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THE EFFECT OF TEMPERATURE ON THE DISTRIBUTION OF THE MAYFLY FAUNA OF A STREAM

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THE EFFECT OF TEMPERATURE ON THE DISTRIBUTION OF THE MAYFLY FAUNA OF A STREAM

ABSTRACT

Stations along the course of a stream were so selected that temperature conditions between the various stations differed widely, while other environmental factors were similar.

It was found that there is an increase in the number of species of mayflies downstream, resulting mainly from the addition of species to those found at the source, and also that the length of time during which a species is emerging gradually becomes shorter downstream until it is confined to the early summer. These phenomena are correlated with the greater seasonal fluctuation in the temperature of the water in the lower reaches. The shortening of the season of emergence downstream and final elimination of a species are caused by the high temperature of the water. Conversely, the absence near the source of species, confined to the lower parts of the stream, is due to the failure of the water to rise to a temperature sufficiently high to allow these species to grow and complete their development. Closely related species occur in the same habitat but are seasonally isolated from one another. They differ in morphological characters which may be the result of their adaptation to growth at different temperatures. Species confined to the upper part of a stream are northern in their general distribution, while species confined to the lower parts of the stream have a more southerly distribution.

INTRODUCTION

The object of the survey was to study the distribution, in regard both to season and habitat, of the mayfly (*Ephemeroptera*) fauna of the streams, and such factors of the environment as might influence this distribution, special attention being paid to the temperature of the water.

Mayflies were selected for several reasons: (1) they are a group with which the author had had some previous experience in the field, and of whose bionomics he had some knowledge; (2) the species, numbering about fifty-five, occupy every part of the stream from the source to the slow-flowing reaches; (3) they are to be found in the water in an immature state at all times of the year, and their development is gradual, so that the life-history is not complicated by long resting periods in a pupal stage, as is the case with holometabolous insects.

Although only the *Ephemeroptera* were studied intensively, observations on some of the other groups in the stream, *e.g.*, the *Plecoptera*, *Trichoptera*, and *Amphipoda*, indicate that the results obtained in a study of the mayflies probably apply equally well for other aquatic organisms.

The investigations set forth in the present paper were made in two tributary streams of the Nottawasaga river in central Ontario, and ran from the end of May, 1930, to May, 1932. These streams are typical trout streams of the basic water type. Observations were made at a number of points, called stations, along the course of the streams, characterized by as wide a variety of temperature conditions as possible but similar in all other respects, such as depth and rate of flow of the water, character of the bottom, amount of aquatic vegetation, and exposure to sunlight. For this purpose ten stations were selected: three, *viz.*, 1, 2, and 3, in the Pine river; three, *viz.*, 4, 5, and 6, in the lower part of the Mad river; and four, *viz.*, A, B, C, and D, in the upper part of the Mad river.* In the case of most of the rapid-water stations, these were located in rapids of rather limited length, alternating with more slowly-flowing reaches, thus minimizing the probability of there being migration of nymphs out of, or into, the stations.

A general description of the Nottawasaga river system is given below, followed by a description of the Mad and Pine rivers, the two tributary streams along the courses of which the stations were selected. A description of the stations follows the description of the streams in which they occur.

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DESCRIPTION OF STREAMS

Nottawasaga river

The map (plate I), shows the drainage area of the Nottawasaga river, most of which is to the east of the Niagara escarpment or cuesta, which is shown running across the map in a general north-south direction. The superficial layer of rock immediately to the west of the escarpment and forming its brow is the Lockport dolomite of the Silurian, the hard durable strata of which have withstood erosion better than the underlying layers, and so have been the main factor in preserving the vertical wall of the escarpment. The dolomite is covered by a thin layer of glacial deposit. The lower ground to the east of the escarpment is more deeply covered with glacial deposit in the form of hills and mounds.

Some altitudes are shown on the map, including all that were obtainable, since contour maps of the district were not available. Those known are: mainly along the provincial highway from the town of Orangeville to Owen Sound; along the railway line which runs from Beeton to Collingwood; the levels of the lower part of the river itself, of Georgian bay, and of lake Simcoe which is east of the Nottawasaga system and not a part of it. The highest point in the vicinity is 1,706 feet at the town of Dundalk on the height of land between lakes Huron, Erie, and Ontario. In the vicinity of this town tributaries of three rivers take their rise. The tributary of the Saugeen flows west into lake Huron; that of the Grand flows south to empty into lake Erie; and two of the Nottawasaga—the Mad flowing north-east and the Noisy flowing east—finally empty into Georgian bay on lake Huron. The Pine river, another tributary of the Nottawasaga, also rises on the same height of land several miles south-east of the town of Dundalk.

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*The sequence of the stations and the reasons for selecting this sequence will be explained later in the paper under the description of the stations.

The changes in altitude of the Nottawasaga river system are illustrated by following the Mad and Pine rivers from their sources to Georgian bay. The former rises at an altitude of a little less than 1,700 feet, and flows north-east on a shallow grade to the brink of the escarpment just a little east of the village of Singhampton, from which point it drops rapidly through a deep, rocky gorge to the village of Glen Huron, where the altitude is 1,034 feet. Through this gorge the river is rapid throughout its course, with several small cataracts. Below Glen Huron the altitude drops gradually to 850 feet at Creemore, to 600 feet at its junction with the Nottawasaga proper, to 580 feet at the mouth, the level given for lake Huron. There is thus a total drop of over 1,000 feet from the source to the mouth of the river; about 500 feet of this drop occurs in a distance of about six miles in the vicinity of the Niagara escarpment. The Pine river follows much the same course, rising at over 1,600 feet and beginning to drop quickly as it flows east through a deep gorge in the escarpment.

Due mainly to this altitude and to the exposure of the country to wind, winter on top of the escarpment is very severe, with heavy snowfall as compared with the lower ground east of the escarpment. This severity of the climate is reflected in the crops grown in the region. Very little corn is grown, no fall wheat is sown, and only the hardiest apples thrive. On the eastern slope of the escarpment and to the east of it, a great deal of corn and fall wheat is successfully grown.

It will be seen by referring to the map on plate I that the drainage area of the Nottawasaga system covers a small portion of the eastern part of Grey county, the southern part of Simcoe county, and the eastern half of Dufferin county. The greater part of the area lies to the east of the Niagara escarpment, the branches from the west, only, having their sources in the high ground above it. The branches from the south and east are more gently flowing throughout because of the lower land through which they flow.

Mad river

In the first eight miles of its course the Mad river is rather slow-flowing with only occasional small rapids; lower down it is rapid, even torrential in places. In the upper part there is abundant aquatic vegetation, including *Nymphaea*, *Potamogeton*, and *Chara*. In places the bottom is deeply covered with silt and in others with clear gravel and marl. A goodly portion of this part of the stream is through swamp and bushland, the trees of which afford shade. The remainder is through open pasture-land, where the aquatic vegetation is much more abundant than elsewhere. There is a distinct fauna of mayflies in this upper part of the stream, including *Ephemera simulans* Walk., *Blasturus nebulosus* Walk., *Blasturus cupidus* Say, *Stenonema tripunctatum* Bks. (Traver, 1933), *Cloeon simplex* McD., *Cloeon rubropicta* McD., and *Centroptilum convexum* Ide. In the more rapid reaches of this upper part, the fauna resembles that found lower down in the rapid portions of the stream, and includes *Epeorus humeralis* Morg., *Stenonema canadense* Walk., *Heptagenia hebe* McD., *Ephemerella subvaria* McD., *Ephemerella deficiens* Morg., *Baetis parvus* Dodds, *Baetis vagans* McD., and *Baetis cingulatus* McD.

The great profusion of aquatic vegetation and its photosynthetic activity are of considerable importance, since they affect greatly the oxygen content of the water of this part and the stream below, as shown in the graph (figure 3, plate II), where temperature and oxygen content in cubic centimetres per litre are shown plotted for a bright day in August.

Farther downstream below the village of Singhampton on the Grey-Simcoe line, the river becomes very rapid in its course through a gorge in the escarpment. In the very rapid portion of the river below Singhampton there is little aquatic vegetation, and this is mainly moss and algal coatings on the submerged and partly submerged stones.

Pine river

The Pine river takes its rise from permanent cold springs in the vicinity of Horning's Mills in Dufferin county, township of Melancthon. Several small streams, originating as springs, join to form the main river which flows east through a gorge in the escarpment. The streams are fairly rapid and rocky from the sources to the plain below. The only really static water is made by several artificial millponds fairly near the sources of the streams. One of the tributary branches at Horning's Mills was made the subject of special investigation. The stream rises in a cedar thicket from several springs which maintain a fairly uniform flow throughout the year and have a temperature of approximately 7.5° to 8.0° C.

DESCRIPTION OF STATIONS

Station 1

This station was selected in a shallow rapid about 100 feet from the source of a tributary of the Pine river, at a point where the stream emerges from a cedar thicket surrounding the springs. The station was exposed to the sun from the east, south, and west. The stream here was about six feet wide and three to eight inches in depth. The bottom was of flat and rounded fragments of limestone from one to three or four inches in greatest diameter, covered with a brownish algal coating, making them slimy to the touch. The rapid here was very limited in extent and was followed by a sluggish stretch below the station, which would prevent the down- or upstream-migration of stone-clinging forms such as were found there, unless, of course, they were also active swimmers. The temperature of the station was low, varying but a few degrees during the day and indeed through the year, thus providing a very uniform environment in regard to temperature. On warm, summer days the temperature rises as high as 11° C.; on colder days the rise is much less, approximating 8° C., the temperature of the source. In winter the temperatures recorded were not below 6.7° C., but on very cold days it probably drops to 6° C., or a little lower.

Collections of mayfly nymphs were made at this station on the following days: June 9, June 22, July 6, July 20, July 29, August 11, August 16, October 17, December 19, all in 1931; March 20, April 23, and May 15, 1932. Some additional collections made in June and July, 1928, were also studied.

Station 2

Station 2 was taken lower down in the same tributary in a situation which was similar as far as possible in respect of bottom conditions, rate of flow of the water, and exposure to sunlight. It was a little more shaded than station 1, due to the presence of some poplar trees on the banks. The volume of the water was greater and the stream wider at this point than at station 1, but the depth was the same. The station was about 1,000 feet below no. 1, and about 200 feet from the upper end of an artificial pond of about two acres in extent, into which it emptied. The temperature at station 2 fluctuates more than at station 1, because the water has been exposed for a longer time to the air and the action of the sun's rays. In warm weather, therefore, station 2 is warmer than station 1, and conversely, in cold weather station 2 is colder than station 1. The environment, at least so far as temperature is concerned, is more variable than at station 1, providing colder and warmer seasons in winter and summer respectively than the former. A temperature as high as 20° C. for a hot day in summer was taken and a minimum in winter of 4° C. which would be still lower in extremely cold winter weather. A very usual summer daily maximum here was 15° to 16° C., dropping down below 10° C. during the early hours of the morning.

Collections of mayfly nymphs were made at this station on the following days: June 9, June 22, July 6, July 20, July 29, August 11, August 16, October 17, December 19, 1931; March 20, April 23, and May 15, 1932.

Some additional collections made by the author at this station in June and July, 1928, were also studied.

Station 3

This station was situated in the outlet stream of the millpond mentioned above in connection with station 2. The stream was of greater volume here since the pond is fed not only by the tributary under discussion but also by another of slightly less volume of flow. At station 3, however, conditions of bottom, rate of flow, and depth of water and exposure to sunlight were similar to the two above-mentioned stations, except that here perhaps the water was flowing a little more rapidly in parts of the station.

The temperatures at station 3 were higher in summer than at station 2. The highest recorded was 21° C., when station 2 was 20° C. Also in winter the temperature was 2° C. when the temperature of station 2 was 4° C. A usual summer daily maximum was about 18° C. to 19° C. Most of the water passing the station was from the surface of the pond and so was warmer than the water at the bottom of the pond. Water escaping from the mill flume, which had been tapped from the deeper water of the pond, was colder than that which passed through station 3.

Collections of mayfly nymphs were made at this station on the following days: June 3, June 14, June 19, June 22, July 6, July 20, July 29, August 11, August 16, October 17, December 19, 1931; March 20, April 23, and May 15, 1932. Some additional collections of nymphs made by the author in June and July, 1928, were also studied.

The method in choosing stations, as mentioned above, was to get points along the temperature gradient of the stream and to make the choices in such a way that other conditions such as rate of flow, depth and exposure to sunlight, and type of bottom, would be similar and that differences in the fauna would thus be explainable as effects of temperature or other factors varying with the temperature. An ideal selection of the remaining stations should have been made at points lower down on the Pine river, but this was not done since work had already been started on the Mad river at Singhampton, and a permanent camp established there. In previous summers in the district it was noticed that the mayfly fauna in the Mad, Pine, and Noisy rivers was very similar and probably identical for similar situations in the streams. For instance, with one or two exceptions all the species (along with a few additional species) taken at station 3 in the Pine river were taken in the Mad river just east of Singhampton in the rapid portion mentioned earlier in a description of the Mad river. These additional forms, at least several of them, were collected in previous years from lower down the Pine river, where the temperature of the water was higher in summer than at station 3 and was similar to the temperature in the part of the Mad river in the eastern outskirts of the village of Singhampton. It should, perhaps, be mentioned further that there was only one species of mayfly taken in the Pine river which did not occur in the rapid portion of the Mad river, and this form, *Ephemerella aurivilli* Bengts, was restricted to stations 1 and 2, not appearing at 3, or, in other words, it was restricted to the upper part of the stream where uniform temperature conditions prevailed.

Station 4

This station was situated in the Mad river about half a mile below Singhampton, where the stream is fairly rapid and provides a series of habitats for mayflies similar to those found at stations 1, 2, and 3. The Mad river at this point has a much greater flow of water than the Pine river at station 3, but its greater width (about twenty feet) accommodates the greater volume at approximately the same depth.

A short distance above the station there is a dam which creates a long pond which extends for nearly a mile upstream and on which station D (see below) was situated. Station 4 was subdivided, one location, 4A, being in a rapid similar to those at the other stations, and the other, 4B, being in the quieter, deeper-flowing water about seventy-five feet below the rapid. The temperature here averaged somewhat higher than at station 3, the highest recorded temperature for a very hot day being 27° C. (July 1, 1931). On a very cold day in winter the temperature was 0°C. or very close to it (January 16, 1931, 4.00 p.m.). Usual summer daily maxima were about 20° C. to 22° C.

Immediately below this station there is a fall of about twenty feet, and below this point the stream is very rapid, in some places torrential, with many small cataracts along its course down the gorge.

Collections of mayfly nymphs were made at this station on the following days: May 29, June 11, June 28, July 9, July 24, August 12, September 3, 1930; January 16, March 20, April 23, May 15, May 20, May 23, June 3, July 1, July 8, July 21, July 28, August 12, October 17, 1931.

Station 5

This station was situated at a point about two miles below station 4, and well down in the rocky gorge of the river, the heavily wooded banks of which run up for nearly 300 feet above the station on the north and south sides. At this station there was more protection from the sun's rays because of the trees along the bank. The flow of water was more rapid than at station 4 and deeper in parts. Station 5 was subject to flooding in spring, as also was station 4, which made collecting very difficult on certain occasions. In flood seasons the water was more turbid than at other stations, due to silt being carried in suspension. Although it is farther downstream, this station is colder on the average than station 4, due in part to the protection from the sun's rays afforded by the wooded banks, and to the addition of cold subsoil water during the course down the gorge. It is possible, too, that the effect of evaporation might be of importance in lowering the temperature (Belding, 1928). Evaporation goes on at the surface of the water everywhere, but in exposed situations the cooling effect of evaporation would be offset by the warming effect of the sun's rays. Station 5, then, comes above station 4 in the temperature gradient of the stream. The highest recorded temperature was about 21° C., but this was not on an extremely hot day. From other temperatures taken and a comparison of the rate of heating-up of the water at this station with that at others, utilizing a recording thermometer at station D, it seems probable it would rise to about 23° or 24° C., a little higher than station 3 and lower than station 4.

Collections of mayfly nymphs were made at this station on the following days: May 29, June 11, June 18, June 23, June 28, June 30, July 10, July 23, September 4, 1930; March 20, April 24, May 18, May 23, June 4, June 13, June 17, July 7, July 21, July 28, August 14, October 18, December 21, 1931; March 21, April 24, May 15, 1932.

Station 6

This station was chosen three miles farther down the stream at a point about half a mile east of the village of Glen Huron, where the stream crosses the road which runs from the village to the railroad station. The river here is quite wide and divided into two branches. There is a quantity of sediment immediately below the rapids of the stream proper, and even among the stones of the shallow

rapids are collections of silt which indicate a weakened current. The station was more exposed to sunlight than was station 5, and approached more nearly in this respect conditions at the other stations.

Collections of mayfly nymphs were made at this station on the following days: June 3, June 5, June 10, June 24, July 8, July 22, August 5, August 20, September 5, 1930; January 17, March 21, April 24, May 17, May 23, June 3, June 5, June 9, June 13, June 18, July 1, October 18, 1931.

The habitats just described, namely stations 1, 2, and 3 of the Pine river and 4, 5, and 6 of the Mad river, were typical rapid-water stations of great uniformity in respect of depth and rate of flow of water, character of the bottom, vegetation, and exposure to sunlight, but differing widely in temperature of the water. The next stations to be described, namely, A, B, C, and D of the upper part of the Mad river, were also very uniform in regard to the above-mentioned environmental factors, differing, however, in the temperature of the water at each station. Stations A, B, C, and D differ from stations 1 to 6 in the greater depth of the water and its slower rate of flow, in the presence of more silt on the bottom, and, in parts of the stations, having a luxuriant growth of aquatic plants.

