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with good wishes
T. Macan.

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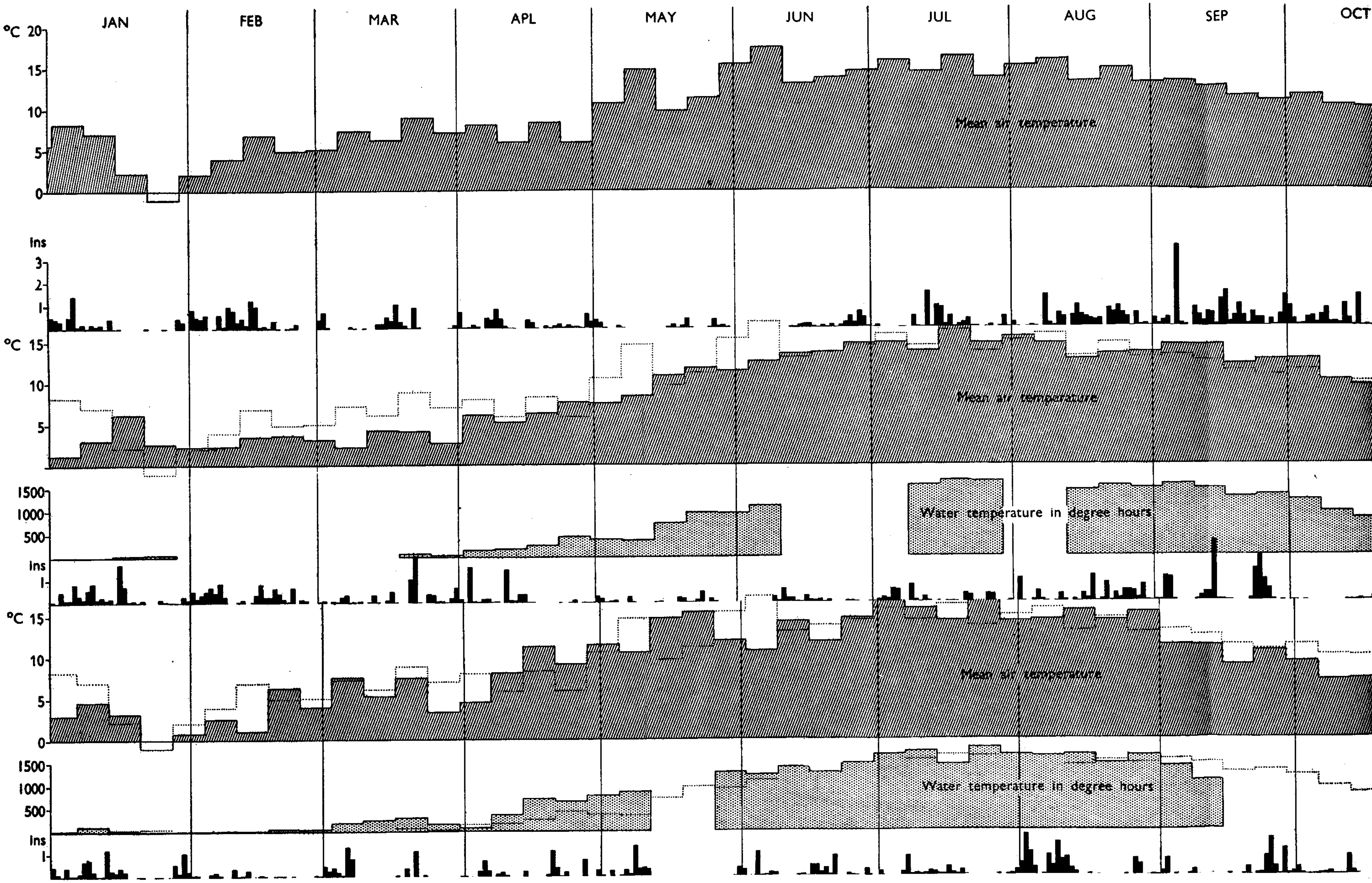
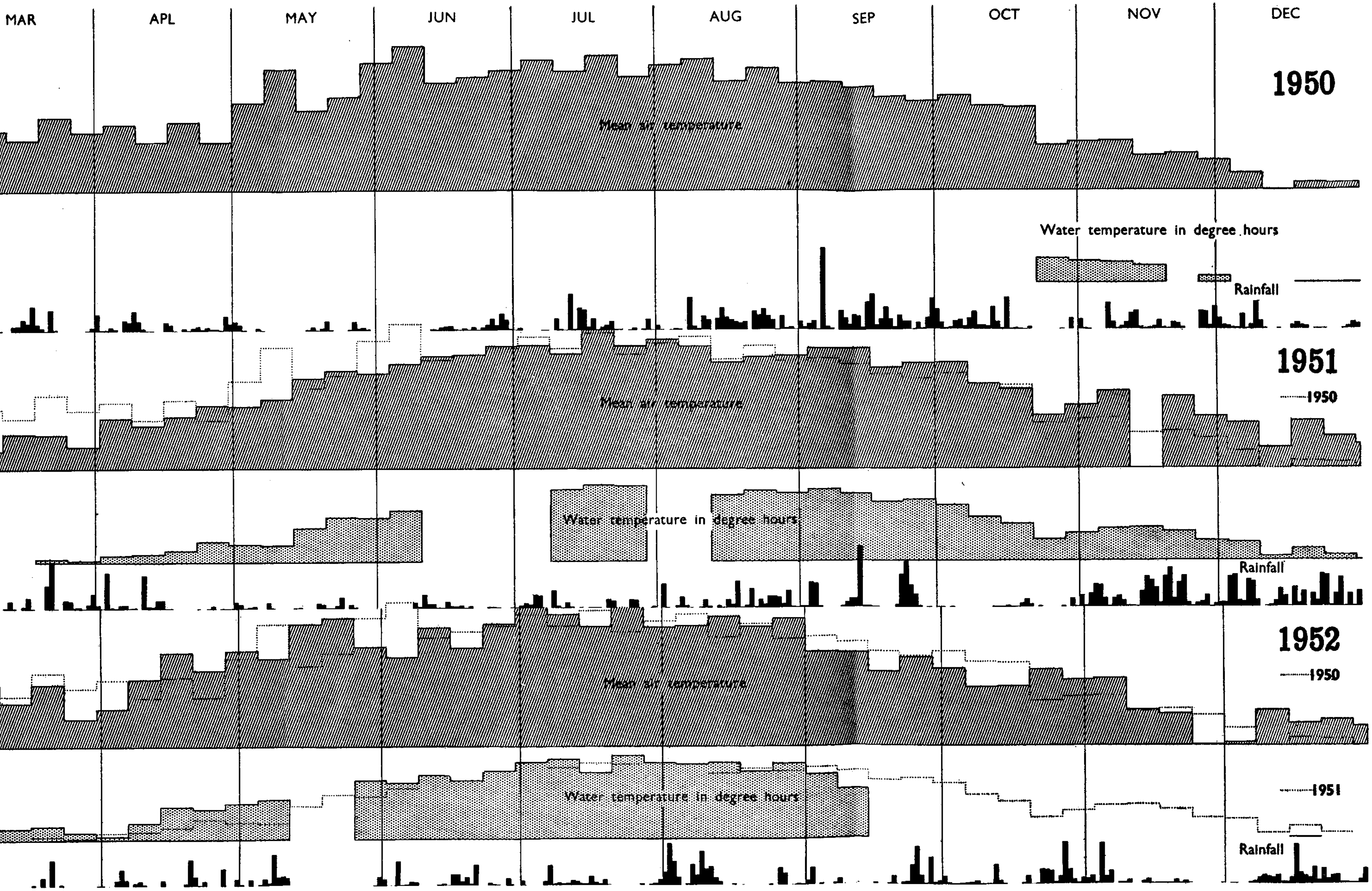


