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# FURTHER STUDIES ON THE BENTHIC ECOLOGY OF SUGARLOAF LAKE, WASHTENAW COUNTY, MICHIGAN

By

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#### INTRODUCTION

Although numerous studies of lake macrobenthos have been made, relatively few (e.g., Eggleton, 1952; Tebo, 1955; Clampitt, et al., 1960; Ball, 1948; Buscemi, 1961) have dealt with the littoral zone. Investigation of this zone has lagged, perhaps because it is so rich in species and lacks the uniformity of the profundal region. Hence, intensive sampling is required for statistical reliability. Investigation is often tedious because identification of many forms to species is either impossible or impractical.

The benthic fauna of the littoral zone of Sugarloaf Lake has been under study for several years by the Institute for Fisheries Research, Michigan Department of Conservation. Seasonal changes in benthos at three stations were recorded by Anderson and Hooper (1956) who also made an estimate of annual production of the midge Tanytarsus jucundus.

Suspecting that considerable variability may exist among seemingly homogeneous areas of the lake, a more intensive survey was conducted (Beatty and Hooper, 1958). Samples of soil,vegetation, and benthos were taken at 22 stations which were located by superimposing a grid over a map of the lake. Distribution of benthic forms was, indeed, not uniform.

The object of this study is to determine the qualitative and quantitative differences between Synoptic Survey I taken on November 23-24, 1955 (Beatty and Hooper, 1958) and Synoptic Survey II taken on January 4, 1958. It was felt that such a comparison would lead to a better appraisal of the magnitude of yearly fluctuations of the benthic population of a shallow eutrophic lake as well as provide further information on variation in distribution of the benthos in seemingly homogeneous substrates.

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## GENERAL DESCRIPTION OF THE LAKE

Physical, chemical, and biotic features of Sugarloaf Lake have been described in several previous publications (Cooper, 1953; Hooper, 1956; Anderson and Hooper, 1956; Beatty and Hooper, 1958) and will only be summarized here.

Sugarloaf Lake, located in the northwestern corner of Washtenaw County, Michigan, is glacial in origin. It has a maximum depth of 18 feet although approximately 87 percent of the total surface area (180 acres) is less than 5 feet deep (Fig. 1). The water is hard; the methyl orange alkalinity varies seasonally from 127 to 171 ppm (Anderson and Hooper, 1956).

The chemical composition of the soil is remarkably uniform over the lake basin (Beatty and Hooper, 1958). <u>Chara predominates</u> in shallow water and <u>Potamogeton</u> in the deeper central depression (Fig. 1). <u>Najas</u> is present in scattered areas. Casual inspection of the vegetation in 1963 did not suggest that it had changed significantly between 1955 and 1963.

Unpublished data in the files of the Institute for Fisheries Research indicate that a winterkill occurs occasionally in Sugarloaf Lake. Further, the lake may thermally stratify during the summer with a thermocline at a depth of about 16 feet and complete oxygen depletion at 18 feet. Since the greatest depth sampled in this study

Figure 1. --Abundance and composition of submerged vegetation in samples taken at 21 stations in Sugarloaf Lake on November 22, 1955. Mean dry weight of plant samples collected at each station is proportional to radius of circle; standard error of the mean is represented by a line indicating increase or decrease in length of the radius. (After Beatty and Hooper, 1958)

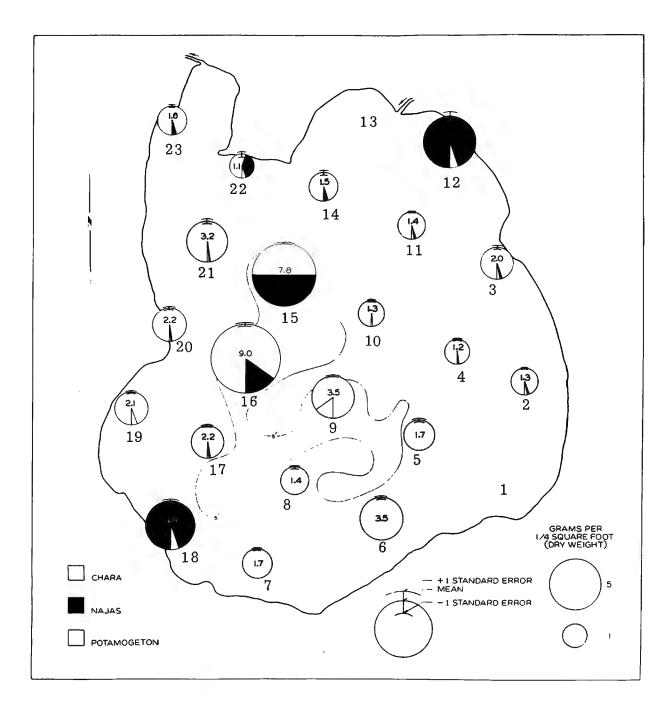


Figure 1

was only seven feet, temperature and oxygen are probably unimportant as ecological differences among the stations.

#### METHODS

Reference is to be made to the publication of Beatty and Hooper (1958) which is the foundation for this study. The original data of the 1955 synoptic survey (Synoptic I) has been made available to me by these authors for comparison with the 1958 survey (Synoptic II). Insofar as possible, the methods that I employed are copied after theirs; where I have departed it is so stated.

#### Sampling Stations and Methods

Those stations sampled in Synoptic I were revisited in Synoptic II with the addition of station 13, which had been located but not sampled. Thus a total of 23 stations were sampled (Fig. 1).

At the time of the 1958 survey the lake was covered with ice. A maximum of four bottom samples were taken at randomly selected points within a circle with a radius of 10 feet from the station locus with a modified Ekman dredge (Anderson and Hooper, 1956). Animals were preserved, picked from the debris, and identified. Since a large number of organisms were to be classifed, only the most abundant or characteristic groups were identified to lower taxons. Estimates of benthic biomass were based on one sample per station in Synoptic I and four samples per station in Synoptic II.

## **Correction Factors**

In Synoptic II biomass was measured by weighing each sample on an analytical balance after it had been centrifuged briefly to remove excess preservative. By weighing and by measuring the volume of the animals in 30 samples, an empirical factor of 1.12 was determined for converting weight to volume in terms of ml. Following the reasoning of Ball (1948), preserved volume, as determined by water displacement, is considered equal to live weight in grams.

Since Synoptic I was taken on November 23 and 24 while Synoptic II was conducted on January 4, it was necessary to correct for growth and mortality occurring during this interval before the synoptics could be compared. From reported seasonal changes in biomass and numbers (Anderson and Hooper, 1956) and additional unpublished data from three other years, an average increase in biomass of 2.2 percent occurs during this interval due to growth whereas a 1.6 percent decrease in numbers occurs because of mortality.

## Statistics

Availability of an IBM 7090 computer has made it practical to make full use of statistical tools in data analysis. Counts of organisms were transformed to  $\log_{10}(x + 1)$  prior to those analyses given in Tables 3, 5, and 7.