Station A

This station was situated near the source of the river in the vicinity of the village of Badjeros. The water was slow-flowing with an unruffled surface and a depth of from one foot to eighteen inches or deeper during the spring flood. The bottom was covered with flat stones varying in size from a few inches up to a foot or more in greatest diameter. There was some silt present. Above and below the station there was abundant aquatic vegetation consisting chiefly of *Nymphaea*. Collections of mayfly nymphs and other aquatic insects were made from the stones and also from aquatic plants in the vicinity. One reading of oxygen content was taken at 2.00 p.m. on August 16, 1930, which showed 9.1 cubic centimetres per litre, which was higher than that found at any other point in the stream at any time. The temperatures taken here varied about a mean of approximately 12° C., a minimum summer temperature of 8° C. being recorded for a cold day (May 31, 1930), and a maximum of 19° C. for a bright, hot day (August 16, 1930). At corresponding times the temperature was always lower by several degrees at station A than at B.

Collections of mayfly nymphs were made at this station on the following days: May 31, June 7, June 17, June 27, July 11, July 25, August 13, September 4, 1930; May 18, June 5, 1931.

Station B

This station was situated about four miles lower down the river than A, at the village of McIntyre. The stream at this point is only slightly shallower than at A, with a somewhat more rapid flow. There were a few tufts of a *Potamogeton* waving in the current and harbouring some mayflies. The bottom was similar to that at station A. Oxygen content determined at 3.10 p.m., August 16, 1930, showed 7.0 cubic centimetres per litre. This was lower than at A at 2.00 p.m. on the same day, but was higher than at two intermediate points. The reason for this is believed to be the presence in the stream immediately above station B of a luxuriant growth of *Nymphaea* and *Potamogeton*, whose photosynthetic activity probably greatly increased the oxygen content. Not many temperatures were taken for station B, seven in all, but of these the minimum was 15° C. and the maximum 19.5° C. for summer temperatures.

Collections of mayfly nymphs were made at this station on the following days: June 14, July 9, July 23, August 6, September 2, 1930; May 15, June 5, July 8, 1931.

Station C

This station was selected about half a mile west of the village of Singhampton, at a point where the water is flowing fairly rapidly, but smoothly, away from a small rapid. This station is more shaded than either A or B, since here and for some distance above, the stream flows through a wooded area. It was similar to A and B in type of bottom, depth, and rate of flow of the water. The temperatures taken indicate that they are higher on the average than at station B. The maximum summer temperature recorded here was 20.7° C. and the minimum summer temperature 11.5° C.

Collections of mayfly nymphs were made at this station on the following days: June 4, June 21, July 10, July 24, August 6, September 6, 1930; January 18, April 23, May 19, June 6, 1931.

Station D

This station was situated a short distance below C at the upper end of a very slow-flowing reach of the stream, in reality a long pond formed by a mill dam below the village of Singhampton. The base camp was established here and a thermometer, which gave a continuous record of the temperature of the water, was installed. In the graph (figures 1 and 2, plate II) the water temperatures are given for most of the summers of 1930 and 1931. This curve is compiled from the weekly graphs by smoothing out the daily fluctuations to give average daily temperatures, and so is slightly lower than the maximum and slightly higher than the minimum for any day.

An oxygen series taken at this station on a bright day in summer is shown in figure 3, plate II, and indicates that in spite of increasing temperature there is an increase in oxygen content, probably caused by the photosynthetic activity of the aquatic plants. The series of readings was taken from 5.15 a.m. to 8.00 p.m., August 14, 1931. The water was deeper at station D than at the other stations and the bottom was of silt along the edges and marl and gravel in the middle. A limited number of flat stones along the edge, however, provided shelter for at least one of the stone-clinging forms found at stations A, B, and C, namely *Stenonema tripunctatum*.

Collections of mayfly nymphs were made at this station on the following days: May 31, June 2, June 4, June 6, June 16, June 21, June 23, June 25, June 28, July 24, August 6, September 6, 1930; January 18, May 19, June 6, 1931.

Temperature relationships of stations

In this section is given a summary of the temperatures at the stations and also the method by which the temperature gradient of the streams was established.

Table 1 gives temperatures (maximum and minimum summer, minimum winter, and average summer), oxygen content of water in cubic centimetres per litre, and pH of the water at the various stations where collections were made. The average summer temperature is the average of temperatures taken at the stations between June 1 and August 31, and to the right of each average is given the number of readings which were averaged.

TABLE 1.—Maximum summer, minimum summer, minimum winter, and average summer temperatures of water at stations; oxygen content and pH.

Station	Temperature				Oxygen cc. per litre One reading	pH
	Maximum summer	Minimum summer	Minimum winter	Average, June 1-August 31		
1	11°C.	8°C.	6.7	9.0 (6)	6.3 cc.	8.4
2	20.0	10.0	4.0	15.0 (7)	5.6	
3	21.0	13.5	2.0	17.5 (8)		
4	27.0	15.0	0.0	17.7 (8)	5.9	
5	20.2	14.5	0.0	17.8 (15)	6.5	
6	30.0	14.5	0.0	21.1 (12)	6.0	
A	15.2	8.0		13.0 (5)	9.1 ?	
B	19.5	15.5		18.1 (4)	7.0	
C	20.7	11.5	0.9			
D	23.2	10.0		16.8 (14)	4.5-6.8	8.4

The maxima and minima listed above are not necessarily the real maxima and minima for the two seasons except in the case of station D where the recording thermometer was installed. The others are merely the highest and lowest temperatures taken on visits to the stations, or in other words, the highest and lowest of the readings taken at random throughout the season at different times of the day. Stations 4 and 6 were visited on a particularly hot day in summer (July 1, 1931), when the extremely high maxima recorded were secured. The table is included to give a general idea of the temperatures met with at these stations and especially to demonstrate the temperature gradient.

Another method was adopted for determining more accurately the temperature gradient in the stream. It was impossible to take readings of temperature simultaneously at the stations since stations 4, 5, and 6 were situated about fifteen miles away from stations 1, 2, and 3 and on another stream. The latter stations were, however, near one another and on July 20, 1930, a series of hourly temperatures of the water was taken at each throughout the day. These temperatures were plotted in three graphs (figure 4, plate II) illustrating the changes in temperature during the day. The maximum temperatures of the water as shown by these graphs were 9.0° C., 16.5° C., and 19.5° C. for the stations 1, 2, and 3 respectively. The maximum air temperature on the same day was 25.0° C. in the shade.

Several series of temperatures of the water at station 6 were taken on summer days. The series of June 20, 1931, showed a maximum of 24.0° C. and air temperatures for that day were almost identical with those of July 20, 1930, so that a direct comparison could be made between the maximum temperatures of stations 1, 2, and 3 and that of station 6.

A more definite check on weather and water conditions on these two days was provided by a thermometer registering a continuous record of the temperature of the water at station D which was situated on the Mad river. The records of water temperature provided by the thermometer were practically identical on July 20, 1930 and June 20, 1931. Although station D was not included in the series the record of the thermometer placed at this point served as a basis for the comparison of temperatures taken at stations 1, 2, and 3 with those taken at station 6.

When the maximum temperature was 24.0° C. at station 6 and weather conditions were similar to those of June 20, 1931, the maximum temperatures for stations 4 and 5 were 21.5° C. and 20.5° C. respectively.

The maxima determined in the above fashion for stations 1, 2, 3, 5, 4, and 6 were 9.0° C., 16.5° C., 19.5° C., 20.5° C., 21.5° C., and 24.0° C. respectively. Although not taken on the same day at all the stations they are comparable as the maxima which would obtain at these stations on a day on which the maximum air temperature was 25.0° C. and other weather conditions similar.

The average of temperatures taken during the day at stations 1, 2, 3, 5, 4, and 6 during the summer months were 9.0° C., 15.0° C., 17.5° C., 17.8° C., 17.7° C., and 21.1° C. respectively.

The comparable maximum temperatures of the water at stations 1 to 6 are plotted in the graph (figure 5, plate III) as the unbroken line WX.

Stations 1, 2, and 3 are spaced along the horizontal axis at distances approximately proportional to their distances from the source. This could not, of course, be done in the case of stations 4, 5, and 6, which were in another river and separated from one another by intervals of two and four miles respectively. The maxima recorded for summer and minima for winter are indicated by the dotted lines WY and WZ respectively. In the latter case the minima are high since temperatures were not secured on a very cold day. The horizontal axis in the diagram, WW, is at the temperature of the source. If instead of these temperatures for a particular day, average summer maxima had been used, the curve would have been essentially similar in slope. The difference between maximum temperatures at adjacent stations in the temperature series for the curve WX are shown in table 2. This difference between maximum temperatures at each station for one day is being taken as the temperature gradient of the stream.

Table 2.—Temperature gradient of stations 1 to 6 (differences between maximum temperatures at stations on one day).

Station	Maximum	Difference between maxima
1	9.0°C.	
2	16.3	7.5°C.
3	19.5	3.0
5	20.5	1.0
4	21.5	1.0
6	24.0	2.5

By an expansion of figure 5, plate III, into a three-dimensional diagram employing all the available temperatures taken at the stations, figure 6, plate III, was produced, which gives in a general way the temperature relations at the stations throughout the year. The vertical axis gives temperatures, the longitudinal axis the stations, and the transverse axis the months of the year in cyclic arrangement, placing the summer months across the top and the winter months across the bottom. The names of the months are shown only for station 6 where they are projected outside the diagram.

The temperatures taken were rather inadequate, especially in spring, fall, and winter, but the best curves were drawn through the points. The temperatures at stations 3 and 5 are combined in order to give a greater number of points, and this is permissible since the temperatures at each are not very different, as shown by the average summer temperature of 17.5° C. for station 3 and 17.8° C. for station 5. The periphery of the blackened area represents roughly the average of temperatures taken during the day at the stations. The periphery would be irregular if accurately taken for any year showing higher and also lower temperatures than are recorded here.

The areas under the time-temperature curves for the stations were determined by a counting-of-squares method. The area above the temperature of the source (8° C.) was taken, which gave comparative areas in the ratio of 143: 115: 92: 66: 32, for stations 6, 4, 3 and 5 taken together, 2, and 1. Another series of areas which is perhaps useful is the total area of each blackened area, including the area above and below the temperature of the source. The relative areas thus determined are in the ratio of 226: 192: 162: 134: 39 for stations 6, 4, 3 and 5 taken together, 2, and 1 respectively.

The diagram figure 6, plate III, shows how uniform the temperature conditions are at the source and at station 1 in contrast to the great fluctuation of temperature during the year at station 6. Organisms at the source are peculiarly insulated from extremes of temperature, either high or low. Organisms at station 6 are exposed to much higher temperatures in summer, and also lower temperatures in winter.

The pH of the water was taken by the La Motte colorimetric method, using phenol red as an indicator. A reading at the source gave a pH of 8.0, and one lower down also gave 8.0, both definitely on the alkaline side. The pH probably varies somewhat at different times of the year and in different parts of the stream, but this variation should not be great since the water is highly buffered. The streams flow from springs in Dolomite limestone and along their courses is a limy precipitate in the form of marl. Any increase in the carbonic acid in the water will dissolve some of the marl and tend to keep the hydrogen-ion concentration constant.

The oxygen content of the water at different stations is quite variable, but in no place in the streams was it lower than 4.5 cubic centimetres per litre. The usual range of oxygen was between five and seven cubic centimetres per litre. On bright days the oxygen content rises rapidly from a minimum occurring very early in the morning to a maximum occurring about four p.m. This rise is probably due to the photosynthetic activity of the aquatic plants. This fluctuation in the oxygen content of the water is not as apparent at the upper stations as at the lower ones, particularly at D. The oxygen content at the source is usually lower than elsewhere, about five cubic centimetres per litre, which is about a fifty per cent. saturation at the temperature of the source (8° C.). Downstream the water tends to become saturated with respect to oxygen, and due to the photosynthetic activity of plants in the water becomes even supersaturated. Individual organisms near the source have only about one-third the growth rate of members of the same species farther downstream. If an oxygen content of six or seven cubic centimetres per litre is sufficient for individuals growing in water of, say, 18° C. it seems very probable that the oxygen concentration of five cubic centimetres per litre, as found near the source, is more than sufficient for the requirements of the organisms living there, since they grow so much more slowly than those in the warmer water.

METHODS

Collecting

The bulk of the material examined was taken from the rapid-water stations, 1, 2, 3, 4, 5, and 6, although collections were also made in other places, principally at stations A, B, C, and D of the upper part of the Mad river.

Collections were made at the stations at intervals of about two weeks during summer months, and at longer intervals in winter. At each collection two or three stones were turned over and all the mayfly nymphs seen, whether large or small, taken from the stones or moss adhering to them and preserved in seventy per cent. alcohol. These collections were later examined and the number of individuals of each species found in the collections recorded together with the approximate stage of development of each individual, determined by a method to be described later. Adult mayflies were also collected from the leaves of trees in the vicinity of the stations. In no case were any but the roughest quantitative data procured, and these only with the commonest forms. In these instances approximately the same number of stones of equal size were examined. With the rarer forms diligent search was required in order to establish their presence at the station on that date.

For some forms it was necessary to dredge with a small sieve along the grass of the overhanging bank, in order to procure specimens. The great majority of the collections, however, was made by turning over stones. The date of each collection was recorded and also the temperature of the water for the hour at which the collection was made. In some instances a series of hourly temperatures was taken for each station throughout most of the day to determine the rate of heating of the water. Some oxygen determinations were made and also determinations of the hydrogen-ion concentration. At station D, as mentioned above, a Negretti Zambra continuous recording thermometer was installed with its bulb submerged about three feet. This record served as a check on isolated readings of temperature taken at the various stations and gave a means of comparing these readings. This was necessary since it was impossible to take readings simultaneously, or even nearly so, at all the stations.

Analysis of collections

The number of stages or instars has not been definitely determined for mayflies and it is a difficult matter accurately to define stages. In a paper not yet published the author gives results of an attempt which has been made to determine the number of stages for two species, and in these cases the number is believed to be between forty and forty-five in one, and between thirty and thirty-five in the other, which is more than had previously been demonstrated by Lubbock in 1867 for *Cloeon dimidiatum.*

The method used in the present paper of determining stages of development was as follows. The collections of each species were subjected to statistical analysis. Measurements of total body length were found to be unsatisfactory because individuals in the same stage vary greatly in size; for example, female individuals are often much larger than males of the same stage, and there were also found great differences in length due to the different degrees of telescoping of the abdominal segments produced by varying effects of the fixative upon the muscles. Frequency diagrams of structures of the nymph which were growing rapidly relative to the growth of the nymph as a whole, however, did give a satisfactory series of stages. For instance, in the later instars the mesothoracic wing-pads are growing out rapidly, and frequency diagrams of these parts separate the various stages fairly well, especially the last five or six. In these frequency diagrams (see diagram 1, plate IV) the measurement of the structure is plotted as abscissa and the frequency of the occurrence of this measurement is represented by the ordinal length of the column, each individual measured being represented by a unit square.

The stages so determined may include more than one instar since between some of the instars there is so little increase in wing-pad length that they are not separated in the diagram. This has been mentioned by Lubbock (1867) and is demonstrated in a paper by the author, not yet published, dealing with the post-embryology of mayflies. The length of the wing-pad was measured from its attachment to the mesothorax to the tip by means of a squared field ocular in a compound microscope, and this length was divided by the length of the seventh abdominal tergite to compensate for differences in size of the nymphs. In measuring the tergum the overall length of the sclerotized part was taken, excluding the length of the closely set spines along the posterior border.

The factor, designated X, for each individual obtained by this means was plotted in a frequency diagram, and the ranges in the value of this factor for each stage thus determined.

This method was found useful only in the separation of the last five or six age groups. For younger stages the number of segments in the antennae was found to be fairly satisfactory. The very young stages were not found in the collections, but were reared in the laboratory.

It must be remembered that the figures given for one species cannot be applied to another species. In each case a new frequency diagram must be constructed, measuring not the nymph as a whole, but parts which are growing relatively rapidly. The methods described above are not sufficiently accurate to discriminate between instars in every case, but they do establish arbitrary points in the life-cycle which have some value in a study of this kind. Stages determined in this way are designated A, B, C, D, E, F, and so on, where A is the last nymphal stage, B the next to the last, and so on. A stage designated A1 means that the nymphs were in the last instar and had blackened wing-pads indicating that they were about to change into the winged state.

The method will be described more fully in the following account given of *Epeorus humeralis*, one of the most characteristic of the mayflies of the rapid portions of the streams.

DISTRIBUTION OF SPECIES AT STATIONS 1 TO 6

Epeorus humeralis Morgan

Diagram 1, plate IV, is a frequency diagram for all the nymphs of this species collected, plotted on the basis of the wing-pad length divided by the length of the seventh abdominal tergite for stages A, B, C, D, E, F, G, H, I, and the number of antennal segments for J, K, L, M, N, O. In this diagram and in others the ordinates represent the number of individuals, and the abscissae represent the factor X described below for the older stages and the number of antennal segments for the younger. This gives fifteen stages which is probably about half the number of true instars.

The accompanying table shows the range of variation for these characters, determined from the frequency diagram, which have been arbitrarily ascribed to each stage.

