

DIURNAL AND SEASONAL CHANGES IN
THE DISTRIBUTION OF THE LIMNETIC
CRUSTACEA OF LAKE NIPISSING
ONTARIO

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DIURNAL AND SEASONAL CHANGES IN THE DISTRIBUTION OF THE LIMNETIC CRUSTACEA OF LAKE NIPISSING, ONTARIO

ABSTRACT

An investigation of the limnetic crustacea of lake Nipissing was made in 1934 and 1935. The following species were obtained in sufficient abundance to determine their distribution.

Cladocera

Daphnia longispina (Müller)
Holopedium gibberum (Zaddach)

Copepoda

Epischura lacustris (Forbes)
Diaptomus oregonensis (Lilljeborg)
Diaptomus minutus (Lilljeborg)
Limnocalanus macrurus (Sars)
Cyclops group.

The horizontal variation in numbers of each of these groups of organisms was determined. Some, notably *Daphnia* and *Epischura*, were found to be nearly uniformly distributed. Others, the *Diaptomus* and *Cyclops* populations, were definitely "bunched" in that they showed marked variations in abundance laterally. These variations necessitated a modification of the treatment of the discussion of seasonal changes in abundance.

The diurnal changes in vertical distribution during the twenty-four hour cycle were analysed. This was necessary to interpret changes in such distribution resulting from differences in absolute light intensity at the time of sampling on the different dates during the season. The movements resulting in the diurnal differences in distribution were correlated with changes in light intensity. There were also specific differences in response to changing environmental conditions, and the type and extent of the diurnal migration of any one species differed at different periods during the season.

The seasonal changes in the vertical distribution of individual species were analysed and a determination of the factors responsible for those changes was made. Field observations and experimental evidence showed that the factors of light, temperature, oxygen, and carbon dioxide were important in determining these changes in vertical distribution. The reaction of the limnetic crustacea to the above-mentioned factors was modified by age, sex, and specific differences of individuals.

In the case of immature *Diaptomus oregonensis*, individuals were found concentrated near bottom in the deepest water of the lake in June. This concentration moved progressively higher in the hypolimnion, correlated with oxygen depletion and the increased carbon-dioxide content of these strata in July and August. Experimental evidence was obtained indicating the extent of change in the content of each of these gases separately, causing comparable avoidance reactions in populations of *Cyclops* and *Daphnia*.

The seasonal changes in the abundance of the different species of Copepoda indicate that the population undergoes two complete reproductive cycles and the production of a third brood of nauplii between April and mid-September.

INTRODUCTION

The plankton crustacea are in a large measure responsible for the transference to the higher organisms, of the food materials synthesized by phytoplankton. The present investigation in lake Nipissing has been directed towards a clearer understanding of the distribution of these intermediate links in the chain.

The point of attack has been through a quantitative analysis of the distribution of the *individual species* of plankton crustacea wherever practicable. The causal factors determining the abundance at any one place have been sought through an analysis of the environmental factors responsible for diurnal and seasonal changes in distribution.

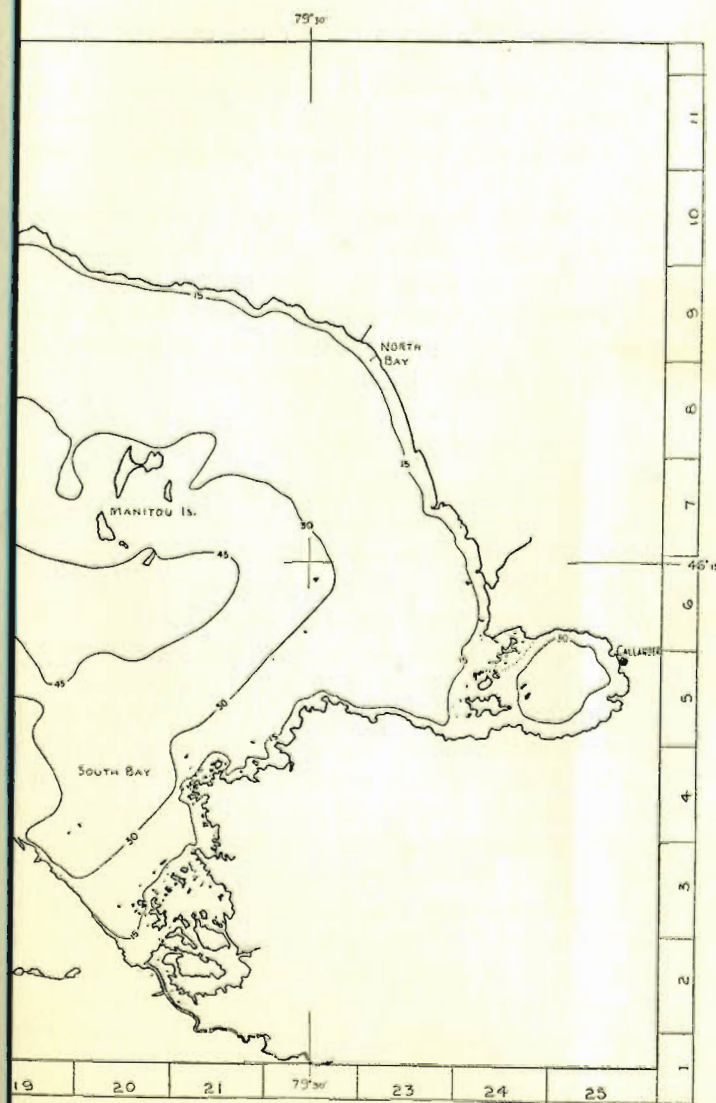
ACKNOWLEDGEMENTS

During the course of the limnological investigation of lake Nipissing carried out during the period from 1928 to 1935 inclusive, by the Ontario Fisheries Research Laboratory, a large body of physical, chemical, and ichthyological data pertinent to the plankton investigation has been obtained. The free use of these data afforded the author, has proved of inestimable value in the advancement of the investigation.

The investigation was made possible by the co-operation of the various members of the Fisheries Laboratory, to whom I take this opportunity of offering thanks. To Professor W. J. K. Harkness, Director of the Laboratory, are due special thanks for his kind assistance and advice, and for his support throughout the period of the investigation.

I wish also to acknowledge the kindness of Drs. Birge and Juday, of the University of Wisconsin, in allowing me the privilege of an extended visit to their limnological laboratory during the summer of 1933. The adoption of methods and technique in use there was a direct result of their generosity in giving of the wealth of their experience.

The physical and chemical data discussed throughout this paper have been taken from the original data obtained by Dr. G. H. W. Lucas and Dr. J. M. B. Corkill, and from Dr.



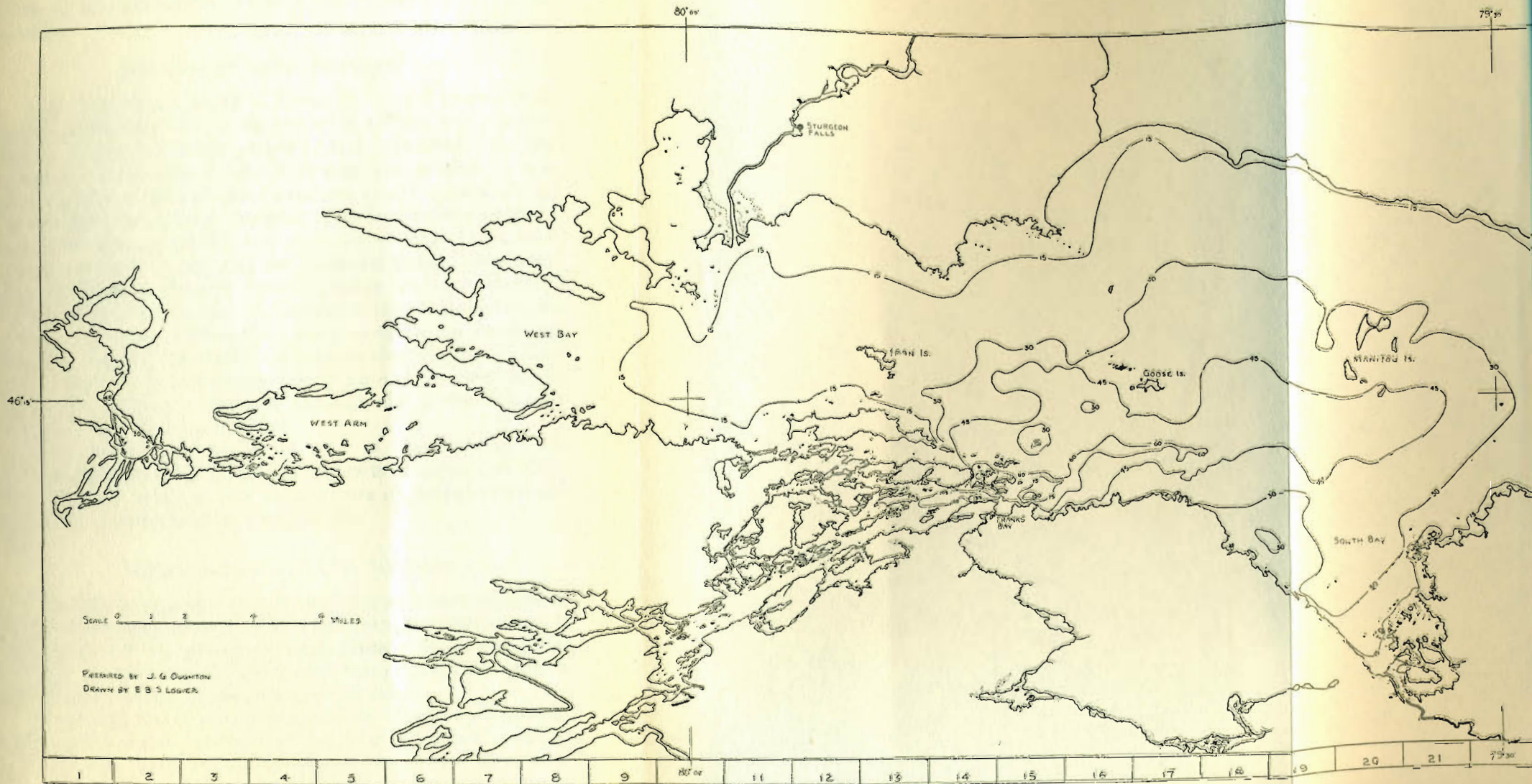


FIGURE 1.—Contour map of lake Nipissing (depth in feet).

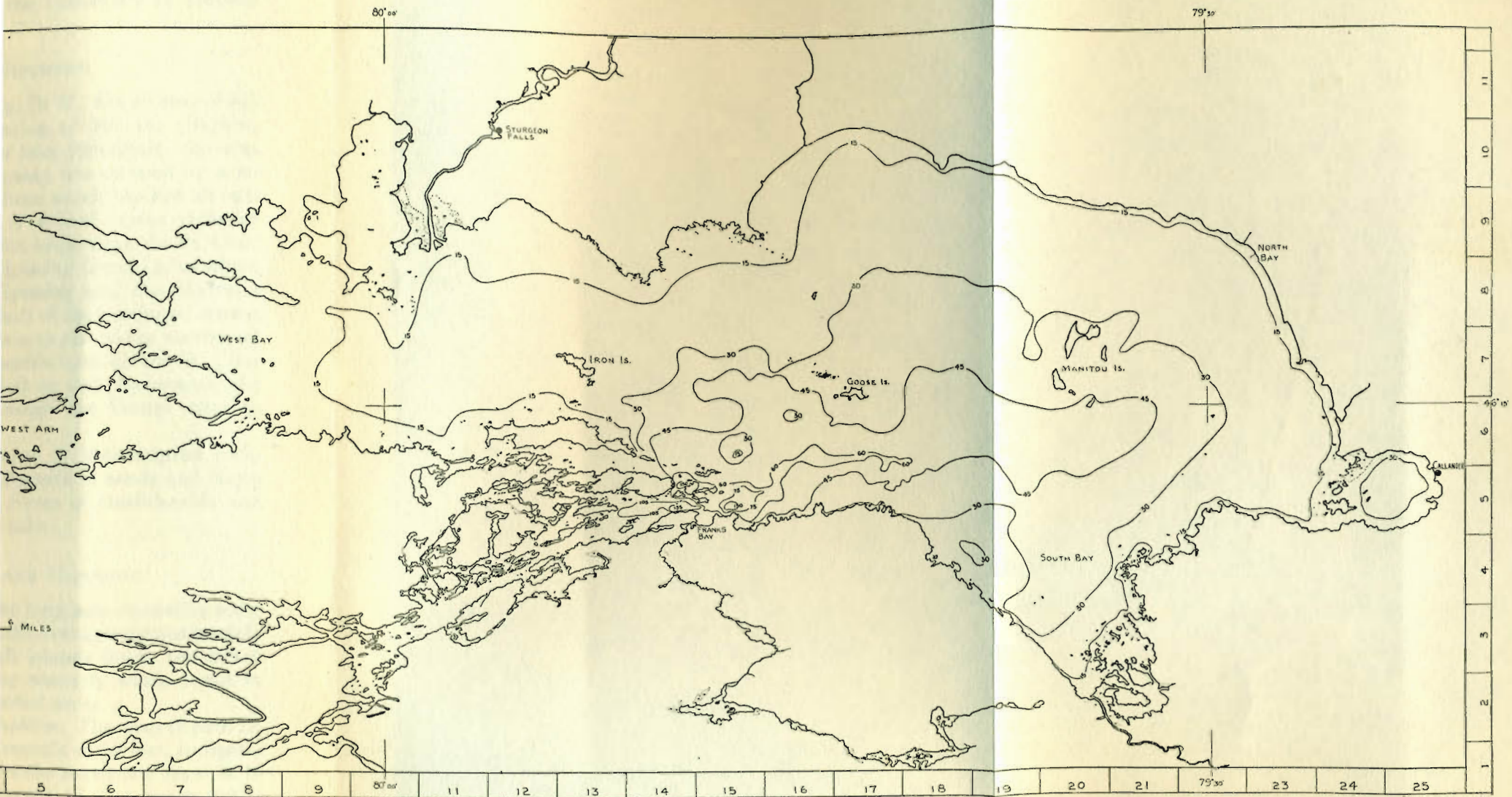


FIGURE 1.—Contour map of lake Nipissing (depth in feet).

Corkill's manuscript, which will be published in the near future in the Biological Series of the University of Toronto Studies.

GEOLOGY OF LAKE NIPISSING

Lake Nipissing, Lat. 46 N. Long. 79 W., has an area of 345 square miles, and lies at an elevation of 640 feet (Barlow, 1907). During the early period of lake Algonquin, the area occupied by the present lake Nipissing was covered by a retreating lobe of the Labrador ice sheet which blocked all outlets for the lake to the north-east. The final retreat of the ice from this region opened a new outlet lower than the St. Clair river, previously in use, and the Nipissing Great Lakes which resulted drained through lake Nipissing and the Mattawa valley to the Ottawa river. As a result of the continued retreat of the ice, the rise of the land in this area and to the north-east finally turned all the water southwards through the St. Clair river. The North Bay channel dried up and the present lake came into existence, draining through the French river to Georgian bay (Coleman, 1922).

The present lake lies in an area of Precambrian rock, covered in large areas by glacial deposits of sands and clays. Several small streams and three rivers of considerable size drain the surrounding area to the lake.

MORPHOMETRY OF LAKE NIPISSING

The lake is long and narrow, the long axis extending some 50 miles from east to west. The width averages approximately 12 miles, and few relatively small islands break the broad expanse of open water. Prevailing westerly winds result in severe wave action in the unprotected areas.

In general the lake is rather shallow. The map (figure 1), showing the depth contours at intervals of 15 feet, indicates that over the major area of the lake the maximum depth is 45 feet. The proportions of the different 15 foot depth zones, together with the percentage of the area within each contour, are given in the following table.

TABLE 1.—The surface area of lake Nipissing divided by 15 foot contours.

Stratum	Percentage of total area	Percentage of area within each contour
feet		
0-15	32	68
15-30	34	34
30-45	22	12
45-60	10.2	1.8
60-75	1.34	0.46
75-105	0.19	0.27
105-150	0.18	0.09
Below 150	0.09	0.00

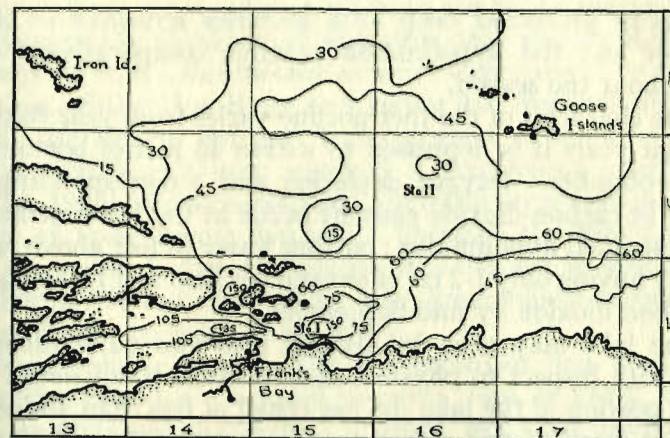
Two-thirds of the area of the lake is less than 30 feet in depth, and only a half of one per cent. is deeper than 75 feet.

This restricted area of deep water has been found to be of extreme importance in the biology of the lake, and has, therefore, been drawn on a much larger scale in figure 2. Reference points are given as in figure 1. Near the south shore there exists a valley-like depression leading towards the source of the French river. It is in this region, and at the source of the river itself, that the only water over 75 feet in depth has been found in the lake. A still greater enlargement of the deep water area just to the east of Frank's bay is given in figure 3. It is clear that organisms limited to depths below 60 feet would be restricted to this region of the lake, and migrants to the deepest of this area would tend to become greatly concentrated.

PHYSICAL AND CHEMICAL CONDITIONS IN THE LAKE

The results of the extensive physical and chemical study of the waters of the lake, from 1929 to 1934 inclusive, are to be published by Dr. Corkill. Some general statements pertinent to the problem at hand may, however, be made here to provide a background for the discussion which follows.

The lake is usually free from ice by the end of April, and spring warming is quite rapid. The extensive area of shallow water which is exposed to wind action, becomes warm, and is well oxygenated throughout all strata during the summer.



Contours in feet scale 0 1 2 miles

FIGURE 2.—Region of lake Nipissing, including stations I and II.

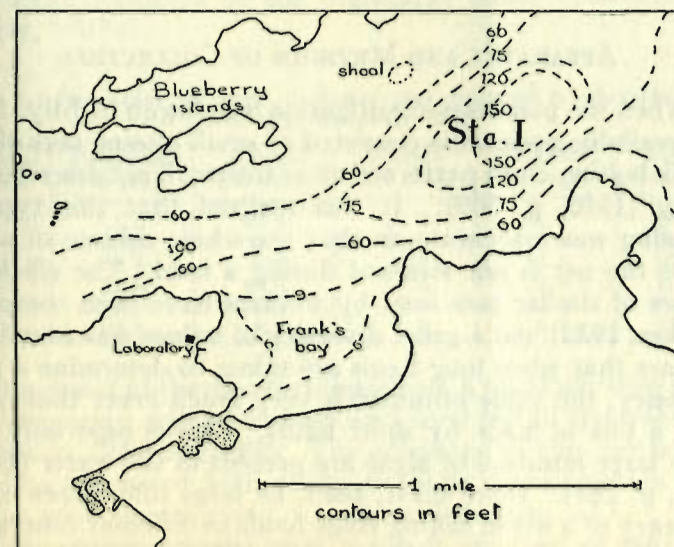


FIGURE 3.—Region of station I, lake Nipissing.

The more protected deep area becomes stratified in early summer and the hypolimnion remains comparatively cold throughout the season.

The character of the thermocline varies from year to year. In most years it is depressed to within 45 feet of bottom by mid-September. Oxygen depletion and a corresponding increase in carbon-dioxide content occur in the lower strata of this restricted hypolimnion; bottom water (3 feet above mud) usually having only 1-2 cc. of oxygen per litre and 12-14 p.p.m. of carbon dioxide by mid-September.

The lake may then be divided into two quite different areas with respect to physical and chemical conditions. The major portion of the lake (88 per cent.) of less than 45 feet in depth is warmed and remains well oxygenated at all depths throughout the summer season. The very restricted area of deep water which is thermally stratified, remains cold throughout the summer, but loses much of its dissolved oxygen and becomes highly saturated with carbon dioxide resulting from respiration and decomposition.

APPARATUS AND METHODS OF COLLECTION

When the plankton investigation was begun in July, 1932, the available apparatus consisted of small closing nets of No. 20 silk bolting cloth patterned after the small net described by Juday (1916, p. 569). It was realized that this type of sampling was inaccurate, in that the whole column of water above the net is not strained during a haul. The efficiency factors of similar nets used by workers have been compared (Ricker, 1932) and a great diversity of values was found. It appears that when long hauls are taken to determine a net's efficiency, the value obtained is very much lower than when such a test is made by short hauls. This is especially true when large numbers of algae are present in the water (Birge, 1897, p. 284). There must, then, be large differences in the efficiency of a net in taking stage hauls in different concentrations of a plankton population, or in different populations.

As an attempt was being made to study the vertical distribution of the plankton, it was clear that results obtained in sampling with a fine meshed tow net were subject to severe criticism. Since Drs. Birge and Juday had discontinued the use of the closing net and had designed a plankton trap (Juday, 1916) and later evolved a continuous centrifuge (Juday, 1926), it was considered advisable to investigate the merits of these newer methods. Through the kindness of Drs. Birge and Juday, the author was enabled to spend the summer of 1933 at their Trout lake limnological laboratory and study the methods in use there.

During the season of 1933, a comparison was made between the plankton trap and the nets used in 1932. These data are discussed elsewhere (Langford, MS.) but table 2 and figure 4 show some of the results obtained. The most striking difference is that of the greatly increased efficiency when sampling by short hauls. Secondly, a variation in the efficiency of catching particular organisms in certain strata is noted. This is no doubt due in part to errors in sampling the very small numbers of the organisms under consideration (Ricker, 1937a).

TABLE 2.—Percentage efficiency of closing net compared to plankton trap, Trout lake, Wisconsin, 1933.

Depth Metres	<i>Diaptomus</i> Per cent.	<i>Cyclops</i> Per cent.	Nauplii Per cent.	<i>Daphnia</i> Per cent.	Mean Per cent.
0 - 2.5	64.0	63.5	55.0	84.5	65.0
2.5- 5	27.3	26.5	36.6	38.5	36.0
5 -10	9.9	8.9	9.2	13.5	10.0
10 -15	15.0	18.3	19.8	13.6	17.0
15 -20	17.0	16.8	9.5	20.3	13.5
20 -29	12.5	8.6	4.8	6.7	11.6

As a result of the above comparison, a plankton trap of 10 litres' capacity was purchased and used for all quantitative samples in 1934 and 1935. The efficiency of this method of sampling compared with pump methods is discussed in connection with the trap and net comparisons (*loc. cit.*).

Light measurements were made at the time of sampling

with a modified "metrophot" photoelectric exposure meter, calibrated to read in foot candles. Samples were taken so far

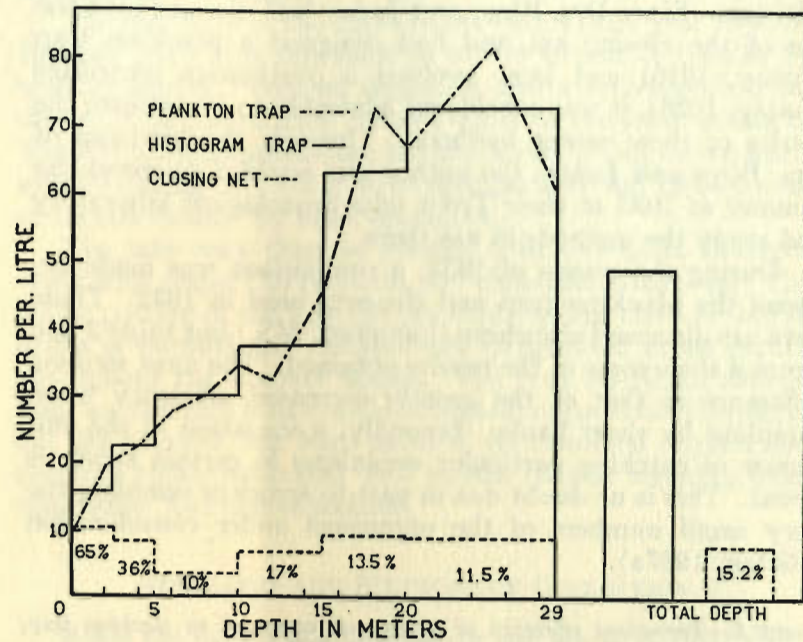


FIGURE 4.—Comparison of the efficiency of net and trap, Trout lake, Wisconsin, 1933.

as it was possible when conditions of light were stable. This was done in order to avoid changes in distribution while sampling.

COLLECTIONS

Two stations were selected as representative, respectively, of the deep and shallow areas of the lake. These stations were marked by observing the position of salient features of the shore line. Station I was situated near the south shore, three-quarters of a mile east of Frank's bay (figures 2 and 3). Depths of 40 and 45 metres were regularly obtained at this

station. Station II was situated some three and a half miles from Frank's bay in the direction of the Goose islands (figure 2). Depths of 10 and 12 metres were found in this region of open water, which was subject to considerable wind action.

In 1932 samples were taken with the closing net at bi-weekly intervals from July till October at both stations. The stage hauls subject to such variations in the efficiency of the net have not been included here. The seasonal variation in numbers, determined from total vertical hauls only, is compared with that for 1934 and 1935, at station I, using an efficiency factor of 6.6 for the tow net. Absolute abundance is, therefore, not to be compared, but rather only the relative changes during the season.

In 1934 trap samples from station I were taken weekly from May 16 until the end of June, bi-weekly during July, and weekly until the middle of September. The series of depths sampled was 0, 3, 5, 8, 10, 15, 20, 25, 30, 35, and 40 metres. Trap samples were also taken from station II at approximately bi-weekly intervals from May 19 until the end of August, the series of depths sampled being 0, 3, 5, 8, 10, and 12 metres.

In 1935 samples were taken with the plankton trap from station I at weekly intervals from May 18 until September 18. Samples were taken at 1 metre and 45 metres in addition to the series given for 1934. The value of the 1 metre sample may be seen from the graphs of many of the organisms, which show wide differences at depths of 0 and 3 metres. Station II was sampled only irregularly during 1935, and the 1 metre level was added to this series as well.

It will be noted that plankton samples have been taken at depths measured in the metric system in order that results may be easily compared to those of other plankton workers. It has been necessary to include certain data and maps involving the English system of linear measure. The error is slight if 1 metre is considered equivalent to 3.3 feet wherever comparisons are necessary.

In addition to the routine sampling, certain special samples were obtained for specific investigations. In 1934 a diurnal series of samples was obtained at station I; the regular series of depths being sampled at critical periods during the diurnal cycle.

In 1935 midnight series, as well as daylight series, were obtained on the dates on which oblique settings of gill nets were made for ciscoes. The data from the enumeration of these are used in comparing the plankton food present at the different levels with that taken by ciscoes caught in comparable strata.

ENUMERATION AND EXPRESSION OF RESULTS

All individuals of each species of the plankton crustacea, with the exception of nauplius and metanauplius stages, were enumerated in the total trap collection. A large counting cell was employed, on which the sample was distributed by stirring. A Leitz travelling binocular microscope was used in observing the plankton, and numbers were recorded by "counters" and later tabulated on suitable forms. The ease with which the objectives could be changed from low to high power proved valuable in determining the *Diaptomus* species.

The numbers of individuals given in the tables, and indicated in the graphs of this paper, are in all cases one-tenth of the count, *i.e.*, numbers per litre. In the case of the diurnal migration study, since there was a certain variation in the total of the vertical series of collections, the data are converted to percentages of the total in constructing these graphs. The actual numbers per litre of all counts are, however, given in the respective tables.

SAMPLING ERRORS

Introduction

Ricker (1937a) has shown that estimates of a plankton population, made from individual samples, are subject to

statistical errors of considerable magnitude. When the population has a random distribution throughout the whole or part of a lake, it can be shown that a series of samples taken simultaneously from that part will constitute a Poisson frequency distribution. Following the methods of Clopper and Pearson (1934), Ricker calculated tables of confidence or fiducial limits, which yield a measure of the accuracy of small samples as an estimate of the population (Ricker, 1937b). For larger samples (*i.e.*, counts of over 50) the standard error is equal to the square root of the count, and the probability that the population lies between given limits may be obtained from the table of the normal probability integral.

It must be emphasized that these statistical limits are acceptable only when the distribution of plankters is proven to be random. This involves the determination of the horizontal distribution of each plankter considered in the individual lake.

Variation in horizontal distribution

(a) **Historical.** From the time of Hensen (1895), who believed his results showed a uniformity of distribution of the oceanic plankton, the subject of horizontal variation in distribution has received a great deal of attention. The question is still, however, far from being satisfactorily settled. Apstein (1892), Reighard (1894), and Ward (1896) have all contended that the plankton studied in their investigations was distributed with great uniformity. Imhof (1892), Zacharias (1894), and Marsh (1897) state that such was not found to be the case in their studies. Birge (1897) agrees with Apstein that two- to four-fold variations are not to be counted as swarms, and hence states, "while therefore I find swarms occasionally present, I find also that the Crustacea of Lake Mendota are in general distributed with marked uniformity".

An analysis of these early reports, and of the results of recent studies, indicates that probably three factors were responsible for these differences of opinion. Firstly, the individual lakes studied probably differed with respect to the distribution of the plankton population therein. That this is possibly true of Cultus lake (Ricker, MS. 1) and lake Nipissing

will be shown later. Secondly, methods of collection and analysis very likely gave different results from this standpoint. A third reason for these differences of opinion, may have been the fact that no exact measure of the variation in distribution was available, and considerable diversity of opinion existed over the definition of what was meant by a "swarm".

(b) **Statistical analysis.** Ricker (1937a) has shown that:

(i) If the plankton population is randomly distributed, the counts of a series of samples at point of time will comprise a Poisson frequency distribution. The mean will in this case

$$\text{equal the variance } \left(\frac{\sum(x - \bar{x}_1)^2}{N_1 - 1} \right).$$

(ii) If the population is bunched together in places, scarce in others, the variance of a series of counts will exceed their mean.

(iii) If the population is "spaced", *i.e.*, if the individuals have a tendency toward remaining a definite distance apart, then the variance will be less than the mean.

The significance of these differences from the mean may be determined by the χ^2 test: "when testing agreement to a Poisson distribution, since the variance should equal the mean $\chi^2 = \sum(x - \bar{x})^2 / \bar{x}$. Reference may then be made to the χ^2 table to determine whether or not the value obtained is unreasonably large or small. Such tables are to be found in Pearson (1924) table 12, or Fisher (1934) table 3" (Ricker, 1937a). We have, therefore, a means of determining with exactitude the type of distribution exhibited by any plankton, provided that sampling methods give results suitable for analysis.

