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PLANKTON STUDIES ON LAKE MENDOTA. II.

THE CRUSTACEA OF THE PLANKTON,
JULY, 1894—DEC., 1896.

BY

David Sahel
E. A. BIRGE, PH. D., SC. D.,

Professor of Zoology, University of Wisconsin.

REPRINTED FROM THE TRANSACTIONS OF THE WISCONSIN ACADEMY OF SCIENCES,
ARTS, AND LETTERS, VOL. XI., PP. 274-448,

WITH THE ADDITION OF TITLE PAGE AND INDEX.

[Issued December, 1897.]

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THE CRUSTACEA OF THE PLANKTON,
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*Edward
Sabel*

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INVERTEBRATE
ZOOLOGY
Crustacea

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WILSON
COLLECTION

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PLANKTON STUDIES ON LAKE MENDOTA. II.

THE CRUSTACEA OF THE PLANKTON FROM JULY, 1894, TO DECEMBER, 1896.

E. A. BIRGE,

Professor of Zoology, University of Wisconsin.

INTRODUCTION.

The following paper is a continuation of the work done by myself with Messrs. Olson and Harder, in the summer of 1894, published in the preceding volume of the Transactions of this Academy. (Birge, '95.) The study carried on in that month showed a vertical distribution of the crustacea so unexpected and peculiar that it seemed to me worth while to continue the investigation throughout an entire year. A few observations were made in the latter part of August, 1894, and on September 18th, regular observations were begun and were continued until the close of December, 1896. During the fall of 1894 observations were taken on 28 days. In 1895 observations were taken on 110 days, and on 126 in 1896. The details of the number of observations and of the days on which they were taken will be found stated in Table A given at the close of this paper. During the late spring and summer months as many as three observations per week were taken. During the winter season, the late fall and early spring, observations were necessarily fewer in number, and occasionally a period of two weeks would pass without an observation. At this time of the year, however, the crustacea are not varying greatly in number, so that small error results from these gaps.

I had intended at first to carry my observations through one year only, but as a peculiar annual development of the crusta-

cea was found in the course of the year 1895, it seemed to me advisable to continue the observations through the season of 1896, in order to determine whether the course of development would be the same as in 1895. Until August, 1896, the number of the crustacea in each catch was determined separately, and the average catch for each two-week period was computed. After that date the catches for each two-week period were mingled together, and the average number only was determined. Up to August, 1896, therefore, the average, maximum, and minimum catches are given for each period, in the tables of the appendix, but after that date it is possible to state the averages only. This "two-week average" is the main number used in this paper.

The net employed was that described by me in my former paper, and the method of counting was substantially the same, except that a smaller fraction than one-sixth was often used to determine the large number of crustacea from the upper levels of the lake—one-tenth to one-fifteenth being ordinarily employed, with a view to making the last figure of the resulting number 5 or 0, in order to facilitate adding and multiplying in subsequent operations.

The multiplications to reduce the catch to the number per square meter of surface were performed by the aid of Crelle's Tables. The products are stated in this paper in thousands and tenths, in order to avoid the constant use of ciphers in the last two places. The result would have been quite as accurately expressed in most cases if the nearest thousand had been stated, but in case of the smaller numbers it was necessary to state the hundreds, and as the products were read off directly in all cases in hundreds, I concluded to leave them in the printed results, although, of course, understanding that no reliance is to be placed on the exactness of the enumeration in the last place of figures if the total is large.

The total number of serial observations was 333 besides 97 single catches, and as there were at least six collections in each series, and from three to eleven species of crustacea to be determined, the number of single observations is very large—over 10,000. It has been my aim in preparing this paper to exhibit

these results in a graphic form so that they might appeal to the eye, and to print only the summaries of my observations; rather than to confuse the reader by presenting him with the great mass of figures which would be needed to exhibit the results of the single observations.

In preparing the diagrams which accompany this paper, the average number of crustacea for each two-week period was determined and was platted at the center of the space representing the period; and the averages of successive periods connected by a line.

It has been found impossible to use the same scale in platting the annual distribution of the different species of the crustacea. Where numbers range from less than 25,000 to over 3,000,000 per square meter, it is not practicable to use the same scale for all species. The scales employed range from 25,000 to one vertical space, to 200,000 for the same distance. In all cases the scale is stated on the margin of the diagram. No attempt is made to show by a curve the rate of variation within the two-week period, since this variation is quite too irregular to permit a curve to be drawn with any accuracy.

I had intended to introduce this paper by a preliminary account of lake Mendota accompanied by a hydrographic map. Some hundreds of soundings have been made by myself and by the Department of Civil Engineering of the University of Wisconsin, but the preparation of the map has been delayed, and it is therefore impossible to insert the account at this place. I must therefore refer to the brief account given in my former paper, merely stating here that the lake is about 6 miles (9 kilometers) in length by 4 miles (6 kilometers) in greatest breadth, of a somewhat regular shape. No greater depth than 24 meters has been found; a large part of the lake is deeper than 18 meters, and the bottom is very flat without irregular depressions. The principal observing station was near the southern side of the lake, about 2,700 feet (850 meters, from the southern shore, and in 18.5 meters of water. The second principal station was about a mile and a half (2 kilometers) from the southern shore, and in 22 meters. The principal station was marked by a buoy, so that the observations were taken at the same spot.

During the winter observations were made through the ice, the net being suspended from a tripod. While it is very easy to make a single haul of the net at any temperature in the winter, it is very difficult to make a series if the temperature is materially below -6° C. At lower temperatures, or even at this temperature on a cloudy day and with northerly wind, the net freezes so rapidly that work is extremely difficult and slow, as time must be taken for the net to thaw in the water before a second haul can be made. The line also becomes so heavily coated with ice and so slippery and stiff that it is impossible to secure accuracy in the time of raising the net. While therefore the pleasant warm days of winter offer the best possible occasions for working the dredge, the average work in winter is extremely disagreeable. It is, however, more difficult to secure continuous observations during the periods immediately preceding the formation and the breaking up of the ice than it is in winter. The lake freezes near the shore so that it is difficult to get out with a boat, while the ice is still too thin to bear the weight of a man; and as there is no current in the lake, the breaking up of the ice in the spring is ordinarily very slow and there is always a number of days in which the ice is too weak for safety. After the breaking up of the ice a continuation of north winds may keep the sludge ice on the southern shore, and thus still further delay observations, as was the case in 1896.

In carrying out this work it has been my endeavor to make a contribution to the natural history of an inland lake as "a unit of environment," to employ Eigenmann's appropriate phrase. (Eigenmann '95, p. 204.) I have, therefore, discussed somewhat freely the causes which seem to me to have contributed to the peculiarities of the annual and vertical distribution of the crustacea. I do not suppose that my conclusions are correct in all particulars, still less that they are complete. The causes determining the biological conditions of a lake are far too numerous and various, and their inter-relations far too complex to be understood at present with any accuracy. It has seemed to me, however, that the aim of plankton investigations should be to reach an understanding of these conditions,

and I have therefore put out the suggestions of the final sections of each part of my paper, with the hope that they will stimulate others to similar attempts and thus lead to an enlargement of our knowledge and to the correction of whatever errors may be present in my conclusions.

THE COEFFICIENT OF THE DREDGE.

One of the most difficult and unsatisfactory portions of plankton investigation has been the determination of the coefficient of the dredge. It is well known that the net when raised through the water offers a certain resistance to the passage of the water, so that a part only is filtered by the net, while another fraction is displaced. The determination of the relative amounts of water filtered and displaced is the determination of the coefficient of the dredge. Many attempts have been made to determine this quantity. The most elaborate investigations have been made by Hensen (Hensen, '87, p. 11, and Appendix; '95, pp. 67-86). Reighard ('94, p. 57) has also devised and carried out another method of determining the coefficient. Hensen has attempted to work out a formula by which the coefficient for a net of given cloth and given area could be determined, and has finally given the best and easiest method of determining the coefficient in lakes abounding in vegetable plankton ('95, p. 92). Reighard's method depends upon mixing with the water a known number of particles and determining the relation between those caught by the net when drawn through the water and the number known to be present. This method was entirely inapplicable to a net constructed like mine, and it was impossible for me to enter upon any elaborate investigation of the coefficients of the cloth which I used. I confined myself, therefore, to a determination of the coefficient of my net under the conditions in which it was used. In the serial investigations which formed the greater and more essential part of my study, the dredge was raised through a distance of three meters. The speed was approximately one half meter per second, although ordinarily a little less, the total time occupied by raising the dredge through 3 meters, being from 6.5 to 6.75 seconds. In order to ascertain the coefficient of the dredge I determined to ascertain the num-

ber of crustacea in a column of water 3 m. in length and 10 cm. in diameter and to compare with this number the catch of the net. For this purpose a tin tube was made, of the size indicated. This tube was provided at the lower end with a slide in which was placed a carrier bearing a net and bucket. The carrier and net could be slipped to one side so as to leave the opening of the tube entirely free, and by means of a cord reaching to the surface, they could be drawn back so as to hang immediately below the opening of the tube. The slide and carrier were made of brass plates carefully scraped and fitted together, so that no crustacea could escape between the bottom of the tube and the top of the net, and the net was closely covered when slipped to the side of the tube.

The tube was lowered into the water with the net moved to one side of the opening and was lowered slowly so that the water within the tube might remain at the same level as that without and no appreciable currents should be set up in the water. The tube was also provided with a close fitting cap on the top, which could be closed after the top of the tube had sunk about one-half meter below the surface. When the tube had been lowered this cap was closed and the slide with the net drawn across the bottom of the tube. There was thus imprisoned a column of water 10 cm. in diameter and 3 m. long. The tube was then slowly raised to the surface and lifted out of the water so that the contained water might be filtered through the net, leaving behind the plankton. Several successive hauls of the tube were made, and the number of crustacea so taken was compared with that obtained from a similar number of hauls of the net made at the same time and through the same distance. The number of crustacea thus obtained was carefully determined, $\frac{1}{16}$ to $\frac{1}{16}$ of the number being counted where the number was great, and $\frac{1}{4}$ where the number was small. In determining the coefficient of the dredge, it was assumed that the tube took all of the plankton in the column of water which it contained, and the number of crustacea caught by the tube was compared with that caught by the net. Since the opening of the net was four times that of the tube the catch ought to have been four times as great, provided all of the water was fil-

tered. As a matter of fact, the net caught about twice as many crustacea as the tube, thus indicating that its coefficient is about two.

In this method of determining the coefficient the quantities compared are by no means uniform; indeed, it is known that the number of crustacea caught in a given haul of the tube may be only one-half the number caught in a second haul within a few seconds. A single comparison has therefore very little value and accuracy in the determination of the coefficient by this method can be reached only by a considerable number of observations. In my own work I made use of six sets of observations, taken on May 14th, October 12th and 25th, 1895, February 25, May 18th, and July 11th, 1896. By distributing the observations over so long a time it was possible to get at the coefficient of the net at different times in its life and under different conditions of plankton. In May the number of crustacea is at a maximum, and the amount of algae is small. In October the number of crustacea is considerable, but the vegetable life is at a maximum; while in February the amount both of animal and vegetable life is of course small. From four to six pairs of observations were taken in each set. The ratio of the catch of the tube to that of the net was computed for each observation in the set, and the average of these ratios was computed, using the method of least squares. As a result of these determinations, the following ratio was established: Tube : net :: 49.85 : 100. The probable error of the determination is ± 1 . The appended table shows the general results

Several facts appear from the table. It will be noticed that the amount of difference between the maximum and minimum numbers caught varies greatly on different occasions. It is plain also that the net shows no greater amount of variation on the whole than does the tube. On the contrary, on those occasions where the numbers are approximately constant in the tube, they are similarly constant in the case of the net; and where the numbers vary considerably in the case of the net, they vary to much the same degree in the case of the tube. There is therefore no reason to suspect any considerable irregularity on the part of the net due to the stoppage of its openings, or to any other cause.

TABLE I.—Results of determination of coefficient of net.

Date.	Pairs of catches.	No. of resulting ratios.	Counted fraction of catch.	CATCH OF TUBE.		CATCH OF NET.	
				Max.	Min.	Max.	Min.
1895, May 14.....	4	16	1-10	2,910	2,400	4,760	2,920
Oct. 12.....	4	16	1-5	1,482	1,170	2,292	1,770
Oct. 25.....	6	36	1-10	8,490	4,290	14,520	10,560
1896, Feb. 25.....	5	25	1-4	1,420	760	3,500	1,750
May 18.....	5	25	1-10	5,940	4,310	12,100	10,480
July 11.....	5	25	1-15	4,215	2,430	8,370	5,680
Total.....	29	143					

Minimum Ratio; Tube : net :: 21 : 100.

Maximum Ratio; Tube : net :: 100 : 100.

Average Ratio; Tube : net :: 49.85 ± 1 : 100.

Area of opening of tube : area of mouth of net :: 1 : 4.

Hence coefficient of net = 2, approximately.

Area of opening of net = 314.1 sq. cm.

Hence to state catch of net in terms of sq. meter of surface, multiply catch by

$$\frac{10,000}{314.1} \times 2 = \text{catch} \times 63.6, \text{ which factor was used.}$$

In determining the number of crustacea caught by tube or net, each species was counted separately. The individual species show just about the same amount of variation as does the total catch; although in the case of less abundant species the maximum number caught was not infrequently three times the minimum. In the case of the tube no difference could be detected in the range of variation of the numbers of species which are active, like *Diaptomus*, and those which, like *Chydorus*, or *Cyclops*, are relatively slow in their movements. During the summer of 1896 an attempt was made to determine the coefficient of the dredge from the number of spherules of *Gloiostrichia*, but as this plant is found mainly in the uppermost strata of the water on calm days, it proved an unsuitable object, and its variations in number in successive catches were greater than those of the crustacea.

It may be added that there was no constant position of maximum or minimum catch in any series which was made, but the numbers varied in a wholly irregular fashion.

In all of the work reported in this paper and done before the 11th of July, 1896, a single net was employed. After that date the net was replaced by one of silk bolting cloth, number 16, containing about 3600 meshes to the square cm. This net was cut from the same pattern as the old one. In order to compare the two nets they were similarly mounted in the same frame, and a series of comparisons made to determine their relative coefficient.

To my surprise the two nets showed practically the same coefficient. The numbers caught necessarily varied considerably, but the average of each of two series of five pairs showed practically the same number of crustacea; the silk net catching on the whole about 5 per cent. less than the old net. It did not seem necessary therefore to alter the coefficient of the dredge with the change of the net. On the 20th of August the dredge, with all its appurtenances, was lost by the accidental breaking of the line, and the work for the remainder of the year was done with a similar instrument of smaller size, having a square opening of 100 square cm. The coefficient of this net was determined by comparing it with the tube, one set of comparisons being made by determining the number of the crustacea. A second set was made by determining the bulk of the plankton caught by the tube and net when allowed to settle for the same length of time in similar tubes. Two other determinations were made by Hensen's last method. (Hensen, '95, p. 92.) The net was fitted with a cover having an opening of 2.5 square cm. Ten successive hauls of the net were made with the small opening and their contents mingled. This was preserved and allowed to settle and compared with the amount of plankton caught with the full opening of the net, the two quantities being similarly preserved and allowed to settle in similar tubes. The result of these three methods of determination of the coefficient of the net was substantially identical, the coefficient varying from 1.81 to 2.04. The coefficient 1.9 was selected, and as a result the catch of this net is multiplied by 190 in order to give the number of crustacea per square meter of surface area.

An important question has been raised, first by Hensen ('87, p. 12) and especially by Kofoid ('97, p. 11) regarding the vari-

ation in the coefficient of the net due to the accumulation of the plankton within it as the net is drawn through the water. Unquestionably the stoppage of the openings of the net by the accumulating catch raises the coefficient, and if the net accumulates a sufficient amount of plankton it will wholly cease filtering the water. In plankton-rich lakes, therefore, serious error may be introduced from this source. Since lake Mendota during the summer and autumn contains very large amounts of vegetable plankton, it was quite possible that the stoppage of the net should cause errors. In order to determine whether these errors existed, I regularly made hauls of the net from the bottom of the lake to the surface during the season of 1895 and compared the number of crustacea obtained in the hauls from the bottom with the sum of those caught in the six successive levels of my series. I append a table showing the number of *Cyclops* caught in the months from January to July, 1895, in order to compare the series and the single haul. It will be seen that the number of *Cyclops* varies, often considerably. Out of 41 cases prior to July 1, the total haul exceeded the sum of the series in 24 cases and fell below it in 17 cases. There was thus no decided advantage on the side either of the series or the single haul. If the amount of variation in this table be compared with the amount shown in the catches of the tube in Table I, it will be seen that the differences are of much the same order as those disclosed by the tube. There is therefore no evidence that under these circumstances the net suffered any stoppage in passing through the 18 meters of the lake which altered its coefficient to any marked degree over that of the net used through 3 meters.

After the first of July *Anabaena* and similar small plants developed rapidly in the lake, and the amount of vegetable plankton increased to a great amount. Under these circumstances the number of crustacea caught in the total haul varied widely and irregularly from the sum of the series, and soon became uniformly lower than the sum. It was found therefore that the coefficient of the net has been raised by the amount of algae present and the catches made by the total hauls were not employed in reckoning the number of the crustacea after the first

TABLE II.— Showing the number of *Cyclops* caught by the net at the same date and place in a series of six hauls of 3 m. each, and in a single haul of 18 m.

Date.	Sum of series.	Single haul.	Date.	Sum of series.	Single haul.
1895.			1895.		
Jan. 6.....	400	460	May 16.....	11,940	14,300
Jan. 9.....	378	550			17,530
Jan. 16.....	505	600	May 18.....	19,470	19,200
		800	May 20.....	11,780	16,000
Feb. 15.....	870	1,220	May 22.....	12,850	11,240
		900	May 27.....	16,710	15,625
Feb. 23.....	2,350	1,180	May 30.....	16,220	17,900
		1,430	June 1.....	13,220	15,200
Mch. 6.....	345	620	June 3.....	10,010	10,080
Mch. 7.....	678	859	June 10.....	8,020	7,800
Mch. 12.....	719	844	June 12.....	8,070	3,640
Mch. 23.....	780	1,355	June 17.....	4,530	5,600
Apr. 12.....	690	710	June 18.....	3,809	3,240
		880			5,680
Apr. 15.....	1,000	600	June 22.....	4,760	3,750
Apr. 18.....	2,520	1,290	June 24.....	3,710	2,120
Apr. 23.....	2,925	3,550	June 29.....	3,299	2,400
Apr. 30.....	9,055	9,510	July 1.....	3,190	3,700
		6,960			3,600
		7,620	July 4.....	3,920	3,800
		5,250	July 6.....	6,105	3,960
May 4.....	15,470	15,450	July 9.....	3,416	2,560
May 7.....	13,630	18,200	July 11.....	2,960	3,080
May 12.....	11,980	19,680	July 19.....	3,434	3,120
			July 24.....	2,791	1,840

of July. The comparisons of net and tube show no appreciable difference in coefficient between the catches of October when the vegetable plankton is at its maximum, and those of February and May, when it is greatly reduced in quantity. There is therefore no reason to suppose that the coefficient of the dredge is appreciably altered by being raised through the distance of three meters. It may be added that results similar to those obtained in the above table would be shown if any other species

of crustacea had been selected, or if the total of all the crustacea had been chosen.

There is still a third question relating to the coefficient to the dredge, namely, does the net function similarly on different occasions, or does its coefficient vary irregularly and in such a way as to vitiate conclusions based on the hauls of the net? This question is partially answered by the determination of the dredge coefficient, as shown in Table I. A second answer can also be given. During the winter the numbers of *Daphnia* and *Diaptomus* do not increase by reproduction, and the successive catches should therefore show no very great variation. In a subsequent section, dealing with the question of swarms, I have given the figures for the catches of these genera during the winter of 1895, from which it appears that the variation in successive catches made within a short time of each other is no greater than may be found between catches made on the same day. *Still further, a diagram is given (Fig. 21), showing the numbers of *Cyclops* caught during the year 1895. This diagram shows plainly that when the average number of *Cyclops* is approximately constant, the individual catches do not ordinarily vary greatly from the average, no more than would be expected from *Cyclops*' necessarily somewhat irregular distribution in the lake. An examination of the maximum and minimum catches in the tables for the different species shows the same result.

I do not pretend that I have determined the coefficient of my nets with absolute accuracy, nor that the coefficient of the net is exactly the same on different occasions; but the careful study whose results are summarized above has convinced me that the coefficient of the net is quite as constant as any of the factors entering into the determination of the plankton. The number of the crustacea certainly varies from point to point in the lake. Where a fraction only of the crustacea are counted, the determination of the number caught is an approximation and is subject to error. This error, is, of course, multiplied greatly in stating the number of crustacea in terms of square meter of surface. Among the variables and approximations which enter into the statement of the results of plankton work, I think it may fairly be said that the coefficient of the net is one of the

most constant factors, and that it may be quite as accurately determined as any other.

TEMPERATURES.

Figs. 1-5.

The following account of the temperatures of the lake is not intended as a complete discussion of the subject. My temperature observations were made at first with the aim of securing approximate results in order to determine the biological relations of temperature. The methods employed until July, 1896, while accurate enough for these purposes, are not sufficiently accurate for other ends. I have therefore refrained from printing the observations of temperature, and discuss chiefly the temperature diagrams, which give the result of my observations by weekly or rather, quarter-monthly averages.

A. Methods.

Surface temperature observations were taken from the beginning of my study, and temperatures from all depths after October 1st, 1894. A water bottle and thermometer were the instruments employed until July 27th, 1896, after which date a thermophone was used. The latter instrument has proved extremely useful and accurate. A full description of the instrument may be found in *Science*, Vol. II. of 1895, page 639. As constructed for my work, the instrument ranges from minus 5 to plus 30 degrees C., each degree being graduated into fifths. There is no difficulty in reading the instrument to less than 0.1 degree C., and its readings are exceedingly accurate, agreeing exactly with those of a standard thermometer with which it has been constantly compared. Observations can be made very rapidly, the time of a single reading varying from one to one and a half minutes, according to the amount of change of temperature from the last reading.

The temperature bottle contained about $1\frac{1}{2}$ litres and had a small neck. It was lowered to the desired depth; allowed to remain from one to three minutes for the glass to acquire the temperature of the water; was then uncorked by a sudden jerk on the



FIG. 1.—Surface and bottom (18 m) temperatures, 1895. Full line, surface; broken line, bottom.

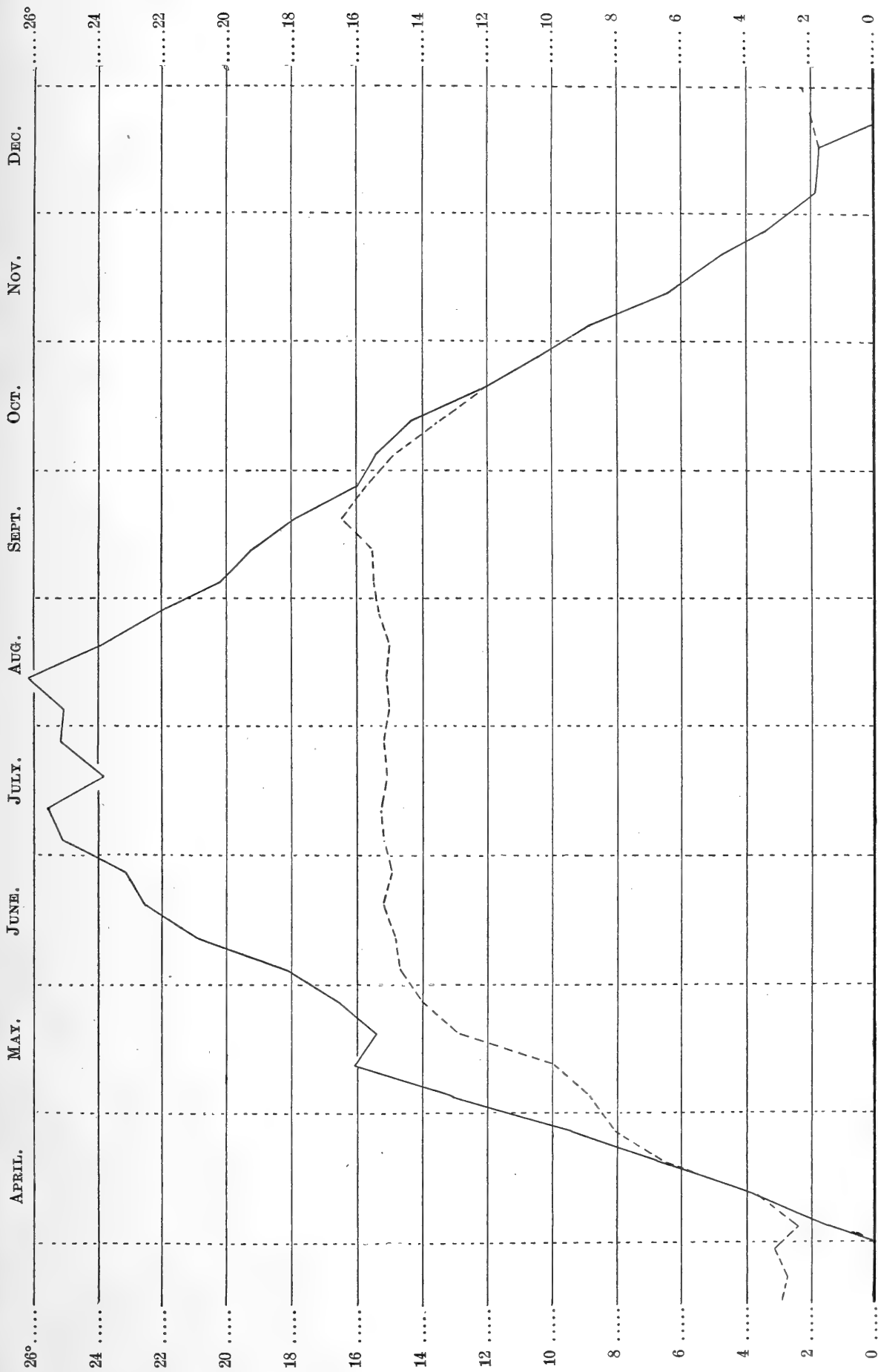


FIG. 2.--Surface and bottom (18 m) temperatures, 1896. Full line, surface; broken line, bottom.



line, and allowed to fill. It was then drawn rapidly to the surface and the temperature read by means of a long-stemmed thermometer graduated to one-fifth of a degree. The time of raising the bottle from the bottom of the lake was ordinarily about ten seconds; and the small size of the opening prevented mixture of the upper water with that in the bottle. The temperature of the water in the center of the bottle, which was measured by the thermometer, did not change perceptibly during the time required for the thermometer to set. The water from the lower part of the lake, however, was somewhat warmed by contact with the glass and the air in the bottle. This error was carefully determined by comparison with the thermophone, and is about one-fifth of a degree C., when the difference between surface and bottom is about 10 degrees.

Errors much more considerable than this occur with the use of the temperature bottle at the thermocline. In this region the temperature may fall as many as nine degrees in a single meter, and not infrequently as much as three or four degrees in a quarter of a meter. It is impossible that the bottle should take in all of its water from the stratum in which its mouth lies as the escaping air sets up currents so that a mixture of the water occurs. A difference of half a degree may therefore occur between the readings of the thermophone and the bottle in this region. In one case the error amounted to two degrees, where the bottle was opened a few inches below the upper level of the cold water and took in a mixture of this water with the lower part of the warm stratum above. The errors at this region, however, while considerable, make little difference in the average results of observations, since their only effect is to make the upper level of the cold water appear to be a fraction of a meter lower than it really is. Since this level is subject to irregular variations, under the influence of the wind, which may amount to two or even more meters, the errors introduced by the bottle are insignificant in the average of a week's readings. It was intended to correct the observations of the bottle by means of the thermophone and to introduce the correction in the diagrams of temperature. It was found, however, that the amount of correction to be introduced in the diagrams

was so small as to make it inadvisable to insert it. In Figure 4 the change from bottle to thermophone is made in the last week of July, and it will be seen that the lines come together with great accuracy.

Above the thermocline the bottle and thermophone agree exactly, except at the surface on calm, sunny days, when the reading of the thermometer is higher than that of the thermophone, since by means of the thermometer the temperature of a very thin stratum can be taken, while the thermophone coil is of such a shape that it reads only the average temperature of a stratum some eight centimeters in thickness.

During the period April — December, 1896, 189 sets of observations were made on 135 days varying from 3 to 6 per week. In 1895, 196 sets of observations were made on 126 days in the same period.

The temperature observations were made at all hours of the day; rarely by night, and must be taken as representing the day temperatures of the water. Little difference, however, would be made in the diagram if the night temperatures had been introduced, as has been shown by an elaborate series of observations made in 1897. Observations were regularly made by single meters by the thermophone, and also by the bottle when the difference between single meters exceeded one-half degree C., and often when the differences were less.

After recording the temperatures, those for meters not directly observed were interpolated, and the average was taken of the observations for each meter and each quarter-month.

In preparing Figs. 3 and 4 the average temperatures for each meter and quarter-month were platted at the proper depth, and in the center of the space representing the quarter-month on the diagram. The position of the full degrees was then platted on the assumption that a uniform decline of temperature is found within a single meter. This assumption is incorrect in the region of the thermocline as the zone of the most rapid decline of temperature is frequently less than a meter in thickness, but as this zone varies in thickness and shifts its vertical position under the influence of the wind, little error results from using this method of plating the average observa-

tions of a week. Lines were then drawn connecting the positions of the full degrees. In 1895 the diagram is carried to 18 meters only, the depth at my regular station. In 1896 the temperatures were carried to 22 meters, observations being taken at that depth nearly every week. Two other temperature diagrams are given, showing the movement of the surface and bottom temperatures from April to December of the years 1895 and 1896.

B. Results.

Winter Temperatures.

Lake Mendota freezes at very different dates during the early winter in different years, and the time of opening also varies greatly. The lake is so large that continued high winds prevent its freezing even after long continued low temperatures, and as there is no large affluent, there are no spring floods to move the ice, which therefore remains until it is greatly weakened by the effect of the sun and is broken up by the wind. In 1894 the lake froze on December 28th, and opened April 8th, 1895, being closed for 100 days. In 1895–96 the lake froze December 6th and opened ^{such} April 28th. The first and last observations through the ice were made on January 1st and March 23d, 1895; and December 9th, 1895, and March 28th, 1896. In the winter of 1896–97 the lake froze December 29th, then broke up again and did not freeze the second time until January 7th, 1897. It opened on April 10th, 1897. The ice usually reaches a thickness of over 60 cm., and in 1895 became nearly 1 m. thick.

During the winter the temperature of the surface of the water is, of course, zero. The water at the bottom when the lake freezes has a temperature which varies in different years. If the lake is prevented by wind from freezing during the first cold weather of December, it may remain open for days or even weeks, cooling very slowly. This was the case in 1894, and the temperature at the bottom on January 1st, 1895, was barely one degree, and at nine meters was about 0.5° . In 1895 when the ice on December 9th permitted observations, the temperature was as follows: 0.5 m., 0.3° ; 5 m., 1.2° ; 18 m., 1.7°

It is, of course, possible that the lake should freeze when the bottom is at any temperature between 4° and zero. It is hardly probable, however, that it often freezes permanently when the bottom is lower than 1° or higher than 2.5° . Below the ice the temperature of the water rises rapidly, being half a degree or even more within less than half a meter of the ice, and below this level the temperature rises very slowly and regularly to the bottom of the lake, the difference between the water at 0.5 m. and the bottom rarely exceeding two degrees. The mud is ordinarily decidedly higher in temperature than the water just above it. (See FitzGerald, '95, p. 81.) The difference between the temperature of the mud and the water half a meter from the bottom was sometimes found to be as great as $0.7-0.9^{\circ}$ in 1894-5, and 1895-6, by the aid of the water bottle; while the thermophone in 1897 showed differences of $0.3-0.8^{\circ}$. This difference varies in different parts of the lake without any assignable reason.

The temperature of the water of the lake rises during the winter, especially during the latter part of February and March (Cf. Apstein, '96, p. 18). In 1895 the temperature reached nearly 2.5° at the bottom, and 1.5° close to the ice on the 27th of March. In 1896, on March 28th, the temperature at one-half meter was 2.9° , at the bottom (18 meters) 3.1° . This was a rise of from 1.5 to 2° during the winter. In 1897, the temperature on January 23rd was: 1 m., 0.6° ; 18 m., 1.8° . On March 29th, at 1 m. the temperature was 1.4° , at 18 m., 2.1° . This warming of the water is due to the sun. If it were due to warm water coming from springs the bottom temperature would necessarily rise to 4° before the change appeared in the upper water. But this is not the case. The temperature at the bottom has not reached 4° , in any of the three winters during which observations have been taken, until after the breaking up of the ice in the spring. It would appear, therefore, that this warming must be due to heat which enters the water from above.

While this rise in temperature is very gradual and is small in amount, it has important biological results. The reproduction of *Cyclops* and of the rotifers goes on very much more rapidly at a temperature above 1.5° than at a temperature near 1° . In-

deed, at the lower temperature the progress of the development of eggs is almost suspended, while at a temperature of 2.5 to 3° the development of eggs into nauplii and of nauplii into young *Cyclops* goes on with considerable rapidity, and at 1.5–2° it is present, though decidedly slower. The history of *Cyclops* in the spring, therefore, depends to a considerable degree on this warming of the water under the ice. If the winter is cold, so that the warming does not take place, or the rise is only slight, the number of *Cyclops* may remain almost unaltered during the winter; while conditions like those of the winter of 1895–96 permit the development of large numbers of young *Cyclops* ready to take advantage of the increased warmth and food in early spring, and so to develop enormous numbers of this genus.

The spring rise of temperature.

A glance at Figs. 1 and 2 will show that the warming of the lake in the springs of 1895 and 1896 was singularly alike. In each year the month of April was pretty steadily warm, and the surface of the lake rose rapidly and uniformly in temperature for about six weeks following the breaking up of the ice. Immediately after the disappearance of the ice the temperature of the lake frequently falls, since the breaking up of the ice is often caused by a north wind accompanied by a much lower temperature than had preceded the breaking up of the ice. This fall in the temperature of the water amounted to over one degree in 1896. But this slight drop is quickly recovered, and if the weekly averages are considered it will be seen that the surface temperatures in both years rose rapidly and steadily. For a time the rise in temperature at the bottom is as rapid as that at the surface. The length of this time varies, of course, with the amount of wind. A succession of warm days, accompanied or followed by high wind, will mix the warmed surface water with the body of the lake and thus secure uniformity in temperature. In neither 1895 nor 1896 were these conditions long realized; the temperature of the bottom began to lag behind that of the surface, and by the middle of May there was a difference of 7° to 8° between the surface temperature and that of the bot-

tom. In six weeks the temperature of the bottom had risen about 5° or 6° , while that of the surface had advanced about 15° .

The relation of the wind to this warming of the lake is well stated by Whipple ('95, p. 207).

In both of the years of observation, and also in 1897, there came in the middle or latter part of May a marked decline in temperature accompanied with high northerly winds. The effect of this was two-fold: first, the surface water was cooled; secondly, the wind mingled pretty thoroughly the water of the lake, thus causing a sharp rise of temperature in the lower strata. On the 12th of May, 1895, the difference in temperature between top (15.6°) and bottom (7.7°) was 7.9° ; on the 16th the difference was only 1.5° , and on the 18th only one degree (12.6° – 11.6°). On May 11th, 1896, there was a difference of 8.3° between top (18°) and bottom (9.7°), and a thermocline was evidently formed between 4 and 6 meters. On May 17th the difference between top (15.6°) and bottom (13.4°) was only 2.2° . Thus in both years there was a rapid rise of 3 – 4° in the temperature of the bottom water. It is probable that if temperatures could have been taken at the most favorable time the lake would have been found nearly homothermous in late May, at a temperature not far from 11° in 1895, and 13.5° in 1896. The effect of the spring warming was therefore to warm a mass of water 18 to 24 meters deep from an average temperature between 2° and 3° in March to an average of 11° to 14° at the latter part of May; with the differences between the top and bottom not exceeding 1° to 2° at the beginning and end of the period.

From these facts it appears that the bottom temperature of the lake may vary greatly in different summers, and that the bottom temperatures of lakes of the same depth, in the same region and season may also vary greatly—much more than the temperatures of the surface. Four factors are effective in determining the bottom temperature; three constant, and one variable: (1) the depth of the lake, (2) its area relatively to its depth, (3) the shape of the lake and the nature of its surroundings as favoring or hindering the influence of the wind, and (4) the amount of warmth and of wind during the spring and the times of occurrence of gales and the succession of warm and cold

waves. The same factors are also the chief powers in determining the position of the thermocline and its rate of downward movement.

Very few of the inland lakes of Wisconsin are more than 25–30 meters in depth, and their bottom temperatures vary more with relation to their area than to any other one factor. In the Oconomowoc lakes, which are in the same region as lake Mendota, and are of the same depth approximately, but are much smaller in area, the temperature of the bottom water does not rise much above 7° during the summer. The same is true of Cochituate lake, Massachusetts, having a depth of 60 feet and an area of less than one and one-half square miles. (FitzGerald, '95.) Green lake and lake Geneva, Wisconsin, both of them not greatly differing in area from lake Mendota, but having a depth of 150 to 200 feet, have bottom temperatures of about 6° .

In a lake of large area, like lake Mendota, and about 24 meters in greatest depth, the temperature at the bottom may differ widely in different summers. In 1896 the bottom temperature at 18 meters at the first of June was nearly 15° ; in 1895 about 12° , and in 1897 about 11.4° . At 22 meters it was about 0.5° lower in each year. Had it not been for the gales in the latter part of May the bottom temperatures would have been much lower; possibly from 7° to 9° . The extreme possible range of bottom temperature in summer for lake Mendota in different years may perhaps be stated as from 8° as a minimum to 18° , as a maximum, and the probable range as from 10° to 15° .

Summer temperatures.

The temperature of the surface rose rapidly and evenly after the fall in the temperature and mixture of water in the latter part of May. In 1895 the weekly average rose from about 13.6° to 22.5° in three weeks, a rate of nearly three degrees per week. In 1896 the surface rose from 15.4° to 25.1° in six weeks, rising somewhat less regularly and at a much lower average rate. The period of the summer maximum was reached about the middle of June in 1895, when the average temperature was 23.5° , and about

the 1st of July in 1896, when the maximum was about 2.5° higher. The maximum surface temperature recorded was 25.2° Aug. 1, 1895, and 27.8° July 23, 1896, both at 5 p. m. After the maximum has been reached there follows a period in which the temperature of the surface is nearly stationary, and in which the weekly averages do not vary more than two degrees. This period was exceptionally long in 1895, lasting from the middle of June to the third week of September, about three and one-half months, in which time the weekly averages were between 22° and 24° . In 1896 it lasted only about six weeks, from the first week of July to the middle of August, at a temperature of 24° to 26° . At the close of this period the surface temperature falls and the decline once started goes on pretty uniformly as shown by the weekly averages, until the lake nears the freezing point. In 1895 the temperature fell 3° in as many days at the last of September. In 1896 there was a fall of 4.4° during the last ten days of August.

At the opening of the summer period the temperature of the bottom rises somewhat rapidly in the latter part of May, gaining perhaps $1.5-2^{\circ}$ in two weeks. After this the bottom temperature is stationary or rises very slowly, not gaining a degree in three months. The bottom temperature at 18 meters lay between 13° and 14° in 1895; close to 15° in 1896, and near 12° in 1897. At the depth of 22-23 meters the temperature was from 0.4° to 0.6° lower in each year. Late in September the water of the lake becomes mingled from top to bottom and the temperature becomes uniform. At this time the bottom temperature rises rapidly by the mixture of the bottom water with the warmer water above.

During the early parts of the period when the bottom temperature is nearly stationary, that of the surface rises until the difference between bottom and surface amounts to 10° and even 15° in late July or early August. As the surface temperature declines, the difference between top and bottom becomes less and usually amounts to between 4° and 5° in late September, just before the time when the lake is rendered homothermous by the fall gales.

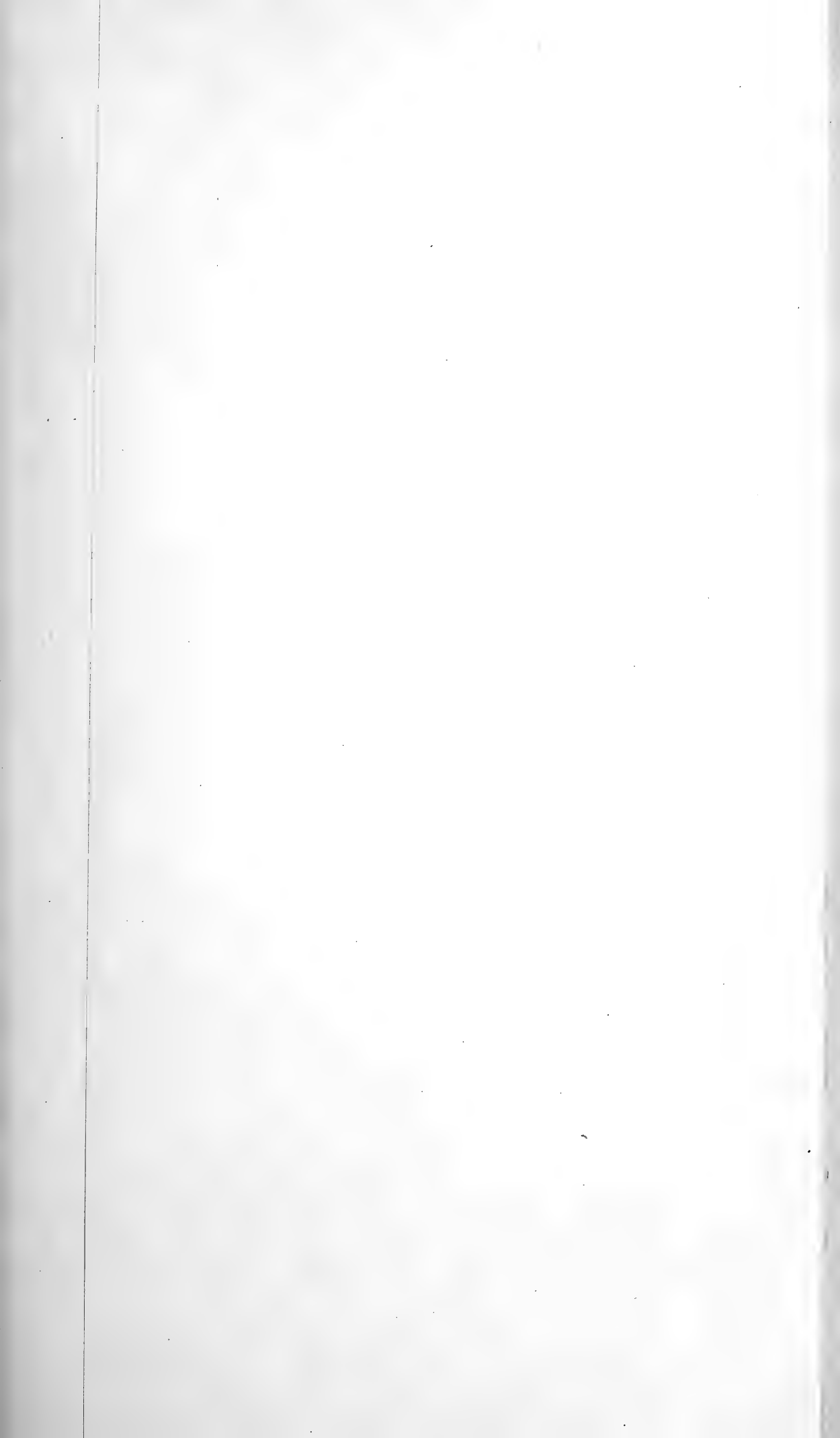
The Thermocline.

During the summer, then, the difference in temperature between the surface and the bottom may amount to 10° , 12° , or even 15° . The decline in temperature from surface to bottom is, however, not uniform as the depth increases. If a series of temperatures is taken about the first of August it will be found that there is a layer of surface water from 8 to 12 meters in thickness whose temperature is nearly uniform, the difference between that of the surface and that at 9 or 10 meters being usually only a fraction of a degree and frequently nothing. Immediately below this mass of warm water lies a stratum in which the decline of temperature is extremely rapid. This stratum may be two or three meters in thickness with a decline of as many degrees per meter. It may be only a meter or even less in thickness, and a decline of as many as nine degrees has been observed in a single meter. This layer in which the temperature changes rapidly may be known as the *thermocline* — the *Sprungschicht* of German authors. Below the thermocline the temperature decreases toward the bottom at first more rapidly and then more slowly as the depth of the water increases, but never showing the sudden transitions which are characteristic for the thermocline, the rate of decline rarely exceeding one degree per meter of depth. The thermocline was first noticed by Richter ('91) in a study of the Alpine lakes. Its origin was attributed by him to the alternate action of the sun warming the surface in the day, followed by a cooling at night. The alternation of conditions resulted in the formation of a layer of water of nearly uniform temperature above the colder bottom water. I do not wish to argue against the correctness of this theory as applied to the lakes which have been studied by Richter and others, but in lake Mendota the concurrence of gentle winds and hot weather are essential to the formation of the thermocline. In other words, the warmth of the surface water, received from the sun, is distributed by the wind through a certain depth of the lake, a depth which is proportional to the violence of the wind and the area of the lake. (Cf. FitzGerald, '95; Whipple, '95.) It can readily be seen that

in a lake of the size of Mendota the water would be of uniform temperature from top to bottom if the lake were always agitated by violent winds. On the other hand, if the weather were perfectly calm, the lake would be warmed only to the depth which the rays of the sun could directly penetrate. As a matter of fact, the formation of the thermocline is due to the concurrence of gentle winds and a temperature high enough to warm the surface water rapidly.

The temperature observations on lake Mendota have been made chiefly at a station about one-half of a mile from the south shore. On bright days in May, with a gentle north (on shore) breeze, it not infrequently happens that a thermocline is formed, there being a mass of water four or five meters in thickness of uniform temperature, below which there is a rapid descent in temperature to the cooler water below. When, however, the direction of the wind changes and blows off shore, this warm water is carried to the other side of the lake, and the temperature shows a fairly uniform rate of descent from the surface to the bottom. If, however, this condition of warm weather and gentle wind continues, there is produced a mass of warm water on the surface, so thick that however the wind may blow there is always a warm stratum floating on the colder water; and when this condition has been established, a permanent thermocline has been formed.

A study of Figs. 3 and 4 will show the formation and movements of the thermocline as disclosed by the weekly averages. It will be seen that in the early part of May the gain of heat is rapidly distributed through the whole mass of water. The bottom lags behind the surface, of course, but the difference in temperature between them rarely exceeds 5° and the temperature of the surface water reaches the bottom in 10 days or 2 weeks. During the rapid warming of the early summer this condition ceases. The surface warms rapidly, the winds are not constant or strong enough to distribute the heat throughout the water, and the downward movement of the isotherms no longer extends to the bottom, but they penetrate for an increasingly shorter distance into the water. In 1895, for example, the surface reached an average temperature of 15° during the last week in May,





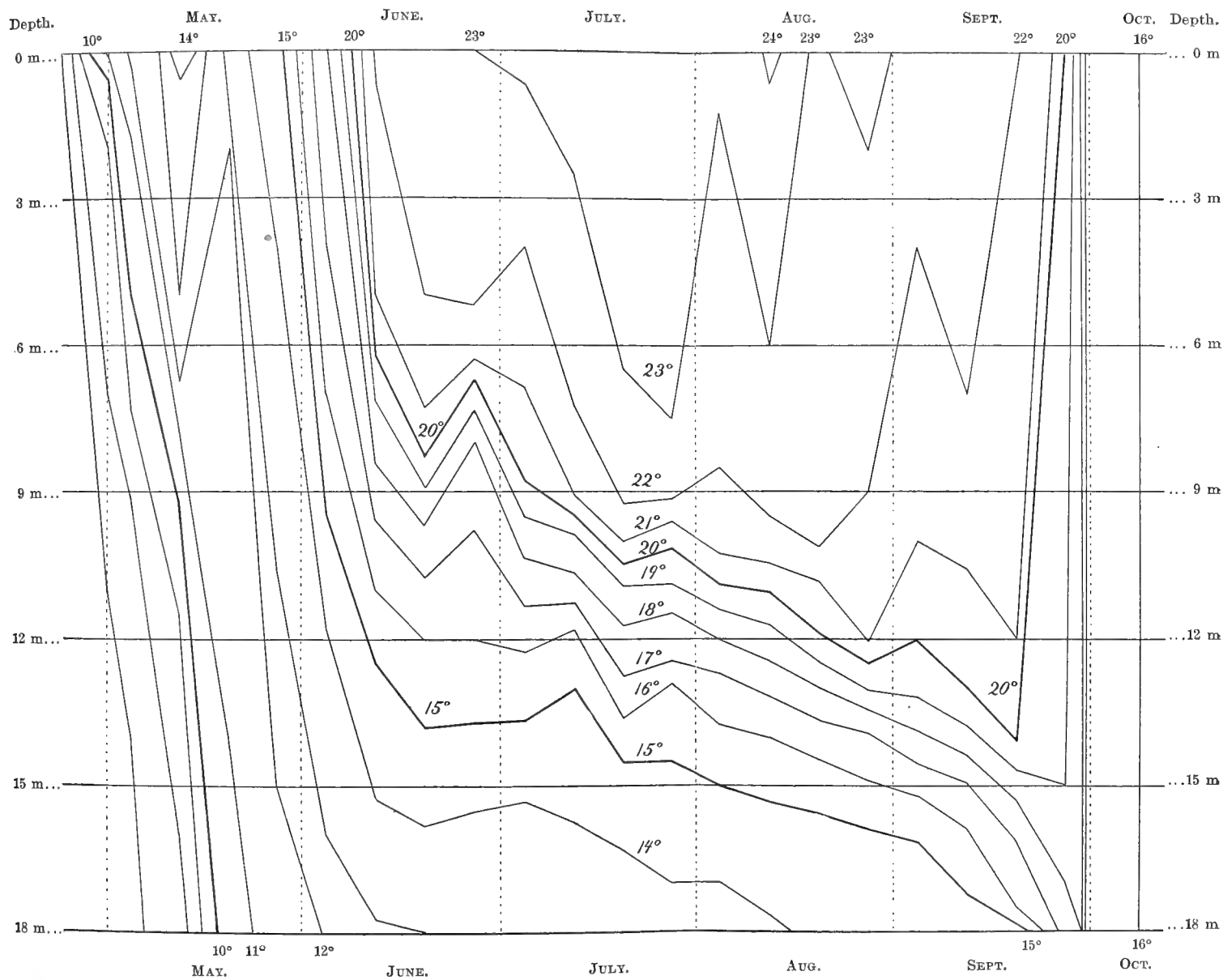
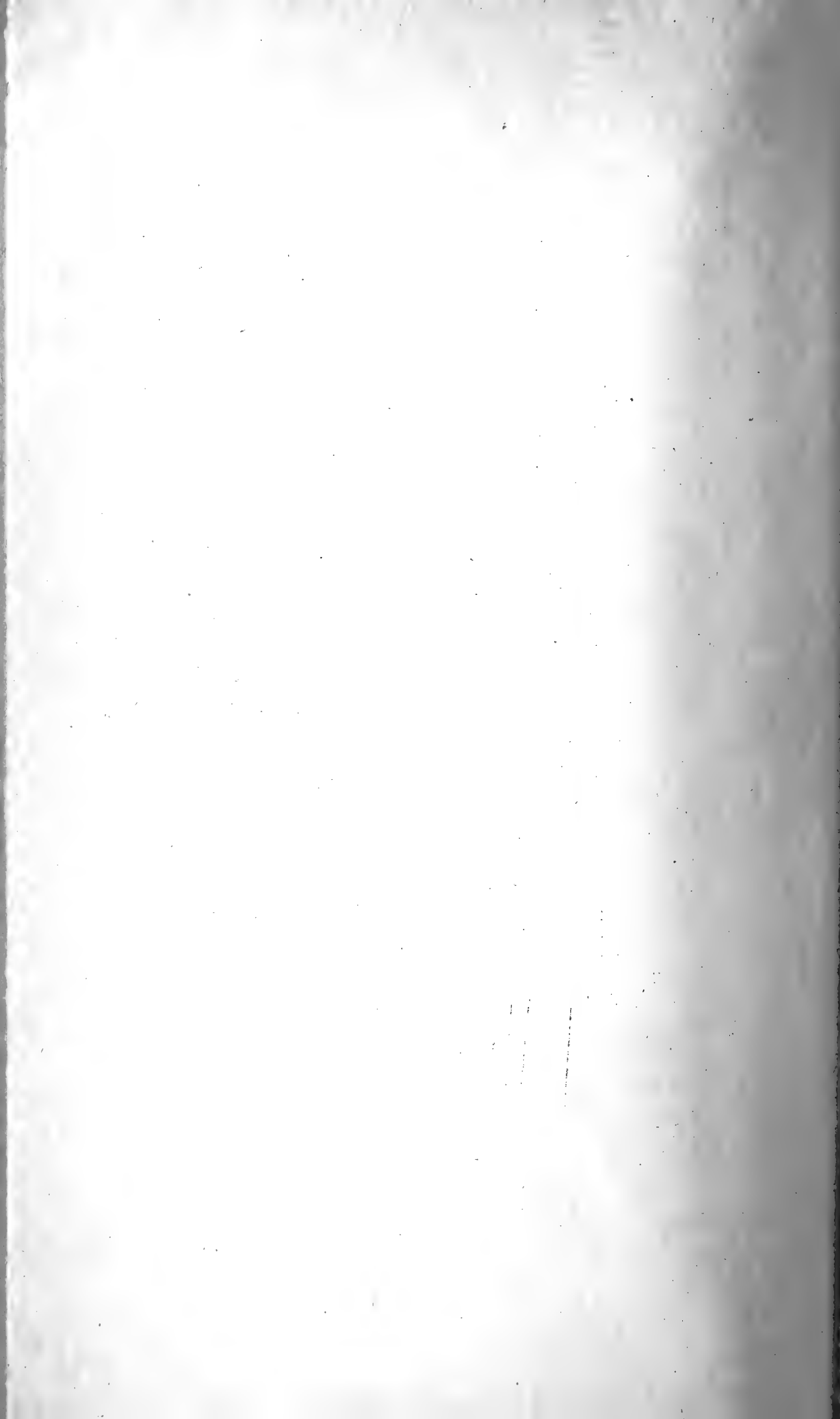
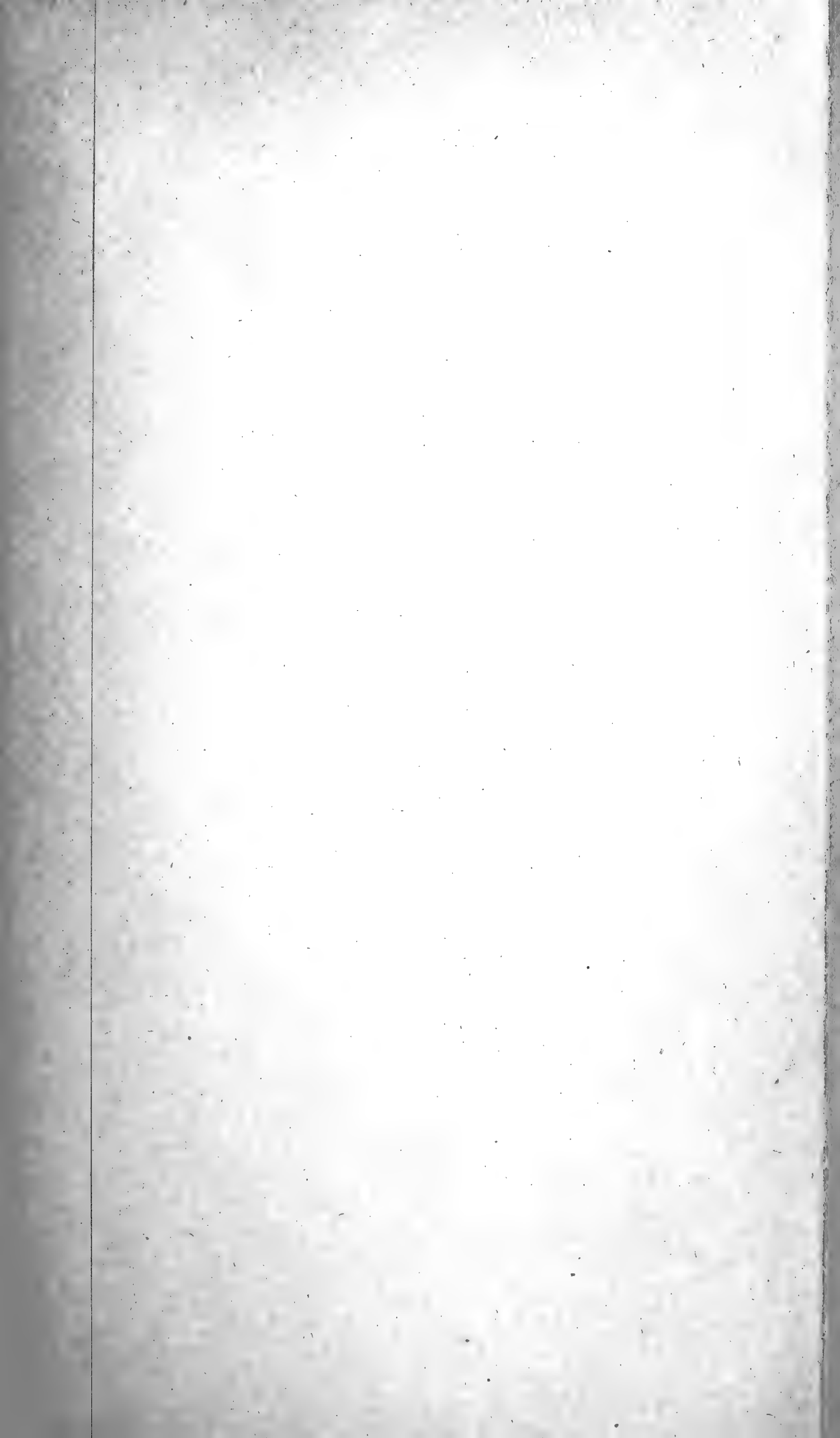


FIG. 3.—Summer temperatures, 1895. See p. 296.