TABLE 3.—The ranges of the factor X, number of antennal segments, and total length used in separating the stages A to O of *E. humeralis.*

Stage	Factor X	Number of antennal segments	Total length in tenths of a millimetre
A	3.80-2.80		
B	2.20-1.55		
C	1.55-1.10		
D	1.10-.80		
E	.80-.65		
F	.65-.53		
G	.53-.40		
H	.40-.30		
I	.30-.20		
J		18-20	28-30
K		15-18	24-27
L		11-15	20-23
M		8-10	15-19
N		5-7	11-14
O		2-4	7-10

Column X of the table is the factor resulting from the division of the length of the mesothoracic wing-pad in tenths of a millimetre by the length of the seventh abdominal tergite in tenths of a millimetre for each stage.

Each day's collection was classified according to this table, and a numerical count of the number of each stage recorded. Then the analyses of the collections were plotted in a graph, according to the date on which collections were made (graph 1, plate III). In the graph the ordinal distances represent the stages designated A, B, C, D, *etc.*, and the abscissae represent the time of the year at which the collection was made. A light disk means that there were five or fewer individuals of the stage represented; a grey disk, six to fifteen; and a black disk, sixteen or more. The upper horizontal line of disks (A1) represents full-grown nymphs whose wing-pads were black, showing that they were about to emerge. The line of disks next below (A) represents full-grown nymphs, and the line below this (B) represents individuals in the next to the last instar or stage, and so on down to the lower stages. As mentioned above, the very earliest stages were not taken in collections.

Epeorus humeralis was entirely absent from station 1. During the summer of 1928 two nymphs were collected at station 2, but none in 1930, 1931, or 1932, so that its occurrence at this station was only occasional. At station 3 it was very rare, although it was plentiful lower down in the Pine river. In this study, however, it was collected in the Mad river at stations 4, 5, and 6, where it was very plentiful, although much more plentiful at 4 and 6 than at 5.

Graph 1, plate III, shows the seasonal distribution of this species at two locations of station 4 through the season of 1930-1. One series of collections was made in the shallow rapid (4A) already mentioned in the description of the station and the second series was taken in the quieter, deeper-flowing water about seventy-five feet below the foot of the rapid (4B). The upper diagram shows the seasonal distribution of the species in the rapid and the lower its distribution in the quieter water below the rapid. Oviposition was observed to take place in the rapids on several occasions, and not below them.

Keeping in mind that the density of the spots represents the abundance of the stage present, it is at once seen that the very young stages, I, J, K, L, M, N, O, are abundant in the rapid 4A, and rare in the location below the rapid, 4B. As the season advances and the nymphs grow, they leave the rapid for the position below. A few well-grown individuals, it is true, remain in the rapids, but it is very few indeed when compared with the numbers found below. This dropping downstream is not gradual, but rather sudden at a certain period of the life-cycle, as is shown in the diagram. It occurs at the time when the nymph is about half grown. Curiously, it is just at this time that there is a sudden metamorphosis in the tarsal claws, which change from a condition in which there are many claws on the distal end of the last tarsal segment to a condition in which there is one large pectinate claw. This takes place at one moult and is described in another paper.

Now, if this is the normal life-cycle, it shows that this species is not adapted to rapid water only, but rather to those habitats in streams where there are small rapids with alternating sections of quieter water. This phenomenon may be more general than is often realized. In 1929 a *Siphlonurus* species was observed ovipositing in a rapid part of a stream in northern Ontario. The nymphs of the species were never found in rapid water later in the season, but in the still water below the rapids.

The seasonal distribution of the adults of *Epeorus humeralis* extended from the last week of May to the first week of August in 1930, at station 4B, and from the last week of May in 1931 to the end of July in 1931. At station 4A the full-grown nymphs apparently persist a little longer than at station 4B, probably due to the fact that this part of the station is more protected from the heating effect of the sun by the presence of trees along the bank. The seasonal distribution of mayflies determined in this way is more accurately represented than by making collections of adults alone, since adults are often difficult to find even when nymphs are plentiful in the stream.

E. humeralis occurred also in abundance at stations 5 and 6 where the seasonal distribution was very similar to that at station 4, where emergence occurred from the end of May to the beginning of July. At station 5, where this species was rarer than at 4 or 6, it should be mentioned that in 1930 records showed that it did not begin to emerge until more than a month later than at station 4, the first specimens with blackened wing-pads having been taken on July 1, as compared with the end of May for stations 4 and 6. In 1931 at station 5 the first blackened individuals appeared about June 15, again noticeably later than at stations 4 and 6 of the same year.

A reference to the graph (graph 1, plate III) shows a few small individuals in both locations which apparently are belated ones which have hatched in spring instead of fall. These individuals do not grow to maturity, apparently disappearing from the stream about the time the last mature nymphs of the species are metamorphosing into adults. It seems likely that they are eliminated by the higher temperature of the water coming at a period in their life-cycle which is passed in the colder seasons of fall and winter by the great majority of individuals of the species. This clipping off of individuals, which would, if they went through with their development, emerge later in the season, provides a mechanism of selection for temperature tolerance. This selection may occur at both sides of the seasonal cycle. For instance, it is quite probable that many of the first nymphs to hatch in summer are killed off by the high temperatures prevailing then, which would virtually trim off the earliest part of the population of the next year. In this connection it should be mentioned that there is a possible mechanism in the time of incubation of the eggs to ensure some individuals surviving the warmest season in the egg stage. In another form, *Stenonema canadense*, eggs of three or four females taken ovipositing on the same day were incubated in a glass receptacle. The hatching of the eggs continued over a period of about six weeks.

Epeorus humeralis is very plentiful in the lower part of the Mad river and is absent from the upper part of the Pine river, although it occurs lower down in the Pine river. It has a long period of emergence extending over most of the summer from the end of May to the middle of August. It is a summer species which will tolerate warm water, at least in the later nymphal and very early nymphal stages. Its habitat apparently is changed during development, the first part being spent in more rapid water than the later part.

Iron pleuralis Bks.

The genus *Iron*, most of the members of which occur in the mountain streams of the west coast of North America, is closely related to *Epeorus*. *Iron pleuralis* was very abundant at stations 1, 2, 3, and 5, occurred sparingly at station 4, and was absent from station 6. It is therefore confined to the upper parts of the streams and overlaps only slightly the territory of *Epeorus humeralis* at stations 3, 5, and 4.

Diagram 2, plate IV, shows the statistical analysis of the collections of this species taken at stations 1, 3, and 5 in 1930, 1931, and 1932. Ordinates represent the number of individuals and the abscissae the factor X (length of mesothoracic wing-pad divided by the length of the seventh abdominal tergite) for stages A, B, C, D, E, F, G, and the number of segments in the antennae for G, H, I, and J.

TABLE 4.—The ranges along the abscissae of the factor X and the number of antennal segments arbitrarily ascribed to each stage of *Iron pleuralis*, at three stations.

Stage	Station 5 X	Station 3 X	Station 1 X	Number of antennal segments
A	4.60-3.00	5.0 ?-3.0 ?	5.10-2.90	
B	2.75-2.15	3.00-2.35	3.00-2.30	
C	2.15-1.80	2.35-1.80	2.30-1.75	
D	1.80-1.40	1.80-1.40	1.80-1.30	
E	1.40-1.10	1.40-1.10	1.45-1.10	
F	1.10-.80	1.10-.80	1.10-.80	
G	.80-.45	.80-.45	.80-.45	12-14
H				9-11
I				6-8
J				4-5

Graph 2, plate V shows the seasonal distribution of this species at the five stations at which it appeared.

A reference to the temperature relationships diagrammatically represented in figure 6, plate III, will help in an understanding of the facts shown by the graph. At station 1, the temperature is very nearly constant so that development goes on at a uniform rate throughout the year and the season of emergence is greatly prolonged, extending from about the middle of April to the middle of August. The individuals to emerge first in the stream are found at this point and they continue to emerge later into the summer than at any of the stations lower down. The young nymphs of the succeeding generation are also in evidence at this station earlier than, or at least as early as, at any of the stations, which fact, together with the slower development at station 1 than at the warmer stations, would indicate that the adults which emerge here early in the season mate and lay their eggs. It seems probable that the length of the season of emergence at this station is determined rather by the air conditions than by the water conditions. In early spring the water at this station is often warmer than the air, so that any individuals which emerged too early in the year would be rendered inactive on coming in contact with the air, and so could not reproduce.

At stations 2, 3, 5, and 4 the length of the season of emergence becomes successively shorter, mainly by its restriction to the earlier summer. At all of these stations (2, 3, 5, and 4) the incidence of emergence is almost simultaneous, apparently about the middle of May, although there is some indication that emergence begins later at 2 than at 3, and probably later at 3 than at 5. From this diagram one would predict that the species would not be present at station 6, and this is actually the case.

If the lengths of the emergence periods are plotted against the areas under the time-temperature curves (excluding the area below the source temperature) for the stations, there is a resulting straight line except for station 1, which is well off the straight line, as shown in text figure 1.

By plotting the value of the whole blackened area including that portion falling below the temperature of the source, there is again a straight-line relationship between stations 4, 3 and 5 taken together, and 2; station 1 also comes much closer to the same straight line as shown in the broken line in text figure 1.

With *Iron pleuralis*, as in the case of *Epeorus*, the seasonal distribution can reasonably be explained on the basis of a different rate of growth at the different temperatures and the selection by heat at both ends of the series of emerging individuals. The earlier individuals to emerge, or, in other words, that part of the period of emergence adjacent to winter, could be trimmed off or eliminated by high temperatures prevailing the summer before when the young were hatching, and that portion of the emergence period which is adjacent to summer could be trimmed off by the high temperatures of the summer months.

The end of the emergence period at each station has been joined by a line and then these points have been plotted in the inset of graph 2, plate V, at ordinate distances equivalent to the temperature gradient or differences of temperature of the stations as worked out in table 2 above. The result is a straight line showing that the end of emergence at the four stations is directly proportional to the temperature gradient and thus probably determined by it, or by some factor which is varying with it.

Iron pleuralis in its distribution shows marked differences from *Epeorus humeralis*. It extends from the source down as far as station 4, and is absent from 6, whereas *E. humeralis* is restricted to stations 3, 4, 5, and 6, and is also present at other places below station 6.

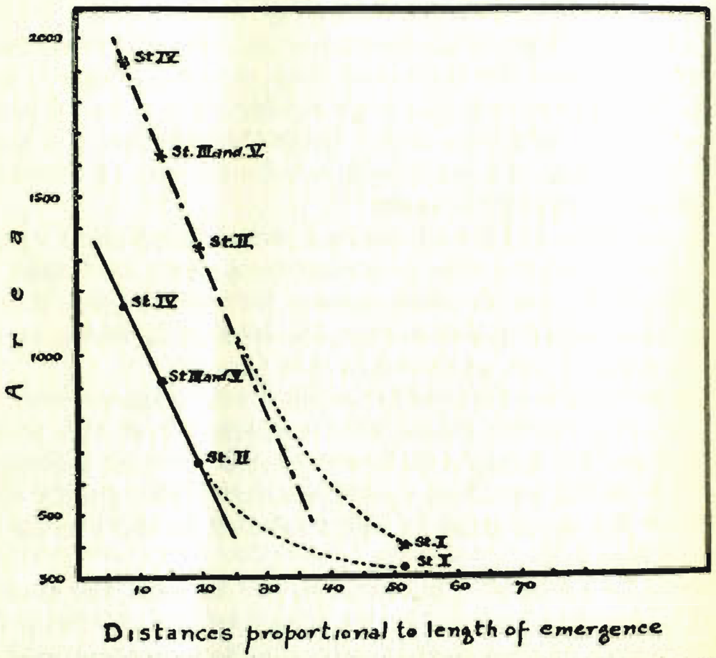

FIGURE 1.—The relationship between the length of the emergence period at the stations and the blackened areas in figure 6, plate III. The unbroken line gives the relationship expressed when the area above the temperature of the source alone is taken and the broken line when the whole area is taken.

At station 4, where *E. humeralis* was emerging for a long period in the summer, *I. pleuralis* was emerging for a very short season in the very early summer only. At station 3, *E. humeralis* was very rare, and the season during which *I. pleuralis* is emerging was extended later into the summer. At station 1 where *E. humeralis* was absent, *I. pleuralis* had a greatly protracted season, which extended nearly as far into the summer as the season of *E. humeralis* at station 4.

Apparently *Iron pleuralis* is able to complete its development and thus reproduce in the stream at a much lower temperature than can *Epeorus humeralis*, and most of the growing period of the nymphs is in the cooler seasons of the year, the spring and fall, except, of course, at the upper stations where the whole summer is a cool season.

Size of *Iron pleuralis* nymphs

One might think that the nymphs growing in the upper part of the stream, where a uniformly cold growing season prevails, would be larger than those growing more rapidly in the lower reaches and that there would be thus a differentiation in size of the species from the source to the warmer stations. When a frequency diagram (diagram 4, plate VI), based on length of wing-pads, was prepared from a measurement of all the full-grown nymphs taken at stations 1 and 5 between May and August, 1931, and from March to May, 1932, it showed that such was not the case. The mode of the diagram for both stations came at approximately the same wing-pad length, the only difference being that the nymphs at station 1 showed a greater range of variation, there being larger nymphs and also smaller nymphs than at station 5.

At the latter station the series is more uniform in size than at station 1, as judged by the length of wing-pads, which seems to be a reliable index of the nymphal size, since a plotting of the length of the seventh abdominal tergum instead of the length of the mesothoracic wing-pad gave a similar diagram. These diagrams for all the last-stage nymphs taken throughout the collecting period were then analysed, a frequency diagram being constructed for each day's collection at stations 1, 3, and 5, the results being shown in diagram 4, plate VI. In each of these three diagrams (plate VI) the abscissae give the length of the mesothoracic wing-pad in tenths of a millimetre, the ordinates of the whole diagram give the times at which collections were made, and the ordinates of the diagram for each collection give the number of individuals measured. All three show the same tendency, namely, the first full-grown nymphs of the season are large, and as the season advances the full-grown nymphs are smaller and reach a minimum size at the height of the emergence and then increase in size towards the end of the season. This shows that the series of individuals, instead of being differentiated in size along the length of the stream, is differentiated from one side of the season to the other. For example, the nymphs emerging at station 1 in the first week in July resemble in size those emerging at station 3 in the first week in June and those emerging at station 5 in the middle of May. This phenomenon cannot be explained by the appearance of one sex at an earlier period, since males and females were present in about equal numbers in all collections.

A similar phenomenon was found for collections of *Epeorus humeralis* taken at one station in 1930. The same distribution in size of the full-grown nymphs is evident in that species.

The decreased variability in the individuals at the lower station in the stream is further evidence in support of the suggestion made above that there is elimination by high temperatures of a great many of the individuals emerging early or late in the season, thus shortening the season of emergence. The only two full-grown nymphs of *Iron pleuralis* found at station 4 gave a measurement of the mesothoracic wing-pads of 16.0 and 15.8 tenths millimetres respectively, which places these individuals near the mode for nymphs taken at station 5.

Heptagenia pulla Clemens

This species in its ecological and seasonal distribution has presented a puzzling problem. It occurs in lakes, particularly on wave-washed shores, often of islands several miles from shore. It also occurs in streams such as the Pine and Mad rivers, where it has a peculiar seasonal distribution.

As with *Iron* and *Epeorus*, arbitrary stages were determined by constructing frequency curves as shown in diagram 3, plate IV. The ranges of the stages A to K are listed in the table below.

TABLE 5.—The ranges along the abscissae of the factor X and the number of antennal segments ascribed to each stage of *H. pulla.*

Stage	X	Number of antennal segments
A	4.0-3.2	
B	2.3-1.6	
C	1.6-1.1	
D	1.1-0.8	
E	0.8-0.5	
F	0.5-0.3	
G	0.3-0.1	
H	0.1-0.0	20-16
I		12-14
J		10-8
K		6-4

X = length of mesothoracic wing-pad divided by length of seventh abdominal tergite.

Classifying the collections according to the table, seasonal graph 3, plate VII, was plotted for stations 1, 2, 3, 4, and 6. Not enough material was available to show its distribution at 5. At stations 1 and 2 there were some individuals which were full-grown and emerging in early summer and at the latter station there were, in addition, a few individuals full-grown and emerging in late summer, the two periods at which individuals were emerging being separated by a period during which there was no emergence. At station 3 there were individuals emerging in late summer and none was taken in early summer, although as the graph suggests these early-emerging individuals would be expected here. At station 4 a few full-grown nymphs were taken on one occasion at the end of May, and no more until July of the same season when the regular emergence occurred. At station 6 no early-emerging individuals were taken, all the emergence occurring in late summer.

It will also be noted that the time of emergence and growth occupies the warmest season at the stations in contrast to the condition obtaining for *Iron pleuralis*, where most of the growth occurred in the fall and early spring. At station 1 there is no division of the emergence period into two, all the individuals at this station emerging at one time. At station 6, also, the emergence all takes place in one summer and most of the growth takes place during the same season. At the intervening stations different degrees of rotation of the season of emergence are evident, depending on the different rates of growth at these respective temperatures, and the winter season splits the emergence into two groups, an early and late summer group. Unfortunately, September is not represented in the collections taken, a rather critical point in the season as it turned out, but taking the growth rates into consideration it would seem that the early-emerging individuals at stations 2, 3, and 4 are the belated individuals of the group, the earlier ones of which had emerged the previous summer. Probably at station 2, for instance, emergence continues on into September and then any individuals which are not ready to emerge stop growing through the fall and emerge in spring when the water reaches a suitable temperature.

