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AN ECOLOGICAL INVESTIGATION OF STREAM INSECTS IN ALGONQUIN PARK, ONTARIO

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AN ECOLOGICAL INVESTIGATION OF STREAM INSECTS IN ALGONQUIN PARK, ONTARIO

ABSTRACT

The effect of several ecological factors on the qualitative and quantitative distribution of stream insects in Algonquin Park, Ontario, was determined from data obtained by use of the cage-trap method of sampling the emergence of insects from unit areas in streams, at regular daily intervals.

Incidents that induced significant alterations in the physical nature of the streams were accompanied by marked reductions in the total insect population and a change in the faunal composition of the affected areas. Such incidents included a severe freshet, cessation of flow and subsequent desiccation of the stream bed, and transformation of a shallow rocky riffle into a deep sedimented pool by construction of a beaver dam.

A correlation was found between the total number of species in rocky riffle areas at different distances from the source, and the average water temperatures. The linear distribution of species was delimited by the water temperatures obtaining in different sections of the stream and this was correlated with the thermal tolerance of the immature stages.

Within the limits set by temperature the distribution of species was affected by other factors including rate of flow and nature of the bottom, two factors which are closely interrelated and fundamentally inseparable. The diversity of the fauna decreased from rubble, through gravel, and muck, to sand as the variety of utilizable microhabitats decreased. The observed distribution on different types of bottom was related to habitat preference and associated morphological adaptations in the species.

The seasonal emergence periods of different species were segregated and the species emerged in the same sequence each year. The date of first emergence and the length of the emergence period of a species differed from year to year and were determined by annual variations in water temperature.

The diurnal emergence of species showed a similar segregation in general, in that any one species emerged at the same time each day while different species emerged at different times. The maximum total emergence from a rapids during mid-summer occurred throughout the evening hours and the most important causal factor involved seemed to be a reduction in light intensity.

It has been suggested that the number of individuals present in any area depends primarily on the utilizable surface area of bottom particles exposed to the water.

INTRODUCTION

Although the importance of aquatic insects in the economy of running waters has long been recognized it has not been until recent years that any intensive work has been done to determine the intimate relationship that exists between the various environmental factors obtaining in streams and the abundance, variety, and distribution of the associated insect fauna. A complete understanding of this relationship is essential for a full appreciation of the complexus of stream populations and a prime requisite for the successful application of any stream improvement policy.

Of the recent publications pertaining to the ecology of stream insects many have treated the biological data purely qualitatively, others quantitatively; few contain analyses of the data from both these viewpoints. There is a scarcity of literature on studies of the invertebrate fauna of streams in which observations have been made at frequent, regular intervals. Although it is not always practicable to carry out such detailed investigations, when these are performed the data obtained are of considerable value in allowing other workers to place the proper interpretation on the results of more casual surveys.

Further, in almost all the stream investigations to date the information has been obtained by sampling the population of bottom fauna. Various methods were used such as the hand-dip method of Ludwig (1922), the Needham square-foot trap (Needham, P. R., 1928), the Peterson trap (Peterson, 1911) and Ekman dredge (Ekman, 1911) used by Gersbacher (1937), the United States Bureau of Fisheries one-foot trap described by Surber (1936), the basket method of Wene and Wickliff (1940), and the circular square-foot sampler devised by Hess (1941), which has been found particularly useful in gravel and rubble areas.

The cage-trap method, which samples the insect emergence from unit areas in streams, was introduced by Ide in 1937 (Ide, 1940). This method was found to be readily adaptable to a wide variety of stream conditions and allowed the investigator to determine the turnover of bottom fauna, rather than merely the population, both qualitatively and quantitatively, at frequent regular intervals. Ide found that his method gave a much higher value for the quantity of bottom fauna present in an area than was obtained by means of bottom sampling.

Ide's method was used in the present investigation which was carried out during the summer months of 1938 to 1941, inclusive, on a section of the Madawaska river system in Algonquin Park, Ontario. Detailed ecological information was obtained on the hourly, daily, seasonal, and annual variations of insect emergence; the effect of an intermittent flow and subsequent desiccation on the insect population of a rapids; the influence of a sudden freshet and concomitant molar action on aquatic insects; the effect of a reduction in the rate of flow and accompanying sedimentation on the insect fauna of a rapids; the role played by temperature in limiting the distribution of species in rocky, riffle areas at various distances from the source; and the distribution of species on different types of bottom in a restricted section of a stream.

HISTORICAL REVIEW

The effect of an intermittent flow and stagnation on the distribution and survival of aquatic insects in a stream of the Panama Rain-Forest was studied by Allee and Torvik (1927), who concluded that pH and dissolved oxygen content of the water were likely the most important factors affecting the distribution. Stehr and Branson (1938) carried out an extensive ecological study of an intermittent stream in Ohio and found that the insect fauna was limited both in numbers and variety during periods of low water.

Many authors have reported marked reductions in bottom fauna following severe floods and freshets in various streams. Moffett (1936) determined the change in the bottom fauna of some Utah streams variously affected by erosion, and found that floods of eroding proportions definitely destroyed existing stream populations. In general, there was a rapid recovery following abatement of the flood. Stehr and Branson (1938) concluded that such areas were repopulated in several ways, including migration of both immature and adult forms, emergence of species from hibernation, and reproduction of species that succeed in holding their positions in the stream.

The role played by current in limiting the distribution of insects in streams has been investigated by many workers including Clemens (1917), Dodds and Hisaw (1924 a and b, 1925 a), Hubault (1927), Muttkowski (1929), and Hora (1930). These studies emphasize the adaptations to and utilization of the current by typical lotic inhabitants. Wu (1931) found that in general the Simuliidae (Diptera) had an "inherent current demand," as opposed to a requirement for a high concentration of oxygen, which limited their distribution. In his work on the function of the gills of mayfly nymphs from different habitats, Wingfield (1939) came to the same conclusion.

Temperature has been shown by several investigators to limit the distribution of stream insects. Dodds and Hisaw (1925 b) determined the altitude range and zonation of the species of Plecoptera, Ephemeroptera, and Trichoptera along the valley of South Boulder creek, Colorado. They found that temperature was the main climatic factor responsible for the observed zonation. Ide (1935) studied the effect of temperature on the distribution of Ephemeroptera in the Nottawasaga river system, Ontario, and determined that temperature sets limits to the distribution of these insects within which are other limits correlated with other environmental factors. Whitney (1939) investigated the thermal resistance of several species of Ephemeroptera from various habitats in a stream and found a direct correlation between the resistance of nymphs to high temperatures and the temperature obtaining in the respective habitats.

Investigations on the effect of type of bottom on the insect distribution in streams have been stimulated, in recent years, through the extensive research on stream improvement that has been carried out in North America. Valuable contributions in this field have been made by Needham, J. G. (1927), Needham, P. R. (1927, 1928, 1932, 1934), Carpenter (1927), Percival and Whitehead (1929, 1930), Pate (1931, 1932, 1933), Moore *et al.* (1934), Morofsky (1935), Tarzwell (1936, 1937), Surber (1936, 1938), Gersbacher (1937), Wene and Wickcliff (1940), Linduska (1942) and others. In general, the quantitative results of these investigations have shown a productivity gradient of bottom organisms related to the types of bottom, decreasing from plant beds and silt through rubble and gravel to sand and bedrock. The qualitative results have shown the existence of distinct habitat preference for specific types of bottom by the majority of stream insects.

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DESCRIPTION OF DRAINAGE AREA, STREAMS AND STATION SITES

Mud creek and its tributary waters are situated along the southeast boundary of Algonquin Provincial Park, Ontario, at 45 degrees 33 minutes north latitude and 78 degrees 15 minutes west longitude. The system extends for 8 miles in a general southerly direction from the headwaters at an altitude of 1,400 feet to its termination in Galeairy lake at an altitude of 1,281 feet, and drains an area of 6 square miles (Topographical Survey of Canada, 1934). Galeairy lake is drained by the Madawaska river which empties into the Ottawa river at the town of Arnprior.

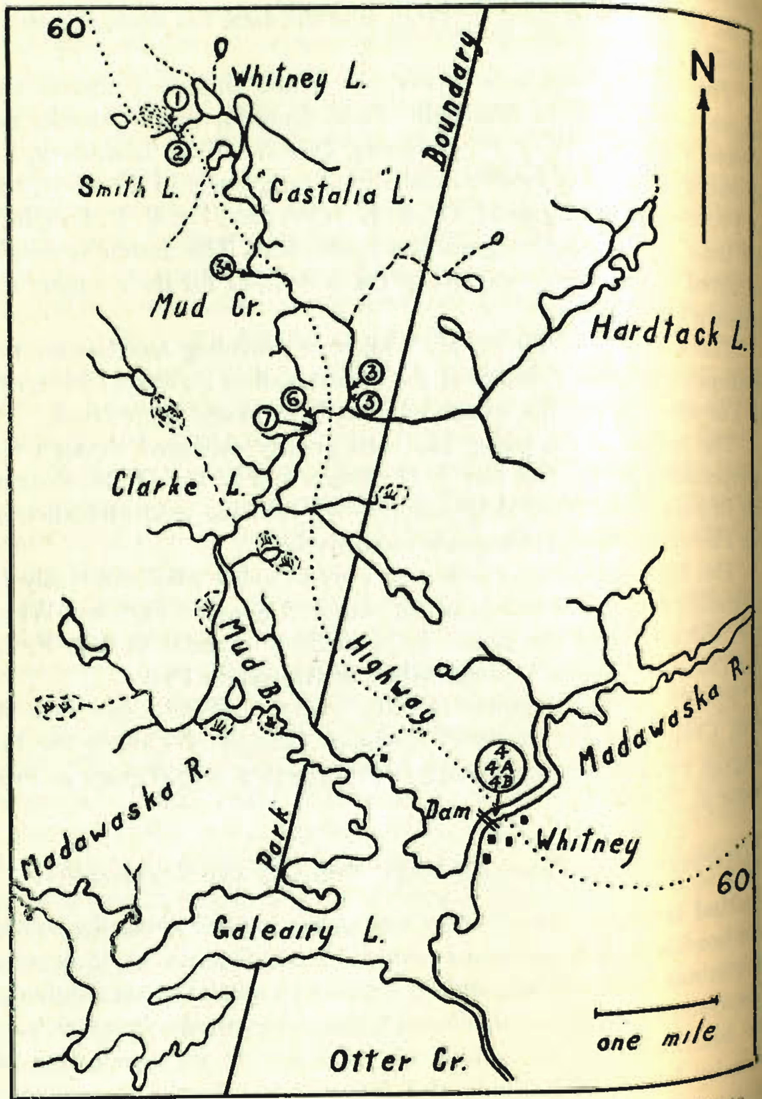

FIG. 1. Map of Mud creek drainage system. The numbers indicate the positions of the station sites used in the investigation.

The district in which Mud creek is located is part of the extensive pre-Cambrian shield area. The rock consists of masses of granitoid gneisses and light-coloured schists, characteristic formations of the Laurentian Period of the pre-Cambrian Era. This district is in the northern portion of the mixed conifer-hardwood forest. Prior to 1900 the area around Mud creek was heavily wooded with red and white pine, but at that time much of the original forest was cleared by intensive lumbering. In 1914 a devastating forest fire swept through this section and left it landmarked with charred rampikes which now jut characteristically here and there among the new growths of subclimax poplar and birch. On the exposed slopes, where the soil cover was thin, the fire burned through, baring extensive areas of rock, while the sheltered slopes and swamp sections were untouched and here considerable stands of conifers and hardwoods are still found.

The annual precipitation averages about 35 inches and this is evenly distributed throughout the seasons with the winter complement falling as snow. The average monthly mean temperatures range from 10 degrees Fahrenheit in January to 65 degrees in July.

Mud creek (figure 1) arises as the outlet of a small lake, 8 acres in area, which is surrounded by steep wooded hills. From its source the stream meanders 400 yards through an open beaver meadow and then widens into a small pond maintained by a beaver dam 8 feet high. The overflow and seepage water from the dam flow intermittently along a narrow rocky channel 3.5 feet wide with vertical banks 2 feet high. The banks support a dense growth of grasses and shrubs which shades the stream throughout most of the day. Station 1 (figure 2) was situated in this section of the stream, 50 yards below the beaver dam. This section of the stream dries up in midsummer in some years.

Station 2 was selected in a rocky riffle area 150 yards downstream from station 1 A small volume of cold water that flows continuously from a sheltered sphagnum bog and joins the stream 50 yards above station 2 provides a permanent flow. The flood channel at station 2 is 8 feet wide with sloping banks covered with grasses and shrubs but these are not dense enough to shade the stream completely during the afternoon period of each day. Extensive tufts of aquatic mosses, including *Fontinalis dalecarlica* Bry. Eur. and *Chiloscyphus fragilis* (Roth) Schiffn., trail in the current from the rocks at the water's edge. From station 2 the stream flows down a steep rocky decline and empties into Whitney lake.

Whitney lake has an area of 22 acres and a maximum depth of 34 feet. In addition to the small permanent stream described above, two intermittent streams that flow only during the spring and periods of heavy rain, empty into the lake. The water passes through a deep narrows into "Castalia" lake which is a shallow, elongate lake of 43 acres and has a maximum depth of 17 feet. One stream with a permanent flow empties into "Castalia" lake and the lake is also fed from Smith lake which has an area of 10 acres, a maximum depth of 25 feet, and one temporary stream flowing into it.

The water in all these lakes is distinctly brown and acid in reaction. There is a sharp thermocline at 15 feet during midsummer. The surrounding shores are characterized by wooded slopes alternating with low marshy areas which support dense growths of alder and various bog plants, while rooted aquatic plants are abundant in the shallow shore areas of the lakes.

From "Castalia" lake to Clarke lake Mud creek averages 10 feet in width and one foot in depth throughout most of the summer. There are frequent riffles where the stream flows rapidly over bedrock, rubble, or gravel, followed by short, deep pools with mucky bottoms. There are several beaver dams in this section which vary in size from mere obstructions to the main current to dams that flood an area as large as 4 acres. The stream is bordered with alder, birch, and poplar, with grasses and sedges at the water's edge. This vegetation protects the stream from direct insolation with the exception of the beaver ponds and wide parts of the stream. Four small streams join Mud creek in this section, three of which have a permanent flow. Stations 3a, 3, 5, 6, and 7 were selected in this part of the system.

Station 3a (figure 4) was situated 800 yards downstream from "Castalia" lake in the centre of a rocky riffle. The flood channel at the station was 8 feet wide with vertical banks which were covered with herbs and bushes. A few sedges occurred at the stream margin. The stream continued along a narrow rocky channel for about one mile and thence emerged into a large open meadow, through which it meandered in a deep, silted channel. The water flowed over a falls 7 feet high at the end of the meadow and passed down a short rocky rapids in which station 3 was established. The flood channel in this part of the stream was 18 feet wide. Station 5 was situated 20 feet downstream from station 3 in a deep placid pool in which the bot-

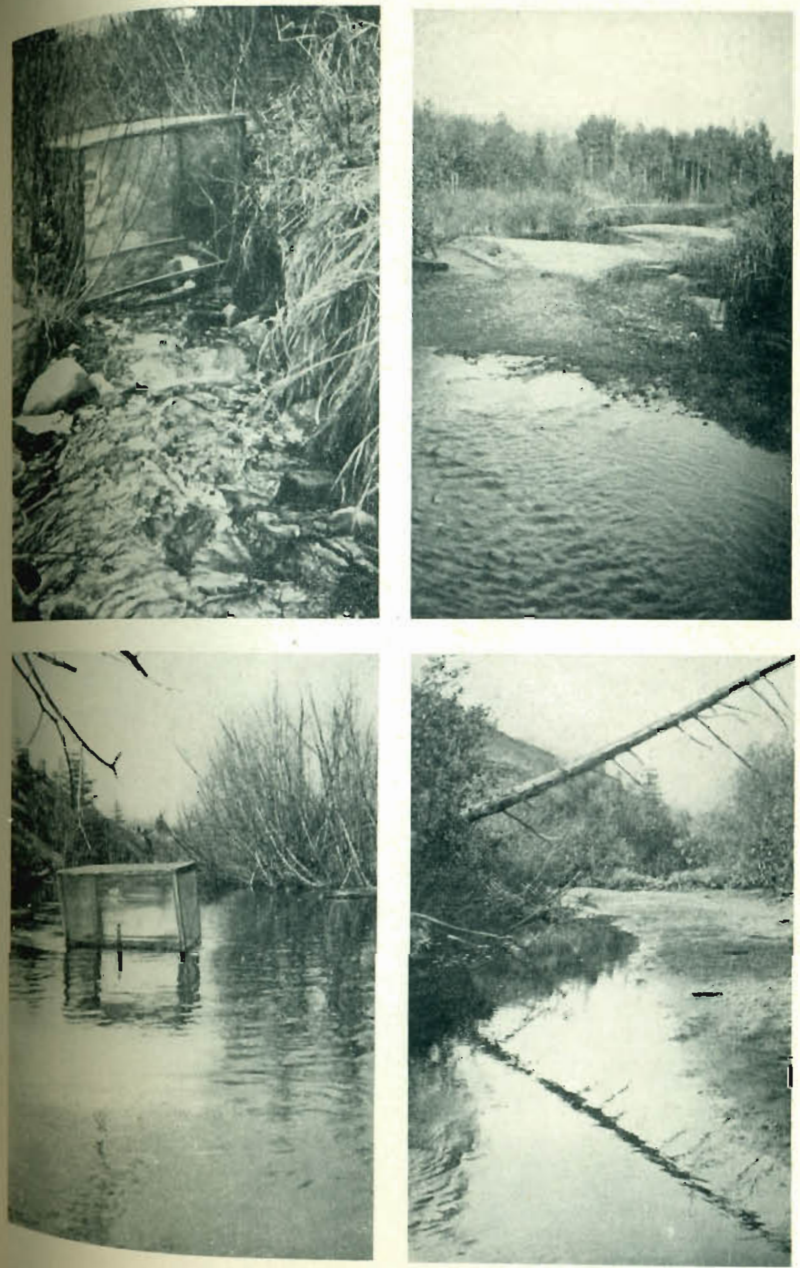

FIG. 2.—Illustrations of stations in the stream.
Upper left—Station 1, spring 1940.
Upper right—View of gravel bar below Station 6, summer 1940.
Lower left—Station 7, spring 1940.
Lower right—View of sand bar below Station 7, summer 1940.