Fig. 1. Climatic data. Top: Mean air temperature per week at Ambleside. Middle: Stream temperature in degree hours above 5° C. per week at Outgate. Bottom: Da



op: Mean air temperature per week at Ambleside. Middle: Stream temperature in degree hours above 5° C. per week at Outgate. Bottom: Daily rainfall at Ambleside.

TRANSACTIONS OF THE SOCIETY
FOR BRITISH ENTOMOLOGY

VOL. 12 27TH MARCH, 1957 PART 5

# THE LIFE HISTORIES AND MIGRATIONS OF THE EPHEMEROPTERA IN A STONY STREAM

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(With 9 figures and 8 tables in the text)

## INTRODUCTION

Monthly collections from five stations in a small stony stream in the Lake District were made in 1950, 1951 and 1952. Seven species of Ephemeroptera were fairly abundant or abundant in the stream, and their life histories and any movements up or down the stream, revealed by the collections, are discussed in the following pages.

These seven species were: *Rhithrogena semicolorata* (Curtis), *Ecdyonurus torrentis* Kimmins, *Heptagenia lateralis* (Curtis), *Baetis rhodani* (Pictet), *B. pumilus* (Burmeister), *Paraleptophlebia submarginata* (Stephens) and *Ephemerella ignita* (Poda).

Other aspects of the work have been written up separately. In a paper submitted to the editor of the *Journal of Animal Ecology*, the population of Ephemeroptera is taken as a whole and differences from station to station, year to year, and stream to stream examined. Articles on the collecting technique, the Plecoptera, the Trichoptera, and *Gammarus* will be submitted to various journals.

