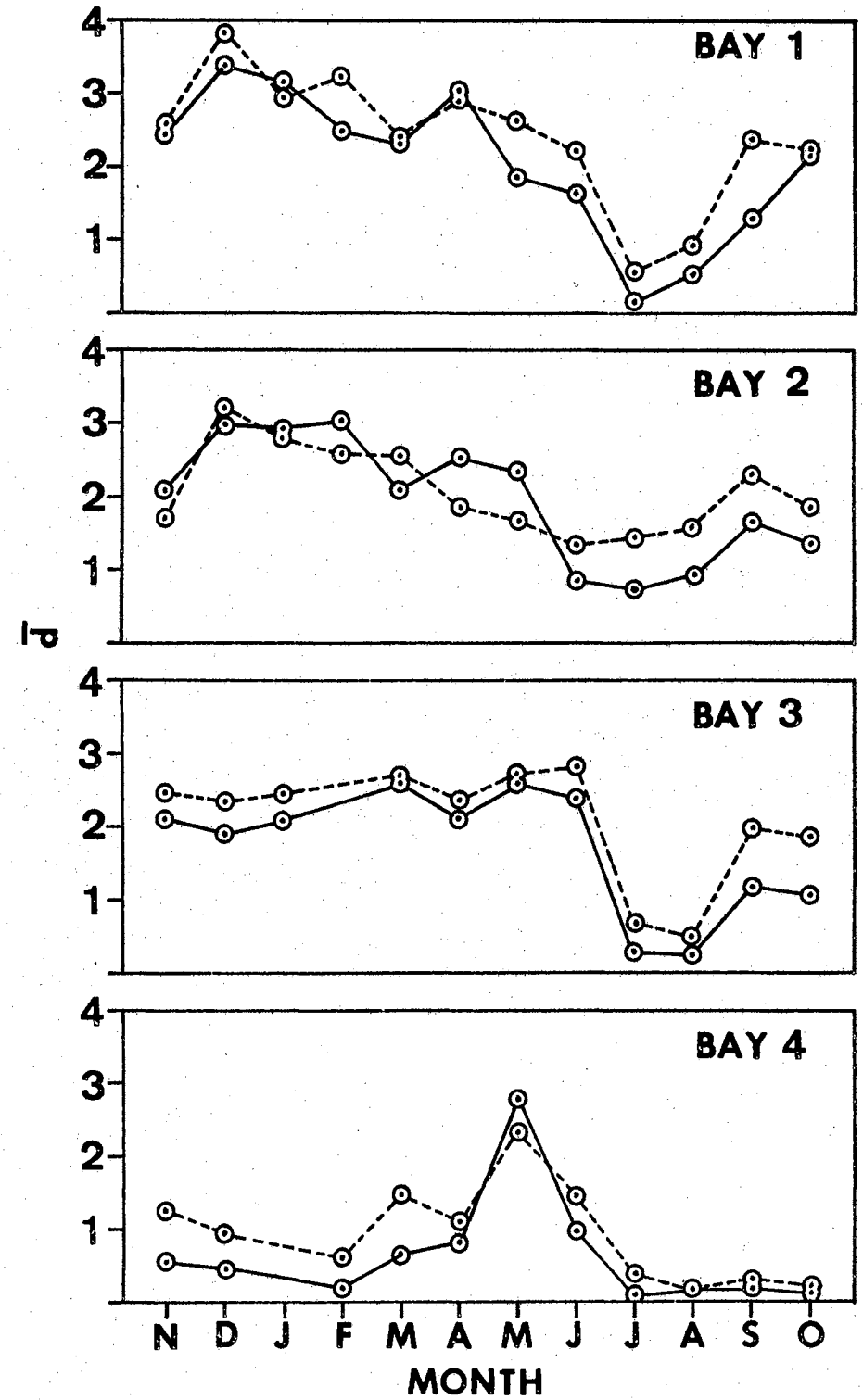

Figure 6. Monthly Variations in Diversity per Individual ($\bar{d}$). Diversity from numbers of individuals = (——), diversity from biomass = (---).