FIG. 3.—The Madawaska river, spring 1940, looking northeast from the dam at Whitney, Ontario. Stations 4, 4A and 4B were established in the right foreground.

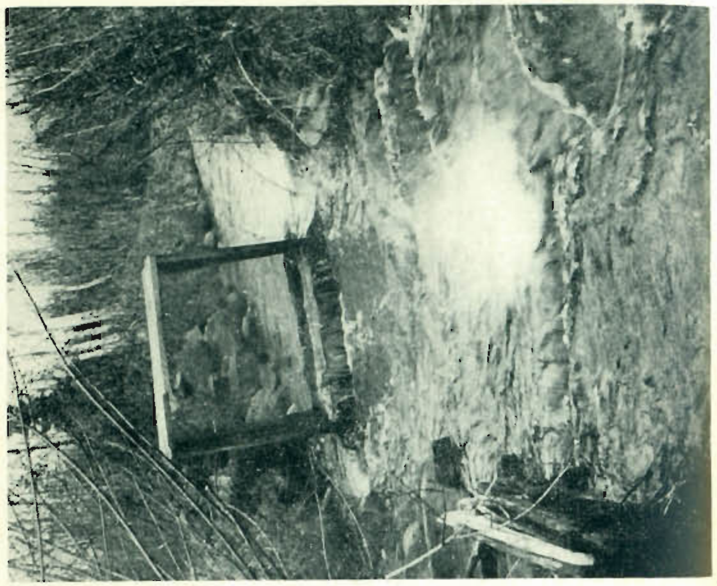

FIG. 4.—A cage-trap in position in the stream. Station 3a, May 10, 1940.

tom consisted of muck and decaying organic matter. Clumps of the sedge, *Carex rostrata* Stokes, were present in the stream but there were no clumps in the station site proper. From station 5 the stream flowed through a dense alder swamp for 400 yards and thence opened into a clearing and flowed down a long, shallow, gravel riffle in which station 6 was located. The flood channel was 16 feet wide and was full and flowing during the spring but the stream was reduced in the summer months and long gravel bars became exposed (figure 2). The banks were covered with herbs and grasses but these were too low to shade the stream during most of the day. Station 7 (figure 2) was located 200 feet below station 6 where the current was reduced and the bottom consisted of fine sand. The flood channel here was 14 feet wide and the banks were covered with grasses, herbs, and alders which effectively shaded this part of the stream. A wide sand bar was exposed here during the summer period of low water (figure 2).

Clarke lake has an area of 51 acres and a maximum depth of 38 feet. The water is dark brown, acid in reaction, and there is a sharp thermocline between 15 and 20 feet in the summer period. Three small permanent streams empty into the lake. From Clarke lake to Mud bay, Mud creek flows sluggishly through a thick alder swamp. The channel averages 4 feet in width and 3 feet in depth and the bottom consists of sand and gravel covered with silt and organic detritus. Mud creek empties into Mud bay through a wide marshy delta in which the stream is diverted into several channels.

Mud bay possesses a relatively narrow channel of open water which is bounded for 200 yards on either side by shallows with numerous stumps and deadheads rising above the water surface. The water level in Galeairy lake is maintained by a dam constructed across the Madawaska river at the town of Whitney. This has flooded Mud bay and Mud creek back as far as Clarke lake so that it seems probable that the stream originally flowed directly into Galeairy lake.

Stations 4, 4a, and 4b were located in the Madawaska river (figure 3) immediately below the dam in a large rocky rapids. The volume of flow through the sluices of the dam was so great that the stations had to be selected to one side of the main current. The flood channel of the river is 150 feet wide and is strewn with large boulders many of which measure 10 feet in diameter. Small stands of poplar and birch, alder clusters, grasses and shrubs cover the river banks, but because of the width of the channel the stations were exposed to direct sunlight throughout most of the day.

The Madawaska river is representative of the large river conditions found in Algonquin Park while Mud creek is representative of the smaller streams so numerous in this district.

PHYSICO-CHEMICAL CONDITIONS

The station sites were selected to provide information on specific phases of the ecology of stream insects. Stations, 1, 2, 3a, and 4 were chosen in the centres of rocky riffles, throughout the length of the river system, in order to minimize the effect of factors other than distance from the source on the insect distribution. In a like manner, stations 5, 6, and 7 were selected in a short section of Mud creek,

TABLE 1.—Average physical and chemical conditions at the stations in the summer of 1938. The figures represent the average of six determinations made on June 17, July 16 and 30, August 11 and 26, and September 9, with the exception of those for the oxygen content, percentage saturation and hydrogen ion concentration at stations 5, 6, and 7 where a single water analysis was made on August 12.

	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6	Station 7
Type of bottom....	Rubble	Rubble	Rubble	Rubble	Muck	Gravel	Sand
Width in feet	1.3	5.8	12.8	85.0	12.5	8.7	9.7
Depth in inches	1.6	3.3	5.7	21.5	14.9	6.7	12.6
Rate of flow in feet/sec.	0.1	0.4	0.9	2.3	0.1	0.8	0.3
Volume of flow in cu. ft/sec..	0.1	0.5	4.8	288.0	1.9	4.0	3.2
Colour.....	69	56	115	32	...	...	...
Dissolved oxygen in cc/l......	6.7	7.6	6.6	6.4	6.9	6.3	6.3
Percentage saturation.	91	97	93	99	91	92	92
Hydrogen ion concentration ...	6.1	6.2	6.6	6.4	6.7	6.5	6.5

close to station 3, where different types of bottom prevailed so that the effect of factors other than type of bottom would be minimized. Sations 4a and 4b were established beside station 4 in an extensive rapids where all conditions were apparently identical.

Observations of certain physical and chemical properties of the water, including rate and volume of flow, colour, oxygen content, and pH, were made only at intervals throughout the investigation, while the depth of water at station 3 and the water temperature at each station were recorded daily.

To illustrate representative water conditions at the stations, table 1 has been prepared from determinations made during the summer of 1938. The values in the table are the averages of six observations made on June 17, July 16 and 30, August 11 and 26, and September 9, with the exception of the pH, oxygen content and percentage saturation at stations 5, 6, and 7 for which the values represent the results of a single water analysis made on August 12. Station 3a, 4a, and 4b are not included in the table since these were not in operation in 1938. However, from observations made in later years, it was found that the conditions at station 3a approximated those at station 3, and at stations 4a and 4b were identical with station 4.

Apparatus and Methods

The water temperature was recorded continuously at station 3 by means of a Negretti and Zambra distance recording thermometer which was in operation in each of the three years. The temperatures at all other stations were obtained from maximum-minimum or hand thermometers. Daily readings were made at the times the stations were visited. All times referred to are Eastern Daylight Saving Time.

The depth of water was recorded daily at station 3. This was determined from a stake graduated in inches which was driven into the stream bed with a zero mark at the surface of the bottom particles. Occasional records of depth were made at all other stations by determining the average of several direct measurements made with a yardstick.

The rate of flow of water was obtained in 1938 by submerging a paddle, attached to a spring, to a standard depth and reading the value from a graduated scale along which the paddle was deflected by the current (Solman, 1939). This apparatus was calibrated so

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that the readings could be converted into rate of flow in feet per second. In the succeeding years the rate was determined by recording the average time required for a small piece of wood to traverse a measured distance in the stream.

The volume of flow was calculated from the equation of Embody (1927) which contains a factor for correction of "bottom drag."

The colour of the water was determined by comparison with a series of coloured glass plates which had been calibrated against a set of platinum cobalt standards (U.S. Geological Survey, 1902).

TABLE 2.—Periods during which collections were made at the stations in 1938, 1939, 1940, and 1941.

Station number	1938	1939	1940	1941
1	May 31 - Sept. 18	May 17 - Sept. 11	......	......
2	May 25 - Sept. 18	May 17 - Sept. 11	May 11 - June 30	May 8 - June 30
3	May 25 - Sept. 18	May 17 - Sept. 11	May 12 - Aug. 31	......
3a	......	......	May 11 - Aug. 31	May 8 - June 30
4	June 6 - Sept. 18	May 17 - Sept. 11	May 25 - July 22	......
4A	......	......	......	July 3 - July 13
4B	......	......	......	July 3 - July 13
5	June 29 - Sept. 17	June 6 - Sept. 11	June 1 - Aug. 31	......
6	June 29 - Sept. 17	June 6 - Sept. 11	May 12 - Aug. 31	......
7	June 29 - Sept. 17	June 6 - Sept. 11	May 11 - Aug. 31	......

The dissolved oxygen was determined by Miller's method as described by De Laporte (1920). The percentage saturation of the water was obtained from Roscoe and Lundt's table; no correction was made for variations in atmospheric pressure.

The pH was determined by means of a Lamotte optical comparator (Lamotte Co., Baltimore, Md.).

Oxygen

The water at all the stations was well oxygenated throughout the summer season with a general increase in the dissolved oxygen content occurring during the latter part of August and into September. In 1938 the values ranged from 5.6 cc/1 at station 1 on June 17, to 9.8 cc/1 at station 2 on September 9. The dissolved oxygen content of the water at station 2 was consistently higher than that at

the other stations and probably resulted from the photosynthetic activity of aquatic mosses which covered the rocks at the station site.

The percentage saturation in 1938 ranged from 84 at station 3 on July 16, to 112 at station 2 on September 9; the average summer value at each station approximated complete saturation.

Hydrogen Ion Concentration

The water at all the stations was acid in reaction with a range of 6.1 to 6.7 recorded during the summer months of 1938.

Type of Bottom

The bottom at stations 1, 2, 3a, 4, 4a, and 4b consisted of rubble and rocks overlying coarse gravel. Station 3 was characterized by this same type of bottom during 1938 and up to the end of June in 1939. However, at this date beavers constructed a dam across the stream, 100 yards below the station, which reduced the rate of flow and altered the nature of the bottom since sand, silt, and organic detritus were deposited among the rubble as the transporting power of the stream was reduced. This condition persisted throughout the remaining years of the investigation.

A thick layer of soft muck constituted the bottom at station 5 and was made up of fine inorganic particles along with a considerable amount of decaying plant remains. Station 6 was selected on a gravel bottom with the individual pebbles averaging about ¾ of an inch in greatest diameter. The bottom at station 7 consisted of fine sand of which 10.9, 72.6, 15.9, and 0.6 per cent was retained in number 10, 40, 80, and 200 standard sieves, respectively.

Flow

A permanent flow of water was maintained at all the stations during the four summers of the investigation with the exception of station 1 where an intermittent flow occurred in the midsummer of 1938.

The rate and volume of flow at the riffle stations increased downstream from the source region, represented by stations 1 and 2, to the lower, large river region of the system which was represented by station 4. The rate and volume of flow at stations, 5, 6, and 7 were directly related to the types of bottom existing at the respective sites. The lowest values at all seasons were recorded at station 5 and increased through station 7 to station 6.

Maximum conditions of flow prevailed at all the stations during the spring flood period in May of each year. After the flood the flow gradually decreased and minimum values generally were recorded in late July and early August, although this depended largely on the weather. Severe thunderstorms or prolonged periods of steady rain induced secondary maxima of short duration which simulated the spring flood in the small source streams.

Depth

In general the average depth of water at the stations increased as the distance from the source region increased. The lowest value was recorded at station 1 and the depth increased through stations 2, 3a, 3, and 4 under normal conditions. The depth at stations 5, 6, and 7, which were characterized by different types of bottom, decreased from station 5 through station 7 to station 6 as the size of the bottom particles increased.

A typical record of the seasonal change is shown in figure 1, Sprules (1941). There is a rapid decrease during May as the spring run-off subsided, followed by a long period of steady decrease in the summer months during which time minor fluctuations occur, dependent on local rainfall. A slight increase in depth was observed in the early fall season which was probably related to the decreased rate of evaporation.

Colour

The water at all the stations was brown, a condition which exists in most waters of this region. The values obtained from water samples taken during the summer of 1938 ranged from 27 at station 4 on August 11, to 145 at station 3 on July 16. The average summer values for 1938 ranged from 32 at station 4 to 115 at station 3. The relatively high values found at station 3 probably resulted from an increased amount of dissolved material added to the water as it meandered through the open meadow above the site of the station.

Temperature

The water temperature at each station was determined once a day, in most cases, at the time the station was visited. Thus a direct comparison of the temperatures at the different stations could not be made, as there was an average time lapse of about 3 hours between the times at which the first and last stations were visited each day. In order to minimize the effect of this difference in times of observation, the average of all the temperature readings obtained from a station for a complete summer was determined, along with the average time at which these readings were made. The average summer temperature at station 3, for the same time of day, was determined from the charts of the constant recording thermometer which was in operation at this station throughout the four years of the investigation. The difference, in degrees Fahrenheit, between the average summer temperature at each station at a specific time of day and the average summer temperature at station 3 for the same time of day, was determined for each year. The average of these differences has been used to obtain an index of the temperature relationships of the stations.

The average summer water temperature at the rocky riffle stations which were selected at different distances from the source, increased downstream from station 2 through stations 3a and 3 to station 4. For the complete period of the investigation the average temperature at station 3 was 62.0 degrees Fahrenheit. The temperature at station 2 averaged 6.1 degrees lower than station 3, station 3a averaged 1.7 degrees lower than station 3 and station 4 averaged 5.4 degrees higher than station 3. Although station 1 was located close to station 2 in the upper section of the stream, the average temperature was only 1.3 degrees lower than that at station 3. The relatively high temperature prevailing at this station, when its position with respect to the source is considered, was dependent on the intermittent nature of the flow at the station.

The average temperature differences between stations 3, 5, 6, and 7, which were selected close together in one section of Mud creek, were small. The temperature at stations 6 and 7 averaged 0.2 and 0.3 degrees Fahrenheit higher than station 3, while at station 5 the average temperature was 0.4 degrees lower than that at station 3.

The largest diurnal temperature fluctuations were recorded at station 3 during the latter part of July and early August each year and amounted to 17.5 degrees Fahrenheit in some instances. The diurnal fluctuations at station 2, which was situated close to the source, and at station 4 where there was a much larger volume of water, were smaller than at station 3. The maximum water temperature recorded during the investigation was 85.0 degrees Fahrenheit which occurred at station 3 on August 16, 1938. Although the average summer temperature at station 4 was greater than that at station 3, the maximum temperature found at the former station was only 79.5 degrees Fahrenheit.

The same seasonal trend of water temperature prevailed at all the stations and consisted of a rapid increase during May followed by a prolonged period of more or less constant high summer temperature and a rapid decrease in September. The temperature at station 2 was lower than at station 3 at all seasons although a much greater deviation occurred in the summer months than in the spring or fall. The average temperature at station 4 was, in general, higher than that at station 3 but during May each year the converse relationship existed resulting from the greater volume of water to be heated at the former station.

In order to obtain an index of the annual temperature variation in the stream, the accumulated temperature above 32.0 degrees Fahrenheit was determined for station 3 from June 1 to September 13 each year by summing the average of the daily maximum and minimum temperatures. Although the total accumulated heat varied significantly from year to year when the values at some particular date during the summers were compared, it was found that the total accumulated heat acquired by the stream over a long period showed little annual variation. Values of 3,470, 3,450, 3,240 and 3,470 day-degrees were obtained in 1938, 1939, 1940, and 1941, respectively. It is probable that the small annual differences observed would be reduced if the early spring and late fall temperatures, from ice breakup to freeze-up, were included in the compilation of these figures. Thus it would seem that the total heat budget in any specific section of a stream shows little annual variation although the seasonal disposition of the heat may vary considerably from year to year depending on annual climatic differences.

Biological Conditions

Apparatus and Methods

The cage-traps (figure 4) used in this investigation were introduced by Ide in 1937 (Ide, 1940), and have been used by him in similar stream studies since that time.

In general, collections were made daily but during the summer of 1938 the cages at stations 5, 6, and 7 were left in position in the stream but were visited on only two consecutive days each week. In this latter case the cages were cleared the first day and a collection made the second day which thus represented the insect emergence for the preceding twenty-four hour interval. Further modifications of the general method were used at stations 4, 4a, and 4b, where occasional diurnal series of collections were made in 1939, 1940, and 1941. These collections were made at one-, two- or four-hour intervals for a twenty-four-hour period.

In the examination of the collections the Plecoptera, Ephemeroptera, and Trichoptera were identified with species whenever possible. These orders were selected for specific determination since they constituted by far the greatest volume of material in the collections. The remaining aquatic insects collected were identified with family only. In the ensuing discussions of the quantitative distribution, the total insect emergence has been considered under six separate headings, the Plecoptera, Ephemeroptera, Trichoptera, Chironomidae (Diptera), Simuliidae (Diptera), and "Miscellaneous." The last heading is composed of a heterogeneous assemblage of insects which occurred in relatively small numbers in the collections and includes Empidae (Diptera), Ceratopogonidae (Diptera), Tipulidae (Diptera), Hemerobiidae (Neuroptera), and Coenagrionidae (Odonata) for the most part.

Sources of Error

There are several sources of error associated with the cage-trap method of collecting aquatic insects. Many of these have been pointed out by Ide (1940). These, briefly, are the introduction of biting insects on the person of the collector, the drifting in of occasional terrestrial forms, passage of small species through the mesh of the cage, reduction in numbers after emergence by the predation of spiders and Empidae, occasional escapes when the cage door is open, shading of the enclosed area, and possible destruction of the aquatic stages through disturbance of bottom when the collector moves about.