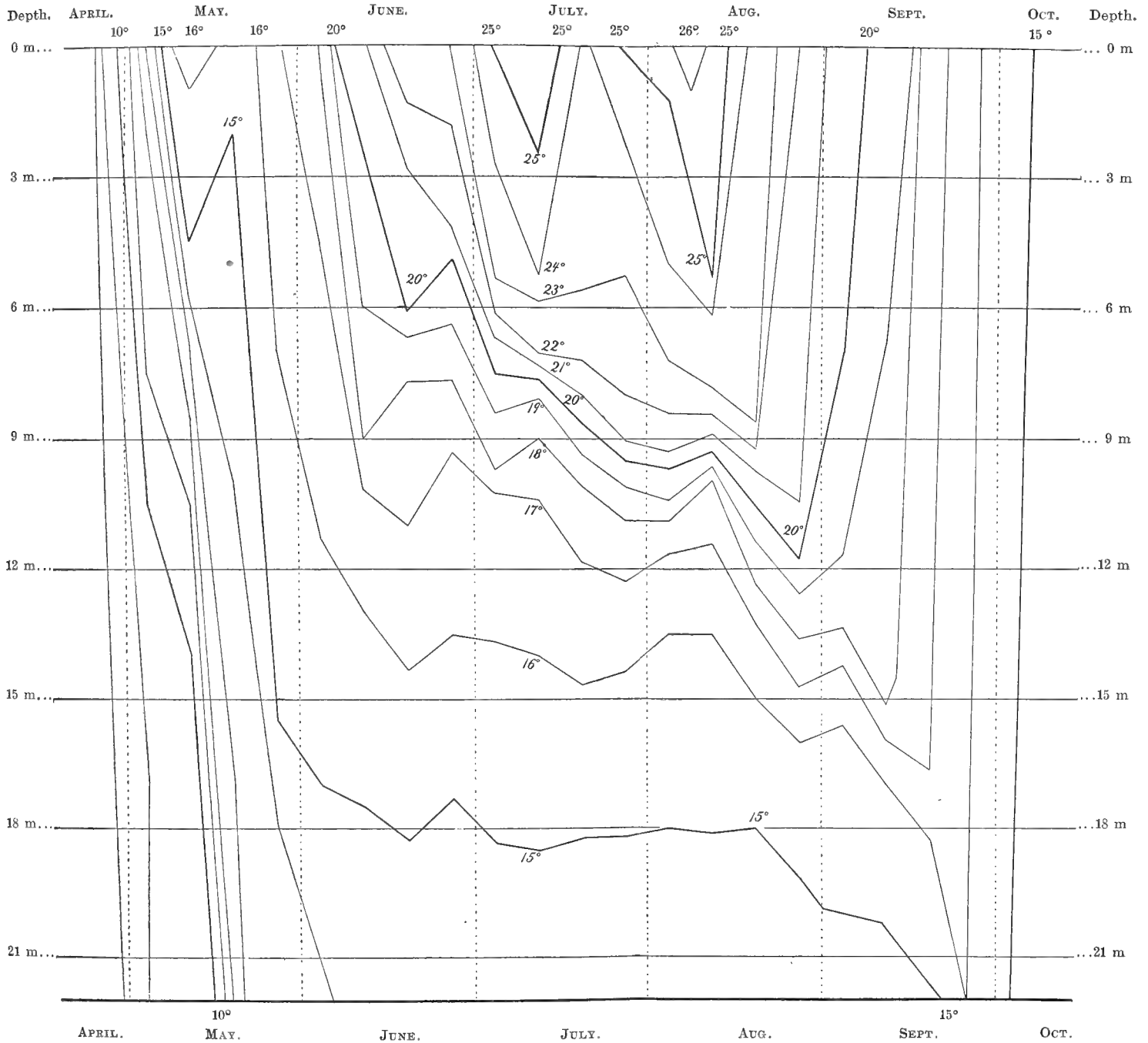


FIG. 4.—Summer temperatures, 1896. See p. 296.



and the isotherm of 15° penetrated nearly 10 meters of the lake in a week; it went down 3 meters further in another week, but thereafter moved downward at a rate little exceeding one meter per month. In 1896 the 15° isotherm was included in the May depression of temperature, but in late May it moved downward nearly 15 meters in one week, 1.5 in the week following, and only one meter in the next two and a half months. As the temperature of the surface rises above 15° the warmth penetrates to a distance increasingly small and the isotherms accordingly bend toward the horizontal at a level nearer the surface. The gain of heat, however, becomes rapidly distributed through the upper water to a depth of 8 to 10 meters, so that the thermocline becomes permanent at about these depths. When the thermocline has once been formed it moves downward very slowly. Beginning at about 8 meters in late June, it descends somewhat rapidly to about 10 meters, but after that moves downward slowly and irregularly, its descent depending rather upon the wind than upon the temperature of the air. In both years the thermocline reached the bottom of the lake in the last of September, which would make its downward movement about 4 meters per month, but the last 5 or 6 meters were passed very rapidly in consequence of the gales of late September.

In 1895 the 18° isotherm was near the center of the thermocline; it oscillated about the 9 meter level in late June, sank nearly 3 meters in July, about 2.5 meters in August, and 4.5 in September, the last 3 in the latter half of the month. In 1896 the 20° isotherm was near the center of the thermocline at the outset and crossed the 6 meter level about July 1st. It lay at 7.5 meters during the first week of July, reached 9 meters about the 20th of the month, oscillated between 9 and 10 meters for more than three weeks following that date—weeks of unusually hot weather—until the middle of August. At that time the weather changed and continued cool with much northerly wind, under whose influence the thermocline rapidly sank more than 2 meters during the last half of the month and continued this downward movement through September until it disappeared in the latter part of the month.

These temperature diagrams, which give the weekly averages of temperature, do not show the actual condition of temperature, and especially the temperature of the thermocline, on any single date. The thermocline oscillates up and down under ordinary conditions of weather through a meter or more; and the effect of averaging the observations of a week is to increase the apparent thickness of the thermocline and thus to diminish the rapidity of descent of temperature in it. Without any considerable change either of wind or temperature the thermocline may oscillate through 2 or even more meters. The action of severe wind is much more apparent. Fig. 5 shows temperature diagrams for August 2, 24, 26, 27, and 28, 1896. It will be seen that the diagrams for the 2nd and 24th of the month were closely similar, although the surface water had cooled a degree or more and the thermocline had descended about 1 meter. On the 24th there was a decided fall in temperature of the air accompanied by violent winds from the northwest. The surface water fell more than one degree in two days, while the thermocline was temporarily depressed at the observing station more than 4 meters. It lay on the 24th between 10 and 11 meters; on the 26th between 14.5 and 16 meters. The temperature at the bottom, 18 meters, was raised about 0.4° , at 14 meters 5.6° , at 12 meters 4.3° , at 10 meters there was a loss of about 0.6° . On the 27th, the wind having fallen to a calm, the thermocline had risen nearly 3 meters, while on the 28th, with a gentle south wind, it had risen still further, and the temperature curve had greatly changed in form. During these three days the temperature to a depth of 8 meters had varied very little—too little to show in the diagram. This example of changes which are going on all the time, shows the following facts: 1. The isotherms of diagrams 3 and 4 represent only the average position of the thermocline. 2. The decline of temperature in the thermocline is ordinarily much more rapid at any given date than is indicated by the average of the week. In other words, the thermocline is not nearly as thick as the week's average would indicate. 3. The greatest daily variation in temperature during summer is found at the thermocline, where a range of 5 or more degrees may be registered in a day. These variations

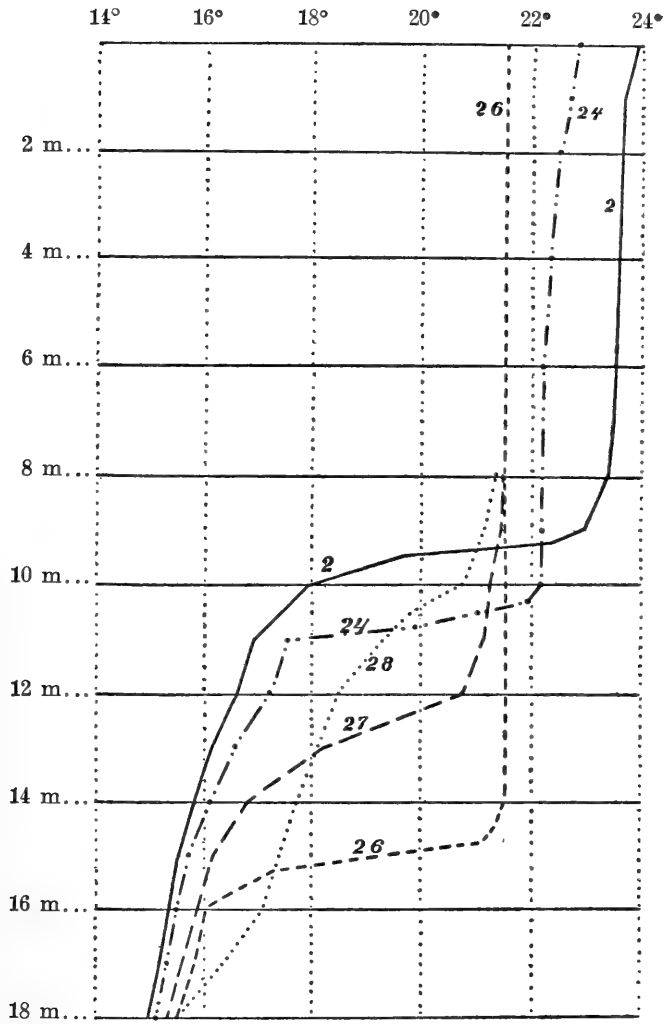


FIG. 5.—Temperatures, August, 1896. See p. 298. The dates of observations are indicated on the temperature curves.



are not caused by the warming or cooling of the water but by the fluctuations in the level of the thermocline. These fluctuations go on to a certain extent without an assignable cause, but the larger movements, at the station where observations were taken, are plainly due to the wind. 4. The upper layers of the cool water become mingled by the action of the wind with the lower part of the warm water above it and are taken into the warm layer. Thus the thermocline moves constantly downward during summer, while the water below it is little or not at all changed in temperature. 5. The water below the thermocline is practically stagnant during the summer, and is cut off from direct exposure to sun and air. As a result, it may become unfit to support most forms of animal life, as is the case in lake Mendota. 6. The larger changes in temperature below the thermocline are due to currents caused by winds.

Autumn temperatures.

By the latter part of September the temperature of the surface water has fallen so that it exceeds that of the bottom by barely 5° . At this time also gales from the north are apt to occur whose effect is to break the thermocline and render the lake homothermous. This result is reached at different dates for different depths, but in both years the lake became homothermous in its deepest parts about two or three days after the time when a similar condition was reached at 18 meters. In each year the homothermous condition was reached at a temperature not much exceeding 16° ; and in general the temperature for the 1st of October may be stated as about 16° .

The breaking up of the thermocline is accompanied by a marked rise in the temperature of the bottom water. In 1895 this rise amounted to 2.8° from the 26th to the 28th of September; and in 1896, to about 1.5° in the same time.

During October and November the temperature falls with singular uniformity, as indicated by the weekly averages, passing the temperature of the maximum density of water late in November. The decline continues steadily until a temperature is reached between 2° and 3° , after which the cooling goes

on very slowly. The difference of temperature between the surface and bottom of the lake during this time is very small. In the morning the lake is entirely homothermous. On bright, calm days, the temperature of the surface rises, and may become as much as 2° warmer than the bottom. This condition of things, however, is uncommon, and ordinarily it is difficult to find differences between the surface and bottom exceeding 0.1° or 0.2° . It is a feature of especial interest in lake Mendota that the fall homothermous period begins so early and at so high a temperature. The autumnal multiplication of many of the species of crustacea goes on after this period has been fully established, and their vertical distribution at this time is therefore independent of temperature. In the deeper lakes, or in smaller lakes of the same depth the homothermous condition is reached much later. In Green lake, as reported by Professor Marsh (Marsh, '97, p. 187), it occurs in November at a bottom temperature of 4.7° , and at a depth of about 45 meters. The rise at the bottom was 1.4° . In Cochituate lake, near Boston, at a depth of 18 meters, the homothermous condition is reached at about the same time, and at the same temperature. (FitzGerald, '95, p. 74.) This lake has an area of less than one and a half square miles.

During the last of November and the early part of December cooling goes on very slowly. The surface temperature frequently falls to zero, as the result of a calm night, and the lake may skim with ice, which is broken up again by the wind.

THE ANNUAL DISTRIBUTION OF THE CRUSTACEA.

I. General Relations of the Plankton Crustacea.

Figs. 6-11.

Lake Mendota has eleven species of limnetic crustacea, which may be grouped as follows:

A. Perennial species —

a. Appearing in great numbers —

Copepoda.

Diaptomus Oregonensis Lillj.

Cyclops brevispinosus Herrick.

Cyclops Leuckartii Sars.

Cladocera.

Daphnia hyalina Leyd.

Chydorus sphaericus O. F. M. var. *minor* Lillj.¹

b. Usually appearing as isolated individuals —

Copepoda.

Epischura lacustris Forbes.

Ergasilus depressus Sars.²

B. Periodic species —

a. Appearing in great numbers —

Cladocera.

Daphnia pulex DeG. var. *pulicaria* Forbes.

Daphnia retrocurva Forbes.³

Diaphanosoma brachyurum Sars.

b. Appearing as isolated individuals —

Cladocera.

Leptodora hyalina Lillj.

To these might be added *Bosmina* of which a very few individuals appear, chiefly in winter, but of which there are never enough to make a fair determination of their number a possi-

¹Sometimes absent but not properly periodic.

²The specific identification is not certain.

³Formerly classed as a variety of *D. Kahlbergiensis* or *D. cucullata*.

bility. Most of the littoral forms of crustacea also appear occasionally in the plankton, especially after storms, as also do Hydrachnids and Ostracoda.

Of these eleven species, the isolated forms do not contribute any appreciable addition to the number of limnetic crustacea. Their combined number is rarely as great as one per cent. of the total crustacea present. They have, therefore, been neglected in determining the total number of crustacea, and this general account will deal with the eight abundant species only.

The limnetic crustacea on lake Mendota show a rhythm of development quite complex, but recurring in closely similar form during the time covered by my observations, July, 1894—December, 1896. (Fig. 6.) Observations less numerous have been continued to the present date, September, 1897, and show a similar development during the present year. The following periods can be distinguished:

Winter minimum.....	December to April, then increase to the
Spring maximum.....	In May, followed by a great decline to the
Early summer depression.....	June or early July,
Mid-summer maximum.....	July,
Late summer minimum.....	Late July or August,
Autumn maximum.....	September and October, declining to the winter minimum, through late October, November and early December.

There are, thus, three maxima and minima which are of unequal value. The spring maximum is by far the greatest, the crustacea reaching a maximum number of 3,000,000 per sq. m. of surface, and in 1896 reaching an average of nearly 2,500,000 for the first half of May. This maximum is due almost entirely to the rapid development of *Cyclops brevispinosus*. After the maximum has passed, this species rapidly declines in number, and the total number of crustacea sinks with it, so that by the middle or last of June the number is reduced to less than half the maximum. This is the early summer depression, which may be greatest at any time from the middle of June to the first week in July. A rapid, but slight, recovery follows, due chiefly to renewed reproductive activity on the part of the species already present in the lake, leading to the mid-summer maximum, in July. Then follows a decline, usually somewhat slow, reach-

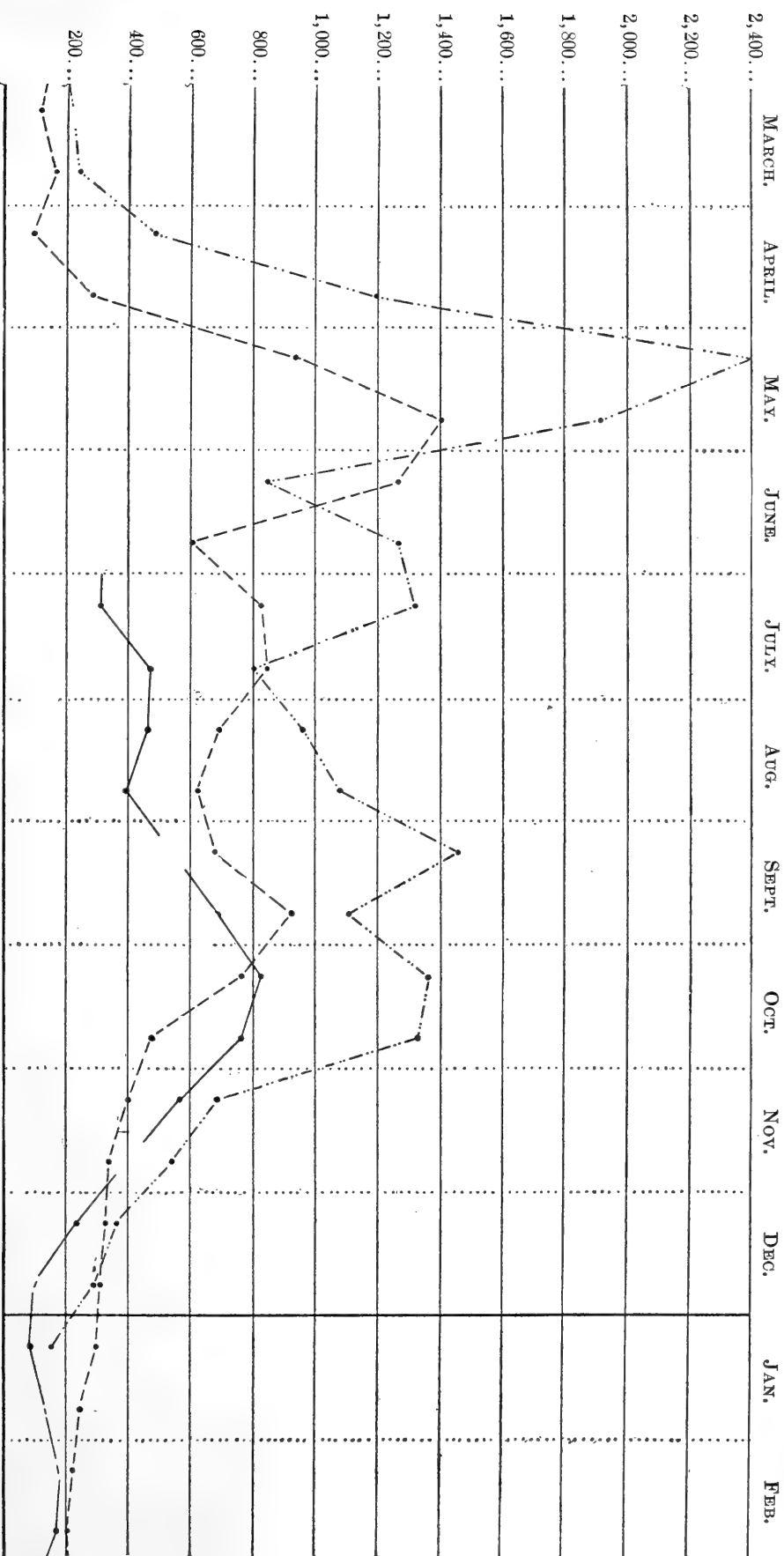


Fig. 6.—Total crustacea, 1894-1896. Scale, 1 vertical space = 200,000 crustacea per sq. meters. See p. 302.

1896.....●.....

1894.....●.....

1895.....●.....



ing a point of greatest depression about the last of August. During this period of decline, most of the periodic species are introduced, but their numbers do not usually compensate for the falling off in the number of the permanent species. In 1896, however, *Chydorus* increased so rapidly during this time as to more than counterbalance the decline in other species.

In September a rise in the number of crustacea begins, caused chiefly by increase in *Daphnia* of all species and in *Cyclops*. This increase culminates in the last of September or in October. This is the fall maximum, which, in general, is decidedly greater than the early summer maximum, the crustacea at this time reaching a number perhaps two-thirds as great as that of the spring maximum. During the later part of the fall and the early winter, the number declines very rapidly at first, and then more or less slowly, until the winter conditions are established with the freezing of the lake in December or early January. The rapidity of the decline varies in different seasons, depending upon the abundance of the periodic forms and upon the number of young *Cyclops* and *Daphnia hyalina*, which are produced in late autumn. The climatic conditions also affect the rapidity of decline; the rate of fall of temperature, the storms, etc., having a decided influence in hastening or retarding the approach of the winter conditions. Near the last of December, however, these conditions are fairly established, and the crustacea pass through the winter with but little change in number and averaging from 100,000 to 200,000 per sq. m. of surface.

A glance at Fig. 6 will show that this complex rhythm recurred with an exactness quite surprising. While the absolute number of crustacea present varies considerably, the shape of the curves indicating the movement of the limnetic population is strikingly similar. The resemblance is the more surprising when we consider that these maxima and minima are due to the increase and decrease of eight species of crustacea, whose numbers are independent of each other, and which appear in very different numbers at different seasons and at the same season in different years. The lines of diagram 6 represent, therefore, the sums of a number of independent variables, never fewer

than three in winter nor more than eight in the period from July to October.

In the study of this rhythm of development, three facts may well be noticed in the first place. First, the number of crustacea in lake Mendota is to a singular extent dependent upon the perennial forms. In other lakes it often happens that the periodic forms are the dominant members of the summer population. Of these forms, *Bosmina* is practically entirely absent from lake Mendota; *Diaphanosoma* appears in small numbers only; and *Daphnia retrocurva* only rarely equals in number the related species, *Daphnia hyalina*. There is, therefore, no great increase in numbers in summer dependent on summer forms alone. Indeed, the influence of the periodic species is not greatly felt until September, and the shape of the developmental curve would not be greatly altered, were the periodic species omitted.

Second, *Chydorus* occupies a peculiar place among the plankton crustacea. It is properly a marginal form, and appears in the limnoplankton only under favorable conditions. Apstein has connected its presence in the limnetic region with that of Chroococcaceae. My observations seem to connect its abundance in the limnoplankton with an abundant development of these and similar plants. In other words, it seems true for lake Mendota that periods when the diatoms and *Ceratium* are the only abundant algae, are periods when *Chydorus* is present in small numbers; while in periods when the Schizophyceae or *Anabaena* abound, *Chydorus* is also abundant. The maxima of this species, therefore, have occurred without close reference to temperature or season, and may come at any time from June to late October. These maxima are also very irregular in amount, number, and duration.

Chydorus, also, is peculiar in the limnoplankton on account of its small size. It contains little more animal matter than a good-sized nauplius, and decidedly less than an embryo *Daphnia*. While, therefore, a great abundance of one form of plankton crustacea usually affects unfavorably the number of other species, *Chydorus* appears to be more independent of the presence of other forms. It seems, as it were, superposed on the regular limnoplankton, rather than a part of the general limnetic life,

and its rise and fall seem measurably independent of the conditions to which the other species respond.

A third fact concerns *Daphnia pulicaria*. This species had a biennial period of development about thirteen months long, extending from July to August of the following year, and a period of rest, in which it was almost entirely wanting in the plankton, extending from late August to the following July. In 1894 a few representatives of this species were found in July, and it wholly disappeared in August. In 1895 they were an important constituent of the crustacean life from July on, increased greatly in late fall and early winter, and continued numerous throughout the winter. In April and May, they increased enormously, producing males and sexually mature females, and then declined, practically disappearing in September. This species was therefore a constant and important factor in the number of the crustacea during the last half of 1895, the following winter, and the spring and early summer of 1896. It was absent during the latter half of 1894 and the spring and early summer of 1895.

I will now pass to a brief discussion of the general crustacean life as it appears in the different seasons. I shall reserve most of the discussion of the causes and conditions affecting the number of crustacea to a later chapter.

The Crustacea in Winter.

All of the perennial crustacea are, of course, constituents of the winter plankton, and their numbers are not very unequal. The number is by no means small, averaging about 125,000 per sq. m. from January to the middle of April, 1895, and about 235,000 from January to April 1st, 1896. The following list shows the species present during the two winters in question.

TABLE III.—Species, with average number of each per square meter.

	1895.	1896.
Diaptomus	24,500	34,800
Cyclops.....	52,100	120,900
Daphnia hyalina.....	46,200	22,700
Daphnia pulicaria		48,400
Chydorus.....		7,900
Total.....	122,800	244,500

It will be seen that in 1895 there were present only three species, while in 1896 two others were added. In 1897 the conditions were essentially similar to those of 1895. Indeed, while the time from which my observations have extended by no means warrants any positive assertion in the matter, there seem to be distinct indications of a biennial periodicity in the plankton in respect to crustacea, algae, and rotifers. Observations must be continued, however, over a much longer time before any definite statement can be made on this subject.

The winter numbers of each species are on the whole singularly constant through the season, as will be seen by reference to the tables giving the numbers of the several species. The death rate must be very low. During the period, January–March, the variation in the number of crustacea taken in twenty or more catches made each winter vary to an extent hardly greater than might be found in catches made close together on the same day. It would be very difficult to prove any considerable decline in numbers of *Diaptomus* or *Daphnia* during the winter and they do not increase by reproduction. *Cyclops* produces eggs much more abundantly than the other species, and the adults seem to become fewer in late winter and late spring, but their number is more than made good by young individuals. In 1895 *Cyclops* began to show numerous egg clusters in February, and about ten per cent. of the specimens were egg-bearing females. These eggs developed very slowly, and few nauplii and almost no young *Cyclops* were seen. In 1896 the reproduction of the *Cyclops* hardly stopped at all during winter. In the middle of January nearly one-half the *Cyclops* bore eggs, and numerous nauplii were present. By the middle of March the nauplii had grown to young *Cyclops*, from three-fourths to seven-eighths of the total number of the species were immature young.

The winter minimum therefore falls in the period before *Cyclops* has begun this winter reproduction. In 1895 the minimum came in January and in February in 1896. Yet throughout the winter months the numbers are so constant that no well marked minimum can be placed at any date. In 1897 the condition of *Cyclops* was intermediate between those of 1895 and 1896.

Young *Cyclops* began to appear under the ice, but the condition of the species in the middle of March resembled that in the middle of February in 1896, and the progress of the development was in general about a month later.

The rotifers also show similar differences in reproduction in different seasons. Of this group there are regularly present during the winter, *Triathra*, two species of *Notholca*, *Anurea aculeata*, *cochlearis*, and *brevispinosa*, *Synchaeta pectinata*, and a species of *Oecistes*. All these reproduce more or less actively, and become quite abundant before the breaking up of the ice. Other species are present in smaller numbers.

The difference in the reproductive activity of these animals in different years seems to depend upon the temperature of the water, as will be explained at length in a later section of this paper. In all seasons there is an abundance of food. One of the chief winter algae is *Aphanizomenon*, which continues its development vigorously throughout the entire winter. Several species of the diatoms are also present, and in 1896 *Fragillaria* and *Diatoma* contributed largely to the plankton algae, but in 1895 and 1897 were insignificant in quantity, as compared with *Aphanizomenon*. There is no season of the year in which the crustacea fully overtake the food supply, except at the time of the spring maximum. During the winter the crustacea are active and fat, but those species which do not reproduce do not increase in size. Careful measurements of numerous individuals of *Daphnia hyalina* showed no appreciable increase in the average size between December, 1894, and April, 1895. When the temperature of the water is between 1.5 degrees and 2.25 degrees C., *Cyclops* develops very slowly or not at all from the nauplius state to that of the immature *Cyclops*, but at temperatures above 2.5 degrees the development goes on, although, of course, more slowly than at higher temperatures.

The Crustacea in Spring.

Lake Mendota has no large affluent, and the breaking up of the ice is slow, since it is due to the combined action of rain, sun and wind. The date of the disappearance of the ice differs greatly in different years. In 1895 the last expedition on the

ice was made March 27th; in 1896, March 29th. The first collection in water was made April 12th, 1895, April 4th, 1896. In general, the lake opens either wholly or over the greater portion of its surface about the 1st of April. The period immediately following the opening of the lake seems to be a time of trial for most of the limnetic crustacea. The temperature of the water increases very slowly at first, or, indeed, may be lowered temporarily; and the surface is, of course, agitated by gales which are so frequent in April.

During the spring *Cyclops* ordinarily increases in numbers with a rapidity dependent on the rise of temperature in the water, and upon the reproductive condition of the species at the time of the disappearance of the ice. *Diaptomus* and *D. hyalina* do not begin to rise in numbers until after the first of May, as may be seen by reference to Figs. 8 and 9. During April these species are wont to decline in number, so that the smallest catches made during the year ordinarily come in the latter part of April or the first of May. *Cyclops*, however, increases with great rapidity. Reference to the diagrams and tables will show that in 1895 *Cyclops* increased more than fourfold in number during two weeks, and that this increased number was nearly quadrupled during the next two weeks. In 1896 *Cyclops* advanced with even greater rapidity and about two weeks earlier than in 1895. In each year the increase in *Cyclops* was about a month in advance of that of *Diaptomus* or *Daphnia hyalina*, and in 1896, about two weeks ahead of the multiplication of *Daphnia pulex*. The spring maximum is reached during the month of May, either in the first or the latter part of the month, according to the temperature. At the maximum the population of the lake consists largely of *Cyclops*, about 70 per cent. of the total in 1895, and 80 per cent. in 1896 consisting of this species.

The multiplication of the crustacea and rotifers during the spring seems to be more rapid than that of the algae, and in late spring at the time of the maximum, the algae are far less numerous with respect to the crustacea than at any other season of the year. In a word, the eaters multiply in excess of the food. This undue multiplication of the crustacea puts a check

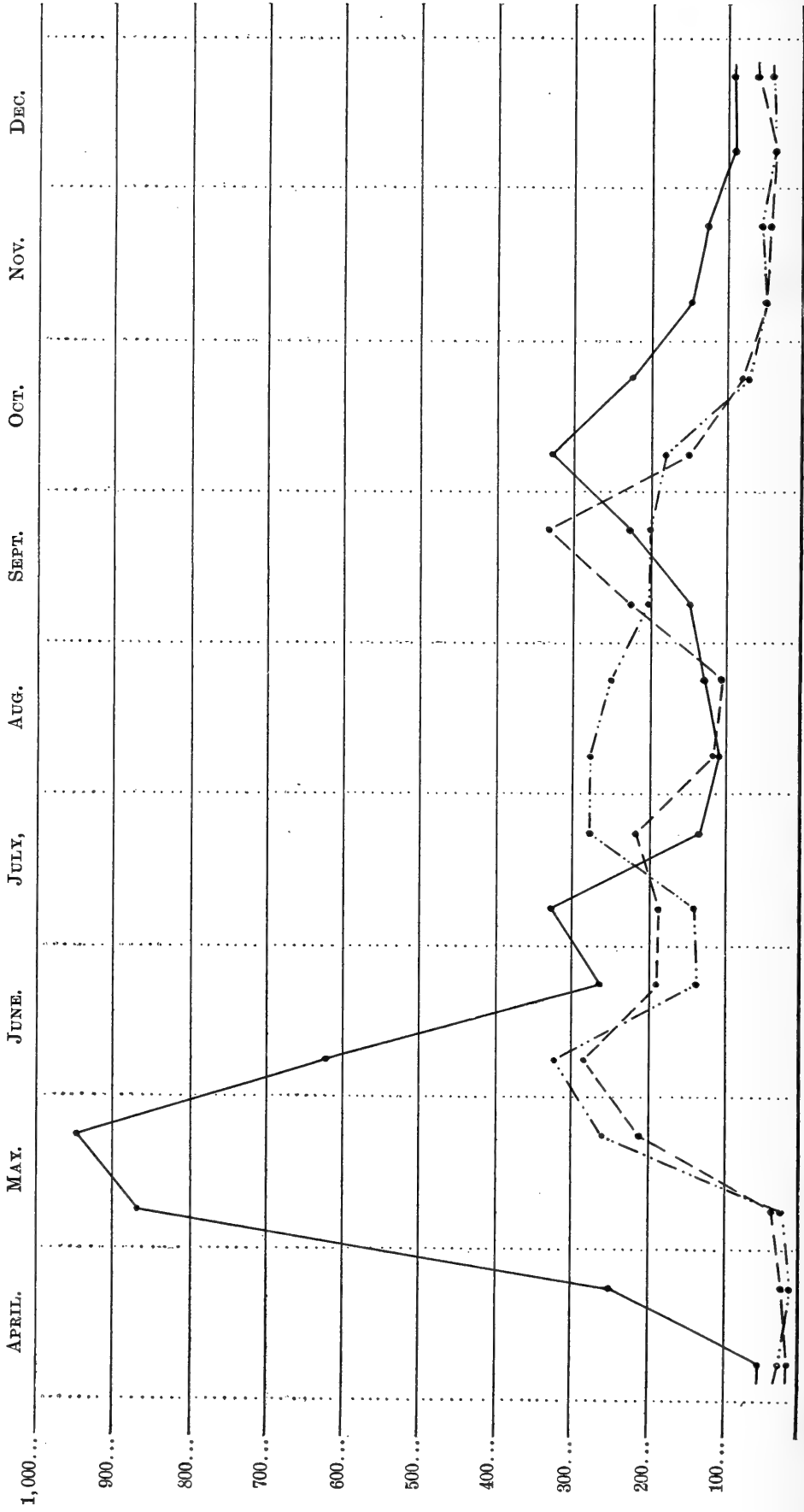


FIG. 8.—Leading crustacea, 1895. Scale, 1 vertical space = 100,000 crustacea per sq. meter. See p. 308, 316.

D. hyalina.....●.....

Cyclops.....●.....

Diaptomus.....●.....

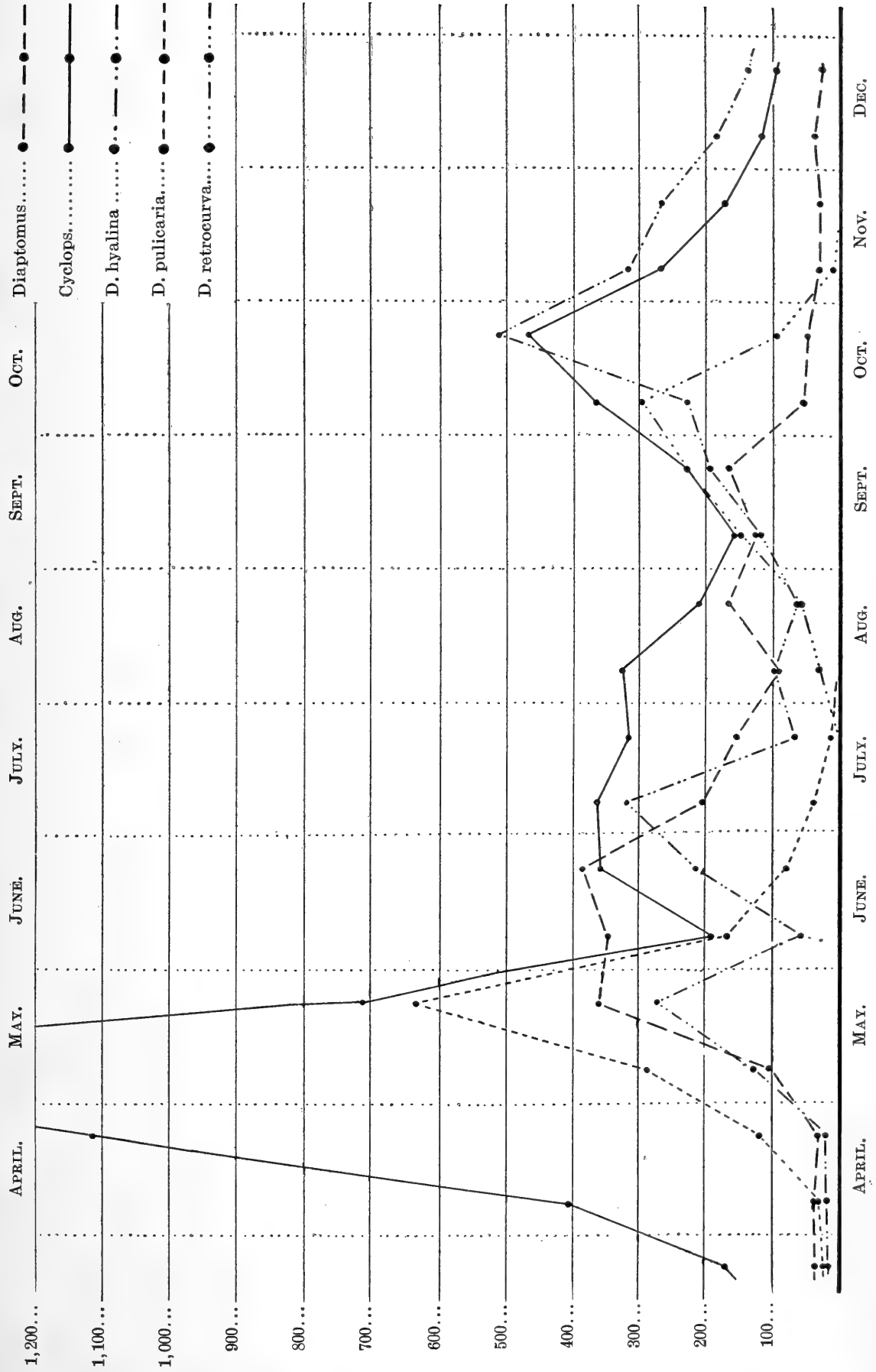
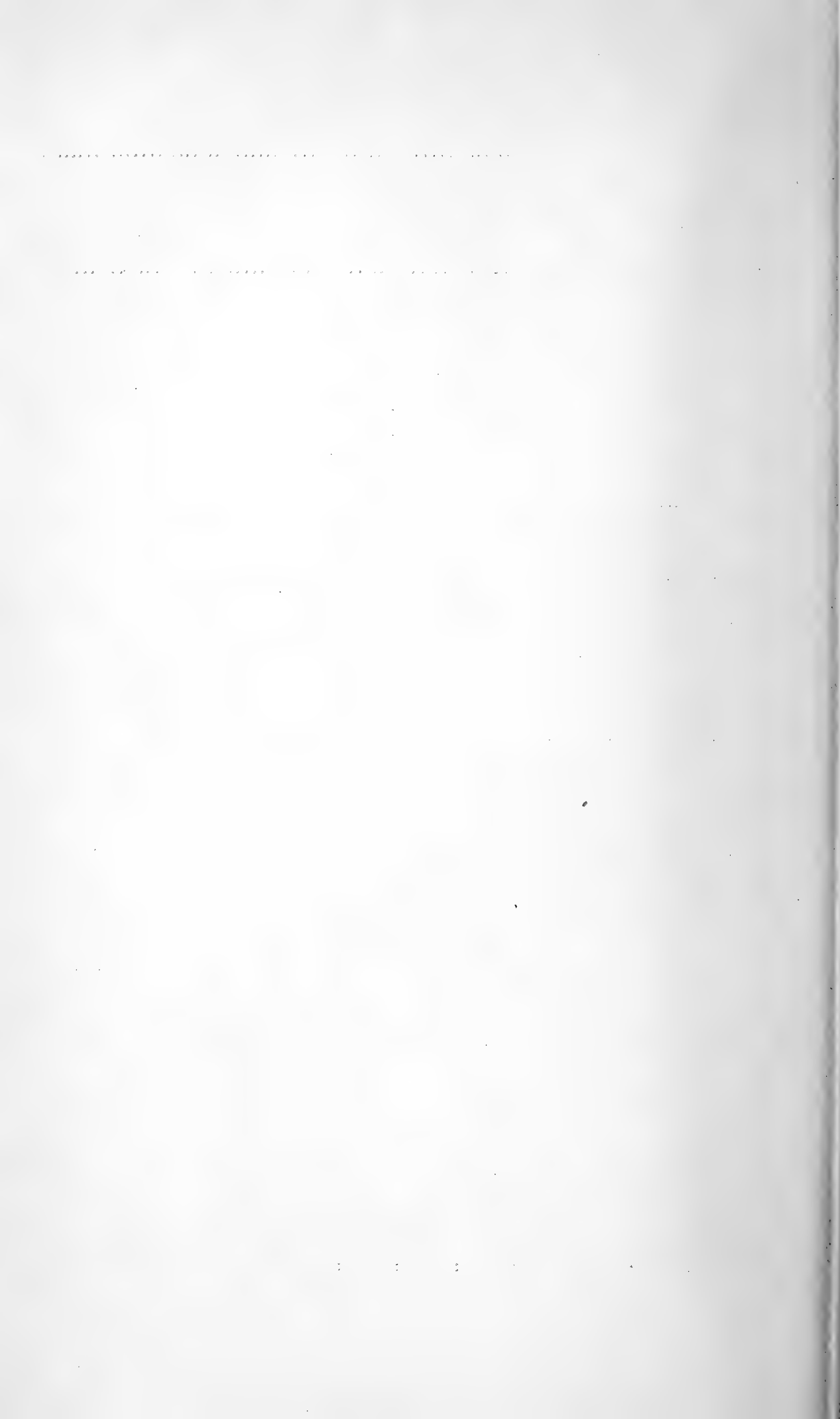


FIG. 9.—Leading crustacea, 1896. Scale, 1 space = 100,000 crustacea per sq. meter. See p. 308, 316.



on their development. At the time of the maximum *Cyclops* may number more than 2,500,000 per sq. m. of surface, but of this enormous number only a very small fraction ever become sexually mature. In any catch made at this season of the year, not more than five per cent. are mature, and not more than one or two per cent. are egg-bearing females. The great majority, therefore, of these *Cyclops* die without reaching maturity, and after the maximum has been passed the number of *Cyclops* decreases even more rapidly than it rose. The decline may go so far that in June the number of this species is scarcely larger than in March.

During this decline of *Cyclops*, the other perennial species are increasing in number, but their combined increase is more than counterbalanced by the decrease in the number of *Cyclops*, so that the late spring and early summer show a marked decline in the total number of crustacea.

The Crustacea in Summer.

The summer life of the crustacea begins with the decline from the spring maximum to the early-summer minimum. This decline is dependent in part on the decrease of *Cyclops*. In part, also, it depends on the fact that both species of *Daphnia* regularly decline after a brief maximum in late May or early June, and in 1895 *Diaptomus* showed the same decline. The total number of crustacea may be thus reduced to one-fourth, or less, of the number present at the spring maximum. The lowest point of numbers was about the middle of June in 1896, and about the first of July in 1895. In 1894, when observations began, during the first week of July, the crustacea were apparently at their minimum, which was exceptionally low in that year, owing to the peculiar character of the vegetation during that season. It was not greater than the number in the winter of 1895-96.

The crustacea increase in number after the early-summer minimum. This increase seems to be due to two causes. First, the development of species hitherto represented in small numbers. In all years there comes at this time an increase of *Cyclops Leuckartii*. The numbers of this species differ greatly in

different seasons. In 1894 it was only a small fraction of the total number of *Cyclops* present, while in 1896 it was quite as numerous as *Cyclops brevispinosus*. In 1896 *Chydorus* developed in great numbers in the latter part of June and early July. This development coincided with the presence of great quantities of *Aphanizomenon*. In 1895, which was characterized by a predominance of diatoms among the plankton algae during the summer, there was no marked development of *Chydorus* until autumn. The second cause of this midsummer increase is the renewed reproductive activity of the perennial species, especially *Daphnia hyalina*. These species has a marked reproductive period and maximum in the spring, (Fig 16) at which time from five to nine eggs may be produced. After the production of the spring broods the reproduction is greatly checked, and the species declines rapidly in number; but when the summer temperature of the water has been established, the species again reproduces, so that its numbers increase rapidly. Only two eggs are, however, regularly produced at once during the summer.

The result of these additions of new forms and increase of old ones gives a marked rise of the total number of the crustacea in late June and early July. This rise was very feeble in 1894, owing to the wholly peculiar condition of the vegetation, as stated elsewhere.

From this mid-summer maximum all of the species, except *Chydorus*, usually decline steadily and somewhat uniformly until the middle or the last of August. Three possible causes may be assigned for this decline: first, the exclusion of the crustacea from the deeper water of the lake; second, the increased temperature of that part of the lake inhabitable by them; third, the great development of *Ceratium*, which regularly becomes a predominant alga during this period, and which is much less available as food than the diatoms and Schizophyceae. *Ceratium* exerts a more unfavorable influence on the number of the crustacea from the fact that the young crustacea are quite unable to eat it. It is so large and its shell is so hard that they cannot master it, yet *Ceratium* occupies, with its enormous swarms, the upper strata of water, which naturally belong to the young crustacea. While, therefore, the adult crustacea may

find abundant food in the deeper strata, the young are unable to develop, and thus the total number of the limnetic crustacea slowly declines. The insect enemies of the crustacea, notably *Corethra*, are also very numerous at this time, but the number of these which I have found is not great enough to account for the decline in the number of the crustacea, and the increase of the crustacea begins in September, before the insect larvae begin to decline. I assign most influence to the first and third of the unfavorable influences which I have named. During this time the periodic species are added but their numbers are usually not great until after the first of September.

The Crustacea in Fall.

The number of the crustacea begins to increase with the opening of September (compare Figs. 6-9) and the increase continues during that month and into October. This increase is due in part to the increase in number of the perennial species. *Daphnia hyalina* and *Cyclops brevispinosus* multiply and reach a maximum in late September or in October. To these species are added the periodic forms, which are present in August, but ordinarily not in sufficient numbers to balance the decline in the other species. During September, however, all increase in number together, and bring the total number at the fall maximum to a point more than half as great as that at the spring maximum. In 1894 the maximum, 821,000 per sq. meter was reached in the first part of October; in 1895, the maximum was 768,000, in the early part of October; in 1896, there were two maxima, one in early September, numbering 1,441,000, of which more than half was due to *Chydorus*. The other, the fall maximum proper, was 1,368,000 and came in early October, or leaving out *Chydorus*, 1,123,000 in late October. The figures are the semi-monthly averages. The difference in these dates is apparently dependent upon temperature. If October is warm and pleasant, the development of the crustacea continues longer, and the maximum is greater than under other climatic conditions. In all seasons food is present in superabundance at this time of the year. The algae are at a maximum, and are enormously in excess of any demands made upon them by the crusta-

cea. The species present are those which are most easily available as food, so that both in kind and quantity of food, the crustacea find the most favorable possible conditions from early September to the latter part of November. Temperature is the predominant factor in influencing their development.

In 1894 and 1896 *Chydorus* was present in great numbers. Both of these seasons were characterized by the great abundance of *Aphanizomenon*. In 1895 and 1897, when the predominant algae were almost exclusively diatoms, the number of *Chydorus* was extremely small. Diagram 10 shows the number of crustacea from July to December, after subtracting *Chydorus*. It will be seen that the form of the curves is strikingly similar in all years, and that the numbers are extremely close for 1895 and 1896, with the exception of a great rise in late October, 1896, which was due to the sudden multiplication of *Daphnia hyalina* at that time.

From the fall maximum the number declines, at first rapidly, and afterwards more slowly toward the winter minimum. The rapidity of the decline depends upon several factors. If a large number of young forms are produced late in the season, many of them die as well as their parents, and the decline in numbers is correspondingly rapid. The number of the periodic species also exerts a great influence. In 1896, when *Daphnia retrocurva* was present in large numbers, its sudden disappearance at the close of its sexual period aided to cause a rapid decline in the total number of crustacea present. The climatic conditions also exert a great influence. A rapid decline in temperature, accompanied by violent storms, causes the numbers to sink more rapidly than a more equable approach of winter temperatures. In any case the number of the crustacea falls off rapidly during November, more slowly during December, and by the middle or last of that month the lake freezes and the winter conditions are fairly established.

The different species of limnetic crustacea enter the winter in very different conditions. *Daphnia hyalina* produces in the late fall large numbers of young, which serve to carry the species through the winter. The old individuals disappear during November and December, very few lingering into January. Dur-

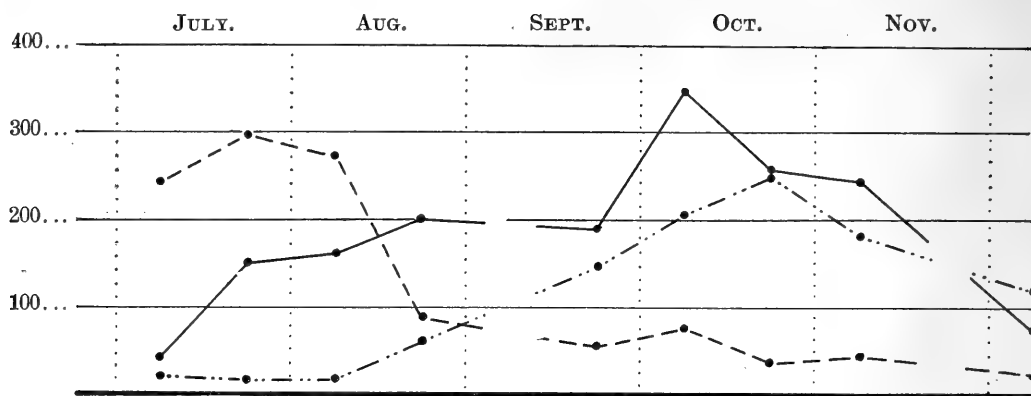


FIG. 7.—Leading crustaceans, 1894. Scale, 1 space = 100,000 crustacea per sq. meter. See p. 308.

D. hyalina..... - - - - -
 Cyclops..... ————
 Diaptomus... - · - - -

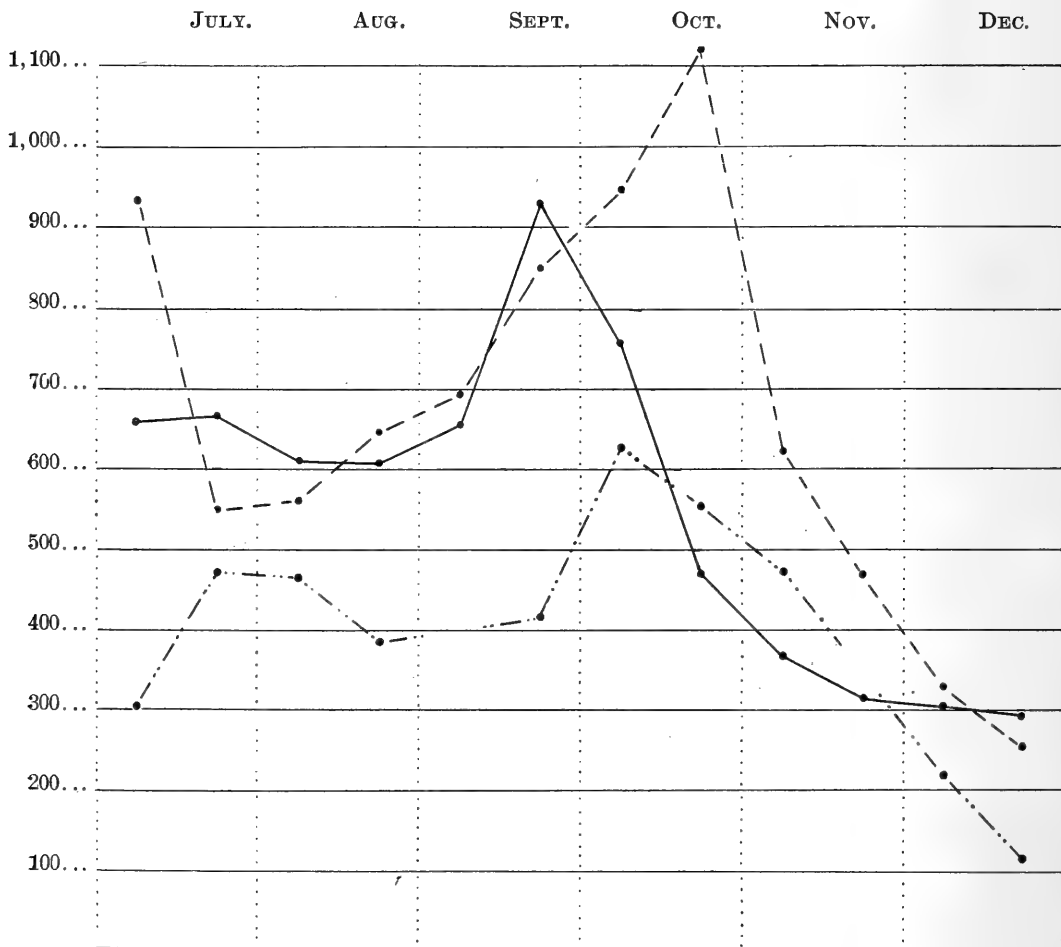


FIG. 10.—Total crustaceans, July-Dec., after deducting *Chydorus*. Scale, 1 vertical space = 100,000 crustacea per sq. meter. See p. 312.

1894..... - - - - -
 1895..... ————
 1896..... - · - - -

ing the same months, those individuals of *Daphnia retrocurva* disappear, which have survived the reproductive period. *Diaptomus* begins its decline in September or early October, and seems to make no special provision for winter forms. *Cyclops* continues its reproductive activity through 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°. Larval Copepods are present in great numbers at all seasons, but their development into later stages is checked in winter. *Chydorus* seems to have the same habit as *Cyclops*; but, for causes as yet unknown, it almost disappeared in the winters of 1894-5, 1896-7, although abundant in the preceding autumns, and present in considerable numbers in the winter of 1895-6. *Daphnia pulicaria* had a marked reproductive period in early December, and continued reproduction at a slower rate throughout the winter. *Diaphanosoma* disappears in October, and *Leptodora* in late November or early December.

TABLE IV.—Average number of crustacea for each two-week period and their sum, stated in thousands and tenths per sq. meter of surface.

