ZOOPLANKTON DIVERSITY IN A TROPICAL LAKE IN RELATION TO PHYSICOCHEMICAL CONDITIONS

By

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CHAPTER I

INTRODUCTION

Zooplankton assemblages have received little attention in tropical areas, although they are important components of lacustrine ecosystems. Recent studies on tropical zooplankton assemblages have dealt with species richness (Patrick 1966) and relative species abundance (Green 1962, 1967a, and 1971). Others have reported on the reactions of populations to environmental pressures (Green 1967b and Zaret 1969, 1972a, and 1972b).

Diversity indices provide a brief and clear way to summarize and compare information concerning the distribution of individuals among species (Patten 1962). The index most commonly used is:

$$\bar{d} = -\sum_{i=1}^{s} p_i \log p_i$$

(Shannon and Weaver 1963), where $\bar{d}$ is the estimate of the diversity from a sample, p_i is the proportion of the i^{th} class in the sample, and s is the number of classes. This index is particularly useful in summarizing the data on the rapid and dramatic fluctuations characteristic of plankton populations since it is based on dominance diversity (Wilhm 1972). This paper addresses itself to fluctuations and their possible causes in zooplankton diversity in a tropical lake.

Attempts have been made to relate physicochemical factors to changes in the structure of zooplankton assemblages. Hutchinson (1967) indicated that temperature normally is the triggering mechanism for changes in the abundance of zooplankton populations. Changes in zooplankton diversity in temperate regions have been correlated to alkalinity, temperature, dissolved oxygen, and conductivity (Kochsiek and Wilhm 1971) and organic enrichment (Ewing and Dorris 1970 and Prather and Prophet 1971). LaBarbera and Kilham (1974) have examined the effect in conductivity on the distribution of copepods in Africa.

Predation also has been shown to effect zooplankton diversity. Selective predation by planktivorous fish on large zooplankters has been reported to favor the development of communities dominated by small zooplankters (Brooks and Dodson 1965, Galbraith 1967, Green 1967a, and Wells 1970). Dobson (1970), Zaret (1971a), and Sprules (1972) have documented other lacustrine examples where the structure of zooplankton assemblages was determined by vertebrate predation. Dodson (1974) has stated that the presence of predacious zooplankters favors the development of communities dominated by large-sized species of zooplankton.

The objectives of the present study were to relate temporal and spatial fluctuations in zooplankton diversity in Lake Atitlan, Guatemala, as estimated by $\bar{d}$, to:

1) temporal and spatial variations in temperature, chlorophyll _a_, and turbidity and
2) fish predation.

CHAPTER II

METHODS

This study was conducted at Lake Atitlan, Guatemala, a mid-elevation (1555 m) tropical lake (latitude 14° 40' N). The surface area is 130 km^2, maximum depth is 324 m, and mean depth is 189 m. The lake basin declines sharply to form a central pool over 200 m deep. Only Santiago Bay has significant littoral habitats (Figure 1). Two permanent rivers flow into the lake on the north shore near Panajachel. No surface outflows exist, but there appears to be a subterranean flow to the river Madre Vieja east of the lake (Weiss 1971). The lake level fluctuates 1-2 m annually between wet and dry seasons. High water levels occur in late November or early December and low levels in early May. Lake Atitlan is a warm monomictic lake with destratification usually occurring in December or January. The hypolimnion has a year-round temperature of 19.5 C, with the epilimnion reaching a maximum of 23.5 C. The 99% level of light extinction occurs below 30 m. The turbidity and temperature profiles for Santiago Bay differ from those of the main basin of the lake.

Weiss (1971) reported that the phytoplankton of the lake is dominated by the diatoms *Melorira* and *Synedra* and the green alga *Closteriopsis*. The zooplankton assemblage includes the following: Rotifera - *Keratella cochlearis*, *Polyarthra* sp., *Brachionus calyciformes*, *Platyias patulus*, *Asplanchna priodonta*; Cladocera - *Ceriodaphnia*

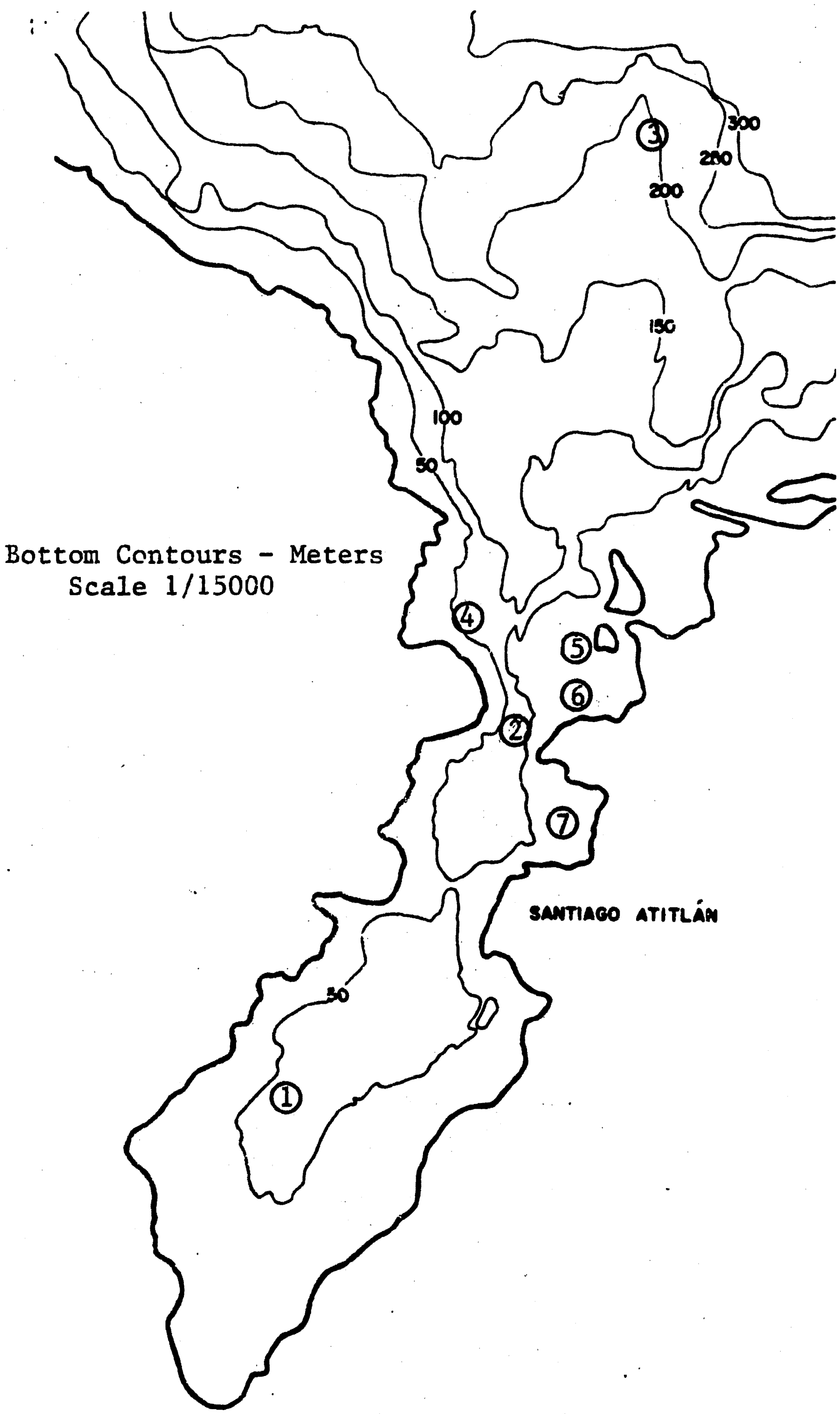

Figure 1. Santiago Bay, Lake Atitlan - Stations 1-7

pulchella, Daphnia pulex, Daphnia ambigua, Bosmina coregoni, Bosmina longirostris, Diaphanosoma brachyurum; Copepoda - Cyclopoidea (1 species).

