THE EFFECT OF A BEAVER DAM ON THE INSECT FAUNA OF A TROUT STREAM[1]

WILLIAM M. SPRULES
Ontario Fisheries Research Laboratory, University of Toronto, Toronto, Canada

ABSTRACT

A qualitative and quantitative investigation of the distribution of aquatic insects in Mud Creek, Algonquin Park, Ontario, has been carried out during the summer months of the last 3 years. Samples of the population present were obtained by trapping the insects which emerged from 1 square yard of water surface.

In the first season the field station described in this report was characterized by a rubble bottom and rapid flow of water. These conditions remained unaltered during the first part of the second season and the insect emergence for this period corresponded closely with that of the previous year. In early July, however, beavers constructed a dam across the stream flooding the riffle section which was under observation. The number of insects emerging immediately decreased as species dependent on a lotic environment were destroyed or forced to migrate. A few species were able to tolerate the new ecological conditions while a numerically small group of species typically found in quiet water entered the area. In the third season the lentic nature of the habitat was continued and the change in the fauna was more complete since the total population approximated that of a slow-flowing, silted stretch of the stream.

INTRODUCTION

The data presented in this paper were obtained unexpectedly in connection with a more extensive stream survey carried out on Mud Creek, Algonquin Park, Ontario, during the last 3 years to determine the qualitative and quantitative distribution of insects in the stream. The conditions reported upon were established in the course of the investigation by the normal inhabitants of the environment and present what may be termed a natural field experiment.

Mud Creek flows along a wide valley flanked by hills which reach an altitude of 1,600 feet, and empties into the Madawaska River, one of the main tributaries of the Ottawa River. The stream averages 12 feet in width throughout most of the summer and possesses many long, shallow riffle sections where the water flows rapidly over gravel, rubble or bed rock, terminating in each instance in deep, slow-flowing, silted pools. The water is slightly acid which is typical of most of the waters found in this Precambrian Shield area. The surrounding country was swept by an intensely devastating forest fire in 1914, which left this portion landmarked by charred rampikes jutting among the new growth of poplar and birch. Beaver dams and ponds are of fre-

[1]This research has been assisted by a grant from the National Committee on Fish Culture of the National Research Council of Canada, to whom the author is deeply indebted.

quent occurrence along the course of the stream, in some sections the latter entirely supplanting the riffles.

In 1938 a field station designated as No. 3 was established in one of the riffle areas and the insect population present was determined. The station was re-established in 1939 in the same position, and up to the end of June the physical nature of the stream here corresponded closely in the two seasons, but early in July beavers constructed a dam across the stream 100 yards below the site of the station. This brought about an immediate change in the physical character of the aquatic environment for almost 200 yards above the dam. This new condition was quite perturbing since it was hoped that a check on the results of the 1938 data could be obtained. Consequently attempts were made to discourage the beavers by breaking a large hole in the dam every day. It soon became evident that this procedure was of no avail and the dam was left relatively undisturbed for the duration of the investigation. The insect emergence was sampled as usual to discover if any significant changes arose which could be correlated with the newly imposed ecological conditions. The results were so marked that the investigation was carried on again in 1940 to cast further light on the problem.

Method

The method used in this survey was identical with that used by Ide (1940) in similar stream surveys for the past few years. A trap or cage consisting of a wooden framework measuring 1 yard in all dimensions, the top and sides of which were covered with 15 mesh to the inch copper screening, was placed in an upright position in the stream covering 1 square yard of bottom. The screening constituting the sides extended well below the water surface but did not come into direct contact with the bottom particles. Thus insects emerging from the water surface covered by the cage were captured while the immature stages were free to move into or out of the area. The trap was visited daily at approximately the same time and completely cleared of the insects which had emerged from the enclosed water surface in the preceding 24-hour interval. The collections were preserved in alcohol and retained for identification.