## DESCRIPTION OF COLLECTING STATIONS

The stream, Ford Wood Beck, was a small one, less than 2 km. long and nowhere more than 2 m. wide. It was a typical moorland beck with a flow fast enough to keep the bottom clear of everything but stones, except in the topmost reach of one tributary, which was not included in the survey. Station 1 was near the mouth. The flow was fair and the bottom composed of stones of all sizes, the largest, derived from an outcrop of rock higher up, being difficult for a man to lift with one hand. Station 2, further up, in a valley filled by ice- or water-borne material, was some distance from a rock outcrop and therefore, should have been floored only with the fairly small stones, which the current could carry down the comparatively gentle gradient of the valley floor. In fact, some larger stones were present, probably relics of wall-building operations. Station 3 was in the region where the beck tumbled over fairly steep rock in a bed of alternating cascades and pools containing stones of all sizes. Station 4 was near the spring and above the entry of the two main tributaries. Stones lay on boulder clay which had not, as in lower reaches, been washed away because there was never a great weight of water. The remaining stations were in the two tributaries Sykeside Beck and Outgate Beck. In Sykeside Beck at the collecting station (Ss in the tables), the current was moderately swift, relative to other parts of the beck, and the bottom of stones of various sizes left behind after the fine material of a glacial deposit had been washed away. Outgate Beck flowed more slowly in an artificial channel with stones of various sizes. Not far above the collecting station (Og in the tables) it originated in a moss now kept dry enough for pasture by a drain right through it.

## METHODS

Collecting was done mainly with a net that had a coarse mesh of 20 threads to the inch. This was used for five or ten minutes to give results that were to some extent comparable. Later, collections were also made with a phytoplankton net (160 threads to the inch), because it was found that an astonishingly high proportion of tiny nymphs passed through the coarser mesh. Some collecting was done with a shovel sampler, by means of which one-twentieth of a square metre of substratum could be removed and tipped into a strong solution of calcium chloride, where the stones and finer particles went to the bottom and the organisms floated to the top.

The work covered three years and each station was visited once a month, except in the first year, when the necessity for such regular sampling was not appreciated. The effective start was at the beginning of 1950 except at station 4 which was not included till April, 1951.

## CLIMATE

Late in 1950 a thermograph was set up in Outgate Beck, but unfortunately it proved to have a defective clock and continuous records have not been obtained until after the end of the present investigations when a new clock was fitted. Such results as were obtained, calculated as total degree hours above 5° C. per week, are shown in fig. 1. 1951 has been superimposed as a dotted line on 1952. It is difficult to gain a true picture of the temperature of a stream from readings taken at one place, and the site chosen, or rather the site forced upon me by the circumstance that nowhere else was there safety and shelter for the recording part of the instrument, was just below an underground stretch. During a hot dry spell when the flow was slight, evaporation in this tunnel cooled the water several degrees.

The water temperature record being incomplete, the air temperature has been included in fig. 1. The readings are those kept by the Lakes Urban District Council at Ambleside, a place some three miles distant. The histograms show the average of the maximum and minimum daily temperatures for a week. 1950 has been superimposed as a dotted line on both later years. It is noteworthy that, from the first week in February till mid-May, 1951 was almost consistently colder than 1950. 1952 was colder than 1950 fairly consistently till the first week in April and then warmer in all but one of the next seven weeks.

Along the bottom of each year is shown the rainfall, also measured at Ambleside. This place is nearer the mountains and therefore receives more rain per annum than Outgate, some 10 inches (254 mm.) on the average. Occasionally there are marked differences in distribution, but, on the whole, the pattern in the two places is the same. Rainfall was rather similar in the three years when the studies were made. Fig. 1 includes no information about 1949 though some mention of the climate of that year must be made, as it was during it that most of the nymphs caught in the first part of 1950 hatched. The summer was exceptionally fine and during the five months May, June, July, August and September only 13.54 inches of rain fell. In the last three months of the year 9.40, 13.28 and 14.43 inches fell respectively. The period June 11-July 12 inclusive was without rain except on one day when .03 inches fell and Sykeside Beck was dry in mid-July.

The following years had wetter summers than this. 1951 was the driest with little rain from mid-April to July though the longest period without rain was shorter than in other years. Sykeside Beck was dry in June. 1950 was similar in that May and June were the dry months of the year but the period of slight rainfall was shorter. In May, 1952, there were nineteen consecutive days that were rainless, except for one, when .01 inches fell. This was a longer continuous dry period than in either of the previous years, but it came immediately after a wet spell and Sykeside Beck did not dry up. There was another rainless period towards the end of the year, and this was the only time, during the three years, that the level of the beck was recorded as low in the winter. Rain was fairly evenly distributed through the rest of the year.

## LIFE HISTORIES AND MIGRATIONS

### *Rhithrogena semicolorata* (Curtis)

The total number of specimens collected per month from all the stations except station 4 is shown in fig. 2, which, however, omits the early part of 1950, because collecting was not regular then. In both the years shown, and in 1950, there is a fair or large population in May and a small one in June. The collecting was done in the third week in the month and therefore it is evident that there is a big emergence of adults in late May and the early part of June. In 1952 emerging adults were trapped and the dots in fig. 2 show the numbers caught. By July there are very few nymphs left and the new generation appears in August, September or October. Clearly this species has one generation per year, emerges in the early part of the summer, and grows throughout the winter.