The dominant fishes in the lake, Lepomis macrochirus, Pomoxis nigromaculatus, and Micropterus salmoides, normally were captured in the littoral zone (Bowman and Summerfelt, In Press). Their spawning season occurred from mid-April to mid-June. An analysis of the stomach contents showed that they fed exclusively on Cladocera in the pelagic zone and both macroinvertebrates and large zooplankters in the littoral zone.

Nine zooplankton collections were taken at Stations 1, 2, and 3 (Figure 1 and Table I) at about two week intervals from February 6 to June 14, 1973. Stations 4 through 7 were sampled during the last six sampling periods. Two replicate samples were obtained at each station with a Clark-Bumpus plankton trap. Columns of water were filtered by raising the trap at a constant speed from near the bottom. The samples were preserved in 5% formalin. In the laboratory, successive fractions of each sample were transferred to a counting disc and examined with a dissecting microscope until 100 individuals had been identified and counted. By calculating the diversity of groups of 50, 100, 500, and 1000 individuals it was determined that the asymptote of the $\bar{d}$ graph was reached with a count of 100. Four count totals for each station were pooled and $\bar{d}$ was calculated using a computer program developed by Wilhm (1970).

Limnological data were taken at Stations 1, 2, and 3 concurrently with zooplankton collections. Light penetration was measured with a GEM submarine photometer (model # 268WA300). To determine chlorophyll a

TABLE I

CONDITIONS AT SAMPLING STATIONS

Station	Depth (m)	Distance to Shore (m)	Macrophytes*
1	60	1000	sparce
2	60	500	sparce
3	200	3000	none
4	15-20	100	sparce
5	15-20	100	abundant
6	5-10	25	abundant
7	10-15	200	abundant

*none - nonexistant
sparce - patchy distribution of individual plants
abundant - bottom completely covered with thick layer of plants

concentration as an index to phytoplankton biomass, two water samples were collected at each station by submerging a weighted, polyvinyl tube (1.18 cm ID) to 60 m. The submerged end of the tube was raised with an attached line. Each column was collected in a glass bottle, mixed thoroughly, and a two liter subsample was taken. The phytoplankton in the subsamples was concentrated on 0.22 mμ Millipore filters and extracted in an acetone solution. After being refrigerated for 24 h the optical density of the solutions was determined at 750, 665, 645, and 630 mμ with a Bausch and Lomb Spectronic 20. The chlorophyll a values were determined by multiplying the OD-665 readings by 14.3 (A.P.H.A. 1971).

To determine how species diversity changed over time, each station mean was compared to itself in a one-way nested analysis of variance. To examine spatial effects on diversity, the eight sampling stations were divided into groups sharing similar environmental characteristics and compared in a one-way classification of linear combinations among means. These combinations consisted of:

1) bay (1 and 2) vs. lake (3) stations;

2) pelagic (1, 2, and 3) vs. littoral (5, 6, and 7) stations;

3) presence (5, 6, and 7) vs. absence (4) of vertebrate predators.

CHAPTER III

RESULTS

Physicochemical

Lake Atitlan was thermally stratified at 45 m on December 15, 1972. By January 8, 1973, the lake had destratified to a nearly uniform temperature of 20 C (Figures 2, 3, and 4). Circulation continued until mid-March with only weak diurnal stratification developing. A persistent thermocline began to form by the end of March and was firmly established by mid-May. An upsurge of cold water in April compressed the lower layers of the thermocline upward. Temperature profiles of the three stations varied little.

Chlorophyll a concentration and turbidity values were different between the lake and bay stations. The chlorophyll a concentration of the lake station (3) remained relatively constant during the entire period, while the bay stations (1 and 2) had a large increase in April (Figure 5). Light extinction values for Stations 1 and 2 were always 10-15% greater than Station 3 (Figure 6). Turbidity increased at all three stations in January, April, and June.

Species Diversity

Zooplankton diversity ($\overline{d}$) values ranged from 1.10 at Station 4 on January 4 to 2.50 at Station 6 on May 22. The mean for all $\overline{d}$ values was