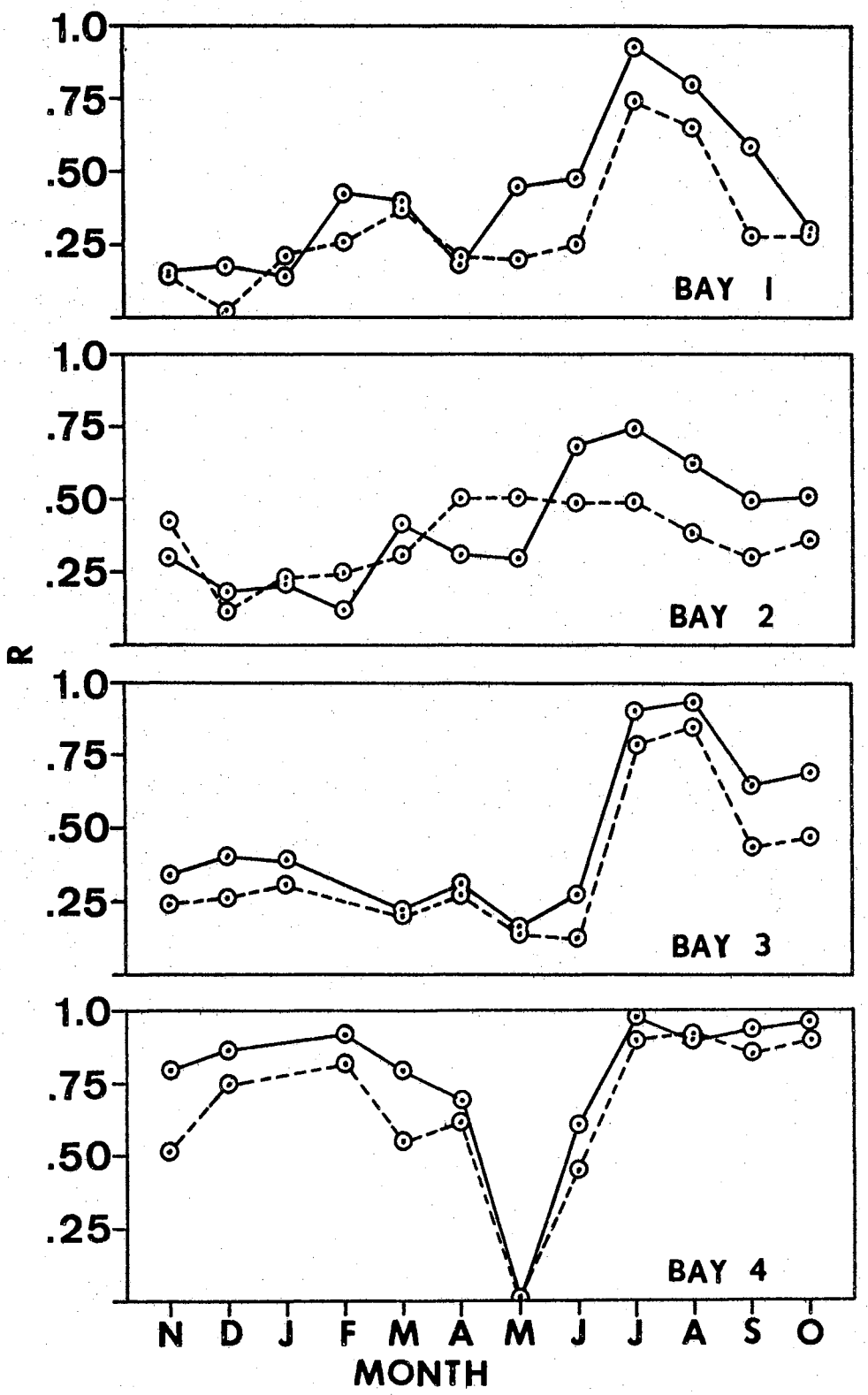

Figure 7. Monthly Variations in Redundancy (R). Redundancy from numbers of individuals = (——), redundancy from biomass = (---).

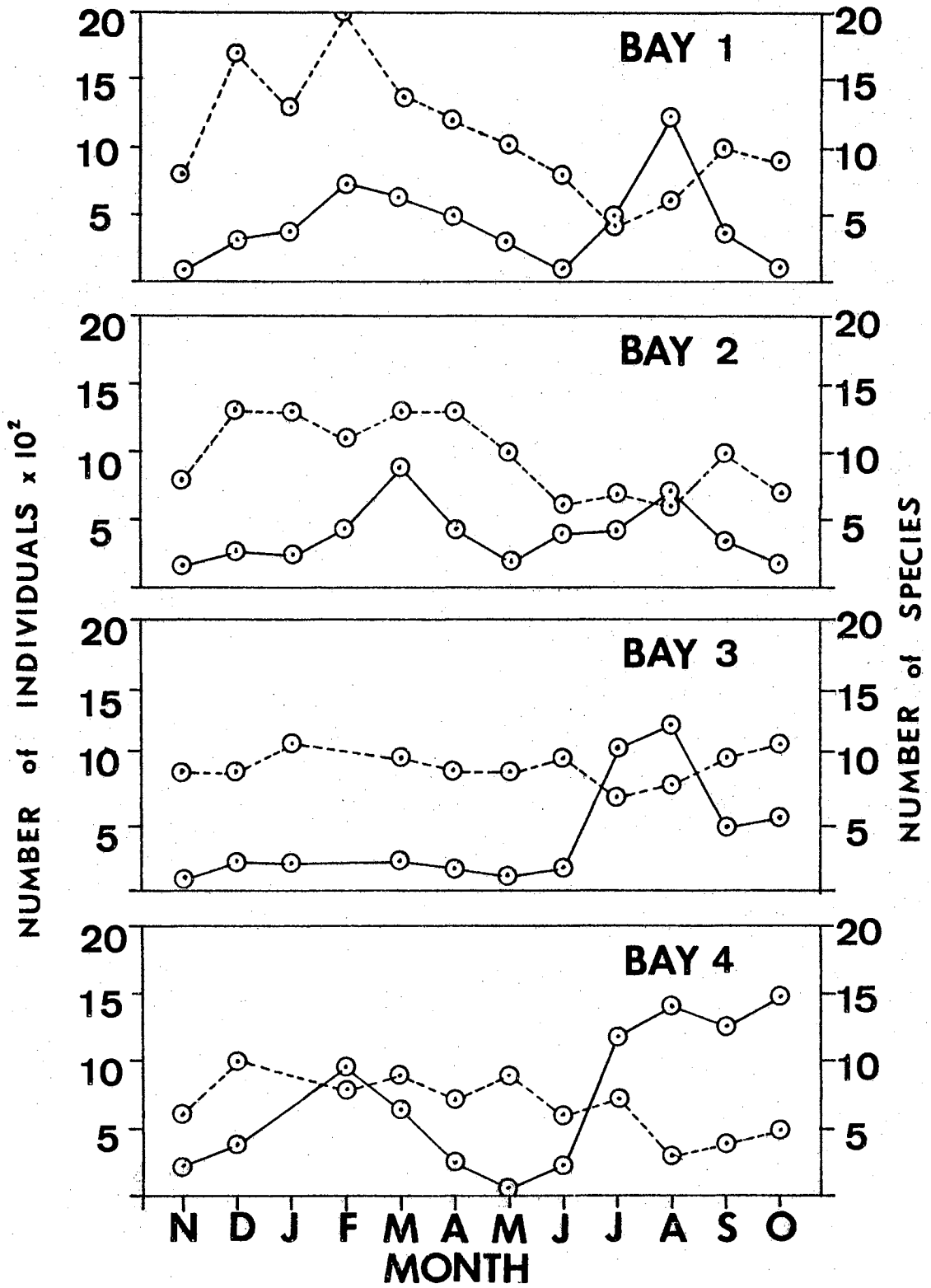

Figure 8. Monthly Variations in Numbers of Individuals and Species. Numbers of individuals = (——), numbers of species = (---).