That this is the life-history of *R. semicolorata* has already been shown by Pentelow in the River Tees (Butcher, Longwell and Pentelow, 1937, pp. 142, 144) and Harker (1952), but, when close comparison is made with Harker's findings, three notable differences are seen. First Harker's specimens reached a greater size, the largest being over 14 mm. long; in Ford Wood Beck in May, 1950, 72% of the specimens were 8-10 mm. long and only 15% over 10 mm. long, the largest being less than 12 mm. long. In the other two years the proportion of large specimens was less. Secondly the emergence of Harker's specimens went on longer (in a letter Dr. Harker writes that emergence began in May and that most adults came out in June and July), and thirdly the new generation appeared in July, earlier than in Ford Wood Beck. Such differences might be due to temperature. Unfortunately Harker was unable to obtain a permanent record and therefore no completely satisfactory comparison is possible, but she does indicate in another paper (Harker, 1953) that the temperature in the middle of the stream never rose above 14° C., in which case her stream was colder than Ford Wood Beck.

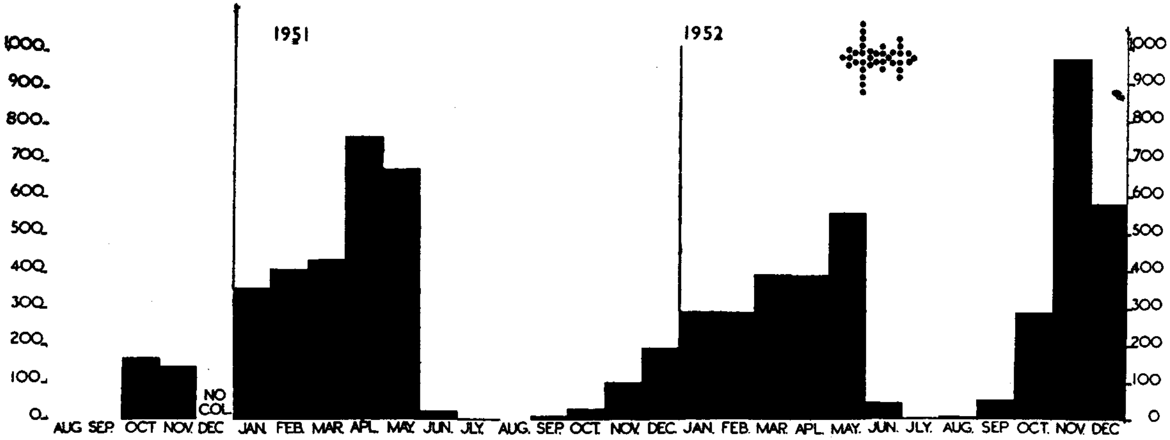

Fig. 2. Total number of *Rhithrogena semicolorata* nymphs caught at five stations with the coarse net. The dots in 1952 represent catches in an emergence trap, each dot being one adult.

There is a feature of fig. 2 that calls for further examination. In both the complete seasons, the histogram has a step-like character; in other words the population is growing denser as the season progresses. This is the opposite of what is to be expected, since it is known that *Perla carlukiana* eats *Rhithrogena* and there must be deaths from other causes too. Suspicion falls first on a faulty collecting technique that misses the smaller nymphs, with the result that more nymphs are caught as the number of large nymphs increases.

