A COMPARATIVE STUDY OF LAKE MICHIGAN MACROBENTHOS[1]

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ABSTRACT
A 1964 study of Lake Michigan benthos was conducted to compare with the results of studies made by Eggleton in 1931 and 1932. The dominant organisms, the amphipod *Pontoporeia affinis*, oligochaetes, and sphaeriids, were the same in the two studies. In both cases there was a concentration of *Pontoporeia* at approximately 40 m and indication of another at approximately 100 m. Neither our data nor Eggleton's show significant differences in abundance of *Pontoporeia* or oligochaetes between May, June, and July. There were 1.5 times more *Pontoporeia*, 2.6 times more oligochaetes, and 4.3 times more sphaeriids, all significant differences, in 1964. At matched pairs of stations from the two studies, there were significantly more *Pontoporeia* and oligochaetes in 1964, but this was not true for sphaeriids.

INTRODUCTION

With increasing age, most lakes naturally undergo a gradual eutrophication with a concomitant increase in productivity. In large lakes this is a slow process, but it can be accelerated by pollution. An objective of a study of Lake Michigan, recently initiated by the Great Lakes Research Division, is a study of the eutrophication of the lake and the effect on this process of the concentrated human activities that occupy much of the shore.

Beeton (1965) concluded that man's activities have accelerated the eutrophication of all the St. Lawrence Great Lakes (except Superior) in the past 50 to 60 years. In Lake Michigan, he found progressive increases in the concentrations of various major ions, total dissolved solids, and some changes in the plankton. He did not, however, report any evidence of changes in the benthos. Wright (1955) and Carr and Hiltunen (1965) have suggested that changes in the benthos in Lake Erie indicate the adverse effects of pollution. The purpose of the present study was to ascertain if notable changes that might provide additional evidence of accelerated eutrophication have occurred in the benthic community of Lake Michigan.

Eggleton (1936, 1937) and Merna (1960) analyzed large numbers of Lake Michigan benthos samples collected in 1931–1932 and 1951–1955, respectively. Their studies provide the only significant data with which present-day observations can be compared. As Eggleton's samples were collected many years before Merna's, they would be expected to reveal much more clearly any changes that have occurred. For this reason, the present study has been designed so that comparisons can be made between Eggleton's results and ours. Merna's results, unfortunately, cannot usually be included in these comparisons because of substantial differences in methods and techniques.

Eggleton's samples were collected with the Petersen dredge, an instrument that has since been shown to be inefficient in the quantitative measurement of Great Lakes benthos (Beeton, Carr, and Hiltunen 1965). However, to obtain data directly comparable with his, we used the same instrument. Relative changes in the benthos could then be studied, although absolute values might be in doubt.

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METHODS

Samples were taken in triplicate at stations on five cross-lake transects and at two

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TABLE 1. *Location of benthos stations in Lake Michigan*

Station	Location	
	N lat	W long
A-1	42°06′30″	86°32′00″
A-2	42°06′00″	86°37′00″
A-3	42°05′30″	86°43′00″
A-4	42°03′30″	87°06′30″
A-5	41°57′00″	87°18′30″
A-6	41°52′00″	87°27′00″
B-1	42°24′00″	86°20′30″
B-2	42°24′00″	86°27′00″
B-3	42°24′00″	86°35′30″
B-4	42°23′30″	87°01′30″
B-5	42°22′30″	87°21′00″
B-6	42°22′30″	87°30′00″
B-7	42°22′00″	87°40′00″
B-8	42°22′00″	87°47′30″
C-1	42°49′40″	86°14′50″
C-2	42°49′40″	86°18′25″
C-3	42°49′10″	86°28′25″
C-4	42°48′50″	86°41′30″
C-5	42°49′00″	86°50′00″
C-6	42°47′40″	87°26′50″
C-7	42°47′30″	87°34′30″
C-8	42°47′00″	87°42′45″
C′-1	43°08′00″	86°23′00″
C′-2	43°12′00″	86°31′00″
D-1	43°57′00″	86°33′00″
D-2	43°56′00″	86°39′30″
D-3	43°54′00″	86°51′30″
D-4	43°48′00″	87°03′00″
D-5	43°38′40″	87°31′00″
D-6	43°44′00″	87°38′00″
E-1	44°37′30″	86°18′12″
E-2	44°37′00″	86°21′42″
E-3	44°34′00″	86°40′00″
E-4	44°30′18″	86°55′18″
E-5	44°25′30″	87°10′18″
E-6	44°27′48″	87°26′25″