Physical and Chemical Changes in the Environment

The most significant changes in the aquatic environment at the station arose in the physical nature of the stream following the construction of the beaver dam and were directly related to the flooding of the area brought about by the retention of water at the dam. As the beavers increased the height of the dam, the amount of water held back increased correspondingly and flooded farther and farther upstream until finally the riffle which was under observation was completely obscured.

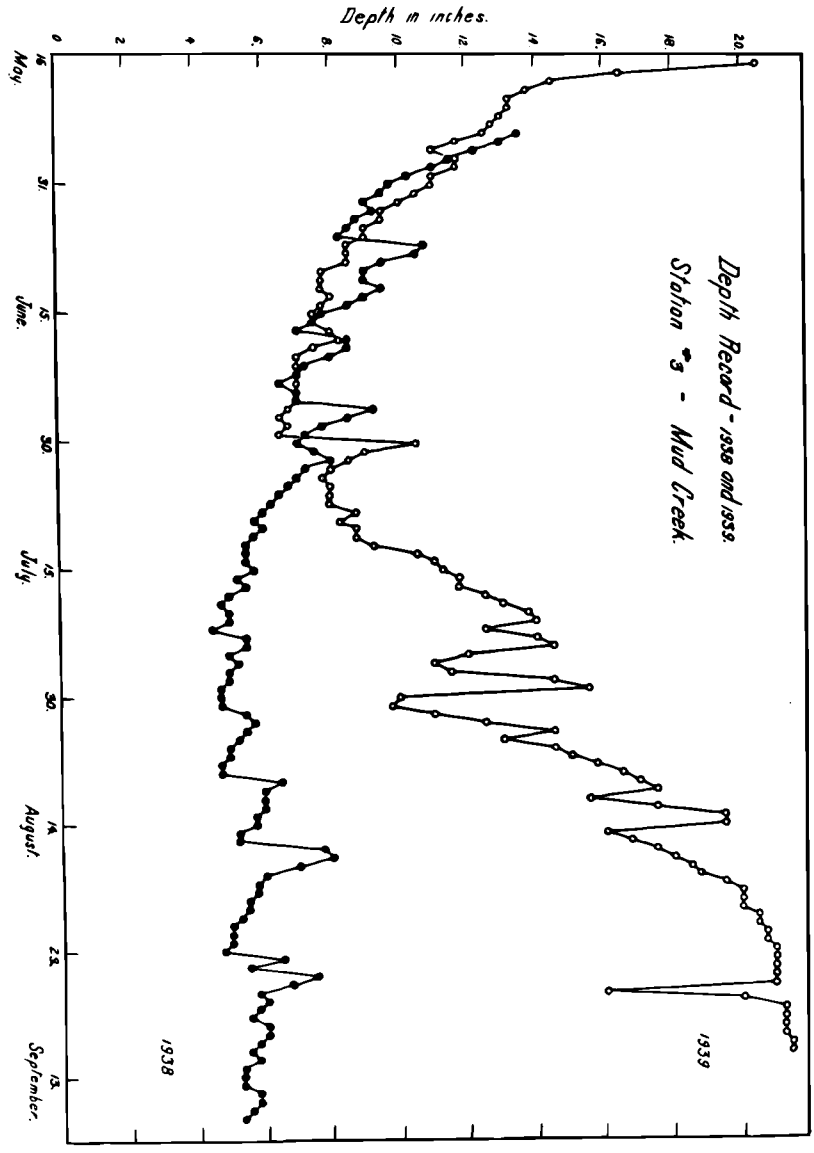

Figure 1.—Seasonal variation in the depth of water at station No. 3, Mud Creek, for the years 1938 and 1939

The depth of water at the station was recorded daily from a graduated stake driven into the stream bed, and these records are illustrated for the first two seasons in Figure 1. In 1938 the water depth decreased continually from the latter part of May to the middle of July with the exception of occasional increases brought about by local rainfall. From the middle of July to the middle of September the depth remained fairly constant averaging 5½ inches. In 1939 the water depth decreased in a similar manner up until the end of June, at which time the depth began to increase, gradually reaching 21½ inches by the middle of September. In this latter period the water level was lowered at intervals by breaking a hole in the dam in order to facilitate collecting at the station. In 1940 the depth averaged 22 inches throughout the season and showed only minor fluctuations.