October. With the large decline in numbers of individuals, due mainly to another C. punctipennis emergence and a slight decrease in number of species, $\bar{d}$ continued to increase through October in Bay 1. There was a decline in $\bar{d}$ from September to October in Bay 2 due to a reduction in number of species.

Diversity per individual ($\bar{d}$) was high, and R was low throughout the winter and spring in Bay 3 (Figs. 6, 7). Numbers of species and individuals remained comparatively constant during those seasons (Fig. 8). The drastic drop in $\bar{d}$ and simultaneous increase in R between June and July was caused by a large increase in Chaoborus punctipennis larvae and a decrease in number of species due to emergence of some tendipedid species. The increase in $\bar{d}$ and decrease in R in Bay 3 between August and September was due to a second emergence of C. punctipennis, the appearance of Dero sp., and the reappearance of some tendipedid species.

The foregoing discussions concerning species diversity calculations on Bays 1, 2, and 3 demonstrate that changes in number of species are reflected in changes in $\bar{d}$ and R. If the species number remains constant, variations in numbers of individuals are reflected only in slight changes in $\bar{d}$ and R. Although changes in $\bar{d}$ and R in Bays 1, 2, and 3 resulted mostly from the emergence of some species, and their reappearance, it is obvious that species diversity calculations could be used to compare reservoirs. A reservoir of poor water quality probably would have few species and a large number of individuals per species at times resulting in a small diversity per individual ($\bar{d}$) and large redundancy (R). Water of a better quality probably would contain a large number of species and a small number of individuals per species of benthic macroinvertebrates, while $\bar{d}$ would be large and R small in

this case. A good example is provided by considering species diversity in Bay 4 where water quality was poorer than that in Bays 1 and 2, and, to a lesser extent, poorer than that in Bay 3. Poor water quality in Bay 4 was attributed to low transparency, or high turbidity, to a substrate of deep silt, and to a consistently higher conductivity.

Diversity per individual ($\bar{d}$) was low, and R was high in Bay 4 during the entire year, except the month of May (Figs. 6, 7). Chaoborus punctipennis larvae dominated the community in Bay 4 to such an extent that $\bar{d}$ and R changes were mere reflections of changes in the life history of that species. The number of species in Bay 4 was less than that of the other bays, and the number of individuals per species, except Chaoborus punctipennis larvae, was lowest (Tables II, III and Fig. 8). The number of species remained relatively constant during the entire year. Large increases from month to month in C. punctipennis larvae accompanied by decreases in the number of species resulted in low $\bar{d}$ and high R through the summer months.

Diversity per individual ($\bar{d}$) calculated from biomass data generally was slightly higher than $\bar{d}$ calculated from numbers of individuals, and R was generally lower when calculated from biomass data (Figs. 6, 7). The presence of tendipedid species, the rarer species, and the annelid worms became much more obvious when biomass was used than when numbers of individuals were used as basic data. The species contributing the largest number of individuals did not always contribute the largest portion of total community biomass.

There was no significant difference at the 95% level between $\bar{d}$ from numbers of individuals as basic data and $\bar{d}$ calculated from biomass as basic data. Duncan's multiple range test at $p = .01$ revealed a

significant difference in $\bar{d}$'s of Bays 1, 2, and 3 on the one hand and Bay 4 on the other. There was no significant difference among Bays 1, 2, and 3.

Species Diversity by Depth

It is obvious that the most diverse communities occurred in the shallower waters (Figs. 9, 10). Tendipedid species, the rarer species, and annelid worms generally were more abundant in the shallower depths. *Chaoborus punctipennis* was the most abundant species in the deeper waters. Diversity per individual ($\bar{d}$) decreased uniformly from the shallow depths to the deeper waters. Duncan's multiple range test at $p = .01$ showed again that a significant difference existed between Bays 1, 2, and 3 on the one hand and Bay 4 on the other. There was no significant difference between biomass $\bar{d}$'s and $\bar{d}$'s from numbers of individuals in any bay.

Physical and chemical estimates changed with depth. Mean $\bar{d}$'s for all bays were compared with mean specific conductance values for all bays (Fig. 11). As depth increased, conductivity increased and $\bar{d}$ decreased. The calculated coefficient of correlation for conductivity estimates versus $\bar{d}$ estimates was -0.93 and for depth versus $\bar{d}$ estimates was -0.97. The coefficients were equal at the 95% level.

