Use of Shannon's Formula in Describing Spatial and Temporal Variation in a Zooplankton Community in Keystone Reservoir, Oklahoma[1]

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INTRODUCTION

Ruttner (1953) and Cushing (1951) state that diurnal movements of zooplankton are exceedingly varied and complicated. Main features of the diurnal migration are a downward movement at dawn followed by an ascending movement at twilight. Downward movement seems to depend on negative phototaxis (Ruttner, 1953). Ascending movement at night is not limited by the lack of light intensity in a given region, but possibly by other causal elements. Oxygen supply, nutrient requirements, and even chemical stratification are undoubtedly important in diurnal movements, but the complete explanation is lacking (Ruttner 1953; Reid, 1961).

Change in the structure of the zooplankton community is typically expressed in units such as individuals/liter, individuals/m^3, or species/m^3. None of these units reflect the meaningful assemblage of species and individuals in the community. Diversity indices enable summarization of the structure of the biotic community in a numerical index. Various diversity indices have been proposed (Fisher, Corbet, and Williams, 1943; Preston, 1948; and Margalef, 1956).

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Brillouin (1960) introduced the formula,

$$H = (1/N)\ (\log N! - \sum_{1}^{s} \log N_i!)$$

as a measure of diversity per individual, where N is the number of individuals in s species and N_i is the number of individuals in the ith species. Shannon and Weaver (1963), using Stirling's approximation to estimate factorials in Brillouin's formula, introduced the transformation,

$$H = \sum_{1}^{s} p_i \log_2 p_i$$

where $p_i = N_i/N$. N_i/N are population values and are estimated from sample values n_i/n to yield the equation,

$$\bar{d} = -\sum_{1}^{s} n_i/n \log_2 n_i/n$$

A diversity index must be independent of sample size. Pielou (1966) has shown that when successive samples are pooled $\bar{d}$ of the pooled sample increases at first and then levels off. Therefore, $\bar{d}$ can be used to compare communities of different numerical abundance. The purpose of this paper is to use Shannon's formula to analyze diurnal variation in zooplankton community structure.

Methods and Materials

Plankton samples were collected every 4 hr from five strata in the Cimarron Arm, Keystone Reservoir. Oklahoma. Strata samples were taken at levels of 0.5, 4.0, 8.0, 12.0, and 16.0 m. Sampling times were 0800, 1200, 1600, 2000, and 2400 hr on 9 July 1968, and 0400 hr on 10 July 1968.

Paired 3-liter Kemmerer bottles were lowered to the appropriate strata, triggered, and the 6 liters filtered through a Wisconsin Plankton Net. The concentrated samples were placed in 30-ml bottles and fixed with formalin.

The survey-count method was used in enumerating all plankton organisms in a 1-ml subsample on a Sedgwick-Rafter slide. Three 1-ml subsamples from each paired total sample were counted so that 6 slides/stratum/time were enumerated. Pooled samples were tabulated for number of individuals per species, species occurrence, total species, and the total number of individuals. Analysis of zooplankton community structure was made using Shannon's formula.

Physicochemical conditions were monitored in the same strata throughout the plankton collecting periods. Light intensity and current were measured during three daylight periods; oxygen, conductivity, turbidity and temperature were measured at all six sampling times.

Results and Discussion

Physicochemical Conditions — Conductivity was relatively constant from 0.5 to 8.0 m and increased sharply below 8.0 m (Table I). The higher salinity at lower depths is characteristic of Cimarron River water. The high conductivity at lower depths could act as a barrier to species that could not osmoregulate, since this would approximate 934 ppm as Cl^- at 12.0 m and 1963 ppm as Cl^- at 16.0 m.

TABLE I. MEAN PHYSICOCHEMICAL CONDITIONS DURING 24-HR SAMPLING PERIOD.

Depth m	Conductivity µmhos	O_2 ppm	Temperature C	Turbidity ppm	Current m/min
0.5	1391	16.0	28.9	14	1.6
4.0	1398	5.0	25.4	23	0.9
8.0	1544	3.8	25.2	23	0.6
12.0	2970	2.1	25.8	15	1.5
16.0	4799	0.5	25.8	24	2.6

Oxygen concentration was high at 0.5 m, with a mean value of 16.0 ppm. Oxygen saturation was 218% at 0.5 m and was less than 64% at remaining depths. The rapid decline in oxygen concentration with depth was influenced by diminution of photosynthesis.

