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by

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Joy E. Prather and Carl W. Prophet*

INTRODUCTION

In general, studies conducted at the community level are concerned with accumulation of data which characterize the general ecological condition of the community in question and which enable ecologists to compare its structure and relative maturity with that of other communities. Community structure refers to the complex of individuals of different species comprising a community. Classically, the ecologist has relied on voluminous verbal descriptions and species lists, such as those by Patrick, Cairns, and Roback (1967) and Gaufin and Tarzwell (1956) to characterize communities; but comparisons based on such information are often difficult to interpret.

Community structure and relative maturity can be quantitatively defined by the use of species diversity indices based on methods derived from information theory (Margalef, 1958). This approach equates diversity with the uncertainty that a randomly selected individual in a community will belong to a given species. In a community consisting of many species of nearly equal abundance, the uncertainity is great and therefore species diversity is large. This is true in a mature community (Odum, 1962). Seral communities and other communities undergoing ecological stress (pollution) tend to have fewer species but great numbers of individuals of some species. In these cases, uncertainty is less and species diversity is low (Wilhm and Dorris, 1968).

Recent studies have demonstrated characterization of water quality by use of species diversity indices. Patten (1962) used diversity and redundancy as ecological variables to describe changes in community composition and to denote precisely the successional status of a community. Patten's study, based on annual net phytoplankton in Rariton Bay, New York, demonstrated a direct correlation between the general circulation pattern of the bay and mean diversity per station. Diversity levels were high in the lower estuary but progressively diminished upbay, reflecting gross pollution occuring at the head of the estuary.

Wilhm and Dorris (1968) drew attention to the use of species diversity indices to characterize water quality of streams. They reported

*Based on a thesis by Joy E. Prather submitted to the Biology Faculty of the Kansas State Teachers College in partial fulfillment for the degree Master of Science. The study was supported by Federal Water Pollution Control Administration Grant WP-00615.

that diversity per individual ($\bar{d}$) values based on benthic macroinvertebrates tended to be less than 1 in grossly polluted streams, 1 to 3 in moderately polluted communities, and greater than 3 in clean water communities. Ransom (1969) found a positive correlation between diversity per individual of benthic macroinvertebrates and conductivity in Keystone Reservoir, Oklahoma. Ransom's work demonstrated the application of diversity indices to characterize water quality conditions in a reservoir.

A preliminary survey of water quality in three U. S. Army Corps of Engineers reservoirs on the Upper Grand (Neosho) River in east central Kansas was made by members of the Limnology Laboratory at Kansas State Teachers College during the 1967 summer which revealed possible differences in physicochemical factors among the reservoirs. A more extensive study, including a comparison of zooplankton community structure, was conducted the following summer to determine if significant differences existed. Results indicated basic differences in physicochemical factors among the reservoirs. There were few significant differences between factors in Council Grove and Redmond, but summer means of most factors in Marion differed significantly from both Council Grove and Redmond values (Prophet, 1969b). This paper attempts to evaluate the possible ecological importances of the observed differences in water quality by comparing summer zooplankton community structure in the reservoirs.

MATERIALS AND METHODS

The general geographical location and morphometry of the reservoirs were described by Prophet (1969b). Five sampling sites were selected in each reservoir, with one station located near the outlet and another near the upstream boundary of each reservoir. The remaining stations were located within the basin to represent variation in depth and other morphometric features (Figs. 1, 2, and 3).

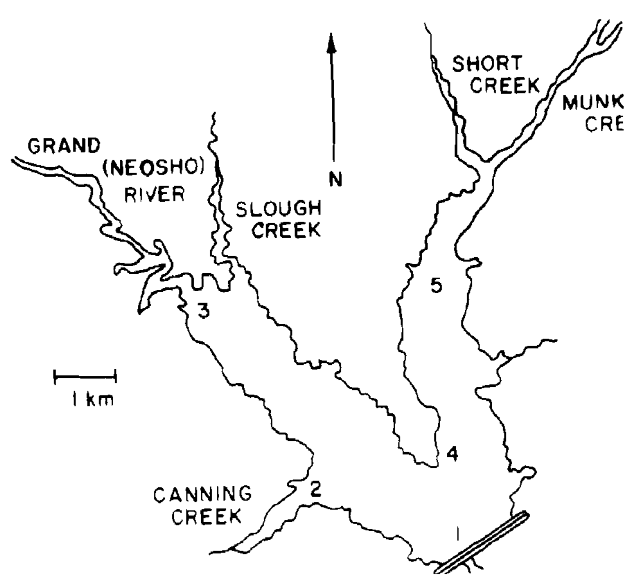

Figure 1. Location of sampling sites in Council Grove Reservoir.