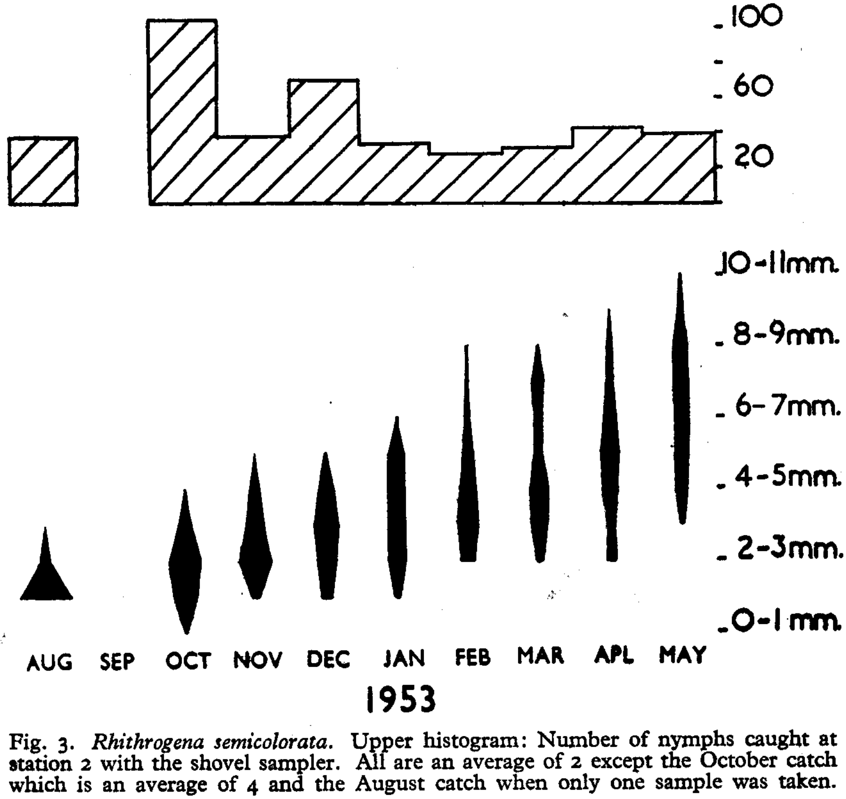

Fig. 3. *Rhithrogena semicolorata.* Upper histogram: Number of nymphs caught at station 2 with the shovel sampler. All are an average of 2 except the October catch which is an average of 4 and the August catch when only one sample was taken. Lower histogram: Nymphs from the same collections arranged in size-groups. The figures have been converted to percentages.

Fortunately two collecting methods were used and the results obtained with the shovel sampler (fig. 3, upper histogram) are available for comparison with those obtained with the net. It is a pity that the two kinds of collection did not overlap completely in time, but the overlap was sufficient to show an entirely different pattern in the two. The shovel caught most nymphs at the beginning of the season, from which it may be deduced that the population is at a maximum then, as is to be expected, and that the net missed many small specimens. There remains the question: at what stage was the error made? Specimens caught by the shovel sampler were dislodged from the stones by a flotation method, but the net-collector relied on the current to wash nymphs into the net. If nymphs were seen still clinging to a stone after it had been picked up off the bottom, it was swilled to and fro in the mouth of the net till they were no longer there, but it is possible that the smaller nymphs were not seen. Some could also have been overlooked during the subsequent sorting. But it seems much more likely that more tiny nymphs were caught by the shovel sampler than by the net because they were mainly on the small stones below the surface layer and not on the larger superficial stones which were the ones chiefly picked up by the net-collector. This is not, however, the complete story, as a glance at the lower part of fig. 3, in which the specimens are arranged in millimetre size-groups in successive months, will show. Nymphs only 1-2 mm. long occur in every month up to and including January. It is possible that some nymphs do not start growing till several months after hatching as do those of the plecopteron *Leuctra fusca* (Brinck, 1949). In the absence of observations on the eggs, comment must be cautious, but the writer inclines to the alternative that some eggs take much longer to hatch than others. Many must take four months, for the majority are laid in June and nymphs were never abundant before October, and it would seem that some take as long as seven months.

This phenomenon of delayed hatching, or delayed growth in the smallest stages, it does not matter which for the present, seems, as will appear in later pages, to be rather common. It has considerable importance from two points of view. First it renders invalid the method of calculating growth rate from the average of monthly measurements used by Harker (1952) and Illies (1952 a and b), because this technique, as Brinck (1949) stresses, is applicable only to populations whose every member leaves the egg or starts to grow within a comparatively short time. Second, it complicates calculations of production. If we assume that each nymph requires what Andrewartha and Birch (1954) call "a place to live," that is an area which provides food, shelter and perhaps other favourable conditions, and that every possible "place to live" is occupied, two extremes are possible. At one, each individual, whatever its size, has a secure retreat and mortality is low; at the other, the number of the "places to live" is inadequate and many of the nymphs that have failed to secure the best ones will fall a prey to predators and other hazards. In the first case, newly hatched nymphs will be forced to lodge in unsuitable places and soon perish; in the second there is a steady drain on all sizes of the population which is continuously made good from the influx of newly hatched specimens. A human sampler might find a population of similar size-structure on two occasions separated by an interval of time but would have no clue that, if the first set of conditions was effective, production was low, if the second, high. Possibly this phenomenon accounts for Allen's (1951) observation that trout apparently ate about seventeen times more than there was to eat in the Horokiwi River. In other words, what Allen missed, and he must obviously have missed something, was the unhatched eggs of the invertebrates he was sampling.

To revert to the growth of *Rhithrogena semicolorata*, it is not possible to do more than gain a rough idea of the rate by looking at the size of the largest specimen in each successive catch. In general, in fig. 3, it has reached the next millimetre size-group each month. In the standard net catches in the

1951-2 season, the largest nymph was in the 3-4 mm. size-group in September, in the 4-5 mm. group in October, and in the 6-7 mm. group in November, after which it was in the next group up in each month till March, when it had reached the 10-11 mm. group. After that there was no increase in maximum length. Results in the previous season were similar though less regular. It is not possible to make out whether the growth-rate was related to temperature, but it is incontrovertible that some nymphs at least are growing all through the winter. This affords a marked contrast to the findings of Illies (1952a, p. 481), according to whom *Rhithrogena semicolorata* did not grow in the months of November, December, January and February.

When an attempt is made to compare the course of events at the different stations, a lack of information about certain points becomes evident. It would have been desirable, had it been possible in the time, to have had an emergence trap at each station, to discover the amount of egg-laying that was done in different parts of the beck, and to collect the smallest nymphs. These, which, as will be seen later, provided a clue essential for the unravelling of the life-history of *Baetis rhodani*, were taken in large numbers only by the shovel sampler, and this instrument was unfortunately not used at all the stations.