(c) **Horizontal distribution in lake Nipissing.** An attempt was made in 1934 to determine whether or not the population was more variable from station to station laterally than at one station in lake Nipissing. Plankton trap samples were taken at a series of depths at ten different stations, within a radius of three-quarters of a mile. Ten samples were also obtained from 8 metres at one station. The samples were all taken between 10.00 a.m. and 1.00 p.m. on July 4, and

light conditions as measured with the photometer remained practically constant during that time. There was no wave action to change the penetration of light, so that there should have been no vertical migration resulting from change in light intensity. The counts of the ten samples at 8 metres together with the mean, the variance, and the χ^2 value are given in table 3. Similarly the series at each of the ten stations is given in table 4.

TABLE 3.—Variation in the number of organisms taken at 8 metres, in ten samples taken at one station, July 4, 1934.

Organism	SAMPLE										Mean	Variance	χ^2
	1	2	3	4	5	6	7	8	9	10			
<i>Diaptomus</i>	140	222	185	173	163	185	134	141	178	164	168.5	703	37.6
<i>Cyclops</i>	22	35	35	32	25	35	18	21	30	20	27.3	52	17.1
<i>Epischura</i>	5	11	7	8	5	3	1	6	7	7	6.0	7.6	11.3
Metanauplii.....	5	12	12	2	3	9	0	5	5	2	5.5	18	28.7
Nauplii.....	569	575	589	555	483	436	423	471	490	514	510.5	3485	61.9
<i>Daphnia</i>	31	37	45	30	25	30	31	35	33	40	33.7	33.1	8.9
<i>Bosmina</i>	4	5	2	8	6	1	1	4	4	5	4.0	5	11.0

From the consideration of the ten counts at one point, 8 metres, it is clear that there was considerable difference in the type of distribution exhibited by the different organisms. *Diaptomus*, *Cyclops*, and their metanauplii and nauplii were definitely bunched, although *Cyclops* were not greatly so. *Epischura*, *Daphnia*, and *Bosmina* appeared to be randomly distributed at 8 metres at this station, with a variance not significantly different from the mean. The influence of errors arising in the transference of samples from the trap to vials has been neglected. It is felt that such errors have not caused the large fluctuations in the numbers of certain organisms since the bunching is evident only in certain species, not in all groups represented in the samples. The 0.05 probability has been taken as the limit of significance.

If we inspect table 4 we find a marked difference with regard to laterally spaced series. In only one case does the variance approach the value of the mean. In this case from a

comparison of the χ^2 value with a table of the same, *Daphnia* is found to have been randomly distributed at 8 metres over the lake. At 10 metres it was bunched, although but slightly. In all other cases the variance is significantly higher than the mean, and *Cyclops*, *Diaptomus*, Nauplii, and *Daphnia*, with the exception noted, were definitely bunched in their horizontal distribution at all depths sampled.

TABLE 4.—Horizontal variation in the number of plankters, 1934. Figures given are in all cases actual counts of plankters in the 10 litre trap samples.

Depth Metres	HAUL										Mean	Variance	χ^2	
	1	2	3	4	5	6	7	8	9	10				
<i>Cyclops</i>	0	11	14	18	37	21	35	12	7	11	32	19.8	121	55.2
	3	45	36	32	35	?	23	62	35	30	?	37.3	138	257.0
	5	31	30	14	53	20	15	55	40	25	50	33.3	239	64.8
	8	22	27	11	20	20	30	45	50	15	25	26.5	154	524.0
	10	16	?	20	25	20	?	10	?	15	10	16.5	306	111.5
<i>Daphnia</i>	0	5	15	9	105	60	115	43	36	55	106	54.9	1725	283.0
	3	110	115	35	155	?	100	227	30	127	?	112.4	4015	250.0
	5	35	75	40	85	32	40	157	40	45	63	61.2	1454	213.0
	8	27	43	45	40	38	35	52	43	30	35	38.8	55	12.7
	10	31	?	42	40	50	?	32	?	52	22	38.4	117	18.3
<i>Diaptomus</i>	0	63	170	215	345	180	280	175	220	270	359	227.7	7917	310
	3	285	215	86	560	?	275	465	200	486	?	321.5	11684	255
	5	160	235	95	325	80	145	410	145	140	304	203.9	12031	532
	8	65	95	80	90	67	95	145	160	50	230	107.7	3033	252
	10	60	?	70	60	70	?	125	?	50	160	85.0	1692	119
Nauplii	0	461	537	742	975	912	1350	802	680	1185	980	862.4	7657	884
	3	426	464	415	627	?	670	815	497	658	?	571.5	20330	249
	5	538	480	371	522	339	440	805	525	490	683	519.3	19113	331
	8	317	272	438	437	300	390	478	563	286	578	405.9	12571	280
	10	202	?	222	258	230	?	310	?	296	400	274.0	4622	101

Even though *Epischura* and *Bosmina* were randomly distributed at 8 metres at one station, this distribution was not found to hold true laterally at other depths over the lake. It is again possible to compare these types of distribution by a statistical method.

If we wish to compare the variation in distribution laterally with that at one station, a test of the significance

of the differences between their variance will tell us if one distribution is more variable than the other. "In testing the difference between two estimates of variance, s_1^2 and s_2^2 from two small samples of N_1 and N_2 the index $z = \frac{1}{2} (\log_e s_1^2 - \log_e s_2^2)$ may be used. Fisher's table 6 shows the distribution of z for probabilities (P) of 0.05 and 0.01 and for various small values of n_1 and n_2 ($= N_1 - 1$, and $N_2 - 1$)" (Ricker, 1937a).

The following example, table 5, illustrates the application of the treatment discussed above to the *Daphnia* population at 8 metres.¹

TABLE 5.—Comparison of the numbers of *Daphnia* at 8 metres in ten samples taken at one station, with ten samples distributed within three-quarters of a mile.

Haul	1	2	3	4	5	6	7	8	9	10	Mean
One station	31	37	45	30	25	30	31	35	33	40	33.7
Horizontal	27	43	45	40	38	35	52	43	30	35	38.8
						One station					
								Horizontal			
Number of samples							10				10
Degrees of freedom							9				9
Variance (s^2)							33.1				55
$\log_e (s^2)$							3.50				4
difference ($\log_e s_1^2 - \log_e s_2^2$)							0.50				
$z = \frac{1}{2} (\log_e s_1^2 - \log_e s_2^2)$							0.25				

Entering the table of z (Fisher's table VI) we find for 9 degrees of freedom for $P=0.01$, $z=.8494$, for $P=0.05$, $z=.5862$. The value of z here, 0.24, is much smaller than the value corresponding to the 0.05 level of significance, and hence the variation at 8 metres over the ten laterally spaced stations was not great enough to be demonstrated by this small number of samples.

A comparison of the variance of the other organisms studied (as indicated in table 6) yields the following results: *Diaptomus*, nauplii, and metanauplii were more variable horizontally at 8 metres than at one point, their z values being greater than the value of z corresponding to the 0.05 level of significance. *Cyclops*, *Epischura*, and *Bosmina* were not so much more variable horizontally at this depth as to be shown by this comparison.

At this date *Epischura*, *Daphnia*, and *Bosmina* appear to

¹Example comparable to one given by Ricker (1937a).

have been nearly randomly distributed at 8 metres, at one point and laterally. *Cyclops* was slightly bunched at 8 metres at one point, and from this comparison was evidently not more variable laterally. *Diaptomus*, metanauplii, and nauplii were definitely bunched at 8 metres at one station and show significantly greater bunching horizontally.

An attempt was made in 1935 to determine whether there would be any trend observable if the ten series of samples were taken in a line. That such was not found to be the case is

TABLE 6.—Comparison of variation in the numbers of plankters at 8 metres in ten samples taken at one station, with ten samples distributed within three-quarters of a mile.

	HAUL										Mean	Variance s^2	$\log_e s^2$	Diff. "z"
	1	2	3	4	5	6	7	8	9	10				
<i>Diaptomus</i>														
Station II...	140	222	185	173	163	185	134	141	178	164	168.5	703	6.55	
Horiz.	65	95	80	90	67	95	145	160	50	230	107.7	3033	8.01	1.46 0.73
<i>Nauplii</i>														
Station II...	569	575	589	555	483	436	423	471	490	514	510.5	3485	8.15	
Horiz.	317	272	438	437	300	390	478	563	286	578	405.9	12500	9.43	1.28 0.64
<i>Metanauplii</i>														
Station II...	5	12	12	2	3	9	0	5	5	2	5.5	18	2.89	
Horiz.	2	6	1	10	5	10	20	30	10	15	10.9	76	4.33	1.44 0.72
<i>Cyclops</i>														
Station II...	22	35	35	32	25	35	18	21	30	20	27.3	52	3.95	
Horiz.	22	27	11	20	20	30	45	50	15	25	26.5	154	5.04	1.09 0.54
<i>Epischura</i>														
Station II...	5	11	7	8	5	3	1	6	7	7	6.0	7	6.2	0.03
Horiz.	1	1	1	0	5	5	10	5	12	6	4.6	15	1.2	0.68 0.34
<i>Bosmina</i>														
Station II...	4	5	2	8	6	1	1	4	4	5	4.0	5	0	1.60
Horiz.	7	4	1	3	0	2	5	5	7	5	3.9	5	6	1.72 0.12 0.06

indicated in table 7. The statistical analysis yields results quite similar to those found in 1934, with the exception of *Daphnia* which is found to have been randomly distributed at the surface, and not greatly bunched at 1 metre.

When we compare this to the results obtained by Ricker on Cultus lake, we find very marked differences. Ricker (1937a) finds that *Epischura* and *Bosmina* are randomly distributed at a point, *Cyclops* and nauplii are "spaced", and *Daphnia* are definitely "bunched". In comparing the hori-

zontal variation of these organisms with that at one station, he concludes (MS. 1): "In most cases their horizontal distribution is approximately the same in the immediate vicinity of the central sampling station as over the entire open water of the lake. In only one case has a more variable

TABLE 7.—Horizontal variation in the numbers of plankters in 10 litre samples taken at ten stations in a straight line, 1935.

Depth Metres	HAUL										Mean	Variance	χ^2
	1	2	3	4	5	6	7	8	9	10			
<i>Daphnia</i>													
0	0	2	7	8	2	5	7	7	3	7	4.8	7.4	14
1	1	0	3	1	0	6	2	5	6	5	2.9	5.8	18
3	27	17	5	13	10	12	20	10	20	10	14.4	42.5	
5	40	40	20	29	30	20	65	12	40	50	34.6	248.7	
8	16	37	20	23	11	25	52	25	23	30	26.2	132.5	
10	22	40	25	40	15	45	32	25	38	25	30.7	94.7	
12	45	40	30	32	20	35	25	?	15	17	28.8	67.3	21
<i>Diaptomus</i>													
0	14	10	12	25	1	10	20	30	20	30	17.2	89.3	47
1	15	8	4	10	12	6	17	17	10	12	11.1	23.2	19
3	50	10	8	54	40	80	35	25	50	10	36.2	547.2	136
5	86	10	42	65	18	145	30	95	150	43	68.4	2480	326
8	72	47	43	50	47	130	65	60	100	25	63.9	941	132
10	80	210	75	80	65	195	90	70	75	20	96.0	3490	327
12	130	480	130	70	85	120	150	?	25	17	134.1	19030	1136
<i>Metanauplii</i>													
0	35	90	130	65	50	125	195	240	205	310	144.5	8350	
1	130	155	145	145	165	255	230	240	205	225	189.5	2120	
3	260	345	360	270	465	255	415	325	355	450	350.0	5740	
5	245	380	690	270	285	310	470	520	405	390	396.5	9580	
8	290	370	290	245	218	355	355	325	395	340	318.3	4790	
10	240	255	220	240	205	285	320	270	325	240	260.0	1600	
12	195	175	240	280	370	315	280	?	250	195	255.5	4725	
<i>Nauplii</i>													
0	165	385	450	525	405	685	680	630	720	805	545.0	36477	
1	310	465	455	490	535	565	695	625	730	646	551.6	16177	
3	660	610	795	660	1225	445	550	550	780	875	715.0	48972	
5	480	440	1355	433	435	320	440	350	595	425	527.3	14544	
8	370	250	370	345	285	365	290	250	300	295	302.0	2040	
10	325	205	255	230	155	175	280	180	262	310	237.7	36750	
12	185	100	165	125	105	90	225	?	245	242	148.2	4294	

distribution over the greater area been demonstrated with certainty, that of *Cyclops* in one of the tests, and the difference was not great."

Whether or not this great difference in the type of dis-

tribution is a result of inherent differences in the two lakes, or whether it is an apparent difference due to difference in sampling methods, is not known. Ricker's samples for comparison were all taken with a Juday closing tow net. The first group was taken with a No. 20 silk net for which he gives net factors of 15.3 on March 17 and 5.9 on October 12. Later a second group was taken with a No. 10 silk net for which he gives a factor of 1.10 (*loc. cit.*).

(d) **Conclusions.** The data presented above are so pertinent to the question of seasonal and yearly fluctuations in abundance, and of comparisons of productivity from lake to lake, that when taken into consideration in such studies they must modify significantly conclusions reached. With regard to seasonal fluctuations in abundance, it should be pointed out that even in spite of horizontal variations, seasonal trends are still noticeable and must be significant. Even though the absolute numbers making up seasonal maxima and minima are subject to large errors, still the trends are so definite, and the differences between such maxima and minima are so great, as to make their existence quite certain. Since the statistical significance of these differences is not known, it will be necessary in the future to modify sampling methods to obviate these fundamental errors when present, if accuracy is required.

In order to overcome the effect of these horizontal variations, both from the standpoint of seasonal abundance and comparative productivity studies, it will be necessary to take a number of duplicating series. Counts of a smaller number of organisms from each, or a fraction of mixed samples from one depth, will yield greater accuracy than is possible from single samples.

In the present study, the extent of horizontal variations was not known until the field work was nearly completed; hence no attempt is made to compare the productivity of lake Nipissing with other lakes, from the standpoint of plankton production. The section of this paper dealing with seasonal abundance contains only a general comparison of the modes in the distribution curves, and no conclusions are drawn as to the relative production in different years.

Throughout the investigation, emphasis was placed upon a study of variations in the vertical distribution of individual species. It was realized that samples must be obtained at short intervals of time, since conditions change rapidly at certain seasons. In the final year (1935), the analysis of a large number of cisco stomachs, in addition to the enumeration of weekly series at station I, and midnight series in connection with food studies, precluded the possibility of attempting more than one series at each sampling date.

In the study of vertical distributions, care has been exercised in analysis in the case of those species which were taken in small numbers. Only outstanding differences have been considered to be at all significant. Minor differences have been disregarded in the analyses.

THE PLANKTON CRUSTACEA OF LAKE NIPISSING

Six species and one group of entomostraca were taken in sufficient abundance to determine their distribution. These are listed below.

Cladocera

Daphnia longispina (Müller)

Holopedium gibberum (Zaddach)

Copepoda

Epischura lacustris (Forbes)

Diaptomus oregonensis (Lilljeborg)

Diaptomus minutus (Lilljeborg)

Limnocalanus macrurus (Sars)

Cyclops group.

Of the Cladocera, *Diaphanosoma leuchtenbergianum* (Fisher), *Bosmina longirostris* (Müller), and *Leptodora kindtii* (Focke) were taken in such small numbers that distributional studies were impossible. The same was true in the case of the malacostracan *Mysis relicta* (Lovén).

The family Cyclopidae is represented by three species in lake Nipissing. These three species, *Cyclops bicuspidatus* (Claus), *Cyclops viridis* (Jurine), and *Mesocyclops obsoletus* (Koch), were too difficult to separate in enumerations, and have therefore been combined under the genus *Cyclops*.

PART I: DIURNAL MOVEMENTS OF LIMNETIC CRUSTACEA

It has for many years been recognized that plankton crustacea react to changes in light intensity. This results in a difference in their vertical distribution at different times of the twenty-four hour cycle. In the studies of vertical distribution of the lake Nipissing plankton crustacea, collections were made so far as possible at times when light conditions were similar, yet light measurements indicated the existence of different light intensities on different dates. In order properly to understand and interpret the results of this vertical distribution study, it is desirable to have definite information on the diurnal movement of the plankton crustacea occurring in lake Nipissing. The results of a study of their movements throughout the day and night of June 27, 1934, is therefore given, and those movements occurring during the cyclic changes of daylight and darkness are here considered as diurnal movements.

Vertical series of trap hauls were taken at critical periods of the day and night beginning at noon on June 27, 1934. The thermocline was not well marked at this date, the steepest gradient (1.5° C. in 2 metres) occurring between 13 metres and 15 metres. The temperature from surface to 13 metres decreased gradually from 17.8° C. to 16.6° C. The diurnal variation in vertical distribution of the different plankton crustacea is indicated in figure 5, and the numbers of organisms involved is given in table 12 (p. 121). The lowermost panel represents on a logarithmic scale the differences in the light intensity at the surface throughout the period.

In 1935, midnight series of trap samples were obtained in connection with the study of the utilization of plankton crustacea by the cisco. Comparable samples were taken the previous day in each case, and these permit a comparison of diurnal movements at different dates during the season. The actual numbers involved are given in table 13 (p. 124). Table 9 (p. 117) records the light intensity values at the time of daylight sampling. Temperature relations at different depths during 1934 and 1935 are indicated in table 10 (p. 118) and figure 12 (p. 51).

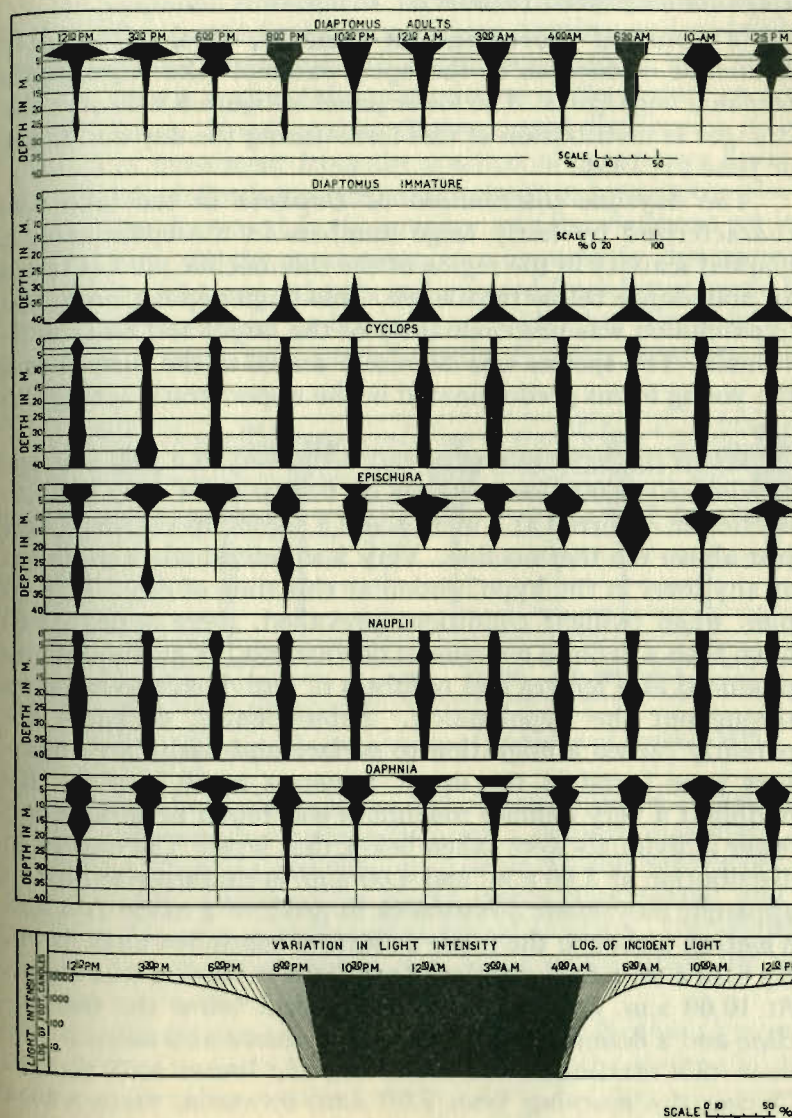


FIGURE 5.—Diurnal changes in the vertical distribution of plankters, station I, June 27, 1934.

Daphnia longispina (Müller)

(a) **Diurnal movement on June 27, 1934.** The only abundant cladoceran in the open water of lake Nipissing is *Daphnia longispina*. The lower panel of figure 5 indicates the changes in distribution of this form during the day and night of June 27, 1934.

The daytime distribution of *Daphnia* in the lake was characterized by fairly large numbers in the epilimnion, a marked scarcity in the region of the thermocline, and at times an abundance below that level. This large population in the hypolimnion was predominantly of the larger and older individuals. The species was definitely scarce at the surface and the young forms predominated in the upper strata during the day.

When the light intensity had decreased to a value of approximately 2,000 foot candles by 6.00 p.m., a very definite maximum occurred at 3 metres and a second mode was found just above the thermocline. Very few individuals were taken at any level in the hypolimnion at this time of day. At 8.00 p.m. when twilight conditions prevailed, there appeared to have been a definite movement downwards. A maximum was produced at 8 metres and numbers of individuals were taken throughout the hypolimnion. Subsequently, darkness apparently caused a migration to surface and fairly large numbers were found in the upper 5 metres at 10.30 p.m. By midnight a very definite maximum was found at surface and fewer individuals were taken below that level. The change in distribution at 3.00 a.m. and 4.00 a.m. is characterized by an apparent movement downwards to produce a mode at 5 and 8 metres, although the mode at surface continued until dawn. By 6.30 a.m. a fairly typical daylight distribution was found. At 10.00 a.m. large numbers were taken below the thermocline and a definite maximum was produced at 3 metres. By noon this maximum was found slightly lower, at 5 metres. During the morning from 3.00 a.m. onwards, there was a gradual evacuation of the surface stratum, and between 10.00 a.m. and noon the 3 metre stratum was affected similarly.

(b) **Seasonal differences in diurnal movements, 1935.**

From figure 6, which gives the various daytime and midnight distributions throughout the season, we observe that at no time was there such a definite maximum at the surface as discussed above. If we consider the nocturnal distribution to be a result of movement from the position of occurrence during the day, the following movements appear to have taken place as the light decreased in the evening, or after darkness set in.

On June 22 the movement was apparently downwards from zero and 1 metre levels and upward from lower levels to produce a maximum at 5 metres at midnight. On July 5 a slight movement took place into the 1 metre stratum. On

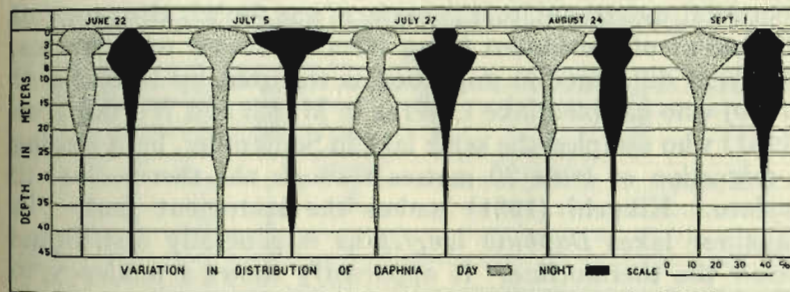


FIGURE 6.—Seasonal differences in diurnal movement of *Daphnia*, 1935.

July 27 the individuals in the hypolimnion (below 12 metres) penetrated the thermocline to form a definite maximum at 5 metres. Contrary to this, on August 24 and September 1, the daytime maximum in upper strata disappeared and a more or less even distribution occurred at night. On September 1 the population of the zero and 1 metre strata did not appear to be materially affected.

(c) **Conclusions.** Juday (1903) says of *Daphnia hyalina*: "with one exception [in nine lakes studied] the young did not show so great a movement as the adults, for they were nearer the surface in the daytime." The difference in distribution between young and adult *Daphnia* noted in lake Nipissing is similar to that found by Juday, but Southern and Gardiner

(1932) and Worthington (1931) have found the exact opposite in Lough Derg and lake Lucerne respectively. Dice (1914) with regard to the question states: "young individuals of *Daphnia pulex* are more strongly positively phototactic and negatively geotactic than adults. They also sink less rapidly in water. For these reasons they are usually found nearer the surface than the adults. There is a downward movement (*i.e.* in distribution) due to the ageing of the individuals."

The differences in the movement of *Daphnia* throughout the season do not appear to have been generally observed. Juday (1903), in sampling ten lakes at different times during the summer, mentions no differences for *D. longispina* correlated with seasonal differences. In eight of the lakes a nocturnal movement to the surface was found, the range of the extent of movement being from $\frac{1}{4}$ metre to 7 metres. No great difference in migration is reported by Burckhardt (1900) who sampled lake Lucerne in March and Worthington (1931) who sampled the same lake in September, both finding a migration of some 30 metres through the thermocline to surface. Kikuchi (1931) makes the statement that: "In Japanese lakes *Daphnia longispina* is generally distributed below the thermocline. It apparently shows a tendency to move upward at night, but not a single individual was found above a depth of 5 metres or in the epilimnion at night. However, *D. longispina* came up near the surface in winter, when the temperature of the water decreased."

From the above it is evident that *D. longispina* reacts very differently in different lakes, and it is therefore not surprising to find that its reaction in lake Nipissing varied under the changing conditions of the season.

Epischura lacustris (Forbes)

(a) **Diurnal movement on June 27, 1934.** Panel four of figure 5 represents the percentage distribution of *Epischura* at different periods during the day and night of June 27, 1934. Numbers taken in any one sample were small, so that too much reliance must not be placed on individual counts. Certain trends are, however, quite evident and are taken as significant, since several samples are involved in each case.

The daytime distribution was characterized by a bimodal curve, one maximum occurring near surface and another in strata below the thermocline. It is questionable whether or not the marked congregation of individuals occurring at 6.00 p.m. was significant, since with continued decrease in light intensity the typical daylight distribution was observed at 8.00 p.m. Throughout the hours of darkness, however, maximum numbers were taken in upper strata and no individuals were obtained below the thermocline. Two hours after dawn a downward movement was observed, and later the species was again taken below the thermocline. The individuals found below the thermocline in daylight definitely moved through the thermocline to upper layers at night. Whether or not this was a result of a change in geotropism is not known.

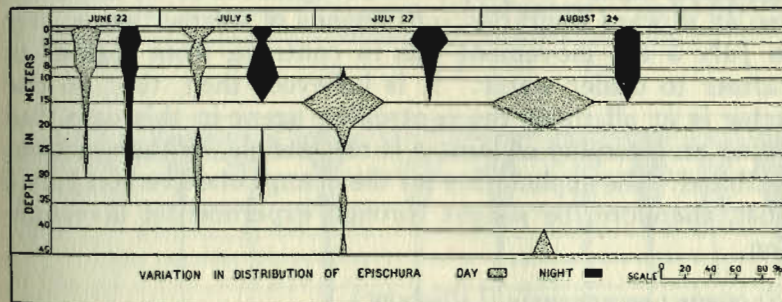


FIGURE 7.—Seasonal differences in diurnal movement of *Epischura*, 1935.

(b) Seasonal differences in diurnal movements, 1935.

Figure 7 indicates the differences observed in the diurnal movements of *Epischura* in the summer season of 1935. On June 22 there was no definite movement of the species. On July 5 a downward trend was evident in the epilimnial population, and on July 27 and August 24 there was a definite upward movement at night.

(c) **Conclusions.** Marsh (1897) says of the species: "*Epischura* prefers warm water but avoids bright light. In the daytime during the hot months it is most abundant in the upper layers, but not at the immediate surface. In the dark-

ness of the evening however, it is no longer repelled from the surface by the light." From night hauls in late August, 1893, he observes: "In these three night hauls, there was an average of 82 per cent. in the 0-5 metre stratum, while the average in the day hauls in the same stratum was 33.32 per cent." Again he states: "On the contrary it appears that in October nights it migrates to greater depths. It appears to be probable that temperature is the controlling cause of both the diurnal and seasonal migrations."

It is true in the case of lake Nipissing that in June when the temperature was approximately 16°C. from surface to 20 metres, no nocturnal movement was noticeable in 1935. In 1934, on June 27, when the upper 10 metres of water were definitely warmer than those below, there was a movement upward at night. On July 27 and August 24, 1935, there was also an upward migration into regions of warmer water, but on July 5 the movement was in contrast, from regions of warmer to colder water. It is believed, then, that no one factor is at all times the controlling agent in this case, but rather an interplay of factors is responsible for the reactions exhibited. The explanation for the change observed on July 5 must, therefore, be sought through experimental investigation.

Diaptomus oregonensis (Lilljeborg)

(a) **Diurnal movement on June 27, 1934.** The second panel of figure 5 represents the distribution of copepodid stages of *D. oregonensis* which were taken near bottom in deep water. Small numbers of adults did occur above the thermocline but were relatively of slight importance in this study.

It is clear that the copepodid stages did not exhibit any marked diurnal movement at this time.

(b) **Seasonal differences in diurnal movements, 1935.** The copepodid stages below the thermocline did not exhibit any marked diurnal movement on any of the dates when day and night series were taken (figure 8). This is in conformity with the data from the diurnal study on June 27, 1934. Considerable difference was, however, observed in the movement

of the adults above the thermocline. On three of the dates, June 22, July 27, and September 1, a definite upward movement was observed at night. On the other two dates, the daylight and midnight distributions were not greatly different, and there was apparently no diurnal movement of these mature individuals.

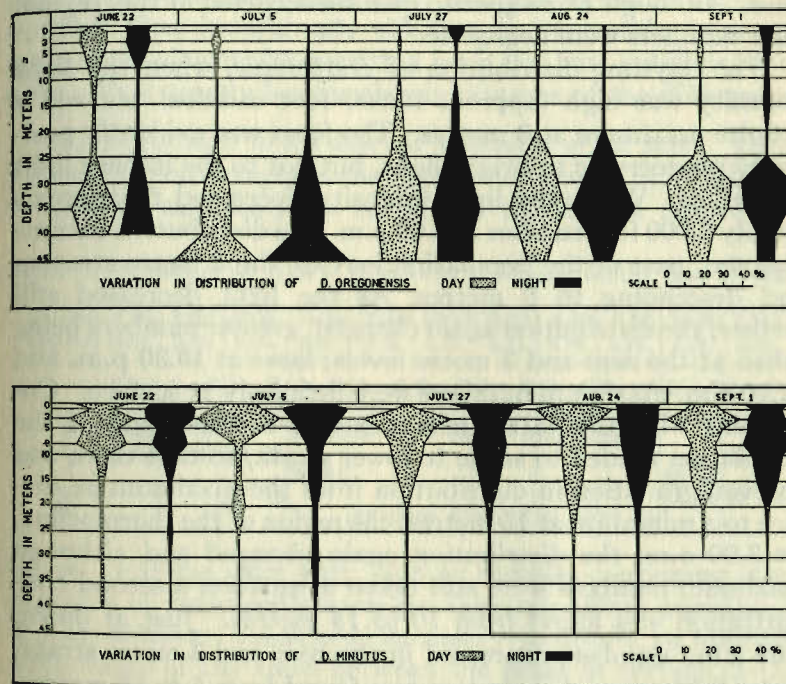


FIGURE 8.—Seasonal differences in diurnal movement of *Diaptomus* group, 1935.