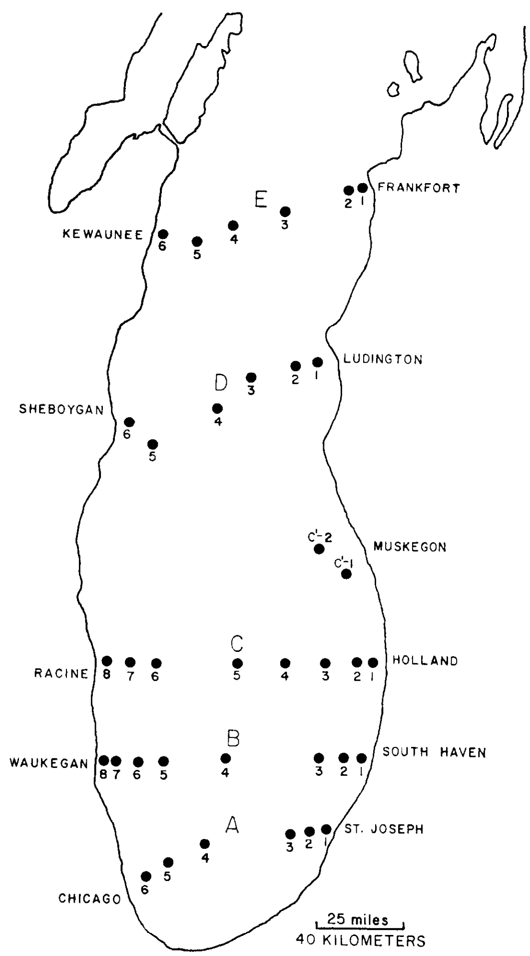

FIG. 1. Index map of Lake Michigan benthos stations sampled in 1964.

additional stations off Muskegon, Michigan (Fig. 1, Table 1). Transects A and B and the first five stations on transect C were sampled once each in April, May, June, and July 1964; the other stations were sampled once each in the latter three months. Some, but not all, of our stations were near one or more of Eggleton's stations. His 1931 samples were taken in the southern two-thirds of the lake, while his 1932 samples were from the northern third, including many from Green Bay. Because our sampling was limited to the southern two-thirds of the lake, the comparisons in this paper, unless otherwise stated, are restricted to the 1931 data.

The samples were washed from the dredge into washtubs and then into the elutriating device described by Powers and Robertson (1965). This device used a 0.5-mm mesh screen sleeve to separate the animals from most of the sediment. The samples were preserved with buffered formalin. In the laboratory, the various types of macroscopic animals were sorted on a white background and counted.

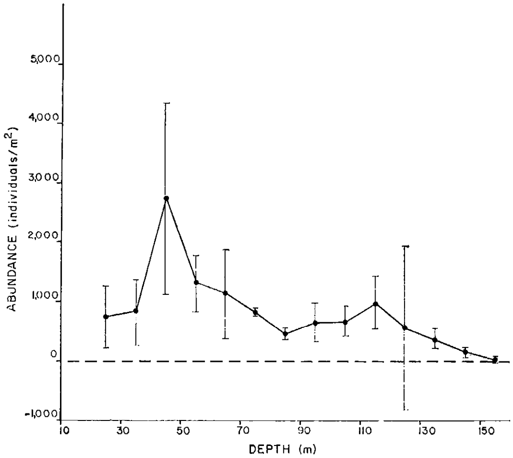

FIG. 2. The mean abundance of *Pontoporeia* in Lake Michigan in a series of 10-m depth ranges in 1931–1932 with 95% confidence limits. The dashed line represents zero abundance.