	Diap- tomus.	Cy- clops.	D. puli- caria.	D. hya- lina.	D. retro- curva.	Chy- dorus.	Diap- hano- soma.	Total.
1894.								
July 1-15	242.2	39.8	6.4	19.8	a	a	a	306.2
July 16-31	298.9	151.0	8.3	13.3	a	a	0.8	472.3
August 1-15.....	218.7	161.0	1.1	16.6	a	a	6.3	401.1
August 16-31.....	87.4	200.3	0.8	60.7	a	15.0	18.0	382.2
September 1-15.....								
September 16-30.....	54.6	190.1	a	148.4	a	278.9	19.6	691.6
October 1-15.....	67.6	347.1	a	207.6	a	193.3	5.2	820.8
October 16-31.....	38.3	261.3	a	252.5	a	202.0	3.0	757.1
November 1-15.....	44.0	246.4	a	183.1	a	97.9	a	571.4
November 16-30.....								
December 1-15.....	23.9	75.0	a	121.5	a	9.5	a	219.9
December 16-31.....	(16.7)	(44.5)	a	(49.0)	a	(1.65)	a	(111.9)
1895.								
January 1-15	17.5	21.5	a	40.8	a	1.3	a	81.1
January 1-15	(15.9)	(40.0)	a	(55.9)	a	(2.0)	a	(111.8)
February 1-14	(44.5)	(80.8)	a	(75.3)	a	a	a	(200.6)

TABLE IV.—Continued.

	Diap- tomus.	Cy- clops.	D. puli- caria.	D. hya- lina.	D. retro- curva.	Chy- dorus.	Diap- hano- soma.	Total.
1895.								
February 15-28.....	28.0	73.1	a	65.8	a	a	a	166.9
March 1-15	28.3	55.7	a	34.7	a	a	a	118.7
March 16-31	34.7	66.2	a	63.6	a	a	a	164.5
April 1-15.....	14.0	53.9	a	26.4	a	a	a	94.3
April 16-30.....	20.6	242.5	a	16.3	a	scat.	a	229.4
May 1-15.....	34.4	864.9	a	28.9	a	12.1	a	940.3
May 16-31.....	207.9	944.4	a	250.7	a	16.5	a	1419.5
June 1-15	285.0	616.9	a	319.2	a	36.7	a	1256.6
June 16-30	190.6	262.6	a	135.6	Scat.	21.9	a	610.7
July 1-15	187.4	323.6	Scat.	139.9	9.7	156.8	Scat.	817.6
July 16-31	217.8	131.4	11.6	275.3	31.5	163.4	6.9	837.9
August 1-15.....	110.5	107.6	19.9	273.0	68.2	78.6	31.5	689.1
August 16-31.....	101.3	129.6	38.1	252.8	50.1	18.7	32.2	622.8
September 1-15.....	224.6	142.0	33.8	202.8	23.8	15.6	27.1	669.7
September 16-30.....	331.5	226.0	98.2	201.6	53.6	Scat.	17.2	923.1
October 1-15.....	148.4	327.5	26.9	180.5	72.5	8.6	3.4	767.8
October 16-31.....	79.7	219.7	23.5	76.6	70.9	8.1	a	478.5
November 1-15	55.8	144.7	49.6	56.2	59.3	25.9	a	391.5
November 16-30.....	46.0	135.4	53.3	48.2	24.2	19.7	a	331.8
December 1-15.....	33.6	90.2	141.1	35.0	5.0	15.9	a	320.8
December 16-31.....	58.0	89.1	99.8	44.6	0.7	20.9	a	313.1
1896.								
January 1-15.....	48.6	111.0	88.2	36.2	a	10.1	a	294.1
January 16-31.....	23.3	151.0	24.8	17.3	a	19.5	a	240.9
February 1-14.....	38.9	91.6	64.1	19.6	a	4.8	a	219.0
February 15-29.....	35.0	82.0	43.9	27.0	a	3.8	a	191.7
March 1-15.....
March 16-31.....	33.3	212.5	20.9	13.5	a	1.4	a	231.6
April 1-5.....	35.2	400.7	28.0	14.6	a	1.9	a	430.4
April 16-30.....	29.9	1,011.2	118.2	15.2	a	9.8	a	1,134.3
May 1-15.....	102.3	1853.4	284.9	124.6	a	28.0	a	2398.2
May 16-31.....	360.2	705.9	533.6	270.8	a	30.8	a	1901.3
June 1-15.....	343.5	189.5	168.6	55.6	a	87.6	a	844.8
June 16-30.....	386.2	358.7	73.2	211.1	a	230.8	a	1,265.0
July 1-15.....	202.9	371.0	39.3	319.0	a	332.0	a	1,314.2
July 16-31.....	152.1	317.5	11.8	65.5	2.5	245.1	Scat.	776.5

TABLE IV.—Continued.

	Diap- tomus.	Cy- clops.	D. puli- caria.	D. hya- lina.	D. retro- curva.	Chy- dorus.	Diap- hano- soma.	Total.
1896.								
August 1-15.....	91.9	326.8	3.7	95.2	27.6	406.5	8.9	960.4
August 16-31.....	167.0	209.0	5.9	60.9	57.1	426.0	147.4	1073.3
September 1-15.....	125.9	157.1	23.5	120.4	157.7	748.6	108.3	1440.9
September 16-30.....	163.4	228.6	3.4	192.5	228.6	263.0	32.9	1112.4
October 1-15.....	52.8	364.8	0.4	228.0	199.3	423.7	0.4	1368.4
October 16-31.....	48.8	469.5	a	511.5	92.7	191.9	a	1314.8
November 1-15.....	29.8	267.7	Scat...	314.6	9.9	62.7	a	684.8
November 16-30.....	23.5	173.9	Scat...	266.0	a	69.3	a	537.7
December 1-15.....	29.3	115.5	Scat...	182.8	a	38.2	a	365.8
December 16-31.....	24.7	93.1	Scat...	138.9	a	28.1	a	284.8

In this table maxima are indicated by bold faced type and minima by italics. a, means absent; scat., scattering individuals not enough to count. Parentheses indicate that observations were made on a single date in the two week period; —, indicates no observations.

Although the general course of the development of limnetic crustacea is so nearly the same in successive years, yet the composition of the crustacean population may differ very widely. This will readily be seen from the tables, and still more easily by the diagrams which show the numbers of the individual species of crustacea in the different years. A single illustration is given in Figs. 11, 12, and 13. These diagrams represent the average number of the crustacea in the latter half of September, 1894, 1895, and 1896. The area of the circles is proportional to the total number of crustacea, and the size of the several sectors is proportional to the number of the individual species. It will be seen that while the total numbers are not very widely different, there is a great divergence between the individual species. *Diaptomus*, for example, is by far the most numerous in 1895, while in 1894 it is the next to the smallest. In 1894, on the other hand, *Chydorus* is by far the largest; while in 1895 it is not represented at all. *D. retrocurva* is one

of the most important species in 1896, and had a fair development in 1895, while in 1894 it was wholly absent. No reason can be given in most cases for these variations in individual species; but where a cause can be assigned, the subject is discussed in the section which deals with the single species in detail.

Diagrams 8 and 9 show on single charts the numerical relations of the most important limnetic crustacea during the seasons of 1895 and 1896. Several facts become very plain from these diagrams. First, the development of *Cyclops* precedes that of *Daphnia* and *Diaptomus* by nearly a month, and precedes that of *D. pulicaria* by something more than two weeks. This relation held in both years, although the development of all the crustacea was some two weeks earlier in 1896 than in 1895. Second, in both years *Daphnia hyalina* and *Diaptomus* began their development together in the spring and rose together to the spring maximum. This coincidence was probably due to the rapid warming of the lake in both seasons. Figs. 1 and 2 show that the temperature of the water rose with much the same rapidity in the two years. *Diaptomus* requires a higher temperature for its development than does *Daphnia*, as is shown by the fact that it declines steadily after the lake falls below a temperature of 20° , while *Daphnia* has its great autumnal period of reproduction in the month of October when the temperature is below 15° . In the spring of 1897 the warming of the lake was slower than in either of the two years covered by my study, and the development of *Diaptomus* lagged decidedly behind that of *Daphnia*. I am not able, however, to give the exact numerical relations.

Diagram 9 shows also that *Daphnia pulicaria* began its course of development about two weeks in advance of *Daphnia hyalina*. Another fact is disclosed by Figs. 8 and 9, namely, that in each summer some one species of limnetic crustacean appears to take the lead, and decidedly dominates the other forms. In 1894, as shown by Fig. 7, this species was *Diaptomus*. In 1895, as shown by Fig. 8, *Daphnia hyalina* maintained its numbers full through July and August, gradually declining through the autumn, and being nearly twice as numerous as

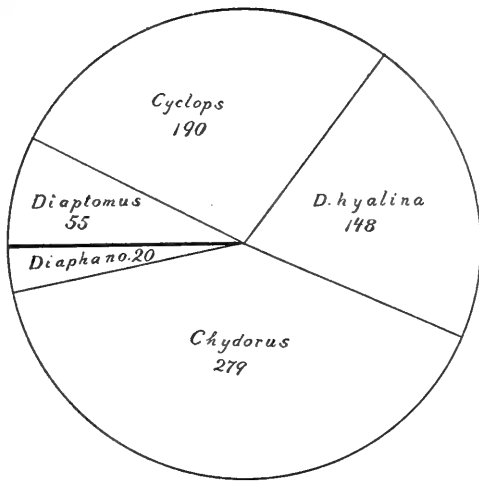


FIG. 11.—Crustacea, Sept. 16-30, 1894.

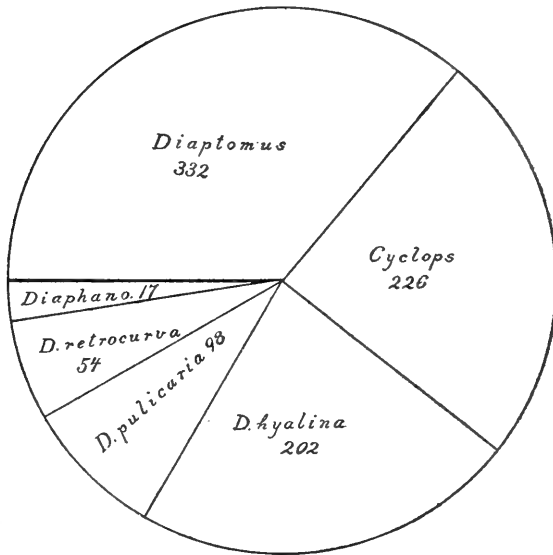


FIG. 12.—Crustacea, Sept. 16-30, 1895.

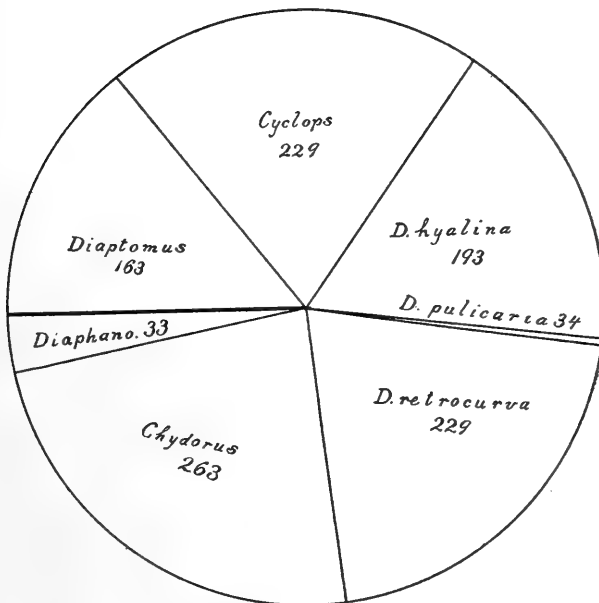


FIG. 13—Crustacea, Sept. 16-30, 1896.
See Table IV and p. 315.



the other two leading genera. In 1896 *Cyclops* held a similar place, recovering rapidly from its early summer depression and maintaining its numbers full throughout July and the early part of August.

The diagrams show further how all the species of crustacea increase in September, and that the rise persists to different dates in the later autumn. In 1895 *Diaptomus* showed a maximum in late September, and that of *Cyclops* came in the first half of October. In 1896 *Daphnia hyalina* and *D. retrocurva* rose together from the latter part of August to the middle of October, when the former species had a period of enormous reproduction, while *D. retrocurva*, which had produced its ephippial eggs, rapidly declined in number. The increase of *Cyclops* in this year also continued until late October. The diagrams show further how all species rapidly decline in number in November, and then more slowly during December, reaching their permanent winter condition in December, or at latest about the first of January.

The feature of the annual distribution of the crustacea which surprised me most in the progress of my work is the great difference between the numbers of the same species of crustacea present in successive years. I do not refer so much to the larger or smaller numbers of forms like *Cyclops*, for whose variations causes can be assigned, at least in part, but rather to such facts as those shown by *Daphnia retrocurva* and by *Diaphanosoma*, which are either absent, or present in very small numbers in one season and appear in great numbers in another year. For such variations it is very difficult to assign even conjectural causes.

A similar fact has appeared in the succession of the algae. It is not true for lake Mendota that the forms of algae succeed one another in a definite order in successive seasons, so that one can be sure of finding certain forms at certain times of year, as would be the case with plants of woodland or prairie. For example, in the winter of 1894-95 *Aphanizomenon* and *Clathrocystis* were the predominant algae after the early part of January. In the succeeding winter these plants were almost entirely absent and *Diatoma* was the predominant form. In the

winter of 1896-97 *Aphanizomenon* and *Diatoma* were present together; the latter form being more abundant at the opening of the winter and the former relatively increasing towards spring. *Asterionella* has been regularly present in all years as a small part of the summer plankton, but never has been predominant except during a short time in the spring of 1897. *Ceratium* has been a leading alga in the summers of 1895 and 1896, but in 1894 and 1897 there was no *Ceratium* period. *Lyngbya* predominated in July, 1895, but scattered filaments only were present during the succeeding two seasons, while in August and September, 1897, it was again present in considerable numbers, though nowhere near as great as in 1894. The summer of 1895 was definitely a diatom season, as was also that of 1897, very few of the Schizophyceae being present; while in 1896 the latter plants predominated, although a considerable number of diatoms were always present. In the autumn there has always been a diatom period, but the predominant forms have been *Diatoma*, *Fragillaria*, and *Melosira* in different seasons. The first alga to develop in the spring is one of those which has predominated during the winter, but the order of succession in the forms which follow is wholly uncertain, as the few illustrations given above sufficiently indicate.

LARGEST NUMBER OF CRUSTACEA PER CUBIC METER.

The following list shows the largest number of crustacea found per cubic meter. It is computed on the assumption that the animals are equally distributed through the three meter space covered by each haul of the net and gives the average per cubic meter for the distance of three meters. In reality the maximum at the stratum of greatest abundance would be greater than the table shows. Probably 600,000 would not be too high as the maximum for the total number in a cubic meter. The numbers are given as thousands per cubic meter. All, except *D. pulicaria* are from the upper, or 0-3 meter level.

Table V.

<i>Diaptomus.</i>	<i>Cyclops.</i>	<i>D. hyalina.</i>
June 17, 1894 88	October 8, 1894..... 56	July 24, 1895 101
June 12, 1895 84	May 18, 1895..... 180	Aug. 21, 1895 102
September 16, 1895..... 98	May 8, 1896..... 290	June 29, 1896 145
June 5, 1896 120	July 7, 1896 170
June 10, 1896 157	Oct. 26, 1896..... 122

<i>D. pulicaria.</i>	<i>Chydorus.</i>	<i>Total crustacea.</i>
Aug. 22, 1895..41, 9-12 meters	Sept. 22, 1894..... 71	May 9, 1896 347
Sept. 22, 1895..41, 15-18 meters	July 12, 1895..... 45	May 18, 1896 392
Dec. 23. 1895..73, 0- 3 meters	June 22, 1896..... 96	June 19, 1896..... 415
May 18, 1896..78, 0- 3 meters	July 7, 1896..... 131	June 22, 1896..... 337
.....	Aug. 6, 1896..... 111	July 7, 1896 426

It thus appears that where most thickly massed, the crustacea number nearly one to 2 ccm. of water.

Diaptomus Oregonensis Lillj.

Figure 14. Table D, Appendix.

The numbers of *Diaptomus* have varied from season to season less than those of any other species of the limnetic crustacea and they are also the least variable in daily numbers. Possibly the greatly developed locomotor organs of the animal aid in securing uniformity of distribution and also enable it to obtain so much food in times of scarcity, that its numbers remain constant when others decline.

Diaptomus does not reproduce during the winter and its numbers show little variation during that time, as the following table will show.

TABLE VI.—*Diaptomus*. Average number expressed in thousands per square meter of surface.

	1894-5.	1895-6.	1896.
October 1-15	67.6	148.4	52.8
October 16-31	38.3	79.7	48.8
November 1-15.....	44.0	55.8	29.8
November 16-30.....		46.0	28.5
December 1-15.....	23.9	33.6	29.3
December 16-31.....	(16.7)	58.0	24.7
January 1-15.....	17.5	48.6
January 16-31.....	(15.9)	28.3
February 1-15.....	(44.5)	38.9
February 16-31.....	23.0	35.0
March 1-15.....	28.3
March 16-31.....	34.7	33.3
April 1-15.....	14.0	35.2
April 16-30.....	20.6	29.9
May 1-15.....	34.4	102.3
May 16-31.....	207.9	360.2

Numbers enclosed in a parenthesis rest on observations made on a single day during the half-month.

These figures show that *Diaptomus* begins to decline toward its winter condition early in the autumn. There is no marked reproductive period in the fall which supplies the individuals which are to live over winter, but the numbers steadily and rather rapidly decline after the time when the lake has decidedly cooled from its summer temperature. The table also shows that the mortality must be very small in winter. In spite of the fact that there is no reproduction, the numbers show very little decline after the winter conditions are fairly established, and only a slow decrease in the late autumn. Indeed from the middle of October until the first or middle of May, the semi-monthly averages show no more variation than might easily appear in two catches made on the same day at the same place. This persistence of the numbers of the species must be attributed to the absence of competition and of enemies during this season. The food supply is ample for the winter stock of crustacea and

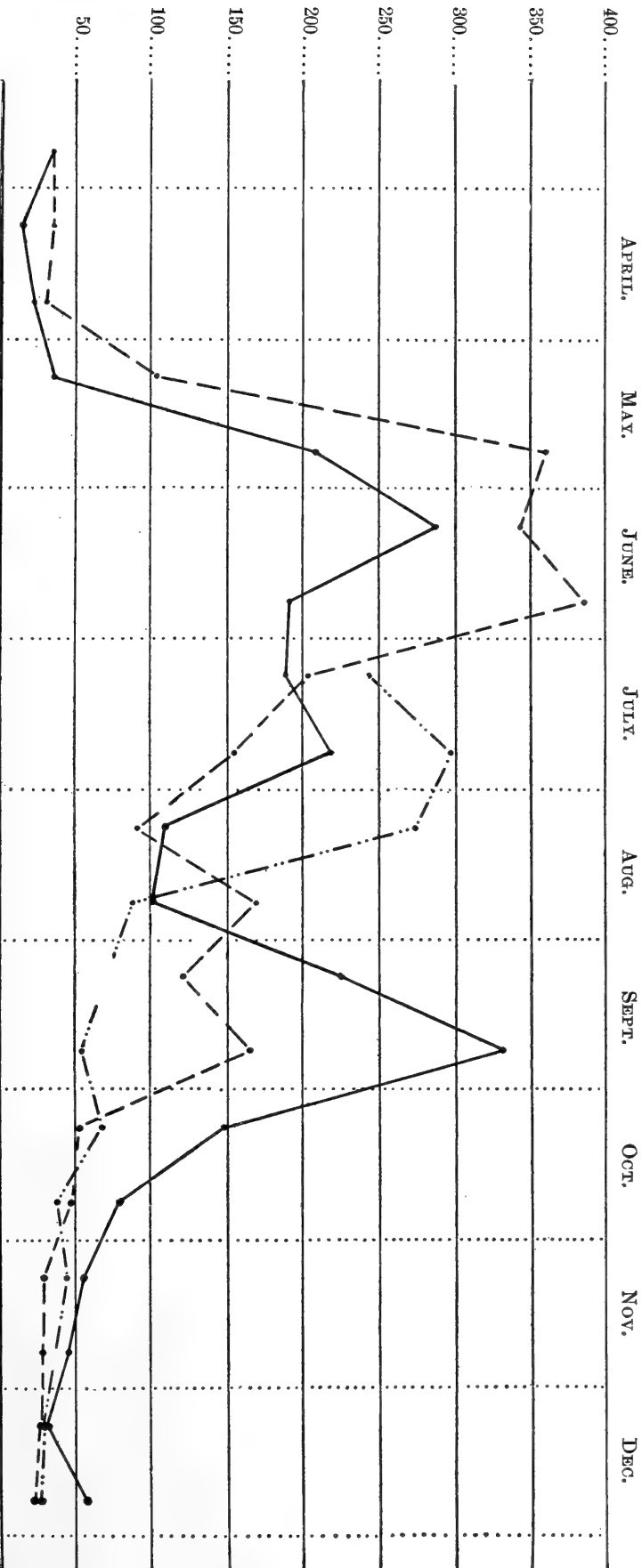
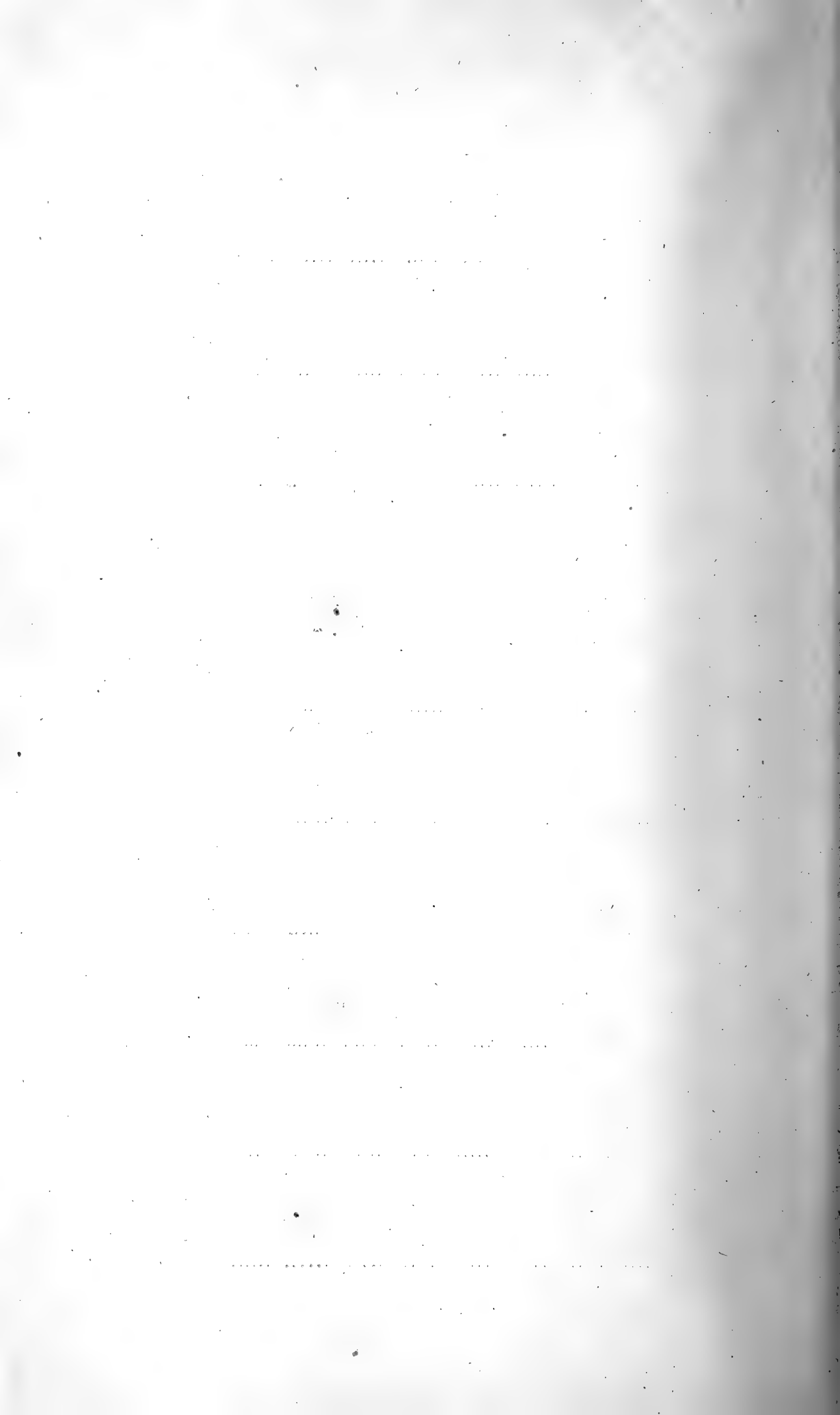


Fig. 14.—Diaptomus. Annual distribution, 1894, 1895, 1896. Scale, 1 vertical space = 50,000 crustacea per sq. m. See p. 319.

1895.....●——●——
1896.....●——●——●——●——



the reproduction of the crustacea in winter is slower than that of the algae. It is not impossible that the slight decline in numbers noticeable in 1895-6 may be attributable to the multiplication of *Cyclops* in that winter. The decline in *Diaptomus* is too small to allow of certainty in the inference, but the adult *Cyclops* fell off rapidly in March of that year as they did not in the preceding winter when little reproduction took place. Food also became much more scanty in the spring of 1896 than in the preceding year. The amount of food material in the spring of 1895 was estimated as at least four times as great relatively to the number of crustacea present.

The chief enemies of the crustacea are the larvae of insects and the young fish, both of which are absent or few during the winter. *Leptodora* also, though living chiefly on *Cyclops* and *Daphnia*, must devour some *Diaptomi* during the summer; while it is wholly absent in winter. At this season the perch, which also feed on the small crustacea, are at the bottom and apparently do not feed at all. There seem therefore to be no enemies of the crustacea during the winter and their numbers are correspondingly constant.

Throughout this season also *Diaptomus* is fat — fatter than in summer, as the drain on tissue for reproduction is absent.

In April after the ice breaks up the crustacea are wont to decline in numbers. This is especially true for those species whose reproductive period comes somewhat late in the spring, and in which only the individuals which have lived all winter are present in the spring. These find the conditions of the open water of the early spring harder than those under the ice, especially as they are exposed to the competition of the increasing swarms of *Cyclops* and sometimes of *D. pulicaria*. The smallest catches of *Diaptomus* which are met during the year, are obtained in the latter part of April when the number of *Cyclops* has risen greatly — more rapidly than the food has increased.

In May there comes a great increase in the number of *Diaptomus*. It shows itself first by the presence of a great number of immature animals in the upper strata of the water. In both years the appearance of these new members of the species was very sudden, as will be seen from the following table.

TABLE VII.—*Showing the actual number of Diaptomus caught during May.*

1895.		1896.	
May 4.....	270	May 2.....	730
May 7.....	410	May 4.....	660
May 12.....	710	May 6.....	980
May 16.....	780	May 8.....	600
May 18.....	2,200	May 9.....	560
May 20.....	1,650	May 11.....	1,945
May 22.....	3,820	May 15.....	6,110
		May 18.....	10,250
		May 21.....	3,690

It will be seen that these catches divide very sharply into two sets, the division coming between the 16th and 18th of May in 1895 and between the 9th and 11th in 1896. Catches earlier than those given in the table show the same general character as those given, as also do those taken later. There is no earlier catch which is larger than 1000, nor one later in May smaller than 2,000 in 1895 or 3,500 in 1896.

There is no reason to think that the increase of numbers is due to small, local aggregations of the species. The increase persists without intermission for long periods of time during all conditions of wind and weather. This alone shows that the large numbers must occur over great areas of the lake. On May 15, 1896, observations were made at different points, and the numbers were found practically constant at a distance of 2.5 kilometers in various directions from the regular place of collecting.

It will be seen that the spring increase came just a week earlier in 1896 than in 1895—on May 11th and May 18th, respectively. This acceleration of development, which was shared by all of the crustacea, was chiefly due to the higher temperature of the water in the latter year.

In 1895 the ice went out on April 8th, in 1896 on April 2d. In each year cold and rainy weather followed the departure of the ice and at the middle of the month the temperature of the water was almost the same in both years.

April 15.	1895.	1896.
Surface.....	4.5°	4.0°
Bottom.....	4.2	3.9

Later the temperature showed a nearly parallel rise at the surface, but a marked acceleration at greater depths for 1896, the following table shows:

	SURFACE.		BOTTOM.	
	1895.	1896.	1895.	1896.
April 18.....	6.0°	7.2°	5.0°	6.1°
April 24.....	8.0	8.0	5.8	7.4
April 30.....	11.5	9.6	6.9	8.5
May 7.....	10.8	16.4	6.3	9.9
May 18.....	15.5	15.2	11.2	13.4

It thus appears that the average temperature of the water was decidedly higher in 1896 than in 1895, and to this fact I attribute the earlier appearance of the spring swarms of crustacea. There was nothing apparent in the increase of the algae to make any difference.

When the young *Diaptomus* appear the number rapidly rises to a maximum which is maintained for some weeks, as the table shows:

TABLE VIII.—Average number of *Diaptomus* during late spring and summer stated in thousands per square meter of surface.

	1894.	1895.	1896.
May 1-15.....		34.4	102.3
May 16-31.....		207.9	360.2
June 1-15.....		285.0	343.5
June 16-30.....		190.6	386.2
July 1-15.....	242.2	187.4	202.9
July 16-31.....	298.9	217.8	152.1
August 1-15.....	273.3	110.5	91.9
August 16-31.....	87.4	101.3	167.0

It will be seen that the numbers found in all three years are closely parallel. Indeed the July averages for the three years

differ no more widely than catches might differ though made on the same day and close together.

In each of the two years where the conditions of the preceding winter were known, the summer maximum was close to ten times the winter average. In all three years there was a marked decline of numbers to a late summer minimum in August; at which time the average number is $\frac{1}{3}$ to $\frac{1}{4}$ of the maximum. In 1895 there was a very marked drop in numbers about the first of July; while in 1896 the maximum number was maintained throughout June and early July and then there was a steady decline for a month or more. In 1894 observations began on the first of July. *Diaptomus* was practically stationary during the month and rapidly declined after the early part of August.

These variations in number in different years are at present without complete explanation. Yet the most singular fact—the notable drop in numbers about July first, 1895—certainly extended to the species all over the lake. Observations were made between the first and tenth of July in that year even in the remoter parts of the lake, and with substantially uniform results. Whatever the cause it was probably the same as produced a similar fall in the numbers of *Daphnia hyalina* at the same time.

The autumnal condition of *Diaptomus* varies with the temperature of the early fall. In 1894 and 1896 there was substantially no recovery from the August minimum. 1896, indeed, showed minor variations of number but on the whole the number did not increase. In 1895 on the other hand there was a very marked rise of numbers in September, culminating in the third week of that month. We shall hardly be wrong in attributing this additional brood of *Diaptomus* in 1895 to the higher temperature of the water in that year. There was very little decline of temperature until the very last days of the month as the following observations will show:

1895.	Sept. 2, 6 a. m.	Sept. 26, 6 a. m.	Sept. 30, 6 a. m.
0 meters.....	21.9°	20.0°	16.3°
10 meters.....	20.9	20.0	16.5
18 meters.....	13.9	17.7	16.5

Thus the decline of temperature for the month occurred in the last three days. In 1896 the temperatures at the opening and close of the month were much the same as in the preceding year, but the decline was pretty equably distributed.

1896.	Sept 1, 9:30 a. m.	Sept. 17, 4 p. m.	Sept. 28, Noon.
0 meters.....	21.2°	18.4°	16.0°
10 meters.....	20.2	18.2	15.75
18 meters.....	15.3	16.1	15.6

It therefore appears that the long continued warmth of 1895 gave *Diaptomus* a chance for an additional brood which did not appear in 1894 or 1896. Food, of course, is always present in superabundance during September.

TABLE IX.—*Diaptomus.* The autumnal numbers stated in thousands per square meter of surface.

	1894.	1895.	1896.
September 1-15.....		224.6	125.9
September 16-30.....	54.6	331.5	163.4
October 1-15.....	67.5	148.4	52.8
October 16-31.....	38.3	79.7	48.8
November 1-15.....	44.0	55.8	29.8
November 16-30.....		46.0	28.5
December 1-15.....	23.9	33.6	29.3
December 16-31.....	(16.7)	58.0	24.7

The winter numbers are seen to be reached early in the season — at latest in the first part of November. The winter numbers are also seen to be not very different in the three years in question and are strikingly independent of the condition earlier in the season. The number in September, 1895, was nearly six times as great as in the preceding year, while in December the difference was less than 50 per cent. in favor of 1895.

The maximum catches of *Diaptomus* were 460,000 June 12, 1895; 651,000 May 18; and 741,000 June 10, 1896. The females carry 20-30 eggs in a single sac, during the spring. In summer the number declines to 9-15.

Apstein ('96, p. 179), finds that *D. graciloides* has its maximum in lake Ploen in winter and in the Dobersdorfer See in summer. Its relations in the latter lake agree very well with those of the same genus in lake Mendota. He concludes from the striking difference in the two lakes that temperature has no effect on the species. Marsh, who finds that *D. minutus* has its maximum in Green lake in September and October ('97, p. 192), also thinks that temperature affects the genus very little. I am unable to agree with this conclusion, so far as the form studied by me is concerned. It is the first of the perennial crustacea to slacken its reproductive activity in the autumn, and this occurs when food is at its maximum. I can attribute this check only to the fall in temperature. Indeed, my observations show that the reproductive activity of *D. Oregonensis* is more promptly checked by the decline of temperature than is that of any other of the perennial species.

Cyclops.

Figures 15, 21. — Table E, Appendix.

There are two species of *Cyclops* which are at times conspicuous in the plankton of lake Mendota, *C. brevispinosus* Herrick and *C. Leuckartii* Sars. *C. pulchellus* Koch was rarely seen. *C. brevispinosus* is by far the more numerous and is practically the only species except in summer. From October to May only scattered individuals of any other species are met, but during summer *brevispinosus* declines and *Leuckartii* may be as numerous as it or even more so. The numerical relation has not been determined because of the great labor involved in discriminating the species, especially in the immature examples which always constitute by far the greater part of the catch.

Cyclops brevispinosus is the most abundant species of limnetic crustacea at almost all times, and at its maximum is far more numerous than any other species ever becomes. It is the only abundant Copepod which reproduces under the ice; *Daphnia pulicaria* among the Cladocera has the same habit.

The winter numbers are as follows, stated in thousands per square meter of surface:

TABLE X.—Winter number of *Cyclops*, stated in thousands per sq. m.

	1894-95.	1895-96.	1896.
November 1-15.....	246.4	144.7	267.7
November 16-30.....		135.4	173.9
December 1-15.....	75.0	90.2	115.5
December 16-31.....	(44.5)	89.1	93.1
January 1-15.....	21.5	111.0
January 16-31.....	(40.0)	151.0
February 1-14.....	(80.8)	91.6
February 15-28.....	73.1	82.0
March 1-15.....	55.7
March 16-31.....	66.2	old. yg. 51.2 161.3
April 1-15.....	53.9	400.7
April 16-30.....	242.5	1011.2

It will be seen that the winter numbers are more variable during the season than are those of *Diaptomus*. This results from two causes; first, the fact that reproduction continues longer in the autumn than in *Diaptomus* and therefore the species reaches its winter minimum at a later date; second, reproduction may begin again during the winter and cause a considerable increase before the opening of the lake in the spring. A third fact ought to be added. During the winter there are often caught large numbers of *Cyclops* in the deeper water, where there are plainly aggregations of the species. Such catches of course raise the average for the two-week period in which they happen to come.

The spring rise comes on immediately after the opening of the lake or, as already said, begins while the lake is still covered with ice. The increase is rapid but by no means so sudden as is the case in *Diaptomus*. This may be seen from the following table of catches, in which by no means all the observations of the periods are given.

TABLE XI.—*Cyclops.* Average number per square meter, stated in thousands per sq. m. of surface.

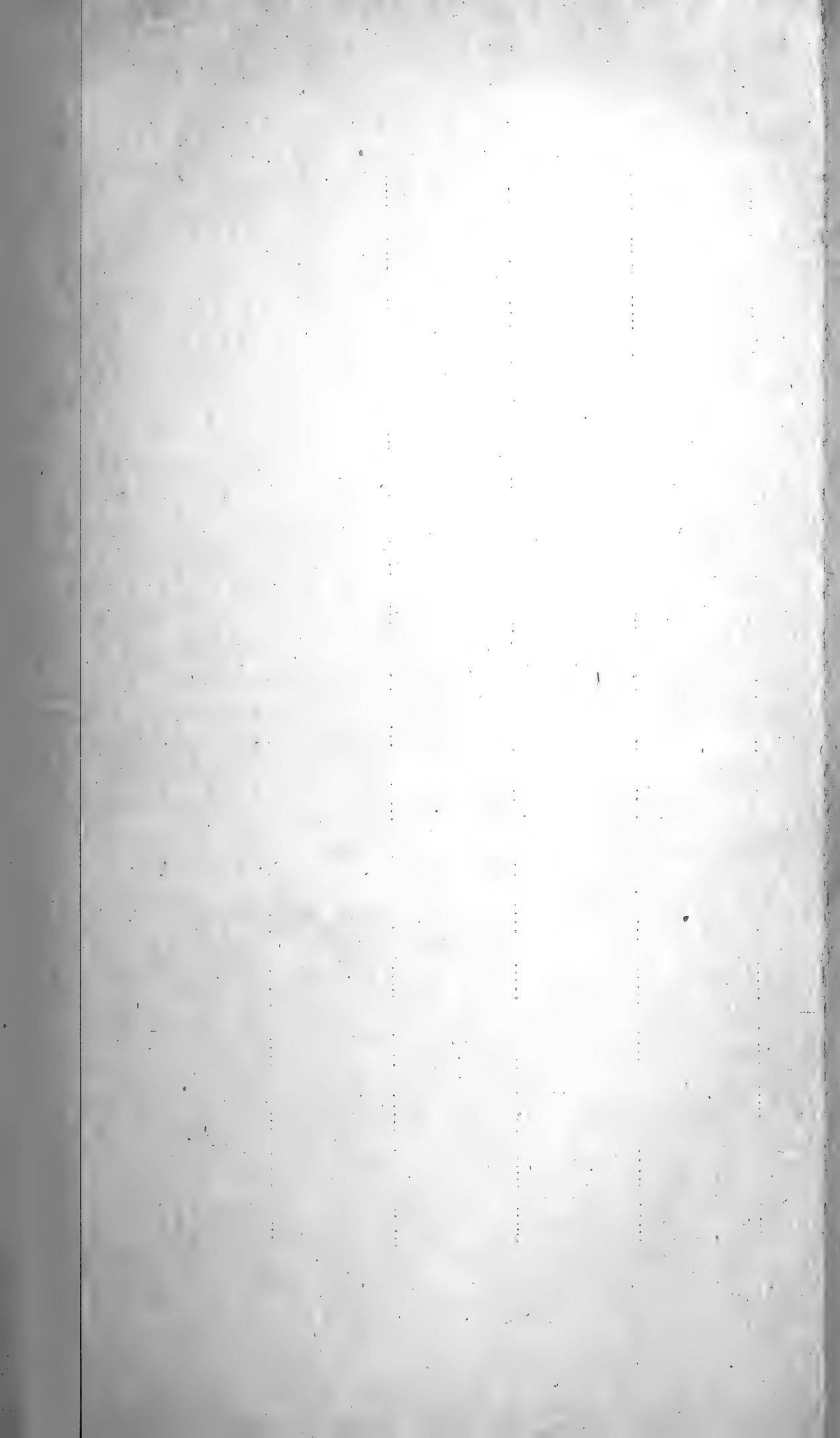
1895.		1896.	
April 12.....	43.8	April 4.....	297.0
April 18.....	90.3	April 11.....	358.7
April 25.....	112.8	April 14.....	863.2
April 30.....	575.8	April 20.....	770.8
May 3.....	979.8	April 30.....	984.5
May 12.....	763.2	May 2.....	1,710.2
May 18.....	1,234.2	May 9.....	2,359.5
May 30.....	1,030.4	May 18.....	1,294.9
June 6.....	636.0	May 26.....	386.6
June 14.....	293.1	June 1.....	176.1
		June 6.....	168.5
		June 15.....	139.2

In each column the numbers begin with the first catch after the disappearance of the ice. It will be seen that on April 12, 1895, there was no evidence of increase over the winter average and that none of the catches prior to that of April 30, are decidedly larger than those of the winter. In 1896, on the contrary the open season begins with numbers far larger than those of the winter and there is a steady and rapid increase from the very first.

TABLE XII.—*Cyclops.* Average for the spring and early summer stated in thousands per square meter of surface.

	1895.	1896.
April 1-15.....	53.9	400.7
April 16-30.....	242.5	1,011.2
May 1-15.....	864.9	1,858.4
May 16-31.....	944.4	705.9
June 1-15.....	616.6	189.5
June 16-30.....	262.6	358.7

The maximum came earlier in 1896 than in 1895. The greatest number were caught from May 18th to 30th in 1895, and from



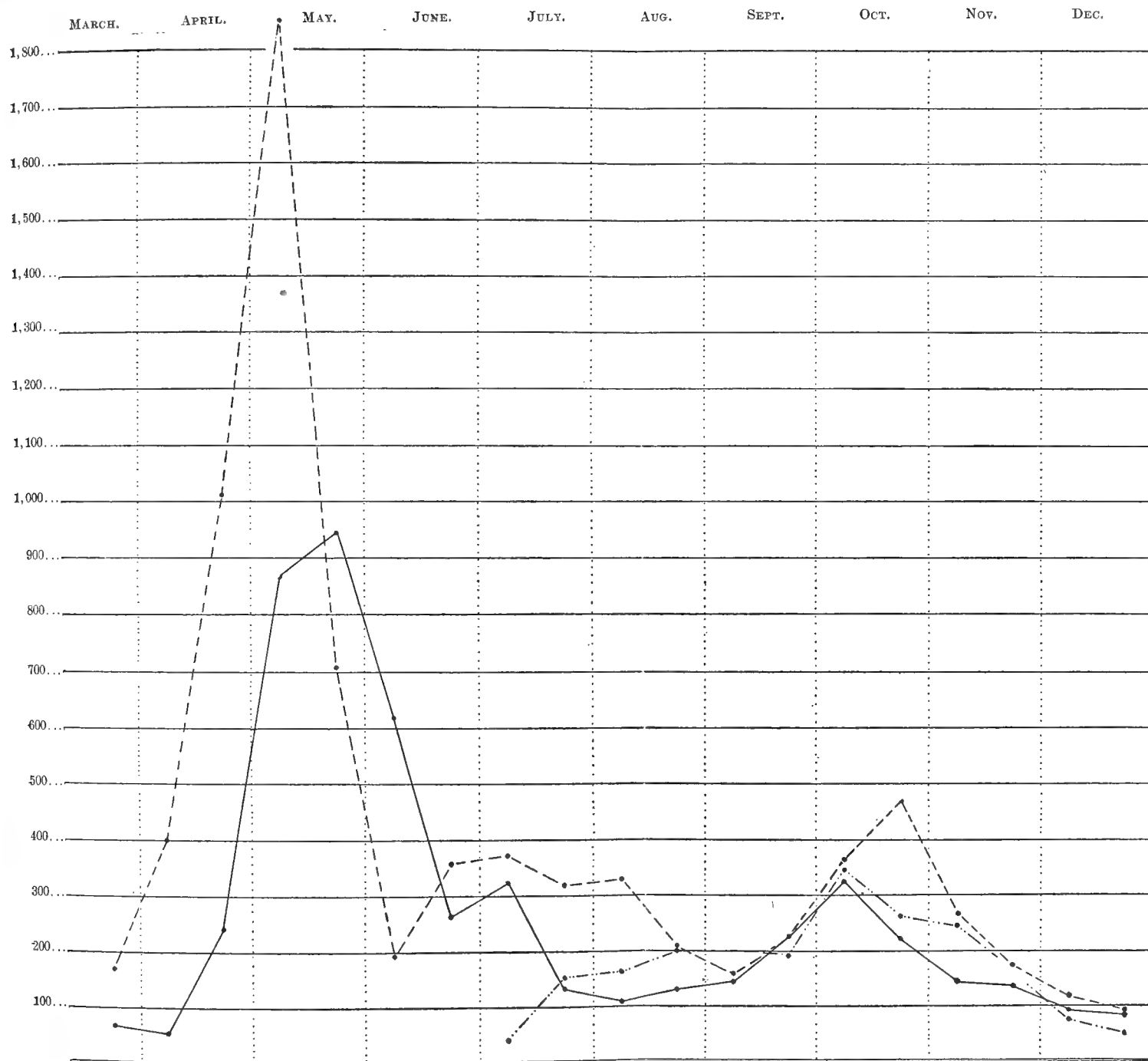


FIG. 15.—Cyclops. Annual distribution. Scale, 1 vertical space = 100,000 crustacea per sq. m. See p. 326.

1894.... ● - - - ● - - -
 1895.... ○ - - - ○ - - -
 1896.... ⊙ - - - ⊙ - - -



May 2d to 9th in 1896. The entire month may be included in the maximum in 1895, as all the catches made between May 3d and June 6th, 26 in number, were between 636,000 and 1,234,000 per sq. m. In 1896 the limits of the maximum period may be set at April 14th and May 20th, during which time the numbers ranged from 763,000 to 2,359,000 per sq. m. The observations were 20 in number. The maximum catch recorded was nearly one-third larger than any other, although there were 7 catches made, ranging from 1,300,000 to 1,700,000 per sq. m.

From these figures and from the averages, it is plain that the numbers were far greater in 1896 than in the former year. I attribute the difference to the earlier start which the species had in 1896. In that year reproduction began under the ice so that the numbers at the opening of the season were three or more times as great as in 1895. While the lake warmed somewhat more rapidly in 1896, the difference was chiefly marked by the higher temperature of the lower water, which would aid the development of the species during the first part of April.

The decline of *Cyclops* is seen from Table XI and diagram 15, to be as steady and rapid as its rise. In 1896 the numbers in the first half of June were smaller than in the latter part of March. In less than two weeks after the maximum the number had fallen to less than one-sixth of the maximum and a week later it was less than one-half of the smaller sum.

This decline is doubtless due to the scarcity of food, to the increasing temperature of the water and, to increasing competition. At no time during the spring rise are as many as five per cent. of the species provided with egg-sacs and almost none of the animals in the lower strata of the water become sexually mature. This fact indicates that the lake becomes so crowded with the early swarms of the species that the food is insufficient to allow their development to maturity. Not only so, but those individuals which are compelled to migrate into the deeper water find there little food and must perish in a short time. At the height of the *Cyclops* period there is very little alga visible in the catch.

The influence of temperature is shown by the fact that the maximum is reached when the temperature of the lake is about

15° and that no considerable rise comes later in the season until the lake has fallen to about the same temperature in the fall. Development, begun actively while the water is little above zero, is gradually checked as the water warms during the spring, yet the nauplii may be very abundant in summer.

A reaction follows the early summer minimum and there is a moderate increase in the numbers of *Cyclops*. This is due chiefly, if not wholly, to the introduction of *C. Leuckartii*. This species is very rare during the cooler parts of the year, though always seen occasionally, and at all times capable of reproduction. In the summer, however, it develops more rapidly and numbers of the species may considerably exceed those of *C. brevispinosus*. This was not true in 1894, especially in July. At that time the number of *Cyclops* was very low, lower indeed than in the winter following. The rise in August of that year was largely although not wholly due to *C. Leuckartii*, and was apparently maintained into September when *brevispinosus* again became abundant. In both the other years *Leuckartii* declined in August and *brevispinosus* did not increase so that there was visible a late summer minimum during the whole or part of that month. The small numbers of 1894 are probably due to the excessive development of *Lyngbya* in the early part of that summer, as is stated more fully on page 353.

TABLE XIII.—*Cyclops*. Average numbers for the last half of the years.

	1894.	1895.	1896.
July 1-15.....	39.8	323.6	371.0
July 16-31.....	151.0	131.4	317.5
August 1-15.....	161.0	107.6	326.8
August 16-31.....	200.3	129.6	209.0
September 1-15.....		142.0	157.1
September 16-30.....	190.1	226.0	228.6
October 1-15.....	347.1	327.5	364.8
October 16-31.....	261.3	219.7	469.5
November 1-15.....	246.4	144.7	267.7
November 16-30.....		135.4	173.9
December 1-15.....	75.0	90.2	115.5
December 16-31.....	(44.5)	89.1	93.1

The foregoing table gives the average numbers of summer and autumn for the three years, stated in thousands per square meter of surface.

The table shows an autumnal maximum in October, followed by a steady decline and a slow one as compared with that which follows the spring maximum. The fall increase is due wholly to *C. brevispinosus* and the maximum comes when the lake is at or below 15° C. The decline is occasioned partly by the gales of autumn causing the death of adults, and chiefly by the increasing slowness of development of the nauplii as the temperature of the water falls. The eggs are still produced and the nauplii hatched, but the young *Cyclops* are slower in coming forward and the deaths exceed the production of young. Food is present in excess of the demands of the crustacea and so forms no factor in the decline.

By the middle of December if not earlier the winter conditions are fairly established although the number of the species may continue slowly to decline until February.

A comparison of the charts showing the curve for *Cyclops* and that for the total crustacea brings out the fact that *Cyclops* is the dominant factor in determining the number of crustacea. All the peculiarities of the general curves are repeated in those for the genus. *Cyclops* is absolutely the most numerous species except in the summer, when it is sometimes surpassed by *Diaptomus* and *Chydorus* and less often by *Daphnia hyalina*. Two causes contribute to this relative disadvantage of *Cyclops* in summer. First, the species is unfavorably affected by the warmth of the water; second, it is unable to retire into the cooler and deeper water as it might do in lakes which are habitable below the thermocline. In such lakes it may well be found that *Cyclops* leads the number of crustacea throughout the year. A few observations indicate this to be true for Pine lake, but the facts are not well known as yet.

Zacharias ('96, p. 54) finds only a fall maximum for *C. oithonoides* in lake Ploen. There is a trace of a spring maximum but very feebly marked. Apstein ('96, p. 178), finds maxima in the Dobersdorfer See in May, September, or July and thinks that the maxima may come at any time in summer. He finds on this

species 5–6 or at most 9 eggs and considers the small number an adaptation to limnetic life. *C. brevispinosus* often carries 18 eggs in each sac without difficulty. He finds no eggs from October to February, while I find egg bearing females at all seasons. Marsh ('97, p. 205), gives the maximum for *C. fluviatilis* in Green lake in the autumn and gives no spring maximum. I think that the difference in our observations is a characteristic of the species rather than of the lakes examined.

Epischura lacustris Forbes.

This species found only occasionally in my collections. It is so large in the adult condition as to be readily distinguishable by the unaided eye and was counted in this way along with *Leptodora*. Young, if present, were doubtless counted as *Diaptomus*. No observations were made on this species in 1894. In 1895 it appeared on June 20th, two specimens being seen. It was not seen again until July, in which month it was found in 6 out of 18 observations, the number not exceeding 2 individuals in any one catch. In August they were seen 6 times out of 13 observations, the maximum being 4, and the total number being seen during the month being 12. In September the number was about the same, but in October the number was greater, averaging 6 in each of the 5 cases where they were seen, with a maximum of 9. In November they were present in every observation, 7 in number, up to the 20th, with an average of 6.5, and a maximum of 19. The species thus showed a decided tendency to a maximum in late autumn. In 1897 the species appeared on May 17th and in the latter part of that month averaged 4 in each catch. In the first half of June the average was 3, and maximum 7; in the last half the average was 4, and the maximum 7. In July the average was 2, and the maximum 7. Only a very few scattered individuals were seen in August, and none were found later.

It is evident that the records of the two years are not at all similar, and that the numbers of the species which were found are too small for profitable discussion.

Ergasilus depressus Sars.

This animal is about the same size as *Cyclops*, although readily distinguishable both by color and form. I am not sure of the correctness of the specific identification, although I can see no differences between my specimens and Sars' description. It is present at all seasons of the year, ordinarily in very small numbers. More than one individual is rarely found when one-tenth to one-twentieth of the catch is counted. This number is so small and the resulting probable error in computing averages so great that it has not been thought profitable to state the numbers in terms of a square meter of surface, and to include them in the total number of limnetic crustacea.

Ergasilus is present throughout the year, although it may often be missed for long periods from the collections. It was first noticed in July, 1895, although doubtless present before, and from 1 to 9 specimens were seen in each collection. The number increased during the latter part of August and in September, when from 10 to 13 specimens were found, indicating nearly 10,000 per sq. m. In the latter part of September the numbers rose to a maximum of 27-30 specimens, or nearly 27,000 per sq. m. In October only 1 to 5 were present, and the species was found occasionally during the winter and spring in single specimens. In July and August, 1896, it became more plentiful; about as is 1895. But no such large number was found in September as in the former year. The animal seems to prefer the stratum of water just above the thermocline, but is not confined to this layer.

Copepod Larvae — Nauplii.

The dredge with which my study was carried on until the middle of July, 1896, was provided with a bucket whose openings were closed by a wire mesh of 1-100 in. This, while retaining the crustacea and a great part of the nauplii, did not retain all of the latter, so that no study was given to these larval forms until work began with the silk net. The following table shows the average number of larvae from the middle of July to the end of December, and also the numbers found in

single observations made since that date. In all cases the larvae of all species of Copepoda were counted together; it being practically impossible to assign them to their proper forms. Unquestionably, however, the great majority of these animals belonged to *Cyclops brevispinosus*. All larvae beyond the nauplius stage were assigned to and counted with their proper genera.

TABLE XIV.—*Nauplii*. Average numbers, expressed in thousands per square meter.

1896.				
July 16-31.....	1113.8		October 16-31.....	712.5
August 1-15.....	529.7		November 1-15.....	477.8
August 16-31.....	685.9		November 16-30.....	350.8
September 1-15.....	310.9		December 1-15.....	613.7
September 16-30.....	408.8		December 16-31.....	606.6
October 1-15.....	200.4			

Maximum, July 18, 2,037,920.

1897.	Nauplii.	Cyclops.		Nauplii.	Cyclops.
January 11.....	1,550	118	April 17.....	204	390
January 21.....	1,234	76	April 28.....	418	619
February 17.....	513	70	May 4.....	357	1,121
March 3.....	722	93	May 10.....	1,007	921
March 29.....	714	87	May 15.....	616	774
April 8.....	726	154	May 21.....	257	1,767
April 14.....	798	560	June 6.....	2,470	1,169

It is difficult to correlate the numbers of the nauplii with those of the older and adult crustacea. While *Cyclops* remained numerous throughout the summer of 1896 there was no such rise of numbers in late July and August as would be expected from the great number of larvae which were present in the latter part of July. The number of nauplii found in the early and middle part of October is not as great as the increase in the number of the crustacea would have led us to expect. It is evident, however, that the decrease of the Copepoda in the late fall and during the winter is due rather to the failure of the nauplii to develop toward the adult form than to the absence of these

larvae, or to the failure of *Cyclops* to produce eggs. It will be seen that the nauplii were exceedingly numerous throughout the winter and into the spring, and during the month of May a certain relation can be traced between the numbers of nauplii present and those of immature *Cyclops*—the nauplii decreasing in number as the *Cyclops* increase. It is evident further that the death rate of these larvae during the winter must be very low, or that the losses are balanced by the production of young which develop to this stage, without going further until the warming of the water in the spring.

During the month from the middle of July to the middle of August numerous determinations were made, from which it appeared that the maximum and minimum numbers of the nauplii vary in about the same ratio as do those of the adult crustacea. In July, out of six observations the maximum was 3.8 times the minimum, and in August the maximum was 3.4 times the minimum. The largest number observed was 2,040,000 per sq. m. of surface on July 18th. A larger series of observations would undoubtedly have shown, in the spring of 1897, numbers equal to this.

Daphnia hyalina Leydig.

Figure 16.—Table F, Appendix.

The autumn numbers in both years show a decline to a minimum which extends throughout the winter and until the first or middle of May. In 1895 this minimum was established in November, but in 1894, not till late December or January. In 1895 there was no marked reproductive period in the autumn. This was apparently due to the continuation of summer conditions until near October 1, and the sudden change at that time. The final reproductive period of this species lies at the end of October or early in November. After the close of this period, the old females rapidly decrease in number, and almost, or wholly, disappear before the first of January. The young grow somewhat rapidly until they have reached about half the mature size, and after that, grow very little or none at all until the following spring. Reproduction is practically wholly absent during the winter, although it occasionally happens that a single female can be found in March, having eggs in the brood-case.