Each of 149 dredge samples were considered an observation in computing correlation coefficients among taxons. In the 2- and 3-way analyses of variance, data from only 13 stations (5, 7, 9, 11, 14 through 22) were used (Model I). Only these stations were replicated four times in both surveys. Rejection level was the standard 5 percent unless otherwise specified.

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#### RESULTS

The Biomass, its Changes and Ecology

The mean benthic biomass of Synoptic I corrected to January 4 was 0.58 ml per one-quarter square foot with 95 percent confidence limits of  $\pm$  0.14 ml. The weighted mean biomass of Synoptic II was 0.48  $\pm$  0.16 ml per one-quarter square foot. Although it appears that benthic biomass of the first year exceeds that of the second, this difference is not statistically significant.

Stations highest in biomass in 1955 were generally also highest in 1958. This was confirmed by a significant correlation of 0.75 (P<.01). On the basis of data from these two years it appears that the relative productivity (as reflected by the standing crop) of various areas of the lake is fixed.

A one-way analysis of variance indicated that differences among the 23 stations of Synoptic II were significant at the 1 percent level. Ecological explanations for these differences were sought using Scheffe's procedure as outlined by Brownlee (1960, p. 252) The following comparisons were made: stations greater than five feet deep (9, 15, 16) versus stations less than five feet deep (4 through 8, 10 through 12, 14, 17 through 23); stations in shallow water where Najas predominates (12, 18) versus those where Chara predominates

(4 through 8, 10, 11, 14, 17, 19 through 21). No statistically significant differences could be found for these comparisons.

After pooling data by stations from both years, however, a correlation of 0.78 (P<.01) was found between benthic biomass and standing crop of vegetation as measured in 1955. That is, those areas with the greatest crop of vegetation tended to have the largest standing crop of benthos. Eggleton (1952) found a similar relationship between numbers of invertebrates and standing crop of plants in Douglas Lake. These observations are readily explainable since luxurient vegetation provides more food, shelter, and living space.

#### Estimates of Standing Crop

Estimates of the benthic standing crop present in November, 1955, and January, 1957, have been made (Table 1). The estimate entitled, Mean at January 1 (Table 1), is the best average estimate of benthic standing crop present on that date.

## Qualitative Changes in Benthic Fauna

Stictochironomus sp. was the only species reported in Synoptic I not found in Synoptic II. Whether the species has disappeared from the lake or simply was not recognized cannot be stated with certainty.

Several new species were first identified in the 1957 samples. Spaniotoma spp., with an average abundance of 3.6 per one-quarter

Table 1. --Estimates and 95 percent confidence limits of benthic

Sample	Entire lake (pounds)	Pounds per acre	Kilograms per hectare		
Synoptic I	40,067 ± 9,671	223 ± 54	$250 \pm 60$		
Synoptic I corrected to Jan. 1	40,948 ± 9,884	228 ± 55	256 ± 61, 1		
Synoptic II	33, 201 ± 11, 260	184 ± 63	203 ± 61		
♥ Mean at Jan. 1	37,075 ± 10,572	<b>2</b> 06 ± 59	<b>22</b> 9 ± 61		

standing crop

 $\Psi$  Mean of Synoptics I and II after correction to January 1.

square foot, were the most numerous of the faunal additions. Other new species occurred infrequently. A revised faunal list of Sugarloaf benthos is given in Table 2.

## Quantitative Changes in Benthic Fauna

A three-way analysis of variance indicated significant differences in total numbers of organisms among years, stations, and species (Table 3). Interaction between years and stations indicated that if stations were to be ranked by total numbers of organisms, the ranking of one year is different from that of the other. Similarly, interaction of species and years indicated that the relative abundance ranking of species and species groups is different between the years. Interaction between species and stations means that the relative abundance ranking of species is different from station to station. Finally, the interaction of all three variables contributes still another significant source of variation.

Changes in the abundance and distribution of the various faunal elements have caused the differences just noted. Referring to Table 4, we see that approximately one third of the species increased in abundance, another third decreased, and the last third changed little or not at all.

Two-way analyses of variance on 13 stations indicated significant yearly increases in abundance for the following organisms

Table 2. -- A revised species list of Sugarloaf Lake benthos. Original table from Anderson and Hooper (1956) with additions from Synoptic I (\*) and Synoptic II (\*\*).

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Turbellaria*	Callibaetis sp.	
Nematomorpha	Siphlonurus sp.	
Gordius sp. **	Heptageniidae Stenonema tripunctatum (Banks)**	
Oligochaeta Lumbriculidae Tubificidae	Odonata Libellulidae	
Hirudinea	<u>Tetragoneuria</u> sp. Coenagrionidae	
Ostracoda	Enallagma sp.	<u>بر</u>
Amphipoda	Trichoptera	14
Hyalella azteca (Saussure)	Phryganeidae	
	Phryganea sp. **	
Decapoda	Banksiola selina (Betten)	
Orconectes rusticus (Girard)	Hydroptilidae	
Orconectes propinquus (Girard)**	Oxyethira sp.	
Hydracarina	Leptoceridae	. • . •
•	Oecetis sp.	
Ephemeroptera	Leptocella sp.	
Ephem <b>eridae</b>	Psychomyiidae	
Hexagenia sp.	Polycentropus interruptus*	
Baetidae	Psychomyiidae sp. A.*	
Ephemerella sp. Caenis sp.	Lepidoptera Pyralididae	
	Nymphula sp. **	

Coleoptera Cryptochironomus digitatus Dytiscidae (Malloch) Dytiscus sp. \*\* Tendipes (Limnochironomus) Chrysomelidae fumidus (Johannsen) Donacia sp. \*\* Tendipes (Limnochironomus) Tlmidae\*\* nervosus (Staeger) Tendipes (Kiefferulus) Diptera tendipediformis (Goetghebuer)\* Culicidae Tendipes (Tendipes) spp. Chaoborus punctipennis (Say) Harnischia (Harnischia) Tendipedidae (= Chironomidae) tenuicaudata (Malloch) Pelopiinae (= Tanypodinae) Heleidae (= Ceratopogonidae) Pentaneura flavescens\* Tabanidae Pentaneura monilis (Linnaeus)\* Tabanus sp. \*\* Procladius spp. Rhagionidae Clinotanypus sp. Atherix sp. \*\* Hydrobaeninae (= Orthœladiinae) Spaniotoma spp. \*\* Gastropoda\*\* Tendipedinae (= Chironominae) Pelecypoda Calopsecra gregarius (Kieffer) Sphaeriidae Lauterborniella sp. Sphaerium sp.\* Microtendipes pedellus (De Geer) Polypedilum (Polypedilum) nubeculosus (Meigen) Polypedilum (Polypedilum) sp. Tanytarsus (Endochironomus) nigricans (Johannsen) Tanytarsus (Tribelos) jucundus (Walker) Tanytarsus (Stictochironomus) sp. Glyptotendipes lobiferus (Say)\*\* Pseudochironomus sp.\*

Table 3 A three-way analysis of va	riance (years, stations, species
abundance) of data from 13 stations.	All F ratios are significant at

Source of variation	df	Mean square	F ratio
Years	1	3.95	66.4
Stations	12	1.60	26.8
Species abundance	29	18.03	303.1
Years $\times$ Stations	12	0.49	8.2
Years $\times$ Species	29	1.25	21.0
Stations $\times$ Species	348	0.59	10.0
Years $\times$ Stations $\times$ Species	348	0.21	3.6
Within	2, 340	0.06	• • •
Total	3, 119	• • •	• • •

the 0.01 probability level. Data transformed to  $\log_{10}(x + 1)$ .