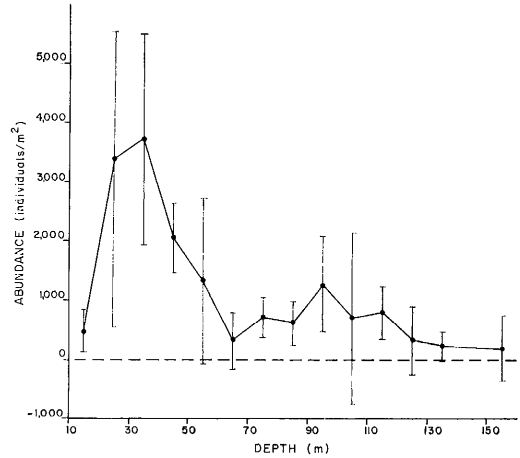

FIG. 3. The mean abundance of *Pontoporeia* in Lake Michigan in a series of 10-m depth ranges in 1964 with 95% confidence limits. The dashed line represents zero abundance.

The sampling methods were generally similar to those used by Eggleton. The dredges, so far as can be determined, were identical. Eggleton's samples were poured into a tub in which they were mixed by hand and then into a cloth net with a fine-mesh, grit-gauze filtering surface. He did not specify the exact mesh size of this gauze; however, he leaves little doubt that this procedure retained almost all the macroscopic organisms. Our method also seemed to retain almost all of these organisms, so it is believed that the two methods are comparable.

In the laboratory, Eggleton visually selected the larger animals and then systematically examined the remaining material with a binocular microscope, a procedure more thorough than ours because we made no microscopic examination. However, for the organisms of major interest, that is, the amphipod *Pontoporeia affinis* (Lindström), oligochaetes, and sphaeriids, our method seemed to recover almost all of the individuals in the sample, and it is considered directly comparable to Eggleton's method for these organisms.

In several cases the names Eggleton used and those we use, for what appear to be the same taxon, are different. The only oligochaetes Eggleton reported were listed as Tubificidae; it is assumed that this includes the same animals as our category oligochaetes. He listed two genera of sphaeriids, *Pisidium* and *Sphaerium*, but reported the latter to be rare. It is assumed that his category *Pisidium* is almost the same quantitatively as our grouping sphaeriids. He used the designation *Pontoporeia hoyi* Smith for animals that we have reported as *P. affinis* following the revision of this genus by Segerstråle (1937).

QUALITATIVE ASPECTS

Eggleton (1937) stated that the benthos is dominated, in order of decreasing abundance, by *Pontoporeia*, Tubificidae, and Sphaeriidae. Merna (1960) finds these groups to be very abundant, with *Pontoporeia* predominant. We found the benthos to be dominated by the same three groups. Our over-all results, however, show oligochaetes to be more abundant than *Pontoporeia.* This arises largely from very high numbers of oligochaetes at several shallow stations in the southern end of the lake. Because these stations are shallower than any sampled by Eggleton in this part of the lake, the order of abundance has also been determined excluding these stations.

TABLE 2. *Monthly mean densities of* Pontoporeia *and oligochaetes in Lake Michigan in 1964 and Friedman* χ_r^2 *values to test whether there are significant monthly differences in density*

Organism	Number per square meter				Friedman χ_r^2	df	Probability
	Apr	May	June	July			
Means based on data from stations that were sampled in all four months							
Pontoporeia	1,089	815	1,222	1,149	3.8	3	$< 0.3, > 0.2$
Oligochaetes	1,559	1,416	1,519	1,380	2.0	3	$< 0.7, > 0.5$
Means based on data from stations that were sampled in May, June, and July							
Pontoporeia		869	1,097	1,140	2.7	2	$< 0.3, > 0.2$
Oligochaetes		1,411	1,176	1,123	0.3	2	$< 0.9, > 0.8$

When this is done the order is the same as that found by Eggleton.