The following table gives the average number of *D. hyalina* from fall to spring.

TABLE XV.—*D. hyalina*. Averages from October to June expressed in thousands per square meter.

	1894.	1895.	1896.
October 16-31.....	252.5	76.6	511.5
November 1-15.....	183.1	56.2	314.6
November 15-30.....		43.2	266.0
December 1-15.....	121.5	35.0	182.8
December 16-31.....	(49.0)	44.6	133.9
January 1-15.....	40.8	36.2
January 16-31.....	(55.9)	17.3
February 1-14.....	(75.3)	19.6
February 15-28.....	65.8	27.0
March 1-15.....	34.7
March 16-31.....	63.6	13.5
April 1-15.....	26.4	14.6
April 16-30.....	16.3	15.2
May 1-15.....	28.9	124.6
May 16-31.....	250.7	270.8

Numbers enclosed in a parenthesis rest on observations made on a single day.

The females which have lived over winter produce at least three broods of young, and die in June, chiefly in the early part of the month. Those individuals which have lived over winter are readily distinguished from those hatched in the spring by the smaller size and different shape of the head. It is easy, therefore, to determine the average length of their life at about six to eight months, from early October to early June, as a maximum. It is not possible to get similar data for the summer form of this species, for the shape of the head-crest gradually alters in all individuals as the water cools in the autumn.

The swarms of young produced in October rapidly diminish in number at first, but an equilibrium is reached by the first of January, and thenceforward the decline through the winter is very slow, or imperceptible. The statements made regarding *Diaptomus* fully apply to this species also. During April and

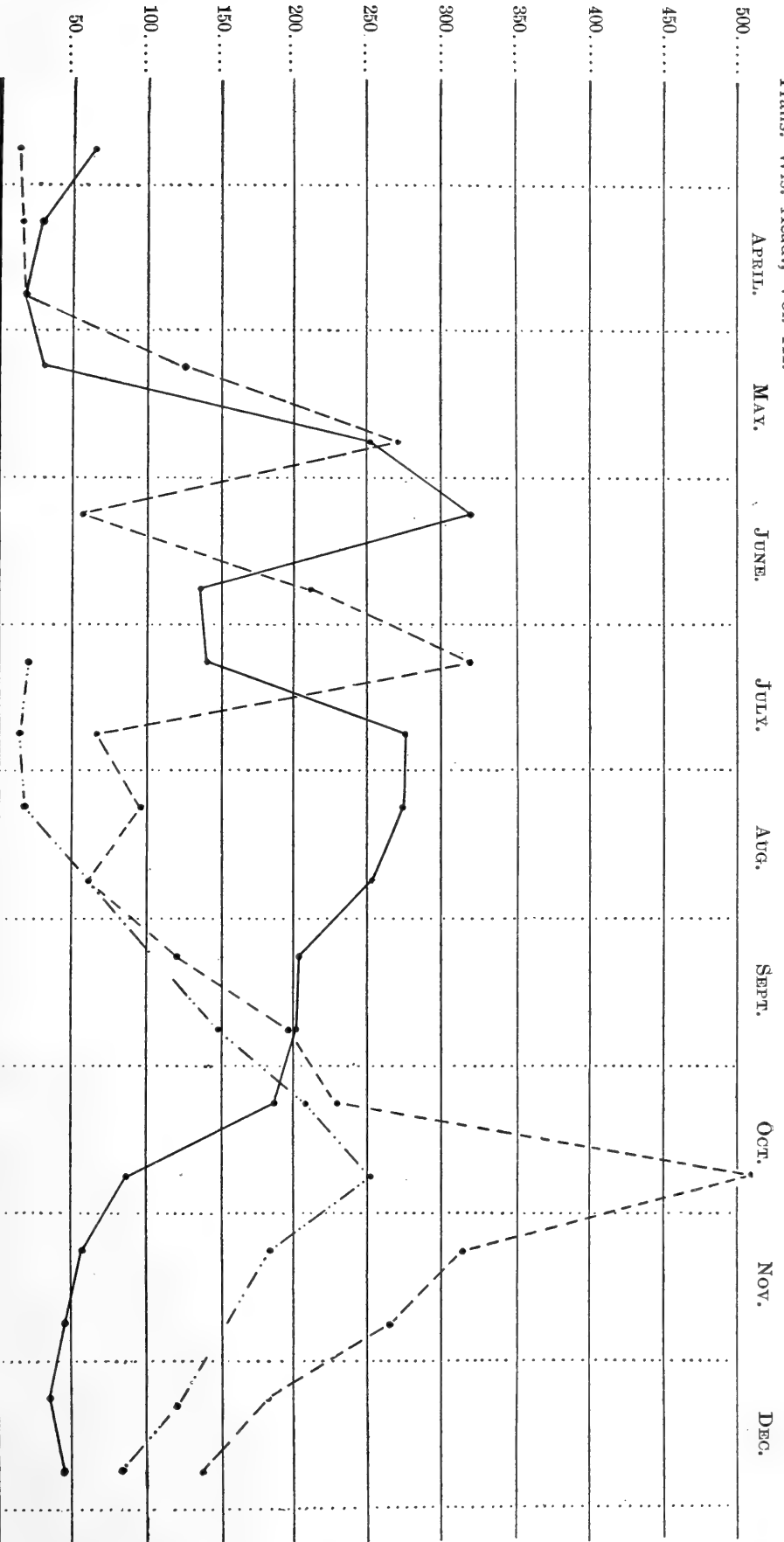


Fig. 16.—*D. hyalina*. Annual distribution. Scale, 1 vertical space = 50,000 crustacea per sq. meter. See p. 335.

1894.....●●●●●●●●●●●●●●●●

1895.....●●●●●●●●●●●●●●●●

1896.....●●●●●●●●●●●●●●●●



and the early part of May, the species declines on the whole, and the smallest catches of the year have been made at this time. The rise in number in the spring comes on very rapidly. The species apparently reproduces first in the warmer and shoaler waters at the edge of the lake, and the individuals thus produced are distributed over the surface of the lake by favorable winds. This supposition is necessary in order to account for the extraordinarily rapid increase in numbers which the species shows. The following table gives the actual number caught in 1895 and 1896 on the dates stated:

TABLE XVI.—*D. hyalina.* Actual number of specimens caught.

1895.		1896.	
April 25.....	144	April 22.....	380
April 30.....	510	April 27.....	120
May 7.....	442	April 30.....	140
May 12.....	1,000	May 2.....	1,360
May 16.....	380	May 4.....	1,140
May 18.....	3,060	May 8.....	1,600
May 20.....	1,210	May 11.....	1,620
May 22.....	4,820	May 15.....	5,660
May 27.....	4,510	May 20.....	4,900
		May 26.....	5,460

It will be seen that the number of the species increased nearly tenfold in two days, and that this sudden increase was held with fair uniformity, so that, while all the catches up to May 16, 1895, and April 30, 1896, were small, all those made after those dates were large.

In 1895, the appearance of the eggs was carefully studied. On April 15th, when the surface temperature was 4.5° C., all of the specimens seemed to have freshly molted, and one contained eggs. Three days later more than a third of the specimens contained eggs, which were mostly young. On the 25th all had eggs, many of which were half developed. On May 4th, young were found. On May 12th, a very few young were seen, including one male, but many had no doubt been hatched at this time, as on the 18th the numerous young were developing ovaries,

and the head-crest was fairly well grown. On the 22d, a very few of the first generation born in the spring, had laid eggs. On May 12th males were first seen, but 175 females were counted without finding any males. On June 3d, it was noted that many of the individuals which had lived over winter were affected by a microsporidial disease, and the young in the brood sacs were attacked and killed by fungus. They were also attacked by bacterial diseases. At this time, or a little earlier, the old individuals were settling into the lower strata of the water, and on the 6th of June nearly all were gone.

In 1896 the development of the species was in general parallel to that of 1895, but was some two weeks earlier, owing partly to the more rapid warming of the water and partly to the fact that the temperature of the water in winter was slightly higher, and the animals emerged from the winter life in a more advanced condition of development. In each season the surface water had reached an average temperature of 15° C., when the marked rise in numbers occurred.

The summer numbers of this species appear from the following table:

TABLE XVII.—*D. hyalina*—Average numbers, June—December, stated in thousands per square meter.

	1894.	1895.	1896.
June 1-15.....	No	319.2	55.6
June 16-30.....	Obs.	135.6	211.1
July 1-15.....	19.8	139.9	319.0
July 16-31.....	13.3	275.3}	65.5
August 1-15.....	16.6	273.0	95.2
August 16-31.....	60.7	252.8	60.9
September 1-15.....	No obs.	202.8	120.4
September 16-30.....	148.4	201.6	192.5
October 1-16.....	207.6	180.5	228.0
October 16-31.....	252.5	76.6	511.5
November 1-15.....	183.1	56.2	314.6
November 16-30.....	No obs.	48.2	266.0
December 1-15.....	121.5	35.0	182.8
December 16-31.....	(49.0)	44.6	138.9

The table shows that the summer history of this species was very different in the three years of my study. In July and August of 1894 the numbers were exceedingly small smaller than in any of the three winters during which I have studied the species. In 1895 the numbers were large and remained large throughout the summer, gradually declining in September and October, and falling off rapidly in the latter part of October to the winter minimum without showing any marked reproductive period in late autumn. In 1894 and 1896 the numbers, which were small and nearly equal in the latter part of August, rose steadily through September and October to a maximum in the latter part of October, and then fell off rapidly to reach the winter minimum in December or January. In late October, 1896, there were present enormous broods of new hatched Daphnias, which raised the number for that period beyond the records of any other. In 1896 the spring maximum was followed by a minimum about the middle of June, in which the numbers were scarcely one-quarter of the maximum. From this minimum there was a rapid recovery, which lasted for about a month and was followed by another marked depression. In 1895 the spring maximum continued into June, and the early summer minimum came about the first of July. Portions of this minimum are included for the averages of the latter part of June and the early part of July, so that the number at the minimum appears greater in the tables and diagram than it actually was. As a matter of fact, there was very little difference in the number present in 1895 and 1896. In 1895 the recovery of the species from the early minimum came on as in 1896, but there was no reaction from the increase, and the number remained substantially unchanged through the entire summer.

No observations were made in the spring of 1894, but the probable history of the species was similar to that in the other years. There was a spring maximum followed by a marked minimum from which there was no reaction. This failure of the species to develop a summer brood seems to have been due to the presence of *Lyngbya* in the upper strata of the water.

The largest catches of this species were 331,000 per sq. m., Oct. 17, 1894; 565,000 June 6, 1895, and 1,049,000 Oct. 26, 1896.

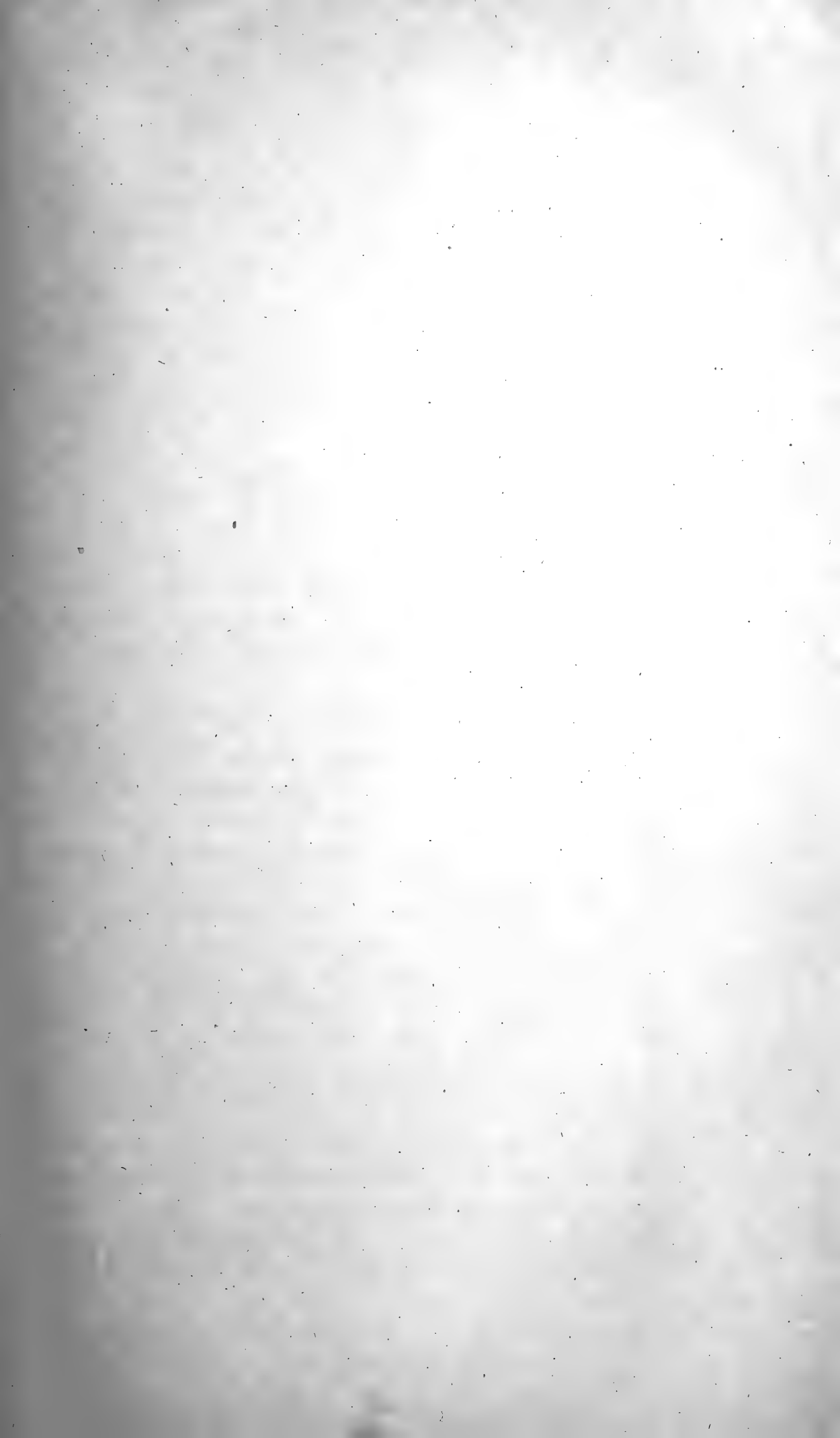
Males are found during and after the spring and fall reproductive periods, although in very small numbers, never exceeding 4 per cent. of the number of females and rarely being as numerous as this. Ordinarily it is only possible to find one or two males by careful search through the entire collection. These males are somewhat more abundant after the fall reproductive period than earlier, and may be found as late as the middle of December or even the first of January. It seems, therefore, that originally this species had two main reproductive periods, in the fall and spring. Each of these was probably closed by the production of males and the development of ephippia. The sexual reproduction has, however, almost entirely disappeared, and the species has practically passed into a acyclic condition.

Apstein ('96, p. 167,) finds that *Daphnia hyalina* is present from September to July, with a maximum in winter. This history is so wholly different from that of the species as found in lake Mendota that no profitable comparison can be made.

Daphnia pulex var. *pulicaria* Forbes.

Figure 17.—Table G, Appendix.

The following table gives the average number of *Daphnia pulicaria* taken during the period of my investigation. From this and from the diagram it appears that the species was present in very small numbers during July and August, 1894; that it then entirely disappeared until the early part of July, 1895; it increased in numbers during the summer and autumn, increased greatly during December, and was present in considerable numbers during the winter. About the middle of April, 1896, a period of rapid reproduction began, the species rising to a maximum in the latter part of May. At this time, and in the early part of June the males appeared and not infrequently numbered from one-third to one-fourth of the total catch. The females developed ephippia and the sexual eggs were produced early in June. The species rapidly declined after this date, although present in somewhat larger numbers early in September. Scattering individuals only were found from the first of October through the winter of 1896-97. The species entered upon



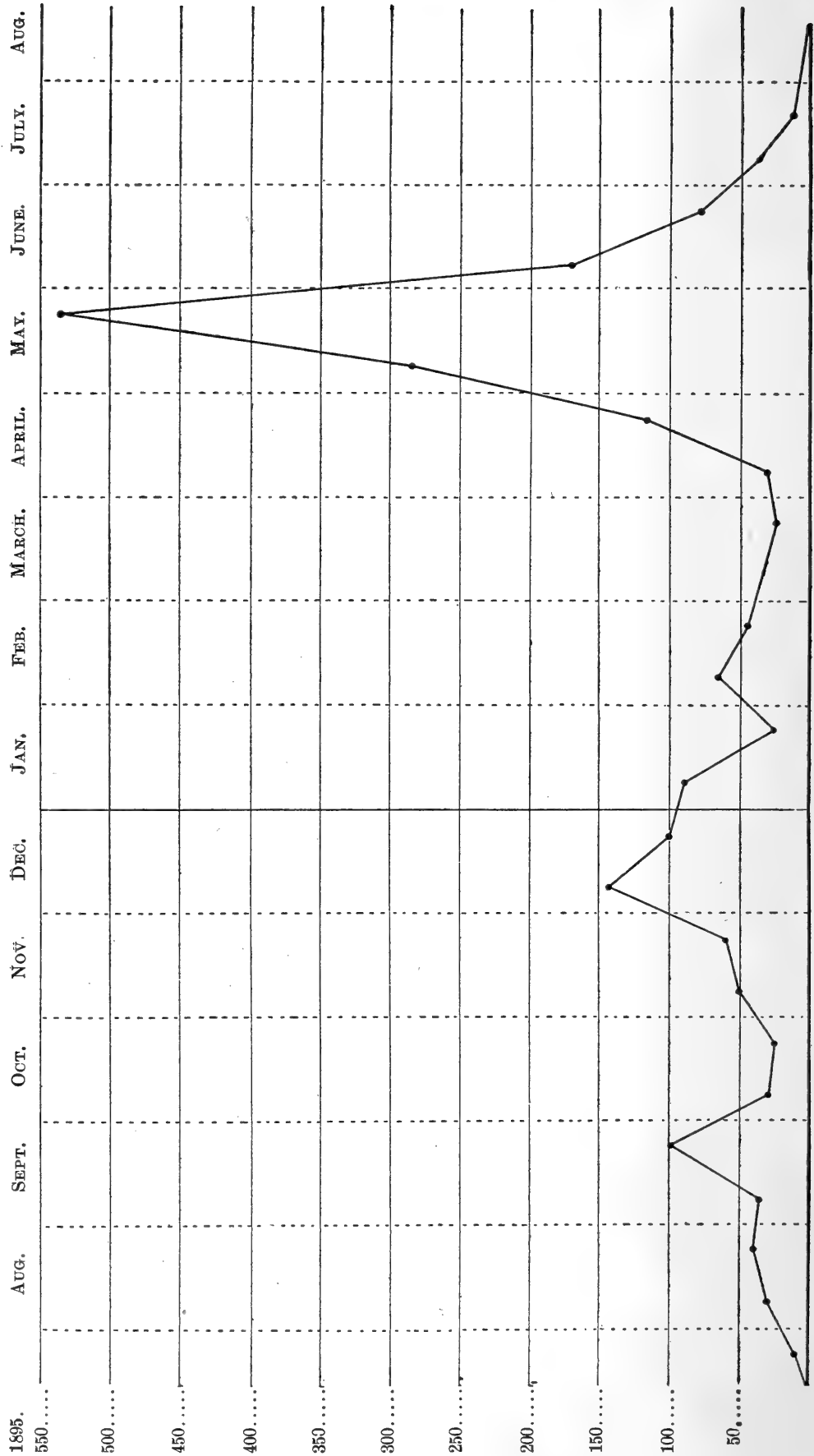


Fig. 17.—*D. pulicaria*. Annual distribution, 1895, 1896. Scale, 1 vertical space = 50,000 crustacea per sq. m. See p. 340.

a new period of development in July, 1897. From this statement of fact it appears that *Daphnia pulicaria*, as found in lake Mendota, has a biennial period of development extending from July of one year to July of the next, followed by a year in which the species is either absent or its numbers are exceedingly small. The study made in July, 1894, seems to have taken the species at the very end of its developmental period after the production of the sexual eggs. One entire cycle was included from July, 1895, to July, 1896, and a second period when the numbers were extremely small, although never entirely absent, from July, 1896, to July, 1897.

TABLE XVIII.—*D. pulicaria.* Average number per sq. meter, expressed in thousands.

	1894.	1895.	1896.
January 1-15.....		a	88.2
January 16-31.....		a	24.8
February 1-14.....		a	64.1
February 15-28.....		a	43.9
March 1-15.....		a
March 16-31.....		a	20.9
April 1-15.....		a	28.0
April 16-30.....		a	118.2
May 1-15.....		a	284.9
May 16-31.....		a	533.6
June 1-15.....		a	168.6
June 15-30.....		a	78.2
July 1-15.....	6.4	s	39.3
July 16-31.....	8.3	11.6	11.8
August 1-15.....	1.1	19.9	3.7
August 16-31.....	0.8	38.1	5.9
September 1-15.....	a	33.8	23.5
September 16-30.....	a	98.2	3.4
October 1-15.....	a	26.9	0.4
October 16-31.....	a	23.5	a
November 1-15.....	a	49.6	s
November 16-30.....	a	58.3	s
December 1-15.....	a	141.1	s
December 16-31.....	a	99.8	s

a, absent; s, scattering individuals only.

The following statement shows the general numerical relations of the species, observations beginning in July, 1894:

Season.	1894.	1895.	1896.	1897.
Spring.....	? Abundant ..	Absent	Abundant....	Very few...
Early summer	? Ehippia ..	Few.....	Adult males and females	Increasing.
Late summer	Few.....	Abundant....	Few.....	Abundant..
Autumn	Absent	Abundant....	Very few.....
Winter	Absent	Abundant....	Very few.....

As was stated in my former paper, (Birge, Olson, and Har-der, '95, p. 473), this species is found through the summer in the deeper water only. Scattering individuals may be found extending to the surface, but even where one-sixth of the total number of crustacea was counted, the number of this species found rarely exceeded one individual; and in my studies during 1896, no individuals of the species were found from the upper levels of the lake. As will be stated more at length on the section on vertical distribution, *D. pulicaria* is confined in lake Mendota during the summer to the space immediately about the thermocline. It is unable to rise higher on account of the high temperature of the water, and is unable to descend lower on account of the impurity of the deeper water in late summer and early autumn. This fact limits greatly the number of the species during the warm season of the year, and in lakes whose bottom water is cold and not contaminated by decomposition products the number of the species is far greater during the summer months, and the period of active sexual reproduction is a much longer one.

This species varies much more in numbers from day to day than does any other of the species whose numbers are at all considerable. The station at which most of the observations were made was not far from the southern shore. As a result of the action of the wind the thermocline is subject to considerable variation. A violent southwest wind, especially has the effect of driving out the warm water near the bottom of the lake, and thus temporarily raising the temperature of the

deeper levels at the station. Under these conditions the members of this species which ordinarily live between the station and the shore become driven out from their ordinary place of abode, and the numbers at the observing station are correspondingly increased. Thus on August 21, 1895, the number of this species caught was 493, a number not far from the average of the month up to that time. On the next day, the wind being strong from the southwest and the thermocline lying at an unusually low level, the number caught was 2,600. On the following day 954 were taken, and four days later only 85. The following table shows the details.

TABLE XIX.

Date.	Wind.	Depth.	Temp.	No. <i>D. pulex</i> .
1895. Aug. 21.....	Southeast.....			Above 9 m. 0
		9 m.	21.4°	9-12 m. 480
		12 m.	18.4°	12-15 m. 5
		15 m.	15.4°	15-18 m. 5
		18 m.	13.8°	
Aug. 22.....	Southwest. Strong all day...			Above 9 m. 90
		9 m.	21.7°	9-12 m. 2,120
		12 m.	20.4°	12-15 m. 360
		15 m.	17.3°	15-18 m. 18
		18 m.	14.7°	
Aug. 23.....	Nearly calm.			Above 9 m. 90
		9 m.	22.0°	9-12 m. 640
		12 m.	20.8°	12-15 m. 220
		15 m.	14.8°	15-18 m. 40
Aug. 27.....	Calm.....			Above 9 m. 0
		9 m.	22.0°	9-12 m. 0
		12 m.	20.8°	12-15 m. 80
		15 m.	17.3°	15-18 m. 5
		18 m.	13.9°	

In September of the same year 415 specimens were taken on the 18th, 2980 on the 22nd, and 3615 on the 25th. The conditions of temperature in the deeper water were much the

same as on the former occasion. The rise in numbers shown by the tables and diagram in the latter part of August and in September are therefore due to these unusual accumulations of the species and do not indicate a corresponding average rise in numbers extending over any considerable area of the lake. The case is wholly different with the increase which comes in late November and December. This is occasioned by a very rapid multiplication of the species. The brood-sacs contain from 5 to 9 eggs. This reproductive period does not begin until after the temperature of the lake has fallen below 10° , and multiplication continues, although at a slower rate, throughout the winter.

In the spring comes the main period of reproduction; and during May, 1896, the numbers were uniformly large, yet even here they were subject to very considerable variation. At the time of the maximum, the species was the most abundant of the limnetic crustacea, with the exception of *Cyclops*, and since the individuals are so much larger than *Cyclops*, the species was the most important constituent of the crustacean plankton.

It would seem necessary to suppose that the ephippial eggs deposited in June and July of one year remain unhatched for nearly a year. This is a very long period, and I have no direct observations which would make the conclusion certain. I am sure, however, that the species was practically absent from the plankton after August, 1894, since it was carefully looked for and only one specimen was found, and that in December. There was also no reproductive period in 1896 after the first of August, the increase in numbers in September of that year depending on an aggregation of individuals corresponding to that in 1895, there was no reproductive period during November or December, and the species declined in number, so that it was not practicable to enumerate it in the plankton. The winter eggs of *Diaphanosoma* must remain unhatched from about Oct. 1 to June of the next year.

The peculiar history of *Daphnia pulicaria* in lake Mendota is conditioned in great part by the fact that the species is unable to live in the cooler water of the lake below the thermocline. In lakes which are relatively plankton-poor, the

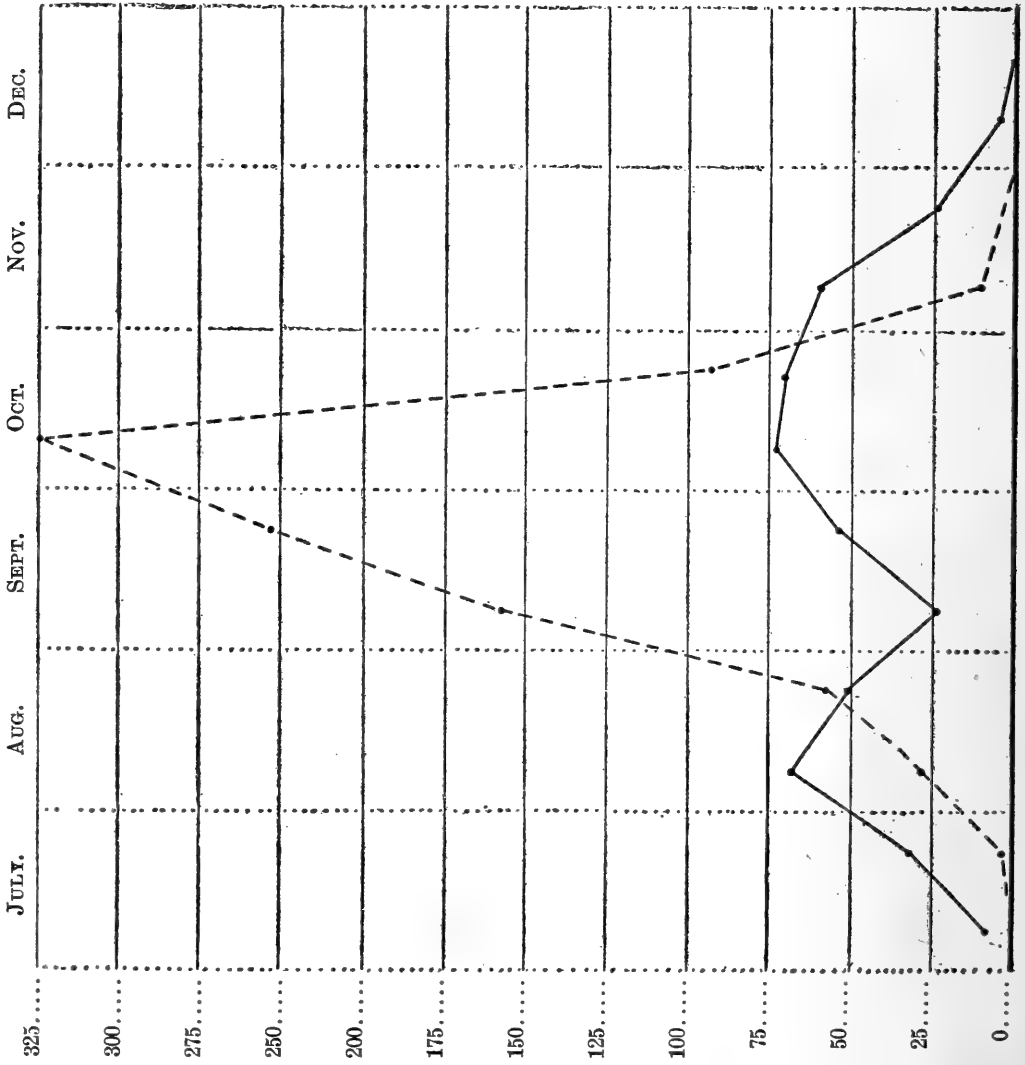


FIG. 18.—*D. retrocurva*. Annual distribution, 1895, 1896. Scale, 1 vertical space = 25,000 crustacea per sq. m. See p. 345.

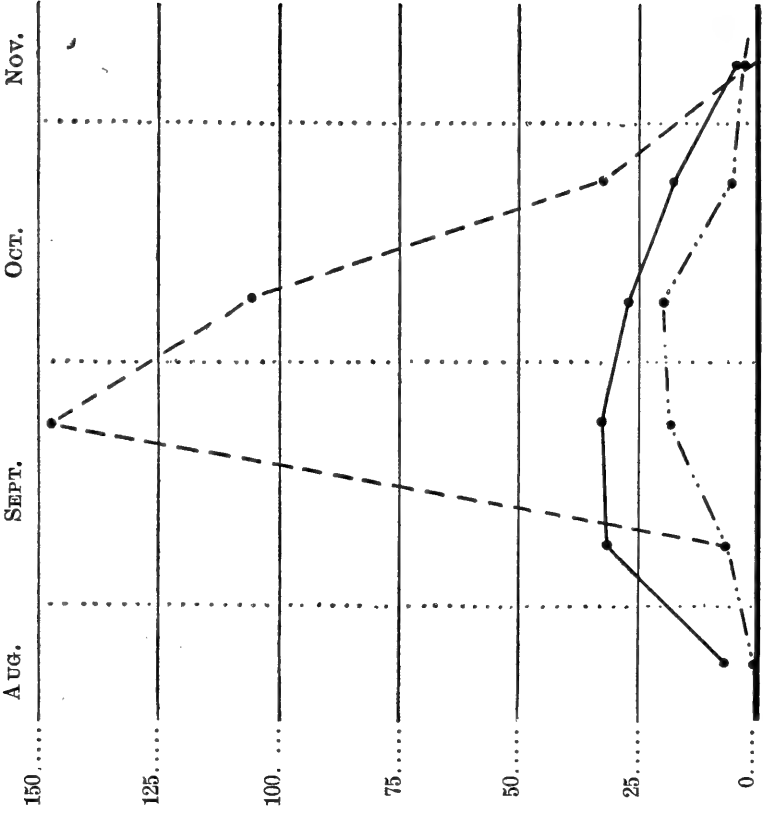


FIG. 19.—*Diaphanosoma*. Annual distribution, 1894, 1895, 1896. Scale, 1 vertical space = 25,000 crustacea per sq. meter. See p. 347.

1896....○---○---
 1895....○---○---
 1894....○---○---

species is found in far greater abundance during the summer in the cool, deeper water, and extends to the bottom of the lake. In the lakes of the Oconomowoc group, this species is abundant and is by far the most conspicuous of the crustacea which are found below the thermocline.

Daphnia retrocurva.

Figure 18.—Table H, Appendix.

TABLE XX.—Number per sq. meter of surface stated in thousands.

	1895.	1896.
June 16-30.....	s	a
July 1-15.....	9.7	s
July 16-31.....	31.5	2.5
August 1-15.....	68.2	27.6
August 16-31.....	50.1	57.1
September 1-15.....	23.8	157.7
September 16-30.....	53.6	228.6
October 1-15.....	72.5	299.3
October 16-31.....	70.8	92.7
November 1-15.....	59.3	9.9
November 16-30.....	24.2	s
December 1-15.....	5.0	s
December 16-31.....	0.7	a

Daphnia retrocurva belongs to the periodic crustacea, and its numbers have been very different in the three seasons of my study. In 1894 the species was practically absent; two specimens only were seen in July, and none were found in later months. In 1895 it was present in moderate numbers, and in 1896 the numbers in September and October were very considerable. The small number in 1895 is probably the result of the absence of the species in 1894. Perhaps also the competition of *Daphnia hyalina* had something to do with preventing the increase of the species in 1895. In that year *Daphnia hyalina* was present in large numbers throughout the late summer and the autumn. In 1896 *D. hyalina* declined greatly in numbers in

August, and in the latter part of the month both *retrocurva* and *hyalina* were practically equal and their numbers rose together during September and October. It is quite possible also that the lower temperature of the water in September, 1896, as compared with the same month in 1895, favored the development of both species. In 1895 the summer temperature of the lake was maintained until late in September. The result of this was apparently a great increase in the number of *Diaptomus*, and a steady decline in the number of *Daphniae*.

D. retrocurva first appears in the latter part of May. The numbers are small, but two or three specimens can be found by search in almost every catch. During June it apparently disappears, or is much more rare than on this first appearance. It is not possible to estimate its numbers with any accuracy before July or August. The males begin to appear in late September or in October. They were first noticed on September 17th, 1895, and October 1st, 1896. The ephippia developed during October, and the species declines rapidly in November, and finally disappears from the lake by January 1st. The ephippia float, and many of them are doubtless driven to the shore, so that if the level of the lake is much lower in the spring and summer than it was in the fall, these ephippia may fail to develop, and thus cause a scarcity of the species.

The maximum of this species coincides with the presence of the males. These, when at their greatest abundance number from 18 to 50 per cent. of the full number caught. They are always more abundant, relatively, in the upper strata of the water than are the females, agreeing in this particular with the young of most species of the limnetic crustacea.

The food of this species agrees with that of the other members of the same genus. It eats *Anabaena* and diatoms in preference to other plants. It makes very little use of *Ceratium* and avoids *Clathrocystis* whenever possible.

Marsh ('97, p. 210) assigns the maximum of *D. Kahlbergiensis* to late October, thus agreeing with the corresponding species in lake Mendota. He does not say anything about males and since the species was present during the winter of 1894-5 it would seem to belong to the perennial crustacea of Green lake.

Zacharias ('96, p. 53), gives August and September as the maximum, and also says nothing about males. The species was only occasionally present in the winter. Apstein ('96, p. 170), gives August as the date of the maximum for all species of *Daphnia*. He does not mention a sexual period, though he gives no especial attention to the subject. Had there been such a period as is shown by *D. retrocurva* it could not have been missed.

Diaphanosoma brachyurum Sars.

Figure 19. — Table I, Appendix.

TABLE XXI.—Average number per square meter of surface, stated in thousands and tenths.

	1894.	1895.	1896.
July 1-15.....		s	s
July 16-31.....	0.8	6.9	s
August 1-15.....	6.3	31.5	8.9
August 16-31.....	18.0	32.2	147.4
September 1-15.....	No obs.	27.1	108.3
September 16-30.....	19.6	17.2	32.9
October 1-15.....	5.2	3.4	0.4
October 16-31.....	3.0	0.0	0 0

This species is the least numerous of the limnetic crustacea which appear in large numbers, and has the shortest season. Scattering individuals may be seen as early as the middle of May, but they do not become a regular constituent of the plankton catch before the middle of July or the earlier part of August. They disappear in October, and are greatly reduced in number by the cold storms which usually come in late September. Males appear about the middle of September, and the winter eggs are then produced. The species was far more abundant in 1896 than in either of the two preceding years, which agree with each other fairly well. For this difference I can assign no reason. The numbers were constantly greater in 1896, so that the increased number was not the result of a few large

catches. The life history of this species practically belongs to the period when the temperature of the upper water of the lake is above 20°.

Apstein ('96, p. 166), Frič and Vávra ('94, p. 103) find the relations of *Diaphanosoma* quite as I have done. It does not seem to belong in lake Ploen. Marsh ('97, p. 215) gives the species as present from June to November in Green lake. All find it a little earlier in the spring than I have done.

Chydorus sphaericus O. F. M.

Figure 20.—Table J, Appendix.

TABLE XXII.—*Chydorus sphaericus*. Average number per square meter expressed in thousands.

	1894.	1895.	1896.
January 1-15.....	1.3	10.1
January 16-31.....	a	19.5
February 1-14.....	a	4.8
February 15-28.....	a	3.8
March 1-15.....	a	No obs.
March 16-31.....	a	1.4
April 1-15.....	a	1.9
April 16-30.....	s	9.8
May 1-15.....	12.1	28.0
May 16-31.....	16.5	30.8
June 1-15.....	36.7	87.6
June 16-30.....	21.9	230.8
July 1-15.....	s	156.8	382.0
July 16-31.....	s	163.4	245.1
August 1-15.....	s	78.6	406.5
August 16-31.....	15.0	81.7	426.0
September 1-15.....	No obs.	15.6	748.0
September 16-30.....	278.9	s	263.0
October 1-15.....	193.3	8.6	423.7
October 16-31.....	202.0	8.1	191.9
November 1-15.....	97.9	29.9	62.7
November 16-30.....	No obs.	19.7	69.3
December 1-15.....	9.5	15.9	38.2
December 16-31.....	1.6	20.9	28.1



The above table shows that the number of this species is subject to very great variation; yet there is a certain degree of regularity in its appearance. The years 1894 and 1896 resembled each other in having a maximum in autumn, which was wholly absent in 1895. A large number was also found in July, 1895 and 1896, while practically none were present in 1894. In the winter of 1895-6, *Chydorus* was regularly present; while in that of 1894-5 there were found only isolated individuals from time to time. I believe that these periods of abundance are correlated with the abundance of *Anabaena* and allied algae in the water. The autumn of 1894, and the whole season of 1896 were characterized by a great abundance of these plants; while they were exceedingly rare in 1895 after the spring and early summer. The summer of 1894 was marked by an enormous development of *Lyngbya*, an alga quite too large to serve as food for *Chydorus*, and at the same time occupying the upper stratum of the water to the exclusion of the smaller algae.

The development of *Chydorus* is therefore dependent on the kind of food to a degree unusual among the limnetic crustacea. It is also dependent on temperature. In both 1895 and 1896 it was the last of the perennial crustacea in its development, no marked rise occurring before the last of June or the first of July. This is the more noteworthy, since eggs may be found in the brood sac at any time during the winter.

In 1894 and 1896 the maximum came about the middle of September, while in 1895 only one small maximum was present, and that was in July. In 1896 there was no decline of the species in August, but rather an increase, and in this season *Anabaena* and allied forms were abundant throughout the summer.

In 1894 the number increased very greatly between the 6th and 10th of June, as is shown by the following record of the number of individuals caught.

June 3	90
June 5	450
June 6	120
June 10.....	4,200
June 13.....	4,430
June 17.....	1,740
June 19.....	4,100

Earlier and later catches agree with those given. On the 8th and 9th of the month there was a violent wind from the north and northwest, which probably brought this species out from shore water where it had been developing.

These facts indicate that *Chydorus* is not properly a limnetic form but that it gets into the limnetic region by accident and maintains itself there so long as suitable food is present. I agree with Apstein in regarding this form as characteristic for lakes abounding in Chroococcaceae or, perhaps, Schizophyceae. He has not observed its dependence on the seasonal appearance of these plants in the lake, as is the case in lake Mendota. In the limnetic region the species is acyclic so far as my observations go. The largest catches of this species were 440,000 per sq. m. Sept. 21, 1894; 221,000, July 28, 1895; 661,000, July 7, 1896; 674,000, Aug. 15, 1896.

Leptodora hyalina Lillj.

TABLE XXIII.—*Leptodora hyalina*. Average catch per square meter of surface.

	1894.	1895.	1896.
June 1-15	No obs.	63	s.
June 16-30	No obs.	680	254
July 1-15.....	324	986	1,208
July 16-31.....	362	827	585
August 1-15	445	2,512	642
August 16-31....	1,081	3,078	1,881
September 1-15.....	No obs.	1,063	2,850
September 16-30.....	871	775	2,945
October 1-15	1,469	457	2,375
October 16-31.....	966	661	1,026
November 1-15.....	95	292	247
November 16-30.....		25	31

The table given above shows the average number of *Leptodora* during the seasons of 1894, 1895, and 1896. The species first appears in May, being first observed May 29th, 1895, and 1896. The nauplii must appear earlier, but I have never seen.

one, although careful search was made for them in both years. The number of the species is so irregular that the average per square meter represents very little. On August 22nd, 1895, the species was present in the upper meter at the rate of nearly 2700 per cubic meter. These were all young females, either without eggs or having the eggs just laid. On October 6th, 1894, three sets of observations gave respectively a catch of 9, 38, and 13 individuals. On July 19th, six catches, at different hours, gave 0, 34, 11, 4, 3, 0. On August 1st and 2nd, there were taken: 4, 24, 16, 10, 4, and 2 individuals at different hours. These examples are sufficient to show that the figures for *Leptodora* are subject to a far greater variation than those of the other crustacea. For this reason, and also because the size and habits of *Leptodora* are quite different from those of the other limnetic crustacea, the species has not been included in the total number of crustacea. The maximum catch was 79, Aug. 7, '95; 75, June 22, 96; about 5,000 per sq. m.

Males of this species appear in October, the numbers decline rapidly during November, and no individuals were caught by the vertical net after November 26th in either year. Horizontal collections, however, show that they were present until after December first. The limits of this species, therefore, extend from the middle of May to the first of December, and the maximum numbers occur in late summer and early fall. It is worthy of note that in no year does the maximum number coincide with the production of males. This is to be expected, as the large summer catches were due to the presence of numbers of young or half grown *Leptodora* at the place where the net was hauled. It is therefore not surprising that these swarms should be irregular, and they would not be expected at the time when the adult females are producing the winter eggs.

Many observations were made upon the food of *Leptodora*, and it was found that they eat chiefly *Cyclops* and *Daphnia*. The attempt of the animal seems to be to squeeze out and swallow the interior of the prey. In a considerable number of instances the intestine or the ovary of *Daphnia*, nearly entire, was seen in the stomach of *Leptodora*, and only occasionally

were any parts of the skeleton of this species found. The legs and similar appendages of *Cyclops* were not infrequently seen. Large *Daphnias* have ordinarily a shell so thick that the weak jaws of *Leptodora* are unable to pierce it, and a very large proportion of the *Daphnias* seized by *Leptodora* escape apparently uninjured.

Apstein ('96, p. 175), notes that this animal in the Einfeld See was very large, over 1 cm. long. It is not at all uncommon to find specimens measuring 18 mm. in lake Mendota. The average size is dependent apparently on the abundance of food. In Green lake and the Oconomowoc lakes the length is decidedly less than 1 cm.

FACTORS DETERMINING THE ANNUAL DISTRIBUTION.

Our knowledge of the conditions of limnetic life is at present far too fragmentary to permit any complete explanation of the factors which determine the number of crustacea present in the plankton. Certain provisional results however, may, be reached as a result of this study of the crustacea. The following factors are present and combine to determine the total number of the crustacea present at any time and the number of the members of each species.

1. The food, both in quantity and quality.
2. Temperature.
3. Competition.

Food.

It is plain that the quantity of available food must set an upper limit to the number of crustacea. Available food must be carefully distinguished from plant material, since all plants are by no means equally edible by the crustacea. *Gloio-trichia*, for example, is present in lake Mendota in considerable numbers from the latter part of July to the early part of September. It is never the dominant alga, as it is apt to be in the plankton-poor lake. But it is often the most prominent alga to the eye, and is present in such numbers as to form on calm days a thin scum on the surface. It does not appear, however, that any species of crustacea regularly eats it. I have given very careful study to this point during three seasons, and have

never seen any evidence that any of the limnetic crustacea feed upon it. Of course in cases of necessity it may be eaten, but even where other food is comparatively scanty, *Gloiostrichia* seems to be avoided. It should, therefore, be subtracted from the quantity of available food.

Clathrocystis and *Coelosphaerium* appear also to be far less readily eaten than other species. I have made very numerous observations upon *Daphnia* of all three of the species present in lake Mendota and have uniformly found that while the diatoms, *Anabaena*, and *Aphanizomenon* are greedily eaten, the colonies of the genera first named are uniformly rejected. During the autumn and winter of 1894-5, *Clathrocystis* and *Aphanizomenon* were almost the only algae present. The food of *Daphnia* was almost exclusively the latter species, and I have seen hundreds of *Daphnia* persistently rejecting *Clathrocystis*, while greedily collecting and devouring *Aphanizomenon*. *Daphnia* eats freely all of the filamentous diatoms, including *Fragillaria*, *Melosira* and *Diatoma*, while *Diaptomus* seems to prefer *Anabaena* and *Aphanizomenon* to the diatoms, when all are present in large numbers. Since these preferences for various kinds of food are so strikingly marked among the crustacea, it may easily happen that a period when vegetation is superabundant in the lake may be one of scarcity for the crustacea. The most conspicuous case of this sort occurred in the summer of 1894, when my observations on the crustacea began. In July and early August of that year a species of *Lyngbya* overgrew all the other species of plants, constituting more than 95 per cent. in bulk of the vegetable plankton. It was so abundant as to constitute a thick scum on the surface of the lake during calm weather. The filaments of *Lyngbya* are large and perhaps for other reasons than size are little available as food. The *Daphnias* present were carefully examined and hardly a single filament of the species was found in them, nor could I find any evidence that the other species ate it, although the remains of diatoms and other species of plants were found in their intestines. The number of every species of limnetic crustacea, except *Diaptomus*, was far smaller during this period than in other years, as the following table will show:

TABLE XXIV.—Number of limnetic crustacea during July, 1894–1896, stated in thousands per sq. m. of surface.

July.	1894.	1895.	1896.
Diaptomus	260.5	202.2	177.5
Cyclops	95.4	227.8	244.2
Daphnia hyalina.....	15.5	207.6	192.2
Chydorus		160.1	313.5

Daphnia retrocurva was entirely absent in 1894, while beginning its regular development in the two latter years.

It seems quite evident that the presence of *Lyngbya* in the lake was the determining factor in causing the numbers of all species except *Diaptomus* to be so exceptionally small. The influence of this alga is not by any means confined to the adults. It is even more important in its action upon the young. In all the species of crustacea the immature forms are found near the surface, and during the day the upper one-half meter, or thereabouts, is occupied by immature crustacea. This is the same region as that in which the *Lyngbya* is most abundant, and since *Lyngbya* is wholly unmanageable as food for the immature crustacea, its presence in the upper water exerts a very unfavorable influence upon the development of the new broods which may be hatched while it is the predominant alga. It is noteworthy that *Diaptomus*, which maintained its numbers through the *Lyngbya* period, is the species of crustacea which combines great locomotive powers with effective means of collecting food. *Daphnia* has the most effective food collector, but is inferior in locomotive powers. *Cyclops* is inferior to both species in both ways, but ordinarily has an advantage in its omnivorous habits and its greater adaptability to different conditions of life.

In late July *Lyngbya* began to decline, and *Aphanizomenon* and *Melosira* began to develop. Parallel with this change in the character of the algae, *Cyclops* and *Daphnia hyalina* increased rapidly, and in late August, when *Melosira* was the predominant alga, *Cyclops* and *Daphnia* were the predominant crustacea. *Chydorus* had fairly entered upon its period of rapid multiplication at this time but its numbers only became large as *Aphanizomenon* multiplied in September.

Ceratium offers an instance of an alga which, while not absolutely unavailable as food, is far less rapidly eaten than other species. So far as my observations extend, the adult *Cyclops* devour it more freely than do any other species of crustacea. *Cyclops*, indeed, is the most omnivorous of the plankton crustacea. It seizes and devours rotifers, nauplii, and other small animals, as well as plants. I have seen it pounce upon and devour *Ceratium* several times, while I have never seen *Diaptomus* do the same, and have only very rarely found fragments of *Ceratium* in the intestine of *Diaptomus*. During 1895 I did not find in a single instance *Ceratium* within the shell of *Daphnia*, but in 1896 I found it in a very few cases. *Ceratium* is a prominent alga during the summer, and at some time ordinarily becomes the dominant form, so that there is fairly a *Ceratium* period. In 1895 this period fell from the middle of June to the middle of July, and for a week on each side of the first of July, *Ceratium* constituted more than 90 per cent. of the plankton algae. In 1896 this period was later, coming in August and early September. It was present in large numbers from the early part of the summer, but seemed to be hindered in its development by the great numbers of *Aphanizomenon*, which were present in the water. For nearly a month it seemed doubtful whether there would be a *Ceratium* period at all, but finally in August, *Ceratium* predominated decidedly over *Aphanizomenon*, although a considerable quantity of the latter species and *Anabaena* was always present. *Ceratium*, like *Aphanizomenon*, occupies the upper strata of the water, and its presence there is a hindrance to the development of the young crustacea, since it is so large and its shell is so hard that it cannot be eaten by them. The *Ceratium* period in 1895 marked the beginning of a decline in the numbers of the crustacea. The same was true to a less marked extent in 1896. I have no doubt that the presence of this alga in great quantity is one of the factors which influences the late-summer minimum in the numbers of the limnetic crustacea. In 1894, *Ceratium* was present, but its numbers were always far inferior to those of *Lyngbya*.

The quantity of food also exerts an influence on the number of the crustacea. In a lake in which the plankton is so abun-

dant as in lake Mendota, the quantity of algae is ordinarily in excess of the demands of the crustacea, and any scarcity of food is wont to be brought about rather by changes in the quality of the algae than by an inadequacy in the total supply of vegetable material. There is, however, one line of facts regarding the quantity of food to which sufficient attention has not as yet been given, namely, the correspondence of the relation of the rhythm of development of the algae with that of the crustacea. As is well known, the successive species of plankton algae come on in waves of development, and between the periods when given species are plentiful, there are intervals, longer or shorter, when the food supply may be small. This relation may be best seen in lake Mendota at the time of the spring maximum. The crustacea, during the spring, increase more rapidly than the algae, and when the crustacea are at their maximum, the mass of plankton appears to the eye to consist of little except crustacea. Under these circumstances the food supply must be inadequate, the number of crustacea must fall off, and, especially, their reproductive power must decline. If the rate of increase of the algae coincided with that of the crustacea, so that the time of maximum amount of food agreed with the time of maximum needs on the part of the crustacea, this quantitative oscillation would be of little importance; but, if at any time the decline of the dominant algae coincides with the reproductive period of a species of crustacea, it may be long before the species recovers from the injury thus caused. This relation between food and crustacea is one of the most important, and at the same time one of the most difficult to investigate, and one to which as yet but little study has been given. It is plain, however, that the number of a species of crustacea must be determined—so far as determined at all by food—by food relations when most unfavorable, and that the quantitative relations of food and crustacea must be followed from day to day, if this relation is to be understood.

Zacharias ('96, p. 60) expresses his surprise that the small crustacea do not increase beyond a certain number when they are provided with so abundant food throughout the year. To this question he states that there is at present no answer. I

am very far from supposing that I can answer the question completely, yet Zacharias's own figures show that at certain times of the year the food supply must be exceedingly small. For example, his figures show that the quantity of plant life is apparently abundant during the spring and early summer, but that in the late summer the amount of vegetation is small in proportion to the number of eaters.

On August 20, 1895, the number of crustacea (l. c., p. 45) was nearly 1,360,000 per square meter of surface, the diatoms less than 30,500; *Dinobryon*, *Eudorina*, and *Ceratium* 459,010; and *Gloiostrichia* 70,650. Thus, including *Gloiostrichia*, there was less than one colony of algae to 2.5 crustacea. On Sept. 20, there was hardly more than one plant to 10 crustacea. Under these conditions a daphnia would have to strain a good many liters of water to satisfy her eternal hunger.

It never happens in lake Mendota that the ratio of food to crustacea falls as low as these observations in lake Ploen, and while I am convinced that the occasional scarcity of food is an important factor in limiting the number of crustacea, I am equally sure that there must be other conditions, still unknown, which at times are even more important. My studies on the vertical distribution of the crustacea in 1895 and 1896 show that all or nearly all of the increase of the crustacea which causes the fall maximum is brought about by the increase in the numbers of the crustacea in the deeper part of the lake from which they are excluded during the summer. In other words, the number of crustacea in the upper three meters of the water remains nearly constant from a date near the close of the spring maximum to the decline in numbers in late autumn. In 1896 the number of the crustacea in the upper strata increased somewhat during the autumn, owing to the occasional presence of large numbers of new-hatched individuals, but even in this year more than three-fourths of the increase in the number of the crustacea was due to the increase of the population of the lake below the nine-meter level. In the upper water, however, the increase of plants is most rapid. It begins in August at latest, and the quantity of vegetation goes on increasing, for two months at least, until in October the amount of food may easily be four

or five times as much as in mid-summer. During this period the conditions of temperature are by no means unfavorable for reproduction, and it is at present impossible to see why crustacea should not increase more rapidly and thus reach a greater number at the period of the fall maximum.

Temperature.

The temperature of the water, as such, independent of its influence on the food supply, determines the reproductive powers of the crustacea and the rate of their development, and thus limits their numbers. Perhaps, also, it exerts an influence on the length of life of the adults, although this influence is less certain.

The different species of limnetic crustacea differ greatly in their relation to temperature. The periodic species are necessarily more greatly influenced by it than are the perennial. *Diaphanosoma brachyurum* is the most stenothermous of the periodic species. The first scattering individuals appear late in May but the species does not become a regular constituent of the plankton until late in July or early in August. The species increases in number throughout August and early September. The males appear towards the middle or last of September, when the species rapidly declines and wholly disappears from the plankton before the 1st of November. Its active period, therefore, lies during the time when the temperature of the water of the lake to a considerable depth equals or exceeds 20° C. The individuals found in October are the survivors of the September swarm, which show no reproduction and which disappear rapidly.

Daphnia retrocurva comes next in its relations to temperature. The species first appears late in May, but develops very slowly, and does not become plentiful enough to be counted as a regular constituent of the plankton until late in July or early in August. Its appearance thus coincides approximately with that of *Diaphanosoma*, but its autumnal history is quite different. The species continues to increase sexually until mid-October. The immature males appear late in September or early in October. The females begin to develop ehippia in the first

half of October. The first ehippial females were seen on October 1st, 1895, and October 12th, 1896. By the middle or last of October nearly all the females bear ehippia, and the ehippia are cast off before November 1st. After this date the species rapidly declines, and the last females practically disappear about the first of December, although scattering individuals may remain until after January 1st. The sexual period of this species, therefore, instead of coming, like that of *Diaphanosoma*, when the temperature of the lake is still in the neighborhood of 20°, does not begin until the temperature has fallen below 15°. It should be remarked that in all these cases of an autumnal sexual period, scarcity of food can play no part in bringing it on. At this time the lake is crowded with algae of those species which are most greedily eaten by the crustacea, and in the case of the *Daphnias* there is always present a large mass of food material between the legs.

Leptodora is closely parallel to *Daphnia retrocurva*, although of course, its numbers are far smaller. I have never been able to see the nauplius of this species, though I have looked for it carefully. The young females appear late in May. The species reaches a maximum in late August or September. The males appear in late September or early October, and the species disappears about the middle or last of November.