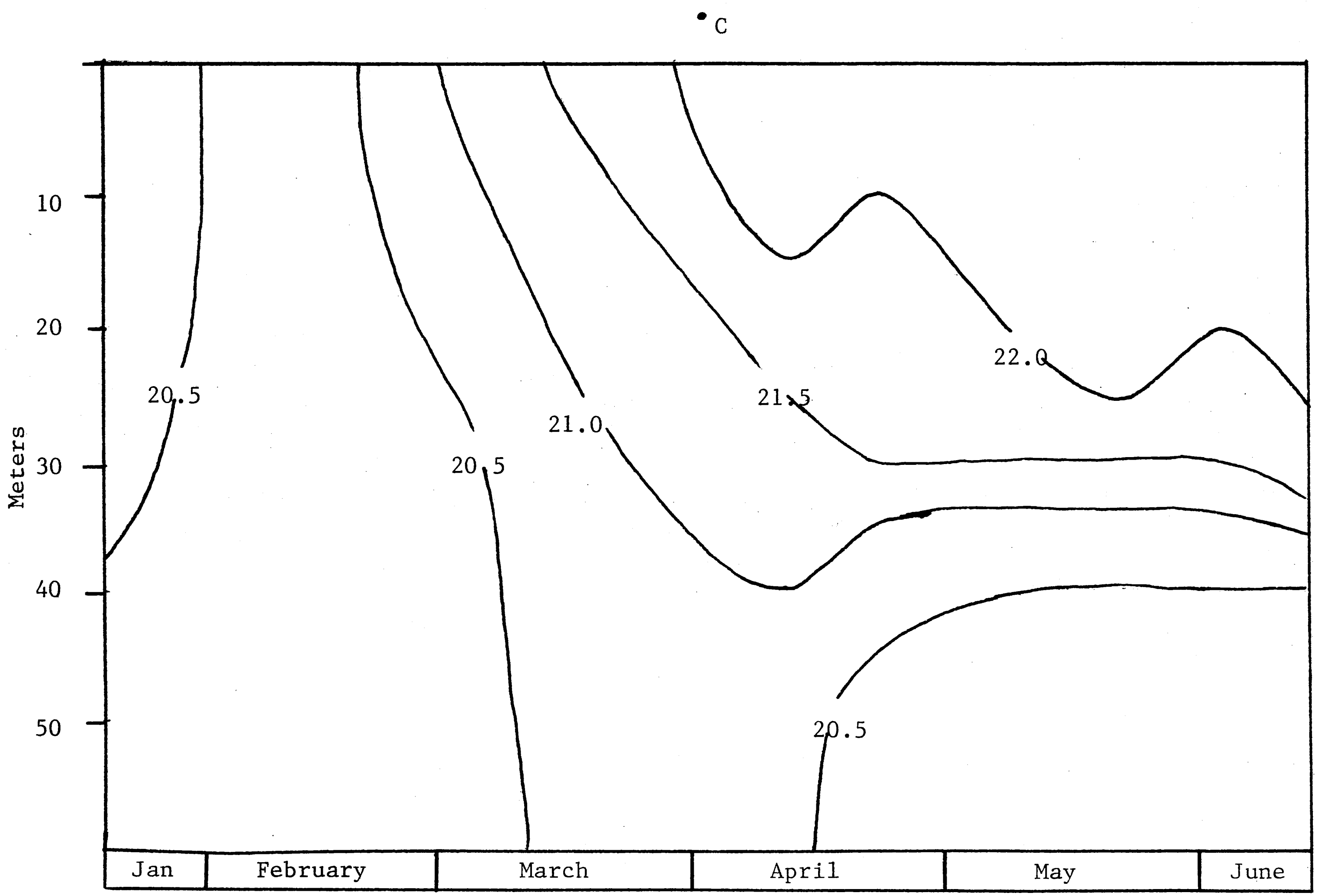

Figure 2. Temperature Profile - Station 1

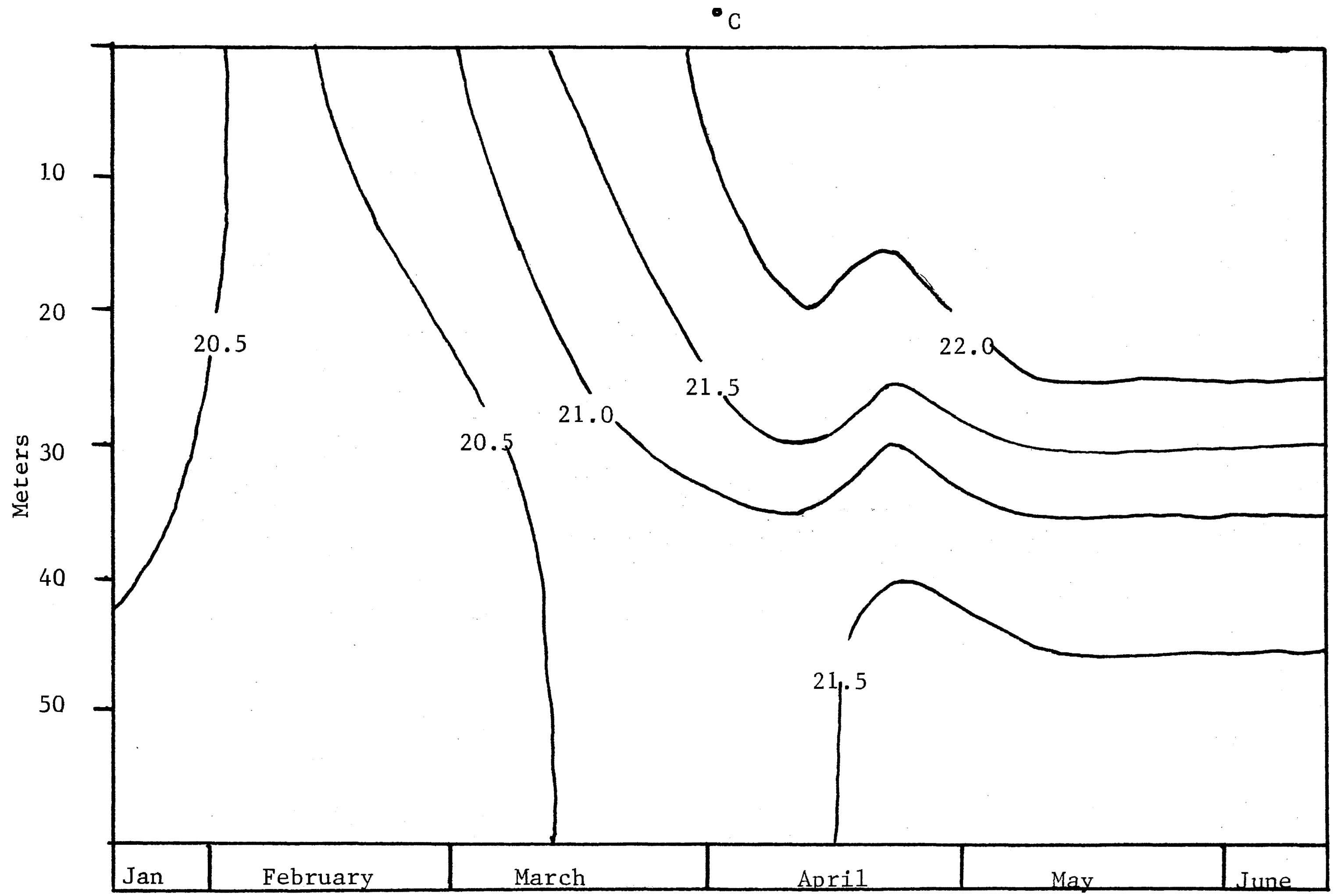

Figure 3. Temperature Profile - Station 2

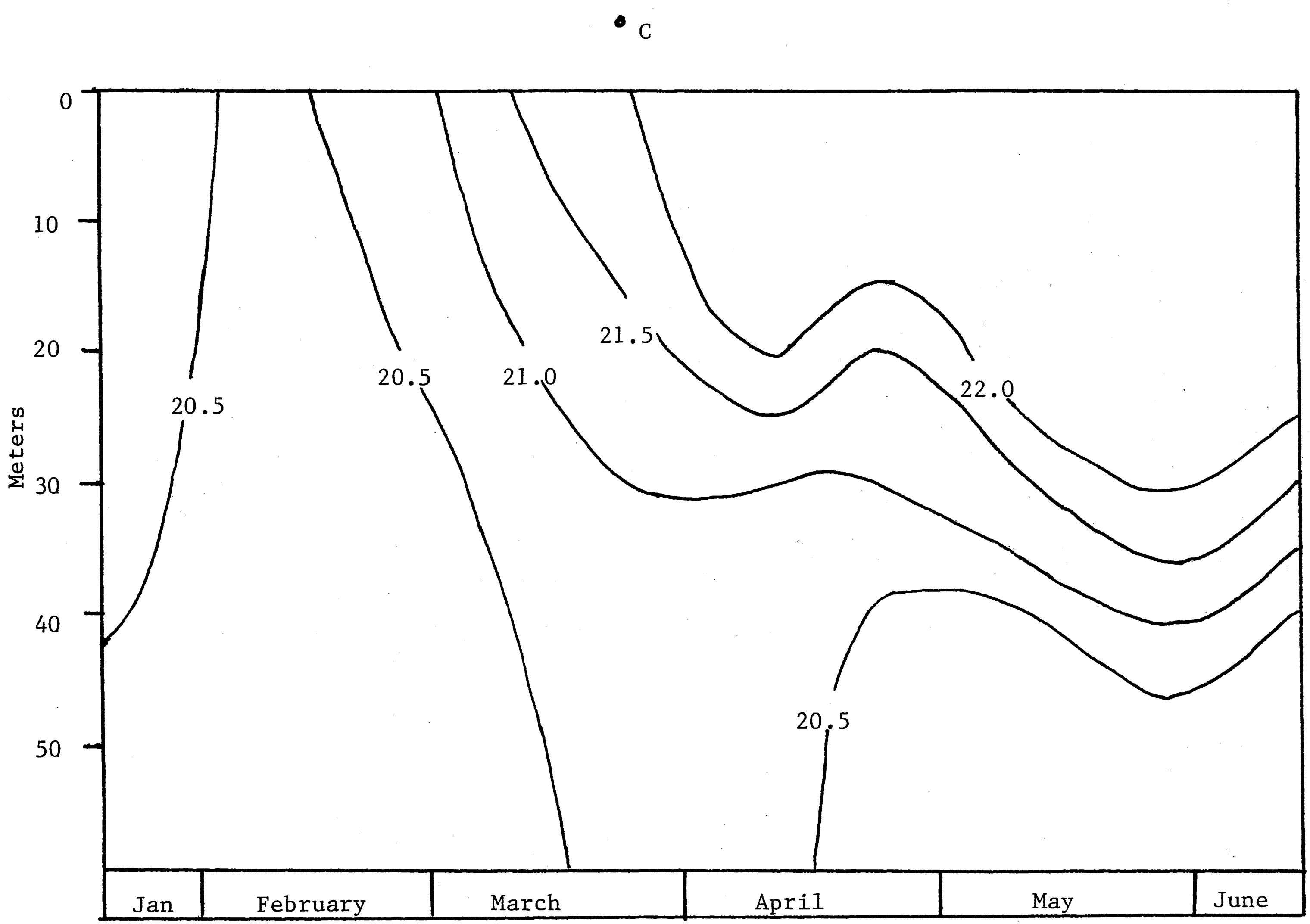

Figure 4. Temperature Profile - Station 3

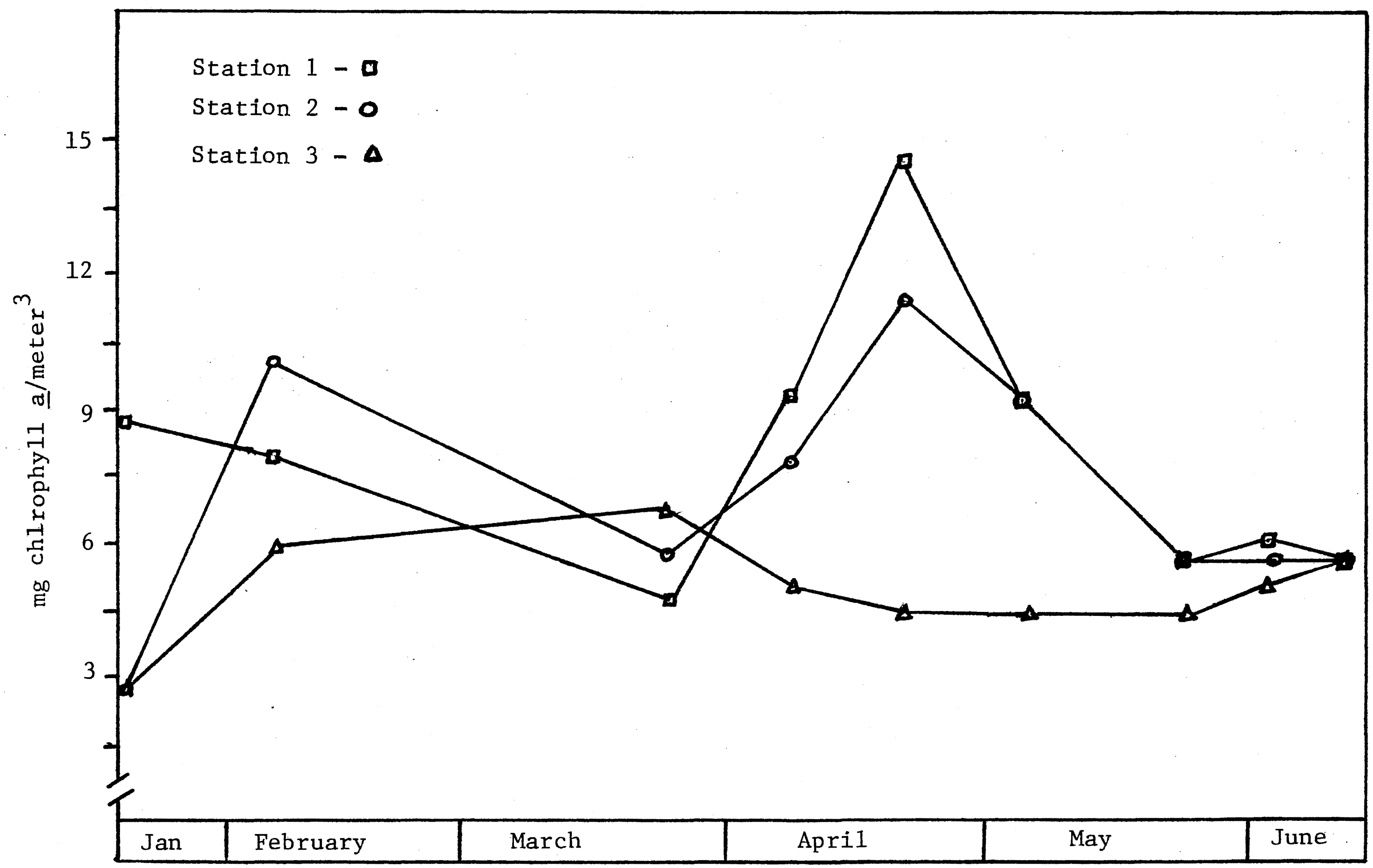

Figure 5. Chlorophyll a Concentration in a 60 m Column

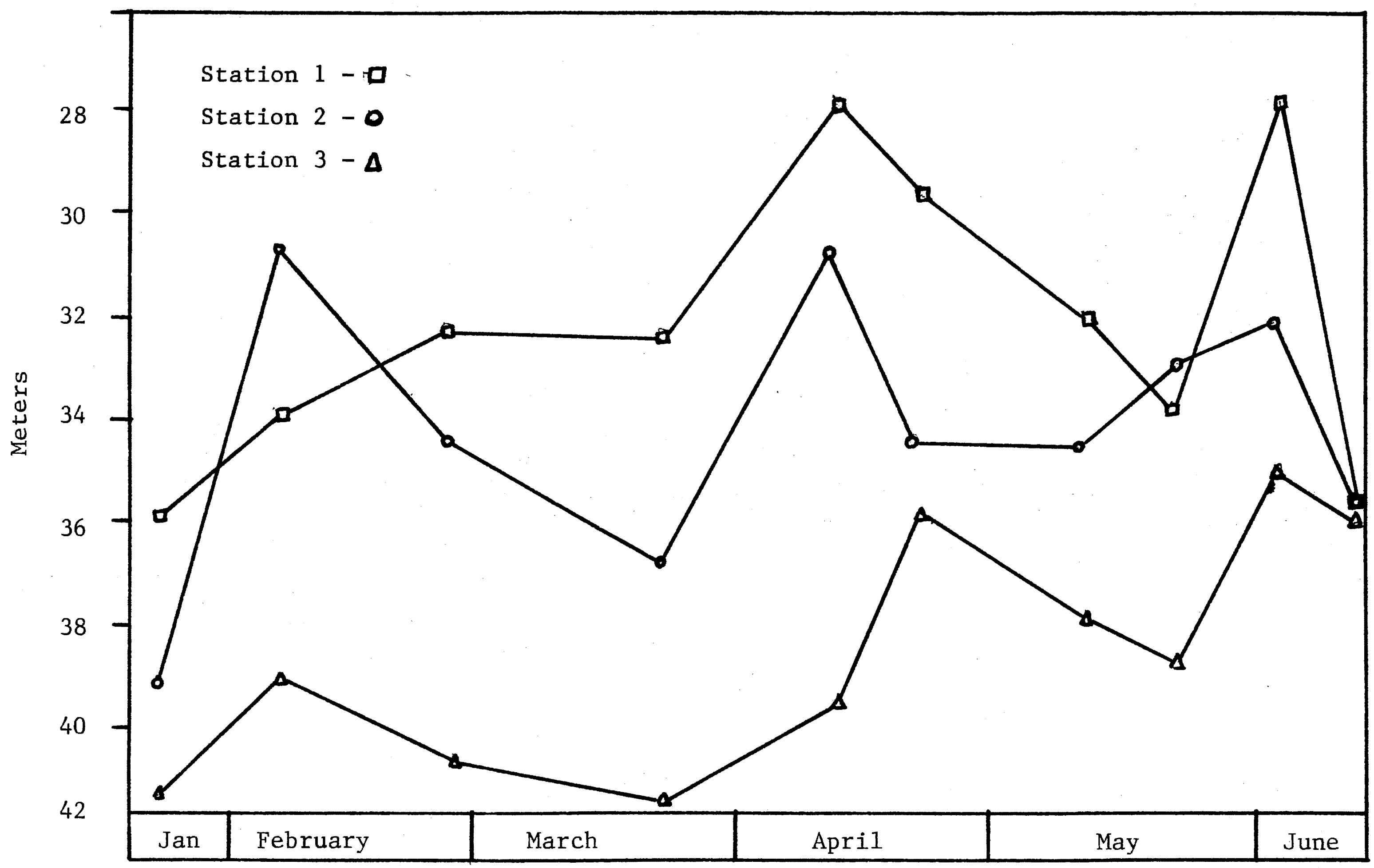

Figure 6. Level of 99% Light Extinction

1.68. Trends in $\bar{d}$ observed at the three deep water stations were similar in slope and magnitude, being highest in April and June and lowest in February and May (Figure 7). The $\bar{d}$ values at shallow water Stations 5-7 oscillated more frequently, showed less similarity, and normally were higher than at Stations 1-3 (Figure 8). Diversity at Station 4, a shallow water station had results similar to the deep water stations. Temporal variation in diversity was significant ($p = .95$) at all eight stations (Table II).

Normally, little statistically significant difference occurred in the diversity values of Stations 1-3 on any given sampling date (Table III). A large amount of variation was found between station groups 1-3 and 5-7 where differences were statistically significant on all sampling dates. Station 4 significantly varied from Stations 5-7 but differed little from Stations 1-3.

The taxonomic groups identified were the same as those reported by Weiss (1971). *Cyclops* sp. was the most abundant species found at each station and usually constituted the bulk of the periodic, rapid increases in total abundance (Tables IV-X). *Brachionus calyciformes* was the most numerous rotifer, being present in all the samples with highest proportional numbers in March and June. *Asplanchna priodonta* was proportionally most abundant in January and February. *Keratella cochlearis*, *Polyarthra* sp., *Platyias patulus*, and the four species of Cladocera were present in relatively smaller numbers. The number of taxonomic groups present at any one sampling station varied from eight to ten on all but one occasion, with the periodically occurring groups being those of relatively smaller abundance.