No correlation exists between the light intensity at the time of daylight sampling and the subsequent nocturnal distribution, nor was there any observable difference in light intensity between the nights when movement was observed and those nights on which adult *D. oregonensis* failed to migrate towards surface. Other factors, the nature of which are not known, must at times limit the response of this species to diurnal changes in light intensity.

Diaptomus minutus (Lilljeborg)

(a) **Diurnal movement on June 27, 1934.** The upper panel of figure 5 represents the changes in distribution of adult *Diaptomus* throughout the diurnal cycle. The diagrams can be taken as indicative of the movement of *D. minutus*, for it was the abundant diaptomid taken in the epilimnion at this time. Although *D. oregonensis* adults occurred in this region, their numbers were negligible.

The daytime distribution of *Diaptomus*, when the light intensity was high (approx. 10,000 foot candles), showed a definite maximum at 3 metres. The form was evidently positively phototropic to bright light, but not to the intense light at surface. When the light intensity decreased to approximately 2,000 foot candles at 6.00 p.m., the distribution became bimodal, part of the population leaving the 3 metre stratum and descending to 8 metres. As the light decreased still further, the distribution again changed, greater numbers being taken at the zero and 3 metre levels; later at 10.30 p.m. and 12.10 a.m. maximum numbers were definitely at surface. Coincident with this latter movement to surface, part of the population tended to settle to lower strata, so that there was an even gradation in distribution from the maximum at surface to a minimum at 15 metres, the region of the thermocline. At 3.00 a.m. the distribution again changed and although maximum numbers were still taken at surface, a second concentration was found from 10 to 15 metres. Just at dawn, 4.00 a.m., numbers decreased in the zero and 3 metre strata, and a fairly even distribution was found from 5 to 15 metres. A light intensity similar to that found previously at 6.00 p.m. failed to produce a bimodal distribution at 6.30 a.m. This was possibly because the light was increasing rather than decreasing. By 10.00 a.m. a unimodal distribution was again produced, the maximum occurring at 5 metres, and by noon it had become bimodal once more, maxima being found at 3 and 8 metres as at 6.00 p.m.

It is, therefore, clear that the population of *D. minutus* in lake Nipissing does react to changes in light intensity, in that

its distribution changes markedly throughout the cycle. Marsh (1897), however, found no such reaction for this species.

The bimodal type of distribution suggested a difference in the composition of the population at the two modes, certain individuals reacting differently from others to existing conditions. A determination of the sex ratio at certain depths suggests a possible explanation. The problem is, however, so complex that its ultimate solution is impossible from the series of small samples resulting from the final subdivision to sexes. This greatly lessens the significance of the differences.

(1) *Differences in the diurnal movement of the sexes.* Table 8 gives the percentages of the males and females of *Diaptomus minutus* in samples from certain of the depths referred to

TABLE 8.—Percentage sex ratio of *D. minutus* at different depths, June 27, 1934.

Depth metres	12.10 p.m.		3.30 p.m.		6.00 p.m.		8.00 p.m.		10.30 p.m.		12.10 a.m.		3.00 a.m.		4.00 a.m.		6.30 a.m.		10.00 a.m.		2.115 p.m.		
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	
0	68	32	72	28			90	10	25	75	17	83	24	76	28	72	79	21					
3	58	42	53	47	92	89																84	16
5							35	65														58	42
8					27	73																38	62
10									52	48	58	42	45	55	50	50	31	69					

above. For the most part, only in samples containing large numbers of individuals were sex determinations attempted. It was, however, considered necessary to obtain an approximate value of the ratio between the sexes in certain of the samples of special significance, even though the numbers were smaller.

The maxima observed at 3 metres at 12.10 p.m. and 3.30 p.m. when light intensity was high were apparently composed of fairly equal numbers of males and females. Above these maxima the surface population was made up of more females than males.

In the upper maximum at 6.00 p.m. females predominated to a marked extent, whereas in the lower maximum at 8 metres, the reverse was true. At 8.00 p.m. the females still

remained predominant in upper layers, while males predominated at the 5 metre level.

At 10.30 p.m. a definite change occurred; males became more numerous at surface and numbers of males and females became equalized at 10 metres. This condition became more marked at the surface by midnight and the proportion of males at 10 metres became slightly lower. The distribution of the sexes at 3.00 a.m. and 4.00 a.m. was apparently quite similar to that at 10.30 p.m.

By 6.30 a.m. a radical change again took place and females predominated at the surface and males were again predominant at 10 metres.

At 10.00 a.m. the maximum at 5 metres was made up of fairly equal numbers of males and females, as were similar maxima at 3 metres the previous day; at 8 metres there occurred a slight predominance of males.

In the mid-day distribution, which was bimodal, the upper mode was predominantly composed of females, the lower predominantly of males, as was observed in the other bimodal distribution at 6.00 p.m.

(2) *Summary.* Both males and females appeared to be positively phototropic to bright light. Females were taken in greater proportion at the surface since they were not sensitive to the same intensity of light as males.

With declining light intensity, when the value reached some 2,000 foot candles, some males separated from the rest of the population and congregated at levels slightly lower, producing a bimodal curve for the total population. Females, on the other hand, showed a slight tendency towards an upward movement, numbers at the surface having increased slightly and males having in part moved downward. Females remained in surface layers when the light intensity decreased still farther and twilight condition existed. Males, however, dispersed in layers slightly lower than where they were previously taken in maximum numbers.

After an hour or more of complete darkness, males definitely moved to the surface, since total numbers at the surface did not change appreciably, and the ratio of males to females

became 3:1 as compared to 1:9 at 8.00 p.m. Similarly it was evident that females must have settled away from surface.

This condition, with slight variation, continued until dawn, at which time fairly large numbers of females were taken at the lower levels near the thermocline, and males still predominated at surface.

Two hours after dawn, with light intensity increasing, the distribution showed the result of an active migration of females towards surface, and males had again moved downwards.

After light conditions had become stable by 10.00 a.m., equal numbers of males and females occurred at the 5 metre maximum, with a predominance of females in the population above that level.

The distribution at mid-day, with a light intensity of 4,000 foot candles, was again of a bimodal type, with a maximum of males at a lower level than that of the females. The distribution at this time is not understood, but may have been a result of variations in light intensity previous to sampling, and hence not observed since light measurements were taken only at periods of sampling.

(3) *Conclusions.* The movement of the population of *D. minutus* in lake Nipissing, throughout the diurnal cycle, appears to be the result of a complex movement of the two sexes, for the differences in sex ratios at different depths have been found to be statistically significant. The distribution under conditions of intense light was unimodal, with a maximum near surface, in which the ratio of the two sexes was approximately 1:1. The movement of males downwards under decreasing light intensity caused a bimodal type of distribution, the upper mode of which was predominantly of females, the lower of males. Females apparently did not react actively to decreasing light, or in darkness, as they only gradually left the upper layers and by dawn were found in largest numbers near the thermocline. Males did react actively in the absence of light, and large numbers occurred at surface shortly after darkness set in, and remained until dawn. When light intensity had increased after dawn, males at first actively

moved downwards and females actively came to the surface. Later the unimodal distribution was produced, in which the sexes were equalized at 3 or 5 metres, depending on light intensity. Above this mode females predominated and below it males were predominant.

Southern and Gardiner (1932) state for *Diaptomus gracilis* in Lough Derg: "The adult males and females do not differ in their vertical distribution." In the population of *Cyclops strenuus* in the same lake, males predominate at the bottom at all times, the preference for the lowest layers being most marked from sunset to midnight. Females of *Cyclops strenuus* predominate at levels above the male population, and are apparently the most active in performing the diurnal migration. Kenzo Kikuchi (1927) shows in the diurnal distribution of *Diaptomus pacificus* in Kizaki lake that females had their maximum at lower levels than males and were more active in performing the diurnal migration. Males and females of *Cyclops strenuus* in the same lake were both most abundant at bottom, 28 metres, but males predominated at 25 and 20 metres. It is evident that in each lake, each species, and the sexes of each species, show an individuality in their reactions to environmental conditions.

(b) **Seasonal differences in diurnal movements, 1935.**

The diurnal movements of *D. minutus* also differed throughout the season (fig. 8, p. 37). On June 22 the individuals from the daylight mode at 3 metres, immediately above the thermocline, evidently scattered out towards surface at night. Certain individuals producing a maximum just below the thermocline apparently did not change their position greatly. On July 5 certain individuals in the daylight maximum at 3 metres moved to the 1 metre level at night, and others scattered downward producing a gradation in concentration from the maximum at 1 metre to a minimum at the thermocline. A similar change took place on the nights of July 27 and August 24, although in these cases the maximum abundance was found at surface. In these three cases males were predominant at the upper mode and females at the lower limit at night. This change is quite similar to that observed in the

diurnal study on June 27, 1934. On September 1 there was a nocturnal movement of males to the surface, and a concentration of females at 8 metres. Detailed temperature relations in this region were not obtained on this date, and the cause of this concentration is not known. It is evident that factors other than diurnal changes in light were affecting the migrations of this species as well. Juday (1903) also found considerable variation in the movement of *Diaptomus spp.* from lake to lake, and in certain lakes at different times during the summer.

Cyclops group

(a) **Diurnal movement on June 27, 1934.** The third panel of figure 5 indicates the diurnal movements of *Cyclops*, as observed over a twenty-four hour period on June 27, 1934.

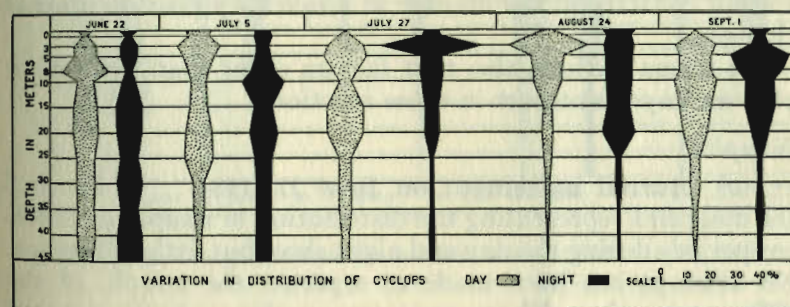


FIGURE 9.—Seasonal differences in diurnal movement of *Cyclops group*, 1935.

It is clear that on this date there was no definite trend to changes in distribution throughout the diurnal cycle. A possible exception was the slight downward movement in upper levels during the night. Daylight apparently attracted some individuals to maxima near the 3 metre level.

(b) **Seasonal differences in diurnal movements, 1935.**

Contrasted with the above lack of movement, we observe marked differences in diurnal changes at different times during the 1935 season (figure 9). On June 22 the most important change was a loss at night of the 8 metre maximum, which was

immediately below the thermocline. On July 5 we note a definite nocturnal movement downward from upper strata and the formation of a maximum at 10 metres. On July 27 a concentrated upward migration from 15 and 20 metre levels resulted in a definite maximum at 3 metres at midnight. On August 24 the daytime maximum at 3 metres changed to a fairly uniform distribution from surface to thermocline region during darkness. On September 1 another upward movement resulted in the production of a maximum at 5 metres at night.

(c) **Conclusions.** The changes exhibited by the combined species of *Cyclops* are indeed diverse. It is quite probable that the separate reactions of the three species is in a large measure responsible for the great difference in behaviour exhibited from time to time. It seems likely also, in view of the comparisons of other specific groups, that even the species are not constant in the manner in which they react to diurnal changes.

It seems obvious also that factors other than light must play an important part in these reactions.

Nauplii

(a) **Diurnal movement on June 27, 1934.** In figure 5 the diagrams representing the distribution of nauplii at different periods during the day and night show but little difference. No attempt has been made to separate the nauplii of the different species. There was apparently no movement of nauplius stages correlated with changes in light intensity at this date.

(b) **Seasonal differences in diurnal movements, 1935.** From figure 10 which indicates variations in day and night distributions throughout the summer of 1935, we observe that this stage was, as was the case for adult copepods, not constant in its reaction to changes of light. On June 22 there was a slight concentration in mid-hypolimnetic layers. On July 5 there was a movement away from surface at night and the formation of a bimodal distribution. On July 27 a more even distribution was produced in the upper 3 metres, as contrasted with the daytime maximum at 1 metre. A second

mode also formed at 10 metres on this night. On August 24 a definite settling downward occurred at night, producing a fairly uniform distribution from surface to 20 metres, the region of the thermocline. On September 1 a similar movement took place, but maximum numbers continued to remain at upper levels, although not in the surface stratum.

(c) **Conclusions.** The daytime distribution of nauplii in lake Nipissing as indicated in figure 10 and figure 26 (p. 84) tended towards maximal numbers at or near surface. This was definite after July 1. The nocturnal movement appeared to be away from the upper levels, although this was more or less imperfectly expressed at times. It is believed

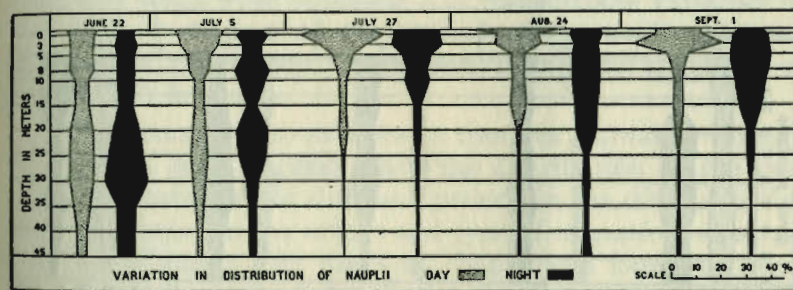


FIGURE 10.—Seasonal differences in diurnal movement of nauplii, 1935.

that the daylight distribution here was the result of a positive phototropism, the lack of which allows the individuals to settle slowly during the night. The sensitivity to bright light appeared to be stronger at that time, when the upper water had become quite warm.

That the above type of distribution and subsequent nocturnal movement is not constant for larval forms of copepods in general, is evident from the following, although Marsh (1918) gives the general statement that "most of the larval forms of copepods are found close to the surface in the daytime". Birge (1897) states: "In all lakes which I have examined in summer, the great majority of the nauplii have been found in the region of the thermocline. I infer therefore

that this distribution is the common one." Kikuchi (1927) finds for the nauplii of *D. pacificus* a "plurimum" at 8 metres in the day and a nocturnal migration to surface. In 1929 Kikuchi makes a general statement that nauplii are "twilight migrators", *i.e.* they migrate to surface in evening and early morning during rapid changes in light intensity, but are away from surface during the hours of daylight and darkness. Juday (1903) states that in several lakes examined, nauplii exhibited no diurnal movement. From even these few references and the distribution found in lake Nipissing, it is evident that no general positive statement concerning the distribution and nocturnal movement of nauplii is of universal application.

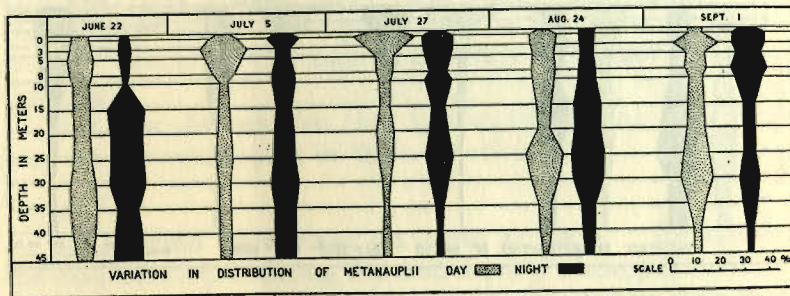


FIGURE 11.—Seasonal differences in diurnal movement of metanauplii, 1935.

Metanauplii

(a) **Seasonal differences in diurnal movements, 1935.** Metanauplii were not enumerated in 1934 but a comparison of the nocturnal changes in distribution at different times during the summer of 1935 may be obtained from figure 11. No marked diurnal changes are exhibited by the metanauplius stages at any time during the year. A slight downward movement from the upper 10 metres occurs on the night of June 22. On July 5 and July 27 the daytime maximum in the upper epilimnion disappears at night, although on the former date some individuals appear to congregate at 1 metre. On August 24 some individuals settle from upper strata and others appear

to scatter into the surface layers in the absence of light. On September 1 there is a slight tendency toward an upward movement at night, larger numbers being taken in the upper 10 metres than during the day.

Summary of Diurnal Movement

Five groups of the plankton crustacea of lake Nipissing were of sufficient abundance that the diurnal changes in their vertical distribution could be detected by 10 litre plankton trap samples. The changes in distribution of each of these groups throughout the diurnal cycle as determined on June 27, 1934, are indicated in figure 5. In 1935 five daylight and midnight series were obtained, and considerable variation in the diurnal changes of the individual groups is apparent throughout the season. These variations are indicated in figures 5-11 inclusive.

Diaptomus minutus exhibited a complex diurnal movement which is in part clarified when the distribution of the two sexes is determined at different periods in the diurnal cycle. Great variation in the extent and type of migration occurred during the season. At times no change was found between daylight and midnight distributions, whereas at other times there is a definite movement to surface at night.

Diaptomus oregonensis in late copepodid stages of development were found in the lower hypolimnion and exhibited only a slight tendency to change their distribution at night. Adults, on the other hand, were found only above the thermocline and differed in their response to changed conditions of light.

The *Cyclops* group, consisting of the combined populations of *Cyclops bicuspidatus*, *Cyclops viridis*, and *Mesocyclops obsoletus*, showed no diurnal change on June 27, 1934, but did show marked differences in their midnight distributions during the season of 1935. Movements away from upper layers, movements producing an extensive maximum at 3 metres by midnight, and movements resulting in uniform distribution in the epilimnion were expressed.

Epischura lacustris, although rather scarce, showed a definite migration on June 27, 1934, but practically no change was observed on June 22, 1935. Later in the season a very definite movement to upper warm strata occurred at night.

Nauplius stages of the above copepoda showed no migration on June 27, 1934. After the upper water had warmed to over 20°C. in 1935, there was a tendency for the nauplii to concentrate at surface in the day, and settle downward at night. This movement was imperfectly expressed at times.

Metanauplii showed no marked diurnal changes in distribution.

Daphnia longispina exhibited a definite nocturnal movement to surface on June 27, 1934, some of the older individuals moving from 15 metres through a rather poorly defined thermocline. During the summer of 1935 considerable variation in the type and extent of diurnal movement was observed.

Discussion

It is not considered advisable to attempt to discuss the many hypotheses involving a great variety of factors that have been put forward in explanation of diurnal migration. Welch (1935), in reviewing the literature, considers light, temperature, food, and gravity to be the important factors involved, but states that: "It is also possible that still other factors may sometimes influence the reactions." Light appears to be the most important factor in this connection, but its effect is without doubt modified by other existing environmental factors. That these are of great importance is clear from the variation in response exhibited at different times during the season in lake Nipissing.

It is because of this great complexity of inter-acting factors that it has been impossible to assign causal factors to the variations in type and extent of diurnal movement exhibited in the lake. It is believed that comprehensive experimental investigations, based upon the field observations of the many workers in this field, are of prime importance in furthering this study. The data discussed above also lend force to a

statement made by Juday (1903) which is in part: ". . . diurnal movement is not a simple phenomenon, which may be attributed to a single factor. On the contrary, the movement in each lake presents complexities which can be solved only by *complete observations that cover a considerable period of time*" (italics are present author's).

Welch (1935), in discussing the dependability of predictions of diurnal movement in uninvestigated lakes, says: "with knowledge of these phenomena still incomplete, the only safe procedure is to make an actual examination of any new situation." The variations in diurnal distributions observed in lake Nipissing illustrate the necessity of considering even different periods of the season as "new situations", and indicate the value of these night samples in the productivity work discussed in a later paper. It is realized that samples taken only at midnight and mid-day do not give a complete picture of diurnal migration. They do, however, serve the purpose of showing the great variations in this phenomenon during any one season. These day and night samples were primarily taken as indicative of the nocturnal distribution of the plankton crustacea, in an attempt to determine the utilization of the different forms by the cisco population.

Conclusions

There are definite diurnal migrations exhibited by the plankton crustacea of lake Nipissing, which are correlated with changes in light intensity. Light appears to be the most important causal factor, but its effect is modified by other environmental conditions.

The diurnal movements of the various plankton crustacea indicate marked differences in the response to changes in environmental conditions. This is noticeable among different species, between the sexes of a species in one case, and among different developmental stages of an individual species, or of a group of species.

The type and extent of diurnal migration of any one species are not constant during the season.

The diurnal migration results in differences in the density of individual species at different levels in the lake, and is of importance in their availability to plankton feeders.

These changes in the concentration of the various species of the population, at different depths, must be taken into account in considering the seasonal differences in their vertical distribution.

PART II: SEASONAL DIFFERENCES IN VERTICAL DISTRIBUTION OF THE LIMNETIC CRUSTACEA OF LAKE NIPISSING

In view of the marked horizontal variation in distribution, and the differences in diurnal migration exhibited during the season, it may appear futile to attempt a discussion of the seasonal differences in the vertical distribution of the plankton crustacea. But differences in the numbers of an individual species at different depths are so marked, and trends in the changes from depth to depth so noticeable, that their significance must be appreciated. Trends in the changes of vertical distribution during the season also lend significance to the differences observed. Even though there are marked horizontal variations in distribution, it is believed possible to observe real differences in vertical distribution by taking a number of vertical series of samples at one station, at weekly intervals. It is also believed that these differences can be correlated with changes in physical and chemical conditions in the lake.

The diurnal movements previously discussed are primarily a result of reactions to changes in light intensity. The effect of this factor in the study of vertical distribution has been minimized by sampling whenever possible, on bright days between 10.00 a.m. and 2.00 p.m. Between these hours light conditions were relatively stable, and, as shown by the diurnal migration study, the plankters do not migrate to any great extent at this period. Since the absolute light intensity has some effect on the vertical distribution of these forms, the light intensity was measured at the time of sampling and will be discussed in the analyses below. Table 9 (p. 117) indicates

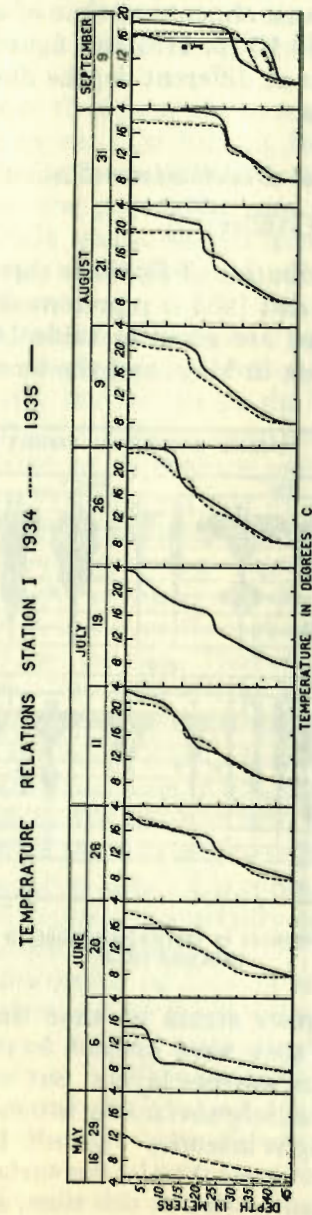


FIGURE 12.—Temperature in degrees Centigrade, at different depths, lake Nipissing, 1934 and 1935.

the light intensity measurements at time of sampling both in 1934 and 1935. Table 10 (p. 118) and figure 12 indicate the temperature relations at different depths during the summer seasons of both years.

Vertical Distribution—Station I

Daphnia longispina (Müller)

The vertical distribution of *Daphnia* throughout the summer seasons of 1934 and 1935 is represented in figure 13 and the numbers obtained are given in table 14 (p. 126). Few individuals were taken in May, and the form was practically

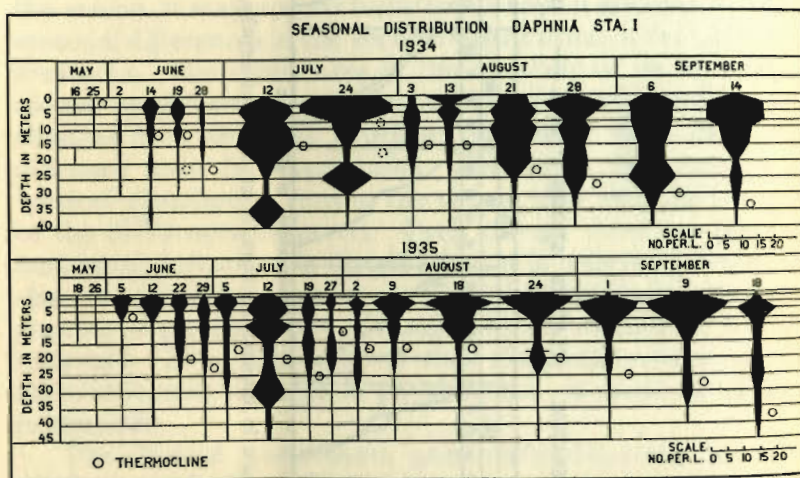


FIGURE 13.—Seasonal differences in vertical distribution of *Daphnia*, station I, 1934 and 1935.

restricted to the upper strata at that time. In June, as numbers increased, they were present in maximum concentrations in the upper warmer layers, but were evidently repelled from the immediate surface by intense light. On June 22, 1935, when the light intensity was only 1,800 foot candles, quite large numbers were taken in the surface catch. It was noted during the enumeration at this time, and subsequently,

that the smaller individuals made up the population in the upper 10 metres, and large individuals predominated below this depth.

During the month of June the water was well populated to the thermocline region. On July 12, 1934, when *Daphnia* increased to an early summer maximum in both years, the major portion of the population was still found above the thermocline. There was a definite decrease in the region of most rapid change in temperature, and a second concentration in deeper strata.

In 1934 the maximum persisted until July 24, but the distribution was markedly different on July 12 and July 24. As opposed to few individuals at the surface and a heavy population to a depth of 15 metres on July 12, extremely large numbers were taken at the surface and a definite concentration existed above 8 metres on July 24. The concentration in the hypolimnion was also 10 metres higher on the latter date.

Two factors are apparently responsible for these differences. (1) The light intensity on the earlier date was the highest observed at any time throughout the summer, having a value of 10,800 foot candles. That measured on July 24 was 7,200 foot candles. The very intense light on the former date apparently repelled all individuals from the immediate surface, and forced the hypolimnial maximum to 35 metres. On the latter date the maximum in the hypolimnion rose to 25 metres in response to the lessened light intensity. (2) A secondary temperature gradient had been formed between 8 and 12 metres on the latter date. The concentration in the warm layers above this gradient apparently occurred as a reaction to these temperature conditions.

In 1935 the maximum on July 12 was not as great as in the former year, and as the thermocline lay at the 20 metre level, there was no marked concentration in upper strata. The light intensity of 8,400 foot candles apparently allowed the hypolimnial maximum to rise midway between that observed in 1934 on the two dates discussed above.

The decrease from maximum numbers was rapid in both years, and the distribution became similar to that observed

in June. The increase toward a second maximum, however, occurred fairly soon. This was more marked in 1934, the interval being of the order of two weeks as compared to a month in 1935. This second seasonal maximum was in both cases practically restricted to the epilimnion.

There was a definite difference in the distribution in August and September in the two years. With the exception of September 14, the autumnal distribution in 1934 was characterized by the presence of large numbers down to the thermocline region (below 20 metres). On September 14 large numbers were taken to a depth of 15 metres. Conversely in 1935 only small numbers were taken below 10 metres from August 18 until September 18. Again two factors appear to be of importance with respect to these differences. (1) As may be seen from the table of light intensities (table 9, p. 117), the light at the time of sampling in each case in 1934 was considerably less than in 1935. As was noted in the day and night series in 1935 (p. 33), the nocturnal movement was away from upper strata, thus destroying daylight maxima near surface. It is possible that the lower light intensities in 1934 did not attract the population to maxima near surface, as was the case in 1935. The definite concentration on September 14, 1934, noted above as an exception, falls into place when it is observed that the light intensity was double that on the preceding dates of sampling. (2) The autumnal temperature relations in 1934 were characterized by homothermous conditions from surface to thermocline, while in 1935 a definite gradient existed from the warmer surface to the thermocline region. It is quite probable that this, too, played a part in the concentration of the population in upper strata in 1935.

Holopedium gibberum (Zaddach)

The cladoceran *Holopedium* was taken in the upper strata of lake Nipissing in the spring, as indicated in the right-hand portion of figure 14. It disappeared from the catches in June, and was not again taken during the summer or autumn as may be seen from table 14 (p. 127).

The disappearance of this form might be accounted for in two ways. Firstly, the increasing temperature in the spring might at some critical point inhibit reproductive activity or prove lethal to the population. In 1934 the form persisted in fairly large numbers until June 19, but in the next year was almost entirely absent by June 12. Table 10 (p. 118) giving the water temperature, indicates, however, that the upper strata were considerably warmer during the former year, when *Holopedium* persisted longer. Secondly, the form may supply certain food requirements of higher organisms, as the ciscoes, to such an extent that its reproductive activity is

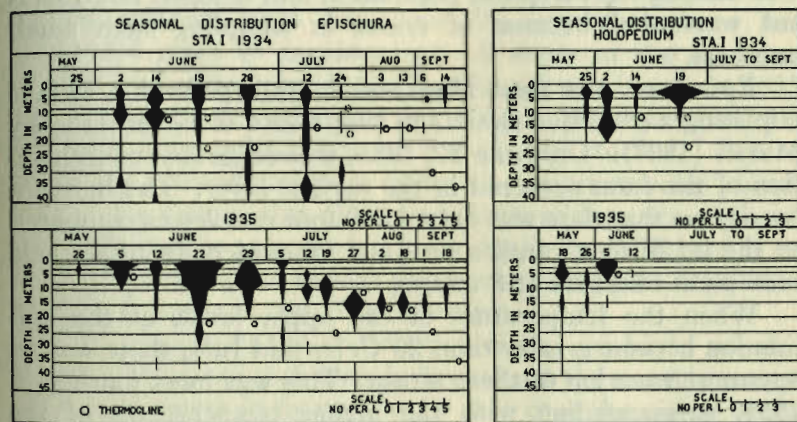


FIGURE 14.—Seasonal differences in vertical distribution of *Epischnura*, and *Holopedium*, station 1, 1934 and 1935.

unable to maintain the population when consumption is at a peak. In 1935 when the utilization of the plankton by the cisco was investigated, it was observed that large amounts of *Holopedium* were taken in the spring, before other food organisms became abundant. The form was evidently "selected" since it appeared in stomachs in greater numbers relative to the other organisms than in the water. Even if *Holopedium* is subject to definite selection, it is impossible to imagine complete extermination by such means. It is possible that both increased temperature and consumption were re-

sponsible for the absence of this organism in the summer months. It is not known how this organism continues to appear in lake Nipissing each succeeding spring. Scattered individuals may live throughout the summer and fall, or ephippial eggs may be produced during the decline in June, to remain inactive until the next spring.