In the perennial species the effect of temperature is chiefly seen in its action upon reproduction. *Cyclops brevispinosus* is by far the most indifferent to low temperatures. Its chief reproductive period is in the spring, and the young may appear during the winter beneath the ice, when the temperature of the water is below 3.0° C. The rate of reproduction increases as the lake warms, but the maximum of the species is reached by the time the surface of the water has been warmed to 15°. During the summer the species makes no marked recovery from the spring decline. In Pine lake this species is found during the summer in great numbers, close to the thermocline, living chiefly in the colder water just below it. It seems probable, therefore, that the species is unable to reproduce rapidly in the warm water of lake Mendota, to which it is confined during the summer. The young of the fall reproductive period do not ap-

pear in large numbers until after the lake has fallen below 15° C. The production of eggs and nauplii continues throughout the year, but the development goes on with increasing slowness as the temperature of the lake falls. When the temperature of the lake has fallen below 2.0° C., there seems to be little or no development of the nauplii into young *Cyclops*, but as the water of the lake warms toward the spring, the development goes on once more. There is, however, no time in the year when female *Cyclops* may not be found in considerable numbers bearing eggs.

In summer the number of Copepoda is smaller than that of the nauplii would lead us to expect. It is fair to conclude that at this time the temperature is higher than the optimum for their development into the adult forms.

Diaptomus does not reproduce during the winter, although a very few females may be found in late February or March bearing egg-sacs. No nauplii of this species have ever been seen during the winter, and the total number seen with eggs has not exceeded a dozen during the three winters of my study. Nor does reproduction begin immediately upon the disappearance of the ice. Females bearing eggs are seen from the middle of April on, but the young *Diaptomus* do not appear in numbers until the water of the lake, to a considerable depth, is near 15° C. Although the numbers of the species vary through the summer, it remains on the whole more constant during the heated term than any of the species, and the late-summer decline in August is apt to be less marked than in other forms. The number of eggs is less in summer than in spring. It may be as great as 30 early in the season but declines to 10–15 later. In 1895, there was a marked rise in the number of *Diaptomus* during September, which was not seen in 1894 or 1896. Since in all years food is abundant at this season, we must look for the cause of this exceptional increase in 1895 to the persistence of the warm weather during September of that year. A glance at Figs. 1 and 2 will show that in 1895 the surface temperature of the water remained practically constant through the summer and to the end of September above or near 20°, while in 1896 the temperature began to decline about the middle of Au-

gust, and the decline continued steadily through September. Similar conditions of temperature to those of 1896 were found in 1894.

There is no fall reproductive season for *Diaptomus*, but as the temperature declines the number of egg-bearing females diminishes, and the number of individuals of the species becomes steadily smaller. The winter level is reached comparatively early, in late October or the very first of November. After this level is reached, no increase takes place until after May 1st of the following year. The number however, remains singularly constant throughout the winter, and the individual members are well nourished, containing large quantities of fat at all times during the winter.

Daphnia hyalina has two great periods of reproduction, in the spring and fall. The ovaries begin to develop before the ice has disappeared from the lake in late February and in March, when the temperature of the water is 2.5° C., or above. A very few of the largest individuals produce eggs at this time, but no considerable number of eggs are found until the temperature of the lake reaches 4-4.5° C., which has been about the middle of April. In 1895 the first numerous broods of young *Daphnias* appeared about the middle of May, when the upper water of the lake had reached an average temperature of about 15° C., and the reproductive period lasted until about the middle of June. During this time the number of eggs is considerable, usually as many as five and occasionally nine, or even more. These eggs are smaller than those produced in the summer, the yolk is peculiar in color, and in general the eggs resemble more nearly those of the ephippia than the eggs produced in midsummer. About three broods are produced during the month by the females. Toward the end of this reproductive period males appear in small numbers. They never exceed 4 per cent. of the total number of the females, and I have never found ephippial females at this season though I have searched carefully for them.

During the first part of June those females die which have lived through the winter, and at the same time there seems to be a break in the reproductive activity of the species. Whether

this is due to the increase in the temperature of the water or not, I find it difficult to decide. In each year, as will be seen by reference to Fig. 16, the number of this species fell off rapidly and greatly at the close of the spring reproductive period, and this decline was followed by an equally rapid rise. So great a fall, followed by so great a reaction can hardly be attributed to the progressive rise of the temperature of the water, and it seems to me probable that this break in reproduction is due rather to a reproduction-pause following the imperfectly indicated sexual period. This species seems to have had originally two reproductive periods, which would naturally have been closed by the production of sexual eggs. There is left now barely a trace of sexual reproduction, but the break in the sexual reproduction is still indicated in the history of the species for spring and early summer.

When reproduction again goes on rapidly during mid-summer, the females produce only two summer eggs, which are large, transparent, and quite different in appearance from those laid in the spring. The number of eggs increases to four in early September if the temperature of the water has fallen from the summer condition.

The period of rapid reproduction in the spring falls at a time when the temperature of the water is from 15° to 18° C. In the autumn the main reproductive period is not entered upon until after the lake has fallen to a temperature of 15° C.

Daphnia pulicaria. The reproductive periods of this species are also limited by temperature. A high temperature exerts an effect more unfavorable than it produces on *Daphnia hyalina*, and the main periods of reproduction come earlier in the spring and later in the fall than do those of its sister species. Reproduction also continues through the winter with considerable rapidity. The period of active reproduction in the fall begins after that of *Daphnia hyalina* closes, and the largest broods appear in late November and early December, when the temperature of the lake has fallen below 5° C. It is apparently not until the lake has fallen below 10° C. that eggs are produced in great numbers, and in the cold water of the late fall, the females deposit in the brood-sacs from five to nine eggs, and the birth

of these broods is followed by a marked rise in number. As the lake cools and freezes, reproduction still goes on, though more slowly than at the earlier date and more slowly than in *Cyclops*. Yet, during the winter of 1895-6, when *Daphnia pulicaria* was abundant, it was always possible to find females bearing in the brood-sac eggs in various stages of development. Active reproduction begins again in the spring, as soon as the ice has disappeared. The temperature of the water rises so rapidly and uniformly at this season that it is impossible to state the optimum temperature, but the large spring broods were produced shortly after May 1st, when the lake had reached a temperature somewhat over 12° C. The maximum number of the species was found about the middle of May, at a time when the maximum rate of reproduction was past. Males appeared in the latter part of May, and the ephippia were ripe early in June and were deposited before the middle of that month. After this date the species rapidly declines, but lingers for a time in the cool bottom water of the lake. The numbers become so few in late July and in August that no fair average can be given. They did not entirely disappear, however, in 1896, as they did in 1894, and it was always possible to find a few individuals in each catch by careful search.

This species is confined to the cool water of the lake during the warm season of the year. In plankton-poor lakes it occupies the whole region below the thermocline. In lake Mendota this region is not inhabitable except at the very top, and the species is confined to the narrow zone which includes the thermocline. It is probable that this unfavorable influence on the life of the species is the cause of its disappearance or great reduction in number during the warm season of the year.

The relations of *Chydorus* to temperature are less definite than those of the regular plankton crustacea. I have already said that *Chydorus* is a littoral form, which occupies the limnetic region only under favorable conditions. These seem to be rather determined by food than by temperature. The active life of the species, however, lies from the first of June to the last of October, and the maxima may fall at almost any time within these limits. In 1894 the species was practically absent

during the latter part of August, rising rapidly to a maximum in September (Fig. 20), and then declining slowly until late October, when it fell off more rapidly and finally disappeared, with the exception of occasional scattered individuals. In 1895 it reappeared in May, reached a small number which it maintained about six weeks, rose rapidly to a maximum in July, and then declined to a small number which was maintained with approximate constancy from the latter part of August, through the autumn and winter, declining, but not quite disappearing, in the following April. In 1896 the species was much more abundant than in either year, a fact which I have connected with the greater abundance of *Aphanizomenon* during that season. The species had a great development from July to the middle of October, reaching its maximum early in September. There was also a minor maximum in early July and one in the first half of October. It appears, therefore, that the maxima of this species have come in July, 1895, in September, 1896, and in October, 1894, and that in other years these months have been marked by the presence of very small numbers of the species or its total absence in other years. It is, therefore, impossible to say more on the relation of temperature than that the maxima fall in the warm season of the year. During the winter of 1895-6, when the species was regularly present, reproduction went on, as was evidenced by the regular presence of eggs in the brood-sac of the females.

Summing up these results of temperature, it may be said that in lake Mendota, temperature exerts a greater control over the number of the plankton crustacea than does food. The number of the crustacea falls off in autumn, while food is still abundant; reproduction is checked in winter, although the food present would permit reproduction; and the reproductive periods of the perennial species are arranged rather with reference to temperature than to food supply.

If I were to sum up my impressions as to factors affecting the numbers, I should state them as follows:

1. Food sets an upper limit to number.
2. The algae of the upper strata of water determine the development or failure of the young broods.
3. Temperature determines the rhythm of reproduction.

Competition.

The connection between the number of a species and the competition to which it is exposed from the other limnetic crustacea is a subject on which little can be said, yet indications of the effect of competition are not wanting in my observations, and it may be worth while to point out some of them. The details of the critical distribution of the crustacea show that while the number of individuals present in the upper strata of the water may vary considerably from year to year, nevertheless the number does not rise beyond a certain maximum during the season, and when this maximum has once been reached the number remains singularly constant. We cannot, therefore, avoid the conclusion that there is a certain number of crustacea which the water can support, and that this number cannot be greatly exceeded. If this is the case, the numbers of one species must exert an influence, more or less unfavorable, on the number of the other forms present.

In each of the summers during which I have studied the crustacea, one form predominated in the plankton, and in each year the species was different. In 1894 *Diaptomus* was more numerous than all the other crustacea put together. In 1895 *Daphnia hyalina* was the predominant species in number, and still more in bulk, as its individuals are so much larger than the other species. In 1896 *Cyclops* was almost equally predominant, although at times *Daphnia* was nearly or quite as important. My explanation of these facts is that when a species secures possession of the water it is difficult for another species to oust it so long as its reproductive power continues. The causes which give an opportunity to any given species thus to occupy the water are still largely unknown, or conjectural. It may be said, however, that as the species become successively predominant, a form whose reproductive period is at hand at the time of the decline of a dominant form will be able to occupy the vacant space for a time.

An instance in which the numbers of a species seem to have been affected by competition is afforded by *Daphnia retrocurva*. In August, 1895 and 1896, the number of this species

was substantially equal, being 57,000 per square meter, in 1896 and 50,000 in 1895, but in 1895 the number of *Daphnia hyalina* was very great, being 260,000 or more during the entire month; while in 1896 *Daphnia hyalina* had fallen off to 61,000 in the latter part of August, being therefore substantially equal with *D. retrocurva*.

The autumn history of *D. retrocurva* was very different in the two years. In 1895 it declined in the early part of September and showed only a feeble rise in October, while in 1896 both species of *Daphnia* rose together at an equal rate, and remained practically identical in numbers until the sexual reproductive period of *D. retrocurva* was passed. I can hardly attribute this difference in the development of the species to anything excepting the occupation of the water by *D. hyalina* in 1895.

Another case in which competition may possibly play a part may be found in the spring development of the crustacea. In no year do *Diaptomus* or *Daphnia hyalina* begin to develop their swarms in the upper water until *Cyclops* has begun to decline, and its numbers in the upper water are greatly reduced. It would seem as though these latter species waited until *Cyclops* was out of the way before they began their main development. But in this case the increasing temperature of the lake is unquestionably a factor in the development, and the relation of competition is accordingly more doubtful.

HORIZONTAL DISTRIBUTION: SWARMS.

“Ob man die Befunde als Beweise der Ungleichheit oder der Gleichförmigkeit bezeichnen will, kann freilich so lange Geschmacksache bleiben, als man den Ausdruck nicht präcisirt. Falls man aber präcisirt und gleichmässig nennt wenn durchschnittlich die Dichte nur um das Doppelte oder Dreifache wechselt, ungleichmässig also, wenn die Vertheilung als so unregelmässig erweisen wird, wie etwa die Bewohnung der Erdfäche durch Menschen oder Thiere, so kann eine Meinungsverschiedenheit nicht wohl bestehen bleiben. Ich betrachte die Bewohnung einer Stadt noch als ziemlich gleichmässig und wenn

einmal an einer Stelle einige tausend Menschen zusammenströmen, so wird dadurch die Bewohnung noch nicht ungleichmässig." (Hensen, '95, p. 172.).

I have placed at the head of this section Hensen's words which seem to me to express with great clearness and wisdom the general truth regarding the still disputed question of the uniformity of the distribution of plankton animals. On no question relating to the plankton are opinions so widely at variance, yet no question is more fundamental to the value of numerical work in investigation. For example, Wesenberg-Lund says ('96, p. 153) that plankton animals occur "saa godt som altid i Svaerme." On the other hand Apstein says: ('96, p. 64) "Es ist bis jetzt nicht ein einziger wohl verbuergter Schwarm beobachtet worden." Thus in the same year opinions diametrically opposed are expressed, each based upon investigation. Under these circumstances the result of my work extending over two and a half years, including some 400 catches, each of which contained from 3 to 12 species, may contribute something to the discussion.

It is not easy to define what is meant by a "swarm." No student of the plankton expects to find the plants and animals distributed with absolute uniformity, and it is impossible to state the degree of variation in distribution which will entitle us to say that the species in question occurs in swarms. I agree with Apstein ('96, p. 53) that two- to fourfold variations are not to be counted as swarms. Apstein computes the actual distance of individuals of *Diaptomus* when the numbers are about 198,000 and 540,000 per square meter, and finds in the first case the average distance would be 2.2 mm. and in the second 1.36 mm. He rightly states that such a difference in distance does not justify the name of swarm. Most will agree, I think, that a ten-fold difference in numbers will justify the statement that such species occur in swarms. Certainly animals whose number differ to that extent are very irregularly distributed, and if they were found in large numbers in compact areas, and the space between these areas was thinly populated, it would not be unfair to say that the species appears in swarms.

In general, there is no evidence of swarms in my observations,

either of all the crustacea or of single species. It will be seen from the tables giving the maximum and minimum catches for each two week period that in the more numerous species the maximum catch is about four times the minimum, when the species is neither increasing or decreasing in numbers to any marked degree. Where the species is present in small numbers, the range of variation is far greater. Thus, in July, 1895, *Lep- todora* showed a variation from 1 to 50 individuals in the 39 catches made during that month. It varied from 1 to 19 in catches made on the same day, and was wholly irregular in its variations during the month. During the same month the catch of *Cyclops* varied from 1290 to 6100; and on no day were two catches made in which one was double the other. In each of 12 days in 1895 and 1896 two catches were made at points about two kilometers apart, and the ratio of the predominant species in these 12 cases was as follows:

	Average ratio.	Maximum ratio.	Minimum ratio.
<i>Diaptomus</i>	A:B::1:1.62	1:2.4	1:1.1
<i>Cyclops</i>	A:B::1:1.55	1:2	1:1.1
<i>D. hyalina</i>	A:B::1:1.58	1:2	1:1.1

In each case A denotes the smaller catch, which was about equally divided between the two stations.

Again, if comparisons are made of catches extending over a period of time when the average number remains nearly constant, and when there is no reproduction, the distribution can readily be inferred. Fifty-six catches of *Diaptomus* were made between December 1st, 1894, and March 30th, 1895. Of these there were:

Below 10,000 per square meter, 1 catch.	Between 40,000 and 50,000, 5 catches.
Between 10,000 and 20,000, 14 catches.	Between 50,000 and 60,000, 2 catches.
Between 20,000 and 30,000, 21 catches.	Over 70,000 per square meter, 1 catch.
Between 30,000 and 40,000, 12 catches.	

The figures also show that all of the December and January catches were below 30,000, all of March above 20,000, and only about one-fourth of them below 30,000; while the February

catches were scattered from 15,000 to 50,000. While there is considerable variety in these catches, yet, when the length of time and the number of observations are considered, the extent of variation lends no support to the theory of occurrence in swarms.

TABLE XXV.—*Diaptomus* and *Daphnia*.—December, 1894—April, 1895.
Expressed in thousands per sq. meter.

	<i>Diapto- mus.</i>	<i>Daphnia.</i>		<i>Diapto- mus.</i>	<i>Daphnia.</i>
December 3	19	103	February 15.....	17	51
	13	144		32	42
December 5	28	154	February 19.....	38	76
	27	93		41	109
	24	100		35	83
	23	116		29	86
	18	78	February 23.....	36	54
	25	91		43	60
December 7	26	133		48	66
	17	118	March 6.....	24	30
December 19	17	57		29	41
	23	41	March 7.....	31	48
January 1	13	45		32	69
	17	52		51	45
	25	55	March 9.....	36	56
January 2	12	48		27	26
	22	65	March 12	28	28
	22	41		45	63
January 6	15	36		56	60
	8	39		27	39
	11	36	March 16	34	83
January 9	29	54		45	102
	16	57		33	86
	20	60		71	103
January 16.....	16	53	March 18	32	69
	13	61		34	72
	23	53	March 23	33	39
February 14	23	43		27	40

The foregoing table shows the numbers of *Diaptomus* and *Daphnia hyalina* during the winter of 1894-5. Similar results

were found in the same species during the winter of 1895-6 and indeed similar tables could be constructed for any species fairly numerous, and neither increasing nor declining in numbers.

On July 21 and August 15, 1896, a series of catches was made extending across the lake some 5 kilometers, at approximately equal distances. The result of the latter catch is given in the accompanying table; the other was substantially the same.

TABLE XXVI.—Collections on August 18, 1896, expressed in thousands per square meter.

	I.	II.	III.	IV.	VI.	VII.
Diaptomus	27	51	40	80	74	83
Cyclops	184	203	142	136	127	145
D. pulicaria	57	31	3.3
D. hyalina	37	31	15	33	33	38
D. retrocurva	13	16	7	11	3.3	20
Diaphanosoma	10	18	13	27	33	49
Chydorus	35	217	184	154	174	147
Leptodora	0.7	1.5	0.2	0.5	0.5
Ergasilus	17	16	3.3	8.9	0.5
Nauplii	241	337	?	236	134	167
Corethra	6	8	1.1	1.2	1.3	4.4
Asplancha	114	101	33	66	40	45
Total crustacea.....	631.7	921.5	*407.6	686.1	678.8	650

* No nauplii included.

The number of *Cyclops* when at its maximum showed surprisingly little variation. In 1895 from May 1st to June 6th, 26 catches were made on 13 days. The catch ranged from 10,000 to 20,000 individuals actually caught. In 1896, 18 catches were made on 16 days. The numbers ranged from 9,000 to 37,000. A figure is added (Fig. 21) showing the number of *Cyclops* caught during the year 1895. It will be seen that the diagram gives no warranty to the conclusion that this species appears in swarms. Similar illustrations could be taken from any year, and from almost any species, with the qualification that the range in number is greater in the case of those species whose numbers are small.

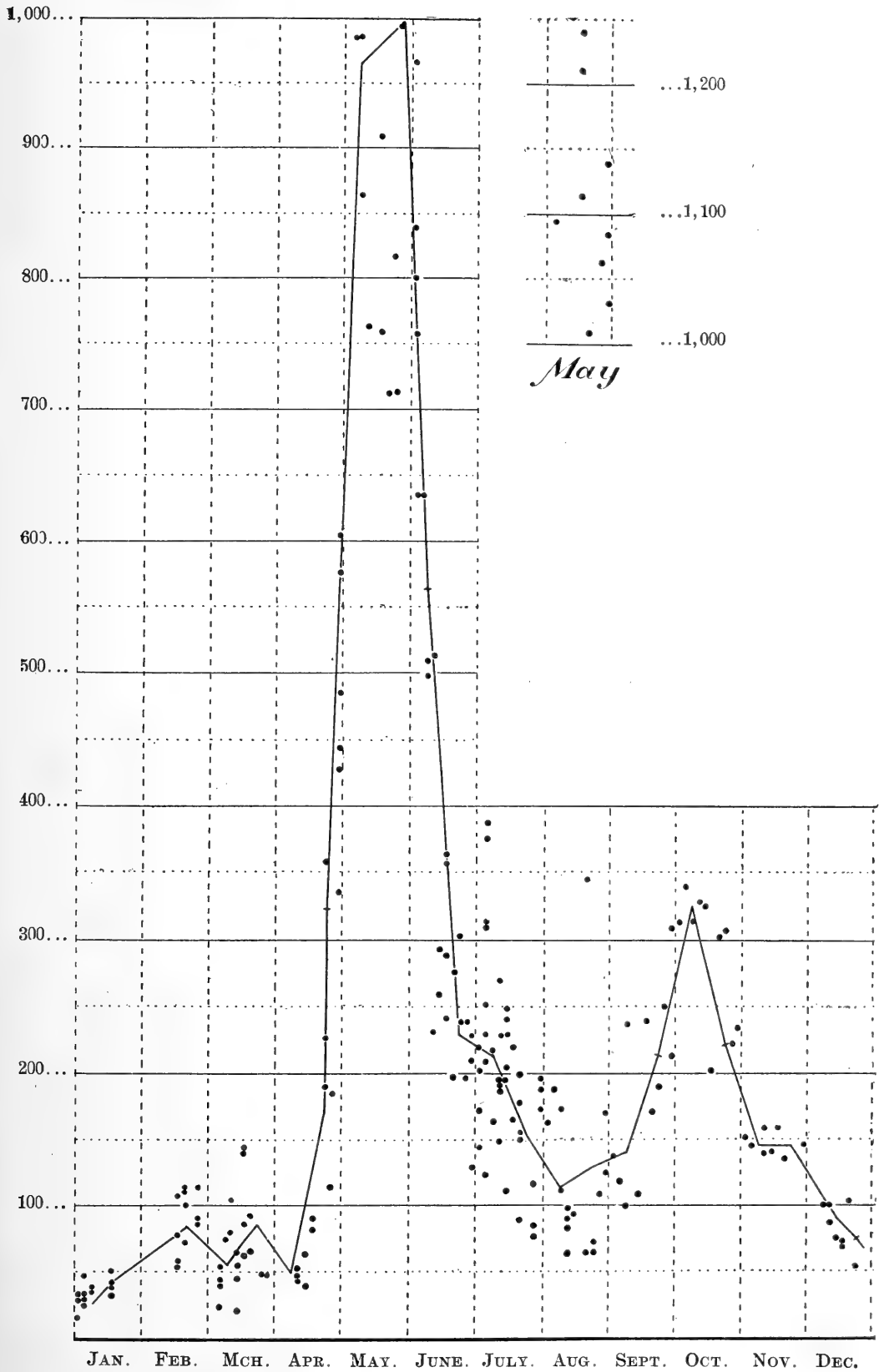
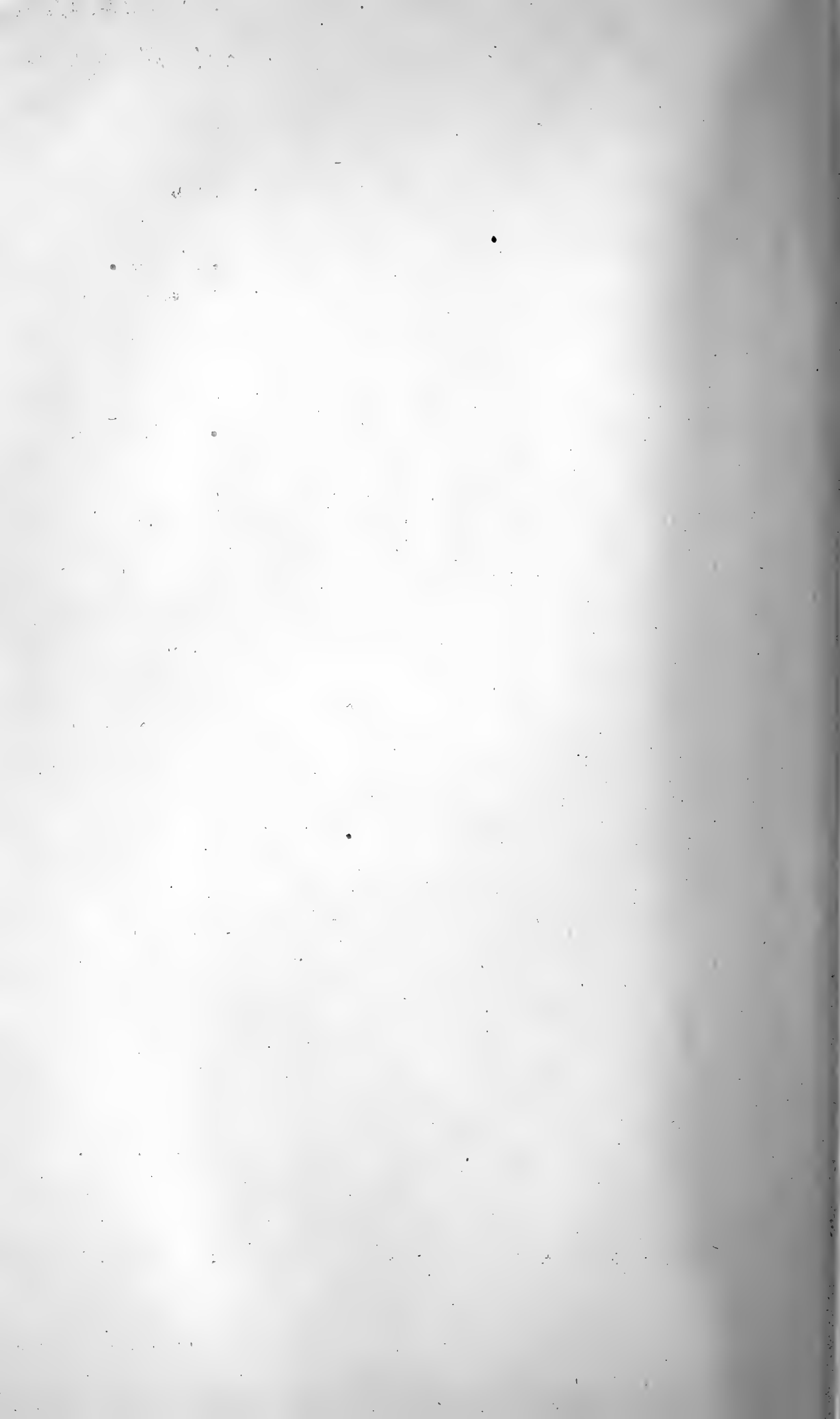


FIG. 21.—Cyclops. Number of each catch, 1895. The curve indicates the average. Scale, 1 vertical space = 100,000 crustacea per sq. m. See p. 370.



The following table gives the variations of the total number of the crustacea during three months of 1896. It will be seen the variations are somewhat smaller than are those of the single species but are of a similar character, and also resemble those of Table XXVI.

TABLE XXVII.—Total crustacea, May—July, 1896.

	Average.	Maximum.	Minimum.	No. observations.
May 1-15.....	2,398	2,966	1,615	8
May 16-31.....	1,901	2,963	1,177	8
June 1-15.....	845	1,977	561	9
June 16-30.....	1,265	1,908	890	9
July 1-15.....	1,314	2,332	1,005	6
July 16-31.....	795	1,266	511	11

I think that I have given here and in the tables of the appendix, sufficient evidence to enable the student to understand the extent of the variation in the distribution of the crustacea. I do not know whether the figures will be interpreted as showing an equal or unequal distribution. I judge that Marsh, from his discussion of the subject ('97, p. 218, ff.) would regard the distribution as irregular. I think that it is quite as uniform as Apstein would expect. For myself, I have never supposed that every square decimeter of the surface of the lake covered an equal number of crustacea. I have been surprised that a net 20 cm. or 10 cm. in diameter should disclose such a uniform number as it actually shows, especially in the case of organisms so highly organized as the Entomostraca.

On the other hand, there is clear evidence for swarms in certain species of crustacea, and at certain times. (1) The distribution of *Daphnia pulicaria* is very irregular, far more so than that of any of its congeners. This species in lake Mendota is confined during summer to the region of the thermocline, and as this stratum works downward through the lake in summer, the area inhabitable by the species is contracted around the edge of the lake, and the crustacea as they move out from the shore to keep in the cool water, may accumulate in swarms. These have already been mentioned in connection with

the species. The most conspicuous case occurred in August, 1895. On the 21st of the month the catch of *Daphnia pulicaria* was somewhat under 500; on the 22d it was nearly 2,600, and on the 27th it was only 85. This aggregation of the species was due to the wind carrying a current of warm water through the deeper levels at the point of dredging and so driving into deep water the individuals near shore, and the decline in number was due to the removal of the large numbers by currents rather than to the final scattering of the swarm.

When a species has once aggregated in this manner, the aggregation may last for a considerable length of time; and *Daphnia pulicaria* always showed a greater range of variation in its numbers than did any other species, apparently due to these temperature aggregations in summer. For example, on April 18th, 1896, at one point in the lake, 3,060 of this species was caught; while another catch, at a distance of some two kilometers, showed only 230. On December 23, 1895, two catches were made of 260, and 3,440 respectively. See also the lateral distribution in Table XXVI, above, which discloses a similar want of uniformity. A distribution so irregular as this, it seems to me, fairly warrants the title of "swarm." I may add that late in the spring the species become more uniformly distributed, and when at its maximum showed a variation of less than three-fold in 10 catches, distributed over 21 days.

(2) Apstein has found no case where a swarm has been seen. I have observed true swarms of *Daphnia hyalina* on at least three occasions. On October 17th, 1895, about 9 a. m. a large swarm of this species was seen at the surface near the dredging station about 800 meters from the shore. The water was perfectly calm, and the sun was bright. The Daphnias were aggregated at the surface to a depth of about 5 cm. or less and within that depth the water was completely filled with them. The swarm was about 50 meters in width, and its edges were perfectly distinct, as the boat passed slowly in and out of it. The length of the swarm was probably three times the width. All of these animals were adult, so that they were easily seen with the naked eye. The occurrence was the more unusual as the bright sun should have kept this species well below the surface.

Two similar swarms of the same species were seen in 1896 on October 3rd, and on November 3rd; both days when the lake was perfectly calm. On the first occasion there was a fog on the water; on the second occasion the sky was clear. These swarms were nearer the shore and were much more extensive. On the first occasion the *Daphnias* occurred in patches of irregular extent and shape—perhaps 10 meters by 50 meters, and these patches extended in a long belt parallel to the shore. The surface water was crowded by the *Daphnias*, and an immense number of perch were feeding upon them. The swarm was watched for more than an hour, during which the fog passed away, and the water could be seen disturbed by the perch along the shore as far as the eye could reach as one was standing in a boat. After a time a light breeze sprang up and, of course, prevented further observation. On this occasion the number was determined to be 1,170,000 per cu. m. in the densest part of the swarm. On November 3rd a similar swarm was seen, and water was again dipped up from the denser part of the swarm. The crustacea were crowded into an extremely thin layer, not more than 2–3 cm. thick. The surface water only was allowed to fall into the vessel and the number determined in 6 catches made by straining 10 liters of water, was from 800,000 to 1,492,000 *Daphnias* per cubic meter, about 99 per cent. adult. In addition there were present about 1,000 *Cyclops* per cubic meter, but nothing else was found. On this occasion one ephippial female was present, the only one that I have ever seen in this species; the ephippium was fairly developed, but no eggs had been deposited in it. No males were in these swarms.

The highest number is found nearly ten times the maximum number of this species per cubic meter, as derived from the three-meter hauls. It is also nearly fifty per cent. more than the maximum catch of this species as obtained from a depth of 18 meters, and nearly five times as great as the average for November 1–15. On November 3d, catches were made below the swarm from 0.3m. to 3.3m. The average of two gave per cubic meter:

<i>Diaptomus</i>	4,900
<i>Cyclops</i>	26,600
<i>D. hyalina</i>	18,200
<i>Chydorus</i>	15,700

The average of *D. hyalina* in the 0–3m. level for the first half of November was 32,200 per cubic meter, of which at least half were immature, so that the catch of November 3d was not an exceptionally low one. These facts show that the swarm in question was a lateral aggregation and not merely a gathering at the surface of the individuals ordinarily below it.

Great numbers of individuals broke through the surface film of the water on all of these occasions.

This aggregation of *Daphnia hyalina* in swarms is probably more frequent than the number of observations would indicate. The swarms are found in the surface water, so that they are dislodged by the slightest breeze, and it is impossible to see them unless the water is entirely smooth. This condition is not often reached, and I have felt myself exceedingly fortunate in being able to observe this phenomenon on so many as three occasions. I may say, however, that during the autumn of 1896, I looked for these swarms on every calm day when it was possible for me to go out on the lake, but found them only twice.

The significance of these aggregations is difficult to state. The habits of the animal are completely reversed in one respect. The adults are strongly negative in their relation to light, and under the conditions of all these occasions should have been found at a depth of one-half to one meter below the surface. It is possible that these aggregations represent the remains of a former sexual period. This may be indicated by the presence of the ehippial female. I have no doubt that *Daphnia hyalina* had at one time two sexual periods, in spring and fall, of which these swarms may be a remainder, but since the few males which appeared in the fall came at a time decidedly later than the earlier of these aggregations, I do not feel warranted in positively interpreting the swarms in this sense.

These swarms of *Daphnia* seem to be phenomena of the same order as those described by Francé ('94, p. 37). In one case the swarm was near the littoral region, as were those described by him. In the other cases they were well out in the limnetic region. The swarm was confined within vertical limits even narrower than the one meter named by him and in all three cases the swarm was "von weitem erkennbar."

While, therefore, I find swarms occasionally present, I find also that the crustacea of lake Mendota are in general distributed with marked uniformity. Marsh ('97, p. 220) finds an ordinary variation of ten-fold in the numbers of *Diaptomus* and an even greater variation in the case of other limnetic crustacea. With the exceptions already noted the range of variation in lake Mendota has not often exceeded four fold. The number of observations, therefore, necessary to give a fair average for the population of the lake is not so great as that spoken of by Marsh. The examination of my records shows that the general development of the crustacea can perfectly well be determined by catches taken at intervals of a week and that the vertical distribution, if computed from such observations, would agree very closely with that reached from the very much larger number actually used. Of course the larger and rarer forms, like *Epischura* and *Leptodora*, vary in number very greatly. No one would attempt to compute the population of a lake from the presence of a single *Leptodora* in the catch, or from the occasional presence of half a dozen, or more, but the numbers of the crustacea which are the regular constituents of the limnoplankton vary within comparatively narrow limits in lake Mendota, and I feel confident that my averages fairly represent the crustacean population. The variation of the numbers of the crustacea in lake Mendota does not support extreme views either on the side of uniformity of distribution or the opposing theory of swarms.

In connection with reconnoissance observations it may be well to remember the following: Exceptionally large catches are due to the presence of great numbers of young, and exceptionally small ones usually contain few young. A catch containing great numbers of young may therefore be suspected to be unusually large and one with few young, if taken in summer or fall, to be small for the lake from which it comes.

THE VERTICAL DISTRIBUTION OF THE CRUSTACEA.

In making collections to determine the vertical distribution of the crustacea the same general method was followed as that described in detail in my former paper. (Birge, '95, p. 429.) The

dredge was lowered to the bottom of the level from which specimens were to be taken, raised through the proper space, and then closed by means of a messenger sent down the line. It was then drawn to the surface, washed out, and the collection preserved for future study.

My observations show so much variation in catches made at the same place and in succession that I have little confidence in the differential method of determining vertical distribution; unless a very large number of observations is made and averaged, so as to eliminate the chance of variation in the single observation. See p. 281.

The distance employed in all of my collections was three meters. This interval was selected because it divided the lake at the point of observation into six levels of uniform thickness, and also because of the close correspondence between three meters and ten feet. Experience has shown that the distance was fortunately chosen as the number of crustacea begins to decline rapidly between 2 and 3 m. from the surface. The place of regular observation is about 850 meters from shore, where the water is about 18.5 meters in depth or somewhat more when the water is highest in the spring of the year. The greatest depth observed in the lake is between 23 and 24 meters. The slope of the bottom in the deeper water is very gradual, and a depth substantially greater than 18 meters is only reached at a considerably greater distance from the shore. If observations had been made in the deepest part of the lake, the distribution as shown in thousands per cubic meter would not vary from the facts as shown in the tables, nor would the summer percentile distribution be altered, since during the summer the deeper parts of the lake contain no crustacea. During the fall and winter months the distribution is nearly uniform in the lower water. The average percentile distribution would, of course, be changed by the addition of one or more levels during winter, and the aggregations of crustacea, especially *Cyclops*, which are found in the bottom levels, would of course, be moved from the 15–18 m. level to those lying below. Observations were made occasionally in the deeper water, as often as once a week during the summer and fall months; less

frequently during the winter. But as the observations were few in number in comparison with those made at the regular point of observation, they have not been used in the preparation of the tables.

During the last half of the year 1894, 75 serial observations were made, 127 during 1895, and 131 during 1896. These were most numerous during the summer months. In general it may be said that on every day on which observations were made as stated in Table A of the appendix, a series was taken, and on some occasions more than one. The general distribution, of the observations, however, can be ascertained from the table. At least five were made in each two week period from the middle of April to the middle of November. During the winter of 1895, some observations were made by six meter intervals in the lower water of the lake, and the result of these observations was equally divided between the two levels covered by them.

In Table B, accompanying this part of the report, the population of each level is given in thousands per cubic meter, the total population of the level being divided by three on the assumption that the crustacea are equally distributed throughout the level. Under some circumstances this assumption is incorrect. In the 0-3 m. level, the upper meter contains more than one-third of the crustacea, especially when there are large numbers of young. It may contain twice as many as any meter below. On the other hand, on bright calm days, when few young crustacea are present, the upper meter may contain less than one-third of the total catch from the upper level.

In the level which includes the region of the thermocline the population of the single meters varies greatly, as will be shown later in this paper; the crustacea being found in considerable numbers above this stratum and practically absent below it. A third error arises at times when large numbers of crustacea are settling to the bottom and dying. This occurs with *Cyclops* during the winter and spring, and with *Daphnia hyalina* in the early part of June. At such times the lower meter of the lower level would contain more than one-third of the crustacea present in that level. These variations from an approximately uniform distribution are however so varying themselves that it has not been

thought wise to attempt to distribute the crustacea among the three meters of each level on any other assumption than that of uniform distribution.

THE GENERAL VERTICAL DISTRIBUTION OF THE CRUSTACEA.

Figs. 22–28, Tables B and C, Appendix.

Winter — January, February, March.

The months during which the lake is covered with ice show a great equality of distribution on the part of the crustacea. This is due to several facts. First, the lake is thoroughly homothermous, at least in a biological sense. Differences exceeding a degree between the temperature of the water at one meter from the surface and at the bottom of the lake are only found in late winter. Second, the food has no such concentration toward the surface as is found in the summer, though the algae are more abundant in the upper strata. Third, the action of the wind is removed, and the influence of the sun is greatly reduced, both by the snow and ice and by the low temperature of the water. Fourth, there is no reproduction of most species of crustacea and consequently no difference in age to influence distribution.

A few forces act in the other way: First, the food is more plentiful near the surface, as the algae reproduce more abundantly there. Second, when *Daphnia pulicaria* is present it is far more abundant in the upper strata of the water than below. Third, *Cyclops* often appears in swarms near the bottom of the lake. Fourth, If *Cyclops* reproduces during the winter the young are more numerous toward the surface.

Tables B and C of the appendix show that during January, February, and the early part of March, 1895, there was very little difference in the population of the four upper levels. In January of that year the lower strata were decidedly poorer in number than those above; while in the latter part of the winter they were the most populous, owing to the accumulation of *Cyclops* in those levels. In the winter of 1896, the 0–3 m. level was at least twice as populous as any below, owing to the large num-

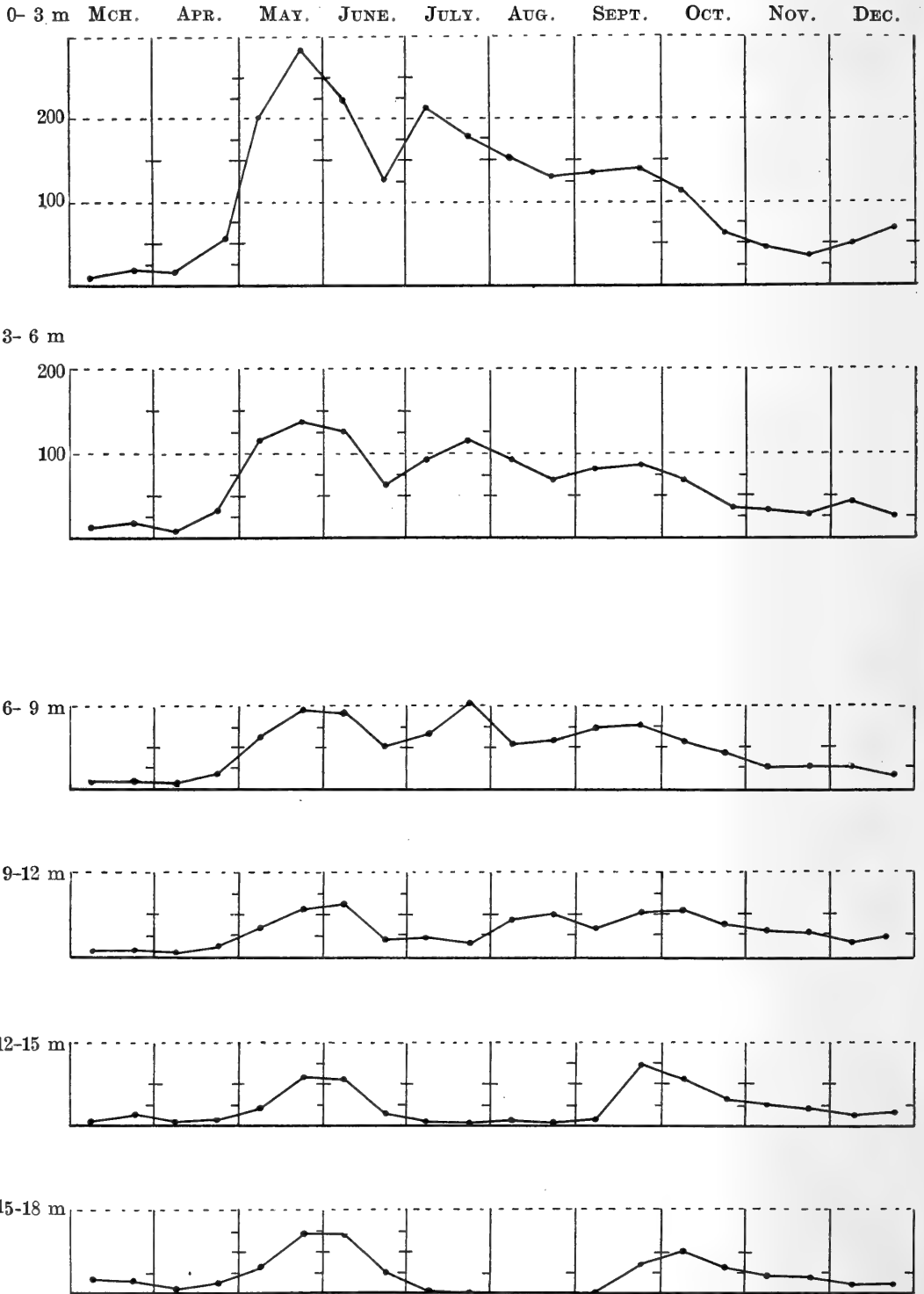


FIG. 22.—Population of the 3 m. levels, 1895. Scale, 1 space = 100,000 crustacea. The 25,000 and 50,000 divisions are indicated. See page 387.

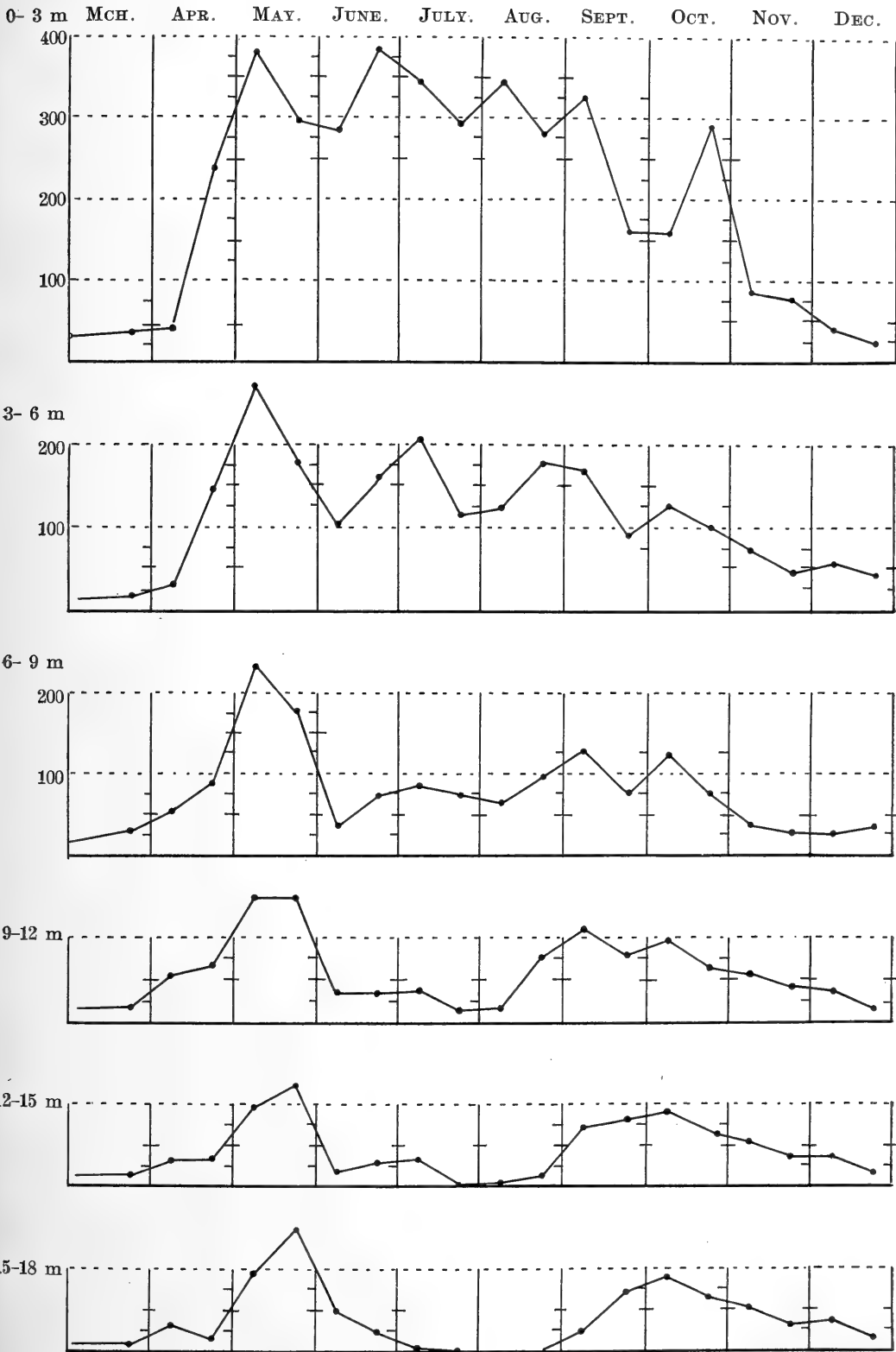


FIG. 23.—Population of the 3 m. levels, 1896. Scale, 1 vertical space = 100,000 crustacea per sq. meter. See p. 387.



ber of *Daphnia pulicaria* present in that winter. The 15–18 m. level was the second in population, except in the early part of January, owing again to the accumulation of *Cyclops* in that region. The middle strata of the lake were the poorest in population in both years.

Some illustrations may be added showing the concentration of the two species in question in the lower and upper water of the lake respectively. On February 15th, 1895, out of 870 *Cyclops* taken by the net, 570 were below 12 meters; on the 19th 880 out of 1,130. On March 9th, 1,017 were found below 15 meters, out of a total of 1,650; on March 12th, 485 out of 710. This aggregation at the bottom was not seen in January, and some few catches of later date did not display it.

In 1896 the same tendency was shown, and began as early as January. On the 7th of that month 1,250 *Cyclops* out of 2,070 were below 12 meters, and similar catches were made through January and February. In March the old *Cyclops* were greatly reduced in number, aggregated only about 640 individuals for the whole depth, and showed no tendency to collect at the bottom. At this time the young *Cyclops* were present, averaging over 2,000 to the catch, and the 0–3 m. level contained about twice as many as any other.

Daphnia pulicaria was absent in 1895 but was numerous in 1896. During January and until the middle of February there were at least five times as many in the 0–3 m. level as in any lower one. As the numbers declined in February they fell off chiefly where they were the greatest and the 0–3 m. level became about twice as populous as any below.

Thus the tables of distribution in winter for 1895 and 1896 show resemblances and differences. In 1895 the 0–3 m. level shows no noteworthy excess over those below, while in 1896 it is about twice as populous. Between 65 and 70 per cent. of the population of this level in 1896 are due to *Daphnia pulicaria*. In both years the bottom water is more populous than that at the middle of the lake, due to the settling of *Cyclops*. This species furnished from 75 to 85 per cent. of the population of the bottom level in both years. The average population per cubic meter is much greater in 1896 than in 1895, especially so in

January; but the population fell off more rapidly in the latter part of that winter, and there was no very noticeable difference in March.

TABLE XXVIII.—*Average percentile distribution for the winter — January, February, March.*

	PER CENT. IN EACH 3 M. LEVEL.						
	Average No.	0-3m.	3-6.	6-9.	9-12.	12-15.	15-18.
1895.....	123,000	18.1	19.3	13.7	12.8	15.8	20.3
1896.....	237,000*	34.1	15.7	14.8	10.8	10.3	13.6

* *Chydorus* omitted on account of its rapid decrease in late winter.

Spring—April and May.

Tables B, C, Appendix.

The distribution of the crustacea during the first half of April is on the whole fairly equal in the different levels of the lake, but with irregularities which mark it as an accidental distribution. The ice breaks up in the first days of April, and the lake is consequently exposed to the action of the wind. The temperature is fairly uniform at all depths, and the algae hardly begin rapid multiplication much before the middle of April. The water at this time has a more active circulation than at any other, as is shown by the presence in the net of numerous particles of vegetable debris from the soft mud at the bottom of the lake.

During this time *Cyclops* begins its rapid increase towards the spring maximum, if the multiplication has not already begun under the ice. Its swarms of young are in the upper strata of the water. It may be laid down as a general rule that large numbers of young of any species of crustacea appear first in the upper levels of the water, and the animals later pass toward the middle of the lake; and later still, occupy the water toward the bottom. It may be said, therefore, in general, that the presence in the upper water of a very high percentage of the catch of any species indicates the beginning of a period of re-

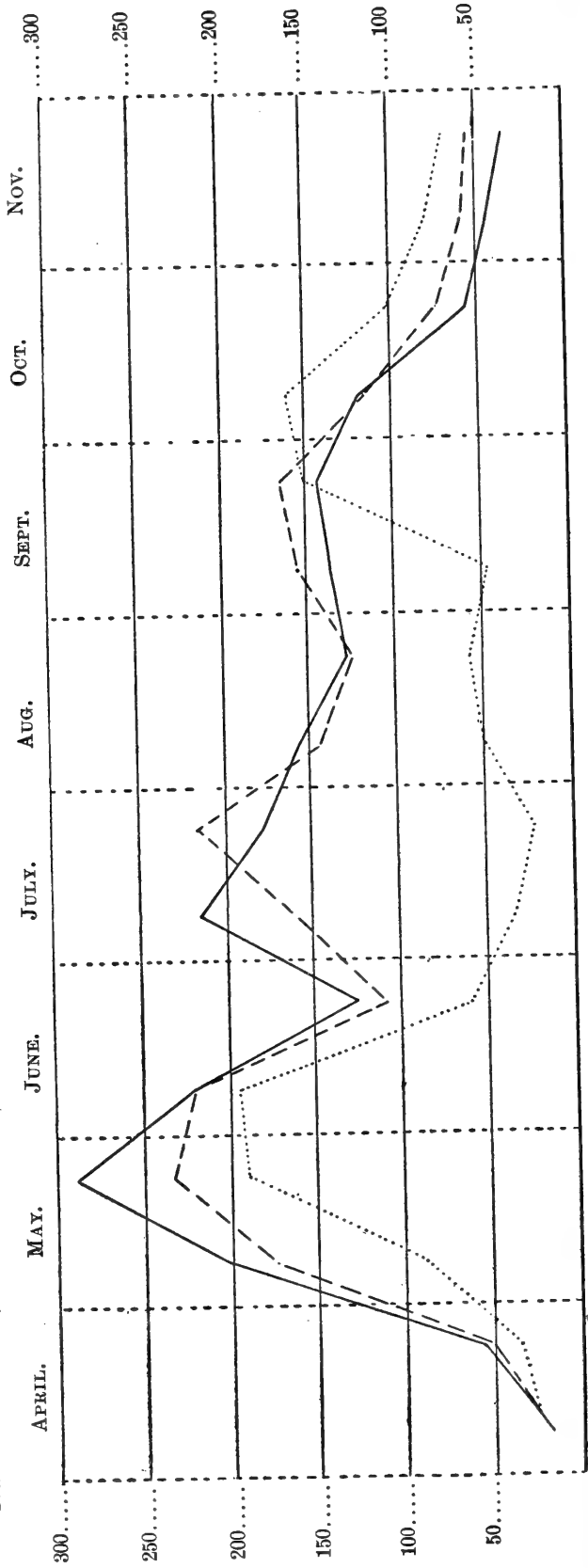


FIG. 24.—Vertical distribution, 1895. Scale, 1 vertical space = 50,000 crustacea per square meter.

0-3 m.....

3-9 m.....

9-18 m.....