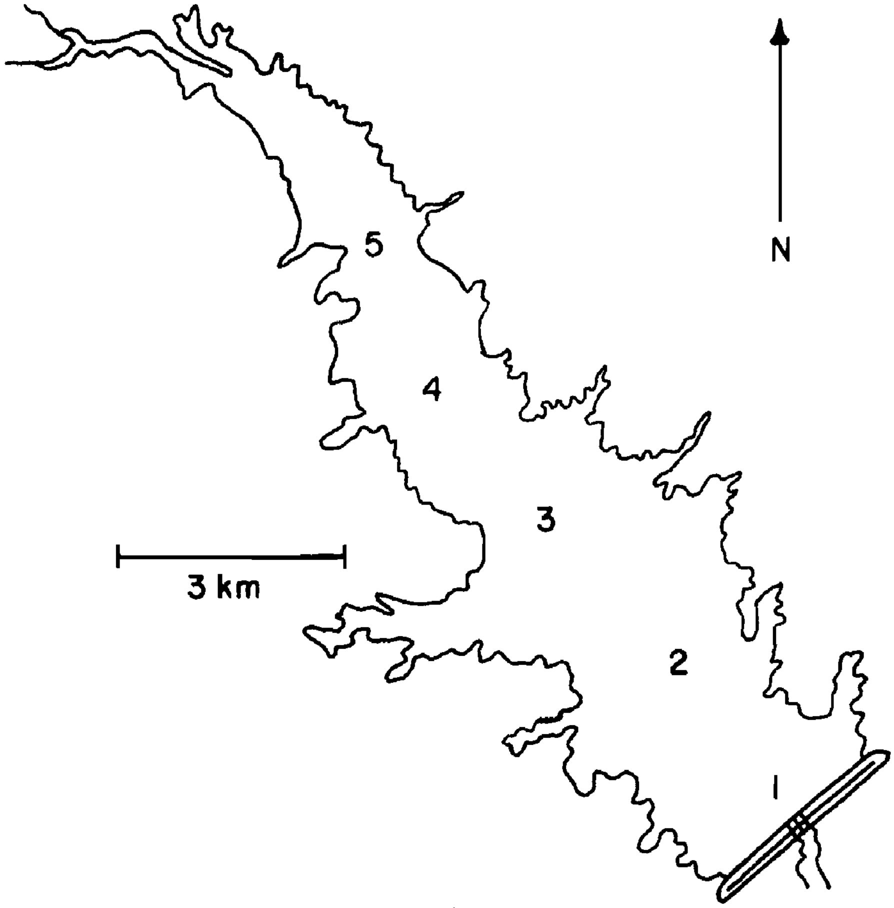

Figure 2. Location of sampling sites in Marion Reservoir.