Temperature decreased rapidly between 0.5 and 4.0 m and was relatively constant from 4.0 to 16.0 m. Slightly higher temperatures at the two lower depths than at 4.0 and 8.0 m was attributed to the denser Cimarron River water flowing through the reservoir.

Light intensity at 0.5 m was 85% of the surface value and at 3.6 m was 1% of the incident radiation. Thus, all sampling depths were below the euphotic zone except the 0.5 m depth.

Turbidity values were greater at 4.0 and 8.0 m than at 0.5 and 12.0 m. Maximum turbidity values were recorded at 16.0 m, presumably caused by large amounts of suspended detritus and silt particles carried by the moving water mass.

Wind activity was greatest at 1600 hr and calm by 2100 hr. Current flow at 4.0 m was upstream, while at 8.0 m movement was circular. Current velocity was greater at 12.0 and 16.0 m as water was moving into the main reservoir to replace that lost by power generation. Outflow at the dam was reported to be approximately 20,000 c.f.s. with the peak flow at 1200 hr, which produced a current of 2.7 m/min at 16.0 m. The 1.6 m/min value at the 0.5 m level was caused by slight winds from variable directions.

Community structure—A total of 20 species of zooplankton were collected during the study. Seven species of rotifers, 4 cladocerans, 8 copepods, and 1 dipteran were counted. Numerical abundance of pooled day and pooled night samples is given in Table II.

Rotifers comprised 63% of the total number of individuals collected. *Brachionus caudatus* and *Trichocerca* sp. were found at all depths and constituted 89% of the rotifers counted. Both species exhibited vertical stratification and were most numerous at 0.5 m during both day and night. Most rotifers were generally more abundant in the upper 8.0 m of water and were relatively rare in the lower depths at night. Over 23% of the total number of rotifers collected during the day were at 12.0 and 16.0 m, while only 5% were taken from the same strata at night.

Cladocera represented less than 1% of the total number of individuals collected. *Daphnia parvula* was collected from all depths and was the most abundant cladoceran. Cladocera were generally absent in the 0.5 samples during the day. The percentage of cladocera in the surface sample increased from 7 during the day to 22 at night. These crustacea were most abundant between 4.0 and 8.0 m throughout the sampling period.

TABLE II. SPECIES FREQUENCY OF POOLED DAY AND NIGHT SAMPLES.

Species	Day						Night					
	0.5	4.0	8.0	12.0	16.0	Total	0.5	4.0	8.0	12.0	16.0	Total
Brachionus calyciflorus	55	8	7		1	71	74	19	8		1	102
B. caudatus	1844	390	274	48	46	2602	1499	357	235	55	16	2162
B. variabilis	19		3	18	29	69	51	7	1	2		61
Hexarthra sp.	3	2				5	11	40	9			60
Keratella cochlearis	25	30	23	8	3	89	24	109	44	1	8	186
Polyarthra sp.	143	23	18	5	7	186	48	12	16		3	79
Trichocerca sp.	669	377	352	640	448	2486	213	110	52	53	50	478
Bosmina longirostris		5	1			6	3	1				4
Ceriodaphnia reticulata		14	8	11		33		7	7	9		23
Diaphanosoma brachyurum	1	30	20	10		61	85	91	32	6		214
Daphnia parvula	19	63	47	29	21	179	1	83	26	39	5	154
Cyclops vernalis	2	196	50	131	141	520	39	95	40	39	18	228
Diaptomus clavipes			6	4		10		2				2

TABLE II, continued

D. dorsalis		32	26	29	16	103	13	36	33	30	1	113
Ergasilus versicolor		3	11			14	1	5				6
Nauplii	38	271	236	211	1061	1817	247	365	199	303	245	1359
Eurytemora affinis		5	10	12	4	31	8	25	4	5	2	44
Mesocyclops edax		10	3	2	10	25	1	12	5	2	2	22
Mesocyclops sp.							8					8
Chaoborus punctipennis								1				1

Copepods were numerous in all samples and constituted 32% of the total number of individuals collected. Nauplii were common and were treated as one species during the study because of taxonomic difficulties. *Cyclops vernalis* comprised 66% of the adult copepods counted and was rare in surface samples during the day. Most copepods were generally found below 0.5 m during the day. Only 40 individuals of one species and nauplii were collected from the surface during the day, while 317 individuals, distributed among six species and nauplii, were taken from the surface during the night.