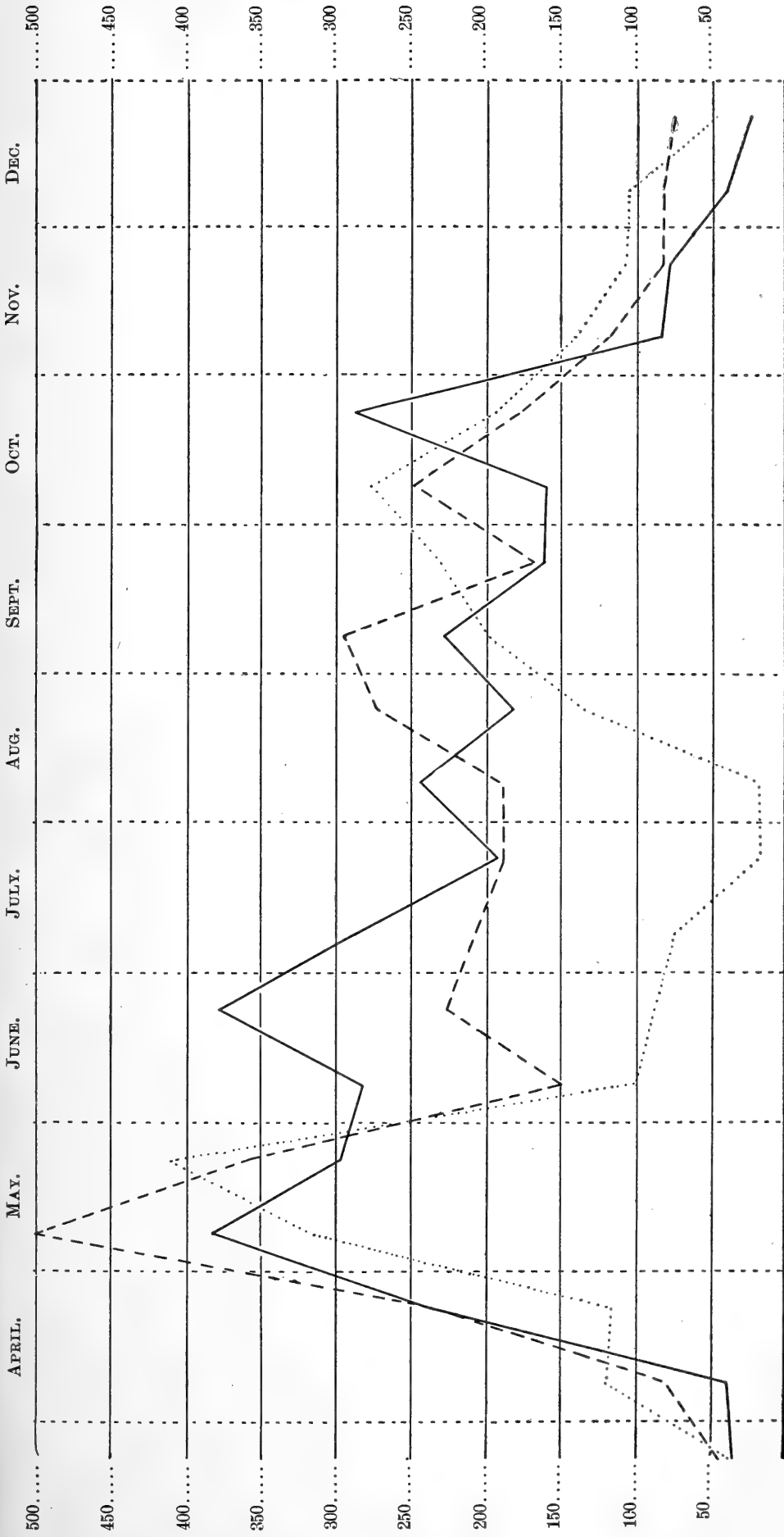
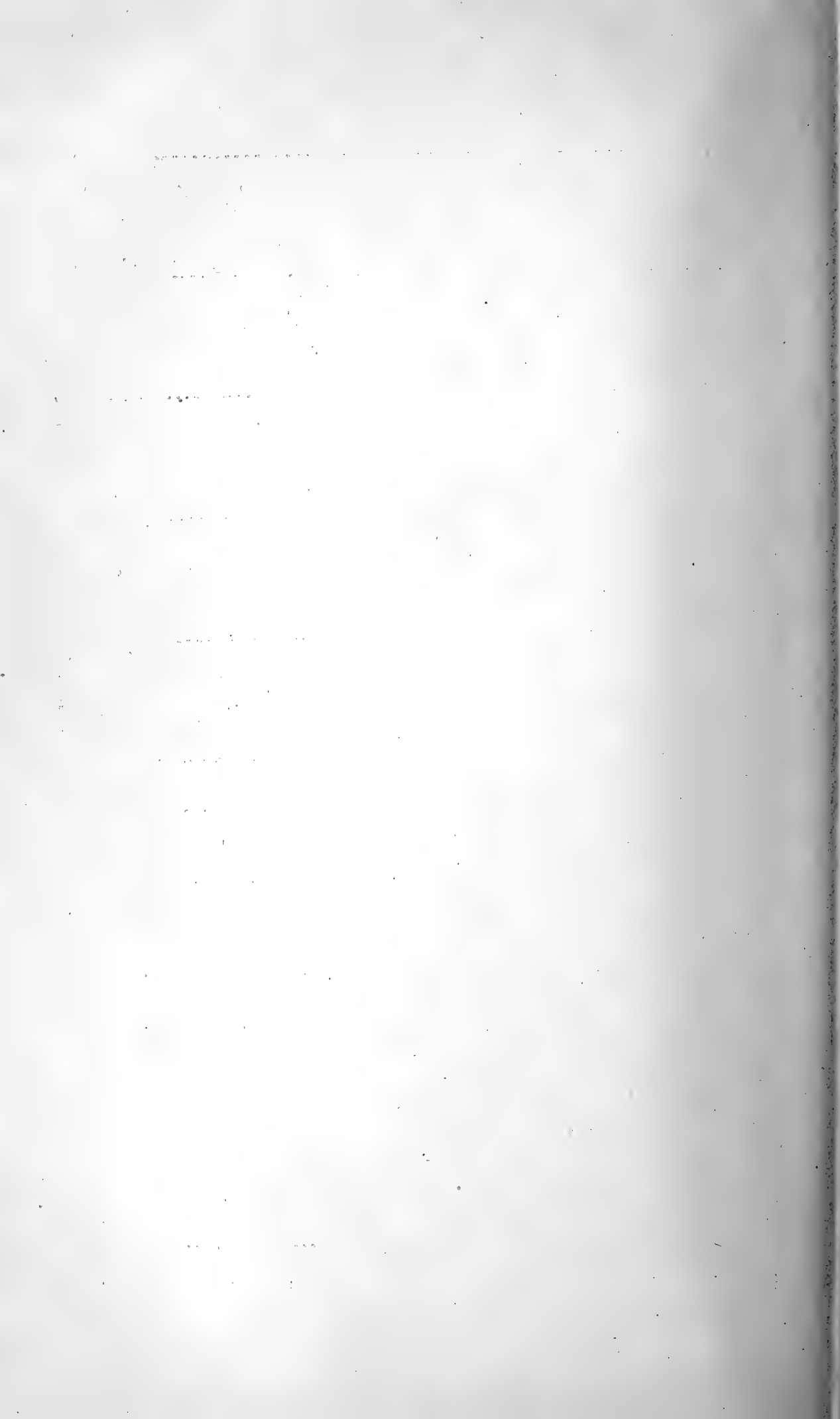


FIG. 25.—Vertical distribution, 1896. Scale, 1 vertical space = 50,000 crustacea per sq. meter. See p. 381.

- 0-3 m.....
- 3-9 m.....
- 9-18 m.....



production of the species, while the presence of a larger number in the bottom water of the lake than in the surface water indicates that the species is past its maximum and is already beginning to decline in numbers.

In both years the numbers of crustacea in the upper water show an increase during April, due to the multiplication of *Cyclops*. This increase went on, as was shown in the early part of this paper, much more rapidly in 1896 than in 1895. As a result, the population both of the surface water and of the lower levels increased much more rapidly in 1896, and the latter part of April, 1896, represents about the same condition of the development of the crustacea, as does the first half of May in 1895. In each case more than 40 per cent. of the crustacea were present in the upper stratum, while the 15–18 m. level had not increased greatly in numbers above its condition in winter. In the latter part of April, 1896, the 15–18 m. level contained less than 3 per cent. of the whole number of crustacea present; and in the first part of May, 1895, it contained less than 7 per cent. As the number of *Cyclops* and *Daphnia pulex* became greater, they moved downward into the deeper water, so that it became relatively more populous. In the latter part of May, 1895, the 15–18 m. level contained 10 per cent. of the crustacea, while in 1896 it contained over 40 per cent. This increase in the population of the lower strata goes on after a considerable decline has come in that of the upper strata. The lower water lags behind the upper both in the increase and decrease of its population, and the maximum population of the lower strata comes from two to three weeks after the maximum population of the lake has passed.

These relations become more obvious if we divide the lake somewhat arbitrarily into three levels, 0–3 m., 3–9 m., 9–18 m. The distribution of the crustacea among these three regions is shown in Figs. 24 and 25. By reference to these it will be seen that in 1895 the two upper levels increased much more rapidly than did the lower half of the lake from the latter part of April to the middle of May. In the latter part of May the reverse is true; and in early June the population of the lower water was stationary, while that of the upper half of the lake

was rapidly declining. In late June the population of all levels declines altogether.

This relation is even more conspicuous in the diagram for 1896. The population below 9 meters did not increase at all until the end of April, while that of the upper levels increased several fold, the 0–3 m. level growing more rapidly than that below. In the first half of May the lower half of the lake gained absolutely more than either of the levels above, its gains per cubic meter being about half as great as those of the upper water. In the last of May the levels below 12 meters continued to gain, while the 9–12 m. level was approximately stationary, and the upper strata fell off rapidly and about equally. At this time the lower half of the lake contained nearly 40 per cent. of the total number of crustacea, nearly equally distributed, while the upper three meters contained only about 28 per cent. In early June all the strata below the 0–3 m. level lost heavily, owing to the disappearance of the spring broods of *Cyclops* and *D. pulicaria*; while the 0–3 m. level remained approximately stationary, the new broods of *Chydorus* and *Diaptomus*, which appeared in that level, compensating for the decline in other species. The result of this decline in the population of the lower water serves to give the 0–3 m. stratum over 50 per cent. of the whole population, and the number in this level continues between 45 and 50 per cent. during the remainder of the summer.

Summer — From the middle of June to the middle of September.

The change from the late spring to the early summer has just been spoken of. The most important fact influencing the vertical distribution at this time is the formation of the thermocline, and the accompanying exclusion of the crustacea from the lower waters of the lake, and ultimately from the entire region below the thermocline. The thermocline was observed in each year about the middle of June — June 11th, 1895, June 13th, 1896 — and was present regularly afterward. The depopulation of the lower waters does not coincide with these dates, as will be seen from the tables. This would be expected since the exclusion of the crustacea is due to the chemical condition of the lower water,

resulting from the temperature conditions. In both years the population of the lower half of the lake in the latter part of June is equal to or greater than that in the same region in the early or even the latter part of April. The population of the 9–12 m. level remained substantially stationary until the middle of June, 1895, and the same was true of this level and the level below until the middle of July, 1896. In June, 1895, the population of the bottom level was high, owing to the accumulation there of large numbers of diseased and dying *Daphnia hyalina*; but as soon as these had died, the numbers rapidly fell off, and the population in the 15–18 m. level was very small in the first half of July.

In 1894, observations begun with the 1st of July, and at that time the population below 9 m. was extremely small, far smaller than in either of the succeeding years. At that time the temperature conditions below the surface were not observed, but it is fair to infer that the thermocline was established at a comparatively early date in that year. A second fact which influenced the distribution in 1894 is the unusual preponderance of *Diaptomus* among the crustacea in that year. A very high percentage of this species is found at all times in the upper water, while *Cyclops*, whose per cent. in the lower water is greater than that of any other species, was represented by very small numbers.

During July the population of the waters below 9 m. declines very rapidly, as will be seen from the table which gives the population of the lower water during the months of June, July and August.

TABLE XXIX.—Population per cubic meter.

	1895.			1896.		
	9-12 m.	12-15 m.	15-18 m.	9-12 m.	12-15 m.	15-18 m.
June 1-15.....	45,000	36,000	46,600	24,000	12,600	30,600
June 16-30.....	13,300	9,200	17,500	24,200	18,800	15,000
July 1-15 ..	14,200	4,200	2,200	25,100	20,900	2,600
July 16-31.....	10,900	2,100	1,400	9,700	700	300
August 1-15.....	27,500	4,100	600	11,200	1,200	20
August 16-31.....	32,700	3,500	550	49,600	6,900	500

While the absolute population of the lake during the summer months has varied very greatly in the three years of my observation, the vertical distribution of the animals has been almost exactly the same, as may be seen from the following table:

TABLE XXX.—Average percentile distribution of crustacea June 15–Sept. 15. (In 1894, July 7–Aug. 23.)

Average No.	PER CENT. IN EACH 3 M. LEVEL.					
	0-3m.	3-6.	6-9.	9-12.	12-15.	15-18.
1894.....406,000	45.5	30.2	16.0	6.7	1.3	0.4
1895.....707,000	44.0	24.6	18.4	8.9	2.2	1.9
1896.....1,116,000	45.1	27.5	14.9	7.7	3.4	1.2

From this it appears that from 44 to 45.5 per cent. of the crustacea were present in the upper three meters of the lake from the middle of June to the middle of September, and from 25 to 30 per cent. more between 3 and 6 meters, from 15 to 18 between 6 and 9 meters, leaving from 8.5 to 13 per cent. for the lower half of the lake.

The percentile distribution of the crustacea during the summer and its relation to the thermocline are shown in Figs. 26 and 27. In each diagram the depth is computed above which were found in each half month, respectively 25, 50, 75, 90, and 95 per cent. of the crustacea, on the assumption that the crustacea in each of the 3m. levels were equally distributed through it. The points representing the depths for the corresponding percentages were platted on the diagram and then connected by lines. There is added in each diagram the position of the isotherm of 20° which lay in the thermocline in both years, although in 1896 the lake cooled below 20° before the thermocline disappeared. In Fig. 26, the temperature for each date was computed from the average of the week preceding and that following the date. The temperature-line of Fig. 27 is taken from Fig. 4.

The diagrams show that 25 per cent. of the crustacea are almost always found in the upper two meters of the lake. No doubt the position of this line would be higher if it had been

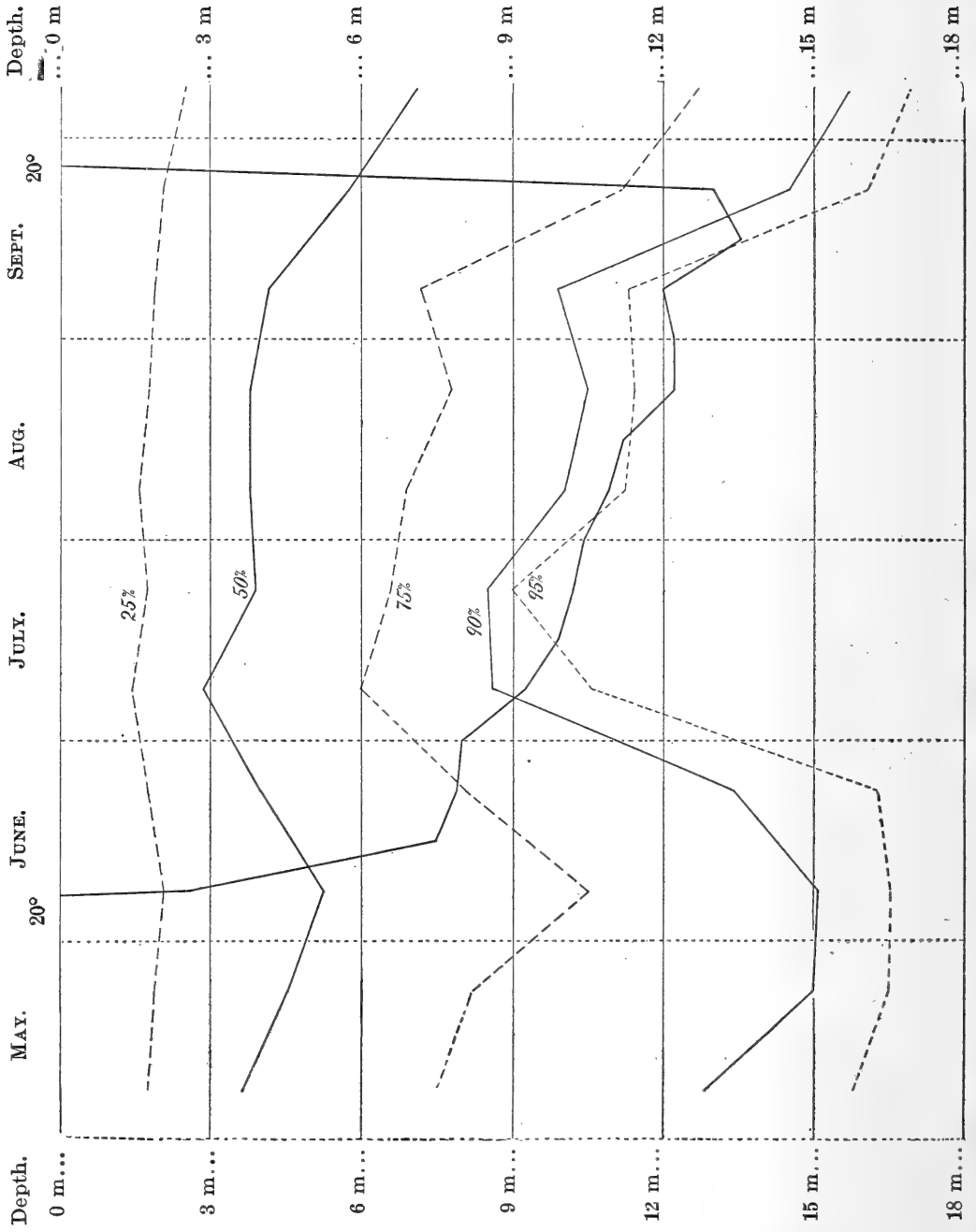


FIG. 26.—Percentile vertical distribution of crustacea, summer of 1895. See p. 384.

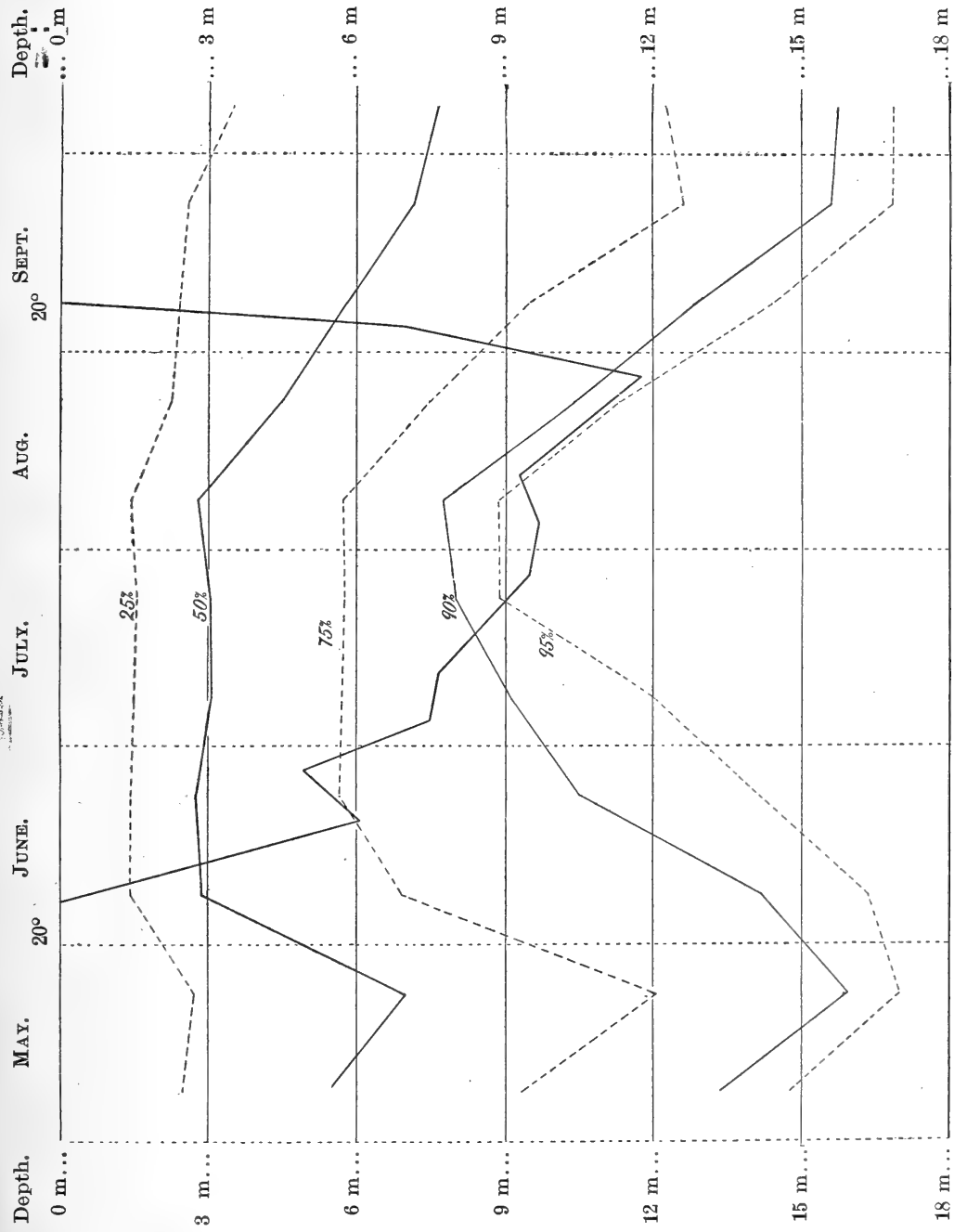
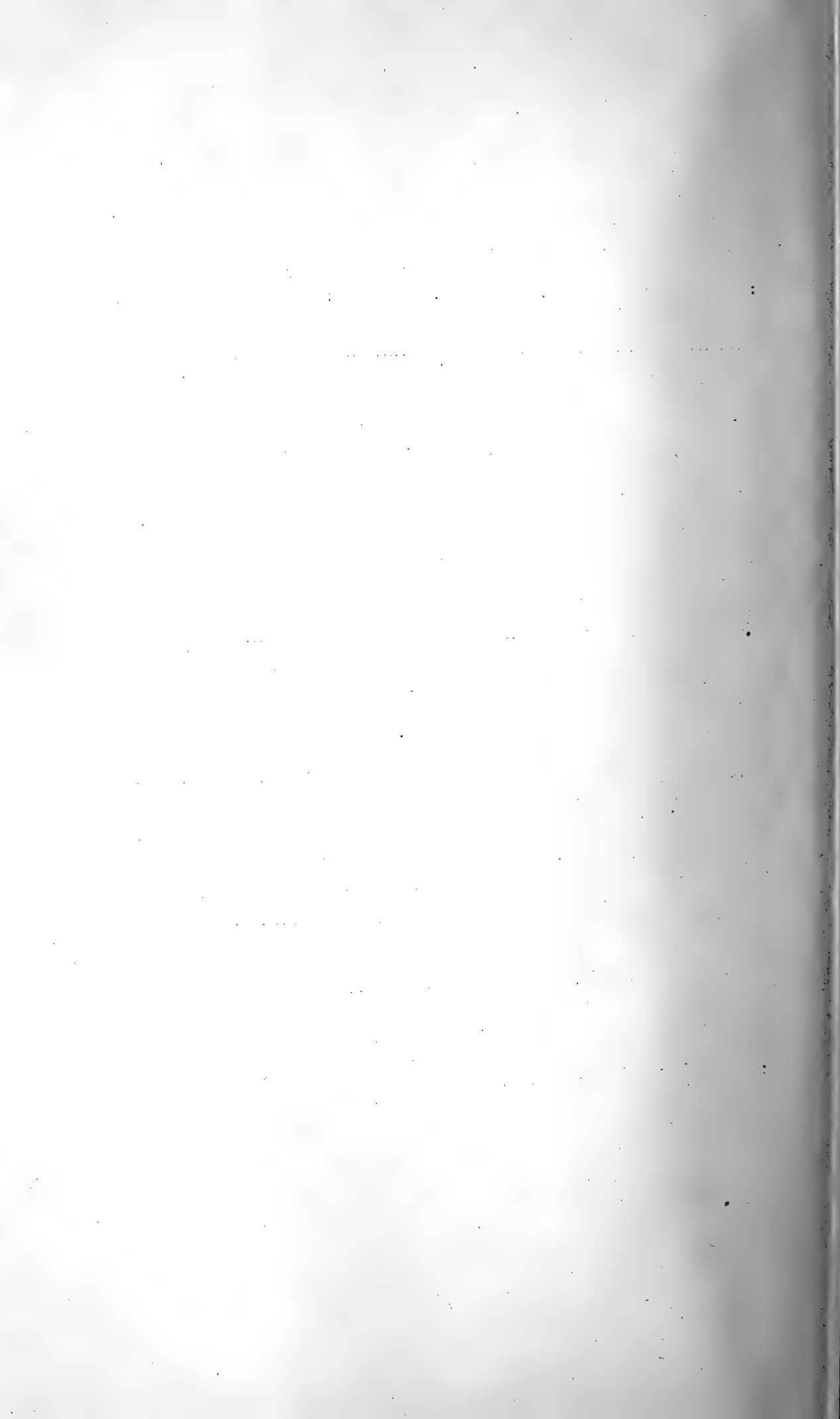


FIG. 27.—Percentile vertical distribution, summer of 1896. See p. 384.



possible to indicate the real concentration of the crustacea in the upper meter. During May the percentage lines all moved downward, owing to the downward movement of *Cyclops* during that month, as its numbers rose to their maximum. The movement extends into June, 1895; while in the early part of June, 1896, the center of population moved upward more than 3 meters, owing to the earlier death of the spring broods of *Cyclops* in that year. The center of population then remains close to the three meter line until the middle of August. In late June and early July of both years there is a rapid decrease of numbers in the lower levels of the lake. The 90 and 95 per cent. lines reach the level of the thermocline early in July, and they remain there through July, August, and early September, closely following the thermocline as it moves downward through the water. The center of population, which remains for some time near the 3 m. level, moves downward rapidly in September, and reaches a depth between 7 and 8 meters in October. If the crustacea were uniformly distributed throughout the lake it should lie at 9 meters. The 90 per cent. level was as high as 8 m. in July and August, 1896; and between 9 and 10 m in 1895, but moves downward to about 16 m. in October.

This practical exclusion of plant and animal life from the lower water during summer is a factor of great importance in the life of the lake, as the following considerations show: First, during this period the number of crustacea and the quantity of the plankton is independent of the depth of the water below the level which the thermocline has reached. Second, the exclusion from the lower water of species unfavorably affected by warmth prevents their appearance in the plankton or causes them to decline during the summer, while in the other lakes in which the deeper water is inhabitable their numbers may go on multiplying. This is pre-eminently true of *Daphnia pulicaria*, whose numbers are small in lake Mendota during the summer, while in many of the Oconomowoc lakes it is abundant during the same period and inhabits the entire depth of the lakes below the thermocline. The summer decline of *Cyclops brevispinosus* may also be due to the same cause. Third, the total number of the crustacea during the summer is far smaller than it would

be if the deeper water could be utilized. It is not impossible also that one factor in determining the small number of the periodic species of crustacea in lake Mendota may be in the fact that the upper water is so completely occupied by the perennial forms as to leave little chance for the development of other species. Fourth, the crustacea are not excluded from the deeper water of the lake by the low temperature of the water, as is proved by the occurrence of the same species in the far colder water of other lakes in the same district. The exclusion is due to the accumulation of the products of decomposition in the lower water, which remains entirely stagnant after the thermocline has been formed and is never exposed to the action of sun and air. This water in lake Mendota acquires an offensive smell and a disagreeable taste, though in neither respect does it go as far as certain waters mentioned by the Massachusetts Board of Health (Drown, '90, p. 553.) It is always clear and bright to the eye.

The products of decomposition of the algae and crustacea of winter and spring remain stored in the deeper water, and undoubtedly the addition of this store of nutritive material to the water of the lake as the thermocline gradually moves downward is one of the factors which occasions the enormous increase of the vegetable plankton in the late summer and autumn.

Autumn—October, November, and December.

The summer conditions of distribution end with the breaking of the thermocline and the resulting establishment of the fall homothermous period. This occurs at different times in different years. The date depends on: First, The rapidity of cooling of the surface; Second, The summer temperature of the bottom; Third, The amount and direction of the winds, especially of gales. In 1895 and 1896, the "turn over" came in the last week of September; in 1894 the distribution of the crustacea shows that it did not come until the first week of October, and it was equally late in 1897. In the year 1894 no observations were made in the first half of September, but the distribution in the latter part of September of that year closely resembles that in the early part.

of the month in 1895, and in the latter part of August, 1896. The distribution in the first half of October, 1894, is not very different from that two or three weeks earlier in the preceding years.

The leading general feature of distribution during the late summer and autumn is the progressive occupation by the crustacea of the deeper strata of the lake as the thermocline moves downward through August and September, and the coincident rise in number of the crustacea toward the fall maximum. It is a fact which was wholly unexpected by me that the 0-3 m. level shows little or no increase in the number of its crustacea after the early summer maximum in early June or late July. In 1895 its numbers steadily declined, or at best were stationary, after July 15th. (See Figs. 22, 23.) In 1896 there was considerable variation in numbers, but on the whole there was no increase except a sharp temporary rise in late October, due to the occurrence of great swarms of young *Daphnia hyalina* at that time. In 1894 the numbers in the upper level rose in the autumn, as would be expected, since they were at an abnormally low level in July, owing to the peculiar condition of the vegetation of the lake in that year.

The crustacea between 3 and 9 meters show also the same relation in their summer and autumn numbers; while those below 9 meters show a great increase, beginning in the 9-12 m. level, as the thermocline moves downward through it in August. The increase steadily proceeds to the the lower levels of the lake. It is very rapid in September and early October, and continues until the storms of late October, when the population decreases in all levels of the water. This result is the sum from 5 to 7 species of crustacea, and of course it does not hold accurately for each species. It is also true that since the broods of young appear in the upper level, they may temporarily increase the number of a species there, but this excess of one species is balanced by a deficiency in another, and often for the single species the semi-monthly averages agree pretty well with the general law.

A good example of the effect of age upon distribution can be seen from the case of *Daphnia hyalina* in the latter part of Oc-

tober, 1896, when great numbers of young appeared on several occasions, and when the old animals were nearly all full grown, so that there were very few half developed individuals. This is given on p. 398.

During November and December the population of the lake falls off pretty uniformly in all levels, more rapidly in November than later, and at this time the distribution of the animals may be more even than at any other period. If *Daphnia pulex* is present it rises toward the surface in December and increases the population of the upper strata. This occurred in 1895. In all years the distribution in November is more uniform than that of December, in which month the population of the lower levels of the lake seem to decline more rapidly than that of the upper stratum.

TABLE XXXI.—Average percentile distribution Oct. 1—Dec. 31.

	Average No.	PER CENT. IN EACH 3 M. LEVEL.					
		0-3 m.	3-6.	6-9.	9-12.	12-15.	15-18.
1894	595,000	25.8	18.8	16.0	15.7	14.0	9.8
1895	436,000	29.7	18.3	14.3	14.9	12.2	10.6
1896.....	759,000	25.9	21.0	15.3	13.9	12.4	11.4

Figures 22 and 23 represent the total population of each of the 6 levels into which the lake was divided. The scale is 100,000 crustacea to each vertical interval. If the scale be divided by 3 the same diagrams will serve to show the population of each level per cubic meter. The relations of the increase and decrease of the population in the several levels are shown very plainly from these diagrams. For instance in 1895 it will be seen that while the two upper levels began to increase during the latter part of April, the population of the lower levels scarcely changed from the winter condition until about the first of May. The population of the three upper levels reached its maximum in the latter part of May, while in the lower part of the lake the population went on increasing, or at least remained stationary, until near the middle of June. The 6-9 m. level

hardly shared in the rise to the early summer maximum until two weeks after the 0-3 m. level, while in the lower part of the lake the population declined, or remained stationary throughout July. In August the crustacea of the 9-12 m. level increased in number as the thermocline moved downward into that level, while no increase was perceptible in the population of the lake below 12 m. until after the middle of September; after which date the numbers rapidly increased.

No increase of population was seen in the upper levels of the lake after the month of July; and if this diagram is compared with Fig. 6 which shows the changes in the total population of the lake, it will be seen that the autumnal maximum, which is clearly indicated, comes entirely from the increase of population in the lower water of the lake.

The same general facts appear in the diagram for 1896, but, if possible, in a form even more striking. The 0-3 m. and 3-6 m. levels follow each other closely, while the spring increase in population comes later in the lower levels of the lake. In the 9-12 m. level the population remains stationary during May, when that of the upper levels is rapidly falling, and at the same time the crustacea in the water below 12 m. are increasing in number; more rapidly in proportion to increased depth. In the 0-3 m. level at the first of June the population was substantially stationary, while that in the water below was falling rapidly. This condition was brought about by the new broods of *Chydorus*, which nearly made up for the loss in numbers of other species.

In 1896 the thermocline moved downward much more rapidly than in the preceding year and as a result of this movement, the crustacea in the lower water began to increase in numbers at an earlier date. (See Figs. 3, 4, 26, 27.) A marked increase occurs in August in the 9-12 m. level and begins about two weeks later in the levels below. As in 1895, so also in 1896, the fall maximum is caused by the increase in the population of the lower water, with the exception that in late October of 1896 there was a great increase in the number of the crustacea in the 0-3 m. level, due to the appearance of great broods of *D. hyalina* at this time. These soon disappeared, so that the crustacea in

this level fell off in number even more rapidly than they had increased — so rapidly, indeed, that no effect was produced by these broods upon the population of the water below 3 m., except perhaps to check in some degree the rate of decrease toward the winter minimum. There was also a small rise in December in the 0–3 m. level, caused by the increase of *D. pulicaria*.

It would seem from these facts that there is a maximum population per cubic meter beyond which the crustacea are unable to multiply and which differs in different seasons. It is difficult to see what it is that sets a limit to this population in the autumn. At this time the food is in enormous abundance as compared with the number of the crustacea, and it would be expected that the numbers in all levels of the lake would increase together. I am quite unable to give a reason for their failure to do so, but the fact recurred exactly in all three years of my observations, making allowance for the peculiar conditions in the early summer of 1894.

Fig. 28 represents the average percentile vertical distribution of the crustacea for Oct. 1–15, 1896, March 1–15, 1895, August 1–15, 1896. The corresponding figures are given in Table C, appendix. In the diagram each horizontal space represents 10 per cent. of the crustacea and each vertical space, 3 m. On each 3 m. line is platted the percentage of crustacea found below it, and these points are connected by a line which extends from 100 per cent. at the surface to 0 at the bottom. From the intersection of these curves with the vertical lines can be seen approximately the percentage of the crustacea above and below the depth indicated at the intersection. If the distribution were uniform there would be 16.6 per cent. in each vertical space and the percentile distribution would be marked by a straight line running from corner to corner of the diagram. The curve for October approximates very closely to this, the percentage being larger in the surface stratum and somewhat smaller below 12 m., but, in general, the line lies very closely parallel to the diagonal. The distribution for March is almost equally uniform, but here the bottom level has an excess, due to *Cyclops*, and the 0–3 m. level is slightly below the average.

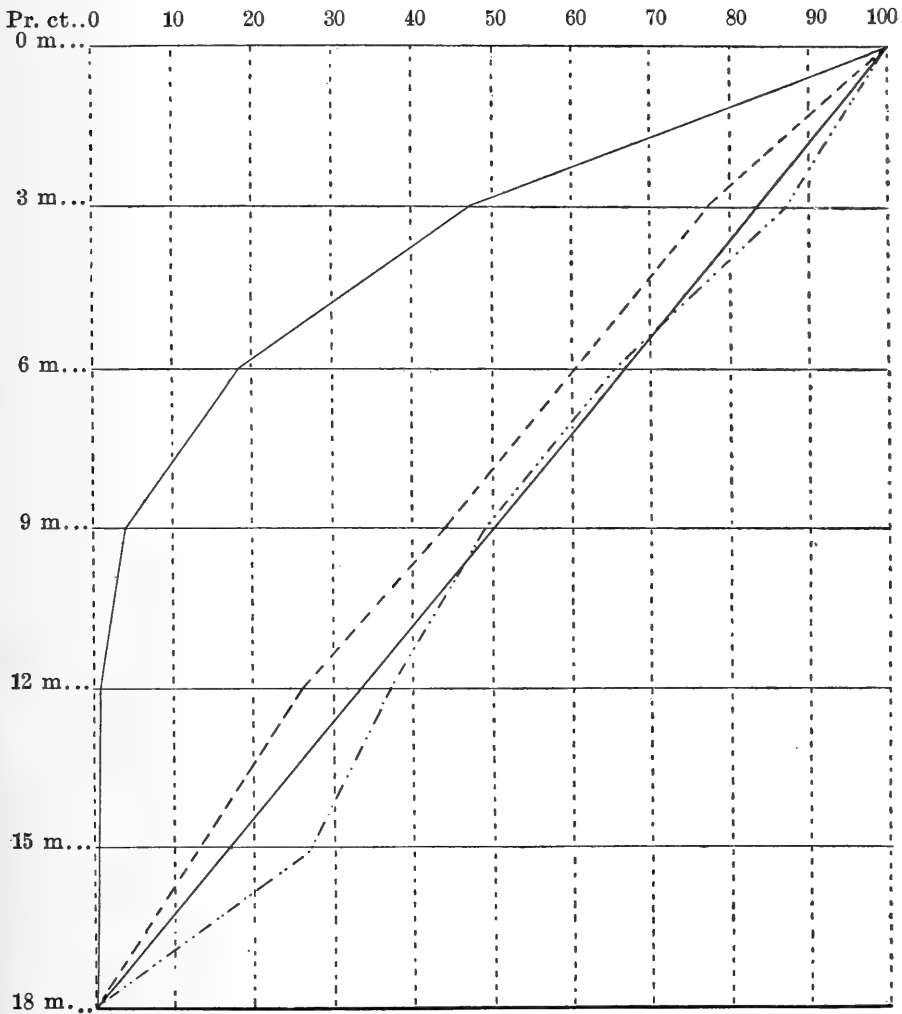
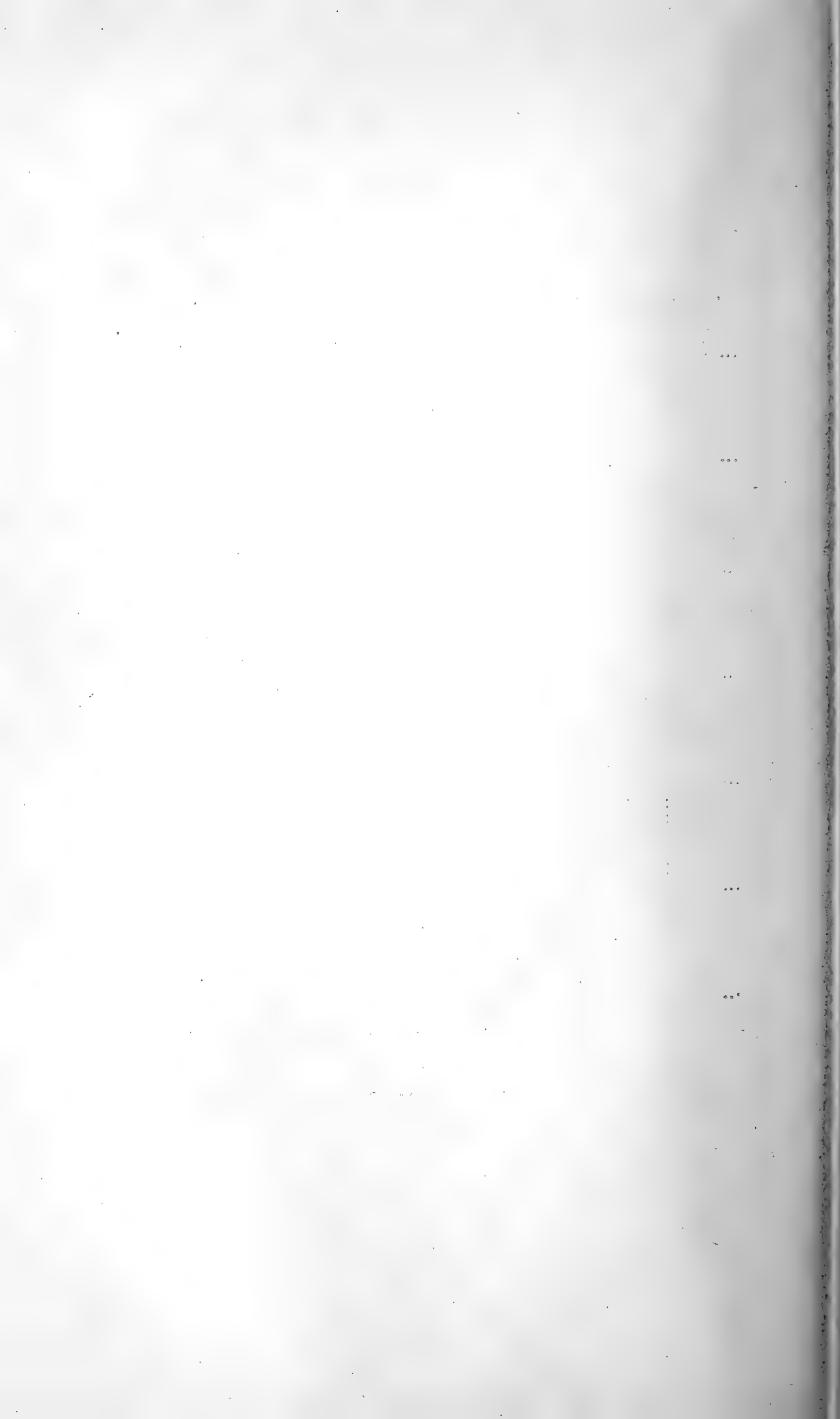


FIG. 28.—Percentile vertical distribution of crustacea, March 1-15, 1895; August 1-15, 1896; October 1-15, 1896. See p. 390.

MARCH

AUG.

OCT.



In October the distribution of all of the species of crustacea is approximately equal. In the winter the equality of distribution is brought about by the excess of *Daphnia* and *Diaptomus* in the upper strata, nearly balancing the excess of *Cyclops* near the bottom. (See Fig. 30.) The curve for August shows a very large percentage in the upper 3 meters and a very small number in the lower water. It is a characteristic distribution for middle summer.

THE VERTICAL DISTRIBUTION OF THE INDIVIDUAL SPECIES.

After this full discussion of the vertical distribution of the total crustacean population I do not intend to describe that of the individual species in similar detail, but I shall confine myself to pointing out the individual peculiarities of each species, devoting more space to those which depart in a marked way from the average vertical distribution. One general law holds for nearly all the species, as already stated: the broods of young appear first in the upper water of the lake and the increase of population extends downward, becoming approximately uniform at all depths as the species reaches its maximum, and later in its life becoming more numerous in the deeper water of the lake. To the first part of this rule the only exception is *Daphnia pulicaria* during summer. There are, however, several factors which prevent the full carrying out of the latter part of the rule. The most important of these is the formation of the thermocline, by which all of the crustacean life is confined to the upper waters of the lake during that period when the development of several species is going on actively. In the late autumn also the numbers of the crustacea decline so rapidly after the fall broods appear that it is not easy to find any accumulation at any low level of the lake. The downward movement of the older forms is shown most clearly by *Cyclops* and *Daphnia hyalina* during the spring, and by the accumulation of *Cyclops* in the deeper water of the lake during the winter, by the disappearance of *D. hyalina* and *D. retrocurva* in autumn. Similar, though less striking, illustrations can be found in all of the species of limnetic crustacea.

Each species of crustacea, also, has individual peculiarities of distribution, which recur from year to year with surprising similarity and which are independent of the absolute number present. These peculiarities appear when the average of any species is taken, although of course it is entirely possible that the distribution should depart widely from this average at any single observation. In general it may be said that the summer distribution of the crustacea follows very closely the figures which are given in my former paper (Birge, '95), and that the variations in the distribution which have been found during the two years and a half succeeding the observations reported in that paper, have been of the same type and in general of the same degree as those which were found during the single month of our first study. It seems to me, therefore, unnecessary to point out again these variations in detail for each species.

In order to show the resemblances and differences in the percentile distribution of the crustacea during the summer months, when their numbers are great and the distribution is most characteristic, I have averaged this distribution for the summers of three years: 1894, 1895, 1896. I have included the three standard representatives of the limnetic crustacea which are regularly present in full numbers during this time; *Diaptomus*, *Cyclops*, *D. hyalina*. The period included is from the middle of June to the middle of September, in 1895 and 1896; and July and August of 1894. It will be remembered that no observations were taken in 1894 before July or during the first part of September, but as the summer conditions were thoroughly established at the first of July of that year and continued until the first of October no noteworthy difference would appear in the averages had it been possible to extend the period. It will be seen from these averages that the distribution of *Cyclops* in the three years in question varies surprisingly little; the percentile difference in the 0-3 m. level being less than 1.5. This close correspondence in distribution exists in spite of the fact that the numbers of the genus were very different in the three years. The same general agreement is seen in the tables of semi-monthly distribution. Compare July, 1894 and 1896 in Table C, Appendix.

TABLE XXXII—Percentile distribution. Summer—*Diaptomus*.

	Average No.	PER CENT. IN EACH 3 M. LEVEL.					
		0-3 m.	3-6	6-9	9-12	12-15	15-18
1894.....	226,000	49.2	29.3	16.6	4.1	0.5	0.3
1895.....	172,000	42.7	29.0	20.9	6.1	0.7	0.6
1896.....	188,000	52.6	27.4	12.4	5.9	1.9	0.5

Cyclops.

1894.....	158,000	40.7	28.4	20.1	9.4	1.7	0.3
1895.....	183,000	39.3	25.2	19.0	10.0	3.1	3.4
1896.....	290,000	40.2	27.1	15.6	10.1	4.8	2.3

Daphnia hyalina.

1894.....	27,000	41.9	23.8	21.4	6.7	1.0	0.3
1895.....	210,000	52.3	20.8	17.6	6.6	1.3	1.2
1896.....	145,000	44.7	22.2	16.1	11.7	4.7	1.3

The variations in the distribution of *Diaptomus* are greater, although its numbers were more nearly constant, but in each year the same characteristics are shown. The percentage of the population found below the middle of the lake is 7.5 or less, while in the case of *Cyclops* the number ranges from 11.5 to more than 17 per cent. *Daphnia hyalina* also varies more in the upper strata, but is in general intermediate in its distribution between the other two genera. The older individuals of *Daphnia hyalina* are much more apt to accumulate in the lower part of the water accessible to them than is the case with *Diaptomus*, and consequently the lower levels are apt to contain a larger percentage of this species. On the other hand the species does not extend to the thermocline in numbers anything like as great proportionately as does *Cyclops*, so that the lower part of the inhabited water always contains a larger proportion of *Cyclops* than of any other species.

The vertical distribution of *Daphnia hyalina*, therefore, differs very considerably in different years. If the species is present in large numbers and the young are constantly appearing, a

very large percentage of the population is found in the upper level of the lake and even in the upper meter. This was the case during the summer of 1895, when this species was the dominant member of the limnetic crustacea throughout the entire summer. Under these circumstances its vertical distribution approximates very closely to that of *Diaptomus*. On the other hand, if the species is declining and the young appear in small numbers, there is a much larger proportion of the species in the lower levels of the lake. This was the case in 1896. In August of that year the numbers of *Daphnia* rapidly declined, so that in the latter part of the month there were present less than half as many as in the latter part of July, and in connection with this decline the population of the three upper levels was nearly equal. In this year the vertical distribution of *Daphnia hyalina* approximated very closely to that of *Cyclops*.

The vertical distribution of *D. hyalina* illustrates very strikingly the dependence of distribution on specific habit rather than on number.

The illustration given in my former paper (Birge, '95, plate VIII) fairly illustrates the characteristic differences in the summer distribution of the different genera, and the percentage diagram, Fig. 29, given herewith indicates the difference in distribution during the summer of 1896.

Diaptomus Oregonensis Lillj.

Figure 29.—Table D, Appendix.

In general *Diaptomus* is more abundant in the upper strata of the lake than in the lower at all seasons of the year. There is rarely less than 70 per cent. of the species in the upper half of the lake even in the winter, and the only times when the average distribution approaches equality are in late fall and at the period of the minimum numbers of the species in the latter part of April, or early in May. The other extreme of distribution is reached when the new broods appear and as their appearance is somewhat irregular the distribution is correspondingly variable. The maximum average number in the 0-3 m. level was reached in the latter half of May, 1895, where the average

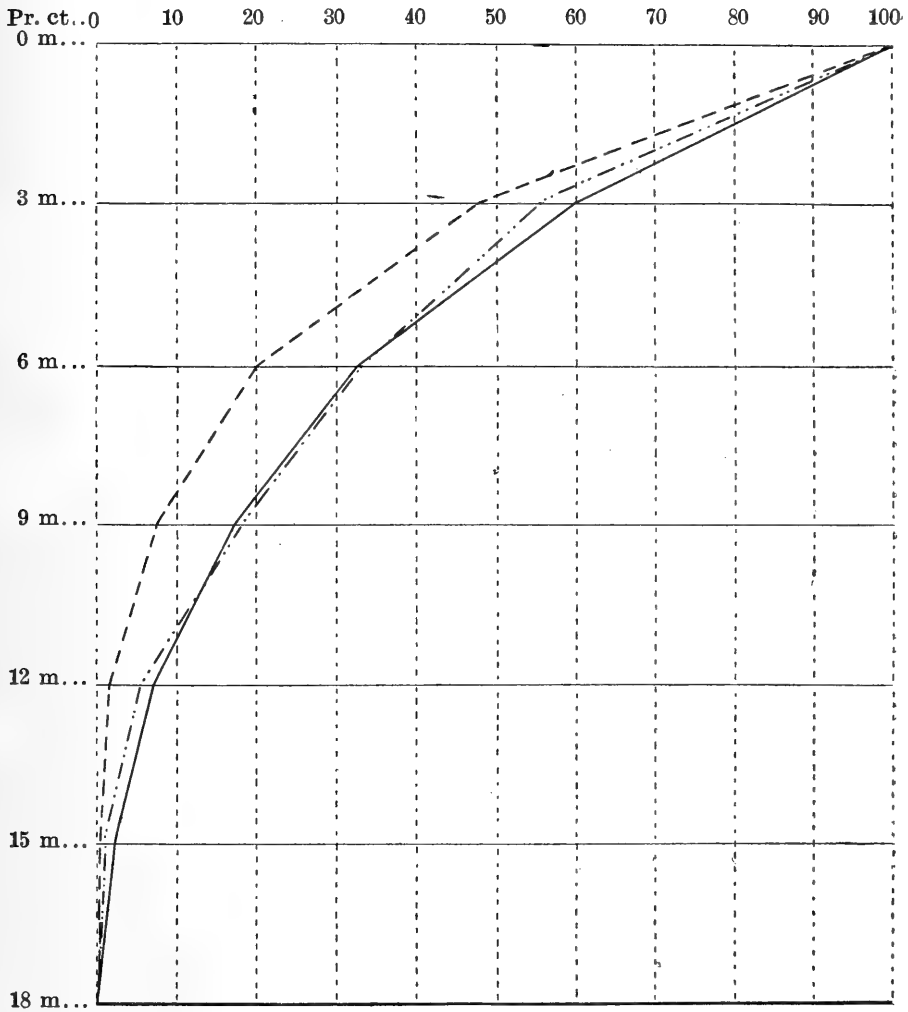


FIG. 29—Summer distribution, 1896. *Diaptomus*, *Cyclops*, *D. hyalina*. See p. 394.

D. hyalina..... - . - . - . - . - .
Cyclops..... —————
Diaptomus.... - - - - -



was 61.5 per cent.; and in June, 1896, where the average for the whole month was 69 per cent. Each of these numbers is higher than the average for July, 1894, which was less than 53 per cent., and higher than the highest average per cent. for any period of July, 1894, which was 63 per cent. in the second period. The variations which are found in the percentile distribution are substantially like those which are recorded in my former paper. (Birge, '95, p. 455.) In no case do the older individuals of this species show a tendency to accumulate in the deeper water of the lake but as the broods which appear in the spring, or later, become older and the water becomes more crowded, they migrate progressively into the deeper levels, but appear to prefer to stay near the surface.

Marsh ('97, p. 194) finds that the vertical distribution of *Diaptomus* in Green lake is uniform throughout the year. This is entirely different from the facts as I find them, since the upper three meters in summer contain more than twice as many of the species as they do in winter. Apstein ('96, p. 80) finds that *Diaptomus* was chiefly in the deep water from January to April. Here again his observations differ from mine, since there was hardly a trace of a descent of the species in lake Mendota. Apstein thinks that this descent in winter on the part of *Diaptomus* and *Cyclops* may be due to their desire to seek the warmer water at the bottom of the lake. This motive cannot hold in the case of lake Mendota, where the temperature of the water is almost the same at all depths during the winter. The aggregations of *Cyclops* in the deeper water are apparently composed of feeble individuals, which do not rise again to the surface.

Cyclops.

Figures 29, 30.—Table E, Appendix.

Of all the limnetic crustacea *Cyclops* seems to be most independent of external influences in its vertical distribution. The maximum percentage in the upper levels is reached when the spring or summer broods appear. While the absolute numbers of these broods in the spring are much greater than in summer, multiplication goes on so rapidly in May that the animals are

quickly forced to move toward the deeper water of the lake, and, since the entire lake is accessible to them in spring, there rarely occurs as great a percentage in the upper stratum as is the case in summer. The highest average per cent. in the 0-3 m. level, reached in the spring of 1895, was 42.7 in the first part of May; and 35 per cent. was the average in the latter part of April, 1896. In July of each year the percentage in the upper stratum rose to about 50, owing to the coincidence of swarms of young in the upper water while the lower strata contained a very scanty population. The fall rise in numbers does not cause any noteworthy increase in the percentage in the upper strata, since at this time the entire lake is accessible to the animals and food is abundant at all levels, and the autumnal gales aid to distribute the species through the lake.

In the winter there is a strong tendency of *Cyclops* toward the bottom and as many as 50 per cent. may be found in the lower three meters, and as many as 70 per cent. in the lower six meters of the lake. Illustrations are given on page 379. Since many of the older representatives of the species die during the winter and the new individuals appear towards spring in the upper water, the population of the lower levels decreases in the early spring, both absolutely and relatively. Diagram 30 shows the percentile distribution of *Cyclops* in the first part of March, 1895, and in the latter part of July of the same year, in which the extremes of its distribution were found.

The spring broods of *Cyclops* show exceedingly well the progressive occupation of the water of the lake by the increasing numbers of the species; the way in which the numbers of a declining species disappear first from the upper waters of the lake, where they first appeared; and the equality of distribution during the decline. The following table shows the spring history of *Cyclops* during 1896. The story for 1895 would be substantially the same.

TABLE XXXIII.—*Cyclops*, 1896. Number per cubic meter stated in thousands.

Depth, meters.	0-3.	3-6.	6-9.	9-12.	12-15.	15-18.
April 1-15	17.2	11.7	18.9	20.3	12.8	15.0
April 16-30	109.4	84.1	52.5	28.8	18.8	9.6
May 1-15	190.2	124.9	117.4	84.5	52.9	42.7
May 16-31	37.0	37.3	34.3	35.2	42.1	64.8
June 1-15	20.5	13.7	7.6	6.7	5.7	14.1
June 16-30	59.2	32.4	17.9	13.4	6.7	9.5

Marsh ('97, p. 204) finds that *Cyclops fluviatilis* is present in great numbers near the surface. Its distribution, therefore, agrees more nearly with that of *Diaptomus* than it does with *C. brevispinosus*. The latter species is present in Green lake in very small numbers apparently in and below the thermocline in summer.

Daphnia hyalina.

Figure 29.—Table F, Appendix.

There are two facts which give the peculiarities of vertical distribution of *Daphnia hyalina* and the allied species *D. retrocurva*. These are: First, a decided tendency of the young animals to accumulate in the superficial strata of the water, frequently in the upper meter. Second, a tendency on the part of the older animals to settle toward the bottom. These species, therefore, show a very high percentage in the upper levels of the lake in periods when they are increasing, and especially at those times when the broods of young appear. On the other hand, when the species is declining in numbers, and in the intervals between the appearance of broods, the distribution may be comparatively equal throughout that part of the lake inhabited by the species. As examples, compare the table on page 398, and the detailed figures of Table F, Appendix.

The percentage in the upper level rarely falls below 25, even in the winter. In May, when the spring broods appear, the average number in the 0-3m. level ranges from 45 to 55 per cent., and the same ratio is found during the summer when the species is increasing in numbers. On the other hand, when the

species declines in numbers, as it sometimes does in August, the percentage in the lower levels may be nearly, or quite, as great as in the 0-3 m. level. (See August, 1896.) At the time of the fall maximum great numbers of young often appear at once. At this time the brood sacs of the females contain from five to nine eggs. There are very few half-grown animals, and the eggs may all hatch in the course of a week. At such a time it is not difficult to determine the difference in distribution of the young and old, and the following tables show these relations in the latter part of October, 1896:

TABLE XXXIV.—*Daphnia hyalina*, per cubic meter.

DEPTH.	OCTOBER 26, NOON.		OCTOBER 27, 8 A. M.	
	Young.	Adult.	Young.	Adult.
0-3m.....	122,200	0	30,400	1,200
3-6.....	27,500	250	13,300	760
6-9.....	15,800	380	1,900	6,300
9-12.....	1,600	4,100	2,500	3,800
12-15.....	0	2,500	2,500	8,900
15-18.....		950	1,300	19,000

After the production of the young in late October or early November, the old females die off rapidly; some few remaining as late as the first of January. In the latter part of May, or the early part of June, according to the progress of the season, those individuals that have lived over winter become weak, are attacked by various diseases, caused by fungi, bacteria, and microsporidia, settle toward the bottom of the lake and die. This downward movement of the older and weaker individuals causes an increase of the number in the lower part of the lake, which was quite conspicuous in June, 1895, and in the latter part of May, 1896.