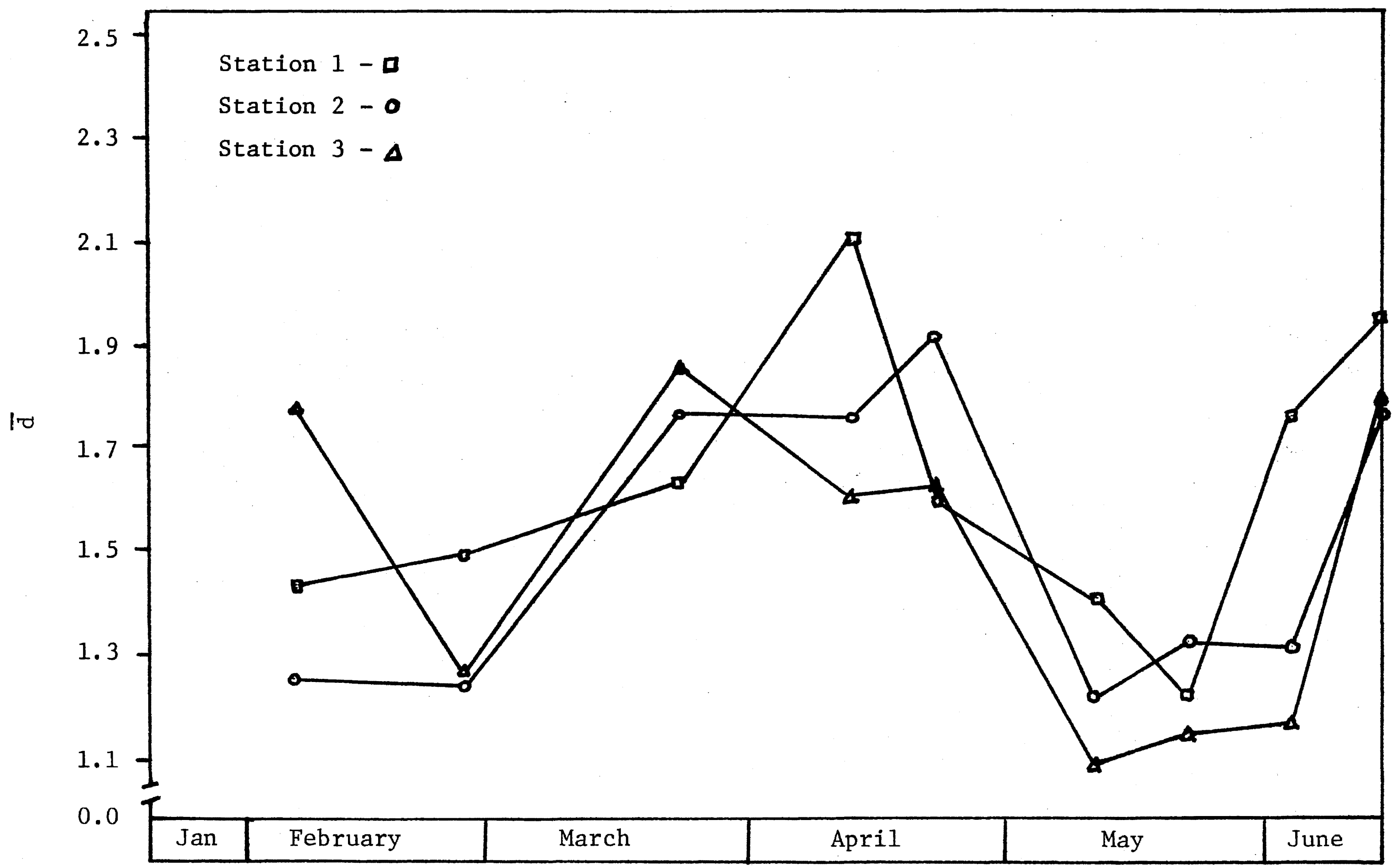

Figure 7. Species Diversity ($\overline{d}$) for Stations 1-3

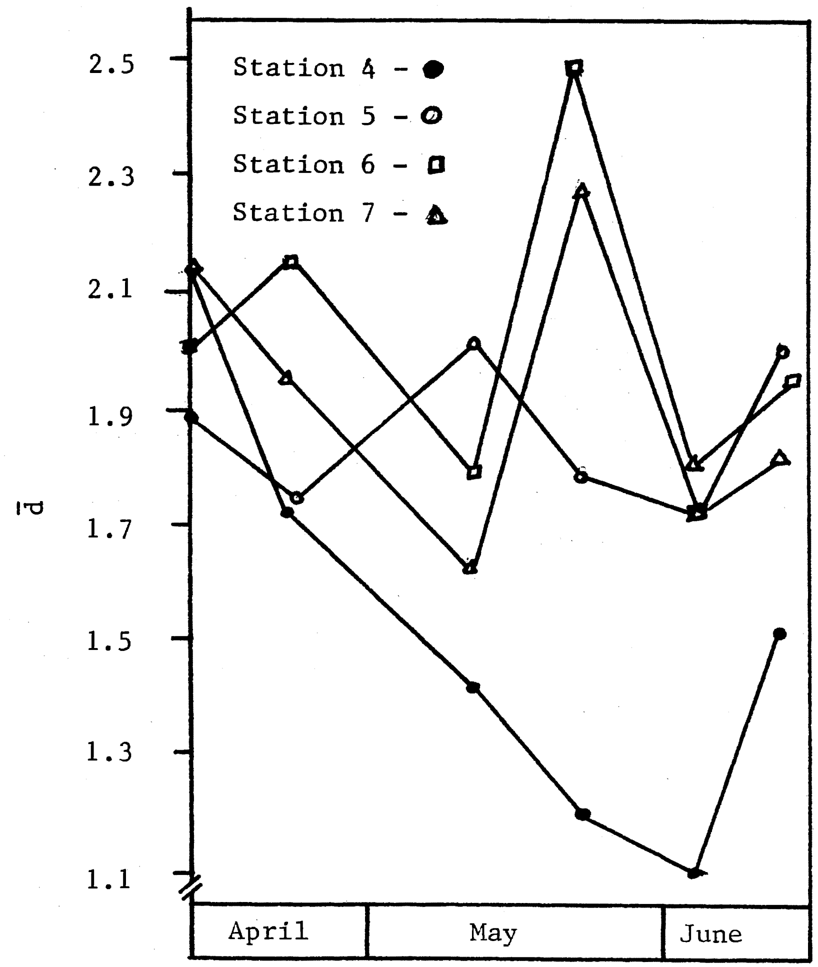

Figure 8. Species Diversity ($\bar{d}$) for Stations 4–7

TABLE II

LEVEL OF SIGNIFICANCE FOR SPATIAL COMPARISONS OF $\overline{d}$ VALUES OF ZOOPLANKTON

Station	1	2	3	4	5	6	7
Level of Significance	0.986	0.997	0.987	0.999	0.952	0.995	0.996

TABLE III

T VALUES FOR SPATIAL COMPARISONS AMONG MEANS OF $\overline{d}$ OF ZOOPLANKTON

Station/Period	2	3	4	5	6	7	8	9	10
1 & 2 vs. 3	3.8393*	3.3596*	0.8366	7.0906**	0.7845	1.5595	0.6207*	2.4372	0.5208
1, 2, & 3 vs. 5, 6, & 7				4.1708**	3.0826*	6.4945**	8.1217**	3.0669*	3.3281*
4 vs. 5, 6, & 7				3.5699**	2.0161	3.3823*	6.0335**	5.2342**	2.8778*
1, 2, & 3 vs. 4				2.4645*	1.4570	1.2099	0.1775	3.0868	2.8775*

*significant at 95% level

**signfiicant at 99% level

TABLE IV

ZOOPLANKTON DENSITY (ORGANISMS/LITER) FOR STATION 1

	Date								
	2/5	2/26	3/23	4/11	4/22	5/13	5/23	6/4	6/12
Cyclops	16.00	9.28	28.98	40.70	31.33	29.26	27.98	63.92	18.13
Ceriodaphnia	2.72	0.48	1.01	4.45	2.12	2.23	2.86	3.18	4.13
Diaphanasoma	2.24	0.48	0.67	1.27	0.71	0.32	0.32	0.32	0.64
Bosmina	0.64	0.08	1.01	5.09	3.72	2.23	1.27	0.64	1.91
Daphnia	1.40	5.60	3.03	1.27	0.71	0.64	0.32	0.32	0.64
Asplanchna	10.88	3.84	6.74	18.44	2.30	4.77	2.23	4.45	5.41
Brachionus	0.80	11.20	19.21	33.07	4.43	4.77	10.81	26.39	35.30
Keratella	0.48	0.24	3.03	12.08	2.30	4.77	1.59	5.09	3.50
Polyarthra	0.16	0.72	0.34	1.27	0.00	0.32	0.32	0.32	1.27
Platyius	0.00	0.00	0.34	0.95	0.35	0.95	0.32	0.32	0.32
$\bar{d}$	1.46	1.51	1.65	2.10	1.61	1.43	1.24	1.77	1.98

TABLE V

ZOOPLANKTON DENSITY (ORGANISMS/LITER) FOR STATION 2

	Date								
	2/5	2/26	3/23	4/11	4/22	5/13	5/23	6/4	6/12
Cyclops	15.04	16.06	19.60	11.83	14.31	22.58	40.93	32.75	19.72
Ceriodaphnia	1.44	0.48	1.43	1.17	1.11	0.64	5.41	1.91	2.54
Diaphanasoma	2.08	0.48	1.20	0.58	0.48	0.32	0.32	0.32	0.32
Bosmina	0.48	0.16	0.24	0.58	2.39	3.50	3.18	2.54	0.64
Daphnia	0.90	0.08	0.96	0.58	0.16	0.32	0.32	0.32	0.32
Asplanchna	4.16	4.13	4.06	2.34	2.86	2.23	3.18	2.54	6.04
Brachionus	0.32	2.23	28.44	13.43	5.72	3.82	13.67	15.90	24.49
Keratella	0.16	0.32	0.96	1.17	2.86	1.91	3.18	2.54	2.86
Polyarthra	0.16	0.48	2.15	0.29	0.16	0.95	0.32	0.00	0.64
Platyius	0.90	0.08	0.96	0.58	0.16	0.32	0.32	0.32	0.32
$\bar{d}$	1.26	1.22	1.79	1.78	1.85	1.28	1.40	1.39	1.77