Our study indicates that gastropods, platyhelminths, trichopterans, and isopods can be added to Eggleton's list (1936) of benthic forms present in Lake Michigan, and Merna (1960) reported these forms as well as specimens of Odonata and Ephemeroptera. Few specimens of the new forms were collected. In general, the kinds and relative importance of the different organisms were the same in 1964 as in 1931.

DEPTH DISTRIBUTION

Eggleton (1937) arranged his data in a continuous series of 10-m depth ranges. He plotted the mean densities for both total benthos and *Pontoporeia* in each range against the midpoint of that range. The two plots have approximately the same shape because *Pontoporeia* constituted 65% of the total benthos. His data for *Pontoporeia* have been replotted (Fig. 2) and 95% confidence limits added for each mean density value. The depth distributions were about the same in the two years Eggleton sampled; therefore, to define more accurately the limits, this plot is of the combined data from the two years. Our data for *Pontoporeia* have been treated in the same way (Fig. 3). The confidence limits were calculated using the method given by Moroney (1956).

Eggleton found that there were two concentration zones: the first at approximately 40 m and a second, less pronounced, at approximately 115 m. Merna (1960) found neither of these zones but observed a decline in numbers from approximately 27 m to approximately 73 m and below that approximately constant values. However, as his first point is near the peak of the first zone and his points are 18 m or more apart, his plot would probably not show these zones even if they were present.

The presence of the deep concentration zone does not agree with other work on Lake Michigan benthos. Powers and Robertson (1965), sampling with a Smith-McIntyre dredge, found a peak in the dry weight of benthos at around 40 m but no indication of a deeper concentration zone. Counts of *Pontoporeia* obtained from the same samples by us, when plotted against depth, likewise showed only the shallower concentration zone. Beeton et al. (1965), from their comparison of dredge sampling efficiencies, concluded that the concentration zones shown by the Petersen dredge samples are questionable.

Our data distinctly show the shallow zone, but the situation is less clear with regard to the second zone. There is some indication of a peak at approximately 100 m with the mean density in the 90–99-m depth range almost twice that of the value on either side. However, this is not a significant difference, because the confidence limits of the 90–99-m mean greatly overlap those of the means on either side. The confidence limits for Eggleton's data indicate that his second peak is not significant either. Yet the fact that both studies show a peak at approximately 100 m makes it difficult to dismiss completely the possibility of the existence of this zone. There are indications

TABLE 3. *The density (no/m²) of the major benthic organisms at a series of stations in Lake Michigan in 1964*