However, it is possible to draw a few deductions reasonably well supported by facts. In 1950 nymphs were first collected in October, by which time most were 3-4 mm. long, the biggest catch being made at station 3 with the population at station 2 nearly as big and at the remaining stations distinctly smaller (table 1). In 1951 and 1952 at the same time the distribution of the population was similar though numbers at station 3 did not exceed those at other stations by quite so much. It seems likely, though confirmation by direct observation is to be desired, that the neighbourhood of station 3 is a favourite oviposition place. It is the most torrential part of the beck and *Rhithrogena* is a species typical of torrential conditions. Oviposition, however, is certainly not confined to this stretch, for it has been observed every year in Outgate Beck.

Later on the percentage of the total catch at stations 2 and 3 tends to drop and this may be due to a dispersal of the specimens to stations both higher up and lower down. An analysis of the numbers of nymphs of different sizes at the various stations showed a higher proportion of larger nymphs in the populations of Outgate and Sykeside Becks than elsewhere. The chi square test was applied to a frame in which the number of specimens was divided horizontally into over and under 8 mm. long, and vertically into stations 1, 2 and 3 together and Outgate and Sykeside together. The result was highly significant in both seasons. Further the average size of nymphs is consistently higher in both the tributary becks. This could be due to faster growth in them, but immigration from a more thickly populated area seems a likelier explanation. Presumably the larger nymphs travel further than the smaller ones. It had been hoped that the drying up of Sykeside Beck in 1951 would provide incontrovertible evidence about migration, but no nymph was found till November and it could have come from an egg laid by one of the last of the adults in early July when the beck filled up.

The total population tends to increase steadily through the winter, but in April, 1951, and May, 1952, there was a big and inexplicable rise. In April of both years the increase in Sykeside Beck was about fivefold. In this beck there was above the station a long stretch that was never investigated, and it is possible that a migration downwards from here caused these large rises. There is evidence that there was some migration towards the mouth at this time of year for in May of both 1951 and 1952 the biggest population was at station 1, which at other times was generally less thickly inhabited than stations 2 and 3. A final point concerns the distribution of the largest specimens. Only 15 falling into the 11-12 mm. size-group were taken in the whole three years; of these 11 were in Sykeside or Outgate Beck. Outgate certainly and Sykeside Beck probably never get quite as warm as the main stream and possibly larger size is associated with temperature, for in the stream studied by Harker (1952), which may have had a lower maximum temperature, nymphs grew bigger than in Ford Wood Beck.

TABLE 1

Numbers of *Rhithrogena semicolorata* caught with the coarse net in ten minutes

| | | St. 1 | St. 2 | St. 3 | Ss | Og | Total |
|---|---|---|---|---|---|---|---|
| 1950 | March | 39 | 78 | 100 | 13 | 24 | 254 |
| | May | — | 93 | 72 | 21 | 11 | 197 |
| | June | 2 | 4 | 27 | 0 | 0 | 33 |
| | July | 1 | 0 | 0 | 0 | 0 | 1 |
| | August | 0 | 0 | 0 | 0 | 0 | 0 |
| | September | 0 | 0 | 0 | 0 | 0 | 0 |
| | October | 13 | 50 | 73 | 18 | 11 | 165 |
| | November | 16 | 62 | 55 | 3 | 6 | 142 |
| 1951 | January | 59 | 141 | 116 | 29 | 13 | 358 |
| | February | 77 | 143 | 120 | 34 | 31 | 405 |
| | March | 125 | 122 | 128 | 16 | 39 | 430 |
| | April | 123 | 227 | 220 | 156 | 43 | 769 |
| | May | 245 | 159 | 146 | 66 | 59 | 675 |
| | June | 23 | 0 | 0 | 0 | 0 | 23 |
| | July | 1 | 0 | 0 | 0 | 0 | 1 |
| | August | 0 | 0 | 0 | 0 | 0 | 0 |
| | September | 0 | 1 | 6 | 0 | 0 | 7 |
| | October | 3 | 10 | 15 | 0 | 0 | 28 |
| | November | 16 | 37 | 37 | 1 | 8 | 99 |
| | December | 34 | 78 | 64 | 1 | 19 | 196 |
| 1952 | January | 51 | 99 | 100 | 3 | 35 | 288 |
| | February | 79 | 111 | 48 | 6 | 46 | 290 |
| | March | 50 | 91 | 181 | 13 | 58 | 393 |
| | April | 94 | 151 | 41 | 57 | 47 | 390 |
| | May* | 178 | 172 | 156 | 10 | 42 | 558 |
| | June | 10 | 15 | 4 | 4 | 9 | 42 |
| | July* | 0 | 2 | 0 | 0 | 0 | 2 |
| | August | 0 | 4 | 0 | 0 | 3 | 7 |
| | September | 3 | 9 | 25 | 3 | 11 | 51 |
| | October | 55 | 64 | 102 | 29 | 39 | 289 |
| | November | 182 | 227 | 396 | 48 | 118 | 971 |
| | December | 164 | 164 | 107 | 42 | 102 | 579 |

* Numbers caught with the fine net in five minutes and doubled.