TABLE VI

ZOOPLANKTON DENSITY (ORGANISMS/LITER) FOR STATION 3

	Date								
	2/5	2/26	3/23	4/11	4/22	5/13	5/23	6/4	6/12
Cyclops	7.84	10.34	23.96	9.64	11.45	13.38	24.17	31.16	59.03
Ceriodaphnia	0.16	0.64	0.32	0.58	0.16	0.24	1.91	1.91	1.20
Diaphanasoma	0.24	0.80	0.00	0.29	0.16	0.24	0.32	0.32	0.24
Bosmina	0.24	0.32	0.00	0.58	0.95	1.43	0.95	0.64	0.72
Daphnia	0.32	3.98	0.48	0.88	0.64	0.96	0.32	0.64	0.72
Asplanchna	1.76	9.70	5.57	1.46	2.07	2.63	2.54	1.27	4.06
Brachionus	0.40	1.11	1.91	9.34	1.59	2.39	7.00	15.90	12.67
Keratella	0.08	0.00	0.00	0.15	0.32	0.49	1.59	2.54	2.87
Polyarthra	0.08	0.16	0.00	0.00	0.48	0.72	0.32	0.32	0.24
Platyius	0.00	0.00	0.00	0.44	0.16	0.24	0.32	0.32	0.00
$\bar{d}$	1.77	1.27	1.85	1.62	1.64	1.67	1.22	1.26	1.81

TABLE VII

ZOOPLANKTON DENSITY (ORGANISMS/LITER) FOR STATION 4

	Date					
	4/11	4/22	5/13	5/23	6/4	6/12
Cyclops	4.05	24.21	17.02	18.09	80.34	30.32
Ceriodaphnia	0.46	2.39	0.53	4.26	2.66	2.66
Diaphanasoma	0.11	0.53	0.00	1.06	0.66	0.00
Bosmina	0.68	2.39	1.06	4.26	0.66	0.53
Daphnia	0.06	0.27	0.53	0.53	0.66	0.53
Asplanchna	2.74	5.05	4.26	5.32	7.30	7.49
Brachionus	4.62	17.29	6.38	13.30	37.85	50.01
Keratella	0.40	0.53	1.06	5.32	3.32	2.13
Polyarthra	0.23	0.27	0.53	0.53	0.66	0.53
Platyius	0.06	0.27	0.53	1.06	0.00	0.00
$\bar{d}$	2.13	1.72	1.43	1.26	1.10	1.50

TABLE VIII

ZOOPLANKTON DENSITY (ORGANISMS/LITER) FOR STATION 5

	Date					
	4/11	4/22	5/13	5/23	6/4	6/12
Cyclops	38.29	24.74	6.12	35.64	24.43	37.24
Ceriodaphnia	9.34	2.13	0.27	6.38	1.77	9.04
Diaphanasoma	0.93	0.53	0.00	0.53	0.35	0.53
Bosmina	2.34	5.05	0.53	2.66	1.77	1.66
Daphnia	1.87	0.27	0.27	0.53	0.35	0.53
Asplanchna	14.01	5.05	2.13	12.24	4.25	10.11
Brachionus	46.23	10.91	3.19	15.42	17.70	43.62
Keratella	1.87	2.39	0.53	3.19	3.89	7.98
Polyarthra	4.20	0.53	0.53	1.60	0.71	4.79
Platyius	0.47	0.27	0.27	0.53	0.35	3.20
$\bar{d}$	1.90	1.74	2.02	1.78	1.70	2.00

TABLE IX

ZOOPLANKTON DENSITY (ORGANISMS/LITER) FOR STATION 6

	Date					
	4/11	4/22	5/13	5/23	6/4	6/12
Cyclops	18.59	19.80	47.40	8.76	21.49	69.60
Ceriodaphnia	0.66	2.87	2.40	1.59	0.25	12.00
Diaphanasoma	0.33	0.29	0.60	0.39	0.25	0.80
Bosmina	2.99	3.44	10.80	0.80	0.00	8.00
Daphnia	0.33	0.86	0.60	1.19	0.25	0.80
Asplanchna	8.96	8.32	14.40	16.32	1.98	63.20
Brachionus	18.92	17.79	21.00	12.34	16.55	53.60
Keratella	1.00	6.03	4.80	11.54	2.96	20.80
Polyarthra	1.33	0.29	0.60	0.40	0.00	0.80
Platyius	0.66	1.72	3.00	3.98	4.69	3.20
$\bar{d}$	2.00	2.16	1.78	2.49	1.70	1.94

TABLE X

ZOOPLANKTON DENSITY (ORGANISMS/LITER) FOR STATION 7

	Date					
	4/11	4/22	5/13	5/23	6/4	6/12
Cyclops	56.00	20.73	36.87	4.47	27.13	50.84
Ceriodaphnia	13.60	0.88	1.07	0.64	2.66	2.79
Diaphanasoma	0.80	0.00	0.00	0.00	0.00	0.31
Bosmina	2.40	9.34	11.46	0.64	4.26	1.24
Daphnia	2.40	0.29	0.36	0.64	0.53	0.00
Asplanchna	0.24	6.72	11.81	12.12	6.38	11.16
Brachionus	93.60	6.13	7.52	8.29	52.67	13.02
Keratella	4.00	1.75	2.15	3.51	7.45	4.96
Polyarthra	0.80	0.58	0.72	0.00	0.53	0.31
Platyius	8.80	0.88	1.07	1.60	1.06	0.31
$\bar{d}$	2.02	1.96	1.63	2.30	1.80	1.78

CHAPTER IV

DISCUSSION

Analysis of Diversity Values

The diversity index defined by Shannon's Formula is dependent on species richness and equitability. The importance of the richness component was examined by determining the correlation coefficient between values of diversity and the number of classification groups which were used in their respective calculation (Sager and Hasler 1969). The low value obtained ($r = 0.19$) apparently indicates that the richness component had little affect on the calculated values. A similar analysis between the $\bar{d}$ values and a measure of evenness (Pielou 1966) resulted in a r value of 0.95 indicating that the main effect being measured in this study was the variation in the equitability component.

These findings are consistent with previous studies. Plankton tends to have a relatively constant number of species present with periodic changes in relative density (Pennak 1956 and Hall 1970). These characteristics suggest that the regulation of plankton diversity is dependent primarily on the equitability component (Tramer 1969). Sager and Hasler (1969) have empirically shown this for phytoplankton in a Wisconsin lake.

The relative abundance of the five most common taxonomic groups controlled diversity fluctuations (Tables IV-X). Diversity was high when one or more of the rotifers increased to a relatively large proportion of the total. Periods of low diversity were found when an extreme dominance by copepods occurred. In one case, however, the richness component significantly influenced diversity (February 26 - Station 3). The number of taxonomic units was reduced by 50% resulting in a reduction in diversity despite a relatively uniform distribution of individuals among the groups present.

Relation of Environmental Parameters to $\bar{d}$ Values

Periods of low diversity at Stations 1-4 coincided with the major environmental changes of lake turnover and the beginning of the rainy season, both of which are known to effect zooplankton abundance (Hutchinson 1967 and Hall 1970). Except at Station 3 in February and March, it appears that environmental conditions gave a competitive advantage to the copepods during these two time periods of change, enabling them to obtain larger numbers than the other species, thus causing a drop in diversity.