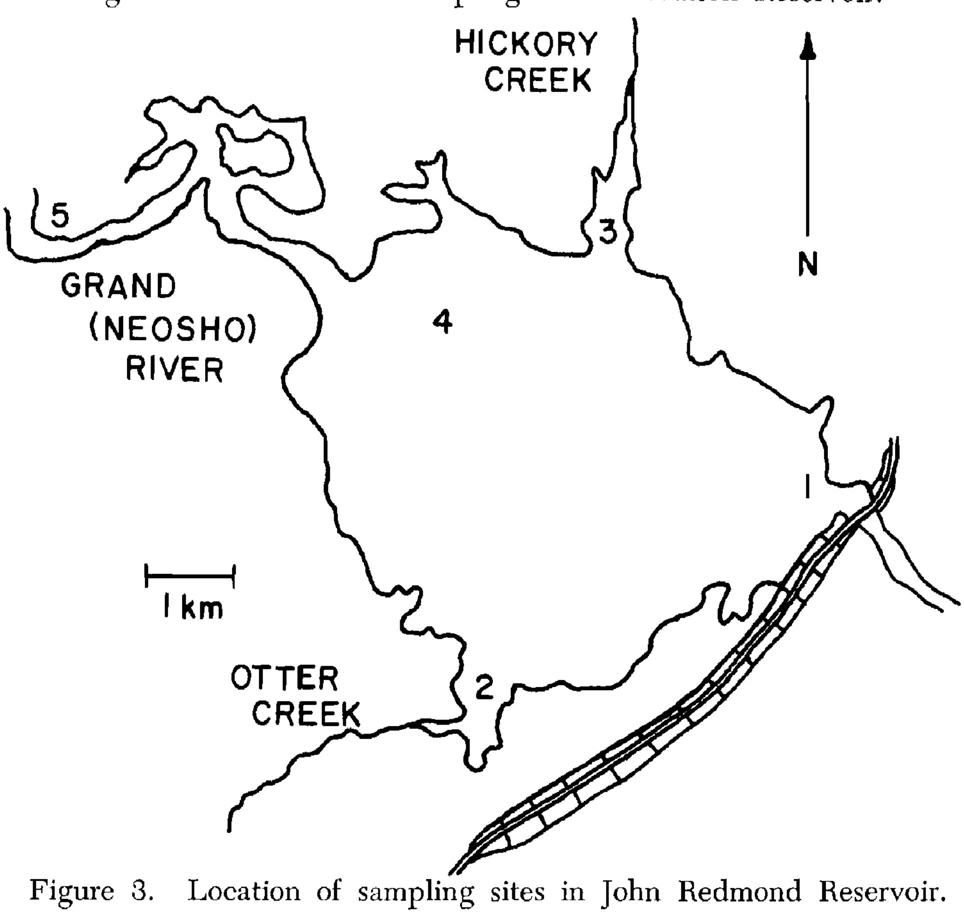

Figure 3. Location of sampling sites in John Redmond Reservoir.

From June 10 to September 6, 1968, townet samples were taken during the same week at monthly intervals in the three reservoirs. Four vertical hauls were made at each station with a 24 cm diameter plankton townet (172 meshes/inch). One haul was made on either side at bow and stern of the boat by sinking the plankton net to the bottom and slowly drawing it to the surface. The length of each tow was recorded for later use in estimating the volume of water strained. Samples were preserved in ten percent formalin and returned to the laboratory for examination.

In the laboratory, one of the four samples from each station was selected at random for examination. Only one sample was used since there was no significant difference between estimates of the number of species and individuals per species at each station based on a single vertical tow and estimates based on all four tows (Fig. 4). Figure 4