Depth (m)	Station	Date	*Pontoporeia*	Oligochaetes	Sphaeriid	Depth (m)	Station	Date	*Pontoporeia*	Oligochaetes	Sphaeriid
10	B-8	18 May	225	12,270	1,365	72	A-3	24 April	637	505	30
13	B-8	11 July	30	5,270	2,060	72	A-4	25 April	930	398	112
14	B-8	17 June	65	5,875	1,700	72	A-3	22 July	825	635	70
15	A-6	19 June	0	80	0	74	B-3	23 April	128	248	8
17	A-6	25 April	120	832	712	74	C-3	15 May	795	75	45
17	A-1	18 June	30	200	26	74	A-4	19 June	755	185	10
17	C-1	17 June	1,640	68	180	74	A-4	22 July	790	130	0
17	C-8	17 June	75	53	8	77	C-3	17 June	1,795	465	80
18	A-1	25 April	105	322	0	79	C-3	8 July	465	495	60
18	A-1	20 May	36	375	30	81	B-6	18 May	355	175	30
18	A-1	22 July	260	240	30	81	B-3	14 July	110	145	0
18	A-6	22 July	105	8,040	0	82	D-2	14 May	965	790	40
18	C-1	8 July	2,175	175	55	83	C-3	19 April	1,312	240	0
19	B-1	24 April	682	4,770	233	83	B-3	18 May	173	413	8
19	A-6	20 May	405	150	26	85	B-6	11 July	765	113	0
19	B-1	18 June	1,550	11,680	2,150	86	B-6	23 April	368	135	15
19	B-1	14 July	510	80	60	86	B-6	17 June	955	225	40
20	C-1	15 May	5,775	360	165	90	C′-2	16 July	2,305	1,190	0
21	C-1	19 April	7,350	5,655	1,395	91	C-4	15 May	180	75	0
22	C-8	16 May	480	960	0	93	C-6	17 June	1,530	120	10
23	B-1	19 May	1,575	12,480	690	95	C-6	15 May	300	90	0
23	C-8	11 July	90	30	0	95	D-2	11 June	1,995	700	70
27	D-1	14 May	2,801	1,020	390	96	C-4	17 June	1,928	68	0
29	D-1	15 July	3,205	1,275	465	99	C-6	10 July	735	550	10
30	D-1	11 June	2,350	1,075	40	103	B-5	23 April	300	158	0
30	D-6	15 July	1,900	835	720	104	D-2	15 July	2,080	705	0
31	A-2	18 June	3,395	6,370	1,365	106	B-5	18 May	135	105	0
31	A-2	22 July	6,185	9,350	900	108	B-5	14 July	290	160	0
32	A-2	25 April	2,580	7,148	285	113	D-5	14 May	638	645	0
33	A-2	20 May	1,305	5,925	120	113	B-5	17 June	570	245	0
35	E-6	15 May	2,895	1,755	1,100	113	D-5	10 June	1,460	335	40
35	D-6	10 June	1,365	1,000	650	117	C-4	10 July	220	290	0
36	C′-1	13 May	8,589	240	30	117	D-4	15 July	995	175	0
36	C′-1	16 July	6,565	2,250	5	119	D-5	15 July	920	290	25
40	A-5	25 April	120	817	712	121	C-4	23 April	240	165	0
40	B-7	11 July	2,520	1,930	555	123	D-4	14 May	590	113	20
41	A-5	20 May	1,140	855	113	126	B-4	23 April	158	113	23
41	E-6	13 June	3,285	1,575	435	133	B-4	18 May	135	165	0
43	B-7	18 May	2,880	2,250	810	133	B-4	14 July	335	95	0
43	A-5	22 July	4,535	1,155	530	137	B-4	17 June	235	200	0
45	B-7	17 June	2,045	1,630	715	147	D-4	11 June	730	110	0
46	E-1	16 May	2,015	1,280	290	150	C-5	17 June	1,410	200	0
46	B-2	18 June	835	970	60	153	E-5	14 July	205	85	0
46	B-2	15 July	1,250	790	0	157	C-5	15 May	293	30	0
46	E-1	14 July	3,700	905	335	162	C-5	20 April	158	60	0
47	B-2	24 April	1,185	1,425	435	162	C-5	10 July	135	120	0
47	B-2	19 May	1,035	1,613	0	165	D-3	15 July	220	100	5
47	E-1	11 June	2,468	1,583	570	170	E-5	16 May	195	110	5
48	C-2	17 June	3,005	2,020	920	170	D-3	11 June	75	60	0
48	C-2	8 July	585	1,440	140	171	D-3	14 May	83	90	0
49	C-7	16 May	2,505	1,253	173	175	E-5	13 June	90	50	10
49	A-5	19 June	1,875	1,240	175	194	E-2	16 May	175	185	5
50	C-2	19 April	2,145	3,510	315	197	E-2	14 July	210	170	0
52	C-2	15 May	180	75	0	198	E-2	13 June	155	115	5
55	C-7	17 June	1,105	0	55	216	E-4	13 June	100	50	0
58	C-7	10 July	1,865	940	155	216	E-4	14 July	65	0	0
63	B-3	18 June	265	450	35	228	E-4	16 May	80	20	0
65	A-3	19 June	530	1,155	115	270	E-3	14 July	25	45	0
68	A-3	20 May	150	1,080	15	271	E-3	13 June	80	40	0
70	A-4	20 May	128	113	0	272	E-3	16 May	110	10	0