This species is noticeably more active than *Epeorus* or *Iron*, or than some of its near relatives such as *Stenonema*, when each is observed at its optimum season.

Although this species is able to withstand cold as indicated by its presence at station 1, it has a much higher temperature threshold of development than either *Iron* or *Epeorus*, and apparently also tolerates much higher temperatures.

Heptagenia hebe McDunnough

This species was not found at stations 1, 2, or 3 in the Pine river, but was found lower down in the same river. It occurred at stations 4, 5, and 6 of the Mad river. Its seasonal distribution has not been quite as carefully worked out as was that of *Heptagenia pulla*, but there is, as far as can be determined from the collections, one generation a year.

At station 6 emergence began about the middle of June or a little earlier and continued at least until the end of August and probably into September. The vanguard of the next season's nymphs passes the winter in about the fourth stage from the full-grown, that is, about the D stage.

It is just possible that the species is broken into two generations with the break occurring from about the middle of July to the middle of August. If this is the case, both generations are completed at this station the same summer and no individuals stay over until the next season.

Another species, *Heptagenia lucidipennis* Clem., did not appear at any of the stations, but was collected at Creemore a few miles below station 6 on the Mad river.

Leptophlebia

Both the Pine and Mad rivers presented ideal habitats for members of this genus and the closely related genus *Habrophlebiodes*. The species of these two genera were represented at the stations in the following way.

Station 1	Station 2	Station 3
L. adoptiva McD.	*L. adoptiva*	*L. adoptiva*
L. debilis McD.	*L. debilis*	*L. mollis* Hag.
		L. debilis
Station 4	Station 5	Station 6
L. adoptiva	*L. adoptiva*	*L. adoptiva*
L. mollis	*L. mollis*	*L. mollis*
L. debilis	*L. guttata* McD.	*L. guttata*
H. americana	*H. americana* Bks.	*L. debilis*
		H. americana

There were two additional species represented in the stream, *L. praepedita* Eaton and *L. moerens* McD., but they were not met with in collections at the stations since they occupied habitats slightly different from those of the stations. No nymphs of *L. debilis* were met with at station 4, although a few adults were taken here late in the summer.

In diagram 6, plate VIII, are shown frequency curves for three species, plotted by the same method as that used with the other species described above, to separate the different stages.

The younger stages were very inadequately represented in collections, due to their small size, but the later stages which are of more importance in the construction of the graph were

TABLE 6.—The stages A to H determined by means of the frequency diagrams, the ranges in the factor X, and the number of antennal segments ascribed to each stage.

	L. adoptiva		*L. mollis*		*L. debilis*	
	X	Number of antennal segments	X	Number of antennal segments	X	Number of antennal segments
A	2.4-10.75		2.70-2.00		2.50?-1.75?	
B	1.30-0.95		1.15-0.90		1.50- 0.90	
C	0.90-0.60		0.90-0.60		0.80- 0.55	
D	0.60-0.20		0.60-0.25		0.50- 0.25	
E	0.20-0.00					
F						25
G		18				18-19
H		13-12				

X = length of the mesothoracic wing-pad divided by the length of the seventh abdominal tergite.

well separated by the frequency diagram. From these data, graph 4, plate IX, was drawn, showing the seasonal distribution of four species of *Leptophlebia* and one species of *Habrophlebiodes.*

The interesting point shown by a study of a genus (*Leptophlebia*) is the increase in the number of species downstream and the relative positions of the species seasonally.

The species emerging earliest at station 6, namely *L. adoptiva*, extends up to the source where its emergence is much more protracted than at station 6. *L. mollis*, the next to emerge at station 6, does not extend up as far as station 2, and the behaviour of its graph at station 4 indicates that the growth rate is slowing down considerably, so that one could almost predict its absence at station 2. It was very rare at station 3 and scarce at station 5, the station immediately above station 3 on the temperature gradient.

L. guttata was present at station 6, was found at station 5, and therefore we would expect to find it at station 4. It did not occur in collections here, but as it was very rare at all stations that is not surprising. We would not expect, however, to find it at stations 1, 2, and 3, because, being adapted to growth in the warmest season at station 6, the growth rate would be so slowed down that it would disappear from the stream at a point lower down than that at which *L. mollis* disappears.

The species of *Leptophlebia* represented here are not very closely related, at least the differences in the male genitalia, by which they are separated, are very striking. The first two species to emerge, however, *L. adoptiva* and *L. mollis*, are more closely related to each other than either of them is to other known species of *Leptophlebia* in America. These two species differ in genitalia and also superficially in the much darker pigmentation of the adult males, so that *L. adoptiva* is brown and *L. mollis* white, or transparent, in the mid-abdominal segments. *L. adoptiva* is larger than *L. mollis* and has darker eyes.

Ephemerella

In their occurrence and time of emergence the *invaria* group of the genus *Ephemerella* closely parallels the conditions just described for *Leptophlebia*. The species found at each station are as follows:

Station 1	Station 2	Station 3
E. aurivilli Bengts.	*E. aurivilli*	*E. subvaria*
	E. subvaria McD.	*E. invaria* Walk.

Station 4	Station 5	Station 6
E. subvaria	*E. subvaria*	*E. subvaria*
E. invaria	*E. invaria*	*E. invaria*
		E. excrucians Walsh

The three species occurring at station 6 are very closely related species, only separable with great difficulty in the nymphal stage, but showing distinguishing characters in the adult stages. At station 6 the three species emerge in the order *E. subvaria*, *E. invaria*, and *E. excrucians*. Some morphological characters show a gradation through this group. The first species to emerge, *E. subvaria*, is the largest, *E. invaria* next in size, and *E. excrucians* the smallest. The distal end of the penultimate segment in the male clasper is very much inflated in *E. subvaria*; in *E. invaria* it is less inflated, and in *E. excrucians* it is scarcely, if at all, inflated. Another gradation is shown in the coloration of the adults. The longitudinal veins of the wings of *E. subvaria* are dark brown, of *E. invaria* lighter brown, and of *E. excrucians* almost colourless. The eyes of the adult males also show a similar gradation. In *E. subvaria* they are dark chestnut brown, in *E. invaria* reddish brown or orange, and in *E. excrucians* pale egg-yolk yellow. The eggs of *E. subvaria* are brownish yellow and those of *E. excrucians* are whitish. Those of *E. invaria* were not observed. *E. aurivilli* is more distantly related to these three species, judging by adult and nymphal characters, and belongs in the same series.

There are other *Ephemerella* species present, of which *E. deficiens* Morg. and *E. serrata* McD. form a series of two at stations 4 and 6. They appear in the season in the order named, and *E. deficiens* is much darker in both nymph and adult than *E. serrata.*

The other *Ephemerellae* present are not very closely related among themselves, *e.g.*, *E. fuscata* Walk., *E. depressa* Ide, *E. needhami* McD., and *E. temporalis* McD., but the last mentioned, at least, is one of a group of closely related species of the *bicolor* group which is more prevalent along the rocky shores of lakes and large rivers, where incidentally *E. temporalis* also occurs. At lake Nipissing, Ontario, 1929, *E. temporalis* was found along the edges of a small stream to the mouth and along the shore of the lake. In the latter habitat it was in company with *E. lutulenta* Clem. and *E. bicolor* Clem., the three of which are members of a closely related group.

To return to the species met with in the stream, the seasonal distribution bears out in general what was found to be the case in *Leptophlebia.* In the first place, all the species have a life-cycle of one year and all the individuals emerge the same season, there being no break in the emergence as was the case with *Heptagenia pulla.* *E. aurivilli* was taken at station 1 as late as July 6 in 1931, after which no nymphs were taken, all having changed into the adult state. At station 2, on the other hand, nymphs were taken in some numbers up to June 9 in 1931, but on June 20 of the same year none could be found. This nymph apparently cannot tolerate warm water, and hence its restriction to the upper part of the stream (stations 1 and 2) and to the early part of the season (before July 6, even at station 1).

We would expect it to be more abundant farther north, which is probably the case, since it has been reported from the Pribiloff islands of Alaska, as well as from Alberta, Ontario, Quebec-Labrador, and Europe (Walley, 1930). It is probably circumpolar.

E. subvaria has apparently finished emerging at station 2 in the first week of July, at station 3 in the third week of June, and at stations 4 and 6 before the end of May.

E. invaria was emerging at station 6 on June 5 and *E. excrucians* followed closely after, and had an even shorter period of emergence than *E. invaria.*

E. deficiens was emerging at station 6 from about June 11 to July 15 in 1930, and at station 4 the emergence was a little more protracted, extending into August. The full-grown nymphs of *E. serrata* were taken towards the end of July at both stations 4 and 6. These two species were absent from stations 1, 2, and 3, although they occurred lower down than station 3 in the Pine river.

E. fuscata was emerging during the last week of June, 1930, at station 5. At station 6 it occurred only in one collection as an immature individual, and was not met with at stations other than 5 and 6. *E. depressa* was taken at stations 2, 3, and 5. At station 5 the emergence in 1930 was during the latter half of June, and at station 3 the emergence was more protracted, a full-grown nymph having been taken here as late as July 21 in the same year. *E. needhami* McD. was rather rare, having been taken, however, at stations 5 and 6. At station 5 nymphs were taken which were ready to emerge about the second week of June.

Stenonema

Stenonema fuscum Clem. was the member of this genus found nearest the source of the stream. It apparently prefers the under side of the stones where the current is not so strong as in most parts of the stations. A few individuals were found at station 2, but none at station 1. It was fairly abundant at station 3 where a full-grown individual was collected as late as August 1 in 1931. At station 6 the species was found in abundance, but here the emergence was over by the middle of July. Enough material was secured here to determine that the vanguard of the new generation does not become full-grown the same summer, but passes the winter in through the dates of the end of emergence at the six stations gives a curve similar to that shown for *Iron pleuralis*.

Baetis cingulatus McD. was absent from station 1, one or two individuals were taken at station 2, and it was rather abundant at stations 3, 5, 4, and 6. This species seems to be one which emerges during the summer months. At station 6 emergence began about the middle of June both in 1930 and 1931, and continued into September. At stations 2, 3, 4, and 5, the data were very meagre, not sufficient on which to base any conclusions as to changes in season at different stations. Nymphs of a size recognizable as this species were never taken during the winter. (*N.B.*—It is just possible that the emergence mentioned above is really that of two generations with the break occurring in August.)

Baetis intercalaris McD. was taken at stations 2, 3, 5, 4, and 6. At station 6 this form gave definite evidence of the occurrence of two generations in the same season. Both in 1930 and 1931, a few full-grown nymphs were taken in early summer up to the first week of June. Then there was a gap until the first week of July, when full-grown nymphs ready to emerge were again taken. In the month in which there was no emergence, only immature nymphs were taken, very young ones in early June, and of increasing size until July, when they were full-grown. This second emergence period lasted until nearly the middle of August, when there was another gap until the first week of September, when nymphs were again full-grown. In collections taken between August 6 and August 21, also, the nymphs taken were very immature, and showed a rapid increase in size between the two dates. Apparently at this station there is a generation emerging from about the first of July to the middle of August and then another emergence in September, some of the late individuals of which overwinter and emerge the following May.

At station 4 the seasonal distribution of *B. intercalaris* was much the same as at station 6. The material collected at stations 2 and 3 was too inadequate to form the basis for any conclusions. At these stations, however, no full-grown nymphs were taken in early summer (May), the only full-grown individuals making their appearance in August. It is

probable that there is only one generation produced at these upper stations in a season.

Baetis parvus is generally distributed in the rapid portions of the streams, occurring at stations 2, 3, 4, 5, and 6. It is not abundant in any place, but the rather scanty data of collections indicate that it has much the same seasonal distribution as B. *vagans*.

Another species which should be mentioned along with *Baetis* is *Pseudocloeon carolina* Bks., which was found abundant in the rapid water of stations 2, 3, 4, 5, and 6. There is apparently but one generation a year.

Isonychia bicolor Walk.

This species occurs at stations 4 and 6, where it apparently has two generations, an early and a late summer one.

Ephemera guttulata Pict.

This large mayfly occurred in great numbers at stations 5 and 6. In contrast to its near relatives it seems to prefer the gravelly bottom of the stream in the rapids and in small collections of silt around stones. The nymphs were frequently exposed by turning over in the rapids stones which were partially buried in gravel. The full-grown nymphs were dredged from the gravel and silt along the border of the stream. This form has been referred to as the *Ephemera* of small rapid streams (Kennedy, 1926). It is not restricted to small streams, however, since it occurs in countless numbers in the Dechenes rapids of the Ottawa river near Ottawa, and in the Lachine rapids of the St. Lawrence river near Montreal, P.Q. In this case, as in others that might be mentioned, it is the micro-habitat, the small collections of gravel and silt among the rocks of the rapids, and the proper temperature conditions, which probably determine whether or not the species will be present and it matters little if these occur in a small or large stream.

SUMMARY OF THE DISTRIBUTION OF SPECIES AT STATIONS 1 TO 6

In discussing *Leptophlebia* it was shown that there is a progressive increase in the number of species of this genus from the source downstream. The same tendency is seen in the distribution of the species of mayflies as a whole. In the rapid-water stations, for instance, the following were present:

Station 1 (7 species)

At each station the name is followed by the number of the station and by the number of any station above at which the species has also occurred. An asterisk is placed in front of the name of a species which is found at no stations lower in the stream.

Iron pleuralis, 1
Heptagenia pulla, 1
Ephemerella aurivilli, 1
Leptophlebia adoptiva, 1
Leptophlebia debilis, 1
Baetis brunneicolor, 1
Baetis vagans, 1

Station 2 (15 species)

Iron pleuralis, 1, 2
Epeorus humeralis (two nymphs only, found on one occasion), 2
Heptagenia pulla, 1, 2
Stenonema fuscum, 2
Ephemerella subvaria, 2
Ephemerella depressa, 2
**Ephemerella aurivilli*, 1, 2
Leptophlebia adoptiva, 1, 2
Leptophlebia debilis, 1, 2
Baetis brunneicolor, 1, 2
Baetis vagans, 1, 2
Baetis cingulatus, 2
Baetis parvus, 2
Baetis intercalaris, 2
Pseudocloeon carolina, 2

Station 3 (16 species)

Iron pleuralis, 1, 2, 3
Epeorus humeralis, 2, 3
Heptagenia pulla, 1, 2, 3

Stenonema fuscum, 2, 3
Ephemerella subvaria, 2, 3
Ephemerella invaria, 3
Ephemerella depressa, 2, 3
Leptophlebia adoptiva, 1, 2, 3
Leptophlebia mollis, 3
Leptophlebia debilis, 1, 2, 3
Baetis vagans, 1, 2, 3
Baetis parvus, 2, 3
Baetis cingulatus, 2, 3
Baetis intercalaris, 2, 3
Pseudocloeon carolina, 2, 3

Station 5 (22 species)

Iron pleuralis, 1, 2, 3, 5
Epeorus humeralis, 2, 3, 5
Heptagenia pulla, 1, 2, 3, 5
Heptagenia hebe, 5
Stenonema fuscum, 2, 3, 5
Stenonema canadense, 5
Isonychia bicolor, 5
Leptophlebia adoptiva, 1, 2, 3, 5
Leptophlebia mollis, 3, 5
Leptophlebia guttata, 5
Habrophlebiodes americana, 5
Ephemerella subvaria, 2, 3, 5
Ephemerella invaria, 3, 5
Ephemerella deficiens, 5
**Ephemerella depressa*, 2, 3, 5
Ephemerella fuscata, 5
Ephemerella needhami, 5
Baetis vagans, 1, 2, 3, 5
Baetis cingulatus, 2, 3, 5
Baetis intercalaris, 2, 3, 5
Baetis parvus, 2, 3, 5
Pseudocloeon carolina, 2, 3, 5

Station 4 (21 species)

**Iron pleuralis*, 1, 2, 3, 5, 4
Epeorus humeralis, 2, 3, 5, 4

Heptagenia pulla, 1, 2, 3, 5, 4
Heptagenia hebe, 5, 4
Stenonema fuscum, 2, 3, 5, 4
Stenonema canadense, 5, 4
Isonychia bicolor, 5, 4
Ephemerella subvaria, 2, 3, 5, 4
Ephemerella invaria, 3, 5, 4
Ephemerella deficiens, 5, 4
Ephemerella serrata, 4
Leptophlebia adoptiva, 1, 2, 3, 5, 4
Leptophlebia mollis, 3, 5, 4
Leptophlebia debilis, 1, 2, 3, 4
Habrophlebiodes americana, 5, 4
Baetis vagans, 1, 2, 3, 5, 4
Baetis cingulatus, 2, 3, 5, 4
Baetis parvus, 2, 3, 5, 4
Baetis intercalaris, 2, 3, 5, 4
Centrophlum bellum, 4
Pseudocloeon carolina, 2, 3, 5, 4

Station 6 (29 species)

Epeorus humeralis, 2, 3, 5, 4, 6
Heptagenia pulla, 1, 2, 3, 5, 4, 6
Heptagenia hebe, 5, 4, 6
Stenonema canadense, 5, 4, 6
Stenonema heterotarsale, 6
Stenonema fuscum, 2, 3, 5, 4, 6
Stenonema (fuscum grp.), 6
Stenonema nepotellum, 6
Isonychia bicolor, 5, 4, 6
Leptophlebia mollis, 3, 5, 4, 6
Leptophlebia adoptiva, 1, 2, 3, 5, 4, 6
Leptophlebia debilis, 1, 2, 3, 4, 6
Leptophlebia guttata, 5, 6
Habrophlebiodes americana, 5, 4, 6
Ephemera guttulata, 6
Ephemerella subvaria, 2, 3, 5, 4, 6
Ephemerella invaria, 3, 5, 4, 6
Ephemerella excrucians, 6

Ephemerella deficiens, 5, 4, 6
Ephemerella serrata, 4, 6
Ephemerella temporalis, 6
Ephemerella fuscata, 5, 6
Baetis brunneicolor, 1, 2, 3, 6
Baetis vagans, 1, 2, 3, 5, 4, 6
Baetis cingulatus, 2, 3, 5, 4, 6
Baetis intercalaris, 2, 3, 5, 4, 6
Baetis parvus, 2, 3, 5, 4, 6
Pseudocloeon carolina, 2, 3, 5, 4, 6

TABLE 7.—A summary of the addition of species at stations 1 to 6, and the dropping out of species downstream.