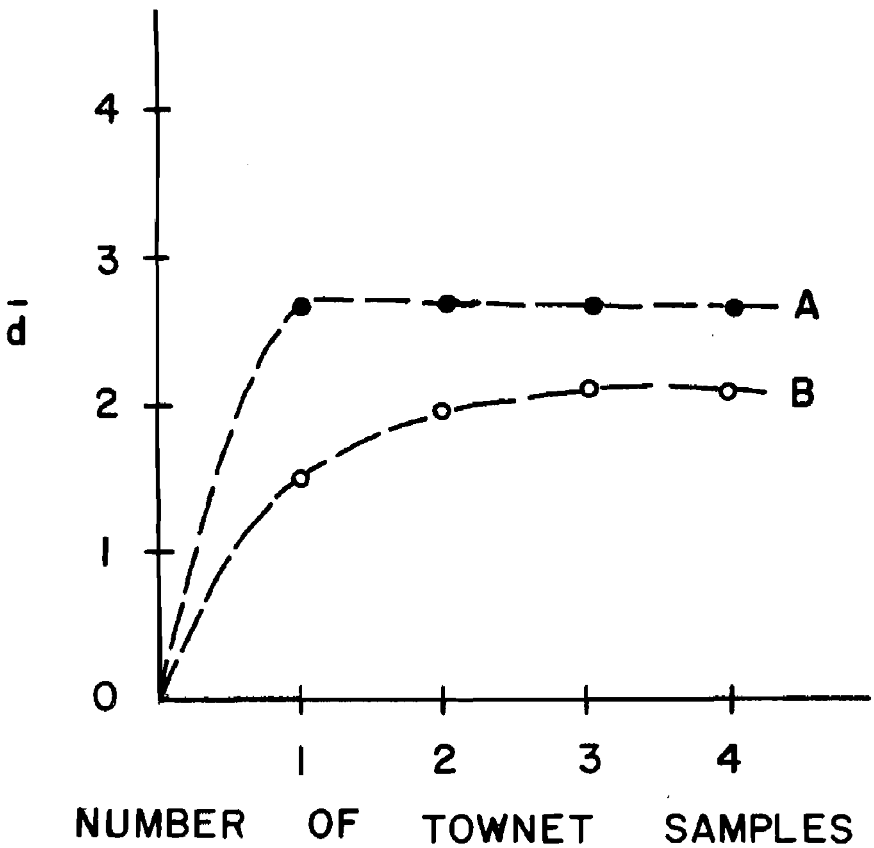

Figure 4. Variation in estimates of diversity per individual ($\bar{d}$) and the number of townet samples used. B = Station 5 in Redmond Reservoir; A = all other stations.

is representative of the relationship between diversity per individual ($\bar{d}$) and the number of pooled townet samples. In most instances, the asymptotic diversity value was reached using the plankters in a single haul. The only exception was Station 5 in Redmond, where all four samples were examined.

Copepoda and Cladocera were identified to species and Rotifera to genus. Identifications were based on *The Systematics of North Ameri-*

can Daphnia (Brooks, 1957), *The Systematics and Evolution of the Moinidae* (Goulden, 1968), *Fresh-Water Invertebrates of the United States* (Pennak, 1953), and *Fresh-Water Biology* (Ward and Whipple, 1959). Identifications of Moindae were verified by Dr. Clyde E. Goulden, Associate Curator of Limnology at the Academy of Natural Sciences of Philadelphia, and the Diaptomidae were verified by Dr. Mildred S. Wilson, Arctic Health Research Center, U. S. Public Health Service, Anchorage, Alaska.

Estimates of population densities were obtained in the following manner. The volume of a townet sample was first made to 60 ml. The sample was then shaken gently and a 1 ml subsample was withdrawn with an automatic pipette before the plankters had settled to the bottom of the container. The material was then transferred to a Sedgwick-Rafter counting cell and plankters identified and enumerated at magnifications of x7 to x440. Population densities of cladocerans, copepods, and rotifers in three separate subsamples were recorded and used to estimate relative abundance of individuals.

The number of subsamples that needed to be examined to provide an adequate representation of each townet sample was determined by comparing estimates of diversity per individual ($\bar{d}$) based on one through six subsamples (Fig. 5). As can be seen, there was virtually no difference between $\bar{d}$ values based on two or more subsamples. It was, therefore, concluded that three 1 ml subsamples provided an adequate representation of $\bar{d}$ for a sample.