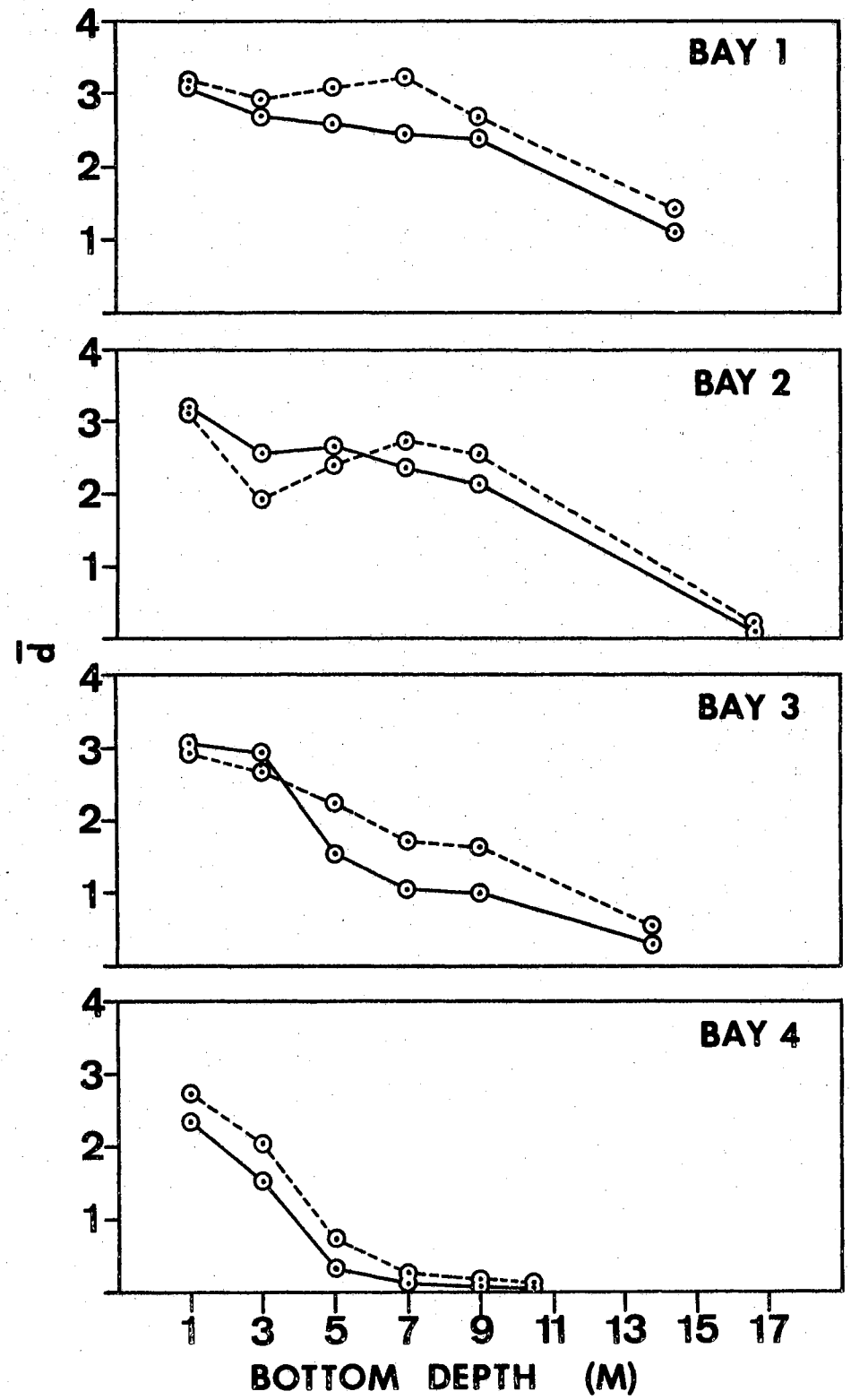

Figure 9. Mean Annual Variations in Diversity per Individual ($\bar{d}$) by Depth. Diversity from numbers of individuals = (——), diversity from biomass = (---).