Precautions were taken to reduce those errors as much as possible. The population of biting insects was taken as double the number of males, which do not bite and thus are not likely to have entered on the collector. Terrestrial insects were disregarded. The cage was tapped to free the door of insects before it was opened. A seat was constructed in one corner of the cage to reduce the necessity of disturbing the bottom.

Certain observations were made during the current investigation which supplement the previous findings. Ide's estimate of 200 as the probable maximum number of Simuliidae to be carried into a cage during a season appears to be low for some situations. A new estimate of the number of insects to enter a cage in this way was obtained from analyses of the collections made at station 5 in 1939 and 1940. This station was characterized by deep, quiet water and a mucky bottom while the larvae and pupae of Simuliidae are found in general in shallow, swiftly-flowing sections of a stream with a rocky bottom. No male individuals were found in the collections while a total of 548 and 826 females were collected in 1939 and 1940, respectively, the majority in both years occurring in the month of June. Under the circumstances it may be taken that virtually all these individuals were carried into the cage by the collector.

The modification of the method of taking daily collections used in 1938 (page 30) created an error in the total number of insects collected at station 6 in that year. A total of 1,942 insects were collected of which 1,753 were Chironomidae (Diptera). These numbers are in error since for a short period in midsummer the number of Chironomidae present the day the cage was cleared each week was so great that these could not all be removed in the time available to complete the collection. Thus, although the collector concentrated on the removal of the representatives of the other insect groups and succeeded in removing all these, a certain number of Chironomidae were left and these augmented the number of insects collected the following day. This particular instance was the only one in which such a discrepancy arose since at all other stations the clearance from the cages was complete each day.

A previously unrecognized error which results from the practice of collecting from the cages only once each day was brought to light from the results of a diurnal series of collections made at the site of station 4. This error is perhaps the most significant of all. In 1939, two series were run at two-hour intervals, the first from 11.00 a.m. August 4 to 11.00 a.m. August 5 and the second during the same

hours on August 14 and 15. In 1940, a similar series was run on July 4 and 5. The results of these collections showed that the number of insects collected over a twenty-four-hour period during which

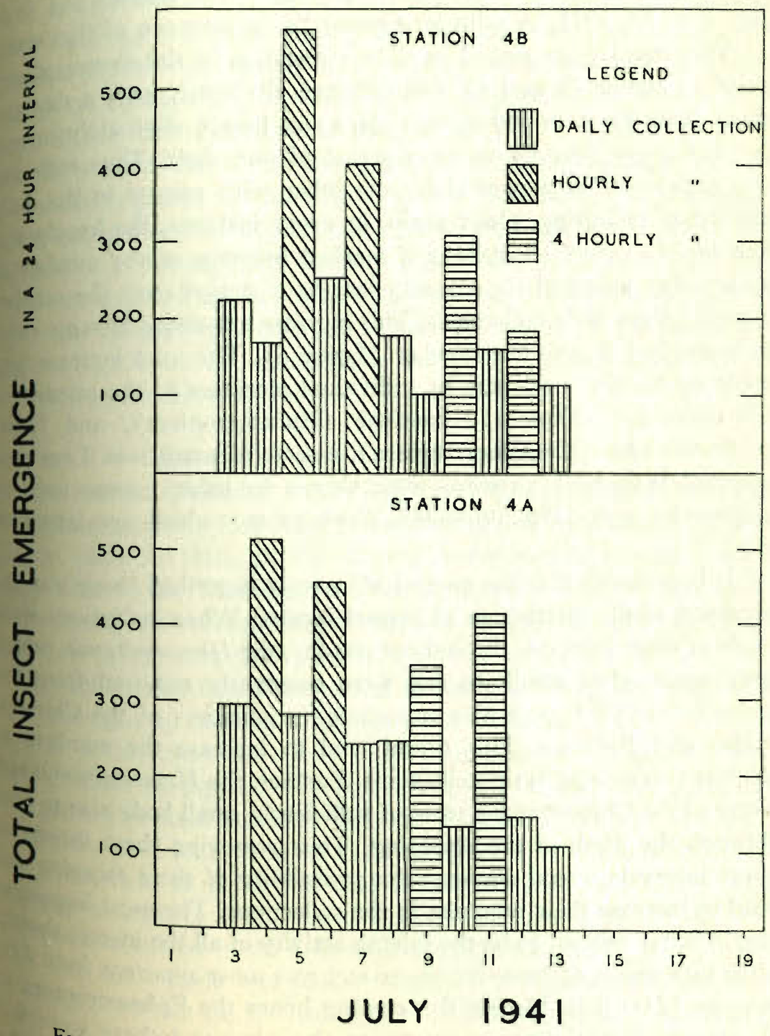

FIG. 5. The total insect emergence for twenty-four-hour periods at stations 4a and 4b from July 3rd to 13th inclusive, 1941, showing the results of collecting the cages once a day, every hour and at four-hour intervals.

collections were made at two-hour intervals was more than double the number obtained when only one collection was made in twenty-four hours.

A somewhat more elaborate experiment was carried out from July 3 to 13, 1941, to estimate further the importance of this error.

Two cages were placed in close association in the stream, designated as station 4a and 4b, and collected alternately once a day and every hour for a period of four days and thence alternately once a day and every four hours for a period of four days. Thus each day one cage acted as a control for the other with respect to the daily method of collecting. Once again, in every instance, the hourly and four-hourly collection showed a marked increase in the number of insects that emerged in a twenty-four-hour period over the number obtained from daily collections. This increase amounted in some cases to more than double the number (figure 5). The total increase was made up for the most part by individual increases in the number of Chironomidae (Diptera), Baetinae (Ephemeroptera), and *Hemerodromia spp.* (Empidae, Diptera), insects of small size. Less pronounced numerical increases were shown by other groups such as *Chimarrha spp.* (Philoptomidae, Trichoptera) which are larger in size.

It is probable that the numerical increase described above was the resultant of the interaction of several factors. When collections were made at short intervals throughout the day, the *Hemerodromia*, which prey upon other small insects, were constantly removed from the cages before they were able to reduce the numbers of the Chironomidae and Baetinae. This would tend to increase the numbers of the last two groups in the collections. Further, the *Hemerodromia* and many of the Chironomidae were of sufficiently small body size to pass through the mesh of the screening. Thus removing these insects at short intervals would decrease the probability of their escaping and tend to increase their numbers in the collections. The most important single factor seemed to be the intense activity of all the insects shortly after they emerged from the water and was most apparent from 7.00 p.m. to 12.00 p.m. During the evening hours the Ephemeroptera in the cages were almost constantly on the wing and these were followed later by the Chironomidae and Trichoptera, which showed the same phenomenon. This activity caused many insects to fall to the

water surface and be carried out of the cages by the current. Collecting at short intervals reduced this possibility and tended to increase the numbers of all the groups in the collections.

It is desirable that a correction factor be established to meet the error resulting from the causes discussed and perhaps others responsible for the discrepancy between the results shown by daily and more frequent collecting methods. This is impossssible at present as a result of the limited amount of data at hand. The diurnal series of collections have shown that the quantitative results obtained in this stream investigation are too low to give a true picture of the actual insect emergence that occurred at the stations. However, since the methods of collecting used fall into a standard pattern, the number of insects collected at each station is probably uniformly relative to the actual number that emerged. Thus the results of the investigation are significant for comparative purposes without application of a correction factor for this error.

The Diurnal Emergence of Insects from a Rapids

The method of making collections from cages at frequent intervals throughout a twenty-four-hour period, which has been discussed previously, provided data on the diurnal emergence of insects from a rocky riffle in the Madawaska river. A detailed analysis was made of the hourly collections taken at stations 4a and 4b from 11.00 a.m. July 3 to 11.00 a.m. July 7, 1941.

In each twenty-four-hour period the hourly emergence was small from midnight up to an hour or two prior to sunset (figure 6). During this period there were only minor fluctuations in numbers, with the minimum emergence occurring between 3.00 and 6.00 p.m. The emergence increased suddenly between 7.00 and 9.00 p.m. and built up rapidly to a maximum at 11.00 p.m. This was followed by an abrupt decrease at 12.00 p.m. and thence returned to the low early morning emergence level. An average of 60 per cent of the total emergence occurred in the four-hour interval between 8.00 and 12.00 p.m. The same cycle was found in the diurnal collections made at two-hour intervals in 1939 and 1940 and at four-hour intervals in 1941.

The separate insect groups showed differences in the time of maximum emergence during a twenty-four-hour period. The Ephemeroptera emerged, for the most part, between 7.00 and 10.00 p.m., although occasional individuals were obtained in the collections made during the late morning hours and early afternoon. The maximum emergence of Trichoptera and Chironomidae occurred between 10.00 and 11.00 p.m., and the coincidence of the separate maxima of these two groups was responsible for the 11.00 p.m. maximum observed when the total quantitative emergence of insects was considered. Both

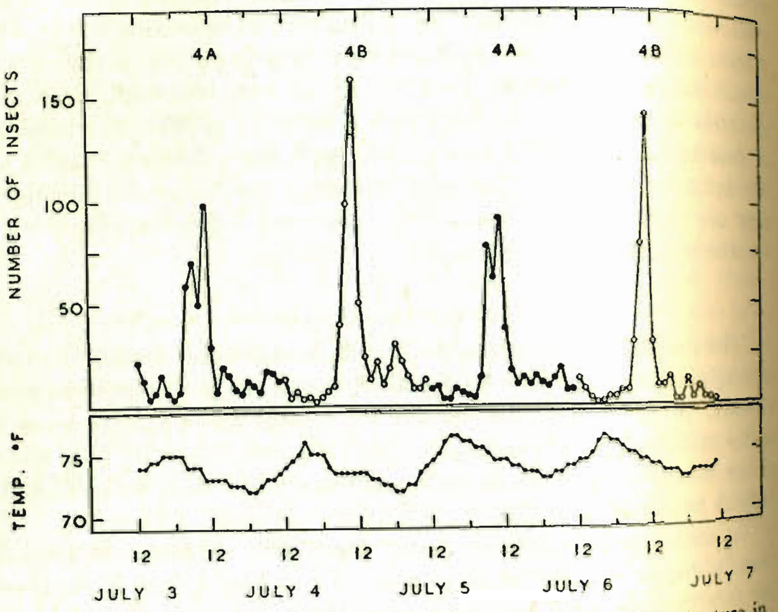

FIG. 6. The total hourly emergence of insects and water temperature in degrees Faharenheit at stations 4a and 4b from July 3rd to July 7th, 1941, beginning at noon.

these groups continued to emerge in reduced numbers throughout the day and night. The Simuliidae emerged throughout the daylight hours and in general were absent from the collections made during darkness. The Empidae ("Miscellaneous") emerged in small numbers during the early afternoon, reached a maximum between 7.00 and 9.00 p.m., and did not emerge during the night. A single species of Plecoptera was obtained during this study and it emerged from 9.00 p.m. to 1.00 a.m. with its maximum emergence at 11.00 p.m.

More detailed analyses of the hourly collections disclosed that the species within any one group of insects emerged at specific times each day. For example, of the Ephemeroptera obtained during the investigation at stations 4a and 4b, *Pseudocloeon virile* was taken only in the 4.00 and 5.00 p.m. collections; *Ephemerella sp.* emerged between 7.00 and 8.00 p.m.; *Baetis sp.* (near *pygmaeus*) between 7.00 and 9.00 p.m. with the maximum in every instance between 8.00 and 9.00 p.m.; *Baetis flavistriga, Leptophlebia volitans, Stenonema rubrum,* and *Stenonema luteum* showed their maximum emergence between 9.00 and 10.00 p.m.; and *Stenonema heterotarsale* emerged between 10.00 and 11.00 p.m. The relation of the times of emergence of these species was observed each day at both stations. One exception was found in that *Isonychia bicolor* emerged between 7.00 and 9.00 p.m. in general, but on July 4 at station 4a this species emerged between 7.00 and 9.00 a.m.

The maxima of temperature and insect emergence did not coincide in any twenty-four-hour period. The maximum temperature occurred, in general, between 3.00 and 5.00 p.m. and the minimum at about 6.00 a.m., while the maximum emergence occurred at 11.00 p.m. The emergence began to build up to this maximum between 8.00 and 9.00 p.m. which corresponds with the onset of sundown and indicates that the final impetus for emergence is related to a decrease in light intensity. It is probable that temperature is of importance in completing the development of an insect on a specific date but emergence does not occur until the following period of decreased light intensity which seems to stimulate activity and result in the completion of the aquatic sojourn of the insect.

Other investigators have obtained similar results regarding the time of emergence of aquatic insects. Miller (1941) found that the emergence of Chironomidae from shallow water in Costello lake, Algonquin Park, occurred between 4.00 and 7.00 a.m. (Standard Time); in the deep water the emergence was equal throughout the day. Scott and Opdyke (1941) investigated the emergence of insects from Winona lake, Indiana, and found that the Diptera emerged, for the most part, between 6.00 and 12.00 p.m., with in one case a smaller mode from 4.00 to 6.00 a.m. (Standard Time). They state that the Trichoptera emerged during the first part of the night, in general, but that a few emerged during the day.

The results of the present investigation showed conclusively that the diurnal insect emergence reached a maximum between 10.00 and 11.00 p.m. in a typical rapids in the Madawaska River. It cannot be assumed, however, that this relationship holds for other streams nor for other seasons in the same stream. Since different species emerge at different times of day, the specific composition of the bulk of emerging insects would affect the time of maximum emergence in any specific section of a stream.

The Effect of a Freshet on the Insect Fauna of a Stream

During a study of the distribution of insects on different types of bottom, a condition arose which afforded an opportunity of determining the effect of a sudden freshet on the insect fauna of a stream. A beaver dam, situated at the outlet of "Castalia" lake, broke suddenly on May 25, 1940, as the result of increased pressure brought to bear by the rise in lake level following an extended period of heavy rainfall. The water level in the lake dropped 3 feet during the day and this enormous volume of water cascaded down Mud creek, overflowing the banks and causing considerable damage in that area. This condition of flood prevailed for 7 days as the water subsided gradually and the stream finally returned to a normal flow. During this period large rocks were observed rolling slowly downstream and gravel and sand sections were moved as a whole and deposited in new areas.

Since the freshet occurred in the early spring, the number of insects emerging each day prior to the flood was too small to determine its immediate effect on the population. Coupled with this was the fact that the cages could not be maintained in the stream during the height of the flood. However, the result of the flood was determined by comparing the insect emergence at stations 5, 6, and 7 for the period June 6 to August 31 in 1939, which may be considered a normal season, and in 1940 (table 3).

The total insect emergence for this period at station 5 corresponded closely in the two years, with 1,932 and 1,827 individuals emerging in 1939 and 1940 respectively, a decrease of 5.6 per cent in the latter year. This decrease probably represents, for the most part, annual variation in the insect emergence, since the station was situated in a deep, slow-flowing pool, to one side of the main current, where the effect of the freshet would be minimized.

TABLE 3.—Number of insects that emerged at stations 5, 6, and 7 from June 6 to August 31, 1939 and 1940.

	Station 5		Station 6		Station 7	
	1939	1940	1939	1940	1939	1940
Plecoptera.	0	1	105	10	7	5
Ephemeroptera. .	608	138	191	64	385	28
Trichoptera.	56	110	34	36	15	20
Chironomidae. . .	1,247	1,575	1,187	595	1,360	757
Simuliidae.	0	0	590	562	10	18
"Miscellaneous".	21	3	88	29	34	44
Total.	1,932	1,827	2,195	1,296	1,811	872

Stations 6 and 7 were located in the centre of the stream in a relatively shallow section where the physical effect of the freshet would be maximal. A total of 2,195 and 1,296 insects emerged at station 6 in 1939 and 1940 respectively, a decrease of 41.0 per cent in the latter year. At station 7 a total of 1,811 and 872 insects emerged in 1939 and 1940 respectively, a decrease of 51.9 per cent in the summer following the freshet. Thus when these percentage decreases are compared with the 5.6 per cent decrease noted at station 5, which represents the probable annual variation in numbers, it is apparent that the freshet brought about a significant decrease in the summer populations at stations 6 and 7.

The total numerical decrease observed at stations 6 and 7 in 1940 resulted from the individual decreases in the numbers of Plecoptera, Ephemeroptera, and Chironomidae, for the most part, while only small differences were found in the numbers of Trichoptera and Simuliidae that emerged each year. The "Miscellaneous" group is too heterogeneous to be discussed satisfactorily. These results indicate that the forms with free-roving immature stages were reduced numerically while those with attached larvae and pupae were not affected appreciably by the freshet.

The role played by freshets in decreasing the population of a stream has been reported by several investigators, including Needham (1927), Tarzwell (1937), Surber (1938), Stehr (1938), and others. In general it has been found that during periods of high water in streams many of the bottom organisms are forced from their ecological niche, carried downstream and deposited in slow-flowing pools. If the gradient in the stream is gradual the freshet may detach only the insects that are free-roving on the surface of the bottom particles, but if the gradient is steep even those forms that adhere tightly to the particles will be moved and thus dislodge or crush the insects present. Stehr (1938) reports that serious floods may carry much of the invertebrate fauna away while the population is restored by minor floods washing individuals into the area and by migration back to the area. Needham (1927) placed a drift net across a stream during a spring flood and found that almost every kind of aquatic organism found in the stream was washed into the net. The majority of these were injured by the grinding action of the bottom particles and even larvae of Simuliidae, which normally live in fixed positions in swift water, were found in the net. Tarzwell (1937) found that a severe spring flood in streams of the Tonto Forest in Arizona reduced the amount of "bottom food" by almost half. This figure is in close agreement with the 41.0 and 51.9 per cent reductions in emergence obtained in the present study.