Station	Number of species	Number of station 1 species	Number of station 2 species	Number of station 3 species	Number of station 5 species	Number of station 4 species	Number of species appearing at this station and at no higher stations	Number of species not appearing at stations lower than this
1	7							
2	15	7					8	1
3	16	6	14				2	
5	22	4	12	14			8	1
4	21	5	12	14	18		2	1
6	29	5	12	14	20	19	6	

There is an apparent discrepancy in the fact that the number of species found at station 5 is greater than the number at station 4, although the latter station is subjected to higher temperatures than the former. The explanation of this is to be found, I think, in the greater complexity of habitats represented at station 5. In parts of the stream at this station the water flowed more rapidly than at other stations.

When the number of species of mayflies found at each station is plotted against the area under the time-temperature curve (exclusive of the area below the temperature of the source) for the corresponding station, we find that there is a fairly good straight line formed, showing that the number of species increases in direct proportion. This phenomenon is illustrated graphically in text figure 2.

Most of the species of mayflies dealt with so far are confined to the rapids in streams. Some, however, extend their range to lakes where favourable conditions are also to be found. Among these are: *Stenonema canadense*, *Stenonema heterotarsale*, *Heptagenia pulla*, *Heptagenia hebe*, *Baetis cingulatus*, *Ephemerella bicolor*, *Ephemerella temporalis*, *Cloeon rubropicta*, and *Cloeon simplex*. In streams these species are found in the less rapid water, for instance along the edge or in parts of the rapids protected from strong currents, where conditions are not very different from those obtaining in the littoral zone of lakes. Frequently such species are found continuously distributed down the stream, and around the shore of a lake into which it empties. In such cases the first individuals to emerge are those at the lower end of the stream, and they emerge much earlier than individuals of the same species in the lake, since the water at the lower end of the stream warms up much more rapidly in the spring than does the water of the lake.

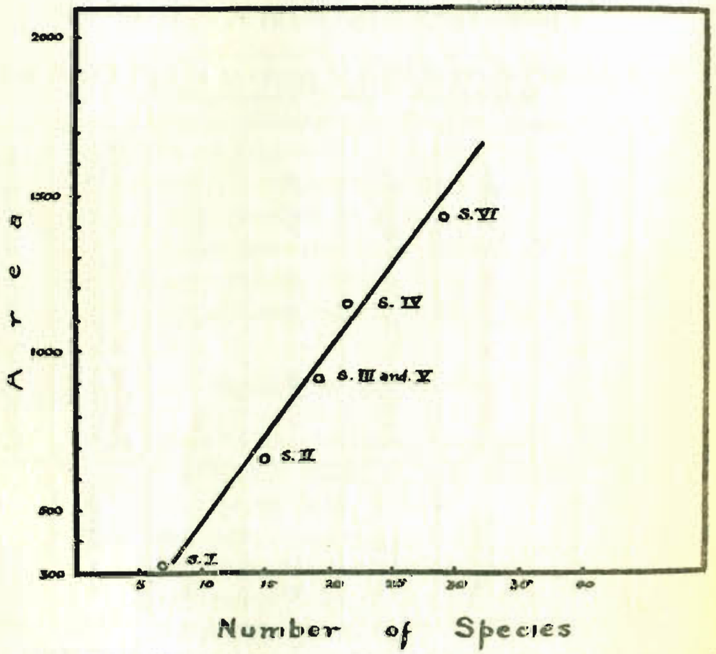

FIGURE 2.—The relationship between the number of species and the area above the temperature of the source under the time-temperature curves of figure 6, plate III.

DISTRIBUTION OF SPECIES AT STATIONS A TO D

These stations as mentioned above were situated in the upper part of the Mad river and, as with stations 1 to 6, were chosen with the view of obtaining the greatest possible similarity in regard to depth and rate of flow of water, type of bottom, aquatic vegetation, and exposure to the sun, and to difference in temperature. The main difference between these stations and stations 1 to 6 was the greater depth and slower rate of flow of the water, resulting in the accumulation of silt on the bottom and the presence of aquatic plants which harboured some of the species of mayflies met with at these stations. The habitats represented at these stations were more varied than at the rapid-water stations, so that they could not be compared with one another so satisfactorily.

In order to determine the effect of the different temperatures of the water on the fauna at the stations, one species, *Stenonema tripunctatum* Bks., was studied in greater detail than the other species, and an account of its distribution is given first.

Stenonema tripunctatum Banks

This species was present at stations A, B, C, and D, where it was found clinging to the under sides of stones. As in the case of the other species, a frequency diagram was plotted, based on the factor X (determined by dividing the length of the mesothoracic wing-pad by the length of the seventh abdominal tergite) for the older stages and the number of antennae segments for the younger stages. In this diagram (diagram 5, plate VIII) as in the others, an individual is represented by one square.

TABLE 8.—The ranges of variation of the factor X and the number of antennal segments of the stages A to K of *S. tripunctatum*; determined from diagram 5, plate VIII.

Stenonema tripunctatum

Stage	X	Number of antennal segments
A	3.50-2.60	
B	1.80-1.40	
C	1.40-1.20	
D	1.20- .95	
E	.95- .80	
F	.80- .65	
G	.65- .45	
H	.45- .25	21-18
I		17-15
J		14-9
K		8-4

X = the length of the mesothoracic wing-pad divided by the length of the seventh abdominal tergite.

Graph 5, plate X, shows the result of plotting the stages represented in the collection taken at stations A, B, C, and D during the summer of 1930 and part of 1931. The graph is not very satisfactory as will be seen at a glance, this being mainly due to the inaccessibility of the stations in winter and the very high water in spring. The best record was secured at station C from which it will be seen that the season's emergence is over before the end of July and that the next generation passes the winter in the B or penultimate nymphal stage. At station D all the nymphs had emerged before the middle of June. It should be mentioned here that the nymphs collected at station D were in very shallow water along the bank of the stream, which warms up rather more rapidly than the main flow of water; this fact probably accounts for the very early emergence of these individuals. At station B the end of emergence was about the end of July and at station A later, probably the end of August. At station A the generation of the next year is fairly well grown by the beginning of September and probably grows during the winter so that emergence will take place at this station very early the next season.

At none of the stations is there a second generation the same summer, but this apparently does occur under some conditions. Along the Rideau canal at Ottawa the author collected some years ago a number of adults of *Stenonema tripunctatum* in October. The individuals were of small size but specifically identical with individuals occurring earlier in the season. The Rideau canal is a body of static water which warms up early in the spring and remains very warm throughout the summer and early fall. Under these conditions, which would supply, by a long-continued high temperature, a much longer growing season than obtained at station D in the Mad river, we would expect that two generations would be produced in the one season, the first generation appearing probably in July and the second in late September and October.

SUMMARY OF THE DISTRIBUTION OF SPECIES AT STATIONS A TO D

The species found in the Mad river in its quieter reaches in the vicinity of stations A, B, C, and D, are listed below.

Station A (11 species)

At each station the name is followed by the letter representing that station and by the letter or letters representing any station above at which the species in question has occurred.

Stenonema tripunctatum Bks., A
Stenonema canadense Walk., A
Stenonema fuscum Clem., A
Centroptilum convexum Ide, A
Arthroplea bipunctata McD., A
Callibaetis americana Bks., A
Blasturus nebulosus Walk., A
Siphlonurus alternatus Say, A
Siphlonurus quebecensis Prov., A
Leptophlebia debilis McD., A
Ephemerella temporalis McD., A

Station B (15 species)

Stenonema tripunctatum, A, B
Stenonema canadense, A, B
Stenonema fuscum, A, B

Ephemera simulans, B
Hexagenia viridescens McD., B
Ephemerella temporalis, A, B
Baetis frondalis McD., B
Baetis pygmaeus Hag., B
Pseudocloeon sp. (not *P. carolina*), B
Centroptilum convexum, A, B
Centroptilum sp. (*bellum*?), B
Blasturus nebulosus, A, B
Leptophlebia debilis, A, B
Trichorythodes atrata McD., B
Caenis sp., B

Stations C and D (21 species)

Stenonema tripunctatum, A, B, C, D
Stenonema canadense, A, B, C
Stenonema fuscum, A, B, C
Heptagenia hebe McD., C
Ephemera simulans, B, C, D
Hexagenia viridescens, B, C, D
Baetis pygmaeus, B, C, D
Pseudocloeon sp., B, C, D
Cloeon sp., D
Cloeon simplex McD., C, D
Cloeon rubropicta McD., C, D
Arthroplea bipunctata, A, C
Centroptilum convexum, A, B, C, D
Centroptilum sp. (*bellum*?), B, C
Leptophlebia debilis, B, C
Blasturus nebulosus, A, B, C, D
Siphlonurus alternatus, A, C, D
Siphlonurus quebecensis, A, C, D
Ephemerella temporalis, A, B, D
Caenis sp., B, D
Trichorythodes atrata, B, D

Of the above-listed species at stations C and D, *Stenonema canadense* and *S. tripunctatum* occurred under stones, in the gently-flowing water. *Ephemera simulans* is a burrower in the marl and fine gravel of the stream in the quieter water, and *Hexagenia viridescens* in the silt among the standing aquatic plants. *Siphlonurus*, *Blasturus*, and *Arthroplea* were found among the plants along the shore, where they were congregated particularly at the time of emerging. *Baetis frondalis* was found on *Potomageton* plants which were waving in the current, *Centroptilum* sp. on plants in the current and sometimes on the stones, from which, however, they usually escaped before the stone was lifted from the water. *Centroptilum convexum*, *Baetis pygmaeus*, *Cloeon* sp., *Cloeon rubropicta*, and *Cloeon simplex* were found always associated with the plants in the quieter water.

TABLE 9.—Summary of distribution of species at stations A, B, C, D.

Station	Number of species present	Number of station A species present	Number of station B species present	New species added
A	11			
B	15	6		9
C and D	21	9	14	4

The habitats represented at these stations are more varied than those at the rapid-water stations, but the same increase in the number of species is well shown from eleven at station A to fifteen at station B to twenty-one at stations C and D which were close together. This increase in the number of species is correlated with increase in temperature downstream.

The foregoing descriptions of the occurrence and distribution of stream mayflies have all been concerned with nymphs which live in the main channels of the streams.

In quieter parts of the stream the temperatures vary considerably from those obtaining in the main channel, becoming much higher in shallow water along the shore, particularly in little pools and inlets along the banks among the emergent aquatic vegetation, so that insects developing in these habitats emerge at a very early season. The best example was found in the case of *Blasturus nebulosus*, which was one of the very earliest mayflies to emerge in the vicinity of station C. A temporary pool was formed by melting snow at least thirty feet above the level of the stream and about 300 feet away from the stream in a meadow. When examined on May 19, 1931, there was no connection between the pool and the stream, although there was evidence in the grass of a former trickle of water from the pool to the stream. The pool had a great abundance of nymphs of this species, and also of *Siphlonurus quebecensis* and *Arthroplea bipunctata.* There were full-grown emerging nymphs taken on this date. These three species were present in the main stream nearby and had found their way up to the temporary pool by way of its outlet. An excellent account of such a migration of nymphs has been described by Neave (1930) for *Blasturus cupidus*.

Such temporary pools form a peculiar habitat from which the mayflies emerge very early in the season. This seems to be due to the warming up of the shallow water in them by the direct action of the sun, in which probably the dark bottom plays an important part. Even on a cold day, if the sun is bright, the water warms up as much as 10°C. above the air temperature. On one occasion, a bright, cold day (April 24, 1932), the air temperature was 9°C., and the water temperature 19°C. Probably here again as in the case of *Iron* at station 1, the air temperature causes many casualties because if the insects emerged they would not be able to fly in such cold air.

A case of this kind was observed with another species, *Ephemera simulans*, at station D, later in the season. The evening was very cold and the water warm from the effect of the sun's heat. The nymphs came to the surface and the subimagos emerged but were unable to fly up from the surface of the water, due no doubt to the cold air slowing down their activity. As a result the surface was very soon covered with hundreds of subimagos floating downstream, an easy prey to the trout.

DISCUSSION AND CONCLUSIONS

Temperature control of the distribution of mayflies in a stream

It has been demonstrated, particularly in the case of the genera *Leptophlebia* and *Ephemerella*, and in general for all the mayflies occurring at the stations, that there is an increase in the number of species at successive stations from the upper ones downstream. Further, the increase in the number of species downstream results from the successive appearance of species additional to those found higher up. In going from station 1 to station 6, about twenty-two species are added and only two (*Iron pleuralis* and *Ephemerella aurivilli*) dropped out. It has further been shown that the emergence at the lower stations of the species represented also at the upper stations is confined more and more to the early part of the season as we go downstream.

Correlated with these facts is the increasing range of temperatures met with at the stations from the source downstream. The extent of the temperature ranges are listed in table 10 and shown graphically in figure 6, plate III.

TABLE 10.—Ranges of temperature of water at stations 1 to 6, between the maximum on a warm, bright day of summer, and the minimum on a fairly cold day of winter.

Station	Summer maximum	Winter minimum	Range	Range above temperature of source
Source	8°C.	8°C.	0°C.	0°C.
Station 1	11	6.75	4.25	3
2	20	4.0	16.0	12
3	21	2.0	19.0	13
5	25 ?	0	25 ?	17
4	27	0	27	19
6	30	0	30	22

At the source the temperature is very uniform throughout the year, at about 8°C. At station 1 the temperature varies more, rising in summer to about 11°C. on very hot days and dropping probably to about 6°C. on cold days of winter. At station 2 the range of temperature is greater than at station 1, the temperature of the water rising to about 16°C. in summer, or even higher on very warm days and dropping on cold days in winter to 4°C. or perhaps lower. At the lower stations the fluctuation in temperature is greater until at station 6 the water temperature closely approximates the air temperature on hot summer days and in cold winter weather drops to 0°C.

The absence of certain species at the upper stations seems to be due to the failure of the water to rise to a temperature sufficiently high to allow the individuals of these species to grow and complete their development. For example, the very slow rate of growth of *Leptophlebia mollis* at station 4 indicates that this species is near the limit of the conditions under which it can survive; its absence at stations nearer the source is, therefore, not surprising. The same condition explains the distribution of *Epeorus humeralis* at the various stations.

On the other hand, the gradual restriction of the emergence to the early season and the final disappearance of a few species at the lower stations seem to be due to the high temperatures prevailing during midsummer at these stations. These phenomena have been dealt with in the case of the absence of *Iron pleuralis* from station 6.

It is interesting to compare the time of emergence and growth rates of closely related species such as *L. adoptiva* and *L. mollis* and *I. pleuralis* and *Epeorus humeralis* at the different stations. At stations at which *L. adoptiva* and *L. mollis* occur together, the former always emerges before the latter and grows as fast even at the lower temperatures prevailing in the earlier part of the season. At stations 1 and 2, where *L. mollis* has been eliminated because of too low temperature, *L. adoptiva* is able to grow, more slowly it is true, than at the lower stations, but yet fast enough to complete its development and emerge. Similarly, at stations at which both *Iron pleuralis* and *Epeorus humeralis* occurred, the former emerged earlier than the latter. *Iron pleuralis* grew at as fast a rate as *Epeorus humeralis*, even at this earlier season when the average temperature of the water was lower. At upper stations, from which *E. humeralis* had been eliminated by its greatly reduced growth rate caused by lower temperatures, *Iron pleuralis* was still able to grow fast enough to reach maturity, although its growth rate was slower than at the lower stations.

From the facts given in the above examples, it seems that low temperatures are detrimental to the mayflies only in so far as the activity and growth of the nymphs are slowed down to such a degree that they cannot complete their life-cycles and so cannot maintain themselves in places in the stream where such low temperatures prevail. *Leptophlebia mollis* and *Leptophlebia guttata* have thus been excluded from the upper stations.

In the case of *Leptophlebia adoptiva* and *Iron pleuralis*, on the other hand, the elimination has been from the lower stations through the action of high temperatures. For *Iron pleuralis* it has been shown (inset of graph 2, plate V) that the date of the end of emergence at each station plotted against the point on the temperature-gradient curve for that station when joined gave a straight line, showing that the latest date at which individuals emerge successfully at a station is determined by the temperatures obtaining at that station. This does not mean that this point is necessarily determined each year by high temperatures of that summer, but perhaps by a process of selection of nymphs by heat over a number of years.