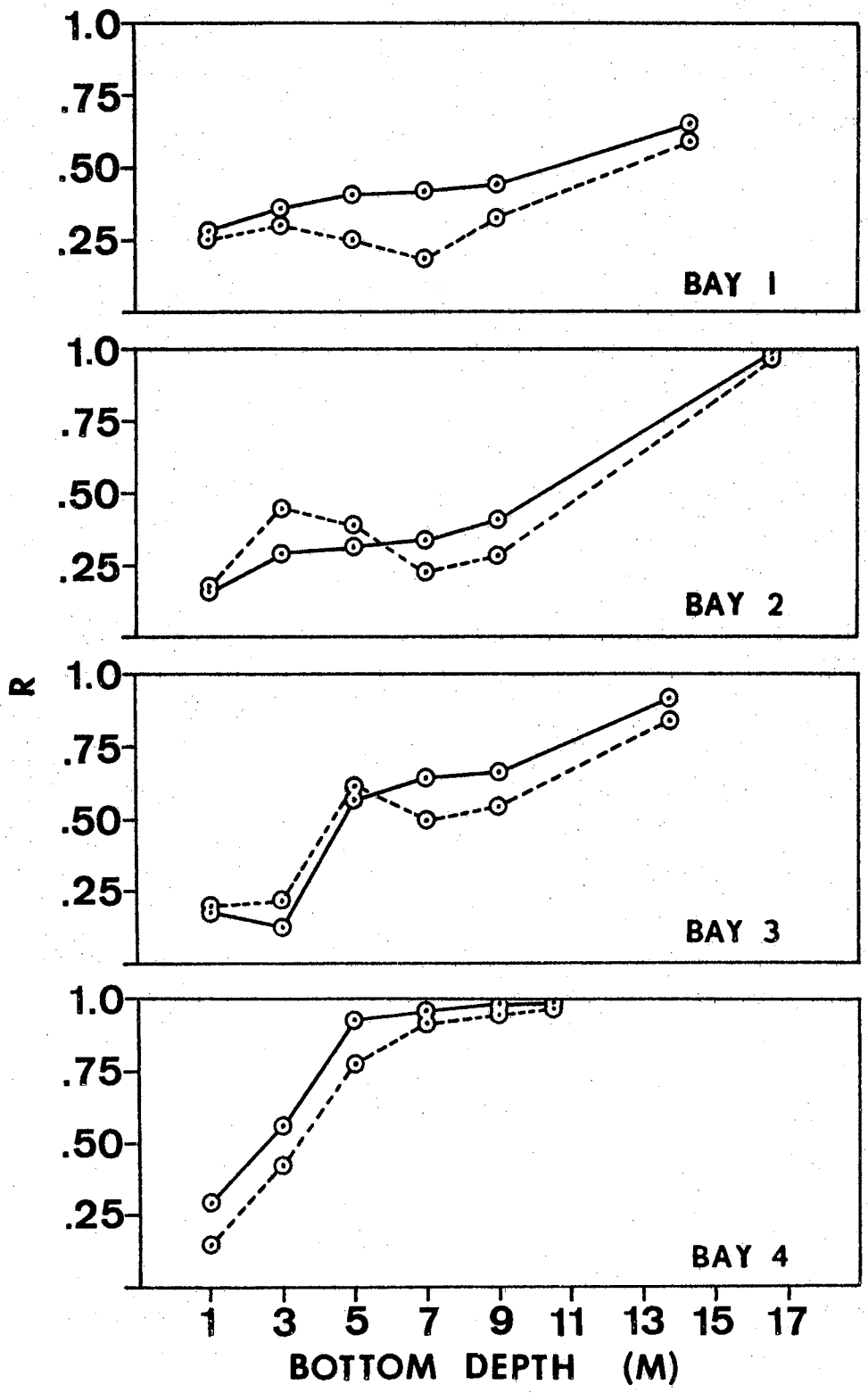

Figure 10. Mean Annual Variations in Redundancy (R) by Depth. Redundancy from numbers of individuals = (——), redundancy from biomass = (---).

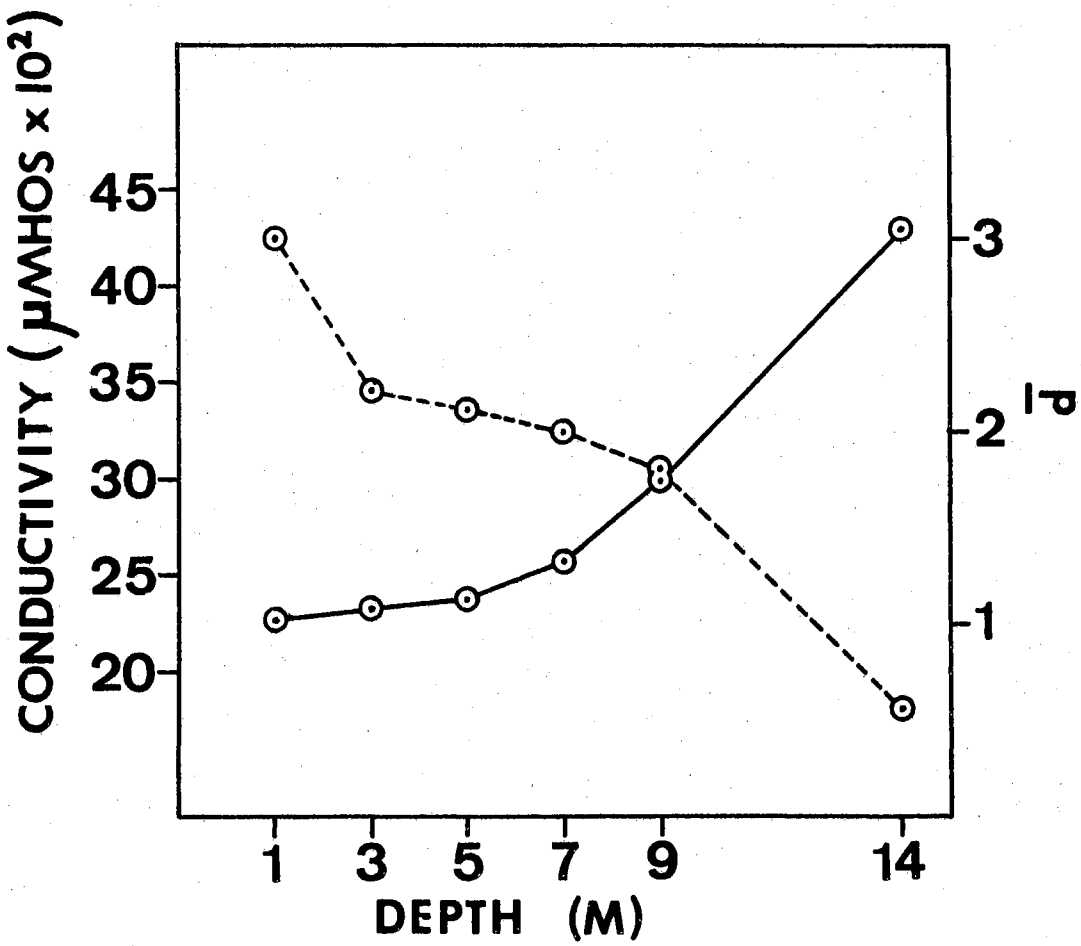

Figure 11. Mean Annual Specific Conductance by Depth and Mean Annual Diversity per Individual ($\bar{d}$) by Depth, All Bays Combined. Specific conductance = (——), $\bar{d}$ = (---).

CHAPTER V

OTHER ECOLOGICAL CONSIDERATIONS

Distribution of *Chaoborus punctipennis* and Tendipedid Larvae

The physiological ecology of aquatic macroinvertebrates has an important role in explaining the distribution of these species. Such studies should enhance understanding of interspecific relations, intraspecific variation, and the bases for ecological ranges (Prosser, 1955). A study of the physiology of some species can, to a large extent, explain ecological distribution (Fromm, 1965).

Chaoborus punctipennis larvae were collected at times from anoxic waters in Keystone Reservoir. Tendipedid larvae were seldom found under anoxic conditions, but occurred often in areas containing as little as 1 mg/L dissolved oxygen. Where both tendipedid and *C. punctipennis* larvae were collected in deep anoxic waters, the number of tendipedid larvae was very small compared to that of *C. punctipennis*.