Epischura lacustris (Forbes)

The seasonal change in the vertical distribution of *Epischura* is graphically represented at the left in figure 14 (p. 55), and the numbers taken are given in table 14 (p. 128). We are here dealing with a sparse population and detailed analysis is not warranted because of errors in sampling such small numbers.

Epischura, was most abundant in the epilimnion in lake Nipissing a condition similar to that found in Green lake by Marsh (1897). On June 22, 1935, a considerable concentration of the form occurred in the surface layer. The light intensity on that date was only 4,800 foot candles as compared to the 9,120 foot candles on June 29, which definitely held maximum numbers at 8 metres.

When the temperature of the upper levels of the epilimnion became greater than 20°C. by mid July, there was an apparent vacation of these strata. This was most marked in 1935, corresponding with the higher temperatures of the epilimnion, and a concentration again occurred at depths with temperatures just below 20°C. With the exception of July 27, these concentrations were just above the thermocline region. That this vacation of upper, very warm strata was not simply the result of limiting temperatures was shown by the fact that the population moved into these strata at night. It appears that the form is more sensitive to light when in warm water than in cold. No marked difference in the transparency of the lake water was noted during the period, and with the exception of July 19, the light intensity was comparable throughout the period.

In 1934 there were apparently more individuals in lower strata than in 1935. No factor or factors have been found to

be clearly responsible for this difference in distribution. The relatively large maximum on June 22, 1935, probably accounts for the greater survival throughout that summer, although too much weight must not be given to apparent differences after that date, since the errors of sampling must be great, due to the scarcity of numbers.

Diaptomus group

(a) **Introductory.** During the enumeration of *Diaptomus* in the plankton trap samples of 1934, it was noticed that samples from the epilimnion contained adults of both *D. oregonensis* and *D. minutus*, but hypolimnial samples were almost entirely large immature *D. oregonensis* in a late copepodid stage of development. A study of the food and feeding of *Leuchichthys artemis* (Le Sueur) was begun in 1935, and it was observed that the larger form, *D. oregonensis*, was the only diaptomid taken by the ciscoes studied. It was, therefore, deemed necessary to obtain a more detailed knowledge of the distribution of the two diaptomid species. Accordingly they were enumerated individually in 1935, and a re-count of the separate species was made on certain of the more important series in the 1934 collection.

The changes in the distribution of the combined population of *Diaptomus* at station I, throughout the summer season of 1934, is shown in figure 15. In each case the region of the thermocline is indicated by a circle to the right of the distribution diagram, and a representation of the temperature relations at different depths over a comparable period in 1934 and 1935 is given in figure 12 (p. 51). The early spring catches indicate the building up of the population by progeny of overwintering individuals. After June 14 each diagram of the series shows a maximum in the epilimnion, a decrease in the thermocline region, and a second maximum in the hypolimnion. The vernal increase involves primarily the group which inhabits the upper strata, and, correspondingly, the seasonal maximum is reached earlier in the epilimnion than below the thermocline.

In order to compare in more detail the production and

distribution of the two species in 1934 with those for 1935, the recounts are represented in figure 16. It should be noted that the distribution of *D. oregonensis* is plotted on half the scale used for *D. minutus* because of the great concentration of immature individuals of the former species in the lower strata. The numbers of each species of *Diaptomus* taken in 1934 and 1935 are recorded in table 14 (pp. 129-30).

(b) *Diaptomus minutus* (Lilljeborg) in 1934. *D. minutus* differed markedly from *D. oregonensis* in its vertical distribution. In general all stages of development appeared to find optimum conditions in the upper warmer layers where food was abundant. The adults were not restricted to the

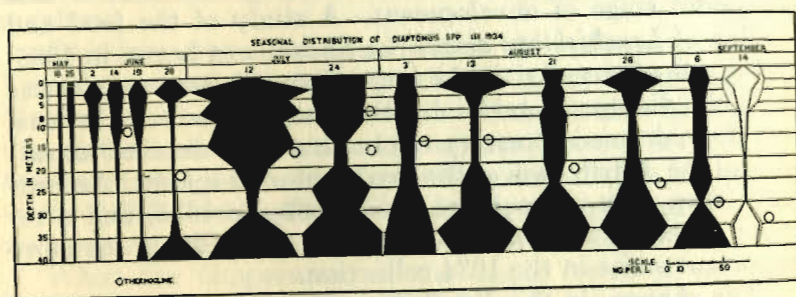


FIGURE 15.—Seasonal differences in vertical distribution of *Diaptomus* group, station I, 1934.

epilimnion to the same degree as those of the other species, for although maximum numbers were in all cases taken above the thermocline, they did extend into the hypolimnion to some extent. The number of adult *D. minutus* was considerably larger than that of *D. oregonensis* at all times during the summer, which might be expected with this form, which does not lose its progeny to a cold hypolimnion where they are consumed in very large numbers, and where, even if they escape such a fate, they develop but slowly. *D. minutus* also reacted more quickly in the spring, in that the population was built up earlier than that of *D. oregonensis*.

An explanation of the differences in vertical distribution is

greatly complicated by differences in temperature and light conditions, as may be seen from the following. On July 12, 1934, although there was temperature gradient at 15 metres, the population extended in fairly large numbers to a depth of 25 metres. On July 24, under similar temperature conditions larger numbers were found at surface, and the lower

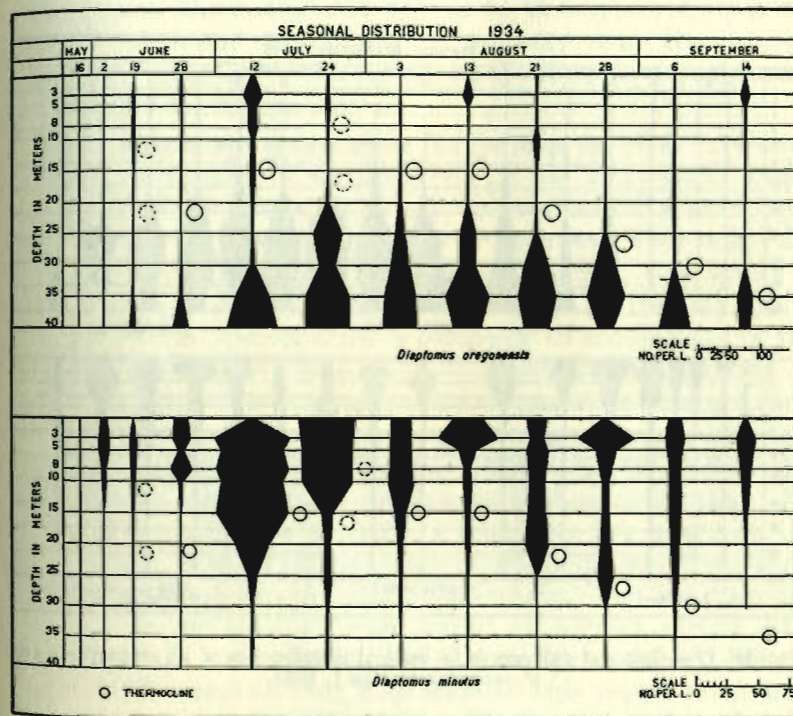


FIGURE 16.—Seasonal differences in vertical distribution of *D. oregonensis* and *D. minutus*, station I, 1934.

limit of distribution for the major part of the population was considerably higher. The difference is here correlated with differences in light intensity. From table 9 it may be seen that the light intensity, when the samples were taken on July 12, was 10,800 foot candles at the surface, while on July

24 it was only 7,200 foot candles. After the beginning of August, the species was again taken only in the epilimnion. With the descending thermocline in late August, the lower limit of distribution is extended progressively to greater depths. From the data at hand, no feasible explanation can be given for the peculiar maxima observed at 3 metres on August 13 and August 28. Conditions of light intensity at the

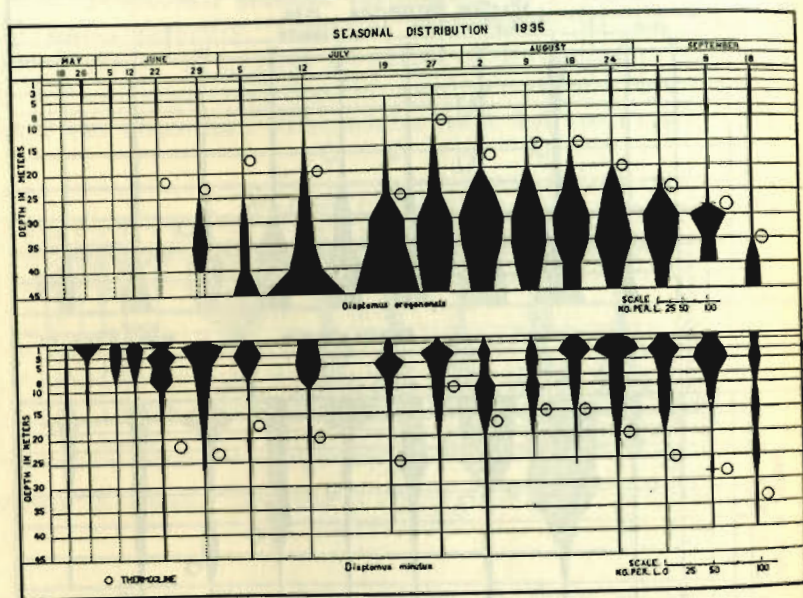


FIGURE 17.—Seasonal differences in vertical distribution of *D. oregonensis* and *D. minutus*, station I, 1935.

time of sampling yield no correlation, and temperature conditions were uniform from surface to a depth of 15 metres.

(c) *Diaptomus minutus* (Lilljeborg) in 1935. From figures 16 and 17 it may be seen that in general the population of *D. minutus* behaved similarly in the two years under discussion. In 1935 the species again reacted quickly to favourable conditions in the spring, and the population soon rose to a maximum. This maximum was composed of fewer

individuals than in 1934 and did not continue as long as in the previous year. In late August and early September a second maximum occurred. The species was largely restricted to the epilimnion, although at times small numbers appeared below the thermocline. In late August and September the population followed the descending thermocline as in 1934. With regard to the difference in distribution within the epilimnion, there does not appear to be any correlation between maximum abundance at or very near the surface, and light intensity at the surface at the time the samples were taken (see table 9, p. 117).

(d) *Diaptomus oregonensis* (Lilljeborg) in 1934. As mentioned previously, the specimens of *D. oregonensis* taken in the epilimnion were almost all adults, and these were practically restricted to that portion of the lake. This is in conformity with the observations of Birge (1897) who states of the species in lake Mendota: "In no case do the older individuals of the species show a tendency to accumulate in the deeper water of the lake. . . ." Below the thermocline in lake Nipissing only late copepodid stages were obtained, and as the season advanced very large numbers congregated near bottom. It is believed that the very restricted area of this deep water is responsible for this marked concentration.

The reproductive activity of relatively few adults in the epilimnion, then, produced large numbers of immature forms which penetrated to the cold hypolimnion. The fact that few nauplii or metanauplii were found in bottom strata after stratification was well established (see figures 26 and 27, pp. 84 and 86) suggests that migration to this region must take place at some copepodid stage. During the period of most rapid growth the immature stages were, therefore, present in upper strata where phytoplankton food was abundant.

The presence of immature *D. oregonensis* in bottom strata was apparent by June 2 (see figure 16), and a gradual increase took place until early July. Maximal numbers were taken during July and at this time they were still most concentrated near bottom. By the middle of August, however, the distribution had changed, and there was evidently a migration

of part of the population to immediately overlying layers. This migration may be the result of at least two factors. As will be shown later, the consumption of this form by the cisco population during July, 1935, was most marked in the lower 10 metres of this deep water area. As this may be considered the usual occurrence for most years, the consumption in 1934 would tend to deplete the population of *D. oregonensis* to the greatest extent in this region. However, it is clear that when the form migrated to the hypolimnion in spring it became most concentrated at bottom. If part of the population were consumed, one would expect a continued migration to take its place unless some other factor prevented such a migration in mid-August. This factor seems to be a change in the dissolved oxygen and carbon-dioxide content in these lowermost layers.

The change in the dissolved oxygen content at different depths during the summer of 1934 is given in table 11 (p. 120) (data from field notes, J. M. B. Corkill). From June until early August there was a gradual reduction in the amount of dissolved oxygen in lower strata, and carbon dioxide increased gradually throughout this period.

These changes were most marked in the bottom stratum (45 metres) where the oxygen content fell to 3.6 cc. per litre and the carbon-dioxide content rose to 10 p.p.m. by the beginning of August in 1934. At 40 metres, the greatest depth at which plankton samples were taken in 1934, the oxygen content did not fall below 4 cc. per litre and the carbon-dioxide content did not rise above 7 p.p.m. until August 9. Between August 6 and 13 there was a rapid decrease in dissolved oxygen at this depth, from 4.1 cc. per litre to 3.3 cc. per litre, and without doubt there was a relative increase in the carbon-dioxide content. As it was at just this period that a portion of the *D. oregonensis* population appeared to evacuate the 40 metre stratum; it is possible that this organism was reacting to these two factors.

(e) *Diaptomus oregonensis* (Lilljeborg) in 1935. As may be seen from figures 16 and 17 (pp. 59 and 60), the most obvious difference between the populations of *D. ore-*

gonensis in the two years was the increased numbers in 1935. This was in part due to sampling in 45 metres of water rather than in 40 metres as in the previous year. It is strikingly evident that this form concentrated in the very deepest water of the lake in early July. Even neglecting that portion of the population below 40 metres, the production in 1935 was still found to be the greater, and this greater population persisted until well into September. The only apparent difference in conditions in the two years was the much greater distribution of heat to lower strata early in the season in 1934. It is diffi-

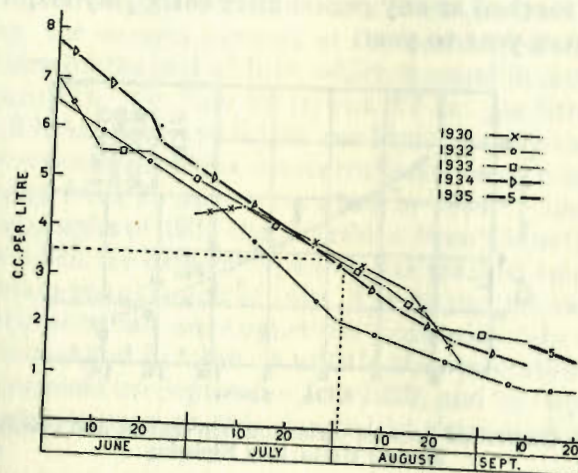


FIGURE 18.—Oxygen depletion at 45 metres at different periods of the season in various years.

cult to assign a definite cause to the greater production of such an organism on the data available, for it was probably dependent upon a chain of events and a combination of factors.

Again, as in the previous year, there was a movement of part of the population from lowermost strata of the hypolimnion to intermediate layers. In 1935 this took place in late July in contrast to the similar movement in mid-August in the previous year.

Although oxygen and carbon-dioxide determinations were not made throughout the summer of 1935, it is believed that

their changes were similar to those observed in 1934, and that oxygen depletion and the corresponding increase in carbon-dioxide content caused the movement of *D. oregonensis* from bottom strata similarly in 1934 and 1935. The stages of oxygen depletion at 45 metres reached at different periods of the summer seasons of previous years are available, and are represented for 1930, 1932, 1933, and 1934 in figure 18 (a modification of plate 28 given by Corkill, 1935). With the exception of 1933, in which year the temperature of the hypolimnion was considerably higher than usual, the stage of depletion reached at any period after early July is quite comparable from year to year.

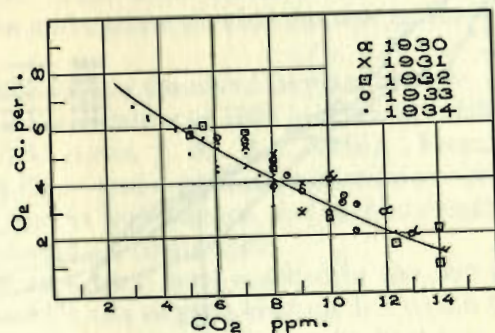


FIGURE 19.—Correlation between carbon-dioxide content and dissolved oxygen in lower strata, lake Nipissing.

Since the stage of depletion reached in early September is similar in 1934 and 1935, and since the temperature of the lower hypolimnial layers was equal after July 1 in the two years, it is quite probable that the oxygen depletion progressed in a like manner in the two seasons.

The correlation between the carbon-dioxide content and dissolved oxygen depletion in the lower layers of the hypolimnion of lake Nipissing is given in figure 19. A considerable number of determinations from different years have been included in the comparison, so that an average relationship is observed. It is clear that a fairly definite relationship does exist, although considerable variation is apparent. It is

realized that both reduced oxygen and increased carbon dioxide may be instrumental in causing the movement of *D. oregonensis* from bottom layers. Due to the variation in the relationship, and to the scarcity of carbon-dioxide determinations, a comparison is attempted between only the depletion of oxygen and the movement of *D. oregonensis*.

If the 1934 dissolved oxygen data (Corkill field notes, 1934) are used without modification in 1935, the following correlation is observed. In 1934 the oxygen at 45 metres decreased rapidly after July 11 (table 11, p. 120). On that date the dissolved oxygen content was 4.5 cc. per litre. Roughly speaking, the oxygen content at the bottom fell to below 3.5 cc. per litre by the end of July, which is usual in normal years (see figure 17). On July 25 it was 3.7 cc. per litre, and by August 2 it had fallen to 3.1 cc. per litre. As discussed previously, it was at about this concentration of oxygen that movement away from 40 metres occurred in 1934. From the distribution graphs of 1935 the migration from 45 metres is seen to occur when the oxygen depletion has reached an estimated similar stage near the end of July. The further migration from 40 metres occurred on August 18, approximately the same time it was noted in 1934. A still further migration from 35 metres occurred on September 1 in 1935, and by September 9 the oxygen content at this depth had decreased to 2.5 cc. per litre.

Concurrent with this upward migration from lowermost layers, the descending thermocline after August 18 carried before it the concentration of individuals in the upper hypolimnion. By September 9 the stage was reached when the thermocline lay between 25 and 30 metres and the oxygen depletion extended from bottom to practically this level. The species was at this time proverbially between the "devil and the deep sea", and apparently its avoidance of low oxygen was the more strenuous, for it penetrated the thermocline to become scattered in the epilimnion by September 18. The descending thermocline, resulting in a concentration of the hypolimnial population, may have been a factor in preventing the migration from 35 metres until the oxygen content fell to

the low figure of 2.5 cc. per litre. In 1934 the depressed thermocline actually increased the concentration at 40 metres on September 6, as it did at 45 metres on September 18 in 1935, although the indications are that many individuals had penetrated the thermocline on these dates. The presence of immature forms above the thermocline at this time lends force to this inference, since reproductive activity in these strata had been slight for some time.

Experimental evidence on the effect of (a) increased carbon dioxide, and (b) decreased oxygen, on vertical movements of plankton crustacea

The peculiar movement of immature *D. oregonensis* from the lower strata of the hypolimnion of lake Nipissing, and its correlation with oxygen depletion and related increase of carbon dioxide, led the author to attempt an experimental analysis of the effects of these two factors separately upon such movement. A series of experiments was conducted employing a vertical gradient tank, designed by Dr. F. E. J. Fry.

The organisms used in this work were *Daphnia magna* (Straus) reared in the laboratory and *Cyclops bicuspidatus* (Claus) obtained in February, 1936, from Grenadier pond, Toronto. A few individuals of *Diaptomus reighardi* (Marsh) were also found in the Grenadier pond samples, but were so scarce that the analysis of their movements was not considered significant. It is interesting to note that with regard to the latter species, so closely allied to *D. oregonensis*, Marsh (1907) says: "It is apparently a rather narrowly localized species, for although collections have been made quite generally in the Michigan and Wisconsin lakes, it has so far, been found only in three localities." In "Freshwater Biology", 1918, he states that the species has been found in only four localities, in Michigan and New York states.

(a) **Apparatus and methods.** The vertical gradient tank consisted of a small aquarium with two glass sides and two wooden sides. A diagram of this tank is given in the scale drawing (figure 20). Through corks placed in the wooden sides, thermometers were inserted at different depths. A cool-

ing coil, through which tap water flowed at a temperature of approximately 10° C., was placed at a height of 7 inches from the bottom. The total height of the water column in the tank was 15 inches. The upper stratum of this column was kept at a constant temperature by means of an electric rod heater, thermostatically controlled with a mercury contact regulator. The immediate upper layers were kept in circulation by rising

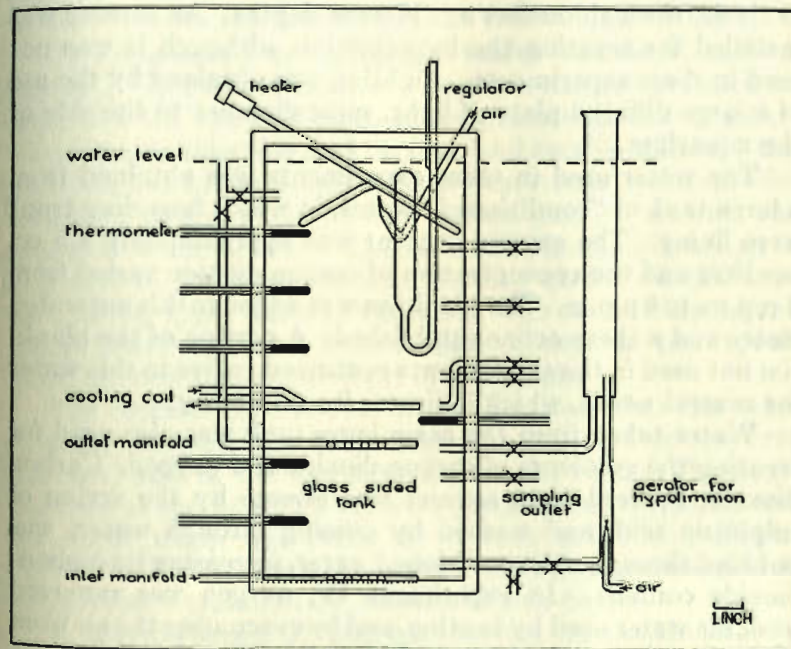


FIGURE 20.—Diagram of Fry's vertical gradient tank.

air bubbles from an inlet 2 inches below the surface. It was possible by cooling the bottom water and warming and circulating the upper layers, to produce a marked temperature gradient at intermediate depths. By modifying the circulation by changing the depth and force of the air jet, it was possible to produce practically any type of "thermocline region" with different relative volumes of "epilimnion" and "hypolimnion" at variously controlled temperatures.

By allowing water, cooled slightly below the temperature of the lower hypolimnion to flow slowly in through the inlet manifold at the bottom, water of high carbon-dioxide content or low oxygen content could be introduced and would remain at the very bottom. This produced a gradient of these gases upward from bottom. An outlet manifold in upper "hypolimnial" layers removed the displaced water without disturbing the system. Water could be removed for chemical analysis, through outlets at different depths. An aerator was installed for aerating the hypolimnion, although it was not used in these experiments. Lighting was obtained by the use of a large diffused plate of light, some distance to the side of the aquarium.

The water used in these experiments was obtained from a large tank of "conditioned" water, in which fingerling trout were living. The oxygen content was approximately 4.5 cc. per litre and the concentration of carbon dioxide varied from 6 p.p.m. to 8 p.p.m. The plankton was added to this untreated water and a thermocline established. A portion of the plankton not used in the experiments continued to live in this water for several weeks, which indicates its suitability.

Water taken from the same large tank was also used for creating the gradients of carbon dioxide and oxygen. Carbon dioxide, evolved from sodium bicarbonate by the action of sulphuric acid, and washed by passing through water, was bubbled through this conditioned water, increasing its carbon-dioxide content. In experiment IV, oxygen was removed from the water used by heating, and by evacuating the air from above in a large winchester. This evacuation with constant shaking was continued for four to eight hours.

The determination of free carbon dioxide was obtained by using the methods given in "Standard Methods of Water Analysis" (1925). Dissolved oxygen content was determined by the Miller method discussed by DeLaporte (1920).

Counts were made of the numbers of individuals at the levels indicated in the diagrams. In the case of *Cyclops*, numbers of individuals were counted at each level by employing a large lens, in front of a narrow opening in a mask. Only

individuals in focus, and within the limits of the mask were counted. This obviated certain errors such as the attachment of large numbers to the glass sides of the aquarium and gave a better average measure of distribution, since the focal point of the lens was approximately at the centre of the tank. The angle iron forming the edges of the aquarium prevented the enumeration of individuals at the bottom in all experiments. Several series of counts within the time interval noted in the figures, were averaged to obtain the values for the diagrams.

(b) **Experiment I. (*Daphnia* under increased carbon dioxide.)** In the first case only *Daphnia magna* were used to determine the effect of an increased carbon-dioxide content. When the thermocline had become well established, and the plankton had had sufficient time to form a steady vertical distribution, cooled water of high carbon-dioxide content was admitted at the bottom. The resultant changing gradient is indicated by the isometric lines showing carbon-dioxide content, in the upper panel of figure 21. The thermocline lay at approximately 4 inches from surface throughout the experiment, as indicated at the right of the graph.

The original distribution of the *Daphnia* after the temperature gradient had been formed is indicated in the first diagram, and in the last diagram at the right. The large numbers at the 14 inch level were predominantly adults, and the upper mode was made up of only small individuals. Below the 14 inch level a still greater concentration was noted, but numbers could not be counted at this depth.

A slight change in distribution was noticeable shortly after beginning the addition of the water of high carbon-dioxide content to the bottom. By the time that 12 p.p.m. of carbon dioxide were determined for the 14 inch level, a portion of the individuals had moved upward, and only large individuals were left. Whether or not these were less sensitive is not known, since they were apparently weighted down, carrying eggs.

The rise in the carbon-dioxide content was so rapid that it is difficult to ascertain the exact concentration responsible for the movement observed. That there was a definite up-

ward movement under the influence of this factor is evident. Apparently the rise in carbon dioxide from 6 p.p.m. to 10 or 12 p.p.m. caused some individuals to move. It is believed that this concentration would not have caused the movement of all individuals even in an extended time. Large females, carrying eggs, were found at bottom at all times. By the time that a value of 48 p.p.m. of carbon dioxide was determined

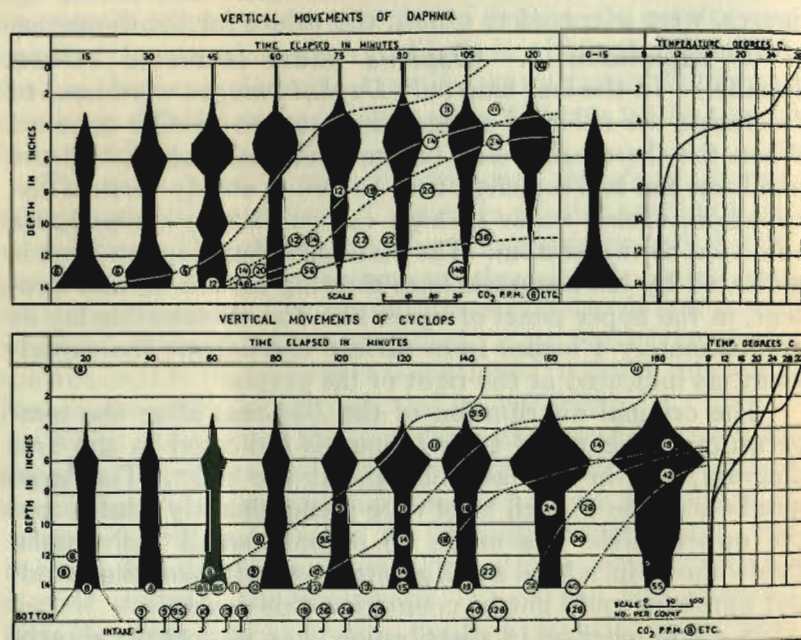


FIGURE 21.—Vertical movements of *Daphnia* and *Cyclops* under conditions of increased carbon-dioxide content at lower levels.

at the 14 inch level, many of the large specimens appeared to be asphyxiated at the bottom. The continued lack of individuals under the 48-56 isometric line is to a great extent due to the asphyxiation of individuals in these strata. Some increase is, however, noted in upper levels in the 120 minute diagram.

These individuals in upper strata show a secondary up-

ward movement as the carbon-dioxide content increases in the lower "thermocline region". The upper limit of the general population is progressively forced higher and higher in the warmer layers at the "thermocline". The upper temperature limit which they will tolerate under these conditions appears to be about 20° C.

(c) **Experiment II.** (*Cyclops* under increased carbon dioxide.) An attempt was made, using *Cyclops bicuspidatus* (Claus), to determine with more exactitude than above the concentration of carbon dioxide necessary to (a) originate and (b) cause a more general movement of this form from lower levels. Carbon dioxide was added gradually at first to the water to be introduced, and later the carbon-dioxide content of this inflowing water was increased more rapidly. As discussed in experiment I the isometric lines indicate the changing carbon-dioxide gradient, and in addition the carbon-dioxide content of the inflowing water is indicated in the lowermost circles in the lower panel of figure 21. It should be mentioned that at the beginning of the experiment a well-defined thermocline had not been established. This, however, was soon remedied and has little effect on the results obtained, as no change in distribution occurred before the temperature gradient became fixed.

There was at the outset of the experiment an apparently uniform distribution from the 6 inch level to the 14 inch level. As indicated by the dotted lines below this level, there was a very great concentration of individuals near bottom. Again as in experiment I, it was impossible to enumerate these.

Very little change occurred during the first hour, except that a slight increase is noted at the 6 inch level in the last counts. When the concentration of carbon dioxide had increased to 12 p.p.m. at 14 inches and incoming water had a carbon-dioxide content of 19 p.p.m., a definite increase was noted at the 14 inch level, and at levels above. These increases must have been due to a movement from the concentrated population at bottom.

As the carbon-dioxide content of incoming water was increased to 28 p.p.m. and an increased concentration was noted

up to 8 inches, a definite mode was formed at 6 inches. This mode became much more marked when the carbon-dioxide content at 14 inches reached 15 p.p.m. and a content of 14 p.p.m. existed to 9 inches.