TABLE 4. *Comparison in a series of depth ranges of the mean densities of* Pontoporeia, *oligochaetes, and sphaeriids found in the present study (P) with those found by Eggleton (E) (1936, 1937)*

Depth range (m)	Number per square meter					
	Pontoporeia		Oligochaetes		Sphaeriids	
	E	P	E	P	E	P
40–49	1,200	2,230	645	1,406	0	364
50–59	489	1,050	465	338	54	70
60–69	390	315	168	895	35	55
70–79	670	793	0	300	8	38
80–89	328	554	146	310	23	20
90–99	522	1,282	80	399	3	13
100–109	628	835	89	323	0	0
110–119	1,080	801	128	330	8	11
120–129	—	—	—	—	—	—
130–139	353	235	40	153	0	0
140–149	430	730	30	110	0	0
>150	48	206	28	82	0	2
Mean	558	821	165	422	12	52
Ratio of 1961 density to 1931 density	1.5:1.0		2.6:1.0		4.3:1.0	

that, in Lake Michigan, the Petersen dredge is a more efficient sampling device in the relatively hard sediments generally found at about 100 m than it is in the softer ones found above and below this depth. So, the apparent deep concentration zone found in Petersen samples possibly arises from a sampling bias.

SEASONAL DISTRIBUTION

Our sampling included only four months and was inadequate to permit any broad conclusions concerning seasonal distributions. However, the monthly mean densities of *Pontoporeia* and oligochaetes have been calculated (Table 2) for the months available. As the more northerly stations were not sampled in April, two sets of means were calculated for each organism. The first gives the monthly means based on the data from the stations that were sampled in all four months; the second gives means for the latter three months based on data from all the stations. Friedman two-way analysis of variance tests (Siegel 1956) were run on each set of means. No significant differences in densities from month to month were detected at even the 10% level for either organism.

Eggleton did not sample in April 1931, but his monthly mean densities for May, June, and July are similar, with the July values usually the highest of the three. Generally, neither our data nor Eggleton's show a distinct seasonal pattern in abundance for the late spring and early summer.

QUANTITATIVE ASPECTS

The mean densities of *Pontoporeia*, oligochaetes, and sphaeriids were calculated for each series of three replicate samples and converted to number of individuals per square meter of bottom to make them comparable with Eggleton's data (Table 3). The values from May, June, and July were arranged according to depth and means calculated for each 10-m depth range. This was done separately for our data and for Eggleton's (Table 4). Only data from May, June, and July were considered because these were the only months when samples were obtained in both studies. Over-all means were calculated by averaging the means from the 10-m depth ranges. This was done, rather than averaging the separate density values from each sample, because the two studies have different station depth distributions. This, together

TABLE 5. *The density of* Pontoporeia, *oligochaetes, and sphaeriids at matched pairs of stations from Eggleton's (1936, 1937) investigation (E) and the present work (P)*