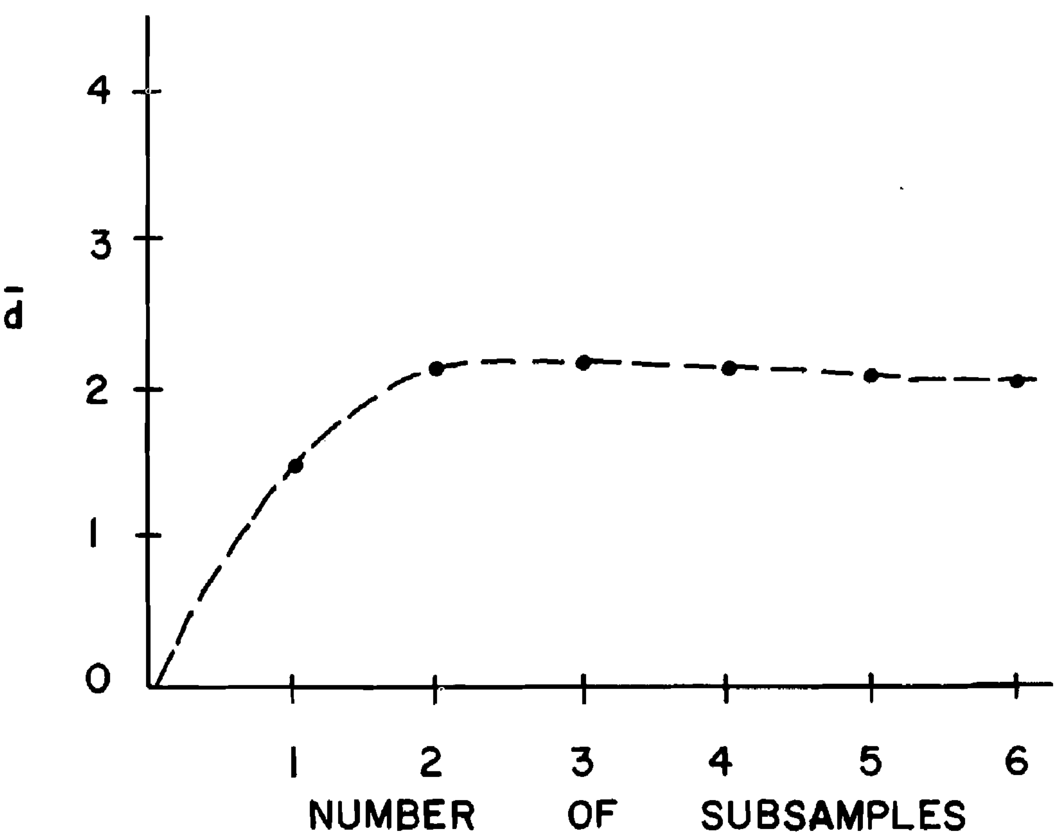

Figure 5. Variation in estimates of $\bar{d}$ of a townet sample based on examination of one to six ml subsamples.

Relative abundance of zooplankton species per townet sample was estimated by the following equation:

$$N = \frac{n\ v}{L}$$

where N is the number of individuals of a species per liter, n is the mean number of individuals per ml of townet sample, v is the volume of the concentrated sample in milliliters, and L is the estimated volume of water strained in liters.

Species diversity indices were calculated using equations from Patten (1962), as later modified by Wilhm and Dorris (1968) and Ransom (1969). The manner in which individuals are distributed among species in a community is reflected by species diversity (d), which was calculated using the equation:

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

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. Species diversity (d) values lie between a theoretical maximum diversity (d_{max}) and minimum diversity (d_{min}). Minimum diversity occurs if all individuals in a sample or community are of one species, and maximum diversity occurs if each individual belongs to a different species. Maximum diversity was determined from the equation:

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

Minimum diversity was calculated from the equation:

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

Diversity per individual ($\bar{d}$) is the ratio of the number of individuals of each species to the total number of individuals in the sample and is represented by the equation:

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

Redundancy (R) is an expression of the dominance of one or more species, and is inversely proportional to the wealth of species (Wilhm and Dorris, 1968). Redundancy is calculated by the equation:

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

Data were programmed and analyzed by the Kansas State Teachers College Data Processing Center, using the above equations. Only $\bar{d}$ and $\bar{R}$ values are reported in this paper. Diversity indices were compared by the F Test at the .05 level. If significant differences were found, Duncan's Multiple Range Test at the .05 level was used to determine which values were significantly different.

RESULTS AND DISCUSSION

SPECIES COMPOSITION OF SUMMER ZOOPLANKTON

Twenty species of Cladocera and Copepoda and eight genera of Rotifera occurred in townet samples collected from the three reservoirs during the 1968 summer (Table 1). There was little difference in the

Table 1. Species list and percent composition of zooplankton in Redmond, Marion, and Council Grove Reservoirs, summer 1968.