Tendipes plumosus larvae inhabit anoxic regions of lakes, but only a few tendipedid species can cope with long periods of anoxic conditions. Mortality rates, being greatest in first and second instar larvae, were as high as 50% for two tendipedid forms under anoxic conditions in Michigan (Curry, 1965). Juday (1908, 1922) and Eggleton (1931) reported the bottom fauna of Lake Mendota and Douglas Lake consisted of species which could withstand complete oxygen lack for the duration of summer. When *Chaoborus* larvae are prevented from migrating under anoxic

conditions, all individuals die within a few days, and all tendipedid larvae will perish soon thereafter under the same conditions (Eggleton, 1931). These studies utilized either the unmodified Winkler method or the Rideal-Stewart modification to determine dissolved oxygen concentration. The unmodified Winkler method, however, is unreliable in the presence of organic matter or ferrous iron, and the Rideal-Stewart technique requires the addition of larger volumes of reagents than the Alsterberg method, but it is also unreliable (Deevey, 1941).

Respiratory metabolism of Chaoborus punctipennis and Tendipes plumosus larvae was investigated to determine distribution of these larvae within the same aquatic environment (Ransom et al., 1967). Measurements were made utilizing standard Warburg manometric techniques, and the direct method and total uptake procedures were used (Unbreit et al., 1957). Total oxygen uptake for T. plumosus larvae was considerably higher than that for C. punctipennis larvae due to a difference in size or mass of the two species (Table VI). T. plumosus larvae weighed about seven times more than C. punctipennis larvae, but total oxygen uptake by T. plumosus larvae was only about six times more than that for C. punctipennis larvae. The Q_{O_2} for C. punctipennis was more than twice the Q_{O_2} for T. plumosus. Reported R.Q. values range from 0.71 to 1.0. The R.Q. values for T. plumosus and C. punctipennis fell within this range.

Total acid production by T. plumosus larvae was greater than that produced by C. punctipennis larvae (Table VI). However, the amount of acid produced per unit dry weight by C. punctipennis was significantly greater than that produced by T. plumosus larvae. C. punctipennis produced a considerable quantity of volatile fatty acids, some of which

TABLE VI

RESPIRATORY MEASUREMENTS ON TWO SPECIES OF MIDGE LARVAE
(30 Individuals of Each Species)

	Chaoborus punctipennis	Tendipes plumosus
Total O_2 uptake - ul	71.54	216.00
Q_{O_2} (ulO_2/mg. dry wt./hr.)	7.95	3.26
Total CO_2 produced - ul	56.64	175.68
Q_{CO_2} (ulCO_2/mg. dry wt./hr.)	6.30	2.65
R. Q.	.79	.81
Total acid produced - u moles	1.23	4.05
Acid produced - u moles/mg. dry wt.	.27	.12
Acid produced - first 50 min. - u moles	.82	2.28
Acid produced - first 50 min. - u moles/mg. dry wt.	.18	.07
Volatile acids - exptl. fluid - meq	0.0250	0.00
Volatile acids - exptl. organisms - meq	0.0775	0.00

was excreted. T. plumosus did not produce volatile fatty acids.

In August, when anoxic conditions prevailed on the bottom at the maximum depth near Bay 4 and light penetrated to about 1 m, all larval stages of C. punctipennis migrated to the upper waters at night (Table VII). Only the first three instars were collected in the upper waters during the daylight hours. In February, when dissolved oxygen was about 12.0 mg/L on the bottom, no larvae were collected from the upper water at any time. The number of larvae in the bottom mud remained essentially the same at each collection time in February. Wood (1956) found the strongest vertical migration from June to August while only 4% migrated in November and 11% in May. Fourth instar larvae of C. punctipennis established an oxygen debt under anoxic conditions (Table VI). These larvae migrate during the summer in order to relieve the oxygen debt. Earlier instars probably cannot cope with anoxic conditions for more than a few hours, and they re-enter the upper waters during the daylight hours but do not move into the level of light penetration.

Probably all feeding by Chaoborus larvae is done at night in the upper waters, although this is open to question (Stahl, 1966). Chaoborus larvae feed upon tendipedid larvae as well as many other animals such as copepods, cladocerans, oligochaetes, rotifers, mosquito larvae, and other Chaoborus larvae (Deonier, 1943; Main, 1953). During the vertical migration investigation in August C. punctipennis larvae were found to be feeding on copepods (probably Eurytemora, Diaptomus, and Cyclops), cladocerans (two species of Daphnia), and the rotifer Branchionus. It is incorrect to assume that the C. punctipennis larvae move to the upper water for the purpose of feeding only. Instead, this

TABLE VII

DIURNAL VARIATIONS IN VERTICAL HAULS OF *Chaoborus punctipennis* (August, 1966)

	Maximum Depth of Vertical Hauls (m)										
	1		3		5		7		9		
TIME	no./haul	no./m^3	no./haul	no./m^3	no./haul	no./m^3	no./haul	no./m^3	no./haul	no./m^3	Bottom Mud no./m^2
1700					25	56	167	266	271	333	3,600
2000	44	543	73	270	134	297	146	232	196	241	378
2300	117	1,445	164	607	177	393	205	326	348	428	178
0200	104	1,284	116	429	121	269	173	275	196	241	267
0500	48	593	59	218	83	184	104	165	126	155	978
0800	11	136	17	63	29	64	46	73	66	81	1,200
1100	16	198	14	52	17	38	16	25	29	36	2,266
1400					19	42	40	64	106	130	2,200

organism's behavior is explainable in terms of its metabolic response to oxygen availability.

T. plumosus larvae establish a temporary oxygen debt under anoxic conditions (Walshe, 1948), but they do not vertically migrate. This may be a partial explanation for the scarcity of *T. plumosus* larvae, as well as other tendipedid larvae, in anoxic waters of Keystone Reservoir. High conductivity in the deeper waters may also be a barrier to tendipedid forms.