The results of this investigation showed that the number of insects that emerged from a scoured section of a stream, following a severe freshet, was considerably lower than would be expected under more normal conditions. It is probable that the number that do emerge from such an area is made up of insects that were able to withstand the increased flow and maintain their original positions in the stream or find suitable shelter, insects that were deposited in the area as the freshet subsided and were able to establish themselves in the new habitat, and insects that migrated into the area to obtain more suitable environmental conditions.

The effect of freshets on insect populations is profound in shallow sections of streams and areas with unstable bottoms, while the effect is greatly reduced in deep sections and areas with relatively stable bottoms. One exception to this generalization is obvious since smooth bedrock, although the most stable type of bottom found in streams, offers no protection during a freshet and the meagre insect fauna associated with this type of bottom would be quickly washed away.

Within any particular habitat, the resistance of the existing species to freshets is related to their mode of life. The free-roving species are readily dislodged unless able to acquire protection in the lee of bottom particles or in crevices, while the species with attached larvae or pupae and burrowing forms are able to withstand a much greater current. However, these species are just as vulnerable as the free-roving types to the destruction wrought by molar action which accompanies severe freshets in areas where the bottom is unstable.

The Effect of Intermittent Flow on the Insect Fauna of a Rapids

Many of the smaller streams of the Algonquin Park area are characterized by an intermittent flow and depend on run-off water and overflow from ponds for their volume. These streams assume considerable proportions during the spring flood and in periods of heavy local rainfall, but are reduced in size and in many cases dry up completely as the summer drought period sets in. A small flow is restored to these streams in the late summer and fall seasons.

Station 1 was situated in such a stream and here the volume of flow was dependent on the volume of water maintained in a beaver pond above. The stream dried up completely for periods during the summer of 1938 but was not completely dry at any time in 1939. An investigation of the insect fauna at the station was carried out to determine to what extent an intermittent flow and desiccation affected the insect population.

Quantitative Results

The insect emergence, when compared in 1938 and 1939 showed marked differences, and these were directly related to the relative drying of the stream bed in the two years. A total of 5,017 insects emerged from June 1 to September 11 in 1938, of which 4,003 or 79.8 per cent of the total emerged prior to July 17, at which date the stream bed at the station became dry, while 1,014 or 20.2 per cent emerged after July 17. The total emergence for the same period in 1939 was 4,899 individuals, which shows that annual variation in the total emergence was slight. However, the seasonal distribution of the insect emergence differed significantly in the two years, since 3,272 or 66.8 per cent emerged prior to July 17, while 1,627 or 33.2 per cent emerged after this date. In both years the majority of insects emerged in the period June 1 to July 17, but a greater proportion of the total emerged after July 17 in 1939 than in 1938. This relationship between seasonal emergence and continuity of flow was the result of definite changes in the different insect groups which were even more directly correlated with the nature of the flow.

All the Plecoptera, Ephemeroptera, Trichoptera[1] and Simuliidae that emerged in 1938 (table 4) were collected prior to July 17 while in 1939, 32.1 per cent of the total number of Plecoptera, 35.2 per cent of the Ephemeroptera, and 9.0 per cent of the Trichoptera emerged after July 17. In 1939, as was the case in 1938, there were no Simuliidae collected at the station after July 17, but since this group completed its emergence early in June each year, it is impossible from the results of this study to determine whether or not the drying up of a stream would affect its emergence. It seems probable from a consideration of the preferred habitat of the Simuliidae that this group should be included with the Plecoptera, Ephemeroptera, and Trichoptera as representative of groups unable to withstand desiccation, at least in their active aquatic stages.

The remaining two groups, Chironomidae and "Miscellaneous," were made up of individuals which were able to survive the desiccation, at least to some degree, since considerable numbers were collected after the stream became dry in 1938. Twenty per cent of the total emergence of Chironomidae in 1938 occurred during the period July 17 to September 11, and 34.7 per cent emerged in the same period in 1939. Part of this difference may be a result of annual variation in the seasonal emergence but it seems probable that, for the most part, it represents a reduction in the population occasioned by the desiccation in 1938.

Of the total number of "Miscellaneous" collected in 1938, 55.9 per cent were obtained in the period July 17 to September 11, while only 13.3 per cent were obtained in the same period in 1939. This apparent lack of correlation between the reduction in number of insects and intermittent flow resulted since the individuals in this group were not identified beyond family, and likely many individuals entered the cage from outside by crawling along the stream bed during the dry period and were, therefore, not truly aquatic. Stehr (1938) reported a rapid influx of terrestrial insects on to a stream bed once

[1]Female individuals were collected while the stream was dry and probably gained entrance to the cage from outside.

TABLE 4.—Analysis of the total insect emergence at station 1 from June 1 to September 11 in 1938 and 1939.

Period	Plecoptera 1938	Plecoptera 1939	Ephemeroptera 1938	Ephemeroptera 1939	Trichoptera 1938	Trichoptera 1939	Simuliidae 1938	Simuliidae 1939	Chironomidae 1938	Chironomidae 1939	"Miscellaneous" 1938	"Miscellaneous" 1939
June 1-30. . . .	14	31	18	62	8	112	126	2	2,216	2,211	45	120
July 1-17. . . .	0	5	41	304	4	11	0	0	1,512	377	19	37
July 17-31. . . .	0	0	0	97	*1	0	0	0	373	71	37	14
Aug. 1-31. . . .	0	17	0	88	*1	11	0	0	522	1,064	40	9
Sept. 1-11. . . .	0	0	0	14	0	1	0	0	36	240	4	1

*Collected while the stream bed was dry. Probably gained entrance from outside.

it became dry, and this corroborates the above supposition since such forms would be included in the collections from the cage and those families which had aquatic counterparts would be included in the quantitative totals.

Qualitative Results

There were seven species of Plecoptera found at station 1 including *Nemoura venosa, Nemoura serrata, Leuctra duplicata, Alloperla mediana, Isoperla montana, Nemoura punctipennis,* and *Leuctra decepta.* The first six species were early summer forms which completed their emergence before July 17, and thus did not show the effect of an intermittent flow. *Leuctra decepta,* on the other hand, which emerges during the late summer, was not found at the station in 1938 but was present in 1939 (figure 7), indicating that it was eliminated in the former years as a result of the drying-up of the stream.

There were six species of Ephemeroptera found at the station. These fell into two main categories, one represented by *Baetis brunneicolor* (figure 7) and *Centroptilum convexum* which completed their emergence in the early summer and thus were not subjected to the drying in 1938, and the second by *Leptophlebia debilis* (figure 7), *Baetis sp.* (near *pygmaeus*), *Heptagenia pulla,* and *Stenonema carolina,* species which emerged later in the summer and were eliminated at the station in 1938.

There were thirteen species of Trichoptera found at the station of which *Hydropsyche betteni, Diplectrona modesta, Psychomyia diversa, Lepidostoma sp., Limnephilus consocius, Dolophilus moestus, Polycentropus pentus, Polycentropus maculatus,* and a species of Hydroptilidae emerged early in the summer and had completed their emergence by July 17 in both years and thus did not provide information on the effect of an intermittent flow on the fauna. *Lepidostoma grisea* (figure 7), *Cheumatopsyche pettiti, Chimarrha aterrima,* and *Polycentropus confusus* emerged after July 17 in 1939, but did not emerge in this period in 1938. Thus this group consists of species which were eliminated when the stream became dry.

Discussion

It has been demonstrated, especially for the Plecoptera, Ephemeroptera, and Trichoptera but also for the Chironomidae, that the

aquatic stages of insects belonging to these groups are eliminated entirely or reduced numerically when a stream dries up. The first three groups have a low tolerance for conditions associated with an intermittent flow and were either killed or forced to migrate from the area as the drying became complete, while the last group seemed to withstand or avoid desiccation, at least to some degree. Since many of

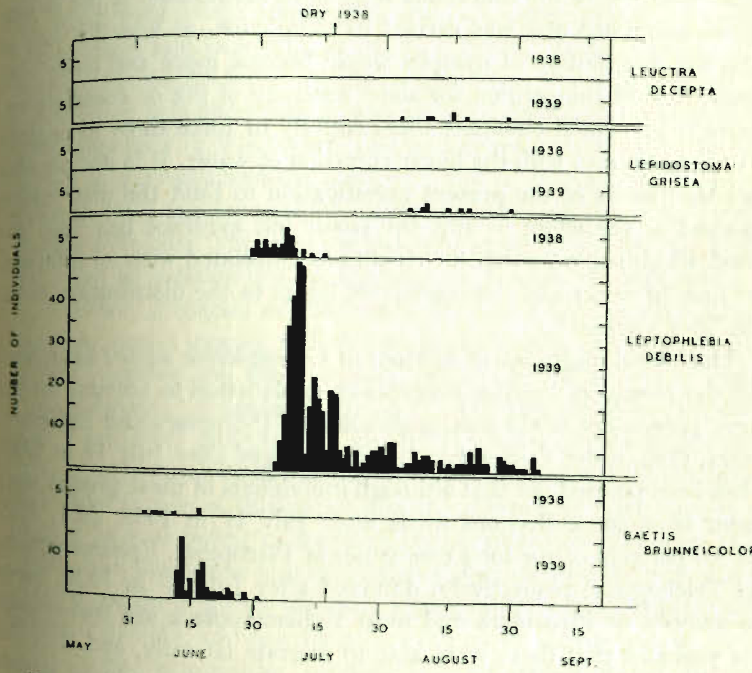

FIG. 7. Emergence polygons of representative species at station 1 in 1938 and 1939, showing the effect of the drying up of the stream on July 17th, 1938, on the insect emergence.

the Chironomidae are known to dwell in the small interstices of the bottom particles, it is probable that these were able to retreat to moist areas under large rocks and here obtain sufficient moisture to complete the aquatic portion of their life-cycles. The numerical reduction observed in the emergence of this group after July 17 in 1938 as compared with that of the same period in 1939 probably represents the number unable to secure such suitable microhabitats.

It was observed during the summer low-water period in 1939 that nymphs of *Leptophlebia debilis,* a species that was eliminated by the drying in 1938, moved gradually towards the centre of the stream as the water receded from the margins. Thus the number of nymphs per unit area increased in the mid-channel and the original wide distribution over the whole stream bed was changed to a concentrated distribution where the conditions were most favourable. If the drying process continued and was carried to completion, as was the case in 1938, the distribution of nymphs would become more and more concentrated until competition for some necessity of life or complete exposure to air would eliminate them entirely or force them to migrate up or downstream with the linear recession of water. It is not possible from the results of the present investigation to limit the distribution observed to the effect of any one factor but evidence has been obtained which suggests that the conditions correlated with an intermittent flow of water and desiccation set limits to the distribution of insects in a stream.

The lateral migration of nymphs of *Leptophlebia debilis* associated with the recession of water suggests an explanation to account for the larger percentage of the total population of Plecoptera and Ephemeroptera, than of the Trichoptera, which emerged after July 17 in 1939. It has been pointed out that although individuals of these groups were absent from the collections made after July 17 in 1938, 32.1, 35.2, and 9.0 per cent of the total emergence of Plecoptera, Ephemeroptera, and Trichoptera, respectively, occurred after July 17 in 1939. Since the nymphs of Plecoptera and most Ephemeroptera are free-roving, it is probable that these were able to migrate laterally, and thus the majority of the population was able to survive in the reduced stream channel during the period of low water in 1939. The Trichoptera, however, showed a much lower survival for the same period than either the Plecoptera or Ephemeroptera. This may be explained by the fixed habit of many larvae and pupae of this group which would prevent or hinder lateral migration as the water receded and thus only those individuals originally situated on the lower bottom particles in the mid-channel would survive.

Although only scattered information was obtained regarding the repopulation of the stream in 1939 following the drying in 1938, it is interesting to speculate on this problem and several possibilities arise. Probably some eggs deposited in the early summer of 1938 were able to withstand desiccation and thus hatch and complete the life-cycle during the late summer and following spring when a flow was restored to the stream. Also late summer oviposition in 1938 would not be affected since a small flow was present at that time. However, these possibilities are not sufficient to account for certain elements of the population found in 1939. It is probable that some individuals were swept downstream from the upper sections during the spring flood and deposited at the station site, while others migrated upstream from the lower sections where there was a permanent flow. Evidence of this phenomenon was obtained during the spring of 1939 when numbers of Plecoptera and Ephemeroptera nymphs were observed at intervals between stations 1 and 2. At each observation the nymphs were concentrated in a different area and this progressed upstream with time. This was not followed in detail but the observations did seem to indicate a slow upstream migration of these forms.

Further, 2 species of Plecoptera, *Nemoura serrata,* and *Alloperla mediana,* and 3 species of Ephemeroptera, *Baetis brunneicolor, Stenonema carolina* and *Centroptilum convexum,* all of which emerged during the early summer at station 1, were also found at near-by station 2 but were absent from station 3a where the temperature conditions were more closely related to those at station 1. It is suggested in a later section of this paper that the absence of these species from station 3a was owing to the high temperatures found there. If such is the case, then these species probably migrate into the site of station 1 from station 2 during the early spring when a large volume of cold water is present, and emerge before the water warms to a lethal level. This faunal composition of station 1 substantiates the suggestion of migration as an active factor restoring the population to this area each year. Stehr (1938) reports that migration is an important factor in the restoration of the insect fauna to an intermittent stream. That the immature stages of certain aquatic insects are capable of extensive migrations, has been proved by Neave (1930) in a report of the movements of nymphs of *Blasturus cupidus* (Ephemeroptera).

A total of 26 species belonging to the Plecoptera, Ephemeroptera, and Trichoptera were found at station 1. This was much lower than the number found at stations 2, 3a, 3, and 4, which also were characterized by a rubble bottom but had a permanent flow. It was found that the number of species at these stations was correlated with the average summer temperatures in the stream (page 68), while the number at station 1 did not follow this correlation. In comparison with the 26 species found at station 1, there were 37 species at station 2 which was located close to station 1 but had a much lower temperature, and 48 species at station 3a where the temperature conditions approximated those at station 1. This lack of correlation resulted from the limitations to the success of aquatic insects associated with an intermittent flow. In such streams a highly variable type of habitat is presented to the insect population and to survive they must be able to withstand or avoid diverse physical conditions such as freshets, still water and desiccation. The greater number of species found at station 1 in 1939 showed that, although a large number of species may be present each year, only the most tolerant forms and those that emerge early in the season are able to complete their life-cycles in the stream when conditions become severe as was the case in the summer of 1938.

The Effect of Flooding by a Beaver Dam on the Insect Fauna of a Rapids

The construction of the beaver dam at the end of June in 1939 transformed the shallow rocky rapids, in which station 3 was located, into a deep sedimented pool. Thus a natural field experiment was set up which provided a considerable amount of information regarding the tolerance of different insect species to varied conditions of current and type of bottom.

These observations have already been published (Sprules, 1941) but because of their interest here will be briefly discussed below.

There was a decrease in the total number of insects taken in the traps as the station changed from a lotic to lentic environment, which could not be explained on the basis of annual variation. Not only was there a change in numbers but also in the proportions of the species in the catch. The Ephemeroptera which constituted about 56 per cent of the catch in 1938 decreased to 46 per cent in 1939 and to 12 per cent in 1940. Similarly the Plecoptera diminished from 2 per cent to about 0.2 per cent. The Trichoptera also dropped about one-quarter of the initial representation. On the other hand the proportion of Chironomidae increased from 31 per cent in 1938 to 84 per cent in 1940.

With respect to the productivity of this area, the effect of the numerical reduction is more pronounced when the volume or weight of the annual emergence is considered. Both the immature and adult stages of the Ephemeroptera, Trichoptera, and Plecoptera groups, which accounted for most of the reduction, are larger and heavier forms than the corresponding stages of the Chironomidae, which is the only group that increased consistently following the introduction of lentic conditions.

Further examination of the material showed that the changes were the result of a differential effect on species. Of the Ephemeroptera, Trichoptera, and Plecoptera, a total of 33 species were wiped out or reduced numerically in the lentic period, 15 species showed no appreciable change in emergence and 10 species appeared at the station during that time. These data indicate the existence of three main groups of species including typical lotic inhabitants which were unable to tolerate the lentic conditions, tolerant species which were able to adjust themselves to either lotic or lentic environments and lentic species which were unable to tolerate lotic conditions.

As a group, the Plecoptera consisted of typical rapid-water dwellers since 9 species were eliminated following construction of the dam, 1 species emerged throughout the investigation, and there were no new species introduced when the pool conditions prevailed. The Ephemeroptera showed a wider range of habitat tolerance since 14 species were eliminated, 7 emerged each year and 7 species were found at the station only after the end of June in 1939. Of this last group some of the species emerged from the area during the late summer of 1939, indicating that the immature stages migrated into the area immediately following the establishment of lentic conditions. Ten species of Trichoptera were eliminated, 7 species emerged under both sets of conditions and 3 species occurred only in 1940. The lack of any new species in the late summer period of 1939 indicates that the immature stages of this group did not migrate as readily as the Ephemeroptera and probably were dependent on oviposition in 1939 to become established in the lentic environment.

The numerical reduction of emergence and subsequent elimination of the typical rapid-water species occurred immediately after the environmental conditions were altered in 1939. In some instances species which were emerging in quantity prior to the flood were entirely absent from the collections made five days after its inception. Although representatives of the still-water fauna did enter the area during the late summer of 1939, the fauna was not established in numbers until the following year.

The decrease in rate of flow, increase in depth, and change in the type of bottom caused by the deposition of silt and other particulate matter over the rubble as the transport power of the stream was reduced were associated with quantitative and qualitative changes in the insect fauna. These three physical factors are closely interrelated in streams and it is difficult to determine the role played by any one of these in limiting the distribution of the insect fauna.