Although *Iron pleuralis* emerges very early in the season at the lower stations, earlier than *Epeorus humeralis* at the same stations, the young nymphs of the next generation of the former species are not to be found in the stream until after those of *Epeorus*. This indicates a longer incubation period with probably a dormant period of the eggs. Fairly definite evidence of such a dormant period is given in graph 2, plate V. At station 5 no nymphs of the species could be found in the middle of October in 1931, and yet by the middle of December nymphs about half-grown were taken. This means that the growth rate was very rapid between these dates. The earliest date at which eggs appeared at this station was about the third week in May. Probably in the middle of October there were very small nymphs present, but it is likely that the eggs remained in an unhatched condition for at least four months. As compared with the rapid growth after hatching, the growth during these four months is practically nothing, making a period of real dormancy extremely probable.

This dormant period has probably been evolved through the killing off by the summer heat of individuals which hatched early and the survival of eggs which remained dormant and were thus carried through the warmest part of the summer in the egg stage. Eggs of this species were not hatched, but eggs of *Stenonema canadense* in their time of hatching give a clue to a possible method of evolution of such a dormant stage in eggs. A series of eggs from several females of *S. canadense*, taken ovipositing the same evening, were incubated in a jar of water. It was found that these eggs continued to hatch over a period of six weeks. Presumably these different incubation times for the eggs are genetic characters, since the conditions were the same for all the eggs. The killing off of early-hatching individuals would result in the survival of the later-hatching eggs, and the propagation of the character.

The restriction of the emergence at the lower stations by high temperatures in *Iron pleuralis* is further illustrated in the case of *Leptophlebia adoptiva*. Although still present at station 6 its very restricted period of emergence at this station indicates its probable absence from points a little lower down the stream.

With both of these species, apparently, no low temperatures that occur in the streams are detrimental, and the restriction of the season of emergence and the final elimination of these two species downstream are caused by the lethal effect of the high temperature of the water during the summer months.

The increase in the number of species downstream is due, as we have seen, to the higher temperatures which prevail in the lower parts of the stream, and the addition of species in this way is more rapid than the elimination of species by high temperatures. This would hold only for the upper reaches of rivers, since in very large rivers such as the Ottawa river at Ottawa and the St. Lawrence river at Montreal, the process of heating the water to high temperatures is much slower, due to the great body of water to be heated, thus allowing many species, eliminated by heat from the lower reaches of small rivers, to be present in the lower reaches of large rivers.

Geographical distribution

The facts brought out by this study appear to throw some light on the subject of the geographical distribution of mayflies. A spring stream, especially near its source, supplies a remarkably uniform environment for mayfly nymphs, wherever the stream occurs—in warm climes, at high elevations on mountains, or in the north. This uniform environment provides a pathway by which organisms may extend their range wherever this environment is present. As one goes north, however, the warm-season forms will be eliminated and the forms of the source, or near it, will still be accommodated farther downstream, and, provided the source becomes colder, there is an opportunity for new forms to appear at the source. The forms near the source are those with a northern distribution in general, and those lower down have a more southerly distribution.

It is probably safe to say that a spring stream in its fauna, taken from the warmer reaches to the source, recapitulates south to north distribution, in the way that a mountain in the torrid zone gives in its fauna and flora, taken from the foot to the top, roughly a vertical section of geographical distribution from torrid to frigid zones.

Temperature as a factor in evolution

The facts with reference to the distribution of mayflies in the stream could be explained on the assumption that there has been an evolution in the direction of an increase in the rate of life-processes among the species of mayflies of various genera, resulting in different rates of growth at the same temperature, and along with these, different thresholds of activity and development, and different lethal temperatures. *Leptophlebia mollis*, for example, has a higher threshold of development and a higher lethal temperature than has *L. adoptiva*. The difference in rates of life processes is well illustrated in graph 4, plate IX, which shows the growth rates of *L. adoptiva* and *L. mollis*. Under low-temperature conditions *L. adoptiva* grows at practically the same rate as *L. mollis* does under high temperatures. Since the growth rate of an insect increases directly with increase in temperature, *L. adoptiva*, if it were able to grow at the temperature at which *L. mollis* thrives, would grow much faster than *L. mollis* at the same temperature. It cannot, however, grow at the higher temperatures because its upper lethal limit is lower than that of *L. mollis*, so that it is barred from the season occupied by the latter.

Paralleling such gradation in physiological characters may be seen gradations in morphological structure such as size, deposition of pigment, and form of the male claspers. In the genus *Ephemerella* we have three very closely related species, *E. excrucians*, *E. invaria*, and *E. subvaria*, giving an illustration of this phenomenon. Using as a criterion the time of year at which these species emerge and their distributions in the stream, it is probable that *E. excrucians* has the highest lethal temperature and the highest threshold of development; *E. invaria* the next highest; and *E. subvaria* the lowest. The morphological characters paralleling these physiological characters have been listed above in the discussion of the genus *Ephemerella*. Some such morphological characters have been claimed to be the expression of physiological differences. For example, different degrees of pigmentation may be caused by the action of different rate genes governing the deposition of the pigment (Goldschmidt, 1923, 1927, 1928), (Ford and Huxley, 1929). Different lengths and shapes of appendages and processes (Huxley, 1931) have been shown to be correlated with increase or decrease in size of the whole organism or part of it, which in turn may be the expression of different rates of life processes.

A consideration of the distribution in the stream and of the season of emergence of such closely related species as *adoptiva* and *mollis* of the genus *Leptophlebia*, and *subvaria*, *invaria*, and *excrucians* of the genus *Ephemerella* leads to the conclusion that temperature requirements and not competition for food explain the occurrence of these species in the situations which they occupy in the stream. So far as one can judge, there is now no competition between the closely related species of the two genera just cited, at least not as much as there is between individuals of the same species. Although the nymphs of all the species of a group may be in the water at the same time, they are of different sizes, thus lessening the element of competition between them. *Leptophlebia adoptiva* does not occupy the seasonal position of *L. mollis*, and *vice versa*, because of their different requirements in regard to temperature for development and limitations in regard to temperature tolerance, and these species are not confined to one season, because of competition with their closest relatives. This suggests that evolution in the case of these species has occurred in the direction of physiological adaptation to different temperature conditions rather than through adaptation to other physical features of the environment.

The appearance of a thermal clone through mutation in *Daphnia longispina*, as described by Banta and Wood (1927), perhaps gives a clue as to the manner in which the different temperature adaptations of these mayflies may have arisen. In the case described by these authors, the new clone or race was developed from a parent strain which had been kept in the laboratory for fourteen years through 363 parthenogenetic generations. After sexual reproduction their thermal clone appeared and was propagated. Its temperature tolerance was different. It could stand a temperature several degrees higher than the parent strain, and its threshold of development was also considerably raised.

If such a clone were to appear in a mayfly in the stream, it would, with its different rate of growth, become seasonally isolated from the species from which it arose. Such physiological differentiation of two species by mutation need not be attended by obvious morphological differentiation, as has been shown in the case of some crickets by Allard (1929). It is probable, however, that some morphological changes do accompany any physiological change although they may not be of adaptive significance at first, so that the species produced occur in the same habitat in the stream, occupying it, however, at different times of the year. Then, with greater morphological differentiation, the species or genera, as the case may be, assemble in new habitats, for example, where the water is less rapid, or where the bottom is covered with silt. We find in these habitats, with different types of bottom and rates of flow of water, new sets of species widely separated in relationship from forms in the rapids, although often of the same genera. They reveal their more distant relationship in their greater divergence in morphological characters. These new sets of species are also limited in their distribution in the stream by temperature conditions. Thus we see that temperature sets limitations on the distribution in the stream, and the nature of the bottom and speed of current set further limitations for the species within the limits determined by temperature.

The distributional data as brought out by this investigation are in accord with Kennedy's (1928) theory, which postulates an evolution in what he terms "metabolic rate" towards higher temperature tolerance. On the basis of the present geographical distribution of dragon-flies in America, their seasonal distribution and their diurnal activities, he finds an analogy between the torrid, temperate, and frigid zones; summer, spring, or fall; midday, morning, or evening. The most active types, or those which have evolved highest in temperature tolerance, occupy the torrid zones and are active during midday of midsummer. The less active or primitive forms occupy the temperate and frigid zones, the spring or fall of the year, and the morning or evening of the day. The older or more primitive species of groups are northern in distribution or, if not northern, are active in the northern in distribution or, if not northern, are active in the cooler seasons of the year or cooler parts of the day. The distribution of the mayflies in the streams appears to be a special case of the same general theory.

Origin of a torrential alpine fauna

The above discussion leads to a consideration of the nature and origin of a torrential alpine fauna. Two views are held as to the origin of this fauna. Étienne Hubault, in his *Contribution à l'étude des invertébrés torrenticoles* (1927), is of the opinion that the torrential fauna as studied by him in streams of the Alps is a relic fauna or in his own words:

> Dans une dernière étude enfin j'ai essayé de donner quelques indications sur l'origine de la faune torrenticole actuelle, fille de la faune des glaciations qui s'est largement propagée dans les cours d'eau par l'intermédiaire des rives des nappes d'eau froide.
>
> Je dirai donc en terminant, que les êtres qui peuplent les eaux rapides, y recherchent des conditions physico-chemiques qui leur sont indispensibles, tout en étant forces de subir le courant, phénomène mécanique et inconvénient auquel ils parent avec des moyens plus ou moins proches de la perfection.

This author says in presenting his view that nothing can be said with certainty. Many presumptions must be made based on analogies and, indeed, in all studies of this kind the most convincing evidence is given by the palaeontological evidence, which is absent here on account of the very evanescent character of the insect exoskeleton.

The opposing view is given clearly by Dr. Sunder Lal Hora (1929) whose summary states:

> In recent years I have studied the invertebrate fauna of torrents in detail, and in every group of animals discussed in the preceding pages I have found evidence of step-by-step colonization [from the slow-flowing reaches of the lower land] . . . . . The animals have become gradually modified under the direct effect of the current, which appears to me to be of paramount importance in their habitat. . . . .

And again

> Of the physical conditions [pp. 174-5] that influence the ecological distribution of the torrential fauna, the principal one is the rate of flow of the current. The high percentage of oxygen in the water is another important factor, but it is dependent on the current to a very great extent. Shallowness and low temperature of the water are also of some importance. Among the biological factors food is the most important.

The evidence provided by the present study indicates that temperature is a most important factor determining where a species may live and where it may not live in the stream. Within the limits set by temperature are other limits set by the strength of the current and the nature of the bottom.

In the alpine stream there are two main factors, the swiftness of the current and the temperature of the water, both of which will exclude certain elements of the fauna from the streams and both of which will be tolerated by other elements. Oxygen content of the water, in cases where it is variable, will also be important. Thus, an insect very well adapted to hold its position in the current might not be able to survive in cold water at the higher altitudes, and hence would not be able to extend its range there. On the other hand, a species might be well adapted to the temperature conditions of the torrent streams but not morphologically adapted to maintain itself in the swift water, and so could not extend its range. But if there were a place in the stream where the water was less swiftly flowing, and there are probably many such places, such a species could maintain itself here and so on up to the highest altitudes. The insect taken in our first example could not possibly find a suitable location at the higher altitudes unless the source of the water were some hot spring. The temperature reaction of the organism, therefore, seems to be of primary importance to the population of alpine streams, and morphological adaptation secondary. This would indicate that the alpine torrential fauna is a cold water (relic) fauna as well as a fauna adapted to rapid water.

There is no palaeontological evidence, as Hubault (1927) has pointed out, to support the view that it is an ancient fauna, but in closely related species such as *Ephemerella aurivilli*, *E. subvaria*, *E. invaria*, and *E. excrucians*, and the species of the genus *Leptophlebia*, there is a stratification according to season and temperature reaction which is perhaps comparable to it.

In the genus *Ephemerella*, the species *aurivilli* has a very extensive northern distribution extending from the Pribiloff islands of Alaska across Canada to northern Europe (Walley, 1930), and is probably circumpolar. *E. subvaria*, *E. invaria*, and *E. excrucians* are American, but it is probable from their seasonal distribution in streams that *E. subvaria* extends farther north than *E. invaria* and *E. invaria* farther north than *E. excrucians*. According to Kennedy's theory, *E. aurivilli* would be the oldest member of the group and *E. excrucians* the most recently developed. From its position in the streams studied, *Ephemerella aurivilli* has a lower temperature range with lower threshold of development and lower temperature tolerance than the other species of the group. *E. excrucians* tolerates higher temperatures than other members of the group, so that it would be placed higher in the scale of evolution in metabolic rate.

In the same way *L. debilis* has a northern distribution in Canada and is found in Europe, where it was described under the name *L. separata* by Ulmer. *L. adoptiva* one might expect would also be found to have a circumpolar distribution, but it is so little known at present, having been just recently described, that its distribution is not known.

From the above evidence it seems fairly safe to state that the fauna of the headwaters of streams and the fauna of alpine streams which are characterized by uniformly cold as well as rapid water are essentially relic fauna, with the oldest species of the genera inhabiting the coldest water near the source. Their adaptation to swift water is secondary to their reaction to temperature.

The data given above, and those to be found in existing records of geographical distribution, are not sufficient to decide whether this group of species of the genus *Ephemerella* had its origin in the north or south. It is perhaps permissible, however, to speculate here as to the evolution of the group.

Ephemerella aurivilli first became separated from the parent stock of *E. subvaria*, *E. invaria*, and *E. excrucians* and with specialization moved northward. This might be considered as a process of senescence or decreasing metabolic activity resulting in the toleration of lower temperatures. Since *E. aurivilli* was separated earliest, it may carry features of the common ancestor not represented in other members of the group, thus being primitive in these features. The next species to be separated was *E. subvaria*, according to this speculation, leaving a generalized stock which later gave rise to *E. invaria* and *E. excrucians*. *Ephemerella subvaria* in this sense is older than *E. invaria* and *E. excrucians* and younger than *E. aurivilli*. *Ephemerella aurivilli* is not as closely related to *E. subvaria* as the latter is to *E. invaria*. This may mean that *E. aurivilli* is the last surviving member of a group, the other members of which have become extinct.

SUMMARY

1. The object of this investigation was to study the effect of temperature on the distribution of mayflies in a stream.

2. For this purpose stations were selected along the course of the stream where environmental factors such as depth and rate of flow of the water, type of bottom, and exposure to sunlight were similar, but where the temperature of the water differed widely.

3. Collections of nymphs were made periodically at these stations over a period of about two years.

4. Collections were analysed to determine the number of species of mayfly nymphs represented, the number of each species, and also the stage of development of the individuals in each collection.

5. Temperatures of the water were recorded corresponding to the time at which each collection was made. From all the temperatures taken, the fluctuations at the various sta-

tions and the gradient in temperature between the stations were determined.

6. It was found that there was an increase in the number of species of mayflies from the source downstream, correlated with the greater fluctuation in temperature downstream.

7. This increase in the number of species results from the addition of species to those already found towards the source. Only two species found near the source are dropped out downstream.

8. The season of emergence of most species occurring near the source becomes shorter and shorter downstream, and is then restricted to the early part of the summer. The elimination of two species occurring near the source is caused by the higher temperatures prevailing at the lower stations in summer.

9. The failure of many of the species occurring at the lower stations to appear nearer the source is due to the fact that the temperature of the water does not rise sufficiently high to allow them to grow and complete their development.

10. Very closely related species in a genus are apparently seasonally isolated by the temperature of the water. In such a group the species to emerge earliest in the season at the lowest station is the species which will extend up to the source; the species next to emerge at the lowest station will not extend up so far.

11. This distribution may be explained by the different growth rates and different thresholds of development and lethal temperatures.

12. Correlated with these physiological characters are certain morphological characters separating these very closely related species, which may be the expression of physiological differentiation.

13. From the evidence available, the forms at the source have a northern distribution on this continent, some being circumpolar. Those which are confined to the lower parts of the stream have a more southerly distribution.

14. Temperature of the water in the stream sets limits to the distribution of the mayflies within which are other limits determined by the rate of flow of the water, type of bottom, and vegetation.

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PLATE V

GRAPH 2.—Shows the seasonal distribution of the different nymphal stages of *Iron pleuralis* at stations 1, 2, 3, 4, and 5 during the summer of 1931 and part of 1932 (in cases in which the collection was made in 1932 a small dot is placed to the right of the disk). X indicates that no nymphs of this species were found in collections taken on that date. The symbols have the same significance as in the case of *E. humeralis* (graph I, plate III). The dates on which the emergence of the subimagos ended at each station, as indicated by the disappearance of nymphs from the water, are joined by a line. In the inset these dates are shown plotted at ordinate distances proportional to the temperature gradient between them, resulting in a straight line, which suggests that this point is determined by temperature or some factor varying with it.

PLATE VI

DIAGRAM 4.—Frequency diagrams of the lengths of the mesothoracic wing-pads measured in tenths of a millimetre for all the last instar nymphs of *Iron pleuralis* taken during 1931 and 1932 (1932 individuals shown as gray squares) at stations 1, 3, and 5. A dotted line is drawn roughly through the mode for wing-pad length of each day's collection, giving a smooth curve. Then the maxima of the curved lines for the three stations are joined by a solid line. The frequency diagrams of the individual collections are summed for each station.

PLATE VII

GRAPH 3.—Shows seasonal distribution of the nymphal stages of *Heptagenia pulla* at stations 1, 2, 3, 4, and 6 during 1931. Symbols and method of plotting the same as for *E. humeralis* (graph 1, plate III). The lines XX and X_1X_1 are drawn through the time of the incidence of emergence at each station, and the lines YY and Y_1Y_1 through the time of the end of emergence. The dotted lines give roughly in their slopes the growth rates.