Organisms	Survey I Mean number per one- quarter square foot	Survey II Mean number per one- quarter square foot	11/1
Ephemerella sp.	0.1	0.7	7
Glyptotendipes lobiferus	2.7	14.1	5.2
Oligochaeta	0.8	2.1	2.6
Polycentropus interruptus	1.2	3.0	2.5
Leptoceridae	1.2	2.6	2.2
Pentaneura spp.	1.0	1.8	1.8
Tendipes spp.	5.8	10.0	1.7
Turbellaria	0.6	1.0	1.6
Pseudochironomus sp.	2.7	4.2	1.5
Hydracarina	0.9	1.3	1.4
Calopsectrini	5.2	6.9	1.3
Heleidae	6.8	7.2	1.1
Clinotanypus sp.	1.5	1.6	1.1
Microtendipes pedellus	5.1	5.2	1.0
Orconectes propinguus	0.2	0.2	1.0
Zygoptera	1.3	1.2	0.9
Tendipes (Limnochironomus) spp.	17.2	16.2	0.9
Anisoptera	1.1	1.0	0.9
Hirudinea	1.1	0.9	0.8
Procladius sp.	11.8	9.9	0.8
Polypedilium spp.	30.5	25.4	0.8
Hyallela azteca	108	86	0.8
Hexagenia sp.	1.4	0.9	0.6
Trichoptera	14.2	7.6	0.5
Cryptochironomus digitatus	1.1	0.5	0.5
Chaoborus punctipennis	4.0	1.9	0.5
Tanytarsus jucundus	11.5	3.6	0.3
Caenis sp.	26.5	5.0	9.2
Psychomyiidae sp. A	11.8	1.5	0.1
<u>Stictochironomus</u> sp.	1.0	0	0

Table 4. --Comparison of average numerical abundance of major species in Synoptic Surveys I and II (based on all samples) (Table 5): Ephemerella sp., Glyptotendipes lobiferus, Oligochaeta, Polycentropus interruptus, and Tendipes spp. Significant yearly decreases in abundance occurred for Stictochironomus sp., Caenis sp., Psychomyiidae sp. A, Tanytarsus jucundus, Chaoborus punctipennis, Hyallela azteca, and Hirudinea. Changes in abundance of Caenis, Psychomyiidae sp. A, Tanytarsus, and Ephemerella were most striking. The large apparent increase in Glyptotendipes lobiferus was due mainly to a single sample containing a concentration of this species.

On the basis of these limited data we may hypothesize that the faunal components may be classified into two groups. One group contains kinds which were not shown to change significantly in abundance. These may tend to have more stable populations perhaps reflecting a steady-state equilibrium condition. The second group contains kinds found to fluctuate significantly. These may tend to have less stable populations. Possible explanations for instability include "recent" entry and colonization in the lake or verging or achieved extinction from it. Of course, large population fluctuations may also reflect intrinsic instability in the population ecology.

There are two examples, already mentioned, which suggest that colonization may have been occurring for one and that extinction may have occurred for the other. <u>Spaniotoma</u> spp. was found in quantity at the time of Synoptic II but was unreported from Synoptic I. Stictochironomus sp., uncommon in I, was not identified from II.

#### Distribution of Benthos

The numerical abundance of all species except <u>Sticto-</u> <u>chironomus sp., Cryptochironomus digitatus, Orconectes propinquus,</u> and Leptoceridae varies significantly from station to station (Table 5). As will be shown later, all of the above except the Leptoceridae are randomly distributed. The Leptoceridae, however, were concentrated at station 12 which was not included in the analysis of variance.

The distribution of species may be described by another method outlined by Andrewartha and Birch (1954) and applied by Lambou (1962). The method has been used in the quadrat type of ecological sampling which is analagous to the sampling procedure used here. If an organism is randomly distributed over an area its distribution will be Poisson. If the statistic  $\frac{\sum (x - \overline{x})^2}{\overline{x} (n - 1)}$  is significantly less than one, the organism is distributed more evenly than random, i.e., uniformly. If, however, this statistic is significantly greater than one, distribution is patchy and the species is said to be contagiously distributed. For a small number of samples significance is given by:

$$\frac{\Sigma (\mathbf{x} - \overline{\mathbf{x}})^2}{\overline{\mathbf{x}}}$$

If the mean is less than the variance this statistic indicates contagiousness (at 5 percent level of significance) when it exceeds the tabular value of Chi square at a probability of 0.05. If the mean is greater than the variance this statistic indicates significant uniformity (5 percent level)

Table 5. --F ratios from a two-way analysis of variance (years, stations) of each species or species group at 13 stations.

Data transformed to  $\log_{10}(x + 1)$ 

	Source of variation									
Organisms	Between	Between	Inter-							
	years	stations	action							
Ephemerella sp.	4.22*	14.12**	18.85**							
Glyptotendipes lobiferus	206.08**	87.89**	89. <b>23*</b> *							
Oligochaeta	21.05**	3.48**	1.82							
Polycentropus interruptus	39.23**	6.83**	4.28**							
Leptoceridae	3.18	0.97	3.61**							
Pentaneura spp.	1.36	9.74**	3.19**							
Tendipes spp.	15.39**	24.93**	5.54**							
Turbellaria	0.05	2.51**	2.41*							
Pseudochironomus sp.	3.66	6.45**	1.06							
Hydracarina	0.18	2.05**	1.61							
Calopsectrini	1.87	3.41**	2.87**							
Heleidae	0.08	5.27**	1.05							
Clinotanypus sp.	0.12	18.05**	2.63*							
Microtendipes pedellus	31.53**	7.43**	1.53							
Orconectes propinguus	2.89	0.84	0.84							
Zygoptera	0.32	2.97**	1.61							
Tendipes (Limnochironomus) spp.	0.08	14.74**	4.30**							
Hirudinea	5.22*	7.55**	1.44							
Anisoptera	2.08	1.98*	1.44							
Procladius sp.	0.89	19.17**	2.09*							
Polypedilum spp.	0.32	14.88**	2.24*							
Hyallela azteca	8.76**	24.73 * *	1.59							
Hexagenia sp.	0.13	13.14**	0.46							
Trichoptera	60.96**	17.15**	5.41**							
Cryptochironomus digitatus	3.57	2.42	1.27							
Chaoborus punctipennis	10.54**	26.17**	1.66							
Tanytarsus jucundus	8.64**	8.90**	2.93**							
Caenis sp.	98.22**	11.28**	9.90**							
Psychomyiidae sp. A	310.61**	16.93**	12.96**							
Stictochironomus sp.	37.18**	1.52	1.52							

\* significant at 0.05 level

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significant at 0.01 level

provided that it is less than the tabular value of Chi square at a probability of 0.95. Distribution of each species during each survey has been tested (Table 6) with 21 df for Synoptic I and 22 df for Synoptic II.