Shortly after this date the crustacea begin to disappear entirely from the lower water, and during the remainder of the summer the life of the species goes on, like that of the other crustacea, in the region above the thermocline.

The vertical distribution of this species does not appear to have been carefully studied by other authors.

Daphnia pulicaria.

Figures 30-32.—Table G, Appendix.

The vertical distribution of this species is so peculiar that it demands a somewhat more detailed account than has been given to the other species. The history of the species begins ordinarily in the early part of July of the odd numbered years. During the first part of July it has been present only in very small numbers, but in the second part of July, 1895, its numbers were so large that it appears in the lists. At that time more than 50 per cent. of the species was found between 6 and 9 meters, in the region of the thermocline, and nearly all of the remainder was found between 9 and 15 meters. In August the species moved downward, following the downward movement of the thermocline, and continued in this position until the coming on of the autumnal homothermous period in late September and October. During October the species was distributed with approximate uniformity through the water of the lake. In November, as the lake cooled, the animals began to move toward the surface, and in late November and December a period of active reproduction began. The young animals were found in the upper level of the lake, most numerous in the upper meter, and as the result of this distribution, the numbers in the upper level were far greater than those in any other portion of the lake. This relation continued throughout the winter of 1895-96, during which time reproduction also continued, although more slowly, until in March and the early part of April reproduction nearly ceased and the numbers of the species declined somewhat rapidly. At this time the distribution was uniform, or such irregularities as were present seemed to be accidental. In the latter part of April the spring period of reproduction began and an enormous number of young were produced in the upper water. At this time as many as 80-85 per cent. of the species were found in the upper level; a larger proportion than has been found there of any other species except *Chydorus*. In the early part of May a reproductive pause occurred, during which the animals were pretty evenly distributed through the water;

the largest number being found in the bottom stratum. A second reproductive period came on in the latter part of May, in which the upper water was again crowded, although the numbers increased so rapidly that the population of all the upper levels of the lake was greatly increased. During the early part of June the distribution became once more equal, with the largest number again in the bottom level, and during the latter part of the month the population rapidly declined, falling off most in the upper levels. At this time more than 60 per cent. of the species was found below the 12 m. level and less than 2 per cent. in the upper level.

Late in June the species began to move away from the bottom water, or perhaps it would be more correct to say that the individuals at the bottom of the lake died off more rapidly than those in the levels immediately above, so that in the early part of July nearly 60 per cent. of the species was between 12 and 15 meters and only 6.5 between 15 and 18 meters. As the species declined in numbers the decline took place chiefly in the lower levels of the lake, so that in July and August the few representatives of the species that were left were concentrated in the region of the thermocline, thus occupying the same position that they had held in the corresponding months of the preceding year. The following table shows the numerical relations.

TABLE XXXV.—*D. pulicaria*, 1896. Population per cu. m. of each level stated in thousands.

Depth, meter.	0-3	3-6	6-9	9-12	12-15	15-18
April 1-15.	1.0	1.5	3.2	2.5	1.3	0.6
April 16-30.	41.6	5.2	0.4	0.7	0.9	0.2
May 1-15.	10.4	12.8	15.5	9.2	13.3	17.8
May 16-31.	55.4	33.7	37.4	28.8	19.8	23.4
June 1-15.	10.3	5.9	8.8	12.5	5.9	10.9
June 16-30.	0.4	1.5	2.8	3.7	10.9	4.4
July 1-15.	0.1	1.1	3.5	7.3	0.8
July 16-31.	3.2	1.7	0.1	0.1

Fig. 31 shows the movement of *D. pulicaria* during the late summer and autumn of 1895. Points were established indicat-

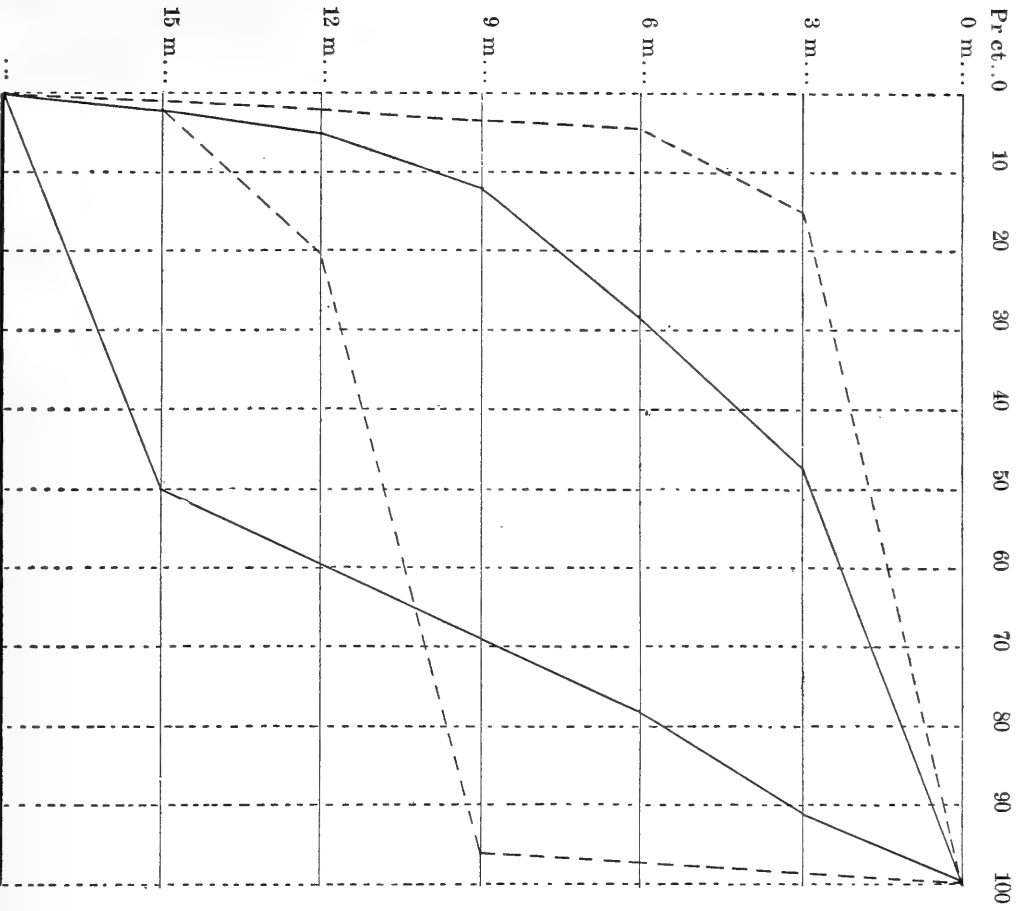


Fig. 30.—Cyclops, March and July, 1896; *D. pulicaria*, August, 1895, and April, 1896. See pp. 396, 399.

Cyclops.....

D. pulicaria — — — — —

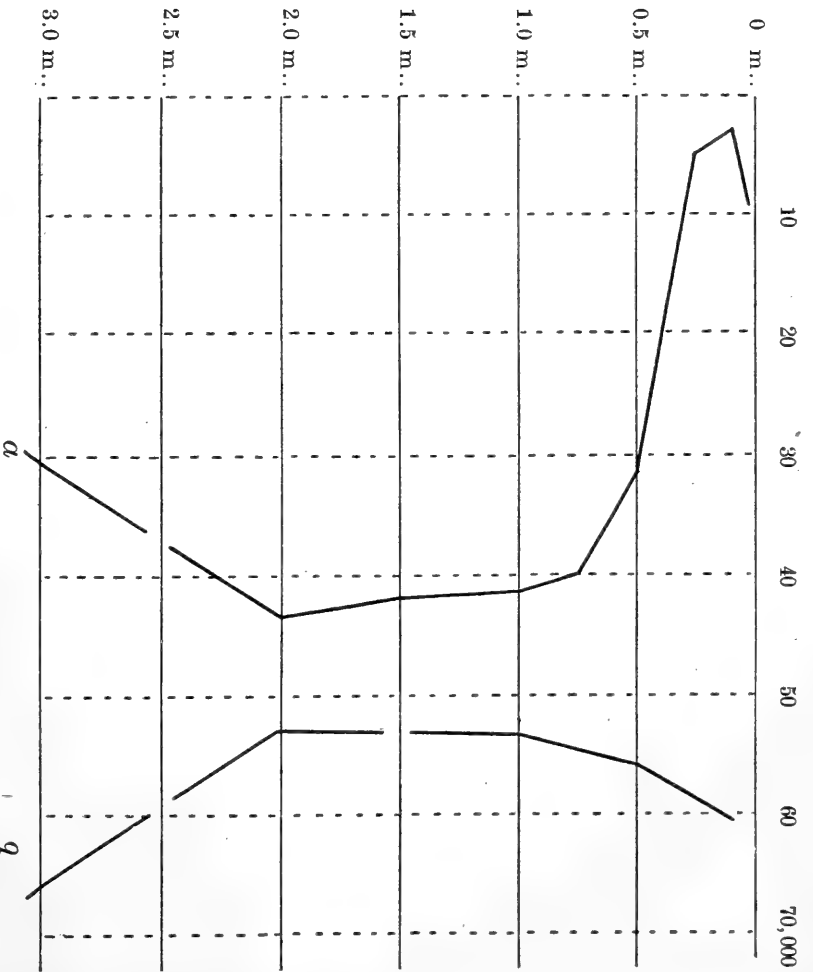
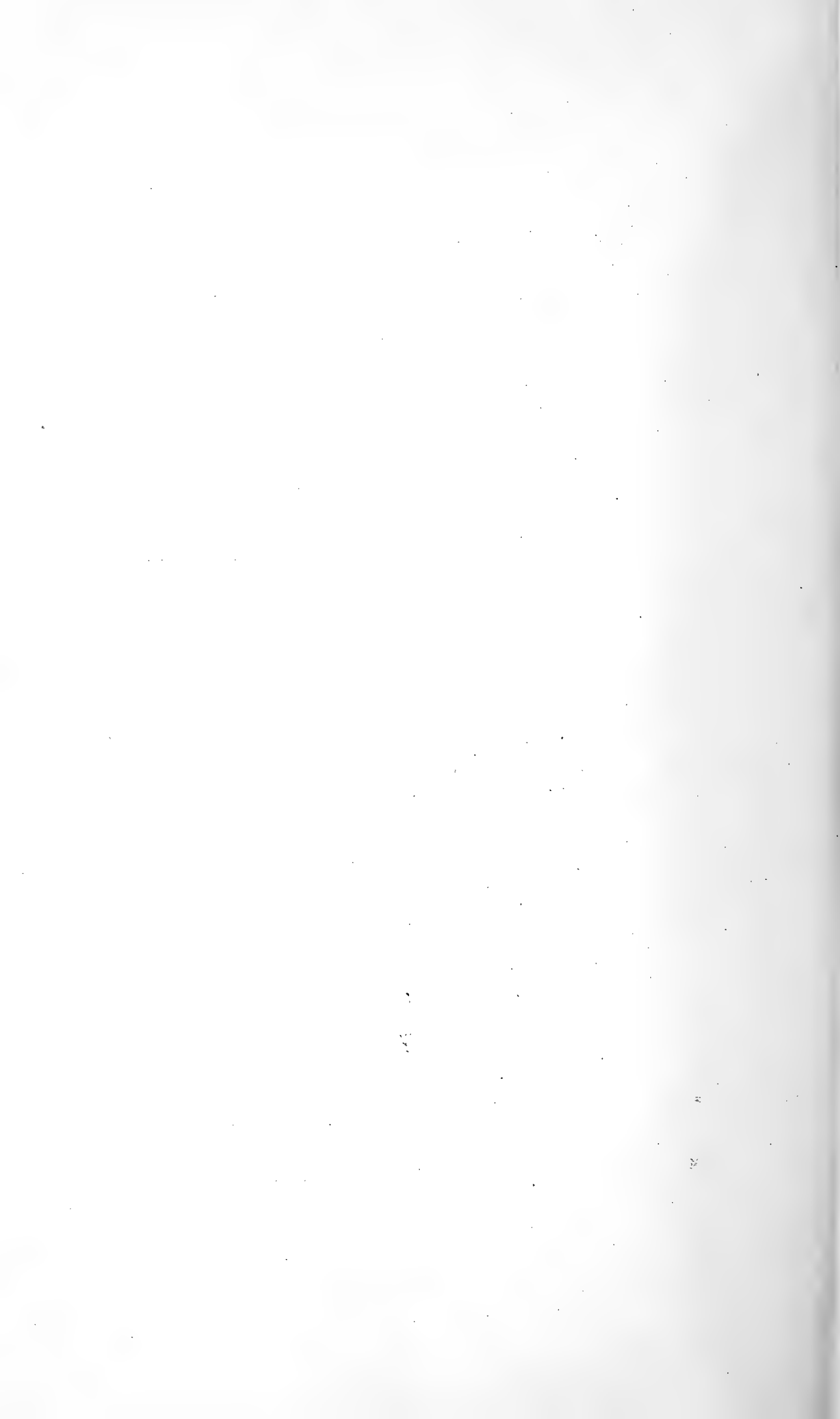


Fig. 31.—Distribution of crustacea, 0-3 m., Sept. 13, 1896, 2 p.m. (a), and 9 p.m. (b). Scale, 1 horizontal space = 10,000 crustacea per cu. m. The lines are interrupted at levels where no observation was made. See p. 413.



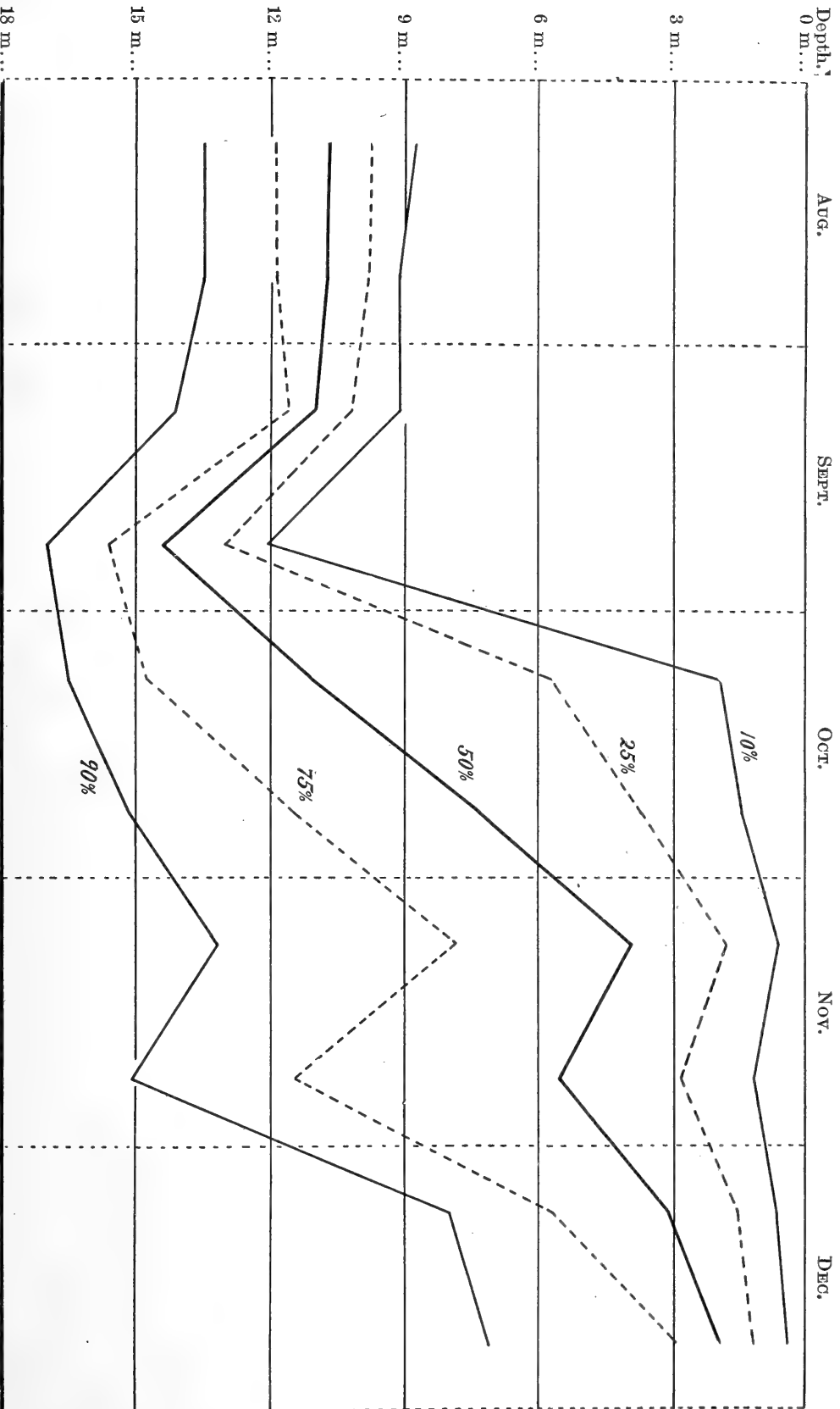


FIG. 32.—Percentile vertical distribution of *D. pulicaria*, August–December, 1895. See p. 401.

ing the level below which the respective percentages of the species were found and these were connected by lines. The distribution is based on assumption that the individuals of the species were uniformly distributed throughout the 3 m. level in which they were found. This assumption is peculiarly incorrect for *D. pulicaria*, since the species is limited to the region of the thermocline. It is often confined within a space of 1 meter, or even less, yet it often passes beyond these narrow limits, as is indicated by the fact that not inconsiderable numbers may be found in two or even three levels. While, therefore, the diagram spreads out the distribution of the species during the summer more than is correct, the general relations are well enough indicated by its lines. It will be seen that in the latter part of August more than 65 per cent. of the species was found between 9 and 12 meters and that the species moved downward during September as the thermocline moved down. In October, after the breaking up of the thermocline, the distribution was much more nearly equal. The center of population rose rapidly and regularly from the latter part of September to the middle of November, lying near 14 meters in late September and at 4 meters in the first part of November. After a small fluctuation in the latter part of November, it rose once more, and in the latter part of December lay about two meters below the surface, where it remained during the early part of the winter, until the decline in numbers came on in March or April. If this diagram were reversed it would serve fairly well to indicate the downward migration of the species in the spring.

In Fig. 30 are given curves for the percentile distribution of *D. pulicaria* for April 16-30, 1896, and August 16-31, 1895, showing the extreme variation of its average distribution. The diagram is similar to that described on p. 384.

I have not found any other case recorded of a *Daphnia* which in summer remains at or below the thermocline. At least one other species of the genus has the same habit in this region. A form which I have identified as *D. longiremis* Sars, belonging to the *cristata* group, is regularly confined to the region below the thermocline in some of the lakes of the Oconomowoc system and in lake Geneva.

Daphnia retrocurva Forbes.

Table H, Appendix.

This species belongs to the periodic crustacea and is present in the lake from July to December. Its numbers during July are small and the proper history of the species does not begin until the latter part of this month, or the early part of August. In 1896, indeed, the numbers were very small until the decline of *D. hyalina* in the middle and latter part of August gave an opportunity for the presence of this species.

In vertical distribution this species agrees very closely with *D. hyalina*, as would be expected. In the early part of periods of increase, from 45 to 60 per cent. may be found in the upper level. This was the case in the latter part of July, 1895. It was also true in late September and early October, 1896, although the crustacea moved rapidly downward so that the two-week averages do not disclose the fact. In the old age of the broods, as the numbers are declining, they are found chiefly in the lower water of the lake. This was especially obvious in late November and in December, 1895, when the species disappeared quite slowly and lingered latest in the lower waters of the lake. In 1896 the formation of the ehippia was nearly simultaneous on the part of all of the females and the species disappeared rapidly and completely in the early part of November, so that this phenomenon of the old individuals lingering in the lower water did not appear.

Marsh (97, p. 210) finds the distribution of *Daphnia Kahlbergiensis* in Green lake very similar to that of *D. retrocurva* in Mendota. He finds, however, a marked difference between the vertical distribution by day and night, which I have not seen. The fact, however, that *D. retrocurva* descends to a somewhat greater depth during the day than does *D. hyalina* seems to indicate a greater sensitiveness to light than that of its congener, although this sensitiveness does not lead to as great movements as Marsh's observations would indicate for Green lake.

Diaphanosoma brachyurum Sars.

Table I, Appendix.

This species belongs to the periodic crustacea, its active development extending from the first of August to the middle of October. It is provided with very large antennæ and is one of the most powerful swimmers among the limnetic crustacea. It is also positive in its relations to light. In both these respects it resembles *Diaptomus* and its vertical distribution very closely agrees with that of the latter genus, although its numbers are very much smaller. In the early history of the species 50 to 70 per cent. of the whole number are found in the upper stratum of the lake. The distribution becomes more equal during the decline of the species and at no time is there found any aggregation of individuals in the lower waters of the lake. The distribution of the small numbers present in the decline of the species is, however, quite irregular and the number in the upper part of the lake becomes smaller than that in the lower water.

Marsh ('97, p. 216) suggests that the vertical distribution of *Diaphanosoma* is controlled by light rather than temperature. He finds it negative to light and thinks that it prefers cool water. In the laboratory *Diaphanosoma* moves toward the light along with *Diaptomus*, so that my observations would indicate that it is positive in its relations to light. I find also uniformly a larger percentage of adult animals in the upper meter by day than I find of the species of *Daphnia*. There is, therefore, nothing in my observations to confirm the idea that the species is negative in its relations to light. Since, however, the absence of crustacea from the upper centimeters of the lake when the light is most intense, indicates a certain negative relation on the part of nearly all forms, it may well be that this species finds the light in the clear water of Green lake too strong, and responds to it more definitely than in lake Mendota.

Chydorus sphaericus.

Table J, Appendix.

This species belongs properly to the littoral crustacea and its presence in the limnetic region depends apparently on the presence in abundance of *Anabaena* and allied forms. Since these plants tend to aggregate in the upper water of the lake, *Chydorus* shows an equal tendency in the same direction and the percentage of this species which may be found in the upper levels exceeds that of any other of the limnetic crustacea. It is true, however, for this species, as for all others, that the largest numbers are found in the upper level at the time when the numbers are rapidly increasing, and that when the numbers are declining the distribution may be more equal, or may vary in an accidental fashion. During the periods of rapid increase from 50–80 per cent. of the individuals are found in the 0–3 m. level. These high percentages have been reached in September, 1894, July, 1895, and June and August, 1896.

In October and later the species becomes quite equally distributed through the water, but it showed no marked tendency to aggregate in the lower water at times when it is declining, until the numbers became very small in late winter, 1896. It is very abundant during the day in the upper meter and, like *Cyclops*, is one of the last forms to disappear at the thermocline.

The fact that *Chydorus* is relatively very abundant near the surface is noted by Apstein ('96, p. 80).

Leptodora.

The number of *Leptodora* caught is so small and so variable that it is difficult to give any positive general conclusions regarding its vertical distribution. The following table shows the average distribution for the months of July, August, and September, 1895, with which that of 1896 closely agrees.

TABLE XXVI.

1895.	Total Number taken.	PER CENT. IN EACH 3M. LEVEL.					
		0-3m.	3-6.	6-9.	9-12.	12-15.	15-18.
July	285	33.3	34.4	24.6	7.4	0.3	0.0
August	680	41.0	28.8	19.5	8.5	1.9	0.2
September	156	34.0	28.2	17.3	9.6	9.6	1.3

This table shows that the average agrees very closely with that of the other limnetic crustacea. During this season a considerable number of observations were made after nightfall, but neither in 1894, nor in this year was there any evidence of a movement of *Leptodora* toward the surface at night, as measured by the three meter intervals. The species is nearly, or quite absent from the upper meter or so during the day, but comes to the surface again with the other crustacea after nightfall.

In August, 1895, the number caught in the 0-3 m. level, ranged from 1 to 43 individuals; in the 3-6 m. level, from 1 to 33; and in the 6-9 m. level, from 0 to 46. Below this level, of course, few, or no individuals were obtained. With this range of variation, the percentages might easily be altered greatly by a single observation.

Nauplii.

Figure 33.

The vertical distribution of the nauplii has been very variable, as may be seen from the following facts: On July 17th 50 per cent. of the very large number taken were caught between 6 and 9 meters and only 7 per cent. in the 0-3 meter level. On the 18th the distribution was substantially the same, while on the 20th 38 per cent. were found between 0 and 3 meters, and 31.5 per cent. between 6 and 9, and on the 21st 49 per cent. were found in the upper level and only 19 per cent. between 6 and 9 meters. On the 5th of August 90 per cent. were found between 6 and 12 meters, and on the 8th 23 per cent. between 9 and 10 meters, and 50 per cent. between 6 and 10.

These observations were all made in the day and under substantially similar conditions of weather and temperature. During August and September, 1897, numerous observations were made by means of net and pump and in nearly all cases the great majority of the nauplii were found in the lower part of the inhabited water, although a considerable number was also found in the surface levels. On the 13th of September a very large number of nauplii were found in the upper half meter, by far the largest number being found at the surface itself. (See Table XXXVIII, J.) The number very rapidly declined from the surface, reaching a minimum at about 1 meter. They began to increase again at about 5 meters and reached a great number in the lower levels, substantially as shown in Fig. 33. The nauplii in the upper water were well developed and apparently about to change into the form of the immature Copepods, while the great number lying between 10 and 13 meters was composed of very young individuals. It seems probable, therefore, that the nauplii during their younger life dwell in the lower part of the inhabited water and move toward the surface when they are about to leave the nauplius stage. The immature forms, both of *Diaptomus* and *Cyclops*, are present in large numbers in the upper strata of the water and the egg-bearing individuals are present in larger numbers in the lower strata, although they are never absent from the upper water. In all the lakes which I have examined in summer the great majority of the nauplii have been found in the region of the thermocline; either just above it, or immediately in and below it. I infer, therefore, that this distribution is a common one.

In October and later the distribution becomes uniform and so continues until late in the winter. In March, as the larvae begin to change into *Cyclops* forms, they approach the surface.

Apstein ('96, Table IV.) does not appear to have found the nauplii more abundant in the deeper water than near the surface.

THE DISTRIBUTION IN THE UPPER METER, AND THE DIURNAL MOVEMENT.

Figures 32, 33.

The observations recorded in my former paper showed uniformly that there was no general diurnal movement of the crustacea and no movement at all which could be detected by the use of three-meter intervals. This conclusion has been confirmed by all of the observations which I have since made. During 1895 and 1896 considerable attention was paid to the distribution of the crustacea in the upper meter, with the design to determining whether or not there was a diurnal movement of the limnetic forms within narrower limits than three meters. A large number of observations were made in 1896 in order to determine the relative number of crustacea in the upper meter and the remainder of the 3 m. level. These observations were begun early in August and continued until the last of November; twenty sets of observations being made in all. In some cases the crustacea were taken meter by meter and the numbers compared. In other cases the crustacea of the upper meter were caught and their numbers compared with those obtained from the entire depth. A single illustration of the former method is given; partly in order to show the results, partly also to illustrate the amount of agreement and difference between the three catches of one meter each and that made through the entire distance of three meters.

TABLE XXXVI.—*Number of crustacea caught August 24, 1895. 6 P. M.*

Depth, meters.	Diaptomus.	Cyclops.	D. hyalina.	D. retrocurva.	Diaphanosoma.	Chydorus.
0-1.....	700	360	2,120	280	140	100
1-2.....	340	360	2,060	200	140	120
2-3.....	460	370	1,150	160	50	50
Total.....	1,500	1,090	5,330	640	330	270
0-3.....	1,780	1,050	4,250	475	350	375

As would naturally be expected, the ratio between the crustacea of the upper meter and those of the entire level varies

very greatly. On some occasions the catch of certain species from the upper meter was larger than that obtained by a second catch from the entire three meters. Such instances were due to the presence of very large numbers of young in the upper meter, with a somewhat irregular distribution, so that the catches varied considerably. Upon the whole, however, the average number derived from these twenty observations agreed surprisingly in all the species. It was found that the upper meter contained an average of 43 per cent. of the entire catch of *Diaptomus* from the upper three meters; 47 per cent. of *Cyclops*; and 50 per cent. of *Daphnia hyalina*. These catches were made during the day and may be taken as fairly indicating the relative number of crustacea in the upper meter during the daylight hours. It will be seen that these observations fully justify the statement made in my former paper (Birge, '95, p. 479) that "a general movement of the crustacea as much as one meter would have been detected," and indicates that at no time is the population of the upper meter of the lake notably deficient. The minimum percentages were very irregularly distributed and depended more upon the presence or absence of young individuals than upon any influence of light, weather, or wind.

These observations also indicate the extent to which the lines of Figs. 29 and 30 should be altered in the upper three meters in order to express the average distribution within that level.

During 1897 observations were made with a view of determining the exact distribution of the crustacea in the upper meter. They were made by two methods: First, a net with an opening ten centimeters in diameter was supported so that it could be drawn horizontally through the water for a known distance at an uniform rate of speed. The crustacea so obtained were counted and the number present at a given level was thus determined. Second, a pump was taken out in the boat, by whose aid the water of the lake was pumped through a hose and strained by the plankton net, the mouth of the suction hose being placed at the successive levels. Water was taken from the surface at a depth varying from two or five centimeters in calm weather, to ten when the lake was agitated by the wind; at one-

half meter; at one, two, and three meters, and sometimes deeper. The results of these two methods were the same and can be stated in general as follows:

1. On calm sunny days the upper ten centimeters of the lake may be almost devoid of crustacea, as was the case on August 1st, 2d, and 25th. At a depth of half a meter, however, the numbers become considerable and may be very great. On August 25th the total population of the water at this depth was at the rate of nearly 70,000 crustacea per cubic meter, without including the nauplii, which numbered 18,000 more. At one meter the population was nearly 200,000 per cubic meter and below that depth the numbers rapidly declined. A large number of similar observations were made on other days, and in one of the cases where the observations with the pump were extended throughout the inhabited water the results have been diagramed and are shown in Fig. 33.

2. The population of the upper meter is largely composed of immature crustacea, the percentage of young varying in different species. It is most marked in *Diaptomus*, *Daphnia hyalina*, and *D. retrocurva*. Great numbers of young are found in the upper meter, as was the case on August 25th, and especially on September 8th, and the adults may be entirely absent. At the depth of a half meter a very few half-grown individuals are present, while they are fairly numerous at one meter and at the same depth the adults begin to appear. Below one meter by far the most conspicuous part of the population consists of adults, although the young may be present in numbers as great as the comparatively few adults. A similar relation of distribution holds for *Daphnia retrocurva*, although the proportion of this species in the upper meter by day seems to be smaller than that of its congener. The adults of *Diaphanosoma* approach nearer the surface when the sun is bright, than those of *Daphnia*, but at least 75 per cent. of the individuals found between the half meter level and the surface are immature. The same statement is true for *Diaptomus*. *Cyclops* shows the least difference; females carrying eggs being regularly found in considerable numbers at half a meter, or even above that level, coming to the surface on cloudy days and occasionally in sunshine. Yet

while it is not easy to determine the exact proportions of young, it is very obvious that the majority of the immature *Cyclops* are near the surface.

3. A far larger proportion of *Cyclops* is usually obtained from the upper five or ten centimeters than comes from any of the other forms of limnetic crustacea, and it may be present at the very surface on hot, calm, sunny days, as on Sept. 13.

4. The nauplii are found in considerable numbers in the upper water during the day and frequently extend to the very surface, yet ordinarily the number at the surface is only a third, or even a smaller fraction of that found at one-half meter. Older nauplii may be found in large numbers at the surface and confined to the upper one-half meter.

5. In windy and cloudy weather the crustacea approach nearer to the surface, the numbers of *Diaptomus* and *Cyclops* being especially increased by the change in the condition of the sky. *Daphnia hyalina* also may come nearer the surface. But the numbers of these species during the day in the upper ten centimeters are always decidedly smaller than at one-half meter, so far as my observations extend.

6. At night the population of the upper meter changes in character. The young, instead of being concentrated in swarms in this layer, become more evenly distributed, and the adults which were found below the one-meter level rise toward the surface. *Leptodora* and larval *Corethra* have been regularly taken at the surface in considerable numbers at night. During the day these animals are rarely, if ever, found close to the surface, although they may be abundant enough above the three meter line. It would appear, therefore, that these animals move toward the surface at night, together with the crustacea on which they feed. *Epischura* seems to have the same habit.

TABLE XXXVII.—Typical catches from the upper water giving the rate of population in thousands per cu. m. at the depth specified.

	Depth, meters.	Diaptomus.	Cyclops.	D. hyalina.	Diaphanosoma.	D. retrocurva.	Total crustacea.	Nauplii.	Leptodora.	Gloiotrichia.	Conochilus
A. Aug. 1. Noon. Light north breeze. Net drawn horizontally 20 meters.	0-0.1	1.2	26.0
	0.5-0.6	22.5	2.5	25.0	12.0	5.0
	1.0-1.1	43.8	5.7	11.7	2.2	63.4	9.2	2.0
	1.5-1.6	14.0	2.4	14.8	1.6	0.4	33.2	2.4	2.2
B. Aug. 2. 5 p. m. Light clouds. Calm. Net drawn 15 meters.	0-0.1	8.2	2.2	1.4	0.1	11.9	1.4	1.4
	0.5-0.6	9.2	7.8	12.0	1.4	30.4	11.6	1.6
	1.0-1.1	11.6	9.2	18.4	2.2	41.4	3.6	0.04	0.04	0.08
	2.0-2.1	9.6	10.4	9.6	2.8	32.4	5.6	0.04	0.08
	3.0-3.1	20.0	8.6	9.0	2.4	41.0	5.0	0.02	0.02
C. Aug. 6, 2 p. m. light clouds, light S. E. breeze. Pump.	0.05	0.4	0.6	0.6	1.6	40.2	12.2
	0.5	22.5	4.1	0.75	0.4	7.8	56.2	8.6
	1	12.0	9.0	6.0	5.0	32.0	77.2	0.05	7.5
	2	22.5	15.0	23.7	12.2	73.4	8.2	s	0.2
D. Aug. 25, noon, calm, clear. Pump.	0.05	1.0	0.5	1.5	6.0	113.0
	0.5	18.5	12.7	4.5	31.5	67.2	18.0	0.1	10.5
	1.0	61.5	21.7	51.7	63.5	198.4	5.2	3.7
	2.0	45.7	18.7	8.7	8.2	81.3	6.0	2.0	4.5
	3.0	10.0	6.0	6.5	4.5	2.0	29.0	1.5	2.0	3.0
E. Aug. 27, 5 p. m. clear, fresh N. W. breeze. Pump.	0.1	6.5	12.0	13.0	12.0	43.5	4.5
	0.5	9.0	15.7	50.3	1.8	13.0	90.0	0.2
	1.0	8.0	17.5	17.0	9.5	51.0	0.1
	2.0	9.0	24.0	12.0	11.5	56.5	0.1
F. Aug. 28, 11 a. m. Cloudy, fresh S. W. breeze. Pump.	0.1	5.6	10.4	3.2	14.8	34.0	13.2
	0.5	10.8	14.0	27.6	12.8	65.2	19.2
	1.0	16.2	17.4	26.4	12.6	72.6	17.4
	2.0	12.0	24.6	17.3	13.8	67.7	16.8
	3.0	15.6	40.8	4.8	9.6	1.8	72.6	12.6
	4.0	7.6	20.0	5.6	6.4	39.6	18.4
	5.0	6.4	12.0	5.2	1.6	25.2	7.2

TABLE XXXVII.—Continued.

	Depth, meters.	Diaptomus.	Cyclops.	D. hyalina.	Diaphanosoma.	D. retrocurva.	Total crustacea.	Nauplii.	Leptodora.	Gloiostrichia.	Conochilus.
G. Sept. 6. Noon. Clear, fresh S. W. breeze. Pump.	0.1	3.5	5.0	4.5	4.0	17.0	27.5
	0.5	1.0	6.0	6.0	6.5	19.5	29.0
	1.0	6.0	14.5	10.5	5.0	36.0	25.0
	2.0	5.0	13.0	10.5	4.0	5.0	37.5	25.5
	3.0	5.4	10.4	3.4	2.0	21.2	13.2

The preceding tables show the results of some of the more important observations of this kind made in 1897. The figures of these tables express the rate per cubic meter found at the given depths, not the actual population between certain depths as is done in the tables based on the vertical net.

In most of these lists, the preponderance of *Cyclops* in the upper stratum is striking. In A, all of the *Diaptomi* at 0.5 and 1 m. were young. The same was true of *D. hyalina* at 0.5 m., and above. In all catches 85–95 per cent. were young at 1 m. on sunny days. The effect of cloud is plainly visible in B, C, and F, and of wind in E and G. The tendency of *Gloiostrichia* to aggregate at the surface is well seen in D.

In the following tables the record for two more complete observations is given, together with one illustration of a night distribution. In the latter there were almost no nauplii, an exception to what has usually been found at night. The population for the given depths in the catch of September 8th has been platted in Fig. 33, and Fig. 32 shows the upper three meters of the two sets of observations on September 13.

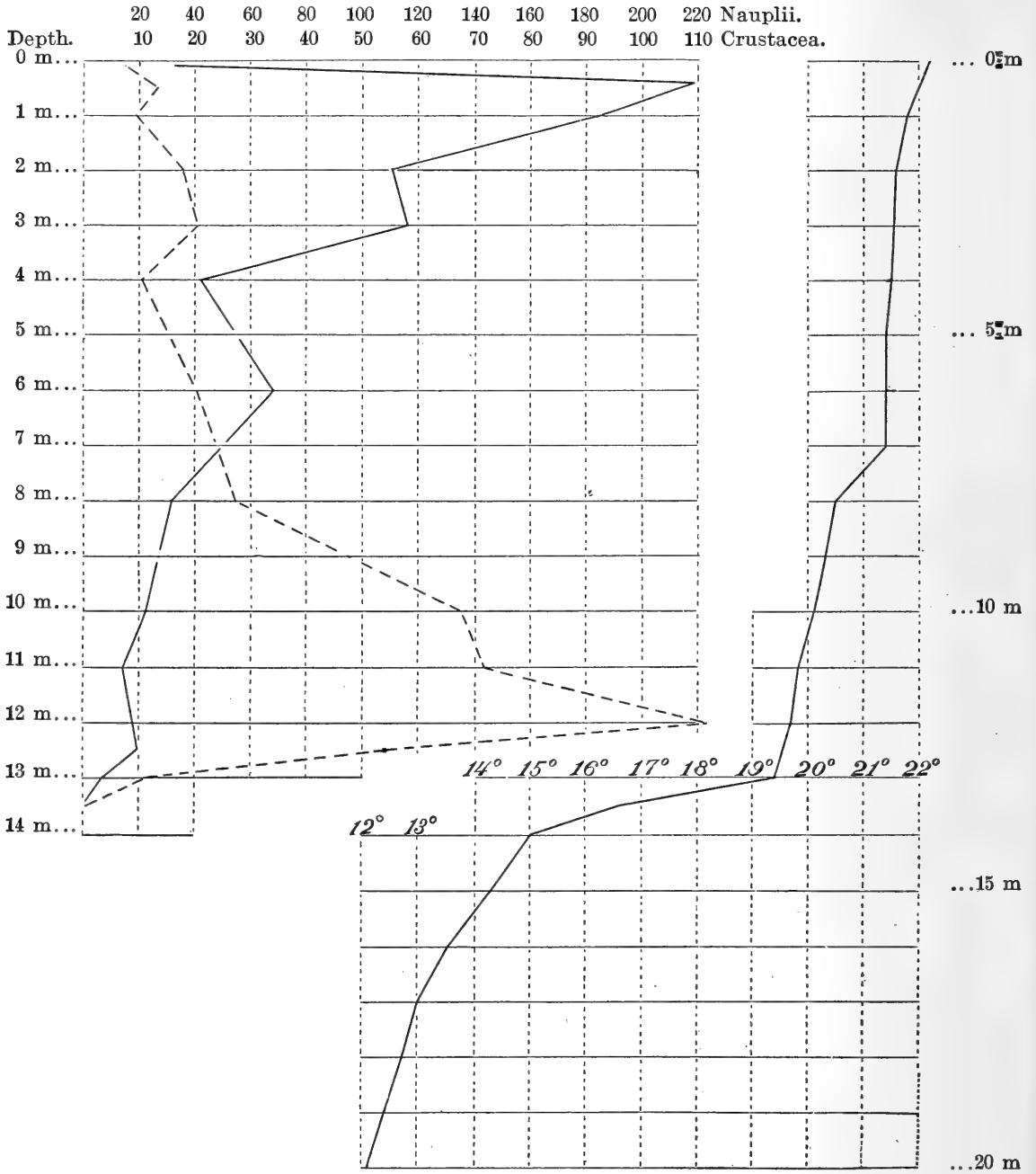


FIG. 33.—Vertical distribution of crustacea, nauplii, and temperature, Sept. 8, 1896, noon. Scale, crustacea (full line), 1 horizontal space = 10,000 per cu. m.; nauplii, 1 space = 20,000; temperature, 1 space = 1 degree. See p. 413.

TABLE XXXVIII—Continued.

	Depth.	Temperature.	Diaptomus.	Cyclops.	Adult <i>D. hyalina</i> .	Young <i>D. hyalina</i> .	<i>D. Retrocurva</i> .	Diaphanosoma.	Ergasilus.	Total crustacea.	Nauplii.
J. Sept. 13. 9 p. m.	0.1	10.5	22.0	3.5	4.5	2.5	12.5	35.5
	0.5	7.5	13.5	5.5	12.5	10.0	11.5	60.5
	1.0	6.0	20.5	7.0	3.5	1.0	14.5	53.5
	2.0	12.5	11.5	6.0	3.5	5.0	13.5	52.0
	3.0	7.5	11.0	6.0	4.5	6.0	32.0	67.0

These observations (and I could adduce many more) show that there is a clearly marked diurnal movement of the crustacea in lake Mendota but that it is confined within the narrow limits of the upper meter, or meter and a half. The day population of the upper centimeters, especially in bright, calm weather, is very small, but the number at one-half meter, even under such conditions, is nearly or quite as large as that at any greater depth, and may be the maximum number. The day population of the upper meter consists chiefly of young and immature crustacea; most of the older individuals of all species being found at greater depths. This relation of age to distribution is most marked in the *Daphnias* and *Diaptomus* and least marked in *Cyclops*. At night the population of the upper meter agrees in general character with that of the water below, the older individuals ascending, and the younger descending. I have found no evidence of an aggregation of adult crustacea close to the surface at night, but my observations have been confined to the hours before midnight.

In general, these conclusions regarding the diurnal movement of the crustacea agree with those of Francé, ('94, p. 35), with the important difference that while the movements described by him are measured by meters, those which I have observed take place within the narrow limits of the upper meter, or even within a smaller distance. There are, however, some noteworthy exceptions to the agreement. I do not find that the

Cladocera aggregate at the surface at night, but find that the upper water, in the early part of the night at any rate, is tenanted by a larger proportion of Copepoda than of Cladocera and that a smaller fraction of adult Cladocera is found among those present at this level than at the depth of half a meter, or more. I do not find that a strong wind brings about an even distribution of the crustacea, although it assists in doing so. In moderate winds the crustacea approach somewhat nearer the surface than in quiet, sunny weather, and during violent winds the distribution in the upper three meters is more uniform than in cloudy weather, but in case large numbers of young are present, there is always a high percentage in the upper meter.

THE DISTRIBUTION AT THE THERMOCLINE.

During the latter part of the summer of 1896 observations were made with the net, in order to determine more exactly the distribution of the crustacea at the thermocline. The net was raised from the bottom of the lake to the bottom of the thermocline and then closed and drawn to the surface. After washing out the collection it was lowered to the depth at which it was closed, opened, raised through one meter and closed again. In this way the population was determined by single meters for the two or more meters including the thermocline and the water immediately above. Great care was taken that the movement of the net should be regular, and the messenger was sent down the line in such a way as to close the net immediately on its reaching the upper level of the meter under investigation. The results show that the crustacean population usually passes into the thermocline and often toward its lower part, but that here it ends often with great abruptness. If the temperature conditions are such that the thermocline is spread out over two or three meters the population ends less abruptly than when the thermocline is concentrated into a meter or a half meter. The observations showed a population per cubic meter of only a few hundred below the thermocline, while in it and above it the population might range from 40,000 to 60,000 per cubic meter. As these observations agree in general with the more exact results reached by the pump in 1897, the details will not be given.

The distribution of the nauplii at the thermocline is especially noteworthy. During the period of the observations there were frequently found enormous numbers of larval Copepods in the lower water. The numbers began to increase at ten or even eight meters, at a point several meters above the level at which the temperature began to fall, so that this distribution does not seem to depend on temperature. The number of nauplii rose to a maximum rate of more than 300,000 per cubic meter in and above the thermocline, but ended with very great abruptness. This termination of the population often took place within the space of half a meter.

The number of algae also declines very rapidly at the thermocline and those which are obtained below this level are dead or dying. The amount of algae thus obtained is, however, far greater than the number of crustacea; indeed the algae below the thermocline are many times more abundant in relation to the number of crustacea present than is the case in lakes like those of the Oconomowoc system, in which there is a large crustacean population in the lower waters. It is obvious, therefore, that the exclusion of the crustacea from these deeper waters is not due to the absence of food.

The algae at times appear to accumulate above the thermocline, and to pass it, as they settle, only after considerable delay. I have attempted to discover whether this delay was due to the greater density of the water, occasioned by the diminution in temperature. A large glass tube, six centimeters in internal diameter and about two meters long, was filled with water and the lower half meter placed in a vessel of ice-water. After a few hours a very marked thermocline was formed, the temperature falling some 6° C. in the space of about 10 cm. Water containing algae, chiefly diatoms, was introduced at the top of the tube and the algae gradually sank through the water. On reaching the artificial thermocline they paused for a few minutes, but rapidly acquired the temperature of the water, as would be expected, and then sank to the bottom of the vessel. The delay at the thermocline could not have amounted to more than five minutes for an individual alga. It seems probable from

these experiments that temperature does not cause the accumulation of algae often found above the thermocline. Their death and consequent rapid sinking in the deeper water account for their small numbers below the thermocline.

In this region *Cyclops* is the least sensitive of the limnetic crustacea to the influences which exclude them from the lower water. *Chydorus* is close to it in this respect when present in large numbers. A larger proportion of these species than of any others is found in the water immediately above the thermocline, and of the few crustacea which are found below that level by far the greater portion is composed of these genera. When *Chydorus* is extremely abundant more individuals of this species than of any other may be found below the thermocline. At one time nearly 70 individuals were taken by the net between eleven meters and eighteen, more than four times as many as all the other crustacea together. An examination showed that all, or nearly all of these individuals were in the process of moulting and had apparently become in some way entangled in the shell, so that their presence in this deeper water was an evidence of injury or weakness. The crustacea below the thermocline are, however, not dead or dying when brought to the surface.

The larvae of *Corethra* are found in considerable numbers below the thermocline and seem to be the only limnetic animal which normally inhabits these waters. Not infrequently the numbers of *Corethra* are far greater than the total number of the crustacea obtained. Indeed this is regularly the case when *Corethra* is present in any considerable numbers. Since *Corethra* can carry a stock of air in its breathing tubes it is easy to understand the possibility of its living in the water below the thermocline. It is less easy to see why it should go there unless it retains in lake Mendota the habits which it has in the far more numerous lakes whose lower waters are habitable by crustacea.

FACTORS DETERMINING VERTICAL DISTRIBUTION.

The following factors contribute to determine the vertical distribution of the limnetic crustacea.

1. Food.
2. Temperature.
3. Condition of the water in respect to dissolved oxygen and other substances.
4. Light.
5. Wind.
6. Gravity.
7. The age of the members of any given species.
8. Specific peculiarities.

Food.

Food influences the distribution of the crustacea both by its amount and its quality. As a general proposition, the crustacea should be most numerous where food is most abundant and least numerous where food is least plentiful. Since, therefore, the reproduction of the limnetic algae goes on most rapidly in the upper strata of the lake, it is natural that the crustacea which feed upon these algae should also be most numerous there. Yet this simple relation of food and eater does not at all cover the facts of vertical distribution. The amount of the algae in lake Mendota is in general so great in proportion to the number of crustacea that the quantity of food is rarely the predominant factor in vertical distribution. In early spring the crustacea, and especially *Cyclops*, increase more rapidly than does the food. But after the opening of summer the food appears to be almost always in excess of the crustacea, and their distribution, therefore, does not follow variations in its distribution.

For example, it is well known that the limnetic algae appear in what may be called successive waves of development. A single species rises to a maximum, predominates for a short time, then declines and nearly disappears, and its place is taken by another species. During the period of decline, especially in the case of diatoms, there is a time when the algae are sinking and

when they are more abundant in the deeper strata of the water than near the surface. At such times the crustacea do not follow the food downward, but retain their normal summer distribution. Again, in the autumn there is a period, beginning a little before the first of October and extending to the freezing of the lake, when the algae are present in immense quantities, and are distributed with approximate equality through the whole mass of the water. Yet the crustacea are not by any means as uniform in their distribution, and at times some species are as closely aggregated near the surface as in summer. Their position depends on age and other factors rather than on food.

The position of *Daphnia pulicaria*, also, cannot be determined by the food. It may be added that the crustacea in the deeper strata of the water are usually less numerous in comparison to the food present than they are in the upper strata.

On the whole, while the quantity of food accounts for many of the larger facts of vertical distribution, it leaves wholly unexplained most of the details of the distribution of all of the species. It entirely fails to account for the position of *Daphnia pulicaria*, or for the absence of crustacea from the deeper water in summer.

The quality of the food at different depths is of some importance in the distribution of the crustacea. *Anabaena*, *Aphanizomenon*, and allied genera of algae are found in larger numbers in the upper strata of the water, while the diatoms, with their siliceous shells, tend to be more evenly distributed and never accumulate at the surface. *Anabaena* and allied forms, also, being small in size and devoid of skeleton, are more readily eaten by the young crustacea than the diatoms, while the diatoms in turn can be very readily eaten by the older and larger crustacea. There is, therefore, a tendency for the young of nearly all species of limnetic crustacea to seek the algae in the surface strata of the lake, and the difference in the distribution of the algae is no doubt one of the factors which keep so high a percentage of the young near the surface.

The fact that the crustacea in the 0-3 m. level do not rise above a certain number (p. 387) shows that food is not the only

regulating factor, since the amount of food in that level in autumn is more than sufficient to support the total crustacean population.

Temperature.

Temperature may be considered under three heads: (1) the rise and fall of the average temperature of the water from spring to late autumn, (2) the diurnal variation of temperature, (3) the vertical distribution of temperature.

I have not been able to discover that the warming or cooling of the water in spring or fall affects directly the vertical distribution of any species except *Daphnia pulicaria*. The movements of this species are undoubtedly determined by the rise or fall of the general temperature of the water. It is a sub-thermoclineal species in plankton-poor lakes and in summer it keeps as near as possible to the cool water in lake Mendota.

The diurnal variation of temperature has no noticeable direct effect on vertical distribution.

The most striking fact in the vertical distribution of temperature is the formation in the lake during summer of the thermocline which forms the lower limit of the crustacea from July on. The crustacea follow accurately the position of the thermocline. This layer has a vertical oscillation of two or even three meters, being affected by the direction of the wind. In every case the lower limit of the crustacea oscillates with the position of the thermocline and follows it downward as it gradually descends during the summer.

The statement made in my former paper (Birge, '95, p. 481) that "during July, only the upper twelve meters are tenanted by crustacea, and over ninety per cent. are in the upper nine meters" should be modified so as to read, that ninety-five per cent. or more of the crustacea are found above the thermocline, which in July is situated from nine to twelve meters below the surface. Yet, close as is this correspondence between crustacea and thermocline, the temperature is not the fact which limits their downward extension. This will be shown under the next head.

I have no doubt, however, that the thermocline is always an

important factor in determining the position of the crustacea. *Diaphanosoma* is pre-eminently a summer form and flourishes only when the temperature of the water is at or above 20° C. It would hardly extend its range into the cold bottom water. In Pine lake and Oconomowoc lake, in both of which many crustacea extend freely through the thermocline, *Diaphanosoma* is confined to the region above it. Marsh states that *Epischura* occupies the same position in Green lake, in which lake also most of the crustacea extend far below the thermocline.

In all small lakes whose deeper water is habitable it will probably be found that the limnetic crustacea (and the rotifers also) can be divided into three sets:

1. Those permanently above the thermocline, including *Diaphanosoma*, *Epischura* (Marsh, '97, p. 195), and probably some forms of *Daphnia hyalina* and *Ceriodaphnia*.

2. Those below the thermocline, including *D. pulicaria* and *Longiremis* and *Limnocalanus* (Marsh, '97, p. 201).

3. Those which are found on both sides of the thermocline, including *Diaptomus*, *Cyclops*, and others. These forms are named on small evidence in most cases, and the list must be regarded as suggestive only. The thermocline and the upper meter or two are certainly the two important strata in vertical distribution.

Above the thermocline there are no differences in temperature which could determine the distribution of the crustacea. There is rarely a difference exceeding two degrees between the top of the thermocline and the surface of the lake, and the variations in the vertical distribution of the crustacea above this layer must depend on other causes than temperature.

After the first of October, lake Mendota is nearly homothermous. Differences exceeding one degree are rarely found, and only in the warmer parts of bright and calm days. This condition is assumed while the temperature is fairly high—16° to 18°—and so early in the autumn that the development of the crustacea goes on actively for a month or more. During this period, therefore, other factors than temperature or food must determine the vertical distribution. Uniformity of distribution, however, is not attained until the decline in numbers of the

several species of crustacea. So long as the crustacea are multiplying, the higher strata may contain as high a percentage as they do in summer. (Cf. p. 398.)

One indirect effect of temperature should be noticed. A higher temperature increases the sensitiveness of the limnetic crustacea to light, and thus aids in driving from the upper strata those species which are negatively affected by light, especially *Daphnia hyalina*.

Chemical relations of the water.

The abrupt limitation of the downward extension of the crustacea in lake Mendota by the thermocline is not due to the change in temperature. This is shown by the fact that in lakes which are poor in plankton the crustacea extend far below the thermocline and in many cases the colder water is the more densely populated part of the lake. The crustacea are excluded from the lower water by the accumulation in it of products of the decomposition of the plankton plants and animals. These accumulate in the stagnant water below the thermocline and their decomposition finally, and in lake Mendota rapidly, fills the water with decomposition products and exhausts the oxygen.

The State Board of Health of Massachusetts in 1889 and 1890 made elaborate examinations of the condition of the deeper water of numerous ponds in that state. It was found (Drown, '90, p. 554) that in the deep water there was "an accumulation of intermediate products of decomposition of nitrogenous organic matter, the hydrogen compounds of carbon, sulphur, phosphorus, and nitrogen, which, owing to the exhaustion of the supply of free oxygen, cannot be further oxidized." It was found also that "in foul water of this character the varieties of animal and vegetable life which we find in water nearer the surface are almost, if not altogether, absent." In 1891 investigations were made of the amount of oxygen in the bottom water, showing (Drown, '91, p. 373) a rapid decline in the dissolved oxygen below the thermocline and its total disappearance from the bottom water of the ponds. It is not possible to state positively whether it is the absence of the oxygen or the presence of the decomposition products which excludes the crustacea from the

lower water, in the absence of more exact investigations on the subject.

In lake Mendota the lower water is always clear, but the whole region below the thermocline rapidly becomes unfit to support life, so that the life in the lower waters ceases very shortly after the formation of the thermocline. In lakes with a smaller amount of plankton the bottom water may become unfit to support life in late summer, although the plants and animals extend far below the thermocline. In Pine lake on September 5, 1896, *Cyclops* was by far the most abundant crustacean in the cold water, and numbered 21,000 per cubic meter between 12 and 15 meters, and 3,000 between 15 and 18 m. It was practically wholly absent between 18 and 24 m., only 8 individuals being taken by the net within that distance, and no other forms of crustacea were taken. In Okauchee lake the crustacea are numerous to a depth of 24 m. in September, but between 24 and 27.5 m. they were very few. In lake Geneva, Wisconsin, the crustacea in September extend to the bottom at a depth of more than 42 meters. This lake is extremely poor in plankton. The statistics given by Marsh for *Cyclops* and *Diaptomus* ('97, p. 191, 204) may indicate a partial exclusion of the crustacea from the lower water of Green lake in late summer and autumn.