PLATE VIII

DIAGRAM 5.—Frequency diagram of all the nymphs of *Stenonema tripunctatum* plotted in the same manner as described above for other species. Males and females are plotted separately and then these diagrams combined and amplified in the lower diagram.

DIAGRAM 6.—Frequency diagrams of the nymphs of three species of *Leptophlebia* plotted in the same manner as described above.

PLATE IX

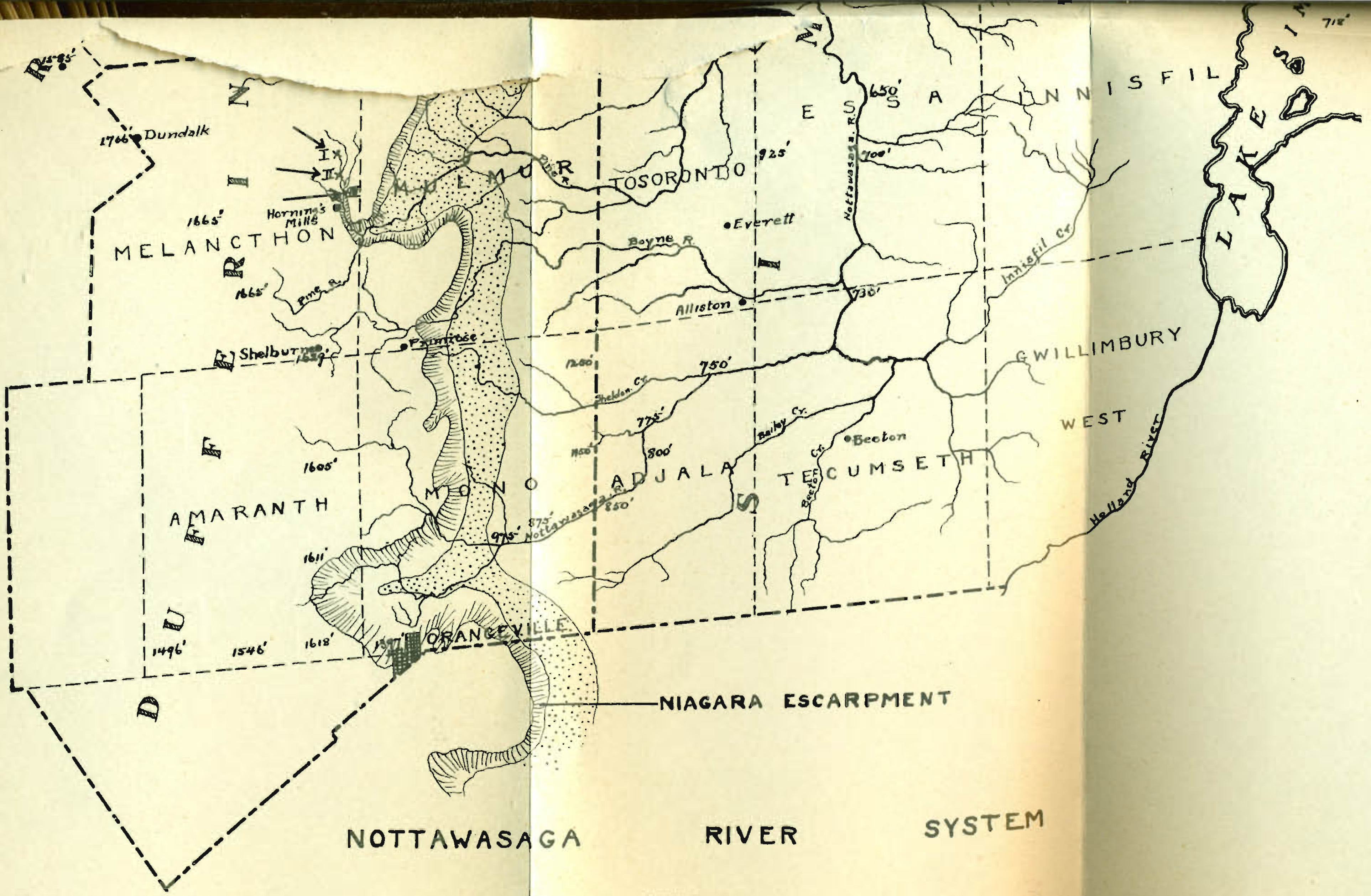
GRAPH 4.—The seasonal distribution of the different nymphal stages of *Leptophlebia adoptiva, L. mollis, L. guttata, L. debilis,* and *Habrophlebiodes americana* at stations 1, 2, 3, and 6, for the seasons 1931 and 1932 (1932 symbols have a small dot placed to the right). In this graph as in preceding ones the nymphal stages A to G are plotted as ordinates and the times on which collections were taken as abscissae. The sloping lines give some indication of the growth rates at the various stations.

PLATE X

GRAPH 5.—Shows the seasonal distribution of the different nymphal stages of *Stenonema tripunctatum* during 1930 and 1931 at stations A, B, C, and D. Symbols and plotting of stages A to J similar to those for *E. humeralis* (graph 1, plate III).

Pl. I.


GEORGIAN BAY
AFORD
MIDLAND
E
580'
Craigleith 599'
COLLINGWOOD
COLLINGWOOD
540
Y
707'
684'
Wasaga
FLOS
Marl L.
589'
Jacks L.
938
Duntroon
713'
Stayner
NOTTAWASAGA
700'
600'
Minnesing
Nottawasaga R.
SUNNIDALE
VESPRA
Little L.
Willow Cr.
Singhampton
C.D.
IV
V
Glen Huron
VI
E
OSPREY
McIntyre
B
1553'
Merton
Creemore
720
New Lowell
700'
Coates Cr.
BARRIE
SIMCOE
718'



NOTTAWASAGA RIVER SYSTEM

PLATE I

Fig. 1.

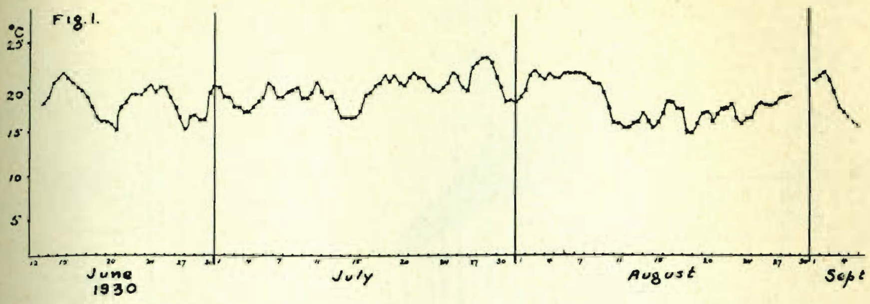


Fig. 2.

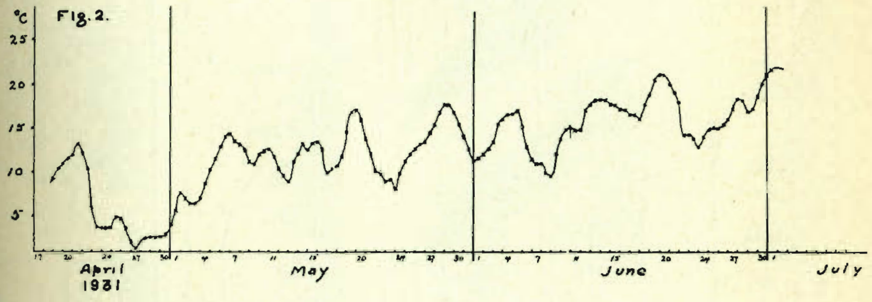


Fig. 3.

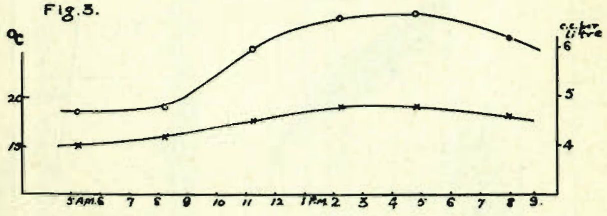


Fig. 4.

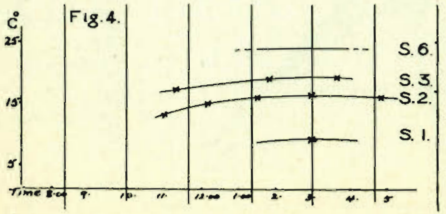


Plate II

Fig. 5

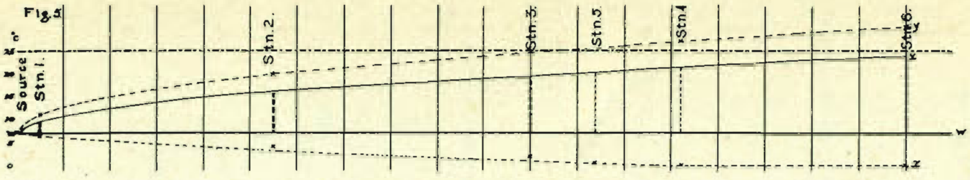
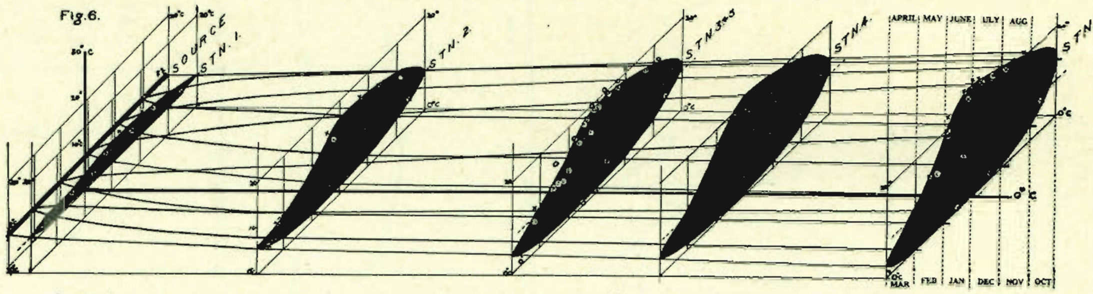


Fig. 6.



Graph. 1.

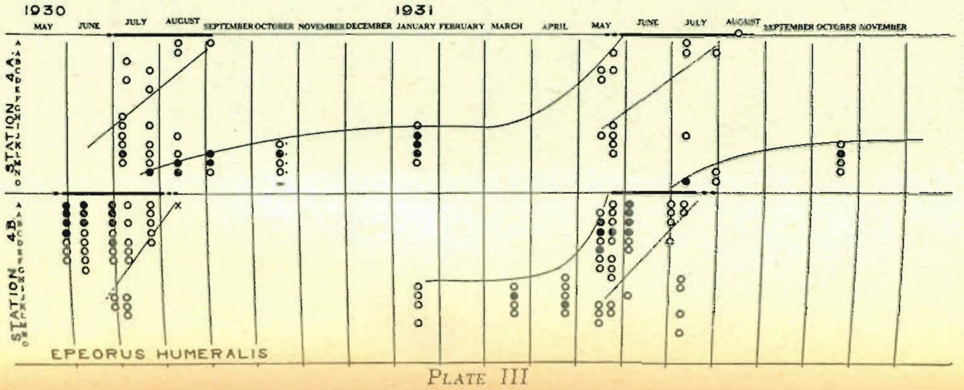
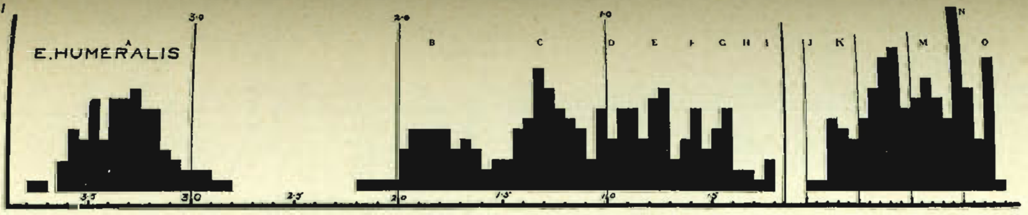
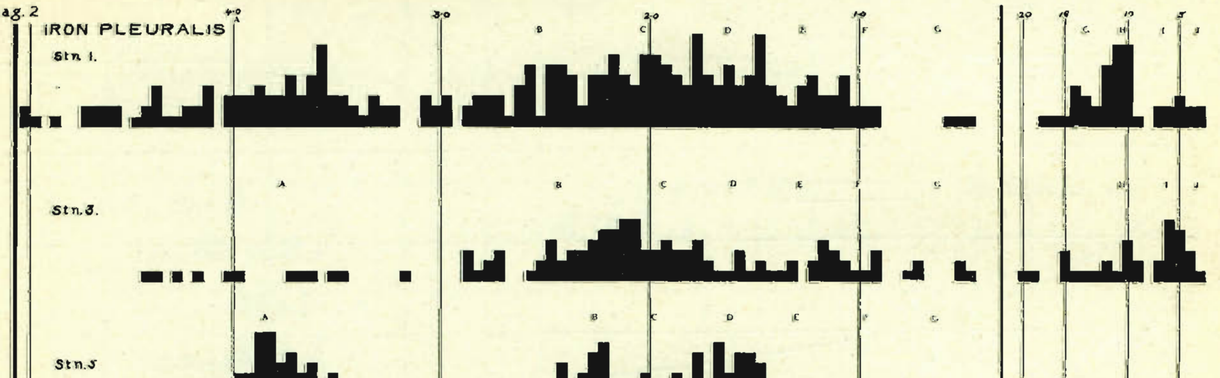


PLATE III

Diag. 1



Diag. 2



Diag. 3

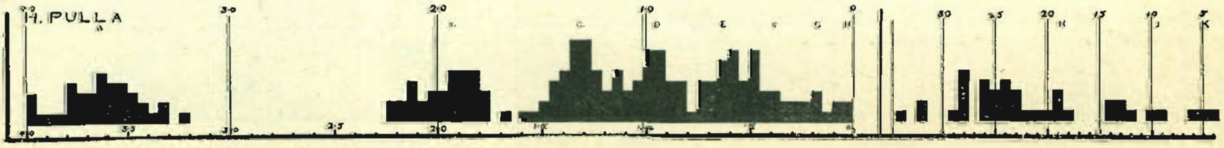


PLATE IV

Graph 24

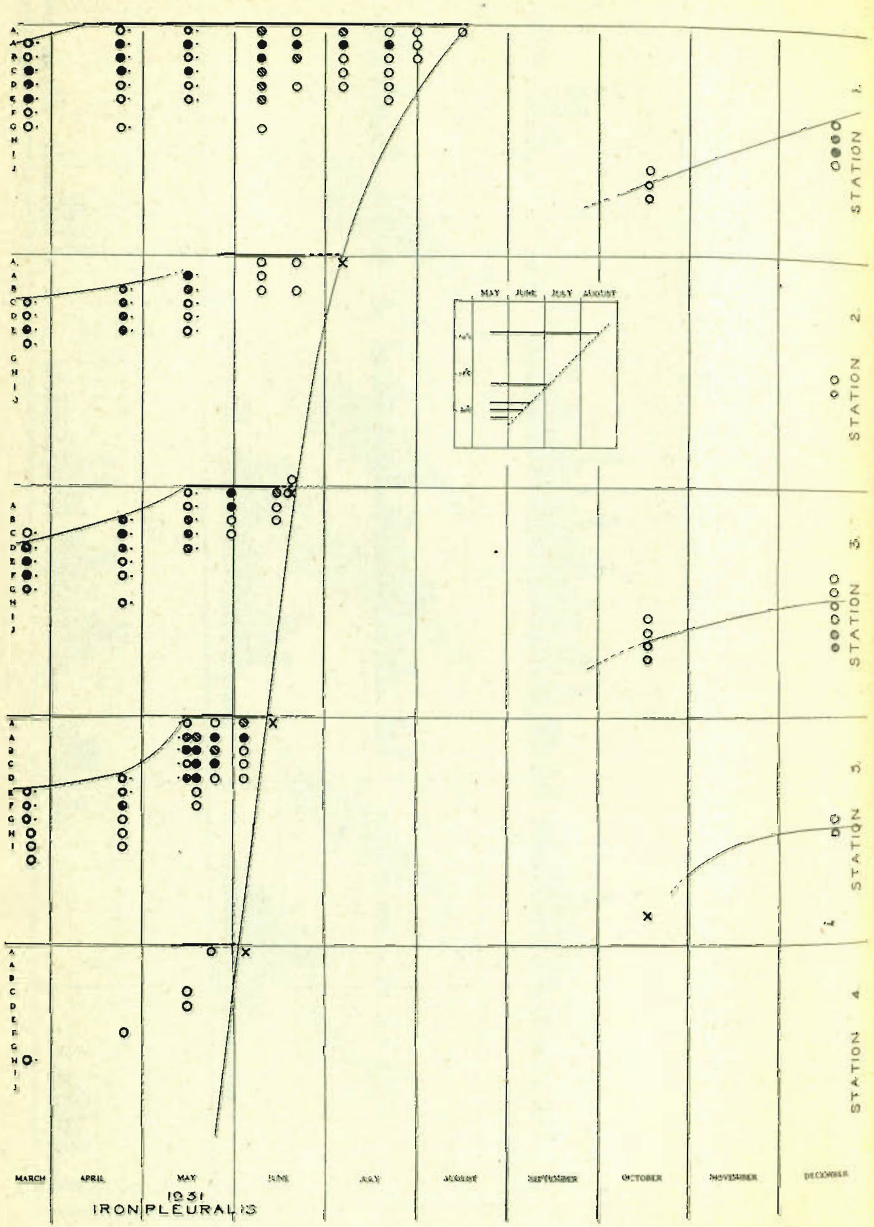


PLATE V

Diag. 4.