Chaoborus punctipennis, the phantom midge, was taken only once during the study, at 4.0 m and 2000 hr.

Species diversity—Figure 1 shows a phase space diagram of spatial and temporal changes in $\bar{d}$. The range of spatial varation in $\bar{d}$ exceeded 1.20 at each time period and the mean range of all time periods was 1.36. $\bar{d}$ varied from 1.03 at 16.0 m to 3.19 at 4.0 m. Spatial variation was

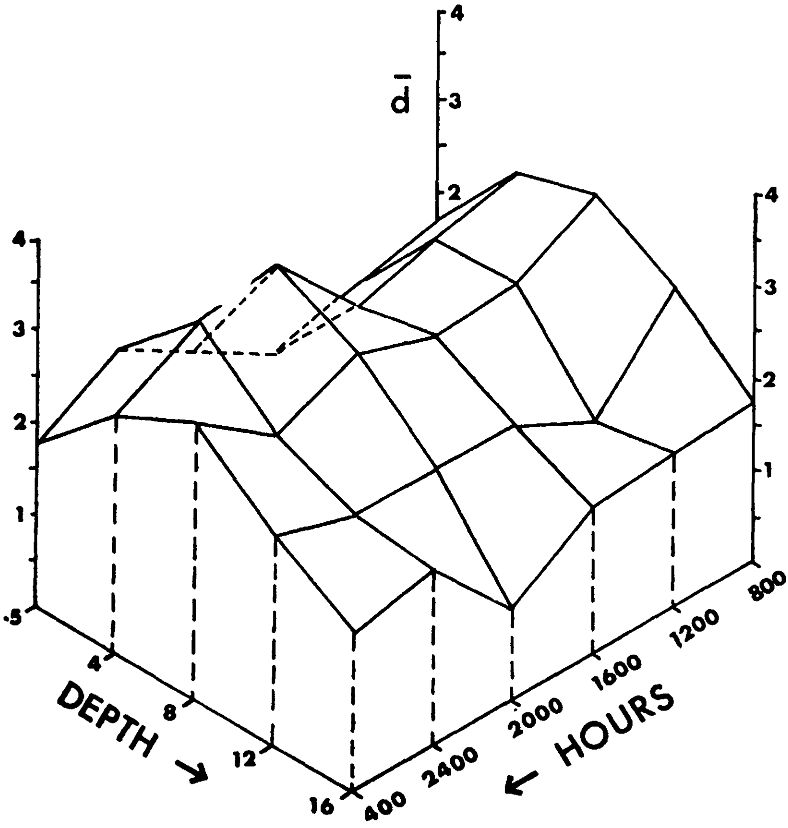

Figure 1. Vertical and temporal changes in $\bar{d}$.

related to physicochemical conditions. Highest $\bar{d}$ values were either at 4.0 or 8.0 m during all time periods. Low $\bar{d}$ values at the surface and bottom strata were associated with relatively harsh physicochemical conditions. High light intensity (Reid, 1961) and temperature (Brown, 1929) probably interacted in such a way as to make the upper strata intolerable to certain species, especially cladocerans and copepods. Low $\bar{d}$ values at 16.0 m may be related to low oxygen and high conductivity.

Despite vertical migration of certain species, variations in numbers of individuals between day and night samples, and the patchiness of species that has been reported (Wiebe and Holland, 1968), temporal variation at a particular depth was less variable than spatial variation at a particular time. The range of temporal variation in $\bar{d}$ was less than 1 at each depth and the mean range of all depths was 0.85. $\bar{d}$ is related not only to the numbers of species in a community, but also to the relative abundance of the different species. A dispersal of a large number of individuals into an area may result in little variation in $\bar{d}$ if the ratios, n_i/n, are relatively unchanged. An immigration of new species may not significantly alter $\bar{d}$, if they are rare. Wilhm (1968) showed that the maximum contribution to $\bar{d}$ is made by a species that contributes 37% of the sample and that the contribution made by rare species is small. In the present study, reporting numbers of species or numbers of individuals would have suggested considerable variation in community structure. However, $\bar{d}$ demonstrated that the pattern of numerical abundance was relatively unchanged in a particular stratum over time. The maintenance of a similar pattern at a specific depth despite changes in numbers of species and individuals merits further study.

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