As the concentration became progressively greater in the lower levels, a large maximum was formed in the upper hypolimnion, but *Cyclops* were apparently more sensitive to higher temperatures than *Daphnia* and did not move into the thermocline as did *Daphnia* in experiment I. This was probably due to the fact that they had been collected from below the ice in Grenadier pond and had been kept in cold water until used in the experiment.

From this experiment it is clear that even a slight change in carbon-dioxide content (from 8 to 12 or 13 p.p.m.) initiates an upward movement, and a concentration of 14 and 15 p.p.m. results in a more marked reaction. It might be argued that higher concentrations than these given (*i.e.* 19 to 26 p.p.m.) were the ones responsible for bringing about the reaction, but it must be understood that incoming water is at once mixed with water in the lowermost strata, thus having its carbon-dioxide concentration diluted. It is believed, too, that the initial stages of this movement were observable after sixty minutes had elapsed.

(d) **Experiment III. (*Cyclops* under decreased carbon dioxide.)** An experiment had indicated that there was no upward movement of either *Daphnia* or *Cyclops* when conditions remained stable. However, the question arose as to whether or not the movements observed in experiments I and II were the result of carbon-dioxide gradients or of agitation in lower strata. After the *Cyclops* population had remained in the gradient tank for twelve hours following the completion of experiment II, the distribution observed was that indicated in the first diagram of figure 22. A maximum abundance was noted in the upper hypolimnion, but large numbers were found in lower strata as well. An even distribution existed from 8 to 14 inches. The carbon-dioxide content in all strata was high but the gradient had not entirely disappeared.

In order to determine whether or not agitation at bottom comparable to that involved in experiments I and II would cause an upward movement of part of the population, fresh water of low carbon-dioxide content was introduced at the bottom of the gradient tank when the distribution was at equilibrium under the conditions mentioned above. The thermocline lying in the 3 to 5 inch stratum was kept constant throughout. The numbers determined at different depths have been converted to percentages of the total counts (mean count 385) obtained in each series. The change in carbon-dioxide content at the depths sampled, resulting from the introduction of the fresh water, is indicated within the circles in figure 22.

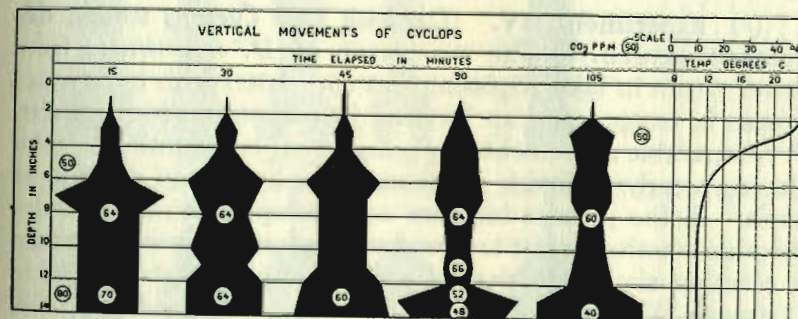


FIGURE 22.—Vertical movements of *Cyclops* under conditions of decreased carbon-dioxide content at lower levels.

When the carbon-dioxide content became equal at 8 and 13 inches, a significantly different distribution was observed. Large numbers were noted in the 12 to 14 inch stratum, and as a decrease in numbers was found at 11 inches, it is likely that movement from the latter level was responsible. A certain amount of leakage had taken place over night, so that inflowing water raised the level of all strata approximately 1 inch. It is believed that this is the cause of the disturbance in the upper hypolimnion.

Progressive decrease in the carbon-dioxide content in lower levels resulted in a definite migration to bottom (15

inches). Since animals at bottom could not be enumerated, the total numbers counted at all levels fell off considerably, so that the percentage graph has been constructed. The very definite movement to lowermost depths is apparent in the last two diagrams of the figure.

It is clear that the effect of inflowing water of low carbon-dioxide content did not result in a movement comparable to that observed in experiment II. Rather the direction of movement has been reversed by a reversal of the carbon-dioxide gradient. The movement downward is very likely expedited by the apparent positive geotropism exhibited by this species under this series of experimental conditions. These movements are then, without doubt, brought about by reactions to carbon-dioxide gradients.

(e) **Experiment IV. (*Daphnia* and *Cyclops* under decreased oxygen.)** The movement of *D. oregonensis* from lower strata in lake Nipissing was correlated with both a decrease in oxygen and an increase in carbon-dioxide content. A comparable movement was induced experimentally by producing a carbon-dioxide gradient at the bottom of a gradient tank. In the present instance an attempt was made to determine whether or not low oxygen concentration would cause a reaction similar to that observed for high carbon-dioxide content. Water treated as discussed under methods on p. 68, was found to contain 1.6 cc. of oxygen per litre when cooled. It was, therefore, necessary to add large amounts of this water to lessen the oxygen content materially in the experimental hypolimnion.

The results of this experiment are graphically represented in figure 23. Oxygen contents at different depths are given in circles. The numbers counted at each depth are again converted to percentages of the total count (mean totals, *Daphnia* 48, *Cyclops* 154) in the column. Three series within each time interval indicated, are averaged in each case.

Certain variations in distribution occurred within the first hour, but no noticeable upward movement took place until the oxygen content at 14 inches decreased to approximately 3.0 cc. per litre. That this is very near the value which initiates

the movement of these two species is indicated by the definite movement observed when the water of the hypolimnion contained only 2.7 cc. per litre. It would appear from the experiment that *Cyclops* were to a slight degree more sensitive to lowered oxygen concentrations than were *Daphnia*.

As has been mentioned previously, difficulty was encountered in decreasing the oxygen content of the experimental hypolimnion, and as may be observed no definite

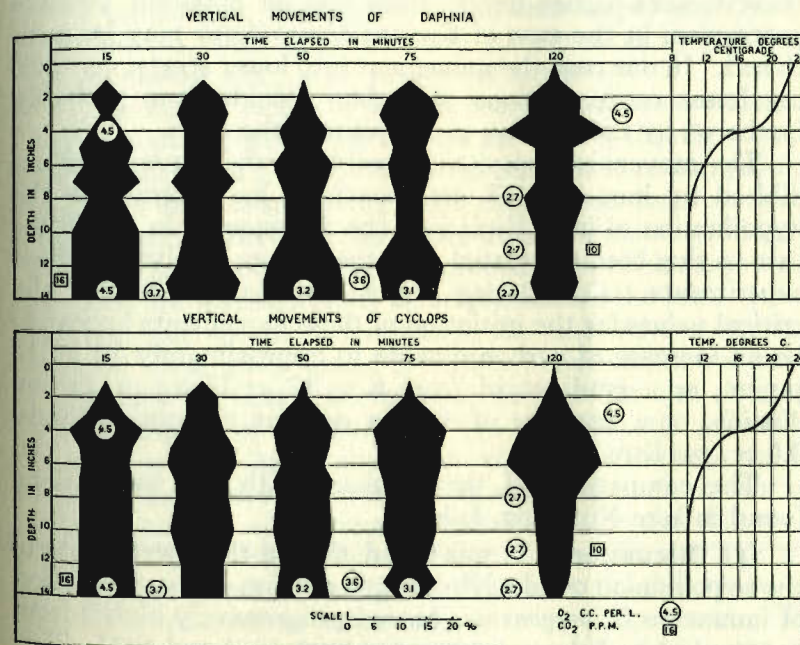


FIGURE 23.—Vertical movements of *Daphnia* and *Cyclops* under conditions of decreasing oxygen content at lower levels.

oxygen gradient was produced. It is clear, however, that low oxygen content did produce a reaction similar to that observed for high carbon-dioxide content. The critical value was apparently about 3.0 cc. per litre of oxygen for *Daphnia magna* and possibly less for *Cyclops*.

(f) **Summary.** By experiments involving gradients of carbon dioxide and oxygen, it has been shown that *Daphnia magna* and *Cyclops bicuspidatus* moved from a region of (a) high carbon-dioxide content to one of low carbon-dioxide content, (b) low oxygen content to one of high oxygen content.

These movements were relatively of considerable extent and involved a fairly large proportion of the population.

In general, the movements counteracted reactions to factors responsible for a definite distribution at equilibrium. Of these factors higher temperature and an apparent positive geotropism in the case of *Cyclops bicuspidatus* may be mentioned. In one case the movement into lower strata, containing lesser concentrations of carbon dioxide, was probably furthered by the positive geotropism of the form.

The movements were comparable to the movements exhibited by immature *D. oregonensis* in lower strata of the hypolimnion of lake Nipissing, the movements in the latter case having been correlated with the factors involved in these experiments. Considering the factors independently, the critical values for the initiation of these movements appear to be an increase of carbon dioxide to approximately 12 or 15 p.p.m., or a gradient of from 8 to 12 or 15 p.p.m. carbon dioxide, or a decrease of oxygen content to approximately 3.0 cc. per litre.

The comparison of these values, with the correlations found in lake Nipissing, follow.

(g) **Discussion.** It was found that in the lower strata of the hypolimnion of lake Nipissing, a portion of the population of immature *D. oregonensis* moved progressively higher from bottom in late July and August of both 1934 and 1935. This movement was apparently correlated with oxygen depletion and the related increase of carbon dioxide in these strata. It seemed evident that this reaction was brought about when the oxygen content fell to about 3.5 cc. per litre and a gradient existed from this value to a higher concentration in strata above.

In figure 19 (p. 64) it was shown that there is a definite relationship between oxygen depletion and increased carbon-

dioxide content in the bottom strata of lake Nipissing. Considerable variation is noted in this relationship, and for the value of 3.5 cc. per litre of oxygen, we find corresponding values of 9, 10, and 10.5 p.p.m. of carbon dioxide, both within the same year at different depths, and in different years at the same depth. The average value would likely be in the neighbourhood of 9 p.p.m. of carbon dioxide.

From experimental evidence, it has been shown that critical values for these two factors, which independently incited comparable movements in *Daphnia magna* and *Cyclops bicuspidatus*, were approximately 12 p.p.m. to 15 p.p.m. of carbon dioxide and 3.0 cc. per litre of oxygen.

That higher values of oxygen content and lower values of carbon dioxide, when the factors are acting together, result in movements of *D. oregonensis* in the lake is not surprising. In fact, what was surprising to the author was the close agreement observed between the values causing similar reactions in *Daphnia* and *Cyclops* under experimental conditions, to those affecting the distribution of *D. oregonensis* in the lake. It was believed that specific differences in the reaction to concentrations of these gases would probably yield results not at all comparable to field observations. It was felt also that the abrupt change of conditions in the experimental procedure would probably bring about the reaction before the values reached the limits indicated. The effect of such an abrupt change may be an alternate explanation for the difference between values which cause these reactions in the lake and under experimental conditions. However, the difference observed is so small as to be only of minor importance. The time necessary to analyse the water samples during the experiment would make difficult a comparison of the above data with those obtained from an experiment involving both factors acting together.

Reference must be made at this point to the comprehensive work of Birge and Juday on this problem. Birge and Juday (1911) state in introduction to their study of dissolved gases: "The animal plankton has not shown any close correlation with the dissolved gases, considered either with reference to

kind or quantity. These gases seem to have no chemotactic effect on the zooplankton, nor do the gaseous products of decomposition, as they exist in lakes, appear to have any unfavorable effect on the animals, such as might determine their distribution in the water of the lake. The zooplankton is excluded from water whose supply of oxygen is too small; but sensitiveness to deficient oxygen does not appear until the supply of the gas is much reduced. These animals do not begin to withdraw from water, until the oxygen supply is reduced to 0.2 cc. or 0.3 cc. per litre, a very small percentage of the normal amount. Few animals remain in water which has less than 0.1 cc."

In view of the above statement, it must be stressed that the movement of *D. oregonensis* was in no case a complete evacuation of the strata under consideration, and in the experimental material it was noted throughout that some individuals remained under conditions from which others had moved.

From a consideration of the data given by Birge and Juday (1911, pp. 116-20 and figures), it is evident that in several cases fairly large numbers of *Cyclops* do occupy regions where oxygen conditions are of the order of 0.3 cc. per litre. It is believed that in most cases—e.g. Mendota, August 8, 24, September 14, 1906; Elkhart, October 2, 1906; Mendota, September 6, 1907; Beasley, August 3, 1908, August 14, 1909; Knights, August 25, 1909; Silver, August 21, 1907 and August 28, 1908—conditions of light or temperature, i.e. an immediately overlying thermocline, or both, were holding concentrations in these strata of low oxygen content. The fact that a temperature gradient or temperature of the order of 20°C. did inhibit the avoidance reaction to high carbon dioxide in the experimental work, is clear from figures 20, 21, and 22, and that the thermocline prevented the upward movement of *D. oregonensis* in lake Nipissing until upper strata cooled considerably is in accordance with this view.

In two cases, Elkhart, July 3, 1906, and lake Geneva, September 25, 1906, modes in the distribution of *Cyclops* occur in strata of low oxygen content, and no tenable explana-

tion can be given on the basis of the above hypothesis. In most cases, with exceptions noted, *Cyclops*, the only group which can be compared directly here, showed definitely smaller numbers in strata having less than 3.0 cc. per litre of dissolved oxygen than in strata containing more than this amount.

In Mendota the rapid decrease of oxygen in the hypolimnion, and the single or far-separated collections from the other lakes, prevent the observation of a correlation, such as was noted for immature *D. oregonensis* in lake Nipissing. Only by a closely spaced series of collections can such a movement be followed, when oxygen conditions are changing rapidly.

It should be pointed out that the critical values in the production of movement given above are far from lethal in effect. The distribution of apparently normal individuals of *Cyclops*, at the beginning of experiment III, in water containing from 64 to 70 p.p.m. of carbon dioxide, is evidence of that fact. These animals lived for several weeks after being used in that experiment. This bears out the statement, made by Birge and Juday (1911), that oxygen depletion to 0.2 cc. per litre and correspondingly high carbon-dioxide content, had no unfavourable effect on the animals. The values given, then, are not limiting values in distribution but rather are critical values which incite avoidance reactions.

(h) **Conclusions.** From analysis of the movements of immature *D. oregonensis* from lower strata in lake Nipissing, correlated with oxygen depletion and related increase in free carbon dioxide, and from subsequent experimental results of the action of these two gases separately, it would seem that the vertical movements of immature *D. oregonensis* in lake Nipissing are of the nature of avoidance reactions to certain critical values of these gases. A comparison of the field observations and experimental data has led the author to believe that a decrease in oxygen to approximately 3.0 cc. per litre or an increase of carbon dioxide to 12 p.p.m. or 15 p.p.m. are sufficient to bring about these reactions, provided that other factors of stronger influence do not inhibit the response. A

steep temperature gradient, moderately high temperatures, and possibly light, may be factors limiting the avoidance of these critical values at times. It appeared that when both factors, low oxygen and high carbon dioxide, were working together in nature, the reaction occurred at slightly higher oxygen and lower carbon-dioxide values than when the factors were working independently under experimental conditions. It is possible that the values given are not of universal application, but it is believed that further observations in nature and more detailed experimental investigation may bear out the hypothesis given.

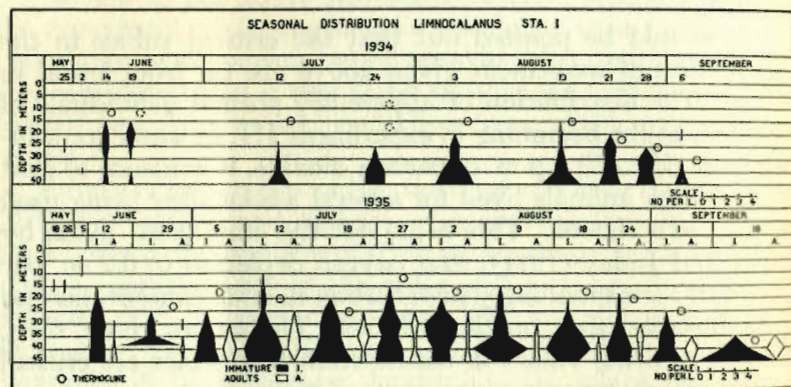


FIGURE 24.—Seasonal differences in vertical distribution of *Limnocalanus*, station I, 1934 and 1935.

Limnocalanus macrurus (Sars)

The vertical distribution of *Limnocalanus* throughout the summer seasons of 1934 and 1935 is indicated in figure 24 and given in table 14 (p. 131). In 1935 both immature and adult specimens were enumerated and their difference in distribution is illustrated in the graph.

By the middle of June both adults and copepodid stages were found concentrated in the deeper strata. This may have been a result of the development of the immature stage from previously unrecognized nauplii and metanauplii, as well as a

definite concentration in the restricted volume of cold water. Marsh (1897) states that "In February, March and April most of the *Limnocalani* are immature in Green Lake, Wisconsin". In May few individuals were taken in lake Nipissing and these were found to be scattered over a wide area.

The numbers remained relatively the same throughout the summer and although some were utilized as food by the cisco, the amount was small and depletion was not noticeable. The form does not carry eggs so that it is difficult to determine reproductive activity, yet the above facts indicate that there must be a slow but steady production throughout the summer.

The errors in sampling a small population such as that of *Limnocalanus* prevent any detailed analysis of their distribution. They were present only in the lower hypolimnion, however, and a marked concentration occurred in mid-September when the thermocline descended to 35 metres. As would be expected the immature forms were considerably more numerous than the adults. The latter appeared to be more restricted to lower strata than the copepodid stages, but their very small numbers invalidate any definite statement that might be made to that effect.

Cyclops group

Cyclops bicuspidatus, *Cyclops viridis*, and *Mesocyclops obsoletus* have been taken in the limnetic region of lake Nipissing. The group as a whole was so poorly represented quantitatively that the individual species were not enumerated, since numbers obtained would have been practically valueless in distribution studies.

The seasonal distribution of the combined *Cyclops* population for the summer seasons of 1934 and 1935 is given by figure 25 and in table 14 (p. 133). Few individuals wintered over, and the group did not increase rapidly in numbers in the spring. Between the beginning and middle of June, a tremendous increase occurred in both years. In 1934 these increased numbers had their maximum in strata below 20 metres and were distributed in large numbers from this level to bottom. In 1935 maximum numbers were taken at 20 metres

and a definite decline was observed below this depth, the group being scarce below 30 metres. It is possible that this scarcity in deep water in 1935 was a result of the lower temperature of the hypolimnion, 9.7°C. to 6°C. below 20 metres, compared with from 12°C. to 8°C. in 1934. When the hypolimnion had warmed up by June 20 in 1935, although the light intensity at the time of sampling was low, producing a maximum at 8 metres, fairly uniform numbers were found from 10 metres to bottom.

In both years the hypolimnion was fairly well populated until the middle of July, after which date *Cyclops* was defi-

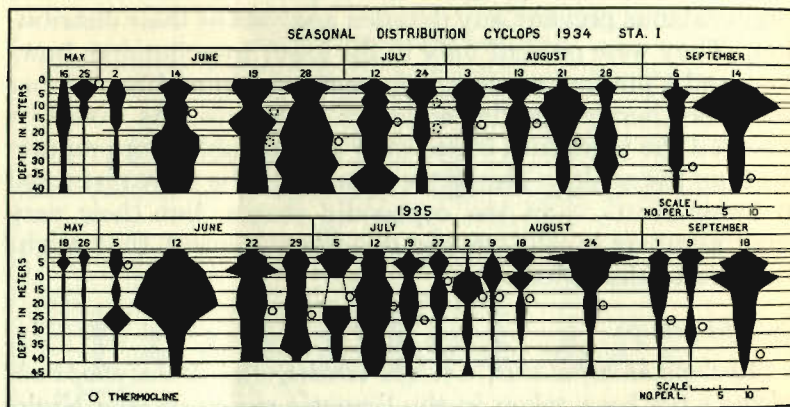


FIGURE 25.—Seasonal differences in vertical distribution of *Cyclops* group, station I, 1934 and 1935.

nately scarce below the thermocline. In both years, also, there was a marked decrease in the concentration of the population in the immediate bottom strata, in early July. Whether this was produced by a definite upward movement as in the case of *Diaptomus oregonensis* is difficult to determine. If such was the case, it suggests that the form is much more sensitive to oxygen depletion than *D. oregonensis*, but Birge and Juday (1911) have found the opposite to be the case. The great differences in the amount of dissolved oxygen at 45 metres in June and early July in the different years, as

indicated by figure 18, and the lack of oxygen data in 1935, prevent detailed comparison in 1934 and 1935. It is, therefore, not possible to make any definite statement with respect to the relationship existing between dissolved oxygen content and the distribution of *Cyclops*. The distribution observed might well be produced only by the effect of more successful survival and reproduction in upper strata, and an inhibition of downward migration by the more pronounced stratification developed in mid-summer. The increase in August definitely remained above the thermocline, as did the final brood observed in late September.

The depressed thermocline in autumn greatly increased the depth of the epilimnion, yet the major portion of the population was found in the upper 10 metres of water in contrast to its distribution in June.

In 1935, on both July 27 and August 2, the light intensity reading at surface when the samples were taken was 8,400 foot candles and on August 9, 18, and 24 the reading was 7,200 foot candles. The tremendous difference in vertical distribution in the upper 10 metres of water on these dates definitely shows the lack of correlation between the distribution of these combined species and light intensity. In all cases the collections were made near midday, and light conditions had been fairly constant for some time. As was shown previously in discussing diurnal movements (p. 44), factors other than light are more important in controlling the vertical distribution at this season.

Nauplii

The nauplius stages of all species of copepods present in the open water of the lake were enumerated together, and their distribution in 1934 and 1935 is indicated in figures 25 and table 14 (p. 134).

The nauplius population was concentrated in the epilimnion in May, although May 16, 1934, proved an exception in that an almost uniform distribution existed from surface to bottom. On that date the light intensity when the samples were taken was only 900 foot candles as compared to 8,400 on

May 25. On May 16 a practically homothermous condition existed from surface to bottom. It is impossible, of course, to be certain, but it seems probable that the distribution found on May 16, 1934, is to be explained by the peculiar light and temperature conditions obtaining on that date.

During June large numbers were found below the thermocline. The hypolimnion as a whole was well populated after the middle of the month, but in all cases the bottom strata had a sparse population. The hypolimnion lost the nauplius stages during July, and they were scarce in that region after

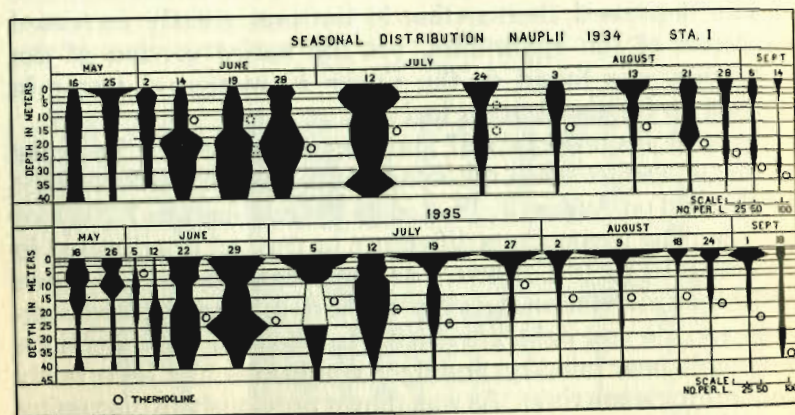


FIGURE 26.—Seasonal differences in vertical distribution of nauplii, station I, 1934 and 1935.

the middle of the month. In 1935 the weekly collections showed a progressive upward vacation of the lower strata and a similar end point was indicated in 1934.

The distribution of nauplii during the month of July was quite similar to that of *Cyclops* and very dissimilar to that of *Diaptomus*. No concentration occurred in bottom layers comparable to that of *Diaptomus oregonensis*. Neither was there an increase in the number of metanauplii in the hypolimnion concurrent with the decrease in the nauplius population there, or correlated with the increase of copepodid stages of *Diaptomus oregonensis*. Since they constitute the

larval stages of several genera, whose vertical distribution differ greatly, and which quite possibly undergo individual ontogenetic changes in distribution, it is difficult to correlate the distribution of the nauplii with the older and adult groups. A similar difficulty was noted by Birge (1897).

The distribution in the epilimnion during late July and throughout August appears to be considerably different in the two years. In 1935 very large maxima were observed at a depth of 1 metre after July 12. In 1934 no samples were taken at 1 metre and the great concentrations at this depth observed in 1935 are absent from the graph. Maximum numbers were taken at surface on July 24 and August 13 and it is possible that maximal concentration did exist just below the surface layer in 1934. In both 1934 and 1935 with few exceptions definitely smaller numbers were obtained at 3 metres than at surface.

Metanauplii

The vertical distribution of metanauplii for the year 1935 is given in figure 27 and table 14 (p. 135); as in the case of the nauplii, in the latter part of May, fairly large numbers were found in upper strata, with a definite scarcity below 15 metres. In June there was a more or less uniform distribution throughout the total depth range, with the exception of the immediate bottom layers. During July maximum numbers were found near surface and the hypolimnion was sparsely populated. When the increase in numbers occurred in August, in contrast to the distribution of the nauplii which produced them, the metanauplii were present in fairly large numbers below the thermocline. In late August and early September, when the numbers again declined, the metanauplii below the thermocline persisted producing maxima there. This may have been the result of a specific difference, or of slower development in the colder hypolimnion.

Vertical Distribution—Station II

The vertical distribution of the limnetic crustacea was also determined at station II in the shallow water area of

lake Nipissing (see figure 2, p. 15). The discussion of the vertical distribution of the various forms at this station, and a comparison with the distribution in the upper strata at station I, follows.

Daphnia longispina (Müller)

The vertical distribution of *Daphnia* at the shallow water station is given in figure 28 and table 15 (p. 136). Few individuals were present in early spring and as was the case at station I the population remained small until July. At that time very large numbers appeared suddenly and then decreased, producing a minimum in late July or early August. A second maximum occurred in late August which continued into September.

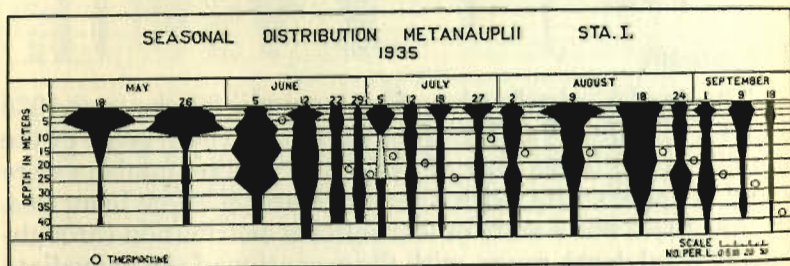


FIGURE 27.—Seasonal differences in vertical distribution of metanauplii, station I, 1935.

The species was quite definitely positively phototropic being taken most abundantly in upper layers, on all dates when light intensity was high. On two dates when the light intensity value was below 4,000 foot candles, however, there was a tendency toward the reverse condition. These data are not conclusive as evidence of a lack of phototropism to these low intensities, since numbers were small on June 9, 1934, and the samples were taken immediately after three days of strong wind on August 21 of same year. Other factors probably play an important part in their distribution on these dates.

Holopedium gibberum (Zaddach)

As shown in figure 28, *Holopedium* was taken at station II only in the spring. When compared to the distribution indicated at station I, it is evident that the form is not evenly distributed over the area of the lake, therefore, as will be discussed later, little can be said with respect to seasonal abundance. The form appeared to be very definitely positively phototropic to low light intensity as indicated by its distribution on June 9, 1934, when the light value was 1,500 foot candles. On June 19, its negative phototropism to the strong light of 9,600 foot candles was quite evident.

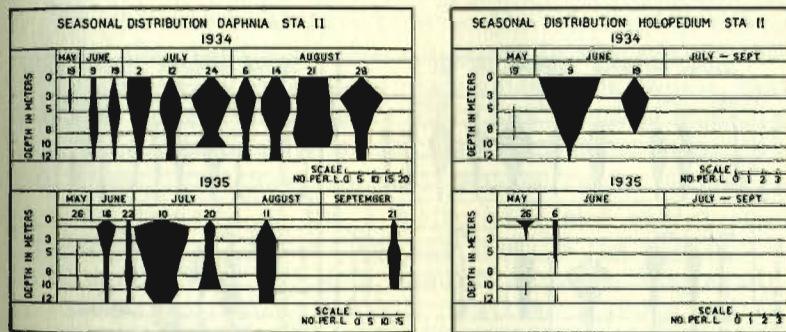


FIGURE 28.—Seasonal differences in the vertical distribution of *Daphnia* and *Holopedium*, station II, 1934 and 1935.

Epischura lacustris (Forbes)

The vertical distribution of *Epischura* throughout the two seasons under discussion is illustrated in figure 29 and given in table 15 (p. 138). The small numbers present prevented detailed analysis, but certain general facts are evident. The species was scarce in the early spring, but numbers increased rapidly in June, decreased in July and August, and practically disappeared by September. The maximum numbers taken during the season were obtained in late June in both years.

As observed in the distribution at station I, we find here that the population of *Epischura* was sensitive to strong light

but positively phototropic to light of moderate intensity. When the light intensity was high, from 7,000 to 9,000 foot candles, only few individuals were taken at surface and maximum numbers were found at the 5 and 8 metre levels. When the light intensity values were near 5,000 foot candles, the levels of maximum abundance were nearer the surface. The presence of a thermocline region at 5 metres may have been responsible for the exception at station II on June 6, 1935. On the dates when surface illumination was below 4,000 foot candles, only one or two stray individuals were taken at 5 metres, and none was found above that depth. It is apparent that moderately strong light was necessary to

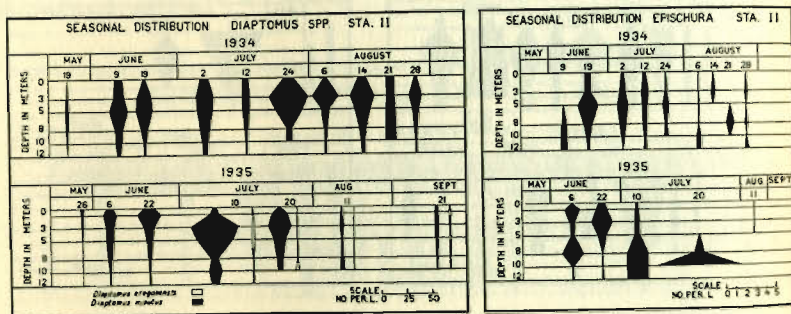


FIGURE 29.—Seasonal differences in vertical distribution of *Diaptomus* group, and *Epischura*, station II, 1934 and 1935.

attract this form to maxima in upper layers, yet excessive illumination repelled them from surface layers to produce maxima in middle depths.