	Redmond	Marion	Council Grove
Diaphanosoma brachyurum	9.8	3.8	8.1
Daphnia parvula	5.1		12.8
Daphnia pulex		8.0	
Daphnia ambigua	1.3		1.2
Daphnia galeata mendotae		0.8	
Ceriodaphnia reticulata	0.4	2.8	5.6
Ceriodaphnia lacustris	*	0.5	3.4
Simocephalus serrulatus		0.1	
Moina wierzejskii	*	6.7	
Moina micrura	0.1	1.2	*
Moina minuta	6.3		
Bosmina coregoni		13.0	
Bosmina longirostris	19.5		10.9
Leydigia quadrangularis	*	*	0.1
Chydorus sphaericus	*	0.6	0.1
Diaptomus siciloides	16.5	25.1	4.6
Diaptomus pallidus	5.7	4.7	7.5
Diaptomus clavipes	0.7	5.9	0.2
Cyclops vernalis	6.4	7.8	7.7
Mesocyclops edax	1.0	*	3.2
Brachionus sp.	3.9	0.5	0.7
Keratella sp.	5.9	17.2	14.3
Hexarthra sp.	*	*	
Trichocerca sp.		*	
Asplanchna sp.	2.1	0.8	2.3
Polyarthra sp.	8.3	0.3	14.0
Filinia sp.	4.6	*	0.4
Pedalia sp.	1.9		2.9

*denotes the presence of a species which contributed less than 0.1 percent to the total density.

number of taxa collected from each reservoir, with 23 taxa present in Redmond, 20 in Council Grove, and 23 in Marion. However, there was less similarity between reservoirs with regard to dominant forms. The dominants in Redmond in order of decreasing abundance were *Bosmina longirostris, Diaptomus siciloides, Diaphanosoma brachyurum, Polyarthra, Cyclops vernalis, Moina minuta, Keratella, Diaptomus pallidus,* and *Daphnia parvula.* Dominant plankters in Marion were *Diaptomus siciloides, Keratella, Bosmina coregoni, Daphnia pulex, Cyclops vernalis, Moina wierzejskii,* and *Diaptomus clavipes.* Those organisms dominant in Council Grove were *Keratella, Polyarthra, Daphnia parvula, Bosmina longirostris, Diaphanosoma brachyurum, Cyclops vernalis, Diaptomus pallidus,* and *Ceriodaphina reticulata.*

Most of the species of Cladocera and Copepoda identified appear to be common in other Kansas impoundments (Prophet, Andrews, and Goulden, 1959; Tash and Armitage, 1960; and Prophet, 1964). However, the occurrence of males and sexual females of *Moina minuta* in September samples from Redmond Reservoir is a new record for North America (Goulden, 1968). Marion was in the initial stages of flooding during this study, which may account for the occurrence of *Bosmina coregoni* rather than *Bosmina longirostris.* Apparently *B. coregoni* occurs during the early history of some natural lakes and is eventually replaced by *B. longirostris* (Goulden and Frey, 1963). Applegate and Mullen (1967) reported that *B. longirostris* was more abundant in the older of two Arkansas-Missouri Ozarks reservoirs on the White River.

Zooplankters were most abundant in Marion and least abundant in Redmond as exemplified by the average summer density. Zooplankton averaged 63 individuals per liter in Marion compared to 20 per liter in Redmond and 28 per liter in Council Grove. Individual contribution of copepods, cladocerans, and rotifers to total density of these zooplankters in each reservoir is given in Table 2. Cladocerans constituted the greatest portion of the zooplankton in Redmond and Council Grove, while copepods were dominant in Marion. Relative to other zooplankters, rotifers were most abundant in Council Grove and least numerous in Marion. Redmond and Council Grove appeared to have the most similarity in associated zooplankters, as 88 percent of the taxa identified in the samples from these two reservoirs were present in both. There was less similarity in species composition between Redmond and Marion, and between Marion and Council Grove (Fig. 6).

Based on these comparisons, it appeared that summer zooplankton exhibited relationships among the reservoirs similar to the trends reported for the physicochemical factors. However, analysis of zooplankton community structure using diversity indices derived from information theory indicated that these similarities were probably superficial.

Table 2. Percent contribution of Copepoda, Cladocera, and Rotifera to total density of the zooplankton community in Redmond, Marion, and Council Grove Reservoirs, summer 1968.