It has been shown that species exhibit different degrees of habitat tolerance in streams. The species that were eliminated from the rapids when it was transformed into a pool showed a narrow range of tolerance and were species typically associated with riffle areas. Species that were present in the area under both sets of conditions were forms that showed a wide range of tolerance and were found in several different habitats in the stream. Degrees of tolerance were exhibited by the species of this group since some emerged in smaller numbers in the lentic than in the lotic habitat while others emerged in equal numbers in both habitats. The species that emerged from the area only during lentic conditions showed a narrow range of tolerance and were types that were typically found in still-water habitats.

It is probable that the reduction in current was of importance in the elimination of rapid-water species. Many of these are dependent on current for respiration and others, such as the net-building Trichoptera, are of fixed habit and depend on current to wash food material into the nets. Further, the deposition of silt which accompanied the reduction of flow would injure the gills of certain species and lead to suffocation in some instances. Many of the free-living species could migrate from the area when the environmental conditions became severe, while others of fixed habit would be unable to avoid the new conditions.

A wide variety of microhabitats is found in rapids where the bottom consists of rocks and rubble. Thus species that show preference for a rapid flow and for rubble bottom would find suitable niches, while in the lee areas species that prefer reduced current or even quiet water, and gravel or sand bottoms, also would find suitable

niches. The latter species are those that showed a wide range of habitat tolerance in this investigation and survived under lentic conditions. The decrease in the number of different microhabitats that accompanied the change of bottom could account for the associated decrease in the diversity of the fauna.

It would seem that current was the most important factor limiting the distribution of the typical quiet-water species. The rapidity with which some of these types entered the area once lentic conditions were established indicates that they were continually attempting to extend their distribution but were not successful until conditions were such as to allow fulfilment of this tendency. The lack of morphological adaptations in these species to withstand a rapid flow would prohibit their establishment in running water. Other factors, such as the increase in amount of organic food material deposited on the rubble when the current was reduced and the reduction of predators through the elimination of rapid-water species, were probably of minor importance in the successful extension of the distribution of these species.

The Insect Distribution on Different Types of Bottom

The smaller streams of Algonquin Park are characterized by the presence of many different types of bottom and several of these often are found in close proximity to one another in a short section of stream. An investigation of the insect fauna associated with different types of bottom was carried out to determine the relationship between size of bottom particles and the existing insect distribution.

During this study two uncontrollable contingencies arose which altered the physical nature of certain stream areas under investigation as well as the normal insect populations, and have made it difficult to make comparative analyses of the data. The first of these was the sudden freshet in 1940 which affected the insect emergence at stations 6 and 7 and may have affected that at station 3a, although this cannot be stated definitely since this station was not in operation prior to 1940 to allow a comparison of results. The second event was the construction of the beaver dam below station 3 in 1939, the effects of which have been discussed in the previous section. These are natural disturbances with which an ecologist is faced frequently in Algonquin Park and the new conditions presented in these instances must be accepted. Although the freshet and beaver dam provided a considerable amount of valuable information on factors affecting insect distribution in streams, they nevertheless disrupted certain of the original plans and have made the interpretation of results more difficult through the addition of extra variables.

Quantitative Results

The number of insects that emerged from different types of bottom in 1938, 1939, and 1940 was determined and the results have been summarized in table 5. In each year the emergence from the sand bottom was numerically less than that from any other type of bottom. Conversely it was found that rubble bottoms with a rapid flow of water produced the greatest insect emergence in 1939 and 1940, while in 1938 an exception to this occurred, since in the period sampled 1,942 insects were collected from the gravel-bottom station and only 1,677 from the rubble. This discrepancy was the result of an error introduced in connection with the method of collecting employed at station 6 in 1938 (page 18). From the collections obtained at station 3, following the building of the beaver dam which transformed the riffle into a pool at the end of June 1939, it was found that a rubble bottom in deep pool conditions produced a smaller number of insects than the rapid-water type. The gravel and muck bottoms were intermediate between the rubble and sand bottoms from the standpoint of total insect emergence. In 1938 and 1939 the gravel produced more insects than the muck, while in 1940 the relation was reversed. This latter instance resulted from the freshet (page 24) which scoured the gravel section, reducing the population considerably, while it had little if any effect on the population at the muck station.

In order to compare the quantitative results of this study more directly, the total insect emergence in each year from the different types of bottom was converted into a ratio with the emergence from sand bottom as the unit. The average values of the ratios for the complete period of the investigation were rubble (rapid) 4.6, rubble (pool) 3.3, gravel 2.1, muck 1.8 and sand 1.0 showing a decreasing productivity of insects from rapid rubble areas to sand.

Results obtained in the present investigation correspond closely to those of other investigators. Needham (1927) found a decrease

TABLE 5.—Analysis of the total insect emergence from different types of bottom in 1938, 1939, and 1940.

	1938 27 daily collections from June 29 to September 18				1939 Daily collections from June 6 to September 11			1940 Daily collections from June 1 to August 31				
Station	No. 3	No. 6	No. 5	No. 7	No. 6	No. 5	No. 7	No. 3	No. 3a	No. 6	No. 5	No. 7
Type of bottom	rubble (rapid)	gravel	muck	sand	gravel	muck	sand	rubble (pool)	rubble (rapid)	gravel	muck	sand
Ephemeroptera	952	57	283	25	195	608	385	469	1,035	64	142	29
Trichoptera	172	26	44	14	36	57	16	102	270	36	109	20
Plecoptera	34	41	0	7	105	0	7	7	450	13	1	5
Chironomidae	480	1,753	859	598	2,131	1,270	1,379	3,227	3,446	620	1,936	786
Simuliidae	0	22	0	2	604	0	10	4	1,554	604	0	18
"Miscellaneous"	40	43	23	24	95	21	3	10	478	32	3	44
Total	1,677	1,942	1,208	670	3,166	1,956	1,832	3,819	7,233	1,369	2,191	902

in the standing crop from rubble through gravel, muck, to sand. Tarzwell (1936) carried out an extensive survey of many grades of bottom in the streams of Michigan and found an increase in population rating from sand to bottoms supporting various aquatic plants. Tarzwell's results converted into ratios give rubble 3.6, gravel and sand 2.6, mucky flats 2.3 and sand and silt 1.0. These agree very closely with those of the present study.

Numbers of individuals are of course not always the best indication of the biomass. A few determinations of the volume of insects produced by different types of bottom were made and from these it was found that the bottoms were related with respect to volume of emergence in the same order as when the number of insects was considered. The ratios obtained from the rubble (rapid), gravel, muck, and sand bttoms were respectively 20.7, 3.6, 1.5 and 1.0. The apparent lack of correlation between volume (20.7) and numbers (4.6) at the rubble station resulted from the preponderance of insects with a relatively large body size, such as Plecoptera, Ephemeroptera, and Trichoptera, which were found in this habitat.

Qualitative Results

(*a*) *General differences.* There are major qualitative differences in the insect emergence at stations associated with different types of bottom in a stream. In order to analyze these differences the number of insects belonging to each of the main groups that emerged from different types of bottom has been expressed as a percentage of the total annual emergence. The average percentage composition of the fauna associated with each type of bottom was determined for the complete period of the investigation (table 6).

TABLE 6.—Average per cent composition of the insect emergence from rubble (rapid), gravel, muck, and sand bottoms, for 1938, 1939, and 1940.

	Rubble (rapid)	Gravel	Muck	Sand
Ephemeroptera	35.5	4.6	20.3	9.3
Trichoptera	7.0	1.7	3.8	1.7
Plecoptera	4.1	2.1	0.0	0.7
Chironomidae	38.2	67.6	74.8	83.9
Simuliidae	10.8	21.4	0.0	0.9
"Miscellaneous"	4.4	2.5	1.0	3.5

Sand. The emergence from the sand bottom consisted for the most part of Chironomidae which made up the greatest proportion of the population each year and averaged 83.9 per cent for the complete period of study. The Ephemeroptera was the next most abundant group averaging 9.3 per cent of the total emergence. The "Miscellaneous," Trichoptera, Simuliidae, Plecoptera followed in order, representing in each case only a small element of the total emergence.

Muck. The emergence from the muck bottom consisted predominantly of Chironomidae which averaged 74.8 per cent of the total emergence over the complete period of the study. The Ephemeroptera was the next most abundant group, averaging 20.3 per cent of the total. Thus the total component of Chironomidae and Ephemeroptera, the two most prevalent groups, was almost identical at the sand and muck stations. The diminution in the percentage of Chironomidae at the muck site as compared with that at the sand was compensated for by an increase in the percentage of Ephemeroptera. The Trichoptera and "Miscellaneous" followed in order of relative abundance. The Simuliidae and Plecoptera[2] groups were not represented at the muck station; this was the most significant faunal difference noted between this station and all others.

Gravel. The emergence from the gravel bottom also consisted for the most part of Chironomidae, which averaged 67.6 per cent of the total emergence during the investigation. The Simuliidae made up a considerable portion of the emergence at this station, averaging 21.4 per cent. The Ephemeroptera, "Miscellaneous," Plecoptera, and Trichoptera followed in order of decreasing numbers and contributed only a small element to the total emergence in each instance. The increased proportion of Simuliidae was the most significant difference observed in the emergence from the gravel bottom as compared with that from sand and muck bottoms.

Rubble. At the rapid rubble bottoms the emergence consisted of more equal proportions of all the insect groups than were found at any other type of bottom. Once again the Chironomidae formed the most abundant element, averaging 38.2 per cent of the total, while the Ephemeroptera followed closely with 35.5 per cent. The Simuliidae averaged 10.8 per cent of the total, and the Trichoptera, Plecop-

[2]One individual taken in 1940—likely washed in following high water.

tera, and "Miscellaneous" followed in decreasing order of abundance, each group making up a larger proportion of the total emergence than was found at any of the other types of bottom.

TABLE 7.—Total number of species of Plecoptera, Ephemeroptera, and Trichoptera that emerged from different types of bottom during the investigation.

	Total number of species	Rubble	Gravel	Muck	Sand
Plecoptera	11	11	8	1	5
Ephemeroptera	34	21	18	19	14
Trichoptera	27	22	12	15	11
Total	72	54	38	35	30

(*b*) *Species differences.* The distribution of species belonging to the Plecoptera, Ephemeroptera and Trichoptera on the different types of bottom was determined. When the total number of species was considered, it was found that 54 emerged from rubble, 38 from gravel, 35 from muck, and 30 from sand (table 7). Thus with respect to the three groups in which species determinations were made, the diversity of the fauna decreased from rubble through gravel and muck to sand. This is the same sequence as was found when the total number and volume of all insects were considered.

Plecoptera. The Plecoptera were represented at the stations by 11 species, all of which were found at the rubble bottom, 8 at gravel, 5 at sand and 1 at muck, which was represented by a single individual (table 8). There were 3 species found only on the rubble bottom; 1 species was common to rubble, gravel, and muck; 2 were confined to rubble and gravel; while 5 species were common to rubble, gravel, and sand. Thus the most diverse population was associated with rubble bottoms followed in order by gravel, sand, and muck.

The distribution of species and the relative abundance of each species on different types of bottom indicated that the preferred habitat for this group was rubble riffle areas. Although there were only 3 species found in the rubble that were not found in the gravel, in almost every case the relative abundance of each species was less in the gravel area. In every instance the relative abundance of the species found on the sand bottom was less than on the rubble or gravel bottoms. The Plecoptera population was negligible on the muck bottom, indicating that the conditions associated with such a habitat are unsuitable for the stonefly fauna found in this stream. This was substantiated by observations made at station 3 in 1939 and 1940 when the rubble riffle was converted into a still pool by a beaver dam. It was found that the Plecoptera disappeared from the area, with the exception of *Isoperla sp.1* which remained in reduced numbers

TABLE 8.—Distribution of Plecoptera and relative abundance of each species on different types of bottom. A—over 50 individuals; F—10 to 50; R—1 to 10; T—1 individual. The abundance represents the maximum annual emergence obtained during the investigation.

	Rubble (rapid)	Gravel	Muck	Sand
Leuctra decepta	A	F		R
Leuctra tenuis	A	F		R
Isoperla sp. 1	F	F		R
Isoperla montana	R	F		T
Hastaperla brevis	R	R		T
Isoperla truncata	F	R		
Alloperla imbecilla	R	F		
Nemoura venosa	F	R	T	
Leuctra hamula	F			
Leuctra sibleyi	R			
Acroneuria abnormis	R			
Total	11	8	1	5

(Sprules, 1940). Frison (1935) found that although the Plecoptera of Illinois were found in many diverse habitats only one species, *Isoperla minuta* Banks, was confined to small muddy-bottomed streams.

Ephemeroptera. The Ephemeroptera were represented by 34 species, of which 21 were found at the rubble stations, 18 at the gravel, 19 at the muck, and 14 at the sand station (table 9). Species that were represented by female imagos only have not been considered in preparing the species list for each station (page 44). There were 5 species confined to rubble, 3 to gravel, and 5 to muck, while no

TABLE 9.—Distribution of Ephemeroptera and relative abundance of each species on different types of bottom. A—over 50 individuals; F—10 to 50; R—1 to 10; T—1 individual. The abundance represents the maximum annual emergence obtained during the investigation.

	Rubble (rapid)	Gravel	Muck	Sand
Baetis cingulatus	F			
Epeorus humeralis	R			
Leptophlebia guttata	R			
Heptagenia hebe	R			
Baetis parvus	T			
Leptophlebia mollis	A	F		
Ephemerella invaria	T	R		
Pseudocloeon carolina	R	T		
Stenonema fuscum	F	T	R	
Habrophlebia vibrans	A	F	A	F
Ephemerella sp. (*bicolor* gr.)	R	R	F	F
Stenonema rubromaculatum	F	R	F	R
Leptophlebia debilis	A	R	R	R
Baetis flavistriga	A	R		R
Heptagenia pulla	A	F		T
Baetis pluto	A	A		R
Baetis sp. (*pygmaeus* gr.)	A	F		R
Centroptilum simile	R		T	R
Stenonema ?vicarium	R		R	
Stenonema canadense	F		R	
Leptophlebia volitans	F		R	
Baetis frondalis		R	T	R
Centroptilum semirufum		R	R	A
Centroptilum convexum		T	F	F
Ephemerella deficiens		F		
Ephemerella sp. (near *serrata*)		T		
Baetis vagans		T		
Cloeon triangulifer			R	R
Caenis sp.			F	T
Cloeon simplex			R	
Cloeon rubropictum			R	
Brachycercus sp.			R	
Blasturus sp.			R	
Ephemerella lutulenta			T	
Total	21	18	19	14

species were found at the sand station alone. Four species were common to all the habitats; 4 to rubble, gravel, and sand; 1 to rubble, gravel, and muck; 3 to rubble and gravel; 3 to rubble and muck; 1 to rubble, muck, and sand; 3 to gravel, muck, and sand; 2 to muck and sand. Thus the most diverse population was found on the rubble bottoms followed by muck, gravel, and sand in decreasing order.

The distribution of species on different types of bottom showed that the species of Ephemeroptera had a much wider range of habitat preference than the Plecoptera. The distribution of species and the relative abundance of individuals on the different types of bottom indicated the habitat preference of each species and the range of habitats it could tolerate. For example, *Heptagenia pulla* occurred abundantly on rubble, frequently on gravel, was represented by a single individual on sand, and did not occur on muck (table 9). Thus, for this species, preference is shown for conditions associated with rubble bottoms, followed closely by gravel, and, although able to tolerate sand conditions, it is unable to tolerate conditions prevailing in a muck habitat. Although no species were found only at the sand station, when the relative abundance of individuals found on the different types of bottom was considered, it was found that certain species such as *Centroptilum semirufum* showed a distinct preference for sand since the maximum emergence occurred there.

Trichoptera. The Trichoptera were represented at the stations by a total of 27 species, of which 22 were found on the rubble bottoms, 12 on the gravel, 15 on the muck, and 11 on the sand bottom (table 10). There were 5 species confined to rubble, 4 species to muck, while none were found only on the gravel or sand bottoms. There were 4 species common to all the habitats; 4 to rubble, gravel, and sand; 2 to rubble, gravel, and muck; 2 to rubble and gravel; 3 to rubble and muck; 1 to rubble and sand; 1 to rubble, muck, and sand; 1 to muck and sand. Thus this group showed the same general distribution as the Ephemeroptera, since the most diverse fauna was found on rubble, followed by that on muck, gravel, and sand in decreasing order.

The Trichoptera showed a wider range of habitat preference than the Plecoptera but not as wide as the Ephemeroptera, since there were no species confined to either the gravel or sand habitats. In fact, all the species found on the gravel bottom were found on the rubble bottom and in no instance was the relative abundance of a species greater in the gravel than in the rubble area. Thus the gravel fauna consisted almost entirely of species that showed a preference for the rubble habitat but were able to extend their distribution into a gravel

TABLE 10.—Distribution of Trichoptera and relative abundance of each species on different types of bottom. A—over 50 individuals; F—10 to 50; R—1 to 10; T—1 individual. The abundance represents the maximum annual emergence obtained during the investigation.

	Rubble (rapid)	Gravel	Muck	Sand
Cheumatopsyche campyla	R			
Lepidostoma grisea	R			
Neophylax autumnus	R			
Psychomyella flavida	R			
Agapetus sp.	R			
Rhyacophila fuscula	R	R		
Athripsodes angustus	R	R		
Nyctiophylax vestitus	F	R	F	
Phylocentropus placidus	T	T	T	
Plectrocnemia cinerea	R	R	F	R
Psychomyia diversa	R	R	F	R
Cheumatopsyche pettiti	F	R	T	R
Hydroptilidae	T	T	T	R
Philopotamus distinctus	A	R		T
Chimarrha aterrima	A	F		R
Hydropsyche sparna	F	R		R
Hydropsyche betteni	F	F		R
Stenophylax guttifer	R		R	T
Polycentropus confusus	R		R	
Athripsodes dilutus	R		R	
Mystacides sepulchralis	R		F	T
Rhyacophila carolina	R			T
Oecetis inconspicua			F	
Lepidostoma costalis			F	
Pycnopsyche aglonus			R	
Platycentropus indicans			R	
Molanna sp.			T	
Total	22	12	15	11

riffle. In the same way the sand fauna consisted in general of species which were found in a rubble riffle where the relative abundance was at least as great. Two exceptions occurred to this generalization.