The avoidance of temperatures above 20° C. was marked at station I where *Epischura* was able to penetrate to depths below such warm water. At station II the avoidance of water above this temperature was marked on July 24 and August 6 in 1934, and on July 10 and 20 in 1935. On the last date a definite concentration was noted at bottom, probably as a result of low light intensity as well as an avoidance of the warm upper layers.

Diaptomus group

Figure 29 and table 15 (p. 139) indicate the vertical distribution of *Diaptomus* at the shallow water station in 1934 and 1935. In 1935 both *Diaptomus oregonensis* and *D. minutus* were enumerated and their distribution is illustrated in the lower panel of the graph.

Since the shallow water of the lake is quite unprotected from wind action, it is kept in a homothermous condition from top to bottom throughout the summer. Under this condition differences in light intensity probably play the primary role in determining distribution. In all cases maximum numbers of *Diaptomus* were taken in the upper 5 metre stratum, but as was the case at station I no simple relationship existed between the position of this maximum in the stratum and the light intensity at the time of sampling. On June 9, 1934, the light intensity was least, being but 1,500 foot candles. With the exception of August 21, the value on all other dates was above 7,000 foot candles. Maxima were present on these latter dates at the 3 metre level and only a small proportion of the individuals occurred at the surface. It would appear that high light intensity caused a congregation of individuals a short distance from the surface, but the effect of low intensities of light is not clear from these data.

On August 21, 1934, samples were taken after three days of strong wind and the even distribution from top to bottom was probably due to circulation of the water, since all organisms enumerated showed a similar dispersion.

In 1935 the two species were enumerated separately and samples were taken at 1 metre as well as at surface and 3 metres. When the light intensity was 4,800 foot candles on June 6 and June 22, definite maxima were observed at 1 metre on both dates. A surface light intensity of 9,100 foot candles depressed maximum numbers to the 3 to 5 metre stratum on July 10, but the upward trend is noted again on July 20 when the light intensity value was 3,840 foot candles. The difference in the ratio between the numbers at 1 metre and 3 metres on July 10 and July 20 is significant since the ratio on July 10 was 19.5 per cent. ± 1.4 as compared to 70

per cent. ± 3.8 on July 20. There was also a definite upward movement from the 8 to 5 metre stratum on the latter date.

It is clear from a comparison of these distributions that the organism was positively attracted to regions of bright light, but repelled from regions where light was intense. Certain optimum conditions of light intensity were probably present, but no clear correlation exists between points of maxima and light intensity at those depths. It is quite probable that detailed sampling at 1 metre intervals together with light measurements would go far in clarifying the picture in this respect.

Only small numbers of *D. oregonensis* were taken at station II in 1935. From the study carried on at station I in 1934 and 1935, it would appear that such is the normal condition in the upper 10 metres of the lake as a whole. Only in the deep water, then, where the species is concentrated as an immature form, could *D. oregonensis* be of very great importance as a food organism.

Cyclops group

The vertical distribution of the *Cyclops* group at station II is given in figure 30 and table 15 (p. 140). The members of this group were scarce in early spring as were the other crustaceans, but by early June fairly large numbers of adults appeared and continued throughout the summer and fall. The picture of seasonal abundance is not as detailed as was that at station I, since the shallow water was not sampled as regularly.

Although *Cyclops* was fairly abundant at all depths in the early summer at the deep water station, they noticeably preferred upper layers at station II. No simple relationship existed between variations in the strength of illumination at the surface and the depth at which maxima occurred. Part of the group at least was positively phototropic to all light intensities encountered in the sampling at this station. It is possible that the separate species are not equally sensitive to light, but the small numbers taken if subdivided to species,

would be subject to such large errors that significant differences could not be obtained. Sampling with a large trap would, therefore, be necessary in order to analyse in detail the distribution of the separate species.

Nauplii

The vertical distribution of the nauplii of the copepoda present at station II are given in figure 31 and table 15 (p. 146). The early rise in numbers in spring and later abundance were due to early production, later to development

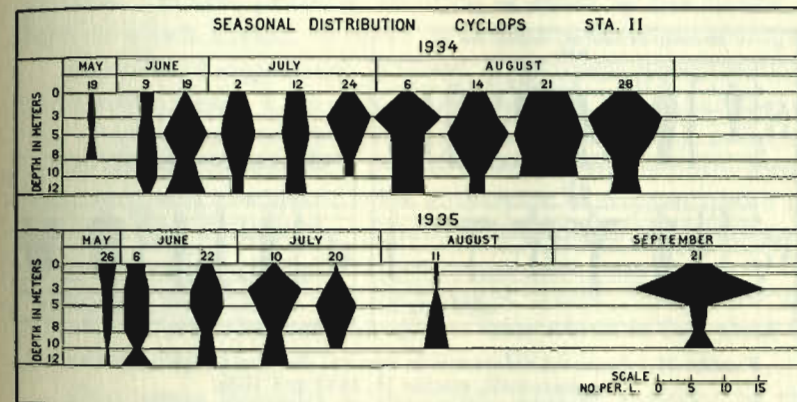


FIGURE 30.—Seasonal differences in vertical distribution of *Cyclops* group, station II, 1934 and 1935.

and to subsequent reproduction of the adults produced. These immature stages increased in numbers early in spring, and fell into a decline just previous to the dates on which adult copepods reached peaks of abundance, metanauplius stages intervening. Further increases occurred after peaks of adult abundance as a result of reproductive activity.

At first sight the vertical distribution of these immature stages appears to have no relationship to light intensity at the time of sampling. On June 19 and August 6 in 1934, and on July 10, 1935, the light intensity at surface was similar, over 9,000 foot candles. There is, however, an obvious

difference in the distribution on these dates. On June 19 and August 6, 1934, and on August 11, 1935, when maximum numbers were taken at the surface, the temperature of the upper layers was considerably above 20° C. The explanation is offered that the nauplii became less sensitive to very intense light at this high temperature. A similar observation was made at station I in this respect. The more usual reaction to light appears to be a positive phototropism to moderate intensities and a negative phototropism or intolerance to the very intense light at the surface.

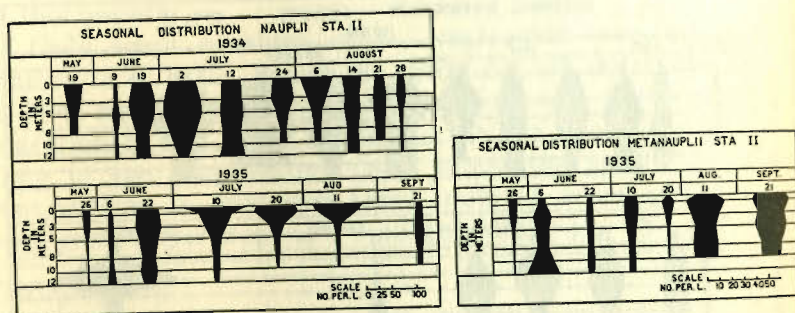


FIGURE 31.—Seasonal differences in vertical distribution of nauplii and metanauplii, station II, 1934 and 1935.

Metanauplii

The metanauplii were counted only in 1935 and the vertical distribution is given in figure 31 and table 15 (p. 142). The data in this case are so scanty that little can be said with respect to the distribution of this stage in the shallow water. On only three dates are the numbers abundant. On June 6 when a thermocline existed at 7 to 9 metres, maximum numbers were taken below this region of rapid change in temperature. On August 11 and September 21, maximum numbers were taken near surface, but the whole depth was well populated.

Summary of Vertical Distribution of the Plankton Crustacea

It is quite evident that the vertical distribution of each individual species is the result of specific reactions to complex environmental factors. The ever-changing environment thus affects the vertical distribution from day to day and from hour to hour, to such an extent that in very few cases can general statements be made as to the existence of any stable distribution of the various forms. In the following summary the more usual type of vertical distribution, together with the general seasonal changes, is given for the individual species studied. Where possible, mention is made of the factor or factors which appear to exert an influence on these changes.

Diatomus oregonensis is found in adult stages only above the thermocline. Late copepodid stages are found only below the thermocline, concentrated at bottom in early summer. Later there appears to be a movement to intermediate hypolimnial layers, correlated with a decrease of oxygen to 3.5 cc. per litre and an increase of carbon dioxide to approximately 10 p.p.m. The great concentration of this form is due to the relatively small area of this deepest water. Only few are taken in the major portion of the lake which is less than 15 metres in depth.

Diatomus minutus is restricted almost entirely to the epilimnion throughout the season. Maximum numbers are usually taken near surface. The form is evidently positively phototropic but is repelled from the immediate surface by intense light.

Cyclops group. As a group *Cyclops* is found in considerable numbers, at all depths, from May until mid-July. After a more definite thermocline is established at this time, the group becomes more or less restricted to the epilimnion. There appears to be little correlation between light intensity and the vertical distribution of these forms. Since the group is made up of three species, a complexity of behaviour is to be expected.

Epischura lacustris is more or less restricted to the warm layers of the epilimnion, although it is definitely repelled

from the immediate surface by intense light. The species showed a definite movement out of strata of over 20° C. during daylight, although an upward movement into such strata was noted during darkness. Whether or not this is a result of a change in sensitivity to light at the higher temperature is not known.

Limnocalanus macrurus was found only in the deep water area during the summer, and in all cases it was taken only below the thermocline region. Temperature is probably the primary factor in controlling its distribution. Numbers of this organism were too small for its distribution to be considered in detail.

Nauplii were found in considerable numbers at all depths from May until mid-July. After a definite thermocline was established, large numbers were found only in the epilimnion. A particular type of distribution resulting in maximum numbers at zero and 1 metre strata was observed in 1935, after the upper layers had warmed to approximately 24° C. This was observed both at station I and station II.

Metanauplii were enumerated only in 1935. In May they were concentrated in upper strata. In June a fairly even vertical distribution was observed, except in bottom layers. During their period of scarcity in July, maximum numbers were taken at surface. In August, when the increase takes place, large numbers extended well into the hypolimnion. This is in contrast to the distribution of the nauplius stage. In late August the hypolimnial fraction of the population persisted, forming a maximum for the group below the thermocline.

Daphnia longispina was taken in maximal numbers near surface when the light intensity was high in June. In July the early summer maximum consisted of a well-populated zone in the epilimnion, a sparse population in the region of the thermocline, and a second maximum at some level in the hypolimnion. The upper population is predominantly young individuals, while in the hypolimnial population adults predominate. The levels of these concentrations appear to be correlated with light intensity.

The second seasonal maximum is restricted to the epilimnion, but its distribution therein appears to be correlated with light intensity.

Holopedium gibberum was taken only during the months of May and June. It was present for the most part in levels above 20 metres. From a comparison of the populations at the two stations, it evidently was "bunched" in its distribution.

Conclusions

Many factors have been given in the past as determining the vertical distribution of the plankton crustacea. Birge (1897) gives a detailed discussion of a number of factors which influenced the vertical distribution in lake Mendota. Welch (1935) lists from the existing literature on the subject the following as important: "(1) light; (2) food; (3) dissolved gases principally oxygen and other dissolved substances; (4) temperature; (5) wind; (6) gravity; (7) age of individuals of a species." This list is essentially the same as given by Birge (*loc. cit.*).

Of these factors, the following appear to be the most important in determining the vertical distribution in lake Nipissing.

Light. Many instances are given in which the prime influence upon the vertical distribution appears to be that of light intensity. In most cases there is evidence that maxima in strata near surface are held there by a positive phototropism, and usually a scarcity exists in the immediate surface layers, evidently caused by the repellent effect of intense light. It should be pointed out that various species are not sensitive to equally high light intensities. It has been observed from the vertical distribution of different species that there are marked differences in existing light conditions in the regions occupied by maximum numbers of their respective populations.

The effect of light is, however, in practically all cases, qualified by that of other factors. As was shown in the discussion of diurnal movements, great differences exist in

the response to changes in light intensity, and these modifications are no doubt conditioned by other environmental factors.

Food. There is no doubt that plankton organisms must be in a position to obtain sufficient food for the purpose of growth and reproduction, or the population will suffer. Although many workers have written at great length in attempts to prove invalid Pütter's arguments, that most aquatic animals must derive the greater portion of their nutriment from dissolved organic matter in natural waters, very little has been accomplished in determining the actual source of food of zooplankton. The importance of the utilization of particulate organic material other than phytoplankton is not known. Naumann (1921) has shown that fresh water *Daphnia* rapidly filter out detritus with attached bacteria. Woltereck (1928) decided that pelagic *Daphnia* cannot make use of detritus, although pond forms do so. The utilization of bacteria by plankton organisms is little known, but may be of considerable importance. Bond (1933) and Stuart, McPherson, and Cooper (1931) have shown that certain bacteria are utilized as food by various plankton organisms.

It is realized that many of the plankton crustacea feed upon phytoplankton forms which are more or less restricted to the upper strata, but abundance or scarcity of phytoplankters should not be confused with abundance or scarcity of food, since other particulate organic material may be utilized. Plankton crustacea are not always numerous where algae and protozoans are most abundant, and until our knowledge of the food relationships is more detailed, no absolute correlation can be expected. It is, of course, realized that other modifying factors may be more influential than the relation between food and feeder in determining the vertical distribution of a population.

Chemical Factors. The decrease in dissolved oxygen content and related carbon-dioxide increase have been shown both by observation and experiment to affect the distribution of certain of the plankton crustacea. It is quite possible

that other substances may play a part in these changes. Oxygen depletion and related phenomena are not as marked in this case as in many others noted throughout the literature. Correspondingly, the deeper water does not become uninhabitable, although there is a marked change in the distribution in the hypolimnion. The scarcity in the hypolimnion, after mid-July, of forms other than *D. oregonensis* may also be a result of these changed chemical conditions, but their very scarcity prevents detailed analysis of their movements. It is believed that conditions less severe than those cited from the literature may be instrumental in bringing about changes in distribution, and that other factors, such as high temperature or bright light, are at times inhibitory to these avoidance reactions. It is quite possible that the critical values discussed are not of universal application.

Temperature. The direct effect of temperature is illustrated by the distribution of several of the species investigated in lake Nipissing. These have been discussed previously in detail. The fact that the copepodid stage of *D. oregonensis* is found only in lower-most layers, and changes its distribution but slightly with change in light intensity, would lead one to believe that temperature is the important controlling factor in this case. *Limnocalanus*, too, is restricted to the cool hypolimnion after the upper layers have become warmed. *Epischura*, on the other hand, definitely shows its preference for the upper warmer layers.

The temperature gradient at the thermocline is an important factor in the vertical distribution of many species. This has not been as noticeable with respect to diurnal movements as is cited in so many instances in the literature, but definite effects have been observed in daylight distributions. In most cases maxima are observed either above or below the thermocline, or in some cases in both epilimnion and hypolimnion. Under such circumstances there is usually a definite scarcity of the species in the thermocline region itself. In very few cases other than in the group *Cyclops* were numbers found in this region equal to, or larger than, those observed either above or below. It would appear that

where a temperature gradient exists, the forms are able to orient themselves and move toward favourable temperatures. In some cases the temperature gradient is observed to be a definite barrier to such selection of habitat.

Indirectly through a change in sensitivity to light, temperature changes appear to affect the distribution of nauplii and of *Epischura*. Our conclusion that the change in the distribution of nauplii under higher temperature conditions was a result of lessened sensitivity to light appears to be contrary to the general view expressed by Welch (1935), ". . . higher temperature increases, while lower temperature decreases the sensitivity". The necessity for experimental investigation of this case is evident.

Wind. The direct effect of wind in causing changes in the vertical distribution of the plankton crustacea has been positively identified in only one instance. On August 21, 1934, collections were made after three days of heavy wind. A fairly uniform distribution from surface to thermocline, of all organisms, with the exception of *Cyclops*, was noted at this time. In lake Nipissing, however, the plankton crustacea reacted to other environmental conditions with sufficient energy to overcome the effects of wind-produced currents.

Indirectly the effect of wind action and cooling, in depressing the thermocline in late summer and fall, increases the volume of the epilimnion, so that its inhabitants, in many cases, scatter. The depressed thermocline, which is here the primary factor limiting distribution, also tends to concentrate the hypolimnial population.

Gravity. The effect of gravity on the distribution of these crustaceans which are heavier than water is omnipresent. In many cases the nocturnal change in distribution has been attributed by us to a lack of an attraction towards light, and a gradual settling to lower strata. The effect of geotropisms has not been discussed, since experimental evidence of its existence is lacking.

Age. Young and adults of some species have been shown to differ with respect to their vertical distribution. Young

forms usually predominate nearer the surface, as in the case of *Daphnia*, and the nauplius stages of the copepods. That the latter is not universal has been discussed. In the case of *D. oregonensis* this ontogenetic difference in distribution is evident.

Sex. The difference in the distribution of the two sexes of *D. minutus*, as discussed on p. 39, is considered to be a result of differences in sensitivity to light. Such differences may be more general than would appear from the literature, yet they escape observation, due to the difficulty of determining the sexes during enumeration.

Specific differences. Throughout the study, it has been observed again and again that each species reacts differently to changes in environmental conditions. The vertical distribution of the limnetic plankton as a whole is a resultant of a complex of specific reactions to interrelated limiting and controlling factors. The effects of ontogenetic differences in reaction and changes in sensitivity under different related conditions further complicate the picture. Only through an analysis of the reactions of the individual species and their developmental stages does any order appear.

Depletion by consumption. The consumption of large numbers of any zooplankter, by definite selection, as is indicated in the case of the plankton feeder *Leucichthys artedi* (Le Sueur), may at times alter the concentration of a plankton form in a certain region. This would affect the observed vertical distribution of the plankter if such distribution were otherwise stable. If the predator were concentrated and feeding heavily this might be of considerable importance, but the extent of such consumption, and hence of the effect on plankton distribution, would be difficult to determine. It is believed that this factor has not been of general importance in lake Nipissing.

Significance of Results

Owing to the great complexity of the interrelated effects of environmental factors on the distribution of a highly organized biota such as the plankton crustacea, it was deemed

necessary to obtain first-hand knowledge of the reactions in the lake. The ultimate analysis of the relative importance of these causal factors affecting vertical distribution will come from experimental investigation. Accurate indices of the effect of individual factors can be determined only under controlled conditions. The types of reactions, and conditions inducing these in nature, must be known, however, before the above indices can be obtained with the expectation of successful correlation with natural phenomena. As was stated in the introduction, it was through an analysis of the distribution and movements of the limnetic crustacea and factors implicated therein that a deduction was made of the factors responsible for observed differences. The tentative explanations of the relative effect of these factors are given in order to clarify the picture for future experimental work. It is hoped that the suggested explanations may be of significant value themselves, and may prove helpful in the furtherance of the problem from this standpoint.

PART III. VARIATIONS IN SEASONAL ABUNDANCE OF THE LIMNETIC CRUSTACEA

Introduction

It has been shown that the plankton crustacea exhibit decided differences in horizontal and vertical distribution, and that the differences in vertical distribution are subject to the seasonal as well as the diurnal cycle of environmental changes. Information on the relative abundance of different species and the changes in the abundance of their respective populations throughout the season is essential for a complete picture of the population of limnetic crustacea. The figures and tables indicating the vertical distribution during the season do not show this seasonal abundance clearly, as the numbers at different depths are plotted separately, and the numbers of each species taken are plotted on different scales. In order to illustrate these differences in seasonal abundance as accurately as possible from the data at hand, the average values for the population throughout all strata, at each date

of sampling, have been calculated from the vertical series of samples. These are indicated in figure 32, for station I in 1932, 1934, and 1935, and figure 33 for station II in 1934 and 1935.

Procedure

In 1932 collections were made from early July until early October, with the "Juday" closing net, No. 20 bolting cloth. The efficiency of this net is known to vary greatly in stage haul collections, and without doubt, considerable variations exist when collecting by total vertical hauls in different plankton populations. Stage hauls taken with this net were compared to plankton trap catches in 1933 at Trout lake, Wisconsin. The average efficiency throughout all strata was found to be 15.2 per cent. An efficiency factor of 6.6 has thus been assigned to this net in the 1932 collections. The varying efficiency of the net (p. 17) makes impossible any comparison of the absolute abundance of the plankton in the net collections of 1932 with that in the trap samples taken in 1934 and 1935. However, the maxima and minima in the seasonal trends may be compared, as they have been below.

The collections made in 1934 and 1935 were in all cases vertical series taken with the plankton trap. To determine the abundance throughout all strata, on a given date, the counts were plotted against depth to 40 metres and the area determined beneath the vertical distribution curve. The average number per metre interval was obtained by dividing the above figure by the depth in metres. This average number per litre, per metre interval, is plotted against time in figure 32.

The effect of horizontal variations in the plankton population has been discussed (p. 21). Indeed, due to the errors in sampling occasioned by wide horizontal variations in the plankton population, it is felt that it is not legitimate to compare absolute abundance in different years even when the plankton trap is used exclusively. Only the trends of a season's samples are considered to be significant. Ricker suggests the use of a running average in comparing a series of collections. However this was found to be insufficient to

overcome the effects of horizontal variation and has, therefore, not been undertaken in this instance, since it is felt that it would tend to give a false impression of accuracy.

In 1932 the two species of *Diaptomus* were not enumerated separately as they were in 1934 and 1935. The upper panel of figure 32 has thus been divided to indicate the seasonal fluctuations of each species in the two latter years. Meta-nauplii were counted only in 1935 as indicated in the third panel. Since the nauplius and metanauplius stages of all copepods are enumerated together, *Cyclops* and *Diaptomus* have been combined in the fifth panel to facilitate a comparison between seasonal abundance of adults and developmental stages. The major portion of the population of *D. oregonensis* is made up of late copepodid stages, as discussed previously.

Variation in Seasonal Abundance—Station I

The seasonal fluctuations in abundance of the different groups, as indicated in figures 32 and 33, show no general similarity and the fluctuations of the population of each group are considered separately. Only the groups in which individuals were abundant are considered.

Daphnia longispina (Müller)

The seasonal variation in the numbers of *Daphnia* taken at station I is indicated in figure 33. Few are taken during May and June, but a marked increase is noted in July. There follows a period of decline and in August and September a second mode is observed.

Diaptomus group

(a) *Diaptomus oregonensis* (Lilljeborg) in 1934 and 1935. In 1934 *D. oregonensis* showed a slight tendency towards a bimodal distribution. Peaks occurred in late July and mid-August, although the slight depression in early August was probably not significant. In 1935 the distribution was unimodal, the definite maximal abundance occurring at a comparable period, although the rise to the peak took place

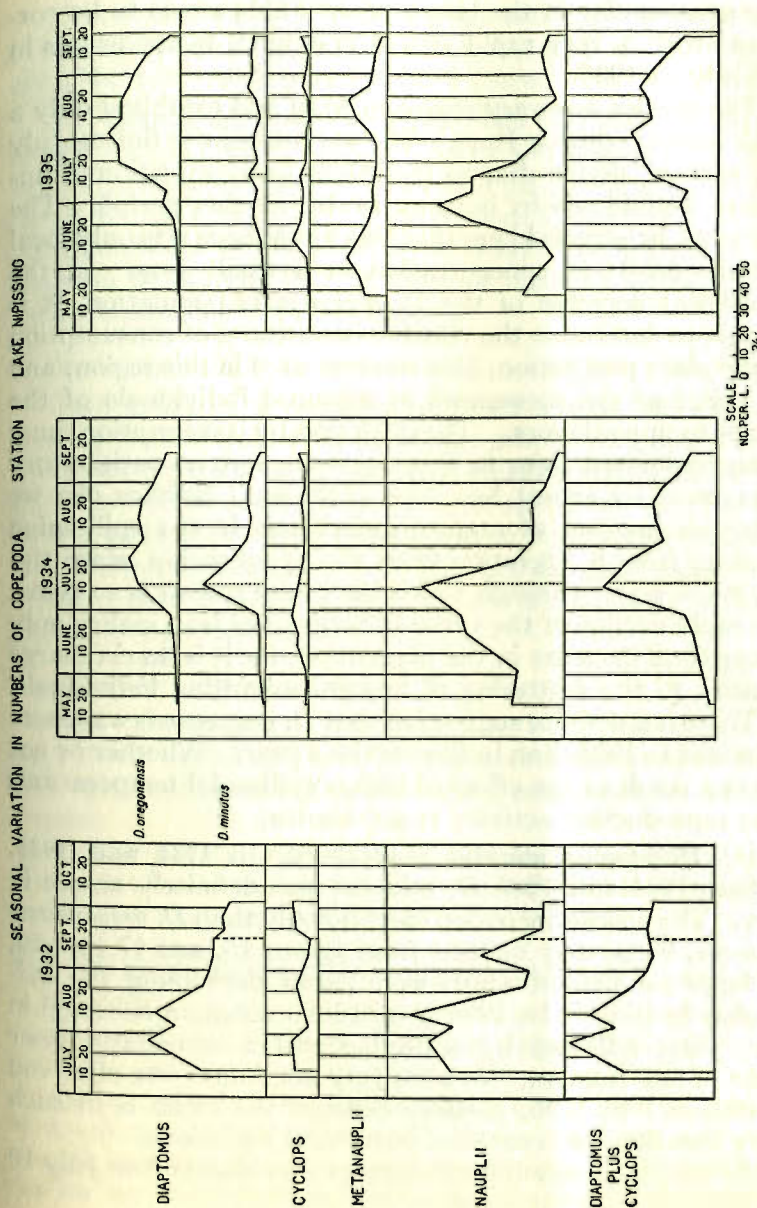


FIGURE 32.—Variation in seasonal abundance of Copepoda, station I, 1932, 1934 and 1935.

somewhat earlier in the latter year. This seems to be correlated with a very rapid rise in epilimnial temperatures in mid-July in 1935.

The species was very scarce in May and exhibited only a slight increase during June. The very rapid rise during July was without doubt due to the marked concentration of immature individuals in bottom strata, at this period. The fact must be stressed here that this abundance was only local and the result of concentration in a small area. In the subsequent decrease of the *D. oregonensis* population, it is difficult to determine the relative importance of consumption by the cisco population, also concentrated in this region, and the effect of the movement of matured individuals of the species to upper layers. The depletion by consumption must be an important item in this decrease, but no satisfactory measure of its extent has been obtained. Neither can we detect an increase of mature individuals in the epilimnion resulting from a migration from the hypolimnion, since the volume of water through which they may spread is so great. The rapid decline of the curve in September is in reality only an apparent decrease in the population, for it is due in a large measure to the scattering of upward migrating individuals.

There is a definite suggestion that *D. oregonensis* was more abundant in 1935 than in the previous year. Whether or not this is a result of the effect of higher epilimnial temperatures upon reproductive activity is not known.

(b) *Diaptomus minutus* (Lilljeborg) in 1934 and 1935. In both 1934 and 1935 *D. minutus* was definitely scarce in May. The species increased more quickly than *D. oregonensis* however, for as may be seen from figures 16, and 17 (pp. 59, 60) large numbers of adults were found throughout the epilimnion in June. In 1934 a definite maximum occurred in early July, followed by a decline and a secondary lesser mode in late August. No such July maximum was observed at station I in 1935, possibly because the mode is of such short duration, or because of horizontal variations.

At station II a definite maximum was observed on July 10 in 1935.

The secondary and lesser mode occurring when the temperature was decreasing in the autumn is apparently significant, since it was observed in both years.

(c) *Diaptomus* group in 1932. The seasonal fluctuations in the two species of *Diaptomus* in 1932 show little more than a maximum production in late July and early August and a decline thereafter. If there were a secondary mode in the abundance of *D. minutus*, it would not appear in this diagram because of the influence of changes in the *D. oregonensis* population at this time.

Cyclops group

This group is a complex of three species as discussed previously, and as is evinced by the graphs no general statement can be made as to the usual seasonal fluctuations. In 1934 and 1935 there was a definite maximum in June and both graphs show an upward trend in September. In 1934 this autumnal trend leads towards a late fall maximum. It is possible that the minor fluctuations are a result of lesser pulses of the different species.

Metanauplii and *nauplii*

The metanauplius stages of the combined copepodid population exhibited a marked bimodal distribution in 1935. The first mode is observed in early June, the latter in mid-August.

Nauplii, on the other hand, show but one large maximum. There are, however, indications of an early mode in mid-May and a later mode in September.

Seasonal relationships between developmental stages and adult copepods

Theoretically, maxima of adult copepods should be preceded by maxima of metanauplius stages, and these in turn should be preceded by maxima of nauplii. This progression is shown more or less definitely. It is evident that the spring nauplii are numerous in May and decrease in early June. As the numbers of copepods in the nauplius stage decrease

in the samples, metanauplius stages increase to their spring maximum. This maximum of metanauplii in turn gives way to the first marked increase of adults (plus copepodid stages of *D. oregonensis*). After this increase in the number of adults comes another peak in the numbers of nauplii. In their turn the metanauplius stages increase and ultimately a second increase in the numbers of adult copepods is found in late August. The correlation is by no means perfect but appears sufficiently clearly defined to lead us to believe that in lake Nipissing the following is a general statement of reproductive cycles. Overwintering individuals begin reproductive activity at least by early May. Nauplii reach their spring maximum by mid-May, and continuing development, produce maximum numbers of metanauplii in early June. These in turn produce the first maximum of adults in late June and early July. Reproduction is rapid at this time and the seasonal maximum of nauplii is produced by these adults. The nauplii develop, resulting in the second maximum of metanauplii in mid-August, producing adults which may be overwintering individuals. The nauplii present in September are presumably progeny of these autumnal adults and may develop slowly during the winter.

It is not known whether reproduction continues throughout the winter. In this regard Birge (1897) states: "*Diaptomus* begins its decline in September or early October and seems to make no provision for winter forms. *Cyclops* continues its reproduction activity throughout the year, at least in periods, when the temperature of the lake is above 2°C., but with a rate of multiplication declining as the temperature falls below 15°C. Larval copepods are present in great numbers at all seasons, but their development into later stages is checked in winter." The statement made above appears to hold for the copepod population as a whole. It is realized that there will be specific differences in production, and that some species may produce more broods of nauplii than the three observed. No study has been made by us of the reproductive activity of the various species as evinced by egg-carrying females.

Variation in Seasonal Abundance—Station II

The seasonal fluctuation in abundance of Zooplankton at station II has been determined similarly to that at station I and is indicated in figures 33 and 34. Fewer series were taken during the season at this station, and this limits the observation of seasonal trends.