A decrease in the rate of flow of water at the station accompanied the increase in depth. In each season the rate was greatest in the early part of the year as a result of the spring flood and decreased continually throughout the remaining months. The average rate of flow of water in the first season was 1.2 feet per second. In the second season the average value dropped to 0.5 feet per second and throughout most of the last season the rate was too small to be satisfactorily measured.

Directly associated with the decrease in the rate of flow of water at the station which followed the construction of the beaver dam there occurred a noticeable deposition of sand, silt and other particulate matter, brought about as a result of the reduced transport power of the water. The interstitial spaces among the rubble gradually became filled with the heavier materials and the rocks covered with a thin layer of silt.

The temperature of the water at the station was recorded continuously throughout the investigation by means of a Negretti and Zambra distance recording thermometer. Although the climatic conditions varied considerably in the three seasons during the spring period, which brought about apparent discrepencies in the comparison of temperatures at this time, the actual accumulated temperature up to any particular date in the summer showed little difference from year to year. On account of the increased depth of water at the station in the latter part of 1939 and throughout 1940 the daily temperature fluctuations in this period were not as great as in the preceding part of the investigation.

A slight decrease in the oxygen content of the water was recorded following the introduction of lentic conditions at the station and a slight increase in the total carbonate content. The values in both cases, however, did not appear to approach a lethal level with respect to the biota present.

Quantitative Change in the Insect Fauna

The numbers of insects that emerged into the trap at station No. 3 during the course of the survey are tabulated in Table 1 as monthly totals. The main aquatic insect orders are treated in separate columns with the exception of the Diptera which are subdivided into the family Chironomidae and a miscellaneous group which is comprised mainly of the families Tipulidae, Empidae and Simuliidae. Only male individuals of the last family have been included in the quantitative data since large numbers of females are carried into the cage on the body of the collector during the peak of their emergence and thus constitute a considerable source of error when quantitative results are considered.

From Table 1 it is evident that the total number of insects that emerged during the months June to August, inclusive, was greatest in 1938 when a running water habitat prevailed at the station, decreased in 1939 when still water conditions were introduced and reached the lowest value in 1940 when the lentic nature of the en-

Table 1.—Monthly totals of the number of insects that emerged at station 3 during the summer months of 1938, 1939 and 1940

	Item	Ephemeroptera	Trichoptera	Plecoptera	Chironomidae	Miscellaneous	Total
Lentic	1938						
	June	1,201	54	18	714	56	2,043
	July	1,744	72	76	515	64	2,471
	August	92	323	22	474	15	926
							5,440
	Percentage of the total population	55.8	8.3	2.1	31.3	2.5	.....
Beaver dam	1939						
	June	1,214	36	36	710	46	2,042
	July	931	47	4	1,020	39	2,041
	August	68	10	2	584	11	675
							4,758
	Percentage of the total population	46.5	2.0	0.9	48.6	2.0	.....
Lotic	1940						
	June	313	30	6	776	5	1,130
	July	141	36	1	1,560	4	1,742
	August	14	35	..	891	4	944
							3,816
	Percentage of the total population	12.3	2.7	0.2	84.4	0.4	.....

vironment had become more firmly established. In July and August, 1939, and throughout the complete 1940 season the Ephemeroptera, Trichoptera, Plecoptera and miscellaneous group showed a distinct decrease in numbers while the Chironomidae showed an increase when the monthly totals are compared with those obtained in 1938.