First, one species found on sand, *Oecetis inconspicua,* was not found on rubble, and from its maximum abundance showed a habitat preference for muck bottom. Thus this species is probably a still-water form which was able to tolerate the conditions prevailing at the sand station but unable to extend its distribution to either the gravel or rubble bottoms where a considerable current existed. Second, the family Hydroptilidae showed its maximum relative abundance on the sand bottom although it was present at all the habitats and thus, as a group, must be considered one which shows a habitat preference for sand but can tolerate the conditions prevailing at a variety of habitats. If complete species identification had been made in this family it is probable that a more diverse distribution would have been obtained for it.

The Trichoptera are known to occupy a wide range of habitats. Certain families, such as the Phryganeidae, are found in still water or slow-flowing habitats, while others, such as the Rhyacophilidae, are limited to rapid streams. Siltala (1906) found several species in the Bay of Finland living under marine conditions and utilizing marine algae for food and larval cases, while one European species, *Enoicyla pusilla* Burmeister, is known to be terrestrial.

Discussion

It is probable that, other things being equal, current is of prime importance in limiting the distribution of aquatic insects in a restricted section of a stream. Wingfield (1939) found that in certain aquatic insects the demand is for current which continually brings a fresh supply of oxygenated water to the respiratory surface rather than for a high dissolved oxygen content as formerly held (Hubault, 1927), and that in some species of Ephemeroptera the gills are used to create a current over the body and are used as secondary respiratory organs only when the oxygen content of the water is extremely low. This could account for the inverse correlation between the gill area of Ephemeroptera nymphs in mountain streams and the dissolved oxygen content found by Dodds and Hisaw (1924b). Wu (1931) found that the Simuliidae had an "inherent current demand" and this was substantiated in the present investigation by the absence of this group from station 5 where the current was negligible. The Plecoptera were also absent from this station and it is probable that this distribuary importance. In the present study it has been found that current and nature of the bottom particles are intimately interrelated and the separate effect of these factors on the distribution of insects in the streams of Algonquin Park could not be distinguished.

Another factor which must be considered when the composition of the fauna is determined for some specific area in a stream is the proximity of one type of bottom to another. Thus in this investigation the muck bottom was situated only a few feet downstream from the rapid rubble station. It is probable that this would allow an influx of insects from the rapids to the muck habitat since certain individuals would be swept down, at intervals, by the current. This was substantiated during the study, since in 1938 and early in 1939 large numbers of *Habrophlebia vibrans* emerged both at the muck and rubble stations. However, when the rapids was converted into a pool in 1939, the number of individuals at both sites was greatly reduced showing that this species was normally associated with a rapid rubble habitat and, although able to survive in the muck, this was not the preferred habitat. The same condition could have existed at the sand station since it was situated in close proximity to the gravel riffle. Thus it is probable that the nature of the stream bottom in the surrounding area, especially in the upstream portion, may have a bearing on the fauna found at any specific site in a stream.

It has been pointed out that the diversity of the insect fauna in any area is related to the number of different microhabitats present in that area. This factor also probably limits the number of individuals in the area, at least to some degree. However, another factor which may limit the number of insects found in any area is the utilizable surface area of bottom particles exposed to the water. It was found that the number of insects that emerged from different types of bottom decreased from rubble, through gravel and muck, to sand. The rubble area provided the greatest area of bottom particles exposed to the water and this was followed by gravel, muck and sand where the utilizable surface area decreased, in order, from the standpoint of aquatic insects. The presence of decaying organic matter on the muck bottom increased the surface area exposed to the water in this habitat.

In the consideration of surface area exposed to the water, the size of organisms must be taken into account. Thus, although few aquatic

insects found in streams could utilize the interstitial spaces in a sand bottom, it has been shown by Pennak (1939) that there is an extensive microfaunal population (Rotifera) found in sandy lake shores. These forms are of small body size and are able to utilize the interstices.

In addition, it is probable that the amount of organic food material limits the number of organisms found in any area and should be considered along with the utilizable surface area of bottom particles exposed to the water.

Tarzwell (1936) carried out an extensive study of the bottom fauna of different types of bottom in a stream and considered many intergrades such as coarse, medium and fine gravel along with various types of aquatic plant beds. The results showed an increase from sand, which was given a population rating of 1, up to beds of *Elodea sp.*, which had a rating of 452. This high population rating could be explained by the original premise since plant beds would afford an enormous surface area exposed to the water as well as an abundant supply of organic food material. Needham (1927) found hardpan and bedrock areas to be less productive than sand. Here the surface area of bottom particles exposed to the water, available cover and amount of organic material present would be minimal. From a few collections made from an area in the Madawaska river where the bottom consisted of large boulders it was found that the population was much lower than that found in the areas of small rubble and rocks. Once again, since the interstitial spaces are reduced in number as the rocks increase in size, such areas would present a less favourable habitat if surface area were considered.

It may therefore, be postulated from such data that there is a direct relationship between the utilizable surface area of bottom particles exposed to the water and the productivity of aquatic insects. Mottley et al (1938) suggested that the number of organisms per unit of substratum exposed to the water might give a better measure of the richness of a stream than the number per unit area of bottom.

Wene and Wickliff (1940) carried out an experiment in Blacklick creek, Ohio, in which the results offer direct substantiation of the above postulation. Wire baskets were filled with denuded medium and small rubble and placed in the creek bottom so that the surface of the rubble was level with the surrounding bottom. When the baskets were placed in a sandy bottom pool it was found that in February, 1938, after the baskets had been in position for approximately one month, the small rubble had about three times and the large rubble five times as many insects as the corresponding check samples from the surrounding sand bottom.

A field observation which further illustrates the relation of surface area of bottom particles and the number of insects may be obtained from observations of the distribution of groups which have a narrow range of habitat preference (such as the Simuliidae and the net-building Trichoptera) where their aggregation in localized positions on the stones may be readily seen.

It was found that the distribution of insects in a stream showed quantitative and qualitative differences which were associated with different types of bottom. It was not possible in this study to attribute these differences to the effect of any one condition that varied with the respective types of bottom, since the fact that the size of the bottom particles differed implies that there were corresponding differences in current, depth, volume of flow, light penetration, oxygen and carbon dioxide content, any one or all of which may play a significant role in limiting the distribution. However, since all these factors are interrelated, the phrase "type of bottom" may be used to represent the characteristics of the habitats referred to, although it must be realized that the various types of bottom cannot be laid down in a stream without accompanying alterations in other conditions. It is probable that the insect distribution found in this investigaton was the resultant of a complex interaction of several environmental conditions of which current and the nature of the bottom are relatively more important.

The Distribution of Insects in Rocky Riffles at Various Distances from the Source

A comparison of the insect emergence at stations 2, 3a, 3 and 4 was made to determine if there were quantitative and qualitative differences in the faunas which could be correlated with change in conditions downstream. These stations were selected at different distances from the source (figure 1) in rocky riffle areas in order to minimize the effect of other factors, such as type of bottom, which were known to affect insect distribution in streams.

The construction of the beaver dam (page 34) disrupted this investigation and made it impossible to compare the emergence at all the stations in any one year, since station 3a was not established until 1940 at which time the original rapids at station 3 had been transformed into a pool. However, it was found in several instances during this stream investigation that annual variation in insect emergence from any area is small. This is particularly true from the standpoint of the species emerging each year and thus the qualitative data probably have been affected only slightly by this circumstance. Although a portion of the differences observed, when comparisons are made of the quantitative data obtained from different stations in different years, may result from annual variation in emergence, it is improbable that the effect of this factor alone could account for all of the differences observed, and it is felt that such a comparison is of considerable value.

Quantitative Results

The total values for insect emergence from June 1 to August 31 at station 2 in 1939, station 3a in 1940, station 3 in 1938, and station 4 in 1939 illustrate the quantitative differences in the populations in rapids at different distances from the source (table 11). For the periods outlined above, a total of 5,393, 7. 175, 5, 440, and 31,505 insects

TABLE 11.—Quantitative analysis of the total insect emergence from June 1 to August 31 at station 2 in 1939, station 3a in 1940, station 3 in 1938, and station 4 in 1939.

	Station 2		Station 3a		Station 3		Station 4	
	No. of Insects	% of Total	No. of Insects	% of Total	No. of Insects	% of Total	No. of Insects	% of Total
Plecoptera	663	12.3	450	6.3	116	2.1	122	0.4
Ephemeroptera	502	9.3	1,035	14.4	3,037	55.8	1,820	5.8
Trichoptera	440	8.2	270	3.8	449	8.3	12,423	39.4
Chironomidae	3,699	68.6	3,446	48.0	1,703	31.3	5,304	16.8
Simuliidae	2	T	1,496	20.8	26	0.5	6,922	22.0
"Miscellaneous"	87	1.6	478	6.7	109	2.0	4,914	15.6
Total	5,393	100.0	7,175	100.0	5,440	100.0	31,505	100.0

emerged at stations 2, 3a, and 4 respectively. Thus the total emergence at the upper three stations showed only slight variation, while the emergence at station 4 was much greater than at any other station, although there was a considerable change in such conditions as width, depth, rate and volume of flow, and average temperature between each station. It was shown in the previous section that the number of insects found in any area is related to the utilizable surface area of bottom particles exposed to the water. This phenomenon is also clearly seen in this instance since the bottoms at stations 2, 3a, and 3 were similar, consisting of a few rocks imbedded in the underlying coarse gravel while at station 4, the bottom was made up of many rocks which were built up in layers with the bottom layer only imbedded.

However when the percentage of the total emergence at the various stations contributed by each of the main insect groups is considered, it is seen that there are changes in the relative importance of each group associated with distance from the source (table 11). The Plecoptera constituted 12.3, 6.3, 2.1, and 0.4 per cent of the total emergence at stations 2, 3a, 3, and 4 respectively. Thus this group made up an important part of the population near the source but decreased in relative importance downstream, until in the lower river region it constituted only a small proportion of the total population. The Chironomidae also decreased in relative importance downstream, dropping from 68.6 per cent of the total emergence at station 2 to 16.8 per cent at station 4. The Ephemeroptera constituted 9.3, 14.4, 55.8, and 5.8 per cent of the total emergence at stations 2, 3a, 3, and 4 respectively. The increase in relative importance of this group between stations 2 and 3 was accompanied by an increase in the number of individuals. At station 4 the number of individuals that emerged was greater than that at either station 2 or 3a, although it made up a smaller proportion of the total emergence than at the latter stations. Thus this group showed its maximum at station 3. The Trichoptera constituted only a small part of the population at the upper stations but was the most important single group at station 4 where it made up 39.4 per cent of the total emergence. The Simuliidae and "Miscellaneous" groups made up an appreciable portion of the total emergence at stations 3a and 4 but were of minor importance at stations 2 and 3.

Qualitative Results

TABLE 12.—Distribution of Plecoptera at stations 2, 3a, 3, and 4, showing the relative abundance of each species. A—over 50 individuals; F—from 10 to 50; R—from 1 to 10; T—1 individual. The abundance represents the maximum annual emergence for each station.

	Station 2	Station 3a	Station 3	Station 4
Leuctra sara	R			
Nemoura trispinosa	R			
Leuctra biloba	F			
Nemoura serrata	F			
Alloperla mediana	A			
Allocapnia pygmaea	R	R		
Nemoura venosa	F	F		
Leuctra decepta	A	F	F	
Nemoura punctipennis	F	R	R	
Leuctra sibleyi	A	A	R	
Leuctra hamula	A	A	F	
Isoperla montana	F	F	R	
Leuctra tenuis		A	A	
Isoperla sp. 1		F	F	
Alloperla imbecilla			R	
Isoperla truncata		F	R	A
Acroneuria abnormis		R	T	A
Hastaperla brevis			R	R
Isoperla transmarina				F
Acroneuria lycorias				R
Isoperla sp. 2				R
Hydroperla subvarians				T
Total	12	11	11	7

Plecoptera. The Plecoptera were represented by a total of 22 species of which 12 were found at station 2, 11 at station 3a, 11 at station 3, and 7 at station 4 (table 12). Thus, in general, the number of species decreased downstream as the distance from the source increased, and this was accompanied by a progressive change in the species comprising the fauna at each station. There were 5 species found only at station 2; 2 species confined to stations 2 and 3a; 5 species common to stations 2, 3a, and 3; 2 species confined to stations 3a and 3; 1 species found only at station 3; 2 species common to stations 3a, 3, and 4; 1 species confined to stations 3 and 4, and 4 species found only at station 4.

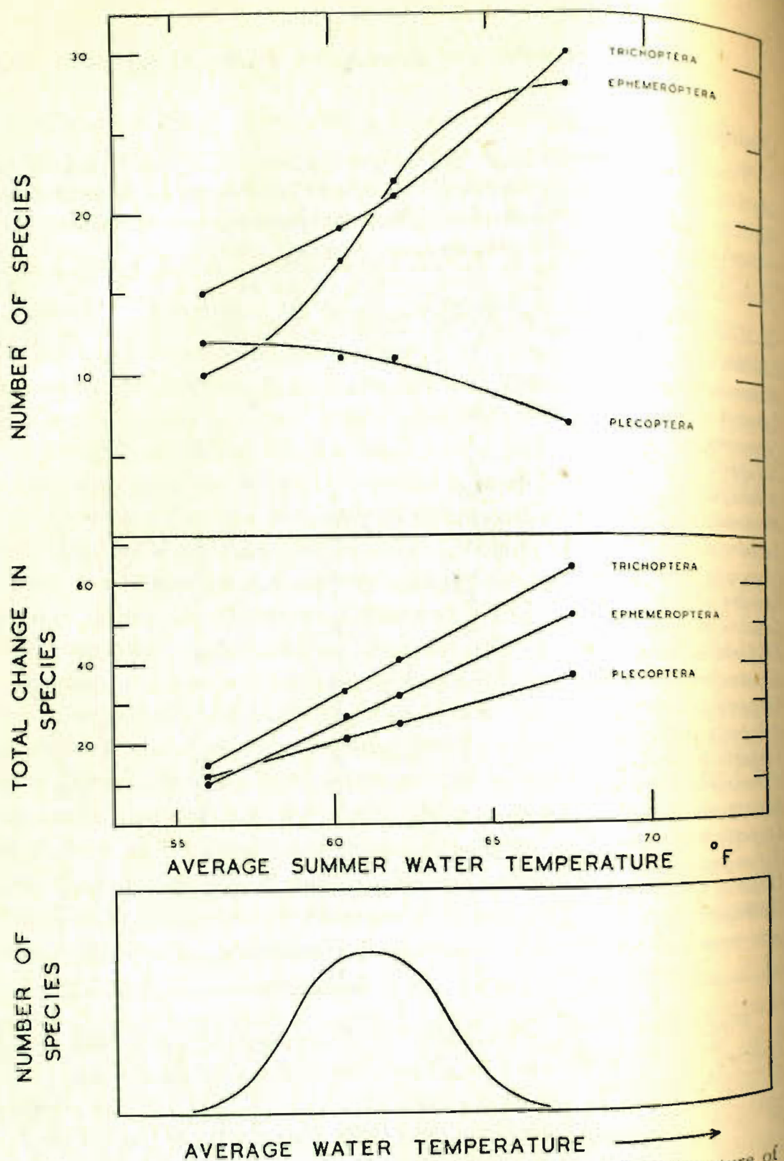

FIG. 8. Relationship of numbers of species of insects and temperature of the water.

Top panel: the relationship between number of species and average summer water temperature.

Centre panel: the relationship between the total change in species and the average summer water temperature.

Bottom panel: the hypothetical relationship between the number of species and average water temperature for any insect group over its complete temperature range in a stream.

There were no species common to stations 2 and 4 which were located at the upper and lower limits of this stream investigation. The faunas at the intermediate stations, 3a and 3, were similar and consisted of some species found at station 2 and others found at station 4, illustrating the progressive change that occurred downstream and the close faunal relationship existing between these two stations.

The change in the fauna downstream resulted from the successive disappearance of species found at the upper stations and addition of species found at the lower stations. The net decrease in the number of species resulted from the more rapid loss of upper-station species than gain of lower-station species (figure 8, top panel). It was found that there was a direct proportionality between the total change of species at successive stations and the average summer water temperature (figure 8, middle panel). There were 5 species found at station 2 which did not occur at station 3a while there were 4 species at the latter station which did not occur at station 2. Thus there was a total change of 9 species between these stations and an average temperature difference of 4.4 degrees Fahrenheit. The fauna at station 3 differed from that at station 3a by a total of 4 species, which included 2 eliminated and 2 added species, and the temperature index differed by 1.7 degrees. Eight species found at station 3 were eliminated at station 4 and there were 4 species at station 4 not found at station 3. This total change of 12 species was associated with an average temperature difference of 5.4 degrees Fahrenheit.

When the number of species belonging to each family occurring at a station was represented as a percentage of the total number of species found there, it was found that in general the Capniidae, Leuc-

TABLE 13.—Relative importance of the families of Plecoptera at the stations. The number of species in each family is represented as a percentage of the total number of species found at a station.