Eggleton's station	Our station	Month	Number per square meter					
			Pontoporeia		Oligochaetes		Sphaeriids	
			E	P	E	P	E	P
18	B-2	June	250	835	223	970	78	60
18	B-2	July	120	1,250	1,200	790	0	0
14	B-3	May	358	173	35	413	55	8
14	B-3	June	108	265	0	450	8	35
14	B-3	July	340	110	220	145	0	0
13	B-6	May	150	355	33	175	0	0
13	B-6	June	240	955	850	225	0	30
12	B-7	May	910	2,880	130	2,250	30	40
12	B-7	June	960	2,045	130	1,630	35	810
4	C-6	May	55	300	0	90	0	715
21	C-6	June	158	1,530	0	120	0	0
21	C-6	July	190	735	0	550	0	10
22	C′-1	July	1,200	6,565	550	2,250	0	10
8	C′-2	July	2,560	2,305	270	1,190	15	5
20	D-5	June	120	1,460	55	335	0	0
20	D-5	July	590	920	35	290	0	40
32	E-2	July	90	210	70	170	0	25
C	E-3	July	35	25	15	45	0	0

with the strong relationship between density and depth, would introduce a bias if the over-all means were calculated from the separate density values.

Ratios to compare the over-all means for the 1964 data with those for the 1931 data showed a greater density in 1964 of 1.5-fold for *Pontoporeia*, 2.6-fold for oligochaetes, and 4.3-fold for sphaeriids. Wilcoxon matched-pairs signed-ranks tests (Siegel 1956) on the paired means in the same depth range showed that *Pontoporeia* ($T = 10$, $N = 11$), oligochaetes ($T = 4$, $N = 11$), and sphaeriids ($T = 2.5$, $N = 8$) were all significantly more abundant in 1964 at the 5% level.

Eggleton's stations were distributed rather haphazardly while our stations were on regular cross-lake transects and were sampled at approximately regular intervals. Thus, the objection could be raised that differences in station location were the real causes of the observed differences in abundance. This objection is believed to be largely invalid, because both studies obtained fairly thorough coverage of the southern two-thirds of the lake for each of the months considered in the comparisons. This should reduce any bias arising from positional differences to minor significance. In some cases, however, a more direct comparison was possible because some of our stations were near 1931 stations. When samples were taken in the same month at both members of one of these pairs, the data were considered directly comparable (Table 5). Wilcoxon tests on these pairs showed there were significantly more *Pontoporeia* ($T = 19$, $N = 18$) and oligochaetes ($T = 25$, $N = 18$) in 1964 at the 1% level. For the sphaeriids, there was no significant difference even at the 5% level ($T = 20$, $N = 13$).

DISCUSSION

The Lake Michigan benthos was dominated by the same three categories of organisms in 1964 and in 1931. There is little doubt that the two most numerous, *Pontoporeia* and oligochaetes, were more abundant in 1964, and there is good evidence that the sphaeriids also were more abundant in 1964. Only two years have been considered, so no definitive conclusions can be reached concerning long-term trends, because the abundance of benthic animals may vary greatly from year to year even in the absence of such trends. However, the fact that all three dominant categories of organisms showed some indication of increased abundance suggests that the differences may at least partially reflect long-term changes.

Damann (1960) found a trend toward increased numbers of phytoplankton in a small portion of southwestern Lake Michigan. If this applies to the entire lake, it may be at least part of the cause of the increased benthos. Detrital organic material is the principal source of nutrition for deep-water benthos, directly or as a medium for bacteria. The greater the amount of phytoplankton present, the greater the amount of detrital organic matter that would be expected to reach the benthic environment to sustain the higher standing crop of benthos.

Beeton (1961) showed that the benthos of Lake Erie underwent extensive changes between 1929–1930 and 1958, including increases in oligochaetes and sphaeriids. (*Pontoporeia* was not reported.) He suggests that these changes resulted from increased organic content in the sediments, as is suggested here for Lake Michigan.

The changes in the Lake Erie benthos were shown by Beeton to be only part of a long series of changes that occurred in that lake as the result of accelerated eutrophication. Many of the changes had deleterious effects on human utilization of the lake for recreation, fisheries, water supply, and so forth. The changes in the benthos suggested by the present work, along with the previously noted changes in chemistry and plankton, imply that Lake Michigan may be undergoing a similar deterioration. Thus, this lake urgently needs further study to establish definitely how it is changing and the significance of the changes to this important resource.

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