The overwhelming majority of species are contagiously distributed (Table 6). None of the four species which were uniformly distributed were so in both surveys (Table 6). Hence uniform distribution is probably not characteristic of these species. <u>Orconectes</u> propinquus, Anisoptera, Zygoptera, <u>Cryptochironomus digitatus</u>, Turbellaria, <u>Ephemerella</u> sp., <u>Oxyethira</u> sp., and Sphaeriidae tend to be more or less randomly distributed on the basis of this test. Oligochaeta, Hirudinea, and Hydracarina are nearly random. All of these are less common kinds of organisms.

It should be noted that the foregoing test does not take into account spatial relations or habitat differences of the stations. Thus <u>Orconectes propinquus</u>, although randomly scattered, was not taken at stations greater than five feet deep. Further, if the test had been applied differently, it would have been obvious that Oligochaeta have a maximum abundance at certain sites (Table 8).

Differences in the distribution of each kind of organism between years is indicated by the interaction term of Table 5. About half the species show significant changes at the 13 stations. Certain conclusions are implied.

Organisms	Synop- tic	$\frac{\Sigma (x-\overline{x})^2}{\overline{x} (n-1)}$	$\frac{\Sigma (\mathbf{x} - \overline{\mathbf{x}})^2}{\overline{\mathbf{x}}}$	Level of signifi- cance	Distribution
Orconectes propinguus	I II*	0.8 0.4	22.7 9.2	0.05	Random Uniform
Hirudinea	I II	0.5 1.6	10.3 34.6	0.05 0.05	Uniform
Hyallela azteca	I II	35 32	736 693	0.001 0.001	•••
Heleidae	I II	4.9 3.3	102 73	0.001 0.001	•••
Caenis sp.	I II	48 13	1,000 274	0.001 0.001	•••
Chaoborus punctipennis	I II	23 17.4	486 382	0.001 0.001	• • •
Anisoptera	I II	0.6 0.7	11.8 15.3	•••	Random Random
Zygoptera	I II	1.6 1.4	32.9 31.4	0.05	Random
Clinotanypus sp.	I II	3.2 2.1	67 47	0.001 0.001	
Procladius sp.	I II	$\begin{array}{c} 4.3 \\ 2.1 \end{array}$	90 <b>4</b> 6	0.001 0.01	•••
Tanytarsus jucundus	I II	78 20	1,638 450	0.00 <b>1</b> 0.001	• • •

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 Table 6. --A statistical test for significant deviation from random distribution. Distribution is

 contagious unless specified.

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(continued)

Organisms	Synop- tic	$\frac{\Sigma(x-\overline{x})^2}{\overline{x}(n-1)}$	$\frac{\Sigma (x-\overline{x})^2}{x}$	Level of signifi- cance	Distribution	
Pentaneura spp.	I II	26.1 1.1	548 25	0.001	Random	
Calopsectrini	I II	3.7 24	77 531	$0.001 \\ 0.001$	• • •	
Microtendipes pedellus	I II	2.9 26	62 564	0.001 0.001	•••	
Polypedilum spp.	I II	26 15	553 330	0.001 0.001	•••	
Cryptochironomus digitatus	I II	1.6	33.3 14	•••	Random Random	
Pseudochironomus sp.	I II	7.6 9.4	160 206	0.001 0.001	•••	
Tendipes spp.	I II	30 37	460 807	0.001 0.001		
<u> Tendipes</u> (Limnochironomus)sp	p. I II	17.2 5.9	360 131	$0.001 \\ 0.001$	• • •	
Glyptotendipes lobiferus	I II	26.7 133.3	560 2,933	$0.001 \\ 0.001$		
Polycentropus interruptus	I II	1.9 $21.3$	39 47	$\begin{array}{c} 0.01 \\ 0.01 \end{array}$	•••	
Psychomyiidae sp. A	I II	10.8 1.3	228 28	0.001	Random	
Leptoceridae	I II	6.2 25.5	131 560	$0.001 \\ 0.001$	•••	

Table 6. -- continued

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(continued)

Table	6.	conclude	đ
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:- <del>x</del> ) <sup>2</sup> n-1)	$\frac{\sum (x-\overline{x})^2}{\overline{x}}$	Level of signifi- cance	Distribution
1.3 2.7	<b>27.</b> 8 59	0.001	Random
1.1 2.1	22.9 47	0.01	Random
0.7 1.5	15.4 33.3	• • •	Random Random
8.8 3.7	184 81	$0.001 \\ 0.001$	•••
0.9 0.9	18.5 20.5	•••	Random Random
0.5 0.7	11 155	0.05	Uniform Random
 8.4	 184	0.001	•••
0.4 0.6	9.3 13	0.05	Uniform Random
	0.6	0.6 13	0.6 13

\* Very few organisms sampled

Considering those species and species groups which are not randomly distributed (Table 3) and which have no interaction (Table 5), certain of the 13 sites tend to have greater numbers of individuals. Hence these sites may be particularly suitable assuming the species have adequate chance for dispersal. Organisms which had the same distribution on the basis of 13 stations in both years are <u>Hyallela</u> <u>azteca</u> (Fig. 2), Heleidae (Fig. 3), <u>Hexagenia</u> sp. (Fig. 4), <u>Pseudochironomus</u> sp. (Fig. 5), and <u>Chaoborus punctipennis</u> (Fig. 6). All are larvae of insects except the amphipod <u>Hyallela</u>. Cther insect larvae which have, by inspection, similar distribution both years are <u>Tendipes</u> spp. (Fig. 7), <u>Clinotanypus</u> sp. (Fig. 8), <u>Glyptotendipes</u> <u>lobiferus</u> (Fig. 9), <u>Tanytarsus jucundus</u> (Fig. 10), <u>Pentaneura</u> spp. (Fig. 11), and Leptoceridae (mostly Leptocella albida) (Fig. 12).

Organisms which show significant differences in distribution probably do not have strong station preferences; that is, relative abundance is not entirely related to site. Examples are <u>Polypedilum</u> spp. (Fig. 13), Psychomyiidae sp. A (Fig. 14), <u>Procladius</u> sp. (Fig. 15), <u>Caenis</u> sp. (Fig. 16), and <u>Polycentropus interruptus</u> (Fig. 17). All are immature insects.