	Station 2	Station 3a	Station 3	Station 4
Capniidae	8.3%	9.1%		
Leuctridae	41.7%	36.4%	36.4%	
Nemouridae	33.3%	18.2%	9.1%	
Chloroperlidae	16.7%	27.3%	45.5%	57.1%
Perlidae		9.1%	9.1%	28.6%
Perlodidae				14.3%

tridae and Nemouridae decreased in relative importance downstream and the Chloroperlidae, Perlidae and Perlodidae increased (table 13). Consideration of the distribution of families at the stations augmented the information obtained from consideration of the distribution of species alone. Thus, although there were no species common to all the stations, one family, the Chloroperlidae, was represented at all the stations and increased in relative importance downstream, since it comprised 16.7 per cent of the population at station 2 and increased to 27.3, 45.5, and 57.1 per cent at stations 3a, 3, and 4 respectively.

When the relative abundance of each species at a station was compared along with the general distribution of species at the stations, it was found that the number of individuals decreased as the species approached the limits of its distribution (table 12). The species found at station 2 in almost every case showed their maximum abundance there and decreased numerically at stations farther downstream, having dropped out completely at station 4. The species found only at station 2 have a narrow range of thermal tolerance when considered from the standpoint of the stations used in this investigation, but it is probable that these would extend farther upstream if their complete distribution were known. The species common to station 4 and stations farther upstream showed a fairly wide range of tolerance, but in general the numbers were reduced at the upper stations, showing that the optimum conditions for the species prevailed at station 4. The species found only at station 4 would be those most likely to extend their distribution farther downstream.

Along with this numerical reduction it was found that the period of emergence for the species was restricted at the limits of its distribution. Those that were eliminated downstream were confined to a short period in the early part of the season at the lower stations, while at the upper stations the emergence occurred later in the season and in general extended for a longer period. For example, in 1940, *Leuctra sibleyi* emerged from June 4 to June 18 at station 2 and from May 31 to June 5 at station 3a. In 1941, this species emerged from May 21 to June 16 at station 2 and from May 16 to May 24 at station 3a. The species that were eliminated upstream from station 4 began to emerge on approximately the same date at the upper and lower stations but the period of emergence was reduced at the upper stations in general. This condition probably resulted from the slower fall cooling and spring warming of the water at station 4 compared with that at station 3 and 3a, and the higher maximum temperatures attained during the summer at the upper stations.

It was found that the period of emergence of Plecoptera at station 4 was restricted to the early summer, from late May to the middle of July, while at stations 2, 3a and 3 the emergence period extended from early spring to late fall. The late summer emergence at the upper stations resulted from the presence of *Leuctra tenuis* and *Leuctra decepta*. These were absent from station 4 as were also the early spring species including *Leuctra biloba* and the Capniidae.

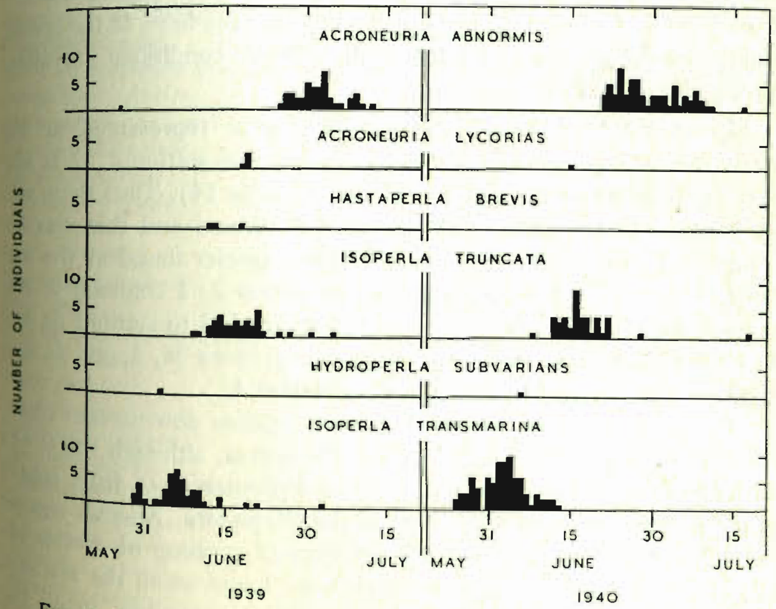

FIG. 9. Seasonal distribution of the emergence of representative Plecoptera at station 4 in 1939 and 1940.

The appearance of the species at a given station followed the same order each year. At station 4 the first species to appear each year was *Isoperla transmarina*, which was followed by *Hydroperla subvarians*, *Isoperla truncata*, *Hastaperla brevis*, *Acroneuria lycorias* and *Acroneuria abnormis* (figure 9). The species at the other stations also followed an orderly seasonal appearance each year. The date of first emergence, length of the emergence period and form of the emergence polygon of any species was subject, however, to annual variation. This seems to depend on the water temperature during the fall and spring preceding the emergence. Thus a warm spring pushed the date of the first emergence of a species forward and if the warm spell continued the period of emergence was short and the number of individuals emerging each day, large. Conversely, a cool spring delayed the date of first emergence, lengthened the period of emergence, and decreased the number of individuals that emerged each day. For example, *Acroneuria abnormis* at station 4 emerged from June 19 to July 11 in 1938, from June 25 to July 12, 1939 (figure 9), and from June 21 to July 17, 1940 (figure 10), and the form of the annual emergence polygons was related to the climatic conditions prevailing during the period of emergence.

Ephemeroptera. The Ephemeroptera were represented at the stations by 40 species, of which 10 were found at station 2, 17 at station 3a, 22 at station 3 and 28 at station 4 (table 14). Thus there was an increase in the number of species downstream and this was accompanied by a progressive change in the species found at the stations. There were 5 species confined to station 2; 1 common to stations 2, 3a, and 3; 4 common to all the stations; 5 to stations 3a and 3; 1 found only at station 3; 7 common to stations 3a, 3, and 4; 4 to stations 3 and 4, and 13 found only at station 4.

The general pattern of distribution of species downstream corresponded closely to that found in the Plecoptera, although there was an increase in the number of species of Ephemeroptera from source to river conditions and a decrease in the Plecoptera. Another significant difference observed was the presence of a group of species belonging to the Ephemeroptera which were found at all the stations, while in the Plecoptera there were no species common to all the stations. The faunas at stations 2 and 4, which were at the upper and lower limits of the investigation, differed markedly while those at stations 3 and 3a were similar.

The progressive change in the fauna downstream resulted from the disappearance of species found at the upper stations and the addition of species found at lower stations. The net increase downstream resulted from a more rapid gain than loss of species (figure 8, top

TABLE 14.—Distribution of Ephemeroptera at stations 2, 3a, 3, and 4, showing the relative abundance of each species. A—over 50 individuals; F—from 10 to 50; R—from 1 to 10; T—1 individual. The abundance represents the maximum annual emergence for each station.

	Station 2	Station 3a	Station 3	Station 4
Centroptilum convexum	T			
Centroptilum semirufum	R			
Ameletus ludens	F			
Stenonema carolina	A			
Baetis brunneicolor	A			
Leptophlebia debilis	A	A	A	
Heptagenia pulla	F	A	A	F
Ephemerella sp. (*bicolor* gr.)	F	R	R	F
Leptophlebia mollis	T	F	A	F
Baetis sp. (*pygmaeus* gr.)	T	F	A	A
Leptophlebia adoptiva		F	F	
Stenonema rubromaculatum		F	F	
Stenonema ?vicarium		R	R	
Epeorus humeralis		F	R	
Centroptilum simile		R	T	
Baetis parvus			T	
Baetis cingulatus		F	F	R
Stenonema canadense		F	F	F
Baetis pluto		F	A	F
Habrophlebia vibrans		A	A	T
Heptagenia hebe		R	R	T
Baetis flavistriga		A	A	A
Leptophlebia volitans		T	F	A
Ephemerella invaria			T	F
Stenonema fuscum			F	F
Pseudocloeon carolina			R	F
Leptophlebia guttata			R	T
Stenonema heterotarsali				F
Stenonema rubrum				A
Stenonema luteum				R
Isonychia bicolor				A
Heterocloeon curiosum				A
Heptagenia ?minerva				R
Ephemerella sp. (near *serrata*)				R
Pseudocloeon cingulatum				F
Baetis vagans				F
Stenonema sp. (near *integrum*)				F
Ephemerella subvaria				T
Pseudocloeon ?dubium				F
Pseudocloeon ?virile				R
Total	10	17	22	28

panel). When the total change of species at successive stations was determined it was found that this change was directly related to the average summer water temperature (figure 8, centre panel).

Consideration of the relative abundance of a species at different stations indicates where optimum conditions for that species occur within the limits of this investigation. For example, *Leptophlebia volitans* was represented abundantly at station 4, frequently at station 3,

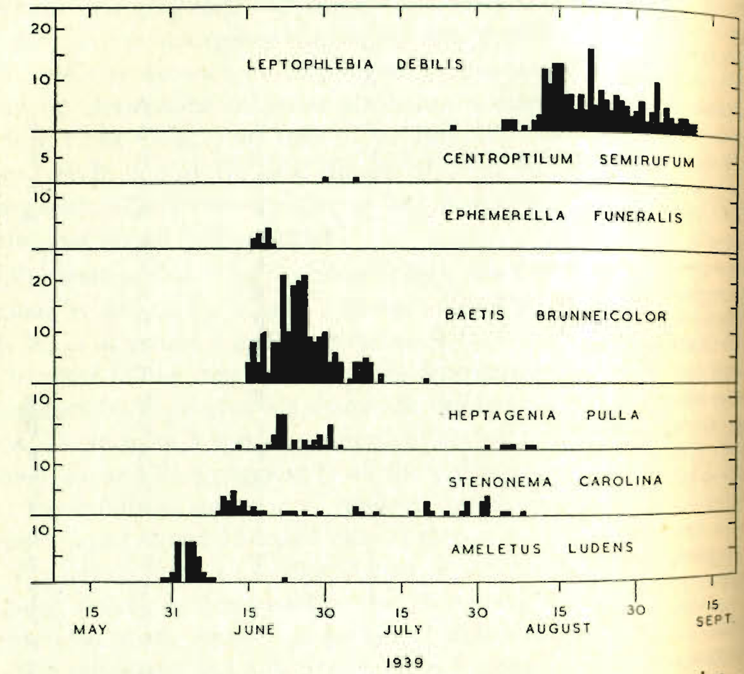

FIG. 10. Seasonal distribution of the emergence of representative Ephemeroptera at station 2 in 1939.

by a trace at station 3a and was absent from station 2 (table 14). Thus, as was found in the Plecoptera, the number of individuals decreased as the limits of distribution of a species were approached. The species found only at station 2 would probably extend their distribution farther upstream while those confined to station 4 would most likely be found in lower sections of the stream. Further, the species that were eliminated downstream emerged earlier each year and had a shorter emergence period at the lower stations than at the upper stations, as was found to be the case in the Plecoptera; the species that were eliminated upstream also had a restricted emergence at the limit of their distribution.

The seasonal distribution of Ephemeroptera showed the same general sequence as was found in the Plecoptera. The species found at any one station appeared in the same general order each year, with some confined to the early season, others to midsummer, others to the late summer, while some emerged throughout the summer months (figure 10). There were no species that emerged as early in the spring as the first Plecoptera species at any station and the emergence continued later in the fall than did that of the Plecoptera.

The date of first emergence and the nature of the emergence polygon of any species varied from year to year and these variations seemed to be directly related to the seasonal water temperature at the station. For example *Ameletus ludens* at station 2 began to emerge on May 29, 1939, and had completed its emergence by June 8 with the exception of one individual which emerged on June 22 (figure 10). Thus the emergence period lasted for 25 days although all but one individual had emerged in 11 days. In 1940 this species began to emerge 5 days later, June 2, and continued until June 27, a period of 26 days, but in this year the emergence was more evenly distributed throughout the period. Associated with this change was a period of high temperature from May 28 to June 2, 1939, following which the temperature dropped, while in 1940 comparable temperatures were not reached until June 2 and 3, following which the temperature dropped.Thus it is probable that the high temperatures attained in 1939 were responsible for the earlier appearance of this species that year as well as for the shortened period of emergence.

Such a period of high temperature does not affect noticeably the date of first emergence of species that appear later in the summer. Thus *Baetis brunneicolor* began to emerge on June 15, 1939, at station 2, while in 1940 it first emerged on June 12, four days earlier. The apparent lack of correlation between the first emergence dates of these two species in 1938 and 1939 probably resulted from the water temperatures effective between the dates of their initial emergence. Miller (1941) proposed that the time required for lake water of different depths to acquire a certain accumulated heat in day-degrees explained the varying time of emergence of Chironomidae at these depths. It is probable that a similar explanation would account for the annual variation in time of emergence of stream insects as well.

Trichoptera. The Trichoptera were represented at the stations by a total of 46 species of which there were 15, 19, 21, and 30 found respectively at stations 2, 3a, 3, and 4 (table 15). Thus there was an increase in the number of species downstream as was found in the Ephemeroptera. There were 7 species confined to station 2; 2 common to stations 2 and 3a; 4 to stations 2, 3a, and 3; 2 to stations 2, 3a, 3, and 4; 3 common to stations 3a and 3; 7 to stations 3a, 3, and 4; 1 to stations 3a and 4; 5 to stations 3 and 4; and 15 found only at station 4.

The changes in the fauna downstream resulted from the elimination of species found in the upper reaches of the stream and the addition of species found in the lower reaches. The net increase in number of species found downstream resulted from a more rapid rate of gain than loss of species (figure 8, top panel). The total change of species at successive stations was determined by summing the number eliminated from the nearest upstream station and the number added, and it was found that this change was proportional to the average summer water temperature (figure 8, centre panel).

As was found in the distribution of Plecoptera and Ephemeroptera, the number of individuals of any species decreased in general as the limits of distribution of the species were approached. For example, *Lepidostoma grisea* occurred abundantly at station 2, rarely at station 3a, while only a single individual emerged at station 3 (table 15). The species found only at station 2, which had the lowest average temperature of any of the stations used in this investigation, showed a narrow range of temperature tolerance and may be described as stenothermal cold-tolerant forms. However, if the complete distribution of such species were known, it is probable that they would show a greater range and would extend farther upstream. Similarly the species found only at station 4, which was located at the other extreme of temperature within the limits of this study, may be termed stenothermal warmth-tolerant species, but would likely extend farther downstream if their complete distribution were known. The species that emerged from two or more stations showed various ranges of thermal tolerance and *Psychomyia diversa* and *Polycen-*

TABLE 15.—Distribution of Trichoptera at stations 2, 3a, 3, and 4, showing the relative abundance of each species. A—over 50 individuals; F—from 10 to 50; R—from 1 to 10; T—1 individual. The abundance represents the maximum annual emergence for each station.

	Station 2	Station 3a	Station 3	Station 4
Hydroptila sp.	R			
Dolophilus moestus	F			
Parapsyche apicalis	F			
Goera stylata	F			
Micrasema sprulesi	F			
Rhyacophila vibox	F			
Lepidostoma ontario	A			
Hydropsyche ventura	F	F		
Neophylax autumnus	R	R		
Philopotamus distinctus	A	A	F	
Rhyacophila carolina	F	F	R	
Stenophylax guttifer	T	R	T	
Lepidostoma grisea	A	R	T	
Psychomyia diversa	R	R	R	R
Polycentropus confusus	R	R	F	A
Cheumatopsyche pettiti		F	F	
Agapetus sp.		R	R	
Hydropsyche betteni		F	F	
Chimarrha aterrima		F	A	A
Nyctiophylax vestitus		F	R	F
Plectrocnemia cinerea		R	R	A
Athripsodes dilutus		T	R	F
Rhyacophilo fuscula		R	R	F
Hydropsyche sparna		R	F	R
Athripsodes angustus		T	R	F
Mysiacides sepulchralis		R		T
Osythira sp.			T	T
Agraylea costello			T	F
Phylocentropus placidus			T	R
Cheumatopsyche campyla			R	A
Psychomyella flavida			R	R
Rhyacophila vuphipes				R
Chimarrha socia				R
Chimarrha lucia				A
Hydropsyche morosa				A
Hydropsyche dicantha				A
Hydropsyche recurvata				A
Athripsodes alces				F
Athripsodes welzeli				R
Oecetis avara				R
Macronema zebratum				A
Neureclipsis crepuscularis				A
Neureclipsis parvulus				F
Micrasema wataga				F
Cheumatopsyche gracilis				A
Cheumatopsyche miniscula				A
Total	15	19	21	30

tropus confusus, which occurred at all the stations, may be described as eurythermal species.

The emergence periods of different species were seasonally distributed throughout the summer months from early May on through September at all stations. The first species to emerge at station 4 each year appeared later than those at the upper stations and this seemed to result from the slower rise in water temperature at this

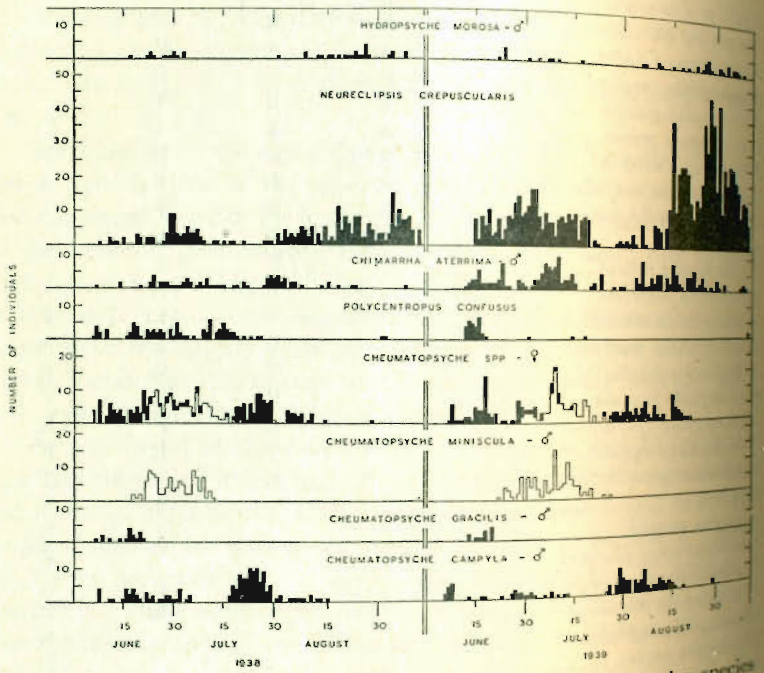

FIG. 11. Seasonal distribution of the emergence of representative species of Trichoptera at station 4 in 1938 and 1939.

station dependent on the greater volume of water to be heated in the spring. The species emerged in the same order each year, and the date of first emergence and length of the emergence period were affected by annual temperature variations as was found for species of Plecoptera and Ephemeroptera. The emergence polygons of a few representative species of Trichoptera have been illustrated in figure 11.