Attempts to relate specific physicochemical parameters to diversity were unsuccessful. The correlation coefficient between $\bar{d}$ and light extinction values was not significant at 0.15 although graphical representations seemed to indicate similar trends (Figures 6 and 7). The correlation coefficient between diversity values and chlorophyll *a* concentration was also low, 0.22. A negative relation existed, however, between chlorophyll *a* and the number of zooplankton. Apparently, the zooplankton act as a limiting factor to phytoplankton as has been found in other studies (Wright 1965, Hargrove and Green 1970, and

Porter 1973).

The diversity values at Stations 5-7 have few common characteristics other than, as a group, being significantly higher than those of Stations 1-4. This would be expected from differences in station characteristics. Stations 1-3 have a simpler physical environment as well as probably no significant vertebrate predation. The same is true for Station 4 which, although a shallow water station, has a bottom composed of boulders with little vegetation. Stations 5-7, however, have a dense cover of macrophytes thus increasing the environmental heterogeneity and suggesting the presence of vertebrate predators, both of which are causes of higher diversity in zooplankton.

The presence of mobile predators can increase the diversity of prey species (Paine 1969 and Hall 1970). Selective feeding gives advantage to competitors of a prey animal. The three dominant fish species in the lake normally feed selectively on large crustaceans (Applegate and Mullen 1967 and Gerking 1966). When large Cladocerans, which apparently have an advantage in food gathering (Brooks and Dobson 1965), are reduced in number, more food is made available to the smaller zooplankters enabling them to increase in number, causing higher diversity.

The studies by Paine and Hall also point out the importance of environmental heterogeneity to diversity. An increase in habitat types increased the number of species present. This could be due to protection from predation offered by the new habitat types or greater ability of the more rare species to compete with the dominants in the new habitats.

CHAPTER V

SUMMARY

1. A study of zooplankton diversity was made in Lake Atitlan, Guatemala, a tropical, mid-elevation lake from February to June, 1973.

2. Diversity values were found to be primarily dependent on the relative distribution of individuals among taxonomic groups.

3. At deep water stations low diversity immediately followed destratification and the onset of the rainy season. No relation was found between diversity and specific physicochemical parameters.

4. Shallow water stations maintained a relatively higher level of diversity which was due to increased environmental heterogeneity, vertebrate predation, or both.

LITERATURE CITED

Applegate, R. L., and J. M. Mullen. 1967. Food of young largemouth bass (*Micropterus salmoides*) in a new and old reservoir. Trans. Amer. Fish Soc. 96:75-77.

American Public Health Association. 1971. Standard Methods for the Examination of Water and Waste Water. 13th ed. Amer. Public Health Ass., New York.

Brooks, J. L., and S. I. Dobson. 1965. Predation, body size and composition of plankton. Science 150:28-35.

Bowman, D., and R. Summerfelt. Progress report on the fishery of Lake Atitlan, Guatemala. (In Press).

Dobson, S. I. 1970. Complementary feeding niches sustained by size selective predation. Limnol. Oceanogr. 15:131-137.

____________. 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55:605-614.

Ewing, M. S. and T. C. Dorris. 1970. Algal community structure in artificial ponds subjected to continuous organic enrichment. Am. Mid. Natur. 83:565-582.

Galbraith, M. G. 1967. Size selective predation of *Daphnia* by rainbow trout and yellow perch. Trans. Am. Fish. Soc. 96:1-10.

Gerking, S. D. 1962. Production and food utilization in a population of bluegill sunfish. Ecol. Mongr. 32:31-78.

Green, J. 1962. Zooplankton of the River Somoto: the Crustacea. Proc. Zool. Soc. Lond. 138:415-453.

________. 1967a. The distribution and variation of *Daphnia lumboltzi* (Crustacea: Cladocera) in relation to fish predation in Lake Albert, East Africa. J. Zool., Lond. 151:181-197.

________. 1967b. Associations of Rotifera in the zooplankton of the lake sources of the White Nile. J. Zool., Lond. 151:343-378.

________. 1971. Association of Cladocera in the zooplankton of the lake sources of the White Nile. J. Zool., Lond. 165:373-414.

Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 14:301-303.

Hargrove, B. T., and G. H. Green. 1970. Effects of copepod grazing on two natural populations. J. Fish Res. Bd. Can. 27:1395-1403.

Hutchinson, G. E. 1967. A Treatice on Limnology, Vol. 2. Wiley.

Koshsiek, K. A., J. A. Wilhm, and Morrison. 1971. Species diversity of net zooplankton and the physiochemical conditions in Keystone Reservoir, Oklahoma. Ecology 52:1119-1125.

LaBarbera, Michael C., and Peter Kilham. 1974. The chemical ecology of copepod distribution in the lakes of East and Central Africa. Limnol. Oceanogr. 19:459-466.

Paine, R. T. 1969. The Pisaster-Tegula interaction: prey patches, predator food preference, and intertidal community structure. Ecology 50:950-961.

Patrick, R., et al. 1966. The Catherwood Foundation Peruvian Amazon Expedition: Limnological and Systematics Studies. Mono. Acad. Nat. Sci. Phila. 118:109-407.

Patten, B. C. 1962. Species diversity in net phytoplankton of Raritan Bay. J. Mar. Res. 20:57-75.

Pennak, R. C. 1955. Species composition of limnetic zooplankton communities. Limnol. Oceanogr. 2:222-232.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. J. Theoret. Biol. 13:131-144.

Prather, J. E., and C. E. Prophet. 1969. Zooplankton species diversity in John Redmond, Marion, and Council Grove Reservoirs, Kansas, summer, 1968. Emporia State Res. Stud. 18:5-16.

Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature (Lond.) 244:179.

Sager, P. E., and A. D. Hasler. 1969. Species diversity in lacustrine phytoplankton: I The components of the index of diversity from Shannon's Formula. Amer. Nat. 103:51-60.

Shannon, C. D., and W. Weaver. 1963. The Mathematical Theory of Communication. Univ. Illinois Press, Urbana.

Sprules, W. G. 1972. Effects of size selective predation and food competition on high altitude zooplankton populations. Ecology 53:375-386.

Tramer, E. T. 1969. Components of Shannon's Formula. Ecology 50: 927-929.

Weiss, C. M. 1971. Water Quality Investigations, Guatemala. Lake Atitlan 1968-1970. Mimeo. U. N. Carolina Environ. Sci. Engin. Publ. 274.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15:556-565.

Wilhm, J. L. 1970. Range of diversity index in benthic macroinvertebrate populations. J. Water Pollut. Contr. Fed. 42:221-224.

___________. 1972. Graphical and mathematical analysis of biotic communities in polluted streams. Ann. Rev. Entomol. 17:223-252.

Wright, J. C. 1965. The population dynamics and production of Daphnia in Canyon Ferry Reservoir, Montana. Limnol. Oceanogr. 10:583-590.

Zaret, T. M. 1969. Predation balanced polymorphism in Ceriodaphnia cornuta Sars. Limnol. Oceanogr. 14:301-303.

___________. 1972a. Predators, invisible prey, and the nature of polymorphism in the Cladocera (Class Crustacea). Limnol. Oceanogr. 17:171-184.

___________. 1972b. Predator-prey interaction in a tropical lacustrine ecosystem. Ecology 53:248-257.

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