### *Ecdyonurus torrentis* Kimmins

Rawlinson (1939) showed that *E. venosus*, in the R. Alyn, had a quick summer generation and a longer one that overwintered. Harker (1952) found that *E. torrentis* also had a quick summer generation, but the life-history was a little more complicated than that elucidated by Rawlinson, because there were three not four generations in two years. The progeny of the summer generation emerged in May of the following year, their progeny in March the year after that, and the third generation completed development within the summer again, emerging in July.

TABLE 2

Numbers of *Ecdyonurus* caught with the coarse net in ten minutes

| | | St. 1 | St. 2 | St. 3 | Ss | Og | Total |
|---|---|---|---|---|---|---|---|
| 1950 | March | 59 | 65 | 28 | 2 | 2 | 156 |
| | May | — | 40 | 11 | 2 | 2 | 55 |
| | June | 2 | 15 | 13 | 0 | — | 30 |
| | July | 14 | 6 | 0 | 0 | 0 | 20 |
| | August | 0 | 1 | 1 | 0 | 0 | 2 |
| | September | 16 | 26 | 8 | 1 | 2 | 53 |
| | October | 93 | 102 | 19 | 20 | 8 | 242 |
| | November | 66 | 20 | 40 | 8 | 5 | 139 |
| 1951 | January | 111 | 7 | 14 | 29 | 11 | 172 |
| | February | 43 | 22 | 8 | 11 | 7 | 91 |
| | March | 103 | 23 | 45 | 12 | 13 | 196 |
| | April | 21 | 13 | 4 | 4 | 3 | 45 |
| | May | 53 | 15 | 17 | 7 | 5 | 97 |
| | June | 66 | 68 | 5 | — | 0 | 139 |
| | July | 26 | 5 | 0 | 0 | 0 | 31 |
| | August | 7 | 15 | 11 | 0 | 0 | 33 |
| | September | 4 | 56 | 10 | 5 | 2 | 77 |
| | October | 36 | 29 | 7 | 13 | 5 | 90 |
| | November | 77 | 103 | 8 | 1 | 17 | 206 |
| | December | 65 | 91 | 7 | 5 | 11 | 179 |
| 1952 | January | 44 | 36 | 4 | 7 | 15 | 106 |
| | February | 58 | 6 | 4 | 3 | 10 | 81 |
| | March | 31 | 5 | 9 | 8 | 12 | 65 |
| | April | 26 | 22 | 2 | 1 | 8 | 59 |
| | May* | 58 | 8 | 2 | 0 | 0 | 68 |
| | June | 13 | 29 | 1 | 0 | 8 | 51 |
| | July* | 10 | 0 | 0 | 0 | 0 | 10 |
| | August | 6 | 16 | 7 | 6 | 10 | 45 |
| | September | 13 | 109 | 70 | 29 | 72 | 293 |
| | October | 16 | 63 | 55 | 14 | 31 | 179 |
| | November | 44 | 125 | 135 | 30 | 61 | 395 |
| | December | 27 | 39 | 27 | 14 | 22 | 129 |

* Numbers caught with fine net in five minutes and doubled.

In Ford Wood Beck *E. torrentis* has a life-history like neither of these, but a simple single-generation-a-year one. Fig. 4 shows the actual numbers taken with the phytoplankton net; collections made in the other years confirm that this is typical. It includes the small ones that could not be identified to species, since the only other possibility, *E. venosus*, was very scarce, and the likelihood that it produced many young, nearly all of which died when very small, is remote. During the winter, there is a big size range, apparently because the population is continuously augmented by small nymphs, as in *Rhithrogena*. Small nymphs continue right up to May, but none could have come from eggs laid the same year, as Harker found, because adults were never seen before May. Emergence continues till September. Tiny nymphs appear in August and grow fast, but not fast enough to emerge the same year. If any specimens complete a generation within the summer, the number must be very small.

Again, it is not possible to calculate growth in the traditional way, because the population is continually being added to. The shape of the histograms and the size of the largest specimen each month in 1950 and 1951 indicate that growth is rapid in the autumn, but slow during the winter.

The life-history of *Ecdyonurus torrentis* is similar to that of *Rhithrogena semicolorata* except that emergence straggles over the summer and is not confined to a period at the beginning of it.

The proportion of nymphs of different sizes was almost exactly the same in shovel and phytoplankton net samples, whereas proportionately many more nymphs of *Rhithrogena* under 2 mm. were taken by the shovel than by the net, a difference that must reflect a difference in habitat. The tiny nymphs of *Rhithrogena* were thought to cling to the smaller stones, and therefore the presumption from these observations is that those of *Ecdyonurus* do not.