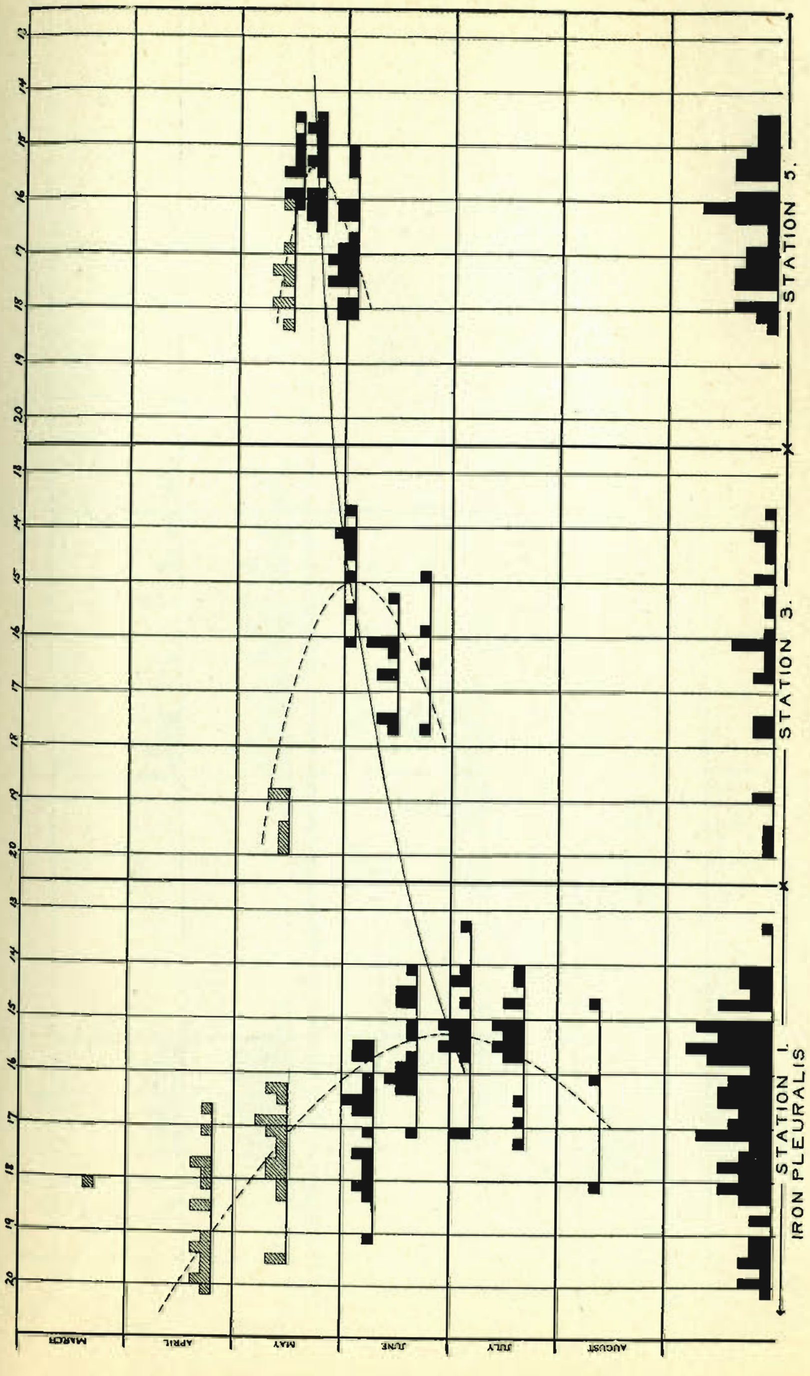
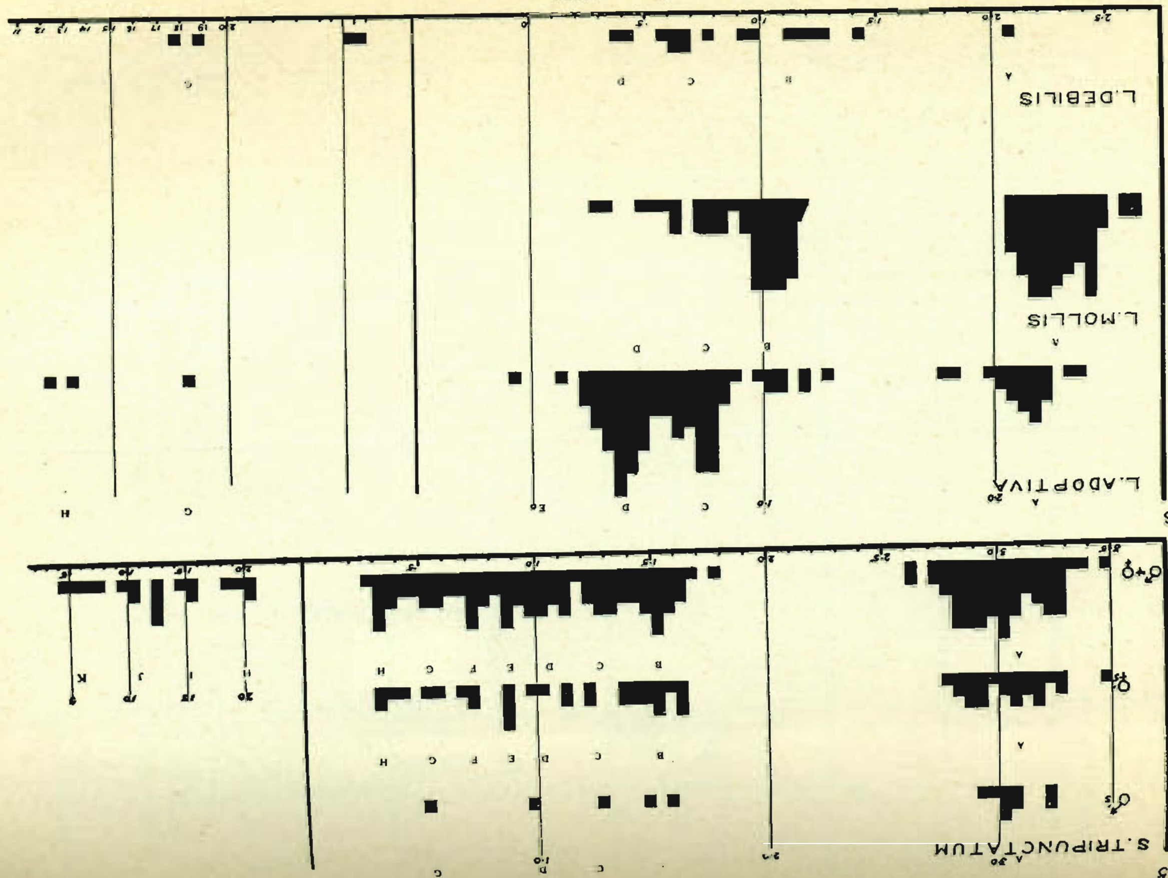


PLATE VI

PLATE VIII



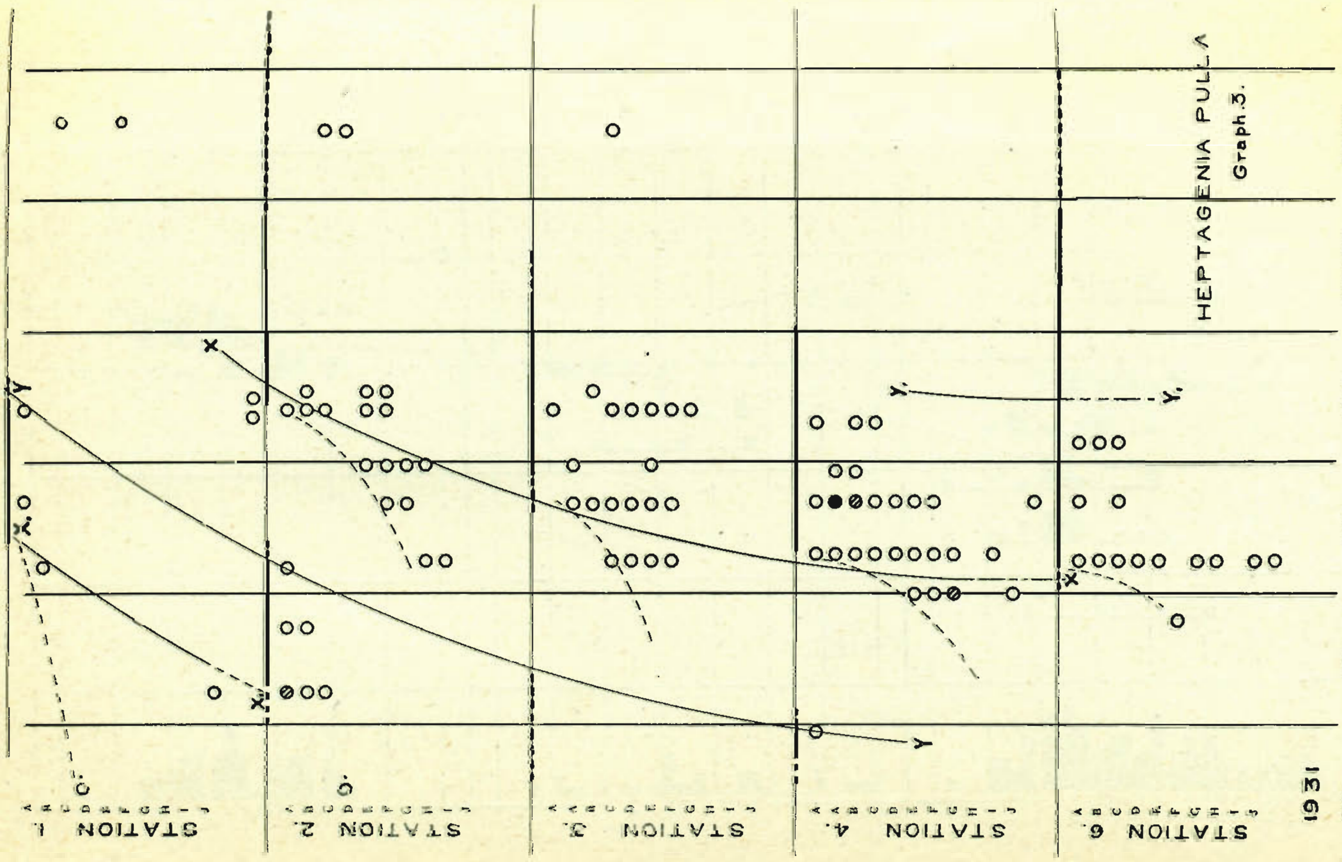


PLATE VII

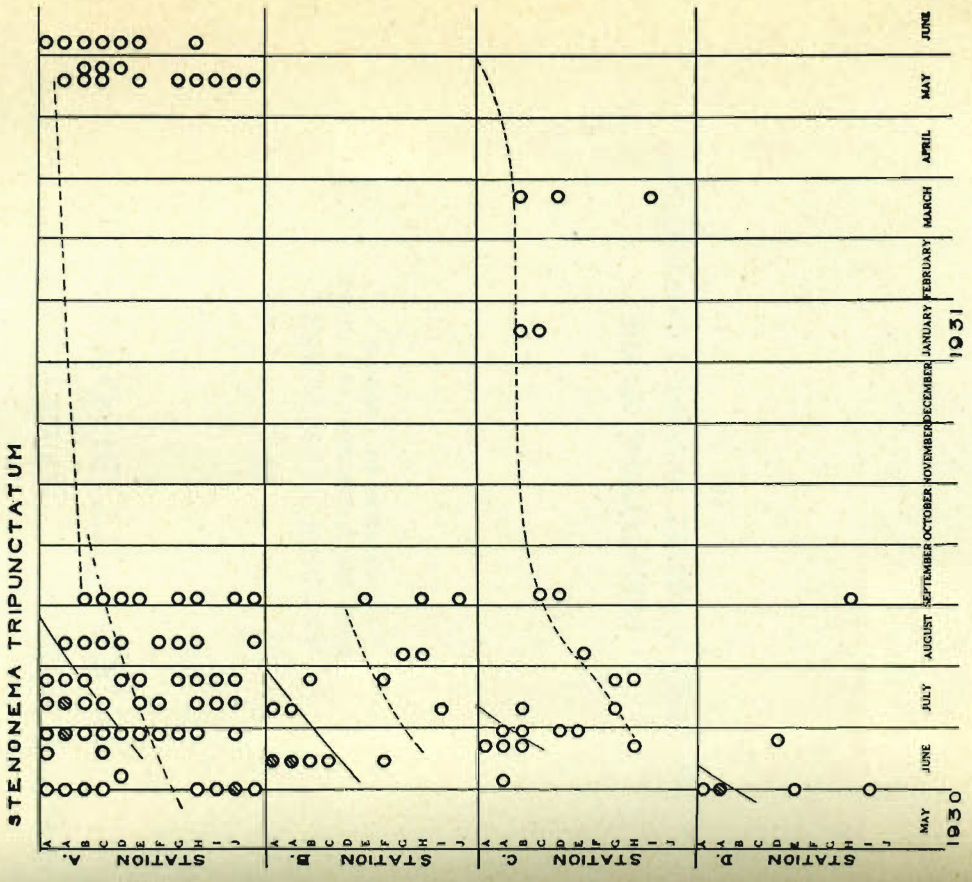


PLATE X

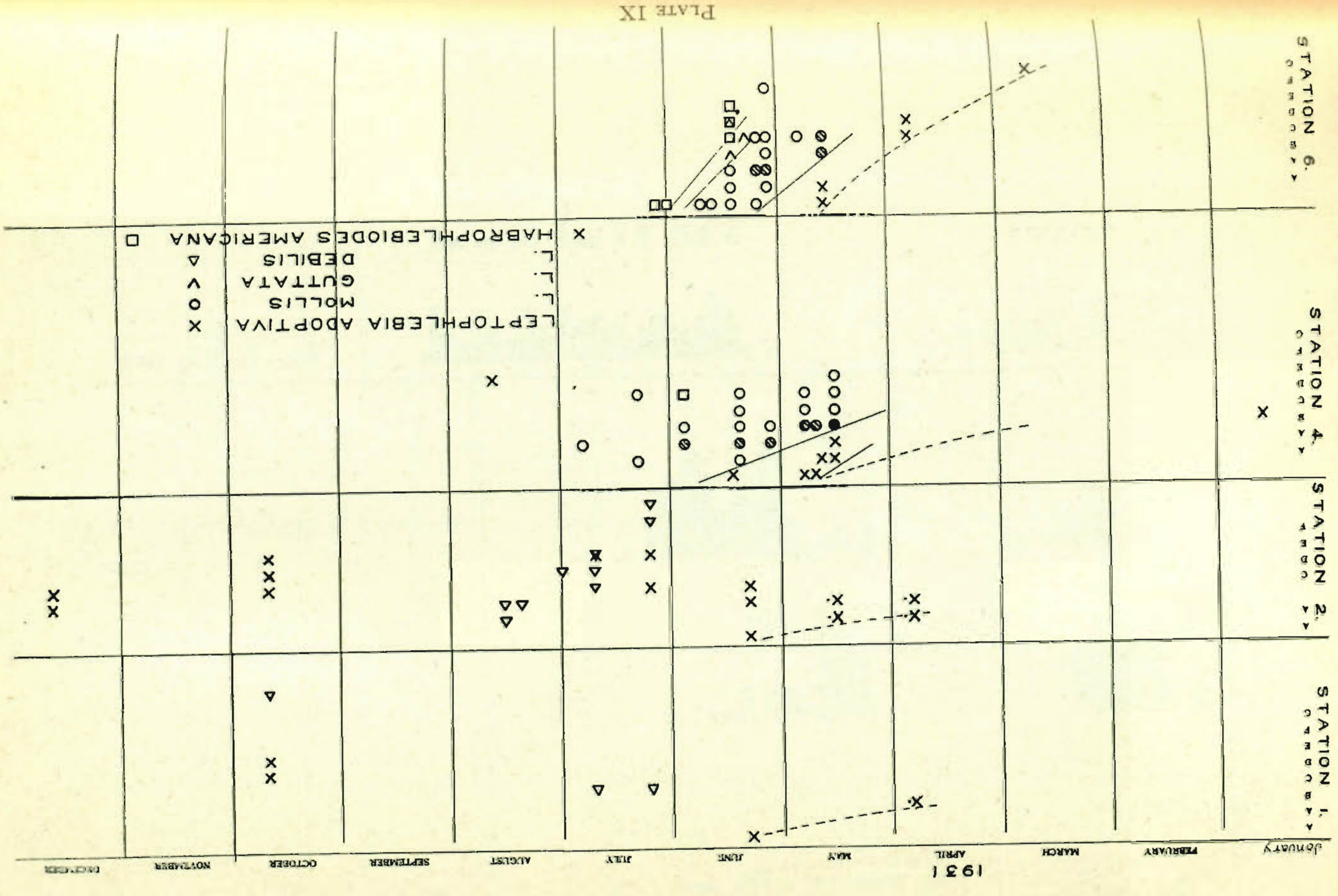


PLATE IX