Shoreward and Return Migrations by Tendipedid Larvae

Eggleton (1931), Berg (1938), Wood (1953), and others have reported "concentration zones" of tendipedid and other larvae occurring in the shallower water of lakes in the spring and in the deeper waters in the fall. These authors have assumed that tendipedid larvae and *Chaoborus* larvae migrate shoreward in the spring because of a temperature stress and reverse the migration in the fall for the same reason. Moon (1940) investigated this particular problem and found no shoreward or return migrations by tendipedid larvae. Certain other larvae, *Sialis* for example, do migrate over the bottom, but for different reasons. It seems unlikely that tendipedid larvae could move a kilometer or more over a rugged bottom and through a long stretch of constant temperature to a location of optimum temperature.

Eggleton (1931) found that midge eggs fall to the bottom, and, if the bottom water is anoxic, hatching is delayed until oxygen is available. He also found that low temperature would delay hatching. Different reasons for the presence of spring and fall concentration of midge larvae seem to be evident here. The last eggs of the fall are laid in both deep and shallow waters. Those laid in the shallower

waters drop onto a bottom of high dissolved oxygen and falling temperature. Most of those eggs do not hatch immediately but continue to hatch slowly through the winter. By early spring there is a large increase in larval numbers. Those eggs laid in the deeper waters probably continue to hatch slowly all winter.

Earlier instars of Chaoborus larvae migrate horizontally, but the reason for such migration is uncertain. Winter temperatures prevent larval change and inhibit growth. Overwintering Chaoborus larvae commence further development in the spring and enter the mud. Large numbers of these earlier instars also enter the mud in the fall.

Concentration zones of benthic macroinvertebrates appear not to be due entirely to horizontal migration. These seasonal concentrations may be explained also in terms of different responses by stages in life history of the organisms to temperature variations and oxygen availability.

CHAPTER VI

SUMMARY

1. Four bays on the Cimarron arm of Keystone Reservoir, Oklahoma, were investigated monthly from November, 1965, through October, 1966. Benthic community structure was subjected to conventional analysis and to species diversity analyses. Causal relationships were established by use of physicochemical estimates and the results of physiological and behavioral investigations.

2. A total of 25 benthic macroinvertebrate species was collected during the year. Tendipedid species comprised 48% of the total. The phantom midge, Chaoborus punctipennis, was the most abundant species collected. A ceratopogonid was the only other midge collected. Two annedid worms, Dero sp. and Limnodrilus hoffmeisteri, were abundant, while the remainder of the species was scarce and included 1 coelenterate, a nematode, and 7 species of other insect larvae.

3. Diversity per individual ($\bar{d}$) was high and redundancy (R) low through the winter months and early spring months in Bays 1, 2, and 3. There was a large drop in number of species and a smaller decrease in numbers of individuals in all three bays from early spring to mid-summer with resulting decreases in $\bar{d}$ and increases in R. There were steady increases in species numbers, numbers of individuals, and $\bar{d}$ in late summer and early fall. Differences in $\bar{d}$ and R were associated with stages in the life history of the benthic invertebrates. Diversity per

individual ($\bar{d}$) was low and redundancy (R) was high in Bay 4 in all months except May. Bay 4 was dominated at all times by Chaoborus punctipennis larvae.

4. Annual $\bar{d}$ and R by depth revealed that the shallower bottom muds contained the more diverse communities. Diversity per individual ($\bar{d}$) was high in the shallower depths and low in the deeper waters of all bays.

5. Diversity per individual ($\bar{d}$) from biomass data were generally higher than those calculated from numbers of individuals. Chaoborus punctipennis larvae were generally the most abundant, but they did not always contribute the most weight to total biomass.

6. Duncan's multiple range test at $p = .01$ revealed $\bar{d}$'s from Bays 1, 2, and 3 were not significantly different while there was a significant difference between Bays 1, 2, and 3 on the one hand and Bay 4 on the other. No significant difference existed at the 95% level between $\bar{d}$'s from numbers of individuals and $\bar{d}$'s from biomass as basic data.

7. Conductivity was high and the reservoir was chemically stratified in all months. Dissolved oxygen was low in the deeper waters in all months. Secchi disc transparency was high in Bays 1, 2, and 3 and low in the highly turbid Bay 4.

8. High turbidity probably contributed to species reduction in Bay 4.

9. Tendipedid larvae generally were scarce in the deeper anoxic waters, while Chaoborus punctipennis larvae were abundant and quite often the only species collected there. Respiratory metabolism measurements on C. punctipennis and Tendipes plumosus larvae revealed tendipedid

forms probably cannot continuously cope with anoxic conditions. Vertical migration behavior of C. punctipennis larvae can be explained in terms of metabolic response to oxygen availability.

10. Concentration zones of benthic macroinvertebrates appear not to be due entirely to horizontal migration. These seasonal concentrations may be explained also in terms of different responses by stages in life history of the organisms to temperature variations and oxygen availability.