The month of June in the first two seasons is the only period in which an annual comparison of the emergence can be made while lotic conditions were prevalent at the station. The total insect emergence

for this month, 2,043 individuals in 1938 and 2,042 in 1939, as well as the separate group totals correspond closely. Thus it seems improbable that the effect of annual variation in the insect emergence is of sufficient magnitude to account for the numerical decrease which occurred following the advent of the beaver dam.

The significance of the quantitative change in the insect population can be pointed out more readily if each group is represented as a percentage of the total emergence for the season and these values compared in the respective years (Table 1). The Ephemeroptera constituted the dominant group in 1938 composing 55.8 per cent of the insects obtained but fell into second place from the standpoint of abundance in 1939 and 1940 composing 46.5 per cent and 12.3 per cent, respectively. In a similar manner the Plecoptera decreased from 2.1 to 0.9, to 0.2 per cent, respectively, and the Miscellaneous group fell from 2.5 per cent in the first season to 2.0 per cent in the second, and 0.4 per cent in the third season. The Trichoptera decreased from 8.3 per cent in 1938 to 2.0 per cent in 1939 and thence increased slightly to 2.7 per cent in 1940. Conversely the Chironomidae showed a continual increase in numbers rising from second position from the standpoint of relative abundance at 31.3 per cent in 1938 to the dominant position represented by 48.6 per cent in 1939 and finally constituted 84.4 per cent of the total insect population in 1940.

With respect to the productivity of this area, the weights or volumes of the daily collections exhibit a more marked decrease than is indicated in the numerical data above. Both the immature and adult stages of the Ephemeroptera, Trichoptera and Plecoptera groups which account for most of the decrease in numbers are heavier and larger forms than the corresponding stages of the Chironomidae which is the only group that was augmented following the construction of the beaver dam.

Qualitative Change in the Insect Fauna

There was a distinct qualitative change in the insect fauna recorded at the station following the construction of the beaver dam and this was to a large extent responsible in bringing about the quantitative change discussed above. In order to determine this change individuals belonging to the orders Ephemeroptera, Trichoptera and Plecoptera were determined to species wherever possible. All other specimens were identified only to family so that the complete qualitative change cannot be estimated.

The insect species have been placed in three main types, based on their reaction to the conditions introduced at the time of the flooding, in order to clarify the discussion. Type 1 includes those that were reduced numerically or completely wiped out of this section of the stream after the beaver dam was constructed and represents typical

rapid water dwellers that were unable to withstand the still water conditions. In this category are included species that emerge early in the season so that no change was apparent in 1939 but were absent in 1940; species that emerge in the mid-part of the summer and thus showed a drop in numbers after July 1, 1939, and were absent in 1940; and lastly species that emerge late in the summer and were present only in 1938. Type 2 includes those species that showed no appreciable change in either 1939 or 1940 as compared with 1938 and thus represent tolerant forms that were able to exist equally well in a lotic or lentic environment. Type 3 includes those species that were recorded only in the period following the flooding and is made up entirely of typical still water forms that were unable to gain a foothold at the station while lotic conditions existed there.

The species obtained at the station, the number captured in the cage each season and the type to which they belong are listed in Table 2. A few species are of doubtful position because of the paucity of individuals taken and these are placed in the type to which they appear to belong followed by a question mark.

A total of 14 species of Ephemeroptera belong to Type 1, 7 to Type 2 and 7 to Type 3. Ten species of Trichoptera fall into Type 1, 7 into Type 2 and 3 into Type 3. Of the Plecoptera 9 species belong to Type 1, 1 to Type 2, while there was no representative of this order belonging to Type 3. Totalling the results for these three orders, 33 species present at the station in 1938 were reduced in numbers or completely wiped out of this area following the construction of the beaver dam, 15 were able to tolerate the new ecological conditions and 10 species were introduced at the station as a result of the changed environment.