An indication of the emergence of two generations during the summer at station 4 was obtained for certain species including *Hydropsyche morosa* and *Cheumatopsyche campyla* (figure 11). Marshall (1939) found two brood flights of some species of Trichoptera in the lake Erie region including *Cheumatopsyche campyla* and suggests the possibility that the individuals of the second brood are the descendants of those of the first, making two generations in one season. Detailed study of the development of the immature stages is necessary before a definite statement regarding second generations may be made. However, no consistent suggestion of two seasonally isolated groups in any species was obtained at the other stations and it is probable that second generations do occur in certain species at station 4 where a high average summer temperature is maintained for a long period. Miller (1941) found evidence of the occurrence of two generations of certain species of Chironomidae in shallow lake water and pointed out that certain species with only one generation a year in northern waters were known to have two generations in their southern range where the summer is longer. He associated the occurrence of two generations with the day-degree requirements for development of the species and it seems probable, from the results obtained for some species at station 4, that a similar explanation would account for the appearance of two seasonally isolated groups within a species in stream environments with a prolonged period of high average summer temperature.

Discussion

The results of this investigation showed that there is a differential linear distribution of insects in rocky riffle sections of a stream which is related to the distance from the source. Associated with this distribution is the increase in the size of a stream as it develops from the source and an increase in the average water temperature. It has been shown that temperature is of prime importance in limiting the linear distribution of species and it is probable that the other factors are of secondary importance in this respect.

A direct correlation was found between the total change of species at successive stations and the average summer water temperatures found there. This total change was derived by summing the number of species eliminated and number of species added at each station. The elimination of species downstream probably resulted from the increase in water temperature. It was found from a series of experiments on the nymphs of Plecoptera that although the lethal temperature was well above the temperatures obtaining in the stream, the value was lower for the species found at the upper stations than for those found at the lower stations. Within this group the species show a gradation of upper limits of temperature tolerance. It would appear from these results that the nymphs are able to withstand the highest stream temperatures, at least for a short period, but prolonged exposure to these may limit the distribution of certain species. Since the experiments were carried out on practically full-grown nymphs in every instance, the possibility that the limiting effect of high temperatures may be active on some other stage of the life-cycle cannot be overlooked. Ide (1935) studied the effect of temperature on the distribution of Ephemeroptera in a stream and found that species dropped out down-stream became successively limited to the early season at the lower stations, he states "that the latest date at which individuals emerge successfully at a station is determined by the temperatures obtaining at that station." He proposed that this resulted from a process of selection on the nymphs by heat over a number of years. This explanation could well account for the elimination of species downstream found in the present study, since it has been shown that the number of individuals in a species decreased as the species approached the lower limit of its distribution, and evidence of the restriction of the emergence period to the early part of the season as the species approached its lower limit was obtained.

The absence of certain species from the upper stations seemed to result from the lower average temperatures found there, which may retard the rate of growth sufficiently to prevent the species from completing their life-cycle. It has been shown that the temperatures prevailing prior to emergence affect the date of first emergence of a species at a station from year to year so that, if the average temperature differences at two stations were great enough, it is probable that this would limit the distribution as Ide (1935) found to be the case in the distribution of Ephemeroptera in a stream. Since the maximum temperatures recorded at stations 3 and 3a were higher than those recorded at station 4, although the latter was farther downstream, it is possible that certain species found at the lower station were eliminated

at stations 3 and 3a by the higher temperatures which may have proved lethal.

Since there were no species of Plecoptera common to stations 2 and 4, located at the extremes of average summer water temperatures found in this investigation, it would seem that the average range of thermal tolerance of this group was small. On further analysis it was found that 45.5 per cent of the species had a range of thermal tolerance extending from either station 2 or station 4 to the intermediate stations 3 and 3a, and 54.5 per cent had a range restricted to one section of the stream. The Ephemeroptera had only 40.0 per cent of the species with a wide range of thermal tolerance, and 60.0 per cent with a restricted range, although there were some species common to all the stations and thus able to withstand the widest temperature extremes obtained. The average range of thermal tolerance of the species of Trichoptera was practically identical with that of the Plecoptera with 45.6 per cent of the species showing a wide range and 54.4 per cent a narrow range.

In all the groups the species that were confined to the upper station are probably stenothermal cold-tolerant forms while those found at the lower station only are stenothermal warm-tolerant species. The species of Ephemeroptera and Trichoptera that were found at all the stations seem to be eurythermal but there were no species of Plecoptera that could be classified in this manner.

Since there was a decrease in the number of species of Plecoptera found downstream it would seem that this group is made up primarily of species adapted as cold-tolerant. This is substantiated by distribution records of the group and the occurrence of winter Plecoptera which complete their life-cycle during the winter with the adults living on the snow and ice at the margins of streams (Frison, 1929). The number of species in the Ephemeroptera and Trichoptera increased downstream; in general it seems, therefore, that these groups are made up primarily of warmer water species. Since the rate of increase of species was decreasing at station 4 in the Ephemeroptera and still increasing in the Trichoptera, it would seem that in the latter group there were more species adapted to warm water conditions, and these to warmer water in general, than was the case in the Ephemeroptera.

Within the temperature limits of the present investigation the observed distribution suggests that species of each group, provided the temperature range were extended, would exhibit a normal curve of distribution along the temperature gradient. The positions of the mode and the length of the distribution diagram would depend on the average optimal temperature and the range of thermal tolerance. The height of the mode would vary also, dependent on the number of species belonging to any insect group. For the perfect expression of these curves, environmental conditions other than those dependent on temperature would have to be uniform. The number of species of Plecoptera decreased downstream as the average temperature increased, while the Ephemeroptera and Trichoptera increased (figure 8, top panel). The nature of the respective increases in the last two groups differed however, since between stations 3 and 4 the rate of increase slowed down in the Ephemeroptera while it continued unabated in the Trichoptera. Thus, considering these distributions in the light of the hypothetical distribution outlined above, the portion of the Plecoptera distribution diagram obtained in this study was a section to the right of the mode and it would seem probable that the mode would occur at a temperature close to that of station 2. The diagram for the Ephemeroptera distribution consisted of a section immediately to the left of the mode and the mode would occur at a temperature close to that found at station 4. The Trichoptera distribution also is illustrated by a section of the hypothetical distribution curve to the left of the mode but no indication of the position of the mode was obtained and it may be assumed that it would occur farther downstream where a higher average temperature prevailed.

Further insight into the role played by temperature in limiting the distribution of insect species in a stream can be obtained from a consideration of the fauna at station 1. There was an intermittent flow at this station and although it was located closer to the source than station 2, the average summer temperature approximated that found at stations 3a and 3. Two species of Trichoptera. *Hydropsyche bettini* and *Cheumatopsyche pettiti*, were found at stations 1, 3a. and 3, but were not found at station 2. Ide (1935) also gives an example of such a station not falling into the direct series. Thus this distribution indicates that temperature sets limits to the distribution of insects and that species are found in widely separated sections of a stream pro-

viding the prevailing water temperatures are within the limits required for development of the species.

The results showed that the total number of insects emerging from one type of bottom at different levels of the stream gradient is not related as closely to temperature as is the number of species. The evidence obtained suggested that the total number of insects is more closely related to the utilizable surface area of bottom particles exposed to the water. However these results are not entirely in agreement with findings elsewhere. Needham (1928) and Pate (1931, 1932, and 1933) showed a relationship between the amount of bottom fauna in a stream and the width. They found that in general small headwater streams are more productive per unit area than the large streams. However it is probable that the stream conditions are much different in the various areas studied by other investigators. In the light of more recent investigation Needham has found that certain large rivers such as the Klamath river in northern California are very rich in the amount of bottom fauna present and that a high organic content was associated with this condition. Further, he states (Needham, 1938) that "It has become quite evident that what is true for one drainage area does not by any means hold true for another. Each presents its own environmental peculiarities and each must be studied individually."

SUMMARY

1. An investigation of the quantitative and qualitative distribution of insects in streams of Algonquin Park, Ontario, was carried out to determine the effect of different environmental conditions on the distribution of insects.

2. The cage-trap method which samples the emergence of insects from unit areas was used in the study since it is applicable to the diverse habitats associated with lotic environments.

3. Data were obtained from ten stations selected throughout the Madawaska river system.

4. It was found that when hourly collections were made from a cage-trap the value obtained for the total *number* of insects which emerged in a twenty-four interval was approximately twice that obtained when only one collection was made in the same interval.

5. In general any one species emerged at the same time each day and different species emerged at different hours throughout a twenty-

four-hour interval. It was found that the maximum total emergence from a rocky riffle in midsummer occurred at 11.00 p.m. each day and that the majority of insects emerged between sundown and midnight.

6. The insect population was reduced in areas where the bottom was scoured by a severe freshet. The reduction resulted from the loss of individuals which were dislodged and swept downstream by the current and the elimination of others through molar action. The effect of the freshet was minimized in areas where the bottom was relatively stable and consisted of large particles which afforded shelter.

7. An intermittent flow and consequent drying of the stream bed limited the number of individuals and species present. It was found that species of fixed habit, such as certain of the Trichoptera and the Simuliidae, were eliminated rapidly as the water receded from the stream margins, while the free-roving forms such as nymphs of Ephemeroptera were able to follow the receding water and thus were not affected by the desiccation in its early stages.

8. The transformation of a shallow rocky rapids into a deep sedimented pool by a beaver dam brought about an immediate reduction in the number of individuals and number of species in the area. The decrease resulted from the elimination of a large group of insects that were dependent on current for respiration and feeding, and the addition of a smaller group of quiet-water species which extended their distribution into the area once the restrictions of current were removed. A small number of species showed a wide range of habitat tolerance and persisted under both sets of conditions.

9. A variation in the number of species and number of individuals was found associated with different types of bottom in a restricted section of the stream. Rocky riffles were most productive, followed in order by gravel, muck, and sand bottoms. The diversity of the fauna found on any particular type of bottom was related to the variety of utilizable microhabitats associated with the bottom type. It has been suggested that the number of insects present in any area is related to the habitable surface area of bottom particles exposed to the water.

10. A change was found in the species composing the fauna of rapid riffles at different distances from the source of the stream. This change resulted from the progressive elimination of species found in the upper reaches of the stream and the addition of species found in the lower reaches. A direct correlation was found between the total change in the number of species in successive riffles at different distances from the source and the average summer water temperature.

11. The emergence periods of different species were seasonally segregated as a result of differences in thermal requirements and the species emerged in the same order each year. The date of first emergence, length of the emergence period and form of the emergence histogram of any species differed annually probably in response to differences in the water temperatures during the developmental period from oviposition to emergence.

12. Species were found in widely separated sections of the stream providing the temperatures in these areas were suitable for the development of the species.

13. The quantitative and qualitative distribution of insects observed in streams results from the complex interaction of many environmental factors, of which temperature, nature and configuration of the bottom particles, and rate of flow are of fundamental importance.

LIST OF SPECIES

The following species belonging to the orders Plecoptera, Ephemeroptera and Trichoptera were identified from the collections made during the investigation.

PLECOPTERA

Classification after Frison (1935).

Nemouridae

Nemoura punctipennis Claassen
Nemoura serrata Claassen
Nemoura trispinosa Claassen
Nemoura venosa Banks

Leuctridae

Leuctra biloba Claassen
Leuctra decepta Claassen
Leuctra duplicata Claassen
Leuctra hamula Claassen
Leuctra sara Claassen
Leuctra sibleyi Claassen
Leuctra tenuis Pictet

Capniidae

Capnia sp.
Allocapnia pygmaea (Burm.)

Perlidae

Acroneuria abnormis (Newman)
Acroneuria lycorias (Newman)

Perlodidae

Hydroperla subvarians (Banks)

Chloroperlidae

Hastaperla brevis (Banks)
Isoperla montana Banks
Isoperla sp. 1
Isoperla sp. 2
Isoperla transmarina (Newman)
Isoperla truncata Frison
Alloperla imbecilla (Say)
Alloperla mediana Banks

EPHEMEROPTERA

Classification modified from Needham, Traver and Hsu (1935).

Heptageniidae

Stenonema canadense Walker
Stenonema carolina Banks
Stenonema fuscum Clemens
Stenonema heterotarsale McDunnough
Stenonema luteum Clemens
Stenonema rubromaculatum Clemens
Stenonema rubrum McDunnough
Stenonema sp. (near *integrum* McDunnough)
Stenonema ?vicarium Walker
Heptagenia hebe McDunnough
Heptagenia ?minerva McDunnough
Heptagenia pulla Clemens
Epeorus humeralis Morgan
Arthroplea bipunctata McDunnough

Baetidae

Metretopinae
Siphloplecton basale Walker

Siphlonurinae
Ameletus ludens Needham
Siphlonurus alternatus Say
Siphlonurus quebecensis Provancher
Isonychia bicolor Walker

Leptophlebiinae
Leptophlebia johnsoni McDunnough
Leptophlebia adoptiva McDunnough
Leptophlebia debilis Walker
Leptophlebia guttata McDunnough
Leptophlebia mollis Eaton
Leptophlebia volitans McDunnough
Blasturus cupidus Say
Blasturus nebulosus Walker
Choroterpes basalis Banks
Habrophlebia vibrans Needham

Baetiscinae
Baetisca laurentina McDunnough

Ephemerellinae
Ephemerella deficiens Morgan
Ephemerella funeralis McDunnough
Ephemerella invaria Walker
Ephemerella lutulenta Clemens
Ephemerella sp. (near *bicolor* Clemens)
Ephemerella sp. (near *serrata* Morgan)
Ephemerella subvaria McDunnough

Caeninae
Tricorythodes sp.
Brachycercus sp.
Caenis sp.

Baetinae

Baetis brunneicolor McDunnough
Baetis cingulatus McDunnough
Baetis flavistriga McDunnough
Baetis ?frondalis McDunnough
Baetis parvus Dodds
Baetis pluto McDunnough
Baetis sp. (near *pygmaeus* Hagen)
Baetis vagans McDunnough
Centroptilum convexum Ide
Centroptilum ?ozburni McDunnough
Centroptilum semirufum McDunnough
Centroptilum simile McDunnough
Heterocloeon curiosum McDunnough
Pseudocloeon carolina Banks
Pseudocloeon cingulatum McDunnough
Pseudocloeon ?dubium Walsh
Pseudocloeon ?virile McDunnough
Cloeon minor McDunnough
Cloeon rubropictum McDunnough
Cloeon simplex McDunnough
Cloeon triangulifer McDunnough

TRICHOPTERA

Classification modified form Betten (1934)

Rhyacophilidae

Rhyacophilanae

Rhyacophila carolina Banks
Rhyacophila fuscula (Walker)
Rhyacophila invaria Walker
Rhyacophila vibox Milne
Rhyacophila vuphipes Milne

Glossosomatinae

Agapetus sp.

Hydroptilidae

Agraylea costello Ross
Hydroptila sp.
Oxyethira sp.

Philopotamidae

Philopotamus distinctus Walker
Dolophilus moestus (Banks)
Chimarrha aterrima Hagen
Chimarrha lucia Betten
Chimarrha socia Hagen

Hydropsychidae

Hydropsychinae

Parapsyche apicalis (Banks)
Diplectrona modesta Banks
Hydropsyche betteni Ross
Hydropsyche dicantha Ross
Hydropsyche morosa (Hagen)
Hydropsyche recurvata Banks
Hydropsyche sp.
Hydropsyche sparna Ross
Hydropsyche ventura Ross
Cheumatopsyche campyla Ross
Cheumatopsyche gracilis (Banks)
Cheumatopsyche miniscula (Banks)
Cheumatopsyche pettiti (Banks)

Macronematinae

Macronema zebratum Hagen

Polycentropidae

Polycentropinae

Neureclipsis crepuscularis (Walker)
Neureclipsis parvulus Banks
Phylocentropus placidus (Banks)
Plectrocnemia cinerea (Hagen)
Polycentropus confusus Hagen
Polycentropus maculatus Banks
Polycentropus pentus Ross
Nyctiophylax vestitus (Hagen)

Psychomyidae

Psychomyia diversa Banks
Psychomyella flavida (Hagen)

Molannidae

Molanninae

Molanna sp.

Leptoceridae

Leptocerinae

Athripsodes alces Ross
Athripsodes angustus (Banks)
Athripsodes dilutus (Hagen)
Athripsodes wetzeli Ross
Oecetis avara (Banks)
Oecetis inconspicua (Walker)
Mystacides sepulchralis (Walker)

Limnephilidae

Limnephilus consocius Walker
Stenophylax guttifer (Walker)
Platycentropus indicans (Walker)
Neophylax autumnus Vorhies
Pycnopsyche aglonus Ross

Sericostomatidae

Brachycentrinae

Micrasema sprulesi Ross
Micrasema wataga Ross

Goerinae

Goera stylata Ross

Lepidostomatinae

Lepidostoma costalis (Banks)
Lepidostoma grisea Banks
Lepidostoma ontario Ross

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