Daphnia longispina (Müller)

Daphnia show a bimodal fluctuation in abundance. Few were taken until the rapid rise in numbers in mid-July, which produced a maximum lasting two weeks. After a short

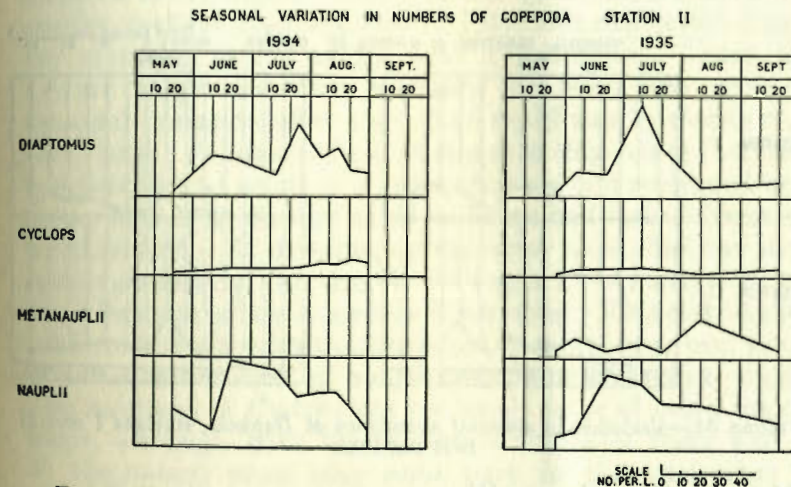


FIGURE 33.—Variation in seasonal abundance of Copepoda, station II, 1934 and 1935.

period of decreased numbers, the second maximum occurred in mid-August and continued into September. The seasonal variation of the form at station II follows fairly well that at station I in 1934, but the paucity of samples in 1935 prevents detailed comparison late in the season.

Diaptomus group

Few individuals of *D. oregonensis* were taken at station II, which may be taken as indicative of conditions throughout

the shallow water area of the lake. The upper panel of figure 33 indicates, in the main, the fluctuations in abundance of *D. minutus*. As was observed at station I, this species reacts quickly in the spring and fairly large numbers of adults are taken in June. The maximum abundance was observed in early July of both years. In general the population declines after this period, but increases slightly in late August and September.

Cyclops group

The number of *Cyclops* does not appear to vary greatly during the summer season in the shallow water region.

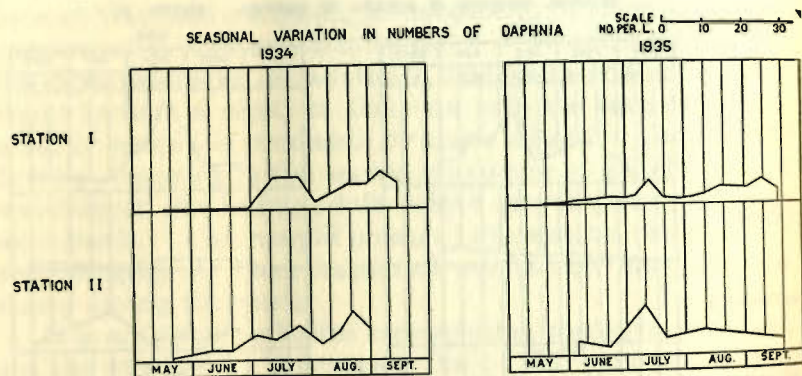


FIGURE 34.—Variation in seasonal abundance of *Daphnia*, stations I and II 1934 and 1935.

Metanauplii and *nauplii*

No spring maximum of metanauplius stages leading to the production of the *D. minutus* maximum in July is observable here. Only two series were taken during June in 1935, and this very probably accounts for its absence. The fall maximum observed at station I is indicated by a peak on August 10 at station II.

Although the nauplii exhibited a trimodal distribution in 1934 at station II, such as was also observed at station I, the lack of numerous collections in 1935 prevents detailed study of seasonal fluctuations.

Summary and Conclusions

The copepod population of lake Nipissing, as a whole, apparently undergoes two complete reproductive cycles and the production of a third brood of nauplii between the break up of the ice, at the end of April, and mid-September. This third brood may, or may not, mature before winter sets in.

An analysis to determine the importance of the individual species of copepods, in the correlation observed between developmental stages and adults, indicates that the population of nauplii and metanauplii of *D. minutus* are dominant in the relationships observed. *D. oregonensis* has a unimodal seasonal distribution. It is believed that production of this species declines after the end of July, and copepodid stages are maturing slowly in the cold hypolimnion. These immature stages are thus probably lost from the cycle of seasonal variation after their first rapid rise in numbers in early July. It has also been shown that this marked increase is primarily the result of a concentration in a restricted area rather than a production of larval forms and their subsequent development. *D. minutus*, on the other hand, has one large maximum in July, and after decreasing in abundance, a second small increase in late August or September. This distribution conforms closely with that expected from the observed variations in abundance of nauplius and metanauplius stages. The numbers of *Cyclops* are too small to be of much importance, although both the immature stages of these and of *D. oregonensis* must play some part in the variations in abundance of nauplii and metanauplii.

GENERAL SUMMARY

The subject has been dealt with progressively in three parts. *Part I* is a consideration of the diurnal changes in the vertical distribution of the limnetic crustacea. *Part II* deals with the seasonal changes in their vertical distribution as effected by changes in environmental conditions. *Part III* is a discussion of the seasonal changes in their abundance and an analysis of the reproductive activity of certain species.

The results and conclusions of each of these phases of the investigation are summarized at the end of each part on pages 47, 93, and 109 respectively.

The general features of the paper are outlined in the following.

Lake Nipissing has an area of 345 square miles, and for the most part is rather shallow. Two-thirds of this area is less than 30 feet in depth, and only half of one per cent is deeper than 75 feet. The restricted area of deep water is, however, of great importance, since it is the only portion remaining cool throughout the season. This deep water loses much of its dissolved oxygen and becomes progressively more highly saturated with carbon dioxide during the summer. The major area of the lake is warmed and remains well oxygenated throughout the summer season.

The limnetic crustacea of the lake are listed (p. 29). Six species and one group were taken in sufficient abundance to determine their distribution.

Through a statistical analysis of a number of collections, it was found that of these entomostracans, none was randomly distributed laterally over the lake at all depths. This was taken into consideration in comparing differences in vertical distribution, and no attempt was made to compare the productivity of lake Nipissing with other lakes.

Definite diurnal migrations were exhibited by the plankton crustacea, and these indicated that light, modified by other environmental factors, was the most important causal factor involved. There were specific differences in response to these changing conditions, and the type and extent of the diurnal migration of any one species differed at different periods during the season.

In spite of the marked variation in horizontal distribution, the great difference in the numbers of individuals of each species at different depths was so marked, and the trends in the change in abundance from depth to depth so noticeable, that seasonal differences in vertical distribution were definitely established.

Field observations and experimental evidence showed that

the factors of light, temperature, oxygen, and carbon dioxide were important in determining these changes in vertical distribution.

Although in most cases there was evidence that maxima in strata near surface were held there by a positive phototropism, usually a scarcity existed in the immediate surface layers, evidently caused by the repellent effect of intense light.

The direct effect of temperature was evidenced by the distribution of several of the species investigated in lake Nipissing. The fact that immature *Diaptomus oregonensis* was found only in lowermost layers, and changed its distribution but slightly with changes in light intensity, would lead one to believe that the important controlling factor was temperature in this case. The temperature gradient at the thermocline was an important factor in the vertical distribution of many species. In most cases maxima were observed either above or below the thermocline or in some cases in both epilimnion and hypolimnion. Under such circumstances there was usually a definite scarcity of the species in the thermocline region itself.

The decrease in dissolved oxygen content and related carbon-dioxide increase have been shown to affect the distribution of certain of the plankton crustacea of lake Nipissing. Late copepodid stages of *D. oregonensis* were found only below the thermocline. These were concentrated at bottom in early summer. Later there was apparently a movement to intermediate hypolimnial layers which was correlated with a decrease of oxygen to 3.5 cc. per litre and an increase of carbon dioxide to approximately 10 p.p.m. in the lower hypolimnial layers.

The reaction of the limnetic crustacea to the above-mentioned factors was modified by age, sex, and specific differences of individuals.

The copepod population as a whole underwent two complete reproductive cycles and the production of a third brood of nauplii between the end of April and mid-September.

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APPENDIX I

TABLE 9.—Light intensity values in foot candles, stations I and II, 1934 and 1935.

		Station I, 1934												
Month Day	V 16	V 25	VI 2	VI 14	VI 19	VI 28	VII 12	VII 24	VIII 3	VIII 13	VIII 21	VIII 28	IX 6	IX 14
	900	8400	7800	9600	9360	4800	10800	7200	3600	6720	4800	4800	3600	8400
		Station I, 1935												
Month Day	VI 5	VI 12	VI 22	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 18
	7800	7800	4800	9120	7200	8400	3840	8400	8400	7200	7200	7200	5760	5160
		Station II, 1934												
Month Day	V 19	VI 9	VI 19	VII 2	VII 12	VII 24	VIII 6	VIII 14	VIII 21	VIII 28				
	9600	1500	9600	7200	7200	7880	9600	9600	2880	12000				
		Station II, 1935												
Month Day	VI 6	VI 22	VII 10	VII 20	VIII 11									
	4800	4800	9100	3840	7800									

TABLE 10.—Water temperatures in degrees Centigrade at different depths, station I, 1934 and 1935 (1934 values from Corkill).

1934

Month Day	V 16	V 29	VI 6	VI 20	VI 24	VI 28	VII 6	VII 11	VII 25	VIII 2	VIII 9	VIII 13	VIII 21	VIII 25	VIII 29		IX 2	IX 9
Depth in metres																Depth in metres		
0	5.4	12.5	16.5	18.1	17.4	17.8	20.0	21.1	22.9	21.5	21.4	20.6	19.6	18.7	17.7	0	17.8	16.5
9	5.4	10.8	16.4	16.1	17.0	17.0	18.5	20.1	21.9	21.3	20.2	20.5	19.5	18.7	17.7
11	16.0	15.0	15.6	...	17.8	19.8	19.8
12	14.8	...	16.6	17.5
14	13.7	13.8	14.2	15.1	16.6	18.7	19.0	19.5	20.1
15	12.6	...	13.9	...	15.9	16.1	18.5	18.1	18.1	20.2
17	17.2	16.8	...	19.5	27	16.8	...
18	...	8.4	12.2	12.6	12.7	12.9	14.9	15.2	16.2	16.3	16.2	17.2	19.5	18.6	17.6	28	14.1	...
20	12.2	13.4	...	14.9	15.7	15.5	15.0	29	11.6	...
22	10.7	13.6	13.8	14.2	...	15.1	16.7	...	30	11.3	15.2
23	13.7	16.4	...	31	...	14.2
25	13.3	13.0	17.2	32	...	13.3
27	...	7.4	9.9	9.6	10.4	11.0	11.8	12.0	12.3	12.5	12.5	12.8	12.3	12.2	12.9	33	...	12.4
32	34	...	10.2
36	...	6.6	8.6	...	8.8	8.6	8.6	9.1	8.8	8.9	8.8	...	9.3	9.2	8.8	35	...	9.6
40	36	...	9.2
45	4.8	7.6	7.9	7.8	8.0	8.0	8.3	8.3	8.4	8.3	8.3	8.3	8.3	37	9.1	...
																45	8.4	8.4

TABLE 10 (continued)

1935

Month Day	VI 5	VI 12	VI 18	VI 20	VI 25	VI 29	VII 3	VII 9	VII 19	VII 27	VIII 9	VIII 22	IX 1	IX 9	IX 18
Depth in metres															
0	15.2	16.2	16.0	15.8	20.9	19.0	19.0	23.2	23.5	24.2	23.2	23.9	20.1	18.6	16.5
5	15.2	15.2	15.2	...	17.6	17.6	18.9	22.2	22.3	...	22.4	22.8	20.1
10	9.5	13.1	15.1	...	16.0	17.3	17.9	21.5	20.4	23.8	21.8	22.3	19.9	18.1	15.0
15	8.9	11.2	14.8	15.6	15.3	16.0	16.8	18.4	18.0	19.6	21.7
18	16.9	15.5	21.0
20	8.4	9.7	12.9	15.2	14.8	15.3	14.9	14.2	16.8	16.8	17.9	21.1	19.4
22	16.8
25	...	8.4	10.2	13.3	13.0	13.3	13.8	13.4	14.6	...	15.7	15.5	18.2	17.5	...
28	14.3	17.0	14.8
30	6.8	7.6	8.7	10.8	10.8	10.7	10.8	11.6	12.1	12.0	11.9	...	12.7	11.4	14.8
35	9.8	14.8
40	6.3	8.8	8.5	9.2	8.5	8.2	8.5	...	8.4	8.7	...	9.1
45	...	6.4	7.2	7.8	8.4	8.4

TABLE 11.—Oxygen content at different depths, station I, 1934 (from Corkill).

Month Day	V 29	VI 20	VI 28	VII 11	VII 25	VIII 2	VIII 6	VIII 9	VIII 13	VIII 21	VIII 29	IX 2	IX 9
Depth in metres													
0	7.3	6.0	5.8	5.4	5.0	5.5	5.5	5.5	5.5	5.6	5.7	6.0	5.9
9	7.5	5.8	5.2	5.2	4.9	5.4	5.4	5.1	5.4	5.5	5.7	5.9	...
18	7.6	5.7	5.4	4.8	4.2	4.0	4.2	4.0	4.1	5.6	5.7	5.9	...
27	7.4	6.3	5.8	5.0	4.4	4.4	4.1	3.8	3.7	3.8	3.8	5.8	...
28	4.7	...
29	4.0	...
30	3.8	5.2
31	4.5
32	4.2
35	2.8
37	7.5	...	6.1	5.3	4.5	4.6	4.1	3.6	...	3.3	3.3	3.0	2.7
45	5.6	4.5	3.7	3.1	3.1	3.2	2.5	2.6	2.0	2.1	1.5

TABLE 12.—Diurnal variation in vertical distribution of plankters, station I, June 27, 1934 (number per litre).

Daphnia

Depth in metres	12.10 p.m.	3.30 p.m.	6.00 p.m.	8.00 p.m.	10.30 p.m.	12.10 a.m.	3.00 a.m.	4.00 a.m.	6.30 a.m.	10.00 a.m.	12.15 p.m.
0	...	0.3	0.3	1.0	3.1	11.5	3.3	3.0	0.6	0.3	...
3	1.7	2.1	5.0	1.2	3.0	3.0	3.0	1.2	3.0	2.8	0.9
5	1.4	1.4	1.7	1.7	4.1	4.4	2.3	3.0	2.5	1.9	1.6
8	1.7	1.5	0.7	2.1	1.0	1.2	1.8	2.0	2.1	0.8	1.2
10	0.8	0.7	1.9	1.3	2.0	0.5	1.0	1.1	0.9	1.0	0.6
15	1.5	0.6	0.3	1.0	0.4	0.9	0.7	1.2	0.6	0.5	0.7
20	0.4	0.2	0.3	0.7	0.4	0.4	0.3	0.1	1.0	0.8	0.4
25	0.1	0.2	0.1	0.3	0.2	0.2	0.3	0.2	0.3	0.3	0.2
30	0.4	0.1	0.1	0.5	0.1	...	0.1	...	0.2	0.1	...
35	...	0.1	...	0.1	...	0.2	0.1	...	0.2
40	0.1	0.3	...	0.1	0.2	0.1	0.2

TABLE 12 (continued)

Epischura

Depth in metres	12.10 p.m.	3.30 p.m.	6.00 p.m.	8.00 p.m.	10.30 p.m.	12.10 a.m.	3.00 a.m.	4.00 a.m.	6.30 a.m.	10.00 a.m.	12.15 p.m.
0	1.2	0.7	1.5	0.3	1.6	...	0.7	0.3	0.7	0.3	0.3
3	1.3	1.7	2.0	0.7	0.5	0.3	0.9	0.8	...	0.7	...
5	0.6	0.9	1.0	1.0	1.2	1.8	0.7	1.2	0.3	0.5	0.1
8	0.5	0.2	0.4	1.0	1.1	1.0	0.6	1.0	0.6	0.2	0.9
10	0.5	0.1	0.3	0.3	0.9	0.5	0.2	0.2	0.7	1.5	0.3
15	...	0.1	0.6	0.4	0.4	0.3	1.1	0.3	0.1
20	0.1	0.1	0.1	0.3	0.5	0.1	0.2
25	0.5	0.2	0.1	0.6	0.1	0.1	0.1
30	0.6	0.5	...	0.4	0.1	0.1	0.1
35	0.3	0.1	0.1	0.2
40	0.1

Diaptomus group

Depth in metres	12.10 p.m.	3.30 p.m.	6.00 p.m.	8.00 p.m.	10.30 p.m.	12.10 a.m.	3.00 a.m.	4.00 a.m.	6.30 a.m.	10.00 a.m.	12.15 p.m.
0	8.0	8.4	22.0	15.0	22.0	27.6	18.0	13.5	18.5	14.0	12.0
3	29.0	23.5	25.5	15.0	18.0	12.0	15.5	12.0	16.5	17.5	16.2
5	6.5	4.5	13.5	10.5	14.5	10.0	10.0	9.0	10.5	27.5	10.0
8	3.5	2.5	22.5	6.5	10.5	8.5	5.5	8.0	6.5	6.5	21.0
10	3.5	2.5	5.0	4.0	8.5	6.5	7.5	7.0	6.5	5.5	6.0
15	1.4	1.0	2.5	2.0	2.5	3.5	6.0	6.0	7.0	3.0	1.5
20	1.0	1.4	1.5	2.0	1.5	1.0	2.0	1.5	2.5	1.5	1.5
25	2.7	1.7	2.0	3.0	0.8	2.0	0.5	2.0	0.5	2.0	0.7
30	3.0	2.0	2.0	3.0	2.5	2.0	2.0	2.3	2.5	4.0	2.5
35	8.2	5.0	5.5	6.5	5.0	7.5	5.5	3.0	4.5	4.0	5.5
40	31.0	35.0	28.5	24.5	24.5	29.5	31.5	25.0	28.5	28.0	28.5

TABLE 12 (continued)

Cyclops group

Depth in metres	12.10 p.m.	3.30 p.m.	6.00 p.m.	8.00 p.m.	10.30 p.m.	12.10 a.m.	3.00 a.m.	4.00 a.m.	6.30 a.m.	10.00 a.m.	12.15 p.m.
0	1.0	1.7	6.0	6.5	4.0	6.0	4.0	8.5	5.0	6.0	10.0
3	9.0	11.0	10.6	4.5	3.5	5.0	4.0	5.0	8.0	10.0	10.0
5	5.5	9.0	8.0	5.0	4.0	4.5	3.5	5.5	6.0	10.0	10.0
8	4.0	6.0	7.0	7.0	7.0	5.0	4.0	4.5	4.0	5.5	8.5
10	5.6	5.5	10.0	8.5	7.0	6.5	6.5	9.0	4.5	7.0	6.0
15	7.6	7.5	12.0	7.0	11.0	11.5	12.0	10.0	8.0	11.0	10.0
20	9.7	8.5	8.0	8.0	8.0	9.5	12.5	9.0	7.5	10.0	6.5
25	8.5	8.0	7.0	9.6	9.0	8.5	9.6	8.0	...	10.5	7.5
30	11.3	8.0	10.0	10.0	8.5	7.0	10.0	6.0	6.5	9.0	7.5
35	8.3	15.0	11.0	9.5	7.5	8.6	8.0	6.5	6.0	7.0	6.5
40	10.0	8.5	8.0	6.5	6.0	7.0	7.0	7.0	6.0	3.0	6.5

Nauplii

Depth in metres	12.10 p.m.	3.30 p.m.	6.00 p.m.	8.00 p.m.	10.30 p.m.	12.10 a.m.	3.00 a.m.	4.00 a.m.	6.30 a.m.	10.00 a.m.	12.15 p.m.
0	36.0	35.0	24.5	23.0	45.5	47.0	26.0	28.0	72.0	64.0	55.5
3	50.0	57.0	66.0	67.5	58.0	48.0	47.0	46.0	64.5	60.0	62.5
5	34.0	33.0	61.0	55.0	52.0	40.0	50.5	39.0	55.0	61.0	76.0
8	38.5	33.5	50.0	46.0	61.0	76.5	55.0	43.0	37.0	40.0	54.0
10	31.0	36.1	25.0	34.0	37.0	45.0	43.5	46.0	52.0	61.5	37.5
15	55.0	39.0	40.0	40.5	32.0	52.0	43.5	35.5	47.5	54.0	77.0
20	80.0	85.0	77.5	84.0	76.5	92.0	81.5	78.0	118.0	86.5	81.5
25	69.5	65.0	50.0	60.0	62.0	61.5	59.0	70.0	61.0	71.0	60.0
30	45.5	49.5	50.0	50.5	41.0	47.5	61.5	58.5	68.0	65.5	60.5
35	38.5	53.0	53.5	43.5	40.5	35.0	40.0	43.0	40.0	41.5	40.0
40	25.4	24.0	21.0	29.0	31.0	25.5	35.0	25.0	35.5	24.5	35.5

TABLE 13.—Depth distribution of plankters at night, station I, 1935 (number per litre).

Month Day	<i>Cyclops</i>					<i>Epischura</i>					<i>Metanauplii</i>					<i>Nauplii</i>		
	VI 22	VII 5	VII 27	VIII 24	IX 1	VI 22	VII 5	VII 27	VIII 24	IX 1	VI 22	VII 5	VII 27	VIII 24	IX 1	VI 22	VII 5	VII 27
Depth in metres																		
0	2.5	2.5	2.0	6.0	2.5	3.0	0.3	0.8	4.5	3.5	5.0	8.5	5.0	33.0	35.5	65.0
1	1.0	3.0	3.0	4.5	1.0	3.5	0.7	1.2	0.2	...	5.0	7.5	13.5	8.5	15.0	30.0	56.3	65.0
3	2.5	2.0	14.5	5.5	2.0	4.5	0.2	1.6	0.2	0.1	6.5	3.5	13.5	7.5	15.5	42.5	33.0	71.5
5	2.5	2.5	3.0	5.0	6.5	3.0	0.5	0.8	0.2	...	5.5	3.5	11.5	7.0	12.0	32.0	33.0	41.5
8	1.0	4.0	3.5	5.0	5.0	3.5	0.8	0.5	0.2	0.1	4.0	5.5	8.0	9.0	17.0	32.5	59.5	28.5
10	2.0	7.0	3.0	4.7	3.0	2.2	1.0	0.4	0.2	...	2.5	5.5	11.5	9.0	13.0	32.5	46.5	34.5
15	4.0	3.0	2.0	4.1	3.5	1.5	17.5	3.5	6.0	14.5	5.5	26.5	18.5	10.5
20	3.5	4.5	2.2	6.0	2.0	1.0	15.5	4.6	8.0	13.5	5.5	51.5	54.0	10.5
25	2.5	3.0	0.5	1.0	0.5	1.7	0.1	16.0	5.0	12.0	17.5	5.5	64.0	48.0	6.0
30	4.0	2.5	0.5	1.5	0.5	0.6	0.2	17.0	6.5	8.0	16.0	9.5	82.5	19.5	4.0
35	2.5	2.5	0.5	0.5	1.0	0.2	9.5	5.0	4.0	8.0	7.0	35.0	12.5	3.0
40	3.5	2.5	1.0	0.5	0.5	13.0	5.0	2.5	6.5	3.5	31.0	12.5	2.5
45	3.5	2.0	0.8	0.5	3.5	4.5	2.5	4.5

TABLE 13 (continued)

Month Day	<i>Nauplii</i>		<i>Daphnia</i>					<i>Diaptomus oregonensis</i>					<i>Diaptomus minutus</i>				
	VIII 24	IX 1	VI 22	VII 5	VII 27	VIII 24	IX 1	VI 22	VII 5	VII 27	VIII 24	IX 1	VI 22	VII 5	VII 27	VIII 24	IX 1
Depth in metres																	
0	16.5	21.0	0.7	10.0	20.0	9.0	4.5	6.0	0.5	23.5	4.0	21.5	21.5	7.0	59.5	21.0	34.5
1	18.5	31.5	1.5	17.0	3.0	11.0	8.0	4.5	0.5	21.3	2.6	20.5	27.5	15.0	35.0	19.5	23.5
3	13.8	34.5	3.0	14.3	2.2	8.5	16.0	5.5	0.5	4.0	2.5	13.5	6.5	11.5	27.5	20.0	30.0
5	15.0	37.0	4.0	6.5	7.5	12.0	13.5	4.0	1.5	2.5	3.5	12.0	14.0	8.0	21.0	17.5	30.0
8	16.0	33.0	3.0	3.0	6.0	6.5	14.0	1.5	2.0	1.0	2.5	5.5	19.5	4.0	25.5	16.0	38.0
10	15.0	27.0	1.5	2.5	4.0	7.0	15.0	0.5	2.0	0.3	3.0	8.0	9.0	3.0	16.5	14.5	24.5
15	12.2	20.5	1.0	1.5	2.2	7.7	14.0	0.5	1.3	8.7	1.5	11.3	3.0	2.7	4.5	9.5	17.5
20	11.4	7.0	1.0	0.8	1.0	5.0	5.0	0.5	1.5	12.5	2.5	3.0	1.5	1.0	2.5	3.0	4.5
25	3.0	7.0	0.5	1.2	0.3	1.5	3.0	1.5	3.5	28.5	30.5	2.5	2.5	1.0	2.0	1.0	2.0
30	4.0	3.0	0.3	1.3	0.5	1.5	1.0	4.0	12.5	...	60.5	80.0	1.0	2.0	...	1.5	1.5
35	2.5	1.0	0.3	2.0	0.2	0.7	0.3	5.5	19.0	65.5	90.5	69.5	1.0	1.0	0.6	0.5	0.5
40	2.5	3.5	0.3	0.5	0.1	0.7	0.5	7.5	18.0	49.5	45.2	30.0	1.0	0.5	0.1	0.5	...
45	6.0	2.5	0.3	0.2	0.2	0.5	0.5	...	49.5	51.5	25.8	27.0	...	0.5	0.5	0.3	...

TABLE 14.—Depth distribution of plankters, station I, 1934 and 1935 (numbers per litre).

Daphnia, 1934

Month Day	V 16	V 25	VI 2	VI 14	VI 19	VI 28	VII 12	VII 24	VIII 3	VIII 13	VIII 21	VIII 28	IX 6	IX 14
Depth in metres														
0	0.1	0.1	...	1.3	0.3	...	0.2	20.0	2.0	2.5	8.0	0.8	4.2	0.8
3	...	0.7	0.5	5.5	4.0	1.7	14.0	28.0	2.5	14.5	9.5	19.0	14.0	17.0
5	...	0.3	0.7	3.3	3.8	1.4	16.5	27.8	4.5	7.5	14.0	14.0	12.5	17.0
8	...	0.1	0.7	1.8	1.3	1.7	11.0	9.0	5.0	3.0	10.5	6.0	12.5	17.5
10	0.1	0.1	1.0	2.2	2.5	0.8	15.0	8.5	3.5	2.5	14.5	10.0	11.5	10.1
15	0.1	0.1	...	0.7	0.7	1.5	17.5	2.5	3.5	2.0	18.0	6.0	8.0	8.0
20	0.1	...	0.3	1.1	0.7	0.4	5.9	1.7	1.5	1.7	10.5	7.5	8.0	1.5
25	0.5	0.2	0.1	1.4	16.0	0.5	0.3	2.0	7.0	14.5	3.5
30	0.2	0.3	0.1	0.4	1.7	1.0	0.5	0.7	1.0	2.0	5.0	2.5
35	1.1	11.0	0.5	...	0.5	0.3	0.5	1.0	1.0
40	0.3	1.7	0.3	0.1	0.6	1.3	0.7	1.0	0.5

Daphnia, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 22	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 9	IX 18
Depth in metres																	
0	0.4	0.1	1.2	0.5	3.0	...	0.5	1.7	...	0.5	1.5	0.1	0.5	9.0	0.5
1	7.0	7.0	4.5	2.0	6.0	7.0	1.5	2.5	0.2	7.5	11.0	22.3	2.5	10.0	1.4
3	0.5	0.2	4.0	7.0	5.5	3.0	7.0	10.0	2.5	3.0	5.0	13.5	21.0	19.0	18.0	25.0	4.5
5	0.5	0.3	3.5	4.0	2.5	4.0	3.5	12.5	4.0	1.0	2.0	7.5	11.0	12.3	16.0	22.5	12.2
8	0.5	0.3	0.5	1.0	3.0	2.5	1.6	6.0	2.2	1.0	1.0	3.0	8.5	4.5	9.0	12.5	5.0
10	0.5	0.2	0.3	0.5	3.5	3.0	2.0	14.0	1.5	0.8	2.0	4.0	10.0	2.5	4.5	7.0	3.5
15	0.1	...	0.5	0.3	3.0	1.8	1.5	3.5	3.5	2.5	1.0	1.5	2.0	2.0	1.5	2.0	2.5
20	0.1	0.3	1.7	1.5	1.5	2.5	2.5	2.7	2.0	1.5	1.0	5.0	2.5	2.0	3.0
25	0.3	0.2	0.7	2.0	4.5	1.0	0.2	2.5	0.3	1.0	0.5	1.0	...	4.0
30	0.3	0.3	0.5	0.7	0.6	10.0	0.3	0.2	0.2	0.3	1.0	0.3	0.8	3.0	2.0
35	...	0.1	...	0.3	0.2	0.5	0.5	1.8	0.2	0.3	0.2	0.3	0.5	...	0.5	0.8	2.0
40	...	0.1	0.1	...	0.2	0.5	0.5	2.0	0.3	0.1	0.1	0.1	0.2	0.5	0.3	0.8	1.5
45	0.3	...	0.5	0.5	1.0	0.2	0.2	...	0.3	0.5	0.5	0.5	...	0.5

TABLE 14 (continued)

Holopedium, 1934

Month Day	V 25	VI 2	VI 14	VI 19	VII 12
Depth in metres					
0	0.9	0.4	...
3	0.8	0.9	0.1	3.5	...
5	0.2	0.7	0.2	1.4	...
8	0.3	0.4	0.2	0.3	...
10	0.3	0.5	...	0.3	...
15	0.1	1.3	0.1	0.3	...
20	0.1	0.1
25
30
35
40

NONE THEREAFTER DURING SEASON

Holopedium, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 22
Depth in metres					
0	0.2	...	0.2
1	0.2	...	1.5
3	0.5	...	1.5
5	1.0	0.2	0.8	0.1	...
8	0.2	0.3
10	0.1	0.1
15	0.3	0.2
20	0.1	...	0.1
25
30	0.1
35	0.1
40	0.1

NONE THEREAFTER DURING SEASON

TABLE 14 (continued)

Epischura, 1934

Month Day	V 16	V 25	VI 2	VI 14	VI 19	VI 28	VII 12	VII 24	VIII 3	VIII 13	IX 6	IX 14
Depth in metres												
0	...	0.1	1.1	1.2	0.3
3	...	0.1	0.8	1.0	1.0	1.3	1.0	0.2	0.3
5	0.4	1.6	1.1	0.6	0.8	0.3
8	0.7	0.6	0.4	0.5	0.3
10	1.2	1.8	0.4	0.5	0.4	0.1
15	0.1	0.4	0.5	...	0.6	0.1	0.1	0.1
20	0.2	0.3	0.4	0.1	0.7	0.1	0.1	...
25	0.1	0.1	0.5	0.2
30	...	0.1	0.2	0.1	...	0.6	...	0.5
35	0.7	0.1	...	0.3	1.1
40	0.4	0.3	0.1