Taxonomic group	Redmond	Marion	Council Grove
Copepoda	30.3	43.5	23.2
Cladocera	42.5	37.5	42.2
Rotifera	26.7	18.8	34.6

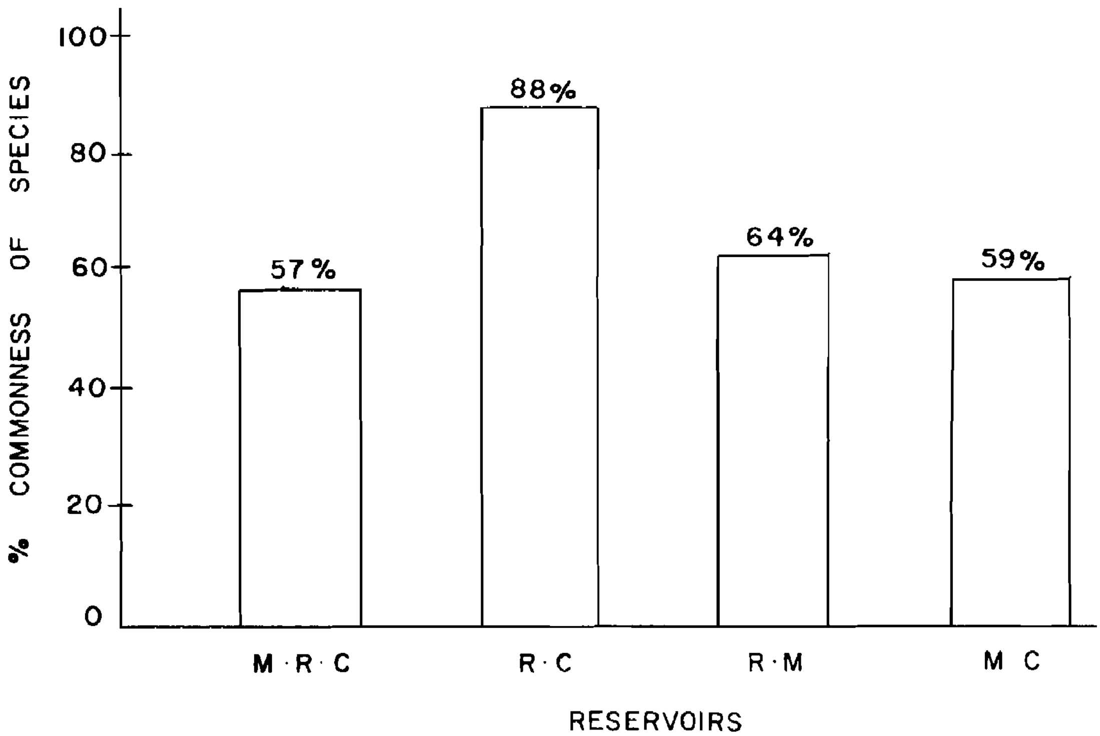

Figure 6. Comparison of species composition of zooplankton communities.

VARIATIONS IN DIVERSITY PER INDIVIDUAL WITHIN RESERVOIRS

There was no significant difference in $\bar{d}$ values among stations in either Redmond or Council Grove. However, there were significant differences among some stations in Marion (Table 3). Diversity per individual based on copepods and cladocerans at Station 5 was significantly different from $\bar{d}$ at Station 4, but the differences between Stations 5 and the remaining stations were not significant. When $\bar{d}$ was based on all three taxonomic groups, relationships changed slightly. In this instance, $\bar{d}$ at Station 5 was significantly different from that of Station 1 as well as Station 4. Thirty-eight percent of all zooplankters collected in Marion were collected at Station 1, while Stations 4 and 5 contributed only 17 and 7 percent, respectively, of the total zooplankton. There were 16 species present at Station 1, 17 at Station 4, and 18 at Station 5. A lower $\bar{d}$ was expected at Station 1, as it contributed the largest number of individuals and the smallest number of species of the three stations. Since Station 5 contributed only 7 percent of the total zooplankters but the largest representation of species, it was expected to have a higher $\bar{d}$ than the other stations.

Table 3. Comparison of mean $\bar{d}$ values among stations within each reservoir.