The distributions of <u>Microtendipes pedellus</u> (Fig. 18) and <u>Spaniotoma</u> spp. (Fig. 19) are particularly interesting. In Synoptic I <u>Microtendipes</u> appeared to be concentrated in a northeast-southwest band which passed through the central portion of the lake. In Synoptic

II it appeared to be concentrated along the northeast shore. <u>Spaniotoma</u> is distributed as if there was a center of dispersal at the southwest corner of the lake.

## Species Associations

Although the substrate of Sugarloaf Lake is quite homogeneous compared to many other lakes of glacial origin, certain differences in the flora and fauna do exist among areas of the lake. In the benthic fauna such differences are chiefly quantitative. Indeed, each species was found to occur with each of the others at one or more stations. Nevertheless, associations between vegetation and invertebrates and among the benthic species were found by Beatty and Hooper (1958) and will be elaborated upon here following the addition of data from Synoptic II.

Correlation coefficients were used to measure association (i.e., the extent to which species have like distributions) among benthic species. Data from 149 samples taken in both years at all stations were used.

The statistically significant correlation coefficients are given in Table 7. Attempts at arranging these into a model which would precisely represent all of the relationships were unsuccessful. The adequacy of even a multi-dimensional model seems questionable.

Table 7. --Significant (P less than 0.05) correlation coefficients between benthic species or species groups. Data transformed to  $\log_{10}(x + 1)$ 

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	genia	a sp.																									
. 50			ironor	nus sn																							
. 46	, 32		notany																								
	. 26	_	Pol			DD.																	•				
••	. 25		, 38		_					•																	
	••	. 29		, 37		allela	azteca																				
	••		. 64	. 32	. 48	B Pro	ocladi	- 18 sp.																			
			. 27		. 35	. 25	Tar	ytarsı	ıs juc	undus																	
••	••			••	. 18			Gly			-	rus															
••	••	••	. 28	. 19	. 35	. 25	. 20	. 25	Tu	rbella	ria																
••	. 21	••		••	-, 25	·	21	••		Oli	gochae	eta															
••	••	••	••	.16	••		. 21	••	۰.		Cry	ptoch	ironom	us dig	itatus												
••	17	••	••	.16	. 42	:	. 22	••		35	. 27	Psy	chomy	iidae :	sp. A												
••	••	••	. 21	••	••	••	••	. 21	. 23	• ••	••	25	Poly	centr	opus i	nterru	ptus										
••	••	••	••	••	••	••	••	••	••	••	••	16	. 24	Orc	onecte	s pro	pinquu	s									
••	••	••	••	••	••	. 16	••	••	••	••	••	••	. 16	••	Eph	emere	lla sp										
•••	••	••	••	••	••	••	••	••	••		24	••	••	••	••	Lep	tocella	sp.									
23	•••	25	••	••	••	••	••	••	. 22			••	. 24		. 19	. 20	Hyd	racari	na								
••	. 26	••	••	••	••	••	18		••	29	••	. 22	••	••	••	. 25	. 24	Caer	nis sp.								
••	••	•••	••	••	••	••	••	16	••	••	••	••	• •	••	••		. 24	. 34	Zyg	optera							
17		28		••	••	••	••	••	•••	••	••	••	••	••	••	. 34	••	. 47	. 31	Hiru							
••	. 25	10	. 23	••	••	••		••	. 26	••	••	••	••	••	, 32	••	, 36	••	••		Calo						
44	•••	29	••	••	••	••	17	••	. 21	••	••	••		••	•••	••	. 25	. 31			. 28		-				
		33	••	••	 16	••		••		••	••	. 20	. 28	••	. 24	••	. 31		. 20	. 24		. 24	Tend	lipes (	Limn	ochir	conomus) spp.
			43				- 33	••	••	••			.18		. 18	. 35	. 34	. 28	. 16	, 49	. 30	••	. 30				pedellus
			27			23		••	••	••	 19	21	••	••	••	. 23	. 35	•••	. 18		. 22	, 25	. 37				spp.
			42					•••	20			••	••	••	••	. 20	.19	. 18	••	. 31	••	. 23	. 39	. 35	. 58		ntanura spp.
			20							 20	••	•••	- 17	••	••	••	••	••	••	••	••	. 20	. 27	. 21	. 47	. 27	
		••				••	••	••	••	-, 20	••	. 30	-, 17	••	••	••	••	. 20	••	••	••	••	••	••	•••	. 23	3 . 29 Stictochironomus

By arranging the order of species so as to group those correlated to the same species, what is felt as the best possible representation was achieved (Table 7). On this basis the species fall either into one of two major associations (upper left or lower right of Table 7), or into a heterogeneous group (Table 7; center) which do not fit well into the others. Obviously the placing of exact boundary lines around these associations could only be done subjectively. It should be kept in mind that some entries in Table 7, as <u>Tendipes</u> (<u>Limnochironomus</u>) spp. and Calopsectrini, represent more than one species and are of uncertain value.

The correlation coefficients measure similarity of distribution but do not indicate the site or the nature of the habitat where species occur together. For these purposes Table 8 has been constructed. Table 8 contains the average number of individuals of each species taken during both surveys at each station. The arrangement of species and stations was made in the following way. Three distinct habitats were recognized on the basis of vegetative differences (see Fig. 1) and stations were arranged accordingly. One habitat, within the 5-foot contour, was characterized by an abundance of <u>Potamogeton</u>. Two shallow-water stations with luxurient growth of <u>Najas</u> comprised the second habitat and the shallow-water stations dominated by <u>Qhara</u> formed the third. The foregoing <u>Chara</u> stations were further arranged geographically. Thus stations along the west shore, to the lee of prevailing westerly winds,

Table 8.--Plant-animal associations of Sugarloaf Lake. Numbers given are the average number of organisms per one-quarter square foot based on a maximum of eight samples taken during Synoptic Surveys I and II. [tr = less than 0.5]