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APPENDIX

TABLE VIII

VALUES OF d, d_{max} AND d_{min} OBTAINED WITH NUMBERS OF INDIVIDUALS AS BASIC DATA BY MONTH

	BAY							
	1		2		3		4	
	d(bits/m^2)		d(bits/m^2)		d(bits/m^2)		d(bits/m^2)	
MONTH	d_{max}	d_{min}	d_{max}	d_{min}	d_{max}	d_{min}	d_{max}	d_{min}
	2,003		3,625		2,222		1,347	
Nov.	2,379	68	5,118	75	3,310	80	6,221	56
	11,392		8,351		4,636		2,053	
Dec.	13,669	187	10,213	137	7,668	90	13,827	108
	13,077		7,835		4,854			
Jan.	15,249	144	9,909	137	7,936	111		
	19,232		14,437				2,421	
Feb.	33,185	245	16,313	122			30,539	93
	16,039		19,933		6,211		4,722	
Mar.	26,068	166	35,123	159	7,907	101	22,055	102
	16,564		12,013		3,934		2,288	
Apr.	19,351	136	17,341	146	5,917	87	7,754	68

TABLE VIII (Continued)

MONTH	BAY 1 d(bits/m^2) d_{max}	BAY 1 d(bits/m^2) d_{min}	BAY 2 d(bits/m^2) d_{max}	BAY 2 d(bits/m^2) d_{min}	BAY 3 d(bits/m^2) d_{max}	BAY 3 d(bits/m^2) d_{min}	BAY 4 d(bits/m^2) d_{max}	BAY 4 d(bits/m^2) d_{min}
May	6,130		4,851		3,620		2,040	
	10,860	105	6,811	99	4,315	83	2,267	76
June	2,108		3,601		4,337		2,479	
	3,838	72	11,125	60	5,881	97	6,081	56
July	686		3,189		3,490		1,266	
	9,263	36	11,998	72	32,177	81	35,820	82
Aug.	7,172		7,678		3,799		2,619	
	34,175	68	20,221	65	40,297	96	24,036	28
Sept.	5,291		5,822		6,397		2,497	
	13,338	108	11,401	106	17,509	111	26,841	41
Oct.	2,498		2,830		6,671		2,536	
	3,603	81	5,765	66	20,800	126	37,312	56

TABLE IX

VALUES OF d, d_{max} AND d_{min} OBTAINED WITH BIOMASS UNITS AS BASIC DATA BY MONTH

	BAY											
	1			2			3			4		
	d/(bits/m^2)			d(bits/m^2)			d(bits/m^2)			d(bits/m^2)		
MONTH	d_{max}		d_{min}	d_{max}		d_{min}	d_{max}		d_{min}	d_{max}		d_{min}
		686			778			339			364	
Nov.	801		57	1,340		62	422		57	735		41
		3,037			2,111			921			485	
Dec.	3,135		154	2,387		112	1,213		69	1,616		81
		3,922			2,263			1,236				
Jan.	4,904		124	2,900		115	1,727		90			
		6,299			3,689						711	
Feb.	8,386		208	4,869		105				3,367		71
		4,330			5,459			2,045			1,530	
Mar.	6,805		141	7,812		133	2,507		86	3,280		80
		4,630			3,030			1,102			466	
Apr.	5,634		117	5,954		128	1,486		71	1,135		52

TABLE IX (Continued)

MONTH	BAY 1 d(bits/m^2) d_{max}	BAY 1 d(bits/m^2) d_{min}	BAY 2 d(bits/m^2) d_{max}	BAY 2 d(bits/m^2) d_{min}	BAY 3 d(bits/m^2) d_{max}	BAY 3 d(bits/m^2) d_{min}	BAY 4 d(bits/m^2) d_{max}	BAY 4 d(bits/m^2) d_{min}
May	1,794	1,457 82	2,568	1,315 87	964	754 65	441	414 57
June	609	469 54	1,704	886 47	762	681 71	914	520 42
July	834	239 26	1,383	730 54	2,833	674 60	3,110	410 61
Aug.	3,856	1,396 53	2,572	1,608 50	3,969	671 73	2,299	256 21
Sept.	1,746	1,301 82	1,529	1,104 80	2,000	1,197 83	2,197	333 30
Oct.	591	442 61	839	565 49	2,782	1,541 97	3,693	398 43

TABLE X

VALUES OF d, d_{max} AND d_{min} OBTAINED WITH NUMBERS OF INDIVIDUALS AS BASIC DATA BY DEPTH

	BAY							
	1		2		3		4	
	d(bits/m^2)		d(bits/m^2)		d(bits/m^2)		d(bits/m^2)	
Depth (m)	d_{max}	d_{min}	d_{max}	d_{min}	d_{max}	d_{min}	d_{max}	d_{min}
	18,245		18,789		7,023		3,998	
1	25,281	238	22,304	163	8,450	134	5,615	97
	30,416		23,415		8,975		9,530	
3	46,638	216	32,891	145	10,342	116	21,676	126
	34,057		23,107		12,193		5,301	
5	54,655	233	33,393	170	28,485	143	54,478	113
	19,791		12,160		12,970		3,365	
7	32,845	195	18,374	136	41,376	135	86,107	118
	22,623		12,507		7,910		1,126	
9	37,709	198	20,769	138	27,087	142	62,964	59
	8,224		702		4,354		355	
M	27,040	129	30,748	42	52,709	112	13,846	38

TABLE XI

VALUES OF d, d_{max} AND d_{min} OBTAINED WITH BIOMASS UNITS AS BASIC DATA BY DEPTH

	BAY							
	1		2		3		4	
	d(bits/m^2)		d(bits/m^2)		d(bits/m^2)		d(bits/m^2)	
Depth (m)	d_{max}	d_{min}	d_{max}	d_{min}	d_{max}	d_{min}	d_{max}	d_{min}
	5,767		4,729		1,688		690	
1	7,823	206	5,666	137	2,034	110	803	72
	8,068		5,840		2,487		2,266	
3	11,245	183	10,754	127	3,151	98	3,823	101
	7,849		6,339		2,710		1,481	
5	10,593	192	10,133	148	4,266	112	6,073	87
	4,739		3,193		2,640		781	
7	5,823	158	4,135	112	5,204	106	8,987	92
	5,052		2,621		1,568		366	
9	7,471	163	3,600	110	3,315	108	6,508	46
	1,219		162		1,034		71	
M	2,872	97	3,165	32	5,669	86	1,417	28

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