$\bar{d}$ Based on Copepoda and Cladocera					$\bar{d}$ Based on Copepoda, Cladocera, and Rotifera				
Redmond Reservoir station no.									
1	2	3	4	5	1	2	3	4	5
1.83	2.04	2.18	1.85	2.04	2.55	2.68	2.70	2.44	2.48
Marion Reservoir station no.									
4	1	2	3	5	1	4	2	3	5
2.15	2.29	2.32	2.46	2.66	2.19	2.30	2.45	2.57	3.02
Council Grove Reservoir station no.									
1	2	3	4	5	1	2	3	4	5
2.44	2.38	2.28	2.54	2.29	2.66	2.84	2.94	3.06	2.79

The numbers 1 through 5 indicate the station number, and the $\bar{d}$ value for that station is given directly below the station number. There is no significant difference between underlined values.

COMPARISON OF DIVERSITY PER INDIVIDUAL AND REDUNDANCY AMONG RESERVOIRS

Diversity per individual and redundancy values were used to compare community structure and relative maturity of the reservoirs (Table 4). In Redmond, mean diversity per individual based on copepods and cladocerans was significantly lower than values for both Council Grove and Marion, but when rotifers were included relationships changed so that $\bar{d}$ was also significantly lower in Marion than in Council Grove.

Table 4. Comparison of mean $\bar{d}$ and R values for Redmond, Marion, and Council Grove Reservoirs, summer 1968.

Based on Copepoda and Cladocera				Based on Copepoda, Cladocera, and Rotifera		
JR	M	CG		JR	M	CG
1.99	2.38	2.39	$\bar{d}$	2.57	2.50	2.86
.27	.26	.16	R	.25	.27	.17

The letters JR = John Redmond, M = Marion, CG = Council Grove Reservoirs, $\bar{d}$ = diversity per individual, and R = redundancy. There is no significant difference between underlined values.

These results raise questions about the possible ecological importances of differences in physicochemical features reported for these reservoirs. Summer means for most physicochemical factors in Marion were found to differ significantly from those in both Redmond and Council Grove while there were few significant differences between Council Grove and Redmond (Prophet, 1969b). Thus, similarities based on $\bar{d}$ were virtually the opposite of those based on physicochemical data and percentages of common species.

Obviously variables other than physicochemical factors were influencing community structure in these reservoirs. In the absence of induced environmental stresses, the structure of a community undergoes change through time. The more mature (closer to the climax state) the community, the greater the diversity in that community. Environmental stresses of either pollution or seral stages reduce species diversity. Although relationships between $\bar{d}$ values varied depending upon the number of zooplankter groups considered, the lower values obtained for Redmond and Marion indicate that both were being subjected to some form of environmental stress. As a result, environmental quality in Council Grove was significantly higher. Marion was in the process of filling during this study, while Redmond and Council Grove had been impounded four years earlier. Because of its recent impoundment, community structure in Marion was less mature than of the other two reservoirs, hence the relatively low $\bar{d}$. Redmond is known to be periodically polluted by runoff from commercial feedlots (Prophet, 1969a). The low mean diversity per individual exhibited by this reservoir reflects the effects of this periodical enrichment.

Estimations of diversity per individual and redundancy did not support our initial assumptions concerning similarities of the reservoirs based on their physicochemical conditions. On the contrary, while physicochemical data indicated a similarity between Redmond and Council Grove, their zooplankton community structure was significantly different. This demonstrates the danger of characterizing ecological conditions in aquatic communities solely on the basis of physicochemical data. Likewise, comparisons based on species lists may also be misleading, especially if relative abundance of species is not taken into consideration.

VALUE OF COMMUNNITY STRUCTURE ANALYSIS

The question of the possible ecological importances of the observed differences in physicochemical factors among the reservoirs cannot be completely answered since it is impossible to ascertain at this time to what extent any of the factors measured influenced the structure of the zooplankton community. Nonetheless, species diversity indices derived from information theory can be a valuable tool to limnologists for characterization of environmental quality of aquatic communities and statistically comparing communities. Diversity indices are especially useful in detecting the occurrence of environmental stresses which might be missed by monitoring only physicochemical conditions. This approach complements rather than totally replaces the use of physicochemical measurements and lists of associated species.

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