										Pr	edomi	nant ve	getat	ion						_		
	Chara (shallow water)															Najas		Potamogeton				
	Windwardstations						Leeward stations										(shallow water)		(d	(deep water)		
	23	22	21	20	19	14	17	11	10	3	4	5	2	1	6	8	7	12	18	9	15	16
Chara Associations																						
Heleidae	23	3	14	11	13	18	7	8	8	5	• 6	5	5	3	10	7	5	2	9	6	3	7
Polypedilum spp.	48	9	31	36	75	36	58	28	26	17	40	29	51	36	31	16	45	67	24	7	4	8
Procladius sp.	16	- 4	8	12	14	16	18	23	12	10	14	16	14	12	8	22	19	11	11	12	2	6
Psychomylidae sp. A	tr	12	17	3	15	16	21	5	9	5	9	14	4	1	6	10	9	1	1	1	3	10
Hynliela azteca	128	5	127	112	223	121	162	108	161	112	104	140	97	78	113	198	199	38	58	13	23	51
Cryptochironomus digitatus	tr	1	1	1	1	3	1	1	2	1	3	1	1	1	2	1	1	••	tr	1		
Turbellaria	1	1	1	1	2	1	1	2	2	tr		2			1	2	3		1	1	1	
Orconectes propinquus	1		1		1	tr	tr	1				tr		tr	tr	••		tr			•••	
Sphaeridae	1		1	1	tr	1	tr	1		1	1		1	1					tr		tr	
Pseudochironomus sp.	5	13	2	6	13	2	2	1	L.	tr	1	1	2	1	16	2	3	tr	2	3	1	4
llexagenia sp.	10	8	2	3	1	1	tr	tr	tr	1	tr	tr		1	tr		1					
Clinotanypus sp.	6	2	6	7	3	1	3	1	3	1	2	1	1	tr	1	1	1		•••		••	1
Tanytarsus jucundus	2	1	3	2	tr	8	3	6	33	6	87	4	27	20	8	8	2		··		1	3
Glyptotendipes lobiferus	•••			tr			1	106	25	1	34	18	6	5		1			tr	••		••
Najas - Polamogeton Associations																						
Zygoptera	2	tr	2	2	1	3	1	1	1	••	1	2	tr	tr		1	3	1	5	3	1	2
llydracarina	1	••	1	tr	2	2	1	2	1	tr	tr	1	1	1	1	1	3	5	2	1	2	1
Hirudinea	••	••	1	••	1	1	1	tr	1	ı	tr	1	1	1	••	2	1	3	2	1	1	1
Leptoceridae	1	1	1	1	1	1	1	1	3	tr	1	••	1	••	1	1	1	26	2	tr	1	1
Oligochaeta	2	2	1	1	1	2	1	2	1	1	1	2	1	1	2	1	3	1	6	6	tr	1
Tendipes spp.	1		1	1	1	1	1	4	tr	1	1	7	3	1		1	9	52	10	9	43	36
<u>Microtendipes</u> pedellus	1	tr	2	1	3	6	1	8	- 4	11	3	3	15	6	5	5	5	44	7	4	10	10
Pentanura spp.	2	tr		1	· 2	2	2	3	2	1	1	2	2	1	1	4	3	4	3	з	7	9
Chaoborus punctipennis	••			tr		1	1	2	1	tr	1	1	1		•••	4	tr	1	3	35	12	5
Anisoptera	2	1	1	1	2	2	1	1	1	tr	•••	1	1	1	1	tr	2	1	2	2	3	3
Stenonema tripunctatum	••	••	••	••	••	••	••	••	••	••	••	••			••		••	••	••	1	1	1
<u>Tendipes</u> (Limnochironomus) spp.	8	2	16	4	20	43	25	30	14	7	7	15	6	2	24	32	21	12	12	30	33	21
Polycentropus interruptus	5	••	2	2	3	3	1	4	3	2	2	2	5	3	tr	8	5	4	1	tr	3	2
Calopsectrini	2	2	3	2	5	2	3	10	3	tr	3	5	1	1	28	6	11	6	4	4	10	6
Caenis sp.	30	2	9	71	20	23	6	20	1	2	3	3	4	1	14	10	8	74	23	6	15	13
Oxyethira sp.	- •		1	tr	tr	1		tr	tr	, 1	••	••	tr	tr		1	1	1	1	1	1	1
Ephemerella sp.	2	1		tr	1	1	1				tr	1		tr	1		tr	1	1	1	••	1

are grouped together. Likewise stations on the east, or leeward, side are grouped. Finally, by inspection, the habitat of maximum abundance of each species was determined, species of similar distribution grouped, and associations blocked out. Several species which did not show a convincing preference for any of these major habitat types were placed at the bottom of Table 8.

Differences among associations are chiefly quantitative. However, <u>Tanytarsus jucundus</u>, <u>Orconectes propinquus</u>, <u>Hexagenia</u> sp., <u>Clinotanypus</u> sp., and <u>Glyptotendipes lobiferus</u> are the most useful qualitative indicators of the Chara association.

Within the <u>Chara</u> association two minor associations may be recognized: (1) <u>Pseudochironomus</u> sp., <u>Hexagenia</u> sp., and <u>Clinotanypus</u> sp., which occurred together along the west shore; and (2) <u>Tanytarsus</u> jucundus and <u>Glyptotendipes</u> lobiferus, with a high coincidence at stations on the east half of the lake. Since the prevailing wind is from the west, these patterns suggest that wind currents may be an important factor in the distribution of these species and in the formation of these associations.

Faunas of the <u>Najas</u> and <u>Potamogeton</u> associations were similar, with several species tending to occur rather abundantly in both. Hydracarina, Hirudinea, and Leptoceridae were most indicative of the <u>Najas</u> association whereas <u>Chaoborus punctipennis</u>, <u>Stenoner</u> a tripunctatum, and Anisoptera seemed more characteristic of the

<u>Potamogeton</u> complex. The species of the genus <u>Tendipes</u> characteristic of the <u>Najas</u> stations are probably of the subgenus <u>Kiefferulus</u> (small forms) whereas a large species of the subgenus <u>Tendipes</u> marked the deep-water stations.

The major and minor associations just described are confirmed, with minor exceptions, by the correlation coefficients of Table 7 and are similar to those described by Beatty and Hooper (1958) based only on data from Synoptic I.

## DISCUSSION

Despite its shallowness, Sugarloaf Lake has relatively low benthic productivity, typical of marlish lakes. Comparison with but a few other lakes indicated that Sugarloaf is similar in standing crop to the northern Wisconsin lakes (Weber, Nebish) studied by Juday (1942) but is well below productive southern Wisconsin waters like Lake Mendota.

The dynamic nature of yearly changes in benthic biomass and species abundance have been reported by others. Rawson (1930) mentions that Lundbeck was unable to explain a doubling of benthos in the Ploner See in the mid-1920's, and also that Alm observed a 100 percent decrease in total bottom fauna in a Swedish lake during the late 1910's. Richardson (1921) and Eggleton (1934) have also noted qualitative and quantitative changes.

Causes for such fluctuation remain to be demonstrated. Population dynamics of those insects which have both aquatic and terrestrial phases in their life histories are particularly difficult to study and subject to influences from both environments. Greater population fluctuations seem likely than in kinds confined to one environment. Borutzky's (1939) study on <u>Corethra</u> is unique in this area.

Closely related to the problem of population fluctuations is that of species distribution. Narrow habitat requirements have been reported repeatedly for certain species of bottom organisms whereas others are known to be quite ubiquitous. There is, however, clear evidence from the Sugarloaf studies that habitat preference or habitat suitability is not an entirely satisfactory explanation for the distributional patterns of some species. Such patterns for Microtendipes pedellus and Spaniotoma spp. (Figs. 18 and 19), in particular, suggest that some consideration other than habitat is involved. Since these midges have winged adult stages, wind may concentrate mating swarms in rather arbitrary areas. If the eggs and larvae are ecologically tolerant and survive, the irregular distribution patterns evident for these and other species might result from this cause. Additional evidence implicating wind as a determinant in distribution comes from the geographic locations of the two minor Chara associations discussed earlier. On the one hand, Tanytarsus and Glyptotendipes were concentrated both years on the leeward side of Sugarloaf Lake suggesting either that this area was particularly suitable or that wind had concentrated mating adults or that water currents had concentrated eggs in this location. Hexagenia, Pseudochironomus, and Clinotanypus, on the other hand, may have tended to seek shelter from the wind along the western shore during mating activities resulting in the observed abundance of their larvae there. Wind may also indirectly influence distribution of benthos by slightly modifying the sediments.