Epischura, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 22	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	IX 1	IX 9	IX 18
Depth in metres																
0	1.2	...	1.7
1	...	0.1	3.0	0.2	4.5	1.0	1.0
3	...	0.5	1.2	1.0	3.5	1.5	0.2
5	...	0.2	1.2	1.0	3.0	2.0	0.5	0.5
8	...	0.1	0.5	0.5	3.0	2.5	0.5	0.1	1.0	0.1	0.3
10	0.5	1.5	1.1	0.3	1.0	1.0	0.1	0.2
15	0.2	1.0	0.6	0.2	1.8	0.7	0.2	1.0	0.4	...	0.1
20	0.3	0.3	0.1	0.1	0.3
25	0.7	...	0.3
30	0.2	0.1
35	0.1	0.1	...	0.1	0.1
40
45	0.1	0.2

TABLE 14 (continued)

Diaptomus oregonensis, 1934

Month Day	V 16	VI 2	VI 19	VI 28	VII 12	VII 24	VIII 3	VIII 13	VIII 21	VIII 28	IX 6	IX 14
Depth in metres												
0	1.0	0.5	1.0	2.0	5.0	3.0	1.0	0.5	4.0	1.0	1.5	0.2
3	0.5	2.5	6.0	6.0	30.0	4.0	1.5	17.0	2.5	8.0	4.0	16.0
5	0.5	1.0	5.0	4.0	16.0	8.0	4.0	20.0	3.5	2.5	2.0	4.5
8	...	2.0	5.0	4.0	17.5	3.0	3.0	10.0	3.5	2.5	2.0	3.5
10	1.5	2.0	5.0	2.0	8.0	2.5	2.0	0.5	10.0	1.5	2.0	3.5
15	1.0	1.0	2.0	1.0	10.0	0.5	4.0	2.5	4.5	1.5	3.0	1.5
20	2.0	1.0	2.0	1.0	6.0	7.0	6.0	2.5	2.5	4.0	4.5	1.0
25	0.5	...	2.0	0.5	4.0	45.0	15.0	24.0	6.5	5.0	3.5	0.5
30	0.5	0.7	1.0	2.0	5.0	27.0	30.5	25.0	40.5	34.5	2.5	0.5
35	1.0	1.5	2.0	5.0	54.0	69.0	48.0	76.5	61.0	60.0	31.0	24.0
40	1.5	?	9.0	25.0	78.0	70.0	55.5	44.5	42.0	26.0	51.0	17.5

Diaptomus oregonensis, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 22	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 9	IX 18
Depth in metres																	
0	0.5	5.0	0.1	...	1.0	...	1.0	0.2	1.6	1.0	1.5	1.5	
1	0.3	1.0	1.0	0.5	3.5	1.0	1.0	0.5	3.0	2.0	1.0	2.5
3	0.3	0.7	1.0	0.5	5.0	1.0	6.0	0.1	...	4.0	...	0.6	1.5	2.5	3.0	3.5	4.0
5	...	0.2	1.0	0.5	3.5	3.5	2.0	0.2	0.5	2.5	...	1.5	0.8	6.0	6.0	4.5	6.5
8	0.5	0.3	0.5	0.2	2.0	1.2	1.5	0.5	1.0	0.3	0.5	0.7	1.2	3.0	1.5	7.5	4.5
10	0.5	0.5	0.6	0.1	1.0	2.0	0.7	0.5	1.5	1.0	6.5	0.7	1.7	0.5	1.0	2.5	3.0
15	0.5	0.1	0.6	0.1	0.5	1.0	0.5	3.0	4.0	9.0	10.0	0.8	0.5	1.7	1.5	0.6	4.0
20	0.1	0.3	0.3	2.0	0.8	0.5	0.5	10.5	8.0	17.0	3.8	7.0	10.5	1.2	0.3	1.2	4.0
25	0.2	0.3	0.3	2.0	1.0	4.5	3.1	20.5	15.0	28.0	54.5	38.0	35.5	36.5	12.0	3.5	3.5
30	...	0.4	0.3	1.5	3.5	17.0	16.0	30.5	71.5	70.5	91.0	68.0	76.0	54.5	74.0	74.0	2.2
35	0.1	0.2	0.2	2.5	7.5	31.0	19.5	39.0	76.0	77.0	81.5	71.5	70.0	74.5	65.0	25.0	2.0
40	0.3	0.3	0.3	2.5	5.0	17.5	18.0	65.0	106.5	68.0	59.0	56.5	37.5	48.5	32.0	34.0	28.0
45	?	?	?	2.0	54.5	161.7	131.0	53.0	45.0	33.0	35.0	28.5	21.0	...	32.5

TABLE 14 (continued)
Diaptomus minutus, 1934

Month Day	V 16	VI 2	VI 19	VI 28	VII 12	VII 24	VIII 3	VIII 13	VIII 21	VIII 28	IX 6	IX 14
Depth in metres												
0	0.5	2.5	2.0	10.0	2.0	44.0	14.0	23.0	16.0	3.0	10.0	2.5
3	0.5	12.5	10.0	14.0	70.0	42.0	16.0	47.0	11.5	15.5	16.0	15.5
5	0.5	8.0	10.0	6.0	50.5	38.0	17.0	14.0	17.0	17.0	11.5	12.0
8	...	6.0	6.5	17.0	66.5	39.0	17.0	6.0	14.0	10.0	9.0	9.0
10	1.5	6.0	4.5	4.0	50.5	40.0	19.0	7.0	13.0	5.0	9.5	6.5
15	1.2	2.5	1.0	0.5	67.0	9.5	9.0	5.0	14.5	6.0	9.0	2.5
20	1.5	1.5	0.5	0.5	25.5	5.5	5.0	4.0	16.5	8.0	7.0	1.0
25	1.0	...	0.5	0.2	7.5	7.0	2.0	2.0	2.0	12.0	5.0	0.5
30	1.0	1.0	0.5	0.5	2.5	4.0	1.5	1.0	0.5	2.0	1.0	0.5
35	1.5	1.0	0.5	0.5	3.0	2.0	1.0	1.0	0.5	0.5	0.5	...
40	2.0	?	0.5	0.5	2.5	0.5	0.5	0.5	0.5	0.5	0.5	...

Diaptomus minutus, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 22	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 9	IX 18
Depth in metres																	
0	1.5	32.5	7.0	8.5	26.0	3.5	11.5	21.8	2.4	1.0	0.5	1.0	5.5	10.0	11.0	18.0	9.5
1	1.0	17.5	11.5	16.5	9.5	43.5	16.5	20.0	8.0	8.0	1.0	4.0	20.5	47.0	16.0	13.5	9.0
3	1.2	4.0	11.5	15.0	30.0	20.0	27.5	24.0	8.7	35.0	12.0	11.0	33.0	36.0	33.0	26.5	8.5
5	2.0	1.8	9.5	10.0	16.5	19.5	19.0	25.5	31.0	21.0	7.5	10.0	13.5	15.0	18.0	34.5	12.3
8	2.5	1.5	1.0	1.8	23.5	12.5	2.5	19.0	9.5	13.0	9.5	8.0	11.0	14.0	11.0	17.0	7.0
10	2.5	2.0	0.4	0.9	6.0	8.0	1.8	22.2	6.5	12.5	20.0	13.0	10.0	15.5	13.0	10.5	7.0
15	2.5	0.1	0.4	0.7	2.5	3.0	2.0	4.4	2.5	6.5	14.0	7.0	3.0	11.0	11.0	3.5	8.0
20	0.2	0.2	0.3	0.5	1.2	3.0	4.0	3.0	0.8	1.0	1.2	0.8	1.8	6.0	1.5	0.7	4.0
25	0.2	0.2	0.2	0.5	1.5	3.0	1.0	1.7	0.5	1.0	1.7	0.3	0.6	2.0	1.0	3.5	7.0
30	0.1	0.3	0.2	0.5	1.0	0.5	0.2	3.0	0.2	0.5	1.0	0.5	0.5	2.0	2.5
35	0.1	0.3	0.1	0.5	2.0	0.5	0.5	1.5	0.5	0.5	0.7	0.2	...	1.0	0.5	0.5	3.5
40	0.2	0.2	0.2	...	1.0	0.5	0.5	1.0	0.2	0.5	0.7	0.5	0.2	1.5	1.0
45	?	?	?	0.5	0.6	...	1.0	0.5	1.0	0.1

TABLE 14 (continued)
Limnocalanus, 1934

Month Day	V 16	V 25	VI 2	VI 14	VI 19	VII 12	VII 24	VIII 3	VIII 13	VIII 21	VIII 28	IX 6	IX 14
Depth in metres													
0
3
5
8
10
15
20	0.5	0.7	0.2	0.1	...
25	0.1	...	0.6	0.3	0.1	...	0.7	0.2	1.0
30	0.1	...	0.2	...	0.2	0.5	0.6	0.7	0.8	1.3	...
35	0.1	0.2	...	0.4	1.5	2.1	1.1	1.0	1.0	0.3
40	?	0.4	0.3	1.6	1.5	3.0	3.0	1.6	1.7	1.1	0.5

Adult *Limnocalanus*, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 9	IX 18
Depth in metres																
0
1
3
5
8
10
15
20	0.1
25	0.1
30	0.1	0.1	0.1	0.4	0.3	0.5	0.2
35	0.1	...	0.5	0.8	0.9	0.2	0.2	0.3	0.1	0.5	0.1	0.3	...
40	0.2	1.0	1.0	0.2	0.2	0.2	0.3	0.3	0.3	1.0	0.4	1.5
45	?	?	?	0.4	...	0.5	...	0.4	0.8	0.5	0.4	0.3	0.2	0.3	0.3	...

TABLE 14 (continued)
Immature *Limnocalanus*, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 9	IX 18
Depth in metres																
0
1
3
5
8
10	0.1
15	0.2	0.1	0.2
20	0.2	0.5	...	0.4	...	0.4	...	0.3
25	0.8	0.1	...	0.3	0.5	0.9	0.7	0.4	0.2	0.2
30	1.2	0.6	0.5	1.0	0.8	1.8	2.6	1.0	0.9	0.5	0.4	0.1	...
35	1.0	0.7	1.2	2.3	0.8	1.3	2.3	1.2	2.5	1.3	1.2	0.9	...
40	4.5	1.5	3.0	2.3	2.0	1.3	4.3	3.5	2.0	1.2	1.0	2.0
45	?	?	?	1.2	...	2.0	2.5	3.5	2.2	1.4	1.1	1.7	1.6	2.6	1.0	6.0

TABLE 14 (continued)
Cyclops group, 1934

Month Day	V 16	V 25	VI 2	VI 14	VI 19	VI 28	VII 12	VII 24	VIII 3	VIII 13	VIII 21	VIII 28	IX 6	IX 19
Depth in metres														
0	0.9	0.5	1.3	1.0	6.5	1.0	0.6	5.0	1.6	1.5	1.5	0.3	0.5	0.2
3	1.5	5.0	2.5	6.5	7.0	9.0	6.0	4.5	5.0	9.5	2.0	4.0	1.0	7.0
5	1.5	3.5	3.5	4.5	5.8	5.5	3.2	5.7	6.0	4.0	6.5	2.5	5.0	9.0
8	1.8	0.9	2.4	3.0	3.5	4.0	5.0	2.5	4.0	1.5	6.5	2.0	2.7	14.0
10	2.0	1.5	2.0	4.5	3.0	5.6	3.5	1.7	4.5	3.0	8.5	1.2	3.0	15.5
15	2.5	0.1	2.0	3.5	8.5	7.6	6.5	2.5	2.2	4.5	5.5	2.5	2.0	3.0
20	1.3	0.3	0.5	8.0	6.5	9.7	4.6	3.0	1.5	3.5	3.5	4.0	2.5	2.5
25	0.9	0.2	0.5	8.5	4.0	8.5	4.7	1.0	1.3	2.5	1.5	3.0	2.5	3.0
30	0.8	0.3	1.0	6.5	4.5	11.3	3.0	1.0	1.0	1.2	2.5	4.5	2.5	3.0
35	0.6	0.1	0.6	6.5	5.0	8.3	9.0	2.0	1.5	1.0	2.5	1.8	1.0	2.5
40	1.3	0.4	?	4.5	5.5	10.0	5.0	2.0	0.5	1.0	0.7	1.0	0.7	1.1

Cyclops group, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 22	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 9	IX 19
Depth in metres																	
0	1.0	...	0.3	1.5	2.5	5.0	4.5	2.5	0.3	2.0	0.3	2.5	...
1	2.0	4.0	1.0	3.0	3.5	4.0	0.8	1.0	0.1	...	3.5	7.5	1.0	2.5	2.0
3	0.5	2.0	2.0	4.5	5.0	3.5	7.5	3.5	2.0	3.0	0.5	1.1	5.5	18.0	4.0	5.0	5.0
5	2.5	1.0	2.5	7.5	5.0	5.0	5.5	4.5	6.0	3.5	0.3	2.5	3.5	7.8	3.0	2.5	9.0
8	0.2	0.5	1.5	10.5	9.5	3.5	3.5	4.0	2.5	2.0	1.0	3.0	0.7	6.7	3.0	2.5	6.5
10	0.5	0.3	0.3	11.0	3.5	3.5	2.5	4.0	1.5	1.0	4.5	3.5	5.0	6.7	4.0	2.0	12.5
15	0.5	0.6	1.5	13.7	5.0	3.0	3.0	7.0	3.0	3.0	5.5	0.8	0.5	2.2	3.0	1.2	5.0
20	0.2	0.2	0.5	15.0	5.5	4.0	4.5	6.0	3.5	3.0	0.8	0.8	1.5	2.5	2.5	0.5	4.0
25	0.2	0.3	5.0	7.5	4.0	3.5	5.0	6.0	2.5	1.0	1.5	0.5	1.0	2.0	1.0	...	4.0
30	0.2	0.2	0.5	3.5	4.0	4.0	2.0	3.6	0.5	1.0	1.8	0.5	1.0	1.0	1.0	2.0	3.0
35	...	0.2	0.5	2.5	3.5	5.5	2.0	4.5	2.5	1.0	0.6	0.2	...	1.0	0.5	0.5	2.2
40	0.1	0.3	4.0	1.5	1.0	4.0	1.0	0.7	0.5	0.5	...	0.5	0.5	0.2	1.5
45	?	?	?	1.5	3.0	1.0	1.0	1.5	1.0	0.6	1.0	0.5	0.1	1.5	0.1	...	0.2

TABLE 14 (continued)

Nauplii, 1934

Month Day	V 16	V 25	VI 2	VI 14	VI 19	VI 28	VII 12	VII 24	VIII 3	VIII 13	VIII 21	VIII 28	IX 6	IX 14
Depth in metres														
0	15.7	105.0	13.3	15.5	14.5	36.0	77.5	65.5	22.5	53.5	20.5	28.0	10.0	16.5
3	17.5	36.0	39.0	20.0	23.0	50.0	106.5	53.5	32.0	60.0	31.5	21.5	16.0	6.0
5	21.8	28.0	32.5	26.0	30.0	34.0	111.5	37.6	34.0	25.7	28.5	15.5	15.0	2.5
8	26.4	31.0	24.6	24.0	37.0	38.5	85.5	27.0	30.5	17.0	21.5	16.0	5.2	1.0
10	28.5	28.5	32.5	26.0	38.0	31.0	56.0	18.5	28.0	22.0	20.0	9.0	3.5	0.5
15	28.0	22.5	25.0	24.5	33.5	55.0	70.5	21.0	14.0	13.0	23.0	10.0	6.5	1.0
20	24.5	20.5	18.0	72.0	68.0	80.0	69.0	28.5	17.0	13.0	36.0	8.5	6.5	3.0
25	22.3	17.0	16.0	53.0	61.5	69.5	51.5	23.5	10.0	5.0	5.0	12.0	13.0	4.5
30	24.5	11.6	14.5	49.5	66.5	45.5	35.5	11.0	7.5	4.5	4.5	3.5	6.0	6.0
35	25.5	11.5	10.5	36.0	57.5	38.5	96.0	6.5	7.0	3.0	3.5	2.0	1.0	2.5
40	33.0	11.4	?	23.5	47.5	25.5	24.8	8.0	3.5	4.5	6.0	2.0	0.7	0.5

Nauplii, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 22	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 9	IX 18
Depth in metres																	
0	26.0	34.5	4.5	2.0	70.0	59.0	143.0	41.0	62.5	70.0	42.0	175.0	28.5	68.0	38.0	25.0	12.5
1	30.0	35.0	3.0	2.0	60.0	106.0	123.0	50.5	161.0	108.0	51.5	200.0	38.5	30.0	37.5	30.0	12.5
3	33.0	36.5	3.0	4.0	55.0	90.0	109.5	46.0	66.0	59.0	32.5	33.0	19.5	34.8	75.0	32.0	14.5
5	40.0	21.0	7.5	3.5	50.0	75.0	67.5	55.5	36.5	26.5	18.5	15.0	7.0	9.0	18.5	25.0	6.0
8	43.0	36.4	9.5	3.5	55.0	61.0	59.0	42.0	16.0	15.0	12.0	10.0	5.5	9.0	9.5	15.0	5.5
10	25.5	48.5	14.0	6.0	31.0	37.0	29.0	64.0	15.0	9.0	12.0	7.5	2.0	8.5	6.5	14.0	5.0
15	31.5	3.5	8.5	10.0	29.5	50.0	32.0	63.0	26.0	5.0	9.0	6.5	2.5	11.0	8.0	16.0	8.0
20	9.5	8.0	10.0	26.0	52.0	58.0	41.0	58.0	24.0	11.5	5.5	5.5	2.0	3.0	5.5	13.5	9.0
25	8.0	7.0	3.0	19.0	54.5	113.5	47.0	50.0	19.0	3.5	3.5	6.5	1.5	1.5	1.0	7.5	7.5
30	7.5	7.5	4.0	14.0	55.0	59.0	37.0	34.0	7.0	2.0	2.5	3.0	1.0	2.0	1.8	2.5	11.0
35	9.0	5.0	3.0	10.0	36.0	31.5	26.0	19.5	5.5	3.0	1.0	3.0	0.5	1.0	1.0	2.5	9.0
40	17.5	9.5	...	10.0	23.0	17.5	12.5	7.5	3.5	1.5	2.5	3.0	0.5	0.5	3.0	4.0	2.0
45	?	?	?	10.0	2.0	4.0	1.0	3.0	5.0	4.0	2.0	2.5

TABLE 14 (continued)

Metanauplii, 1935

Month Day	V 18	V 26	VI 5	VI 12	VI 22	VI 29	VII 5	VII 12	VII 19	VII 27	VIII 2	VIII 9	VIII 18	VIII 24	IX 1	IX 9	IX 18
Depth in metres																	
0	22.0	20.0	8.0	5.5	7.0	1.2	5.0	6.0	2.5	10.0	2.0	14.5	20.5	3.0	5.5	14.3	6.0
1	32.0	31.0	17.0	9.5	7.0	4.0	12.0	9.0	18.0	22.0	11.5	29.5	32.0	11.0	5.0	11.5	4.7
3	43.5	41.0	13.5	27.0	8.5	3.0	20.0	8.5	11.0	14.5	17.0	45.5	29.5	10.0	6.5	18.0	5.2
5	50.0	40.0	20.0	12.7	10.5	6.0	15.5	9.0	6.0	6.5	10.0	27.0	24.5	8.4	7.0	14.5	7.0
8	16.0	54.3	30.0	16.5	9.0	4.5	9.5	6.5	4.0	6.0	12.5	14.0	22.0	9.5	8.0	10.5	4.0
10	12.0	10.0	24.5	15.0	6.5	5.5	3.2	9.0	3.5	4.0	12.5	17.0	21.0	9.0	5.0	7.0	3.0
15	7.5	3.0	34.5	18.0	7.0	6.0	5.0	...	5.5	3.5	8.5	12.5	19.5	6.0	6.0	5.6	2.5
20	2.0	5.0	19.5	18.0	6.5	5.5	6.0	...	5.0	6.0	5.0	16.0	23.5	4.5	6.5	3.0	2.0
25	2.0	6.0	30.0	17.0	7.0	7.0	7.0	8.0	5.0	5.5	12.0	9.5	16.0	15.0	9.5	3.0	3.0
30	4.0	3.0	7.5	11.0	10.0	9.0	5.0	5.5	3.5	3.0	9.0	6.0	14.5	6.7	1.5	3.0	3.0
35	1.5	4.0	6.0	7.0	10.5	6.5	5.0	4.5	2.5	2.0	5.5	5.0	6.5	5.0	6.5	5.5	2.0
40	3.5	4.5	5.0	7.5	9.0	5.0	5.0	3.0	4.0	2.5	5.0	4.5	2.0	4.5	3.0	2.5	1.5
45	?	?	?	6.0	5.0	1.5	1.5	3.0	4.0	5.0	2.0	2.0	2.5	2.5	0.6

TABLE 15.—Depth distribution of plankters, station II, 1934 and 1935
(numbers per litre).*Daphnia, 1934*

Month Day	V 19	VI 9	VI 19	VII 2	VII 12	VII 24	VIII 6	VIII 14	VIII 21	VIII 28
Depth in metres										
0	0.2	1.7	0.2	8.0	1.0	2.0	1.0	2.5	10.0	0.7
3	0.9	2.0	2.8	9.0	7.0	14.5	7.5	10.5	12.0	16.0
5	0.3	3.0	4.5	7.0	8.0	10.5	5.3	10.5	11.5	9.3
8	?	2.5	2.0	3.0	3.0	4.5	2.0	3.7	14.4	4.5
10	?	1.0	1.0	2.2	2.5	10.8	1.8	3.0	11.6	4.2
12	?	0.8	0.7	1.2	3.5	?	3.2	4.0	?	3.2

Daphnia, 1935

Month Day	V 26	VI 6	VI 22	VII 10 day	VII 10 night	VII 20	VIII 11 day	VIII 11 night	IX 21
Depth in metres									
0	...	1.2	1.0	1.5	5.5	...	0.6	11.5	0.4
1	...	7.0	1.5	20.0	27.0	4.0	3.0	12.5	2.5
3	0.1	4.5	2.0	18.5	27.5	3.0	7.5	13.0	2.5
5	...	2.0	1.5	14.7	23.0	3.0	7.0	17.0	5.0
8	0.2	1.5	3.2	10.5	17.0	5.7	6.0	20.0	3.5
10	0.2	1.0	1.0	12.5	14.5	8.0	8.0	6.0	3.0
12	0.1	1.0	1.5	6.0	8.5	?	?	?	?

TABLE 15 (continued)

Holopedium, 1934

Month Day	V 19	VI 9	VI 19	VII 2	VII 12	VII 24	VIII 6	VIII 14	VIII 21	VIII 28
Depth in metres										
0	0.1	4.5	0.1	...	0.1
3	...	3.5	2.0
5	0.1	2.2	0.7
8	...	0.7	0.1
10	?	0.2	?	?	...
12	?	?	?	...

Holopedium, 1935

Month Day	V 26	VI 6	VI 22	VII 10 day	VII 10 night	VII 20	VIII 11 day	VIII 11 night	IX 21
Depth in metres									
0	1.5	0.3
3	...	0.3
5	0.3	0.2
8
10	0.1	?	?	?	?
12	...	0.2	?	?	?	?

TABLE 15 (continued)

Epischura, 1934

Month Day	V 19	VI 9	VI 19	VII 2	VII 12	VII 24	VIII 6	VIII 14	VIII 21	VIII 28
Depth in metres										
0	0.6	0.2	0.2	...	0.1
3	0.7	0.6	0.7	0.2	0.1	0.3	...	0.2
5	2.0	1.1	0.5	0.6	0.2
8	...	0.5	0.8	0.4	0.4	0.2	0.1
10	?	0.6	0.4	0.3	0.2	0.4	0.4	...	0.7	0.2
12	?	0.7	0.2	0.1	0.3	?	0.4	...	?	0.4

Epischura, 1935

Month Day	V 26	VI 6	VI 22	VII 10 day	VII 10 night	VII 20	VIII 11 day	VIII 11 night	IX 21
Depth in metres									
0	0.7	0.2	1.3	0.1	...
1	...	1.5	...	0.3	0.5	0.3	...
3	...	0.6	2.0	0.5	3.0	...	0.1	0.1	...
5	...	0.3	0.8	0.5	3.5	0.1	...	0.2	...
8	...	2.0	0.1	2.0	2.5	0.8
10	...	0.2	0.2	2.2	2.2	8.0
12	...	0.2	0.5	2.0	2.0	?	?	?	?

TABLE 15 (continued)

Diaptomus group, 1934

Month Day	V 19	VI 9	VI 19	VII 2	VII 12	VII 24	VIII 6	VIII 14	VIII 21	VIII 28
Depth in metres										
0	0.5	16.0	3.3	14.4	11.0	19.0	3.5	13.5	14.0	4.7
3	4.0	20.5	29.5	35.0	16.5	77.5	51.0	48.5	16.0	25.0
5	7.0	36.5	33.0	30.0	13.5	51.5	16.5	30.0	18.3	13.5
8	5.3	15.5	12.4	...	5.7	10.5	6.5	12.5	9.0	6.0
10	?	12.2	5.0	11.4	4.0	11.0	3.5	8.0	19.5	3.5
12	?	6.2	2.5	6.7	3.0	?	3.6	6.5	?	4.5

Diaptomus group, 1935

Month Day	V 26	VI 6	VI 22	VII 10 day	VII 10 night	VII 20	VIII 11 day	VIII 11 night	IX 21
Depth in metres									
0	7.0	15.0	21.0	7.0	15.0	1.0	2.5	18.0	5.2
1	3.0	24.0	18.5	19.5	11.0	29.5	3.2	21.5	12.0
3	3.5	17.0	20.4	100.0	24.0	45.0	9.3	28.0	10.0
5	1.0	15.5	11.0	78.5	40.0	25.7	3.1	25.1	10.0
8	0.7	6.5	5.5	15.0	30.5	14.8	5.7	17.5	5.5
10	0.7	3.5	2.5	25.7	25.0	16.5	10.8	18.5	4.5
12	0.7	3.5	3.5	15.0	16.3	?	?	?	?

TABLE 15 (continued)

Cyclops group, 1934

Month Day	V 19	VI 9	VI 19	VII 2	VII 12	VII 24	VIII 6	VIII 14	VIII 21	VIII 28
Depth in metres										
0	0.5	2.0	0.3	2.0	2.5	1.7	1.5	2.6	5.5	3.1
3	0.8	1.5	4.2	4.2	3.3	6.5	11.0	6.0	8.5	11.0
5	0.5	2.5	6.5	5.0	4.0	4.5	5.0	9.0	10.2	9.1
8	1.5	3.1	2.5	...	2.5	1.5	4.6	5.0	7.7	4.1
10	?	3.3	3.8	1.6	2.5	1.2	4.7	2.0	8.5	3.5
12	?	1.0	6.0	1.5	3.0	?	5.0	2.3	?	8.0

Cyclops group, 1935

Month Day	V 26	VI 6	VI 22	VII 10 day	VII 10 night	VII 20	VIII 11 day	VIII 11 night	IX 21
Depth in metres									
0	2.5	2.7	1.5	0.5	4.5	0.1	0.5	3.5	0.5
1	2.0	2.5	2.5	2.5	5.0	0.7	0.5	7.0	2.5
3	1.6	3.7	4.5	8.0	5.5	3.5	0.2	19.5	4.5
5	1.5	3.5	5.0	5.5	2.5	6.0	1.5	2.5	3.0
8	1.0	3.7	1.5	2.0	1.5	3.0	2.7	1.5	5.0
10	0.3	1.0	2.0	3.0	2.0	1.5	3.5	4.5	5.0
12	0.7	4.5	3.0	4.0	1.5	?	?	?	?

TABLE 15 (continued)

Nauplii, 1934

Month Day	V 19	VI 9	VI 19	VII 2	VII 12	VII 24	VIII 6	VIII 14	VIII 21	VIII 28
Depth in metres										
0	36.7	7.0	34.0	52.5	36.5	33.5	62.0	37.5	16.5	11.0
3	27.2	7.5	51.0	72.5	39.5	43.0	39.0	28.5	24.0	18.0
5	16.0	15.7	49.0	77.1	44.5	25.6	20.2	31.0	23.5	10.0
8	16.5	5.5	25.9	54.5	37.0	11.5	11.0	22.0	18.5	4.5
10	?	6.8	26.6	34.3	39.0	12.5	12.5	22.5	18.0	5.5
12	?	6.2	29.6	20.0	49.5	?	16.0	22.5	?	5.0

Nauplii, 1935

Month Day	V 26	VI 6	VI 22	VII 10 day	VII 10 night	VII 20	VIII 11 day	VIII 11 night	IX 21
Depth in metres									
0	15.0	3.5	42.0	120.0	3.5	21.9	99.5	68.0	10.5
1	13.6	8.0	46.0	65.0	2.2	84.0	81.0	81.5	12.5
3	12.2	10.0	50.0	43.5	8.5	30.0	15.5	43.5	15.0
5	3.0	10.0	39.0	20.0	5.0	12.0	7.0	23.0	18.0
8	2.0	6.6	24.5	11.0	29.0	7.0	5.0	27.0	10.0
10	2.0	10.5	31.3	11.0	27.5	2.0	5.0	17.0	10.0
12	2.5	16.0	21.0	7.0	27.5	?	?	?	?

TABLE 15 (continued)
Metanauplii, 1935

Month Day	V 26	VI 6	VI 22	VII 10 day	VII 10 night	VII 20	VIII 11 day	VIII 11 night	IX 21
Depth in metres									
0	6.5	5.5	3.0	8.5	6.0	1.2	12.5	24.5	3.0
1	6.0	6.0	4.0	10.5	6.0	9.5	31.5	29.0	7.5
3	5.0	14.0	5.0	11.0	10.0	5.0	21.5	21.0	7.0
5	2.0	10.5	4.5	7.5	3.0	2.0	16.0	24.5	3.0
8	1.0	9.0	4.0	4.5	8.0	1.5	19.0	16.0	2.0
10	1.0	16.0	5.5	5.0	9.0	1.0	18.5	15.0	1.0
12	...	26.0	4.5	4.5	13.0	?	?	?	?

THE FOOD OF THE LAKE NIPISSING CISCO,
LEUCICHTHYS ARTEDI (LE SUEUR) WITH
SPECIAL REFERENCE TO THE UTILIZATION
OF THE LIMNETIC CRUSTACEA

By

R. R. LANGFORD

(From the Department of Biology
University of Toronto)

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