A few apparent discrepencies may be noted in Table 2 with respect to the type in which certain species have been placed. In these instances a more thorough knowledge of the habits of these forms has been used in conjunction with the numerical data to determine the type to which they belong. Within each type the species included exhibit a gradation between the extremes delimiting the type which may be significant from an ecological viewpoint. For instance, it is probable that within a rapid water community some species utilize only the still water micro-habitats found in the lee of rocks so that these forms although representing Type 2 would tend to increase when lentic conditions spread over this whole section of stream; conversely, some species which are more dependent on current could utilize the flowing water micro-habitats found in a pool but would become reduced numerically since the reduction of the available lotic areas would necessitate the maintenance of a smaller population.

In 1938 the fauna represented at the station consisted in its entirety of forms typically associated with a running water habitat. In 1939 most of these species were recorded again although, as has been shown in Table 2, many were reduced in numbers after July 1 and others

Table 2.—The number of individuals of each species recorded at Station 3, during the period June 1 to August 31, 1938, to 1940, inclusive

Item	1938	1939	1940	Type
EPHEMEROPTERA				
Baetis cingulatis	4	15	..	1
Baetis flavistriga	163	50	..	1
Baetis parvus	1	..	..	1(?)
Baetis pluto	47	20	1	1
Baetis pygmaeus gr.	130	32	1	1
Leptophlebia deblis	50	29	1	1
Leptophlebia guttata	3	4	..	1
Leptophlebia mollis	112	51	1	1
Leptophlebia volitans	19	53	7	2
Heptagenia hebe	6	7	..	1
Heptagenia pulla	111	26	1	1
Epeorus humeralis	2	..	..	1(?)
Stenonema canadense	38	50	38	2
Stenonema fuscum	30	41	25	2
Stenonema rubromaculatum	9	2	28	2
Stenonema vicarium	1	5	5	2
Habrophlebia vibrans	2,297	1,798	311	2
Ephemerella bicolor gr.	4	1	4	2
Ephemerella invaria	1	..	..	1(?)
[1]*Ephemerella subvaria*	..	..	1	(?)
[1]*Brachycercus sp.*	2	..	..	(?)
[1]*Siphlonurus alternatus*	1	..	..	(?)
Pseudochloeon carolina	5	5	..	1
Centroptilum convexum	..	1	26	3
Centroptilum semirufum	..	1	2	3
Centroptilum simile (?)	1	8	..	1
Chloeon minor	..	..	2	3(?)
Chloeon rubropictum	..	1	4	3
Chloeon triangulifer	..	9	9	3
Choroterpes basalis	..	1	..	3(?)
[1]*Baetisca laurentina*	..	1	..	(?)
[1]*Blasturus sp.*	..	2	1	3(?)
TRICHOPTERA				
Chimarrha aterrima	352	12	..	1
Philopotamus distinctus	13	..	..	1
Cheumatopsyche pettiti	25	20	1	1
Hydropsyche betteni	13	2	..	1
Hydropsyche spatna	17	..	..	1
Rhyacophila carolina	5	1	..	1
Rhyacophila fuscula	2	..	..	1(?)
Agapetus sp.	..	2	1	2(?)
Psychomyia diversa	4	1	..	1
Psychomyiella flavida	2	..	1	2(?)
Polycentropus confusus	8	30	5	2
Plectrocnemia cinerea	1	5	14	2
Nyctiophylax vestitus	3	9	21	2
Lepidostoma sp.	1	2	..	1(?)
[1]*Goera stylata*	..	..	1	(?)
Oxyethira sp.	1	..	1	2(?)
Athripsodes dilutus	2	3	13	2
Athripsodes angustus	..	6	..	1(?)
Oecetis inconspicua	..	..	8	3
Mystacides sepulchralis	..	..	8	3
Stenophylax guttifer	..	..	27	3
PLECOPTERA				
[2]*Leuctra decepta* *Leuctra hamula* *Leuctra sibleyi* *Leuctra tenuis*	105	18	1	1
Nemoura venosa	1	..	..	1(?)
Hastoperla brevis	3	5	..	1
Alloperla imbecilla	..	2	..	1(?)
Isoperla montana	2	2	..	1
Isoperla sp.	5	11	5	2
Isoperla truncata	..	4	..	1
[1]*Acroneuria lycorias*	..	..	1	(?)