Other factors which may be important in the distribution of benthos are differences in egg or larval mortality between areas of the lake basin, species interaction, larval and adult behavior, and lake currents. The problem cannot be solved until more is known of the total biology of each species and of the effects of the various habitat forces.

Population fluctuations and variations in horizontal distribution of species necessitates an intensive and statistically sound sampling procedure. Sampling of but a few sites can give erroneous conclusions. An example is provided by <u>Microtendipes</u> which, on the basis of 13 stations, was less abundant (significant at 1 percent) in Synoptic II than in Synoptic I (Table 5). On the basis of 22 stations, however, there was virtually no difference between years (Table 4).

Difficulties of benthic sampling are compounded by the fact that most animals are contagiously distributed. Indeed, contagiousness, although somewhat dependent on sample size, is typical of animal populations in general (Andrewartha and Birch, 1954). However, contagiousness for some benthic species is probably only an expression of the fact that eggs are laid in masses.

The tendency to clump is reflected in sampling and introduces problems in data analysis. As Cole (1949) pointed out, organisms are rarely normally distributed and parametric statistical procedures cannot be properly applied. Cole's criticism was leveled in particular at the use of correlation as a means of measuring species association.

He proposed a nonparametric test which takes into account only presence or absence and thus does not use data on relative abundance. In Sugarloaf Lake, however, where most kinds of animals are present at each station, association will not be detected by the method of Cole with nearly the efficiency of correlation analysis. For example, the highest correlation found, r = 0.64, was between <u>Polypedilum</u> spp. and <u>Procladius</u> sp. Since both were present at every station, Cole's test could not have been applied. Although Cole's criticism of the use of correlation is valid, his test is not an adequate measure of association in all instances.

A third method of measuring degree of association, widely used in plant ecology (see Benninghoff and Cramer, in press), was applied in Table 8. Drawbacks to this graphical method are several. First, there is a danger of bias in arranging the table and delimiting associations. Secondly, the method is limited to two dimensions. Finally, there is no formal statistical test for significance.

In conclusion, no method satisfactory in every respect has been found for the measurement of species association. Provided distribution of data is reasonably normal, correlation seems to have the greatest potential utility.

## SUMMARY

1. By means of synoptic sampling at 23 uniformly spaced stations certain differences in the kinds, abundance, and distribution of benthic organisms in Sugarloaf Lake between two years (Synoptic I, 1955-6 and Synoptic II, 1957-8) have been detected.

2. Biomass did not differ significantly between the two years even though organisms were numerically less abundant in Synoptic II.

3. Biomass differed between stations and was positively correlated with the density of the standing crop of vegetation.

4. Stations which were high in biomass one year were also high the second.

5. The numbers and relative abundance of various species varied from station to station and between years.

6. About equal numbers of kinds of organisms were more abundant, less abundant, and about equally abundant in Synoptic II as compared to Synoptic I.

7. The distributional patterns of certain faunal elements changed appreciably whereas those of others remained essentially the same.

8. Certain data suggest that wind is a factor in the distribution of certain species of bottom organisms.

9. Most of the benthic species were contagiously distributed.

10. Certain species associations have been determined by means of correlation and graphical analyses.

11. A revised species list of Sugarloaf benthos has been presented.

12. The best estimate of average benthic standing crop in Sugarloaf Lake as of January 1 for the 2 years is  $206 \pm 59$  pounds per acre. This value is low, but is comparable to those for certain northern Wisconsin lakes.

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Figure 2. -- Average number of <u>Hyalella azteca</u> per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake. Figure 3. -- Average number of Heleidae per onequarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

Figure 4. --Average number of <u>Hexagenia</u> sp. per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake. Figure 5. -- Average number of <u>Pseudochironomus</u> sp. per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

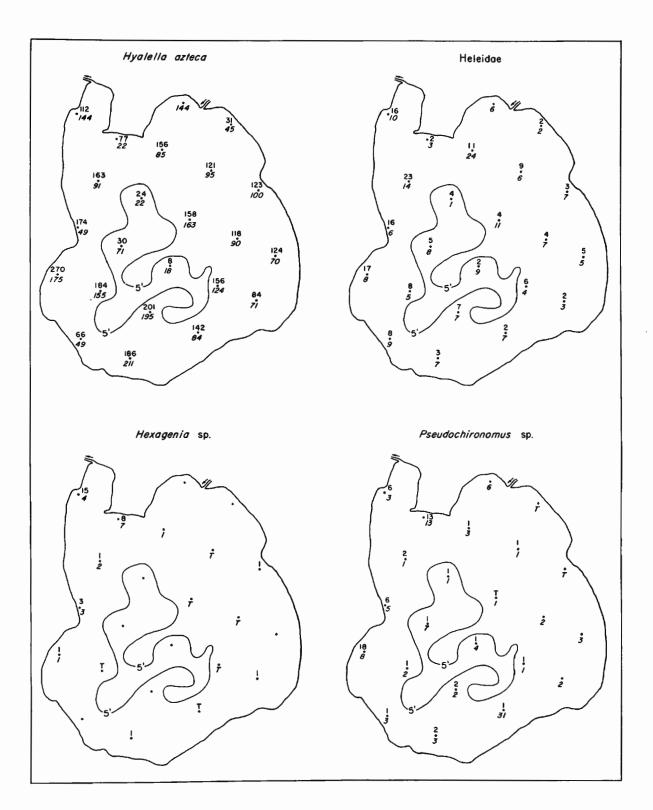


Figure 6. -- Average number of <u>Chaoborus punctipennis</u> per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake. Figure 7. -- Average number of <u>Tendipes</u> spp. per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

Figure 8. --Average number of <u>Clinotanypus</u> sp. per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake. Figure 9. -- Average number of <u>Glyptotendipes</u> <u>lobiferus</u> per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