While the plants and animals of the upper water are excluded by this means from the lower part of the lake, animal life is by no means entirely wanting. Worms are found in the mud at the bottom, as also is *Cyclas*, in considerable numbers. There must, therefore, be oxygen enough in the water to support some life.

Cyclops and *Chydorus* are the least sensitive of the limnetic crustacea to these injurious influences. As shown by the tables on page 416, they always predominate in the lower strata of the inhabited water and form almost the entire population of the water below the thermocline.

It is possible that the exhaustion of the oxygen from the lower strata of the water is the cause of the death of *Cyclops* and *Daphnia hyalina* at the bottom in spring and early summer. I have, however, no positive evidence on this point and in the

case of the latter species a great majority of the old animals are so affected by various diseases as to need no other explanation of their death.

Undoubtedly the condition of the water in summer causes the rise of the survivors of the spring broods of *D. pulicaria* from the bottom to the region of the thermocline.

Light.

In lake Mendota the direct effect of light is confined to the upper meter or two, within which distance it has a powerful influence in determining the position of the crustacea.

Laboratory study shows that the relation of the crustacea to light differs in different species. *Daphnia* in all of the limnetic species has a strongly negative movement. *Diaptomus*, *Diaphanosoma*, and *Chydorus* are strongly positive while *Cyclops* is, on the whole, positive, but is not very strongly affected either way. Yet the vertical distribution of these species is not very different when studied in the lake by three-meter intervals. Compare Fig. 30, and the percentage tables on p. 393 *Diaptomus* and *Daphnia* show an especially close correspondence in spite of their opposite relation to light. These species, placed in a glass vessel near a window, will segregate, *Diaptomus* collecting near the surface and toward the light, while *Daphnia* goes to the bottom and to the side furthest from the light. This movement away from the light is not shared by every *Daphnia* present; some may move toward the light, usually not more than one per cent. of the adult or half-grown individuals. Young *Daphnias*, especially the newly hatched, are attracted by the light. The adult individuals of *Diaptomus* are found in a higher level of the lake than those of *Daphnia*.

The young crustacea have a monopoly of the upper half-meter, or thereabouts, during the day. It is easy to see the advantage of this arrangement to the species. In the upper meter, plant-life is most abundant, and is represented chiefly by small forms like *Anabaena* which are especially adapted as food to the small crustacea. On the other hand, the adult crustacea find an abundance of food suited to their size and masticatory

organs, in the diatoms, which are more uniformly distributed in the water. The young, therefore, are freed in part during the daytime, by the action of light, from the competition of most of the older forms of the same species for the food which is especially adapted to the young.

On August 26th, 1895, there was an alternation of cloud and sun, which made the day especially favorable for the study of the relation of light and the vertical distribution of *Daphnia*. It was found by numerous observations that the adult and half-grown *Daphnias* were approximately one meter below the surface during the sunny periods, but rose to about one-half meter during the cloudy intervals. The rise immediately followed the obscuring of the sun and the return was as prompt when the sun again shone. It was as though the *Daphnias* were depressed by a force against which they were contending, and they rose when the sun disappeared with the promptness of a compressed spring when relieved of weight.

In laboratory experiments *Diaptomus* and young *Daphnias* move quite to the light end of the box in which they are placed. If sunlight is reflected by a mirror, they still move toward it and find no light too strong which can thus be sent to them. It would seem, however, that the direct sunlight of the open lake is too strong for them, or they would be present in larger numbers in the upper centimeters of the lake. If the warmth of the water repelled them we should expect this stratum to be tenanted as the lake cools in the fall, and should also expect that the young crustacea would gradually withdraw during the day as the surface warms. Neither in autumn nor in early morning, however, do we find the crustacea close to the surface. The withdrawal from the upper quarter meter or so continues at least until the first of November, and the crustacea descend from the surface very promptly after sunrise. As already stated, the old nauplii are the only crustacea which I have found in large numbers immediately at the surface on calm, bright days. A high temperature, however, increases the negative action of light and a low temperature lessens or reverses it. In early winter when the ice is transparent, *D. pulicaria* and *D. hyalina* may often be seen in large numbers immediately

below the ice. This is especially noticeable in the case of the former species.

The position of *D. pulicaria* must be controlled by temperature. I have never been able to detect any noteworthy difference between *Daphnia pulicaria* and *Daphnia hyalina* in their relation to light, by means of laboratory experiments. Nor have I as yet been able to find any difference in sensitiveness to light between *Daphnias* brought from a depth of three meters and those from a depth of twelve or more meters.

The conclusion is, therefore, that in the upper meter and perhaps within a range not exceeding two meters from the surface, light is an extremely important factor in determining the vertical position of the crustacea. Below this depth, however, there are no effects which can be definitely ascribed to light. I am not at all inclined to deny that, in lakes whose water is more transparent than that of Mendota, light may influence the crustacea to a greater depth. During the summer the water of lake Mendota is always turbid with vegetation, which cuts off the light very rapidly. My brass-topped dredge can rarely be seen to a depth greater than two meters, and frequently disappears between one-half and one meter. Vegetation, also, is especially effective in cutting off the violet and blue rays, on which the action of the light chiefly depends. In lakes whose water transmits these rays more freely, light may be a far more important factor in controlling distribution.

The diurnal movement of the crustacea, which is clearly present during summer within the narrow limits of the upper meter, is chiefly due to light. Wind or calm alter the conditions of movement but during summer can hardly be considered factors in causing it.

Wind.

On the whole, wind has only a small influence on the vertical distribution of the crustacea, although its effect varies greatly with the season and with the condition of the several species of crustacea. The action of the waves prevents the formation of the dense swarms of young crustacea which are apt to be near the surface during calm weather. These young crustacea seek the

algae which on calm days accumulate near the surface. When the lake is rough the algae are distributed to a greater depth, and the crustacea follow them to some extent; although, even when the wind blows with considerable force, the young crustacea still form the chief population of the upper meter of the water. I have not been able to discover any descent of the crustacea during windy weather, but, on the contrary, have always found the upper meter fully occupied by them even when the lake was so rough as to make it very difficult to go out with a row-boat.

The wind may affect the vertical distribution, also, by creating currents in the water. These are either lateral or vertical; we are concerned only with the latter. During the summer the vertical currents can penetrate no deeper into the water than the thermocline; that is, from six to fifteen meters, according to the time of year. These currents, however, seem to produce very little effect on the distribution of the crustacea—at any rate, at a distance of 850 m. from the shore, where my observations have been made. In the next section it will be shown that crustacea must be able to move through a distance of at least 100 meters vertically per day, and that the larger individuals move through four or five times that distance. There is, therefore, no difficulty in their maintaining any position in the water they may choose to occupy, against the somewhat slow vertical currents produced by the wind. Indeed, the wind affects the vertical distribution of the limnetic algae much less than would be expected. I have frequently collected after severe gales, and, in summer, have never failed to find the algae of the upper three meters far more numerous than those from lower levels. I have never been able to detect vertical currents, produced either by wind or sun, which were capable of distributing the algae uniformly through the mass of water in summer, and of course the active crustacea are far more independent of these currents than are the algae.

In the autumn the entire mass of water in the lakes is put into somewhat active circulation by the autumnal gales. The algae are at a maximum and are pretty uniformly distributed through the water. Neither the quantity nor the quality of the

food, therefore, give any reason to the crustacea for moving to any particular level. The effect of light, also, is lessened by the declining temperature of the water. Hence the crustacea are far more apt to yield to the action of wind and gravity than they do in summer, and become more evenly distributed through all levels of the water.

In the spring a similar distribution occurs immediately after the breaking up of the ice, when the lake is homothermous, and the crustacea and the algae have not yet started their spring development. Very soon, however, the surface strata contain much more food material than those below, and the young crustacea tend to remain near the surface until crowded down by the swarms of newly hatched forms. The lake, too, rapidly becomes heterothermous and the circulation of the water in late April and early May is by no means as complete as it is during the long homothermous period of the autumn.

A slight effect is also produced by the wind on the vertical distribution of the crustacea, since it causes the thermocline to oscillate through one or more meters. In general, it may be said that the on-shore wind tends to depress the thermocline, piling up the warm water on top of it; while the off-shore wind tends to raise it by stripping off the warm water of the surface. This general law, however, is subject to many modifications owing to the irregularities in the outline of the lake and in the conformation of its bottom. Whatever effect however, the wind produces on the thermocline it also exerts, of course, on the lower limit to which the crustacea extend.

Gravity.

The action of gravity has more influence on the position of crustacea than I had supposed on beginning this investigation. Its effects are most plainly seen in *Daphnia*, and least in *Diaptomus*. Gravity does not act as an accelerating force upon the movements of the crustacea, and yet their ordinary movements are adjusted with some reference to it. If Daphnias are watched in an aquarium, it will be seen that they usually remain at about the same level, permitting themselves to sink and then with a few

strokes of the antennæ resuming their former position. In this way they pass up and down through the water utilizing the material available for food. After a time the animal may swim off to a new place, but soon begins to repeat these alternate movements. The movements of *Diaptomus* are far less regular, yet it, too, keeps at about the same level, unless some attraction causes it to move up or down. *Cyclops*, which hunts for food of all sorts, and is decidedly a more predacious animal than either of the first two named, is far less regular in its movements, and *Leptodora*, as a true carnivore, swims actively in all directions.

The amount of energy required of the crustacea in order to maintain their position in the water is not inconsiderable, and is doubtless the main muscular labor demanded of them. They are all of them heavier than water, and sink at a rather rapid rate, which very quickly becomes uniform. The full-grown *Daphnia*, 3 to 4 millimeters long, sinks at the rate of 20–30 centimeters per minute even with expanded antennæ. Small, newly-hatched individuals, one millimeter or less in length, have a rate less than one-third as great, from 5 to 10 centimeters per minute. The specimens experimented upon almost always fell edgewise through the water, with the head down, if the antennæ were folded, and with the head up, if the antennæ were expanded. *Diaptomus* sinks at about the rate of about 12 cm. per minute, and medium-sized adult *Cyclops* without eggs at a rate of 9.5 cm. per minute.

Live *Daphnias* sink at the same rate as those freshly poisoned, as far as the eye can determine. This is easily determined in the case of half-grown and adult individuals, but young specimens are so active that it is hard to be accurate. At the rate given, an adult *Daphnia* would sink through as many as 250–400 meters in a day, and must, therefore, maintain itself against the force which would cause it to fall through this distance. Of course the weight to be lifted is very small, being the excess of the weight of the animal over that of an equal bulk of water. It seems impossible that the animal should ever sleep. As the creatures become older and larger the exertion becomes greater than in the case of young individuals, and the older and, especially, the

feebler animals, tend gradually to sink and accumulate in the deeper waters of the lake.

Such aggregations of *Cyclops* are often found at the bottom of the lake in winter. In March, 1895, for example, from fifty to seventy per cent. of this species were in the lower three meters. *Daphnia hyalina* shows a similar downward movement in late May and early June on the part of those individuals which have lived over winter. In late autumn, also, the adult members of this species are far more numerous in the lower strata than they are at higher levels. Since, at this time, there is a superabundance of food at all depth of the water, and, since the crustacea are relatively few in number, this distribution can hardly be due to any other cause than gravity. (See p. 398.)

Diaptomus and *Diaphanosoma* with their very powerful swimming organs, rarely show this tendency to sink. Perhaps the large amount of fat usually present in *Diaptomus* also aids in preventing sinking.

Age.

It is a general rule that the young individuals of a species appear near the surface. When the crustacea begin to multiply in the spring, the increase appears first in the 0-3-meter level. All very exceptionally large numbers of any species obtained during the summer have been caught in the upper three meters, and usually consisted of young and half-grown animals. No similar aggregations have been found in the deeper water, except as noted for *Cyclops* in the last section.

When a species is declining in numbers, the distribution is more uniform, and as the decline goes on, the lower levels may contain a larger number than the upper. If the crustacea obeyed this law with mathematical accuracy, there would be a sort of progress of the members of a brood from the top to the bottom of the lake, the successive broods of the young continually displacing the older in the upper strata.

Good illustrations of the distribution of the young and adult individuals can be obtained from the fall broods of *Daphnia hyalina*, as stated on page 398

The nauplii of the Copepods seem to form an exception to this rule of age. During the period when the thermocline is present, the maximum numbers of nauplii usually occur in the neighborhood of this layer, although not confined to it. In Pine lake, also, the thermocline and the level immediately below it contained more than sixty per cent. of the nauplii present. In Mendota they cannot go below the thermocline, but they congregate in and above it as shown in Fig. 33. The young *Cyclops* and *Diaptomus*, however, congregate near the surface by day, yet are by no means so closely confined to the surface as is the case with *Daphnia*. In autumn and winter the nauplii are pretty uniformly distributed.

The causes of this distribution by age are to be found in the different relations of old and young to light, food, and gravity. Light and food are probably the most important factors. Certainly it is true that *Cyclops*, which, of all the limnetic crustacea, is least affected by light and most omnivorous in diet, never shows as complete a separation of old and young as do the other genera. Yet even in this case there are more egg-bearing females, in proportion to the total number, in the deeper strata than near the surface. This is possibly due to gravity, which would have a greater effect on females laden with eggs.

Specific peculiarities.

It must be remembered that these various factors affect highly organized animals, which therefore do not respond with the mechanical uniformity of bacteria or of swarm-spores. Yet, in looking over my lists for catches which would illustrate exceptions to the principles given and to the averages of the tables, I have had difficulty in finding them. A few exceptional catches of *Diaptomus* occurred in all summers, where the 6-9 m. level in perhaps half a dozen cases contained more than the 0-3 m. But even such cases are very rare and in general the several species of crustacea follow their law of distribution with the range of variation already noted.

It is in the nature of the response of the species to these factors that the specific differences usually appear, rather than in aberrations from the general law. It has been very interesting to

see how these specific differences regularly presented themselves in my averages in spite of great variations in absolute numbers. Even those so small that they were at first supposed to be merely accidental recurred with great uniformity.

In conclusion I would repeat what I said in my introduction, that this discussion of general causes is to be regarded as suggestive. I shall be quite satisfied if it indicates lines of investigation to students of the fresh water plankton.

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ERRATA.

Page 289, line 18, for April 28th, read April 2nd.

Page 289, line 21, for Dec. 29th, read Dec. 19th.

Page 400, line 2 from bottom, for Fig. 31, read Fig. 32.

Page 412, line 2 from bottom, for Fig. 32, read Fig. 31. Also in Table
XXXVIII, I.

Page 425, line 17, for Fig. 30, read Fig. 29.

In Fig. 13, for D. pulex 34, read D. pulex 3.4.

APPENDIX.—TABLE A.—Dates on which collections were made.

1894.			1895.			1896.		
No. of days.	No. observations.	Dates.	No. of days.	No. observations.	Dates.	No. of days.	No. observations.	Dates.
July 1-15.....	9	7, 10, 11, 14.	Jan. 1-15.....	12	1, 2, 6, 9.....	4	4	7, 8, 14, 15.
July 16-31.....	38	16, 17, 18, 19, 27, 28, 29.	Jan. 16-31.....	3	16.....	2	3	16, 20.
Aug. 1-15.....	12	1, 2, 3, 4.	Feb. 1-14.....	10	15, 19, 23.....	3	4	4, 5, 14.
Aug. 16-31.....	3	23, 24, 25.	Feb. 14-28.....	11	6, 7, 11, 12.....	1	1	24.
Sept. 1-15.....	12	18, 19, 20, 21, 22, 27, 29.	Mch. 1-15.....	8	16, 18, 23.....	3	5	16, 21, 28.
Sept. 16-30.....	7	18, 19, 20, 21, 22, 27, 29.	Mch. 16-30.....	5	12, 15.....	3	4	4, 11, 14.
Oct. 1-15.....	7	6, 9, 11, 15.	Apr. 1-15.....	13	18, 23, 25, 30.....	5	8	18, 20, 22, 27, 30.
Oct. 16-31.....	11	16, 17, 20, 22, 23, 27, 30, 31.	Apr. 16-31.....	9	4, 7, 10, 12.....	5	7	2, 6, 9, 11, 15.
Nov. 1-15.....	5	1, 3, 6, 8, 14.	May 1-15.....	11	16, 18, 20, 22, 27, 30.....	7	7	17, 18, 20, 21, 24, 26, 29.
Nov. 16-30.....	10	3, 5, 7.	May 16-31.....	12	1, 3, 6, 10, 12, 14.....	7	10	1, 3, 5, 6, 10, 13, 15.
Dec. 1-15.....	3	3, 5, 7.	June 1-15.....	14	17, 18, 20, 22, 24, 27, 29.....	7	9	17, 19, 22, 24, 26, 27, 29.
Dec. 16-31.....	2	19.	June 16-30.....	18	1, 3, 4, 5, 6, 9, 10, 11, 13, 15.....	6	6	1, 4, 7, 9, 11, 13.
	46		July 1-15.....	5	17, 19, 22, 24, 27.....	10	10	16, 17, 18, 20, 21, 24, 25, 27, 29, 31.
	109		July 16-31.....	8	2, 5, 7, 9, 12, 14, 15.....	7	7	2, 4, 5, 6, 8, 10, 12.
			Aug. 1-15.....	8	17, 19, 21, 22, 23, 27, 29, 31.....	7	7	17, 19, 24, 26, 27, 29, 31.
			Aug. 16-31.....	5	2, 4, 7, 9, 13.....	7	8	4, 8, 9, 10, 11, 12, 14.
			Sept. 1-15.....	6	16, 18, 22, 25, 27, 30.....	7	7	17, 18, 20, 22, 24, 25, 28.
			Sept. 16-30.....	5	3, 4, 8, 11, 14.....	8	8	1, 2, 3, 5, 7, 8, 10, 12.
			Oct. 1-15.....	5	17, 20, 23, 26, 30.....	7	7	16, 20, 22, 24, 26, 27, 28.
			Oct. 16-31.....	5	1, 5, 10, 11, 14.....	7	7	1, 3, 6, 9, 11, 13, 15.
			Nov. 1-15.....	3	18, 20, 28.....	5	5	17, 19, 22, 24, 30.
			Nov. 16-30.....	4	1, 9, 11, 14.....	5	5	1, 9, 11, 13, 15.
			Dec. 1-15.....	4	18, 21, 23.....	3	5	21, 22, 24.
			Dec. 16-31.....	4		126	144	
	110			187				

TABLE B.—Average number of crustacea per cubic meter in each three meter level, 1895, 1896.

See Figs. 22, 23.

Depth .	1895.						1896.					
	0-3	3-6	6-9	9-12	12-15	15-18	0-3	3-6	6-9	9-12	12-15	15-18
Jan. 1-15... }	6.9	5.0	4.7	5.2	2.6	2.6	41.7	20.6	17.4	8.4	11.9	13.7
Jan. 16-31... }							23.8	9.2	9.3	5.6	5.5	11.8
Feb. 1-14.... }	5.2	8.7	6.6	5.3	14.1	14.1	29.9	11.5	8.3	9.1	8.9	12.9
Feb. 15-28 .. }							20.5	10.8	7.7	7.8	7.8	9.1
March 1-15. . .	5.7	8.4	6.1	5.0	3.7	10.8
March 16-31 ..	12.4	11.7	5.2	5.2	10.1	10.1	23.9	12.3	18.3	11.5	8.0	5.7
April 1-15	10.3	5.8	3.7	3.1	4.1	4.2	26.5	19.6	33.9	35.5	21.2	21.0
April 16-30....	36.1	21.7	12.6	7.6	6.1	9.0	159.2	97.1	58.5	43.5	22.1	11.4
May 1-15.....	134.0	76.8	41.1	22.4	14.1	20.7	254.4	179.6	154.3	98.2	69.3	62.2
May 16-31....	188.0	90.7	64.4	38.4	38.8	47.1	197.8	118.7	117.2	94.4	81.1	99.6
June 1-15.	148.4	83.3	59.9	45.0	36.0	46.6	188.1	69.0	30.4	24.0	12.9	30.6
June 16-30	84.4	41.3	30.3	13.3	9.2	17.5	252.2	106.8	43.8	24.2	18.8	15.0
July 1-15.	142.1	61.4	46.0	14.2	4.2	2.2	230.4	135.2	56.8	25.1	20.9	2.6
July 16-31	119.0	75.8	67.8	10.9	2.1	1.4	127.2	76.9	47.5	9.7	0.8	0.3
Aug. 1-15.	101.1	61.8	34.7	27.5	4.1	0.5	163.0	82.7	42.6	11.2	1.2	0.2
Aug. 16-31	87.1	45.0	38.4	32.7	3.5	0.6	119.9	118.6	62.9	49.8	6.9	0.5
Sept. 1-15.	89.4	60.4	44.8	21.4	6.5	1.7	150.6	111.9	84.8	70.5	47.0	14.4
Sept. 16-30....	93.7	62.6	45.8	34.6	42.0	24.1	107.0	61.1	50.1	51.9	53.2	47.1
Oct. 1-15.....	76.8	39.3	38.2	35.8	36.6	33.9	105.7	84.1	81.3	63.6	61.3	59.8
Oct. 16-31.	41.6	23.9	23.8	25.4	20.8	21.1	192.0	66.9	51.2	41.9	42.5	43.6
Nov. 1-15.....	29.1	22.9	17.1	21.2	17.5	14.0	56.1	47.1	30.9	36.8	28.9	28.2
Nov. 16-30....	23.9	19.3	17.3	18.5	14.1	13.2	52.2	29.8	24.7	27.9	22.7	19.6
Dec. 1-15.	33.2	28.2	17.0	10.6	8.5	6.5	26.5	38.2	15.9	24.6	22.0	23.2
Dec. 16-31....	45.6	16.3	10.0	15.4	9.8	7.2	14.6	27.5	22.0	10.3	10.3	10.4

TABLE C.—Average number and percentile vertical distribution of the crustacea.

	Av. No.	PER CENT. IN EACH 3 M. LEVEL.					
		0-3.	3-6.	6-9.	9-12.	12-15.	15-18.
1894.							
July 1-15	306.2	45.7	29.5	16.9	5.5	1.9	0.5
July 16-31.....	472.3	51.2	30.6	12.3	4.9	0.8	0.1
Aug. 1-15.....	401.1	43.4	27.3	21.6	7.6	0.1	0.1
Aug. 16-31 ...	382.2	42.6	29.0	21.1	7.2	0.1	0.0
Sept. 1-15.....	No	observa	tions.			
Sept. 16-30...	691.6	46.2	26.0	14.5	9.8	3.2	0.3
Oct. 1-15.....	820.8	28.6	20.8	16.2	14.4	11.1	8.9
Oct. 16-31....	757.1	21.0	19.5	17.6	15.8	16.4	9.8
Nov. 1-15.....	571.4	20.7	18.6	15.8	19.8	16.3	8.8
Nov. 16-30....	No	observa	tions.			
Dec. 1-15.....	} 219.9	} 32.8	} 16.2	} 14.4	} 11.8	} 12.4	} 12.4
Dec. 16-31....							
1895.							
Jan. 1-15.....	} 81.1	} 25.5	} 18.5	} 17.4	} 19.2	} 9.6	} 9.6
Jan. 16-31....							
Feb. 1-14.....	} 166.9	} 9.6	} 16.3	} 11.9	} 9.8	} 26.1	} 26.1
Feb. 15-28....							
Mch. 1-15.....	118.7	14.2	21.1	15.6	12.6	9.2	27.2
Mch. 16-31....	164.5	22.9	21.3	9.5	9.5	18.4	18.4
Apl. 1-15.....	94.3	32.8	18.4	11.7	10.0	13.5	13.7
Apl. 16-30....	229.4	38.7	23.3	13.5	8.3	6.6	9.6
May 1-15.....	940.2	43.5	24.8	13.3	7.2	4.5	6.7
May 16-31....	1,419.5	40.2	19.4	13.8	8.2	8.2	10.0
June 1-15.....	1,256.6	35.4	20.0	14.3	10.7	8.6	10.9
June 16-30...	610.7	43.0	21.6	15.5	6.8	4.7	8.4
July 1-15.....	817.6	52.6	22.8	17.0	5.3	1.5	0.8
July 16-31....	837.9	42.9	27.4	24.4	3.9	0.7	0.5
Aug. 1-15.....	689.1	44.0	26.9	15.0	12.0	1.8	0.2
Aug. 16-31....	622.8	42.0	21.7	18.4	15.8	1.6	0.3
Sept. 1-15....	669.7	39.8	26.9	20.0	9.6	2.9	0.8
Sept. 16-30...	928.1	30.9	20.7	15.1	11.4	13.9	7.9
Oct. 1-15.....	767.8	29.5	15.1	14.6	13.7	14.0	13.0
Oct. 16-31....	478.5	26.6	15.2	15.2	16.2	13.3	13.5
Nov. 1-15....	391.5	23.8	18.8	14.0	17.4	14.3	11.5
Nov. 16-30....	331.8	22.6	18.2	16.3	17.3	13.2	12.4
Dec. 1-15....	320.8	31.9	27.1	16.3	10.2	8.1	6.2
Dec. 16-31....	313.1	43.7	15.6	9.6	14.7	9.4	6.9
1896.							
Jan. 1-15.....	294.1	36.6	18.0	15.2	7.4	10.5	12.2
Jan. 16-31....	240.9	36.5	14.1	14.1	8.6	8.6	18.1
Feb. 1-14.....	219.0	37.1	14.3	10.0	11.3	10.1	17.0
Feb. 15-29....	191.7	32.2	17.1	12.1	12.1	12.1	14.3
Mch. 1-15.....	No	observa	tions.			
Mch. 16-31....	281.6	29.7	15.4	22.7	14.1	10.0	8.1
Apl. 1-15.....	480.4	16.8	12.4	21.5	22.5	13.4	13.4
Apl. 16-30....	1,184.3	40.6	24.6	14.9	11.2	5.7	2.8
May 1-15.....	2,398.2	31.1	21.9	18.9	12.0	8.4	7.6

TABLE C.—Continued.

	Av. No.	PER CENT. IN EACH 3 M. LEVEL.					
		0-3.	0-6.	6-9.	9-12.	12-15.	15-18.
May 16-31....	1,901.3	27.9	16.7	16.5	13.3	11.4	14.1
June 1-15....	844.8	53.0	19.4	8.5	6.7	3.6	8.6
June 16-30....	1,265.0	54.7	23.1	9.5	5.3	4.1	3.2
July 1-15....	1,314.2	48.9	28.7	12.1	5.3	4.4	0.6
July 16-31....	776.5	48.4	29.2	18.1	3.7	0.3	0.12
Aug. 1-15....	960.4	54.2	27.4	14.2	3.7	0.4	0.0
Aug. 16-31....	1,073.3	33.4	33.1	17.5	13.9	1.8	0.1
Sept. 1-15....	1,440.9	31.3	23.3	17.7	14.7	9.8	3.0
Sept. 16-30 ...	1,112.3	28.6	16.2	13.4	13.9	15.3	12.4
Oct. 1-15....	1,368.4	23.0	18.4	17.8	14.0	13.4	13.1
Oct. 16-31....	1,314.8	43.9	15.2	11.7	9.6	9.7	9.9
Nov. 1-15....	684.8	24.6	20.7	13.5	16.1	12.7	12.4
Nov. 16-30....	537.7	29.5	16.8	14.0	15.8	12.8	11.1
Dec. 1-15....	365.8	18.0	25.7	11.0	16.6	14.9	15.8
Dec. 16-31....	285.0	15.4	29.0	23.1	10.8	10.8	11.0

TABLE D.—*Diaptomus*. Average, maximum, and minimum numbers. Percentile vertical distribution.

	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3.	3-6.	6-9.	9-12.	12-16.	15-18.
1894.									
July 1-15 ..	242.2	290.6	178.0	48.9	31.6	15.6	3.1	0.4	0.4
July 16-31 ..	298.9	553.3	155.8	53.6	31.2	13.0	2.1	0.07	0.06
Aug. 1-15 ..	218.7	394.3	126.5	45.5	26.8	20.9	6.5	0.2	0.1
Aug. 16-31 ..	87.4	117.9	43.8	49.7	27.6	17.4	5.0	0.2	0.1
Sept. 1-15
Sept. 16-30 ..	54.6	84.5	10.8	58.1	20.4	12.2	8.0	1.0	0.3
Oct. 1-15 ..	67.2	92.8	38.9	38.5	23.2	13.1	11.4	10.1	3.4
Oct. 16-30 ..	38.3	72.0	3.6	25.4	20.3	17.2	14.7	15.9	6.3
Nov. 1-15 ..	44.0	95.4	26.0	28.6	17.6	16.1	16.9	13.0	7.8
Nov. 16-30
Dec. 1-15 ..	23.9	43.2	16.5	} 28.2	15.2	12.5	13.0	16.2	14.9
Dec. 16-31 ..	16.7						

TABLE D.—Continued.

	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3.	3-6.	6-9.	9-12.	12-15.	15-18.
1895.									
Jan. 1-15 ..	17.5	28.9	8.0	} 28.2	23.1	20.2	17.4	5.5	5.5
Jan. 16-31 ..	15.9	22.9	13.3						
Feb. 1-14 } Feb. 15-28 }	28.0	47.7	16.5	22.6	23.1	21.3	12.0	10.5	10.5
Mch. 1-15 ..	28.3	55.6	23.8
Mch. 16-31 ..	34.7	70.5	27.1	22.7	25.6	20.0	14.7	9.3	7.7
Apl. 1-15 ..	14.0	23.5	10.8	28.1	19.0	13.5	13.5	12.9	12.9
Apl. 16-30 ..	20.6	52.7	0.2	32.7	32.1	13.3	9.6	5.5	6.8
May 1-15 ..	34.4	45.1	17.2	58.2	22.6	12.0	3.3	2.0	1.9
May 16-31 ..	207.9	284.2	49.6	61.5	21.7	11.3	3.6	1.1	0.8
June 1-15 ..	285.0	459.8	178.1	57.3	24.1	9.6	3.3	2.6	3.1
June 16-30 ..	190.6	396.9	95.4	51.1	24.9	14.9	5.7	1.3	2.1
July 1-15 ..	187.4	397.5	105.5	41.4	30.1	22.6	4.8	0.8	0.3
July 16-31 ..	217.8	366.3	127.8	31.1	24.9	36.5	6.7	0.5	0.3
Aug. 1-15 ..	110.5	169.8	61.7	47.2	29.9	13.8	8.3	0.5	0.2
Aug. 16-31 ..	101.3	264.5	45.2	45.3	27.7	19.2	7.1	0.5	0.2
Sept. 1-15 ..	224.6	311.6	69.3	40.4	36.4	18.4	3.8	0.8	0.3
Sept. 16-30 ..	331.5	586.3	152.0	40.3	26.1	15.8	10.1	5.4	2.3
Oct. 1-15 ..	148.4	323.1	101.7	27.4	15.4	15.6	13.4	17.2	11.8
Oct. 16-31 ..	79.7	115.1	42.6	22.1	17.7	14.8	17.1	14.5	13.6
Nov. 1-15 ..	55.8	71.8	42.6	13.2	14.7	19.3	20.5	20.1	12.1
Nov. 16-30 ..	46.0	54.1	43.8	12.8	19.8	16.6	17.9	17.5	15.3
Dec. 1-15 ..	33.6	47.1	22.8	13.1	20.0	23.3	20.8	13.1	9.5
Dec. 16-31 ..	58.0	67.4	22.8	25.2	21.4	13.7	20.8	12.1	6.8
1896.									
Jan. 1-15 ..	48.6	62.9	40.0	26.2	24.0	21.9	9.9	9.3	8.7
Jan. 16-31 ..	23.3	34.3	22.8	25.4	16.2	20.7	20.7	14.0	3.0
Feb. 1-14 ..	38.9	57.5	27.3	28.0	24.4	11.9	14.0	14.6	7.0
Feb. 15-29 ..	34.9	33.0	16.3	16.4	14.4	10.8	9.1
Mch. 1-15	24.1	16.0	20.0	18.3	11.7	10.0
Mch. 16-30 ..	33.3	38.8	26.7	19.0	14.6	23.4	30.7	6.0	6.3
Apl. 1-15 ..	35.2	43.4	21.6	26.2	24.0	21.9	9.9	9.3	8.7
Apl. 16-30 ..	29.9	66.7	9.5	16.3	28.3	19.6	19.6	10.9	5.3
May 1-15 ..	102.3	388.5	38.2	48.2	31.3	17.7	1.8	0.9	0.1
May 16-31 ..	360.2	645.5	227.6	38.2	22.4	18.5	10.6	6.1	4.0
June 1-15 ..	343.5	740.9	152.6	67.9	23.7	5.6	1.8	0.4	0.6
June 16-30 ..	386.2	725.6	103.0	69.9	22.9	5.0	1.6	0.2	0.3
July 1-15 ..	202.9	319.2	178.7	49.0	28.0	16.0	5.4	1.3	0.3
July 16-31 ..	152.1	222.6	93.4	62.6	23.2	9.6	4.0	0.3	0.1
Aug. 1-15 ..	91.9	65.0	24.8	8.8	1.0	0.2	0.0
Aug. 16-31 ..	167.0	31.8	37.4	13.6	15.7	1.2	0.0
Sept. 1-15 ..	125.9	37.2	28.2	21.6	7.5	3.1	2.3
Sept. 16-30 ..	163.4	30.1	22.8	13.0	9.3	11.2	13.5
Oct. 1-15 ..	52.8	25.2	19.8	12.6	10.8	22.6	9.0
Oct. 16-31 ..	48.8	39.0	20.6	15.6	14.4	7.8	2.6
Nov. 1-15 ..	29.8	28.9	18.5	23.6	11.5	17.5	0.0
Nov. 16-30 ..	28.5	15.6	18.7	6.3	21.9	15.6	21.9
Dec. 1-15 ..	29.3	19.3	30.0	3.9	19.2	14.5	13.1
Dec. 16-31 ..	24.7	23.1	27.0	20.7	11.6	9.2	8.4

TABLE E.—Cyclops.—Average, maximum, and minimum numbers.
Percentile vertical distribution.

	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3.	3-6.	6-9.	9-12.	12-15.	15-18.
1894.									
July 1-15...	39.8	63.6	11.2	37.4	24.6	21.9	11.3	4.5	0.3
July 16-31...	151.0	347.2	53.2	44.4	31.2	13.8	9.8	1.8	0.1
Aug. 1-15 ..	161.0	297.6	85.2	41.0	28.8	22.5	7.4	0.1	0.1
Aug. 16-31 ..	200.3	270.3	130.3	39.5	28.7	22.4	8.9	0.4	0.1
Sept. 1-15...
Sept. 16-30...	190.1	272.2	129.7	42.3	25.7	16.2	12.1	3.1	0.6
Oct. 1-15...	347.1	421.6	251.8	33.5	21.6	15.7	13.9	8.4	6.9
Oct. 16-31...	261.3	383.1	173.0	15.7	20.1	17.4	17.8	18.4	10.6
Nov. 1-15 ..	246.4	440.1	108.8	12.9	17.8	15.9	22.4	21.2	9.8
Nov. 16-30
Dec. 1-15...	75.0	243.5	44.5	22.7	15.6	13.5	10.8	15.3	22.1
Dec. 16-31...	44.5	46.1	42.6	29.6	14.1	17.4	15.3	12.0	11.6
1895.									
Jan. 1-15...	21.5	48.3	13.3	24.8	17.2	16.0	21.6	10.3	10.1
Jan. 16-31...	40.0	50.9	32.1	5.1	8.8	25.8	25.8	17.2	17.3
Feb. 1-14 } Feb. 15-28 }	82.7	112.6	55.3	5.1	9.1	7.1	8.3	35.2	35.2
Mch. 1-15...	55.7	104.9	39.4	9.3	13.2	8.5	9.9	8.9	50.2
Mch. 16-31...	66.2	143.1	49.6	15.2	17.0	9.9	9.9	24.0	24.0
Apl. 1-15...	53.9	63.6	38.2	29.2	17.1	13.3	10.2	15.1	15.1
Apl. 16-30...	242.5	604.8	82.0	39.3	22.1	13.7	7.9	6.8	10.2
May 1-15...	864.9	1252.8	759.0	42.7	23.8	14.2	7.5	4.8	7.0
May 16-31...	944.4	1234.2	715.3	30.5	17.6	15.3	10.6	11.5	14.5
June 1-15 ..	616.9	966.7	231.5	21.3	17.8	17.5	13.9	12.6	16.9
June 16-30 ..	262.6	361.8	197.7	33.0	22.4	13.9	7.6	7.4	15.7
July 1-15...	323.6	388.0	148.2	52.5	19.3	16.2	7.0	3.1	1.8
July 16-31...	131.4	218.4	85.2	32.8	31.8	25.4	8.9	0.3	0.8
Aug. 1-15 ..	107.6	189.1	64.8	46.0	27.2	14.0	10.1	2.5	0.2
Aug. 16-31 ..	129.6	343.7	108.1	36.4	27.7	20.7	13.5	1.3	0.3
Sept. 1-15 ..	142.0	237.2	169.8	34.7	23.1	24.0	12.8	3.9	1.4
Sept. 16-30 ..	226.0	308.4	169.8	24.5	20.5	18.3	16.3	11.7	8.7
Oct. 1-15...	327.5	338.5	313.5	26.6	15.3	14.9	15.4	14.6	13.3
Oct. 16-31...	219.7	242.3	202.2	23.9	15.2	15.7	18.8	15.6	10.7
Nov. 1-15...	144.7	157.7	138.6	18.2	15.8	14.0	19.7	17.0	15.3
Nov. 16-30...	146.3	158.3	136.1	16.4	14.0	16.2	20.7	16.5	16.1
Dec. 1-15...	90.2	100.4	76.3	14.3	20.0	15.7	17.3	17.1	15.5
Dec. 16-31...	89.1	104.3	52.1	11.2	11.9	14.7	26.6	16.9	18.7
1896.									
Jan. 1-15...	111.0	131.6	78.8	16.0	12.2	13.3	10.0	21.3	27.2
Jan. 16-31...	151.0	237.8	105.5	29.2	13.3	12.6	7.4	9.2	28.3
Feb. 1-14 ..	91.6	108.1	75.6	12.5	10.4	13.2	17.4	16.6	29.9
Feb. 15-29 ..	82.0	22.4	13.3	11.6	13.9	14.7	24.0
Mch. 1-15...
Mch. 16-31...	212.5	239.4	74.4	30.4	15.1	21.1	15.0	11.0	7.5
Apl. 1-15...	400.7	763.2	183.1	17.7	12.0	19.5	20.9	14.3	15.6
Apl. 16-30...	1011.2	1607.8	543.7	34.9	26.8	16.9	12.3	6.0	3.1
May 1-15...	1858.4	2359.6	1071.6	30.6	20.7	18.9	13.6	8.5	7.8
May 16-31...	705.9	1294.8	176.8	14.8	14.9	13.7	13.8	16.8	26.1

TABLE E.—Continued.

	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3.	3-6.	6-9.	9-12.	12-15.	15-18.
June 1-15 ..	189.5	297.6	139.2	30.0	20.0	11.1	9.8	8.3	20.5
June 16-30 ..	358.7	716.1	223.2	42.6	23.3	12.8	9.6	4.8	6.8
July 1-15...	371.0	442.0	341.5	37.0	29.0	14.6	9.0	9.3	1.0
July 16-31...	317.5	412.1	138.0	49.5	30.0	18.7	1.4	0.2	0.1
Aug. 1-15 ..	326.8	48.8	25.2	20.8	4.8	0.3	0.0
Aug. 16-31 ..	209.0	30.0	32.7	10.8	24.0	2.0	0.5
Sept. 1-15..	157.1	33.8	22.5	15.8	12.6	9.9	5.3
Sept. 16-30..	228.6	29.2	13.7	14.4	18.4	14.2	10.1
Oct. 1-15...	364.8	18.3	22.6	18.7	14.3	14.3	11.7
Oct. 16-31...	469.5	27.7	20.8	15.5	12.6	12.2	11.2
Nov. 1-15 ..	267.7	18.1	19.8	12.2	19.2	14.2	16.5
Nov. 16-30 ..	173.9	25.1	13.6	12.0	15.3	12.4	11.6
Dec. 1-15...	115.5	14.3	29.2	10.7	16.0	12.6	17.1
Dec. 16-31...	93.1	6.5	20.8	19.8	13.0	17.0	22.9

TABLE F.—*D. hyalina*. Average, maximum, and minimum numbers.
Percentile vertical distribution.

	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3.	3-6.	6-9.	9-12.	12-15.	15-15.
1894.									
July 1-15....	19.8	32.8	8.5	38.1	23.4	20.2	14.1	3.2	0.9
July 16-31...	13.3	34.4	2.7	43.4	33.5	19.7	2.5	0.9	0.0
Aug. 1-15...	16.6	33.3	9.3	43.5	26.5	23.5	6.2	0.0	0.3
Aug. 16-31..	60.7	82.7	47.8	42.7	29.0	22.2	4.2	0.0	0.0
Sept. 1-15...	No observations.								
Sept. 16-30..	148.4	212.7	74.4	30.6	25.2	21.1	16.3	6.0	0.8
Oct. 1-15....	207.6	461.7	117.3	32.0	26.1	17.5	9.7	6.2	8.4
Oct. 16-31 ..	252.5	531.0	96.3	31.7	19.6	17.1	11.7	11.6	8.3
Nov. 1-15....	183.1	462.6	92.2	37.1	21.3	13.9	12.2	8.9	6.6
Nov. 16-30..	No observations.								
Dec. 1-15... }	121.5	154.2	78.2	41.1	16.0	16.7	12.0	8.7	5.5
Dec. 16-31 }	(48.8)	56.9	40.7						
1895.									
Jan. 1-15....	40.8	65.4	36.7	24.1	18.7	16.7	18.7	10.9	10.9
Jan. 16-31...	55.9	61.0	53.4	30.4	27.7	5.3	11.2	12.7	12.7
Feb. 1-14 }	65.8	109.4	41.9	18.1	19.9	11.0	9.8	20.6	20.6
Feb. 15-28 }									
Mch. 1-15 ..	34.7	69.3	25.6	22.9	26.9	19.2	12.4	9.1	9.5
Mch. 16-31..	63.6	102.3	39.1	28.1	22.7	8.1	8.1	16.5	16.5
Apl. 1-15....	26.4	24.2	12.7	42.7	21.0	10.1	7.5	9.3	9.4
Apl. 16-30 ..	16.3	43.8	3.2	37.5	29.7	9.4	11.3	5.1	7.0
May 1-15....	28.9	81.4	7.9	67.0	22.2	5.7	2.6	1.3	1.1
May 16-31 ..	250.7	349.8	71.2	59.1	24.3	9.9	3.0	2.3	1.4
June 1-15 ..	319.2	564.8	183.1	42.2	19.4	12.5	11.5	6.6	7.8
June 16-30..	135.6	327.5	31.8	51.0	13.3	19.2	6.6	4.3	5.5
July 1-15....	139.9	263.9	21.0	56.1	20.9	17.7	4.4	0.5	0.4
July 16-31 ..	275.3	464.3	129.7	58.3	24.1	15.7	0.9	0.2	0.8
Aug. 1-15 ..	273.0	417.2	78.2	47.6	26.6	13.8	10.7	1.1	0.3
Aug. 16-31..	252.8	428.6	143.1	51.1	17.6	17.8	12.6	0.7	0.2
Sept. 1-15 ..	202.8	349.1	169.8	49.5	23.2	21.3	4.6	1.1	0.3
Sept. 16-30..	201.6	248.0	148.1	37.0	20.8	16.9	11.4	9.6	4.3
Oct. 1-15....	180.5	253.1	123.3	36.9	14.9	12.1	12.5	10.9	12.7
Oct. 16-31 ..	76.6	111.3	54.0	37.9	15.9	15.1	13.0	10.3	7.8
Nov. 1-15 ..	56.2	72.5	38.8	32.8	21.9	12.7	14.7	10.6	7.2
Nov. 16-30..	48.2	60.4	36.2	31.3	15.8	15.0	14.8	12.8	10.3
Dec. 1-15 ..	35.0	41.9	26.4	33.9	32.7	18.7	7.3	4.2	3.2
Dec. 16-31..	44.6	52.7	11.4	38.5	29.2	9.3	12.1	9.5	1.4
1896.									
Jan. 1-15....	36.2	57.8	15.2	31.7	35.8	19.9	4.8	4.2	3.6
Jan. 16-31 ..	17.3	20.3	10.8	41.0	25.4	19.1	6.4	4.7	3.4
Feb. 1-14 ..	19.6	29.6	13.3	26.9	24.2	12.7	10.7	10.6	14.9
Feb. 15-29 ..	27.0	37.6	21.2	15.3	7.0	14.1	4.7
Mch. 1-15
Mch. 16-31..	13.5	27.3	6.9	32.1	14.1	34.9	10.4	4.7	3.8

TABLE F.—Continued.

	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3	3-6	6-9	9-12	12-14	15-18
1896.									
Apl. 1-15 . . .	14.6	18.4	7.6	4.5	9.1	36.4	22.7	22.7	4.6
Apl. 16-30 . . .	15.2	27.9	7.6	21.5	28.6	23.8	11.9	9.5	4.7
May 1-15 . . .	124.6	360.0	52.1	45.0	32.9	16.4	2.5	2.8	0.4
May 16-31 . .	270.8	427.3	78.8	44.9	11.4	16.1	12.1	9.8	5.6
June 1-15 . .	55.6	156.4	6.3	59.4	20.3	12.6	5.6	1.3	0.5
June 16-30 . .	211.1	496.7	106.8	55.0	27.4	13.4	3.4	0.4	0.2
July 1-15 . .	319.0	783.4	132.9	56.4	26.0	13.6	3.3	0.6	0.1
July 16-31 . .	65.5	104.6	40.2	45.3	27.1	17.7	9.4	0.4	0.0
Aug. 1-15 . .	95.2	55.8	18.6	17.5	7.8	0.2	0.0
Aug. 16-31 . .	60.9	36.5	23.2	24.0	14.0	2.3	0.0
Sept. 1-15 . .	120.4	29.1	9.1	17.9	20.5	15.1	8.3
Sept. 16-30 . .	192.5	26.5	18.4	15.4	16.3	12.0	11.4
Oct. 1-15 . . .	228.0	50.5	15.8	7.5	5.4	8.3	12.5
Oct. 16-31 . .	511.5	69.3	7.9	6.3	4.8	4.9	6.8
Nov. 1-15 . .	314.6	31.1	20.2	14.1	14.6	10.7	9.0
Nov. 16-30 . .	266.0	35.2	19.4	12.3	15.2	9.0	8.9
Dec. 1-15 . .	182.8	19.7	24.3	11.0	15.5	15.5	14.0
Dec. 16-31 . .	138.9	20.4	35.7	27.4	8.0	4.8	3.7

TABLE G.—*D. pulicaria*. Average, maximum, and minimum numbers. Percentile vertical distribution.

1895-96.	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3.	3-6.	6-9.	9-12.	12-15.	15-18.
July 16-31...	11.6	17.1	0.2	0.0	0.0	53.1	12.5	32.8	1.6
Aug. 1-15...	19.9	42.3	8.0	0.0	0.0	11.0	65.0	22.0	1.0
Aug. 16-31..	38.1	164.7	5.4	0.0	1.6	2.3	80.2	14.8	1.0
Sept. 1-15...	33.8	57.2	8.3	0.0	2.2	4.5	68.8	22.6	1.8
Sept. 16-30..	98.2	125.9	10.5	0.0	1.5	2.2	3.4	58.8	33.7
Oct. 1-15....	26.9	49.6	12.7	14.1	13.8	14.1	19.2	17.1	21.7
Oct. 16-31...	23.5	46.4	5.4	22.5	21.9	22.3	12.7	9.6	11.0
Nov. 1-15...	49.6	102.3	17.8	42.7	27.3	8.7	9.2	5.5	6.6
Nov. 16-30..	58.3	82.0	39.5	25.2	29.2	19.6	15.1	5.7	5.2
Dec. 1-15....	141.1	221.9	25.0	51.6	35.5	7.9	2.8	1.9	0.2
Dec. 16-31...	99.8	57.2	24.8	37.8	31.1	11.4	11.1	7.7	0.9
Jan. 1-15....	88.2	137.3	40.0	68.3	14.5	12.7	3.5	0.5	0.5
Jan. 16-31...	24.8	31.8	13.3	77.9	8.4	8.4	2.1	2.1	1.1
Feb. 1-14....	64.1	81.4	29.8	75.8	9.1	5.0	2.8	2.4	4.8
Feb. 15-29...	43.9	43.4	20.3	8.7	11.5	8.7	7.3
Mch. 1-15....
Mch. 16-31..	20.9	50.9	10.1	34.0	18.9	27.0	9.4	7.6	3.2
Apl. 1-15....	28.0	47.0	11.4	10.4	14.6	31.2	25.0	12.5	6.3
Apl. 16-30...	118.2	251.8	12.1	84.9	10.6	0.8	1.5	1.7	0.5
May 1-15....	284.9	683.2	85.8	13.1	16.2	19.5	12.0	16.7	22.4
May 16-31..	533.6	763.4	291.2	28.0	16.9	18.8	14.5	10.0	11.7
June 1-15...	168.6	260.7	56.6	17.5	10.0	15.0	21.3	10.1	25.8
June 16-30..	78.2	157.7	13.3	1.9	6.2	11.7	16.0	45.8	18.5
July 1-15....	39.3	52.1	19.7	0.0	0.9	8.6	27.0	57.0	6.5
July 16-31...	11.8	38.2	0.6	0.0	0.0	62.8	33.4	2.0	1.8
Aug. 1-15...	3.7	0.0	10.0	17.0	71.0	2.0	0.0
Aug. 16-31..	5.9	0.0	0.0	0.0	80.0	20.0	0.0

TABLE H.—*D. retrocurva*. Average, maximum, and minimum numbers. Percentile vertical distribution.

	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3.	3-6.	6-9.	9-12.	12-15	15-18.
1895.									
July 1-15....	9.7	14.6	0.0	47.0	25.5	13.1	14.4	0.0	0.0
July 16-31...	31.5	59.7	3.5	50.0	24.0	24.8	1.2	0.0	0.0
Aug. 1-15...	68.2	154.8	8.9	37.1	26.1	16.8	18.5	1.3	0.1
Aug. 16-31..	50.1	96.0	20.5	41.1	21.3	22.7	13.7	1.1	0.1
Sept. 1-15...	23.8	37.5	11.5	46.4	23.5	20.3	6.4	2.9	0.5
Sept. 16-30..	59.6	74.4	21.6	33.8	24.1	15.7	11.6	7.8	6.9
Oct. 1-15....	72.5	103.6	50.9	35.9	15.2	17.9	7.5	11.7	11.7
Oct. 16-31...	70.9	65.5	33.7	29.2	10.0	12.3	10.6	9.1	28.7
Nov. 1-15....	59.3	79.5	42.6	24.2	20.2	12.6	18.4	14.2	10.3
Nov. 16-30...	24.2	37.5	19.1	30.7	20.2	14.9	12.3	10.0	11.9
Dec. 1-15....	5.0	11.4	1.9	3.7	0.0	41.3	17.5	18.7	18.7
Dec. 16-31...	0.7	0.9	0.0	0.0	0.0	27.3	36.4	18.2	18.2
1896.									
July 16-31...	2.5	Irregular	near	surface.			
Aug. 1-15...	27.6	59.0	32.4	8.0	0.4	0.2	0.0
Aug. 16-31..	57.1	36.5	23.2	24.0	14.0	2.3	0.0
Sept. 1-15...	157.7	26.2	17.3	19.3	19.4	12.4	5.3
Sept. 16-30..	228.6	26.5	18.4	15.4	16.3	12.0	11.4
Oct. 1-15....	199.3	26.4	20.0	14.3	10.8	13.0	15.5
Oct. 16-31...	92.7	43.5	18.8	8.8	10.8	10.4	7.6
Nov. 1-15....	9.9	29.0	30.7	0.0	0.0	13.5	26.8

TABLE J.—*Chydorus*.—Average, maximum, and minimum numbers.
Percentile vertical distribution.

	Av.	Max.	Min.	PER CENT. IN EACH 3 M. LEVEL.					
				0-3.	3-6.	6-9.	9-12.	12-15.	15-18.
1894.									
Sept. 16-30..	278.9	440.7	96.6	55.0	26.9	10.6	5.6	2.0	0.0
Oct. 1-15....	193.3	251.2	92.8	12.3	13.3	16.4	21.6	21.6	14.8
Oct. 16-31....	202.0	304.6	82.0	14.2	17.8	18.0	18.7	19.9	11.3
Nov. 1-15....	97.9	261.3	13.3	7.3	15.5	18.6	28.4	19.3	10.8
Dec. 1-15....	9.5	15.9	3.8	16.7	20.6	13.3	16.7	18.7	14.0
1895.									
June 1-15 ...	36.7	92.8	11.1	41.9	24.9	13.0	9.4	5.0	5.6
June 16-30 ...	21.9	45.7	6.9	83.1	13.4	2.4	1.1	0.0
July 1-15....	156.8	271.5	13.3	61.1	25.3	11.0	2.2	0.4	0.0
July 16-31....	163.4	283.6	89.0	42.8	35.2	20.3	1.2	0.2	0.2
Aug. 1-15 ...	78.6	157.7	16.8	43.2	30.4	18.4	7.3	0.5	0.1
Aug. 16-31 ..	18.7	48.7	5.0	32.7	33.3	21.8	11.2	1.1	0.0
Sept. 1-15....	15.6	39.4	8.9	45.5	23.6	22.8	4.8	3.4	0.0
Sept. 16-30..	Scattering only.							
Oct. 1-15....	8.6	14.3	5.0	17.6	17.6	6.6	12.5	14.7	30.9
Oct. 16-31....	8.1	12.0	3.8	46.8	14.1	7.8	23.5	7.8	0.0
Nov. 1-15....	25.9	46.4	10.8	11.4	15.3	14.3	24.3	21.3	13.4
Nov. 16-30...	19.7	29.8	13.9	9.2	18.8	24.0	21.6	16.1	10.3
Dec. 1-15....	15.9	19.7	12.0	26.0	6.6	18.2	10.5	16.8	22.0
Dec. 16-31...	20.9	36.8	8.9	23.0	18.6	11.8	22.6	17.6	6.3
1896.									
May 1-15....	28.0	48.3	19.0	15.9	23.4	23.8	16.2	8.9	11.8
May 16-31....	30.8	68.6	13.3	34.0	23.6	15.9	19.9	4.3	2.3
June 1-15....	87.6	279.8	4.4	77.6	15.8	4.7	1.0	0.4	0.3
June 16-30..	230.8	346.0	145.6	65.0	24.4	7.0	2.6	0.5	0.3
July 1-15....	382.0	661.4	169.8	57.0	33.6	6.9	2.0	0.3	0.0
July 16-31...	245.1	465.5	129.1	43.2	34.1	20.0	2.7	0.2	0.0
Aug. 1-15....	406.5	54.8	32.0	10.4	2.2	0.5	0.0
Aug. 16-31 ..	426.0	32.4	36.2	21.0	8.5	1.7	0.1
Sept. 1-15 ..	748.6	34.9	26.7	17.0	15.2	5.6	0.7
Sept. 16-30..	263.0	25.0	14.8	14.9	12.2	18.1	14.9
Oct. 1-15....	423.7	10.3	15.0	25.8	21.0	14.5	13.4
Oct. 16-31....	191.9	16.9	18.1	17.1	12.8	16.6	18.4
Nov. 1-15 ...	62.7	18.7	22.4	13.0	13.4	12.7	19.8
Nov. 16-30 ..	69.3	21.3	12.0	26.7	17.3	10.6	12.1
Dec. 1-15....	38.2	15.0	16.2	13.4	19.1	16.2	20.1
Dec. 16-31...	28.1	12.8	25.0	15.0	17.6	19.6	10.0

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