[1]Species represented by adult females alone; probably washed into the cage during oviposition.

[2]The genus *Leuctra* is treated as a unit since the female individuals could not be satisfactorily separated taxonomically.

which emerged late in the season were absent. Along with these forms a few species which are normal inhabitants of still water areas were taken at the station in the latter part of the summer. The introduction of these species must have been brought about by migration of individuals that were present in the quiet water along the riffle margins and in the pools, into the sampled section of the stream once the lentic conditions spread over this portion. The predominant migrant group was the Ephemeroptera which were apparently able to migrate more readily than the Trichoptera which may be impeded somewhat by their cases and fixed habit. No new Plecoptera were taken and this is as would be expected since these forms are almost exclusively rapid-water dwellers. In 1940 the change had progressed further and with the exception of an occasional single individual of a species the total population consisted of forms commonly associated with a still-water habitat. The result of oviposition in 1939 would be an important factor in establishing a more stable lentic population in 1940 since the lack of riffles in this section of the stream would favour the oviposition of still-water species.

There was a net decrease in the emergence after the beaver dam was constructed, since the loss of the truly lotic species from this area more than offset numerically, the gain brought about by the newly introduced lentic forms. From the results of another investigation on the emergence of aquatic insects from different types of bottom in Mud Creek it has been found that rubble in a rapid stretch of stream is more productive from the standpoint of insects than is the mucky bottom found in pools. Comparable results have been obtained by other investigators such as Needham and Pate who found that pool bottoms produced only one-third as much weight of potential trout food as did a rubble bottom (Needham, 1938). Thus it seems improbable that the lentic fauna would at any time approach the fauna that was found at the station during the period of lotic conditions unless a growth of aquatic plants were to arise thereby causing an increase in the lentic fauna.

A few of the actual emergence polygons of the species found at Station 3 are recorded graphically in Figure 2. These illustrate both the quantitative and qualitative change in the insect fauna which followed the building of the beaver dam. Representing what has been referred to above as Type 1 are the species *Baetis flavistriga, Chimarrha aterrima* and the genus *Leuctra,* including the species *sibleyi, hamula, tenuis* and *decepta,* which has been recorded as a unit since the female individuals could not be distinguished satisfactorily. In all three instances the general correspondence in the emergence up until July 1 in 1938 and 1939 is evident as is the decrease in the period after July 1, 1939. *Stenonema canadense, Polycentropus confusus* and a species tentatively listed as *Isoperla* sp. are representative of Type 2. It is apparent in Figure 2 that these species were not noticeably affected by the altered conditions found at the station after July