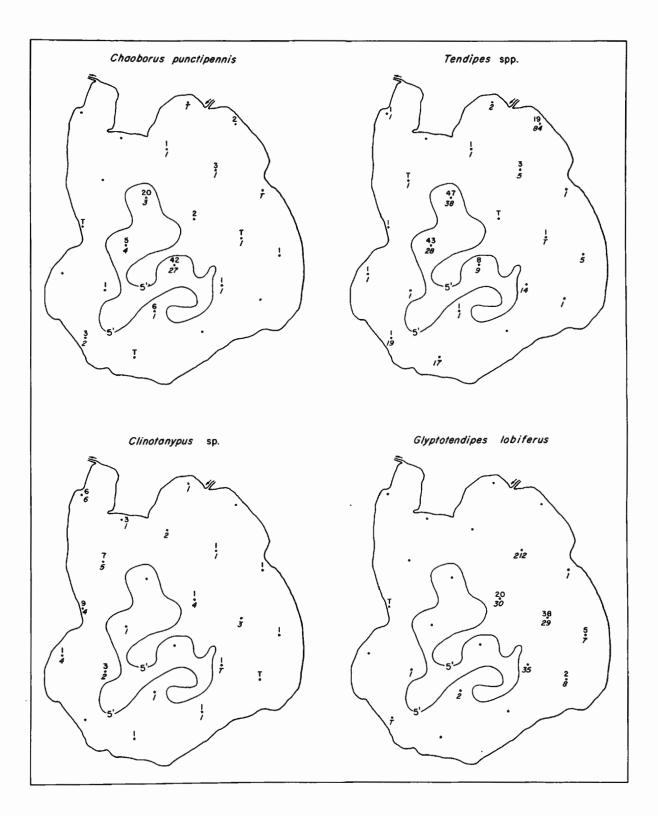
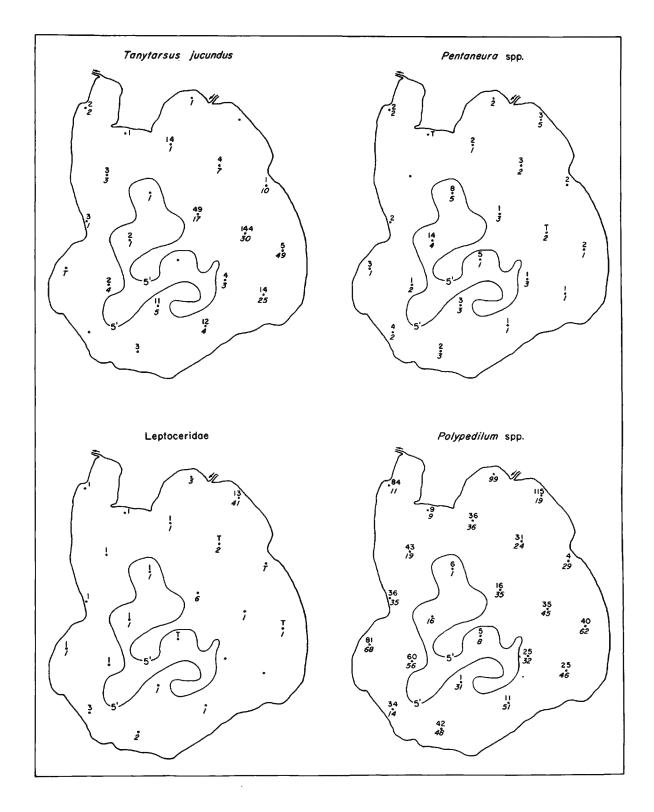


Figure 10--Average number of <u>Tanytarsus jucundus</u> per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake. Figure 11. --Average number of <u>Pentaneura</u> spp. per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

Figure 12. -- Average number of Leptoceridae per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake. Figure 13. --Average number of <u>Polypedilum</u> spp. per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.



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Figure 14. --Average number of Psychomyiidae sp. A per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

Figure 15. -- Average number of <u>Procladius</u> sp. per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

Figure 16. -- Average number of Caenis sp. per onequarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake. Figure 17. -- Average number of <u>Polycentropus inter-</u> <u>ruptus</u> per one-quarter square foot fluring Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

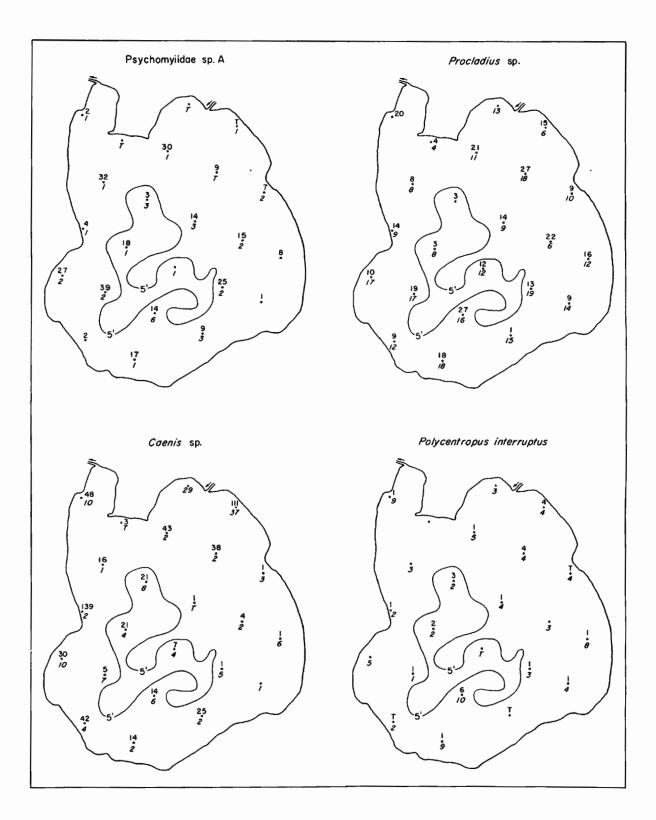
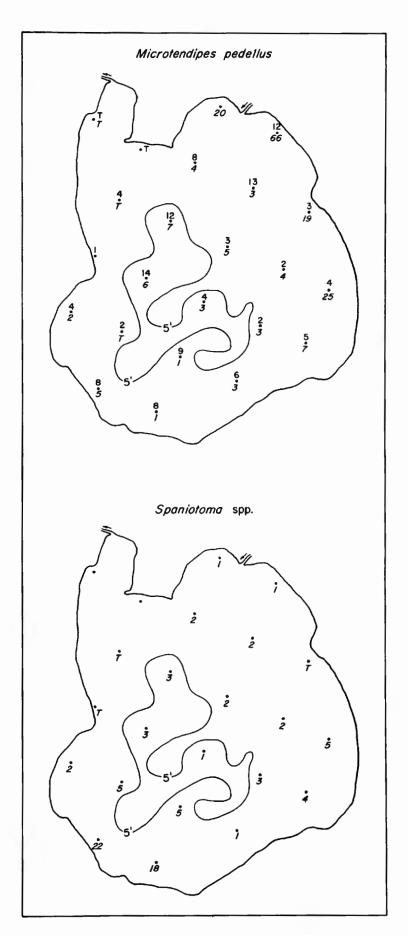


Figure 18. -- Average number of <u>Microtendipes pedellus</u> per one-quarter aquare foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.

Figure 19. -- Average number

of <u>Spaniotoma</u> spp. per one-quarter square foot during Synoptic I (Roman type) and Synoptic II (Italics) in Sugarloaf Lake.



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