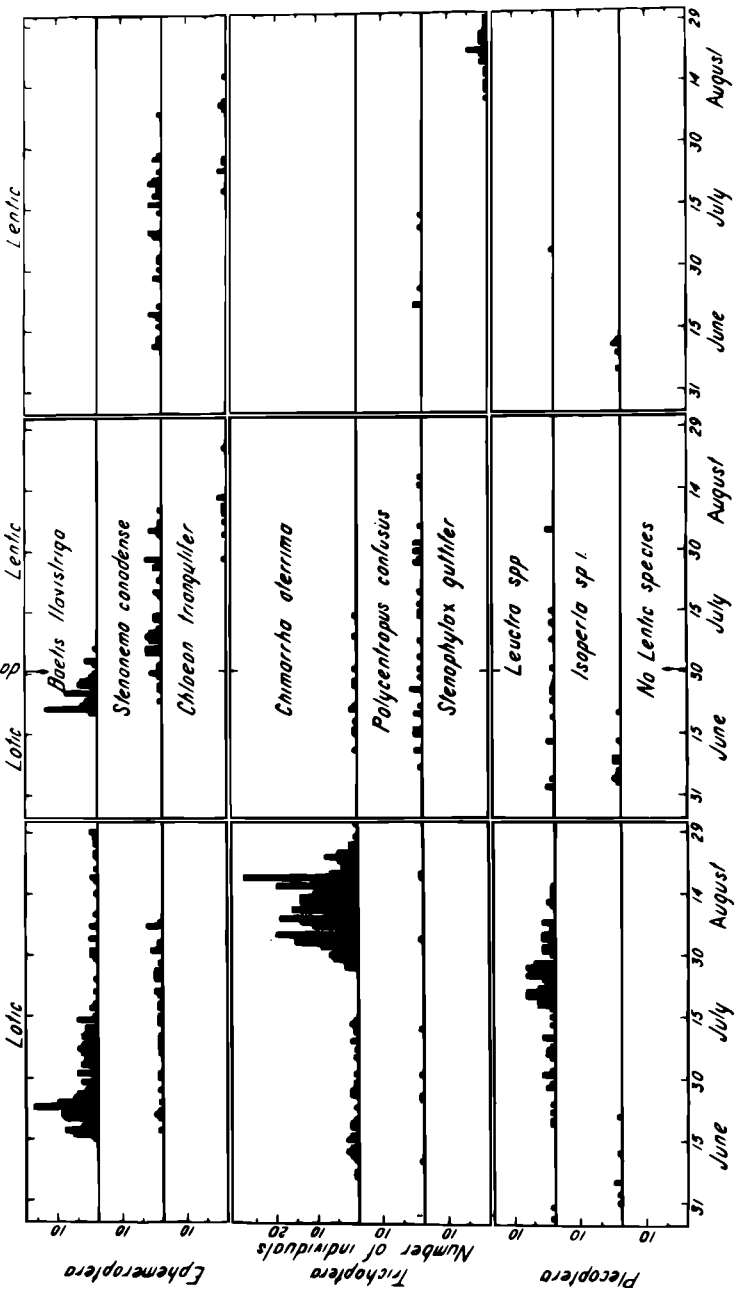

Figure 2.—Actual emergence polygons of a few representative species which occurred at Station 3

1, 1939. The relation is not so clear in the case of *Polycentropus confusus* since this form seems to have dropped off considerably in 1940 as compared with 1939. However, the emergence in 1940 approximates more closely that of 1938 and it is probable that the 1939 figure merely indicates a more favourable set of conditions for this species bringing about a large annual variation. The remaining panels in Figure 2 are examples of Type 3. *Chloeon triangulifer* was present both in the latter part of 1939 and in 1940 and illustrates a form which likely migrated into the area in the former season; *Stenophylax guttifer* on the other hand represents a form which was not able to migrate into the area in 1939 and was only present in 1940 following the altered oviposition instigated in late summer of the 1939 season.

The most important single factor affecting the insect fauna at the station following the construction of the beaver dam appeared to be the decrease in the rate of flow of the water. In the light of recent investigation it has become evident that the current is of fundamental importance to insects dwelling in rapids (Wingfield, 1939). In these forms the inherent demand is not a high dissolved oxygen content as formerly held, since this is generally well above the lethal point in all lotic environments, but rather a definite flow of water causing a circulation about the individual which brings fresh oxygenated water to its body surface and also breaks down the diffusion layer of carbon dioxide in contact with it. The gills are important respiratory organs in the burrowing Ephemeroptera but in other forms are used for the most part in a mechanical way to produce a current and are important respiratory agents only under adverse conditions such as when the oxygen content falls to an extremely low level. This would account, to a large extent, for the marked depletion of the typical lotic fauna after July 1, 1939. Further, certain of these forms, such as the net building Trichoptera larvae, are dependent on the current for their food supply and many of these were found on the rocks in the spring of 1940, in which development had ceased at various immature stages reached during the preceding summer.

In a like manner the current would be the most important limiting factor preventing the appearance of normal still water inhabitants in the rapid water sections. The lack of adaptations in the former species for maintaining their position in running water would restrict these forms to still water habitats.

Summary

1. When a section of stream characterized by rubble bottom and a rapid flow of water was changed into a slow flowing pool through flooding by a beaver dam a net numerical decrease in the insect population resulted in the period immediately following the change.

2. The Ephemeroptera, Trichoptera, Plecoptera and miscellaneous Diptera groups were decreased in numbers while the Chironomidae were increased.

3. Species dependent on lotic conditions were reduced in numbers or wiped out of the area completely following construction of the dam while species typically associated with lentic conditions were introduced. A few more tolerant forms were not significantly altered.

4. In the period immediately following the advent of the dam some still water forms migrated into the area but a more stable quiet water population was established the following year as a result of successful oviposition in the latter part of the previous season.

5. The change in the insect population was correlated with the decreased rate of flow of water and the physical factors associated with this such as increased depth and deposition of sand and silt which filled the interstitial spaces on the rubble bottom as a result of the flooding brought about by obstruction of the stream.

Acknowledgments

This study was carried out at the Ontario Fisheries Research Laboratory which provided funds and facilities for the field work. The author would like to take this opportunity of thanking the members of the laboratory for their assistance throughout the investigation and to express sincere thanks to Dr. F. P. Ide, whose guidance in the field and active cooperation in the identification of the material collected has made this paper possible.

The value of the study has been enhanced through the work of Dr. T. H. Frison and Dr. H. H. Ross of the Illinois Natural History Survey, who identified the species obtained belonging to the groups in which they are specialists.

Literature Cited

Ide, F. P.
1940. Quantitative determination of the insect fauna of rapid water. Univ. Toronto Stud., Biol. Ser. No. 47, Pub. Ont. Fish. Res. Lab., No. 59, pp. 1-20.

Needham, P. R.
1938. Trout streams. Comstock Publishing Company, Inc., Ithaca, N. Y. 233 pp.

Wingeld, C. A.
1939. The function of the gills of mayfly nymphs from different habitats. Jour. Exper. Biol., Vol. 16, No. 3, pp. 363-373.

Discussion

Mr. Harkness: I assume there are trout in this stream; do you know enough about the food of the trout to know how the beaver dam would affect the food of the trout as a whole? Would it diminish it?

Mr. Sprules: Up to the present time I have not been able to carry out a volumetric analysis of my material. Trout are present in the stream, as you suggest, but only in the early part of the season, after which time they are forced to migrate downstream due to high temperatures. I certainly believe that al-

though the numerical increase is not perhaps overly significant, the volumetric changes are of significance. Those that were wiped out were large forms, by volume and weight, while the Chrionomidae, which are increasing, are smaller. The trout would certainly have to take many more chironomids to make up a suitable diet in comparison with mayfly, stonefly and caddisfly foods.

THE PRESIDENT: Do you know how long the chironomids and mayflies remain as larvae before they emerge?

MR. SPRULES: For the most part they have a 1-year cycle. Some of the larger stoneflies and caddisfly groups have a 2-year cycle, but these did not occur in the situation investigated.

DR. IDE: Can Mr. Sprules say whether a balance was reached in the one season?

MR. SPRULES: I think not. Once the lentic conditions are more firmly established in the years to come, plant growth should occur, and this should somewhat increase the invertebrate fauna.

MR. PAUTZKE: Was any evaluation made as to the effect of the constant flow of water upon the organisms below the dam?

MR. SPRULES: At the particular point I was investigating the creek is approaching the lake into which it empties, and from there on the bottom was gravel and sand. I could not, therefore, obtain a proper comparison of the rubble nature of the bottom which I had investigated in the 1938 season.