Numbers were always relatively low in August. This was to be expected in the month when the last of the old generation had gone and the new had only just appeared. In the next four months, the population was generally highest at station 2; to be exact, in eleven catches the population was highest here eight times, at station 1 twice and at station 3 once. In the other months of the year, by contrast, the population was nearly always greatest at station 1, often by a considerable amount. It was highest elsewhere, in fact station 2, only four times in seventeen catches and, inexplicably, three of the four were in June (table 2).

It is not possible to offer an explanation of these observations. That the new generation was most abundant at a point further upstream than the old generation, could have been due to movements of the adults before the eggs were laid or to movements of the nymphs after the eggs had hatched. The point cannot be settled without observations on the eggs, but no such observations were made. The concentration at station 1 after the turn of the year could have been due to migration downstream or to greater mortality higher up that at station 1. The actual numbers taken do not illuminate this problem, because big fluctuations from catch to catch are typical of *Ecdyonurus torrentis*. Dr. Janet Harker, in a painstaking piece of work involving marking nymphs and making frequent collections, found an upstream migration of nymphs of *Ecdyonurus torrentis* during November. These observations have not been published, but were described at a meeting of the Ecological Society of which there is an account on p. 418 of vol. 22 of the *Journal of Animal Ecology*. There was probably upstream migration in Ford Wood Beck, because the proportion of nymphs over 9 mm. long was higher in the stations furthest upstream, as shown by the following figures:

Number of specimens collected

| | Season 1950-1 | | | | | Season 1951-2 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Size | St. 1 | St. 2 | St. 3 | Ss | Og | St. 1 | St. 2 | St. 3 | Ss | Og |
| Over 9 mm. | 86 | 80 | 17 | 32 | 13 | 63 | 31 | 7 | 13 | 39 |
| Under 9 mm. | 504 | 222 | 143 | 36 | 40 | 349 | 344 | 62 | 31 | 45 |

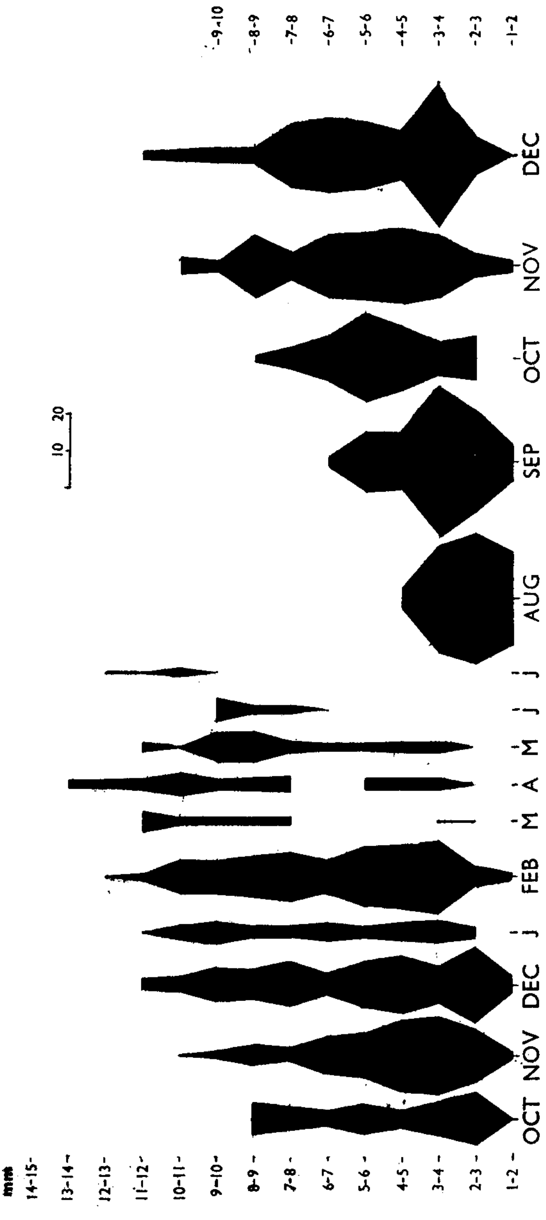

Fig. 4. Actual numbers of *Ecdyonurus torrentis* caught with the fine net arranged in mm. size-groups (season 1951-2).

The differences are highly significant.

### *Heptagenia lateralis* (Curtis)

September was the month in which small nymphs were first found in fair numbers in both 1951 and 1952 (fig. 5). There was some growth in the autumn, little in the winter, and a start again in February or March. Fair numbers were caught each month until June, 1952, and July in 1951, when a big drop was presumably caused by emergence.

This species was never taken in the cage at station 1, which was not unexpected because most of the nymphs were in the upper parts of the stream. To judge from the nymphs, the emergence period was short but, because numbers were not large, it is impossible to be certain about this. In the beck studied by Harker (1950) the species differed in exactly the way *Rhithrogena semicolorata* did, that is the nymphs grew larger, the adults appeared later, and the eggs hatched sooner.

*Heptagenia lateralis* resembles *Rhithrogena semicolorata* and *Ecdyonurus torrentis* in having one generation a year but it grows less in the winter than *Rhithrogena* and does not start to emerge until later than both of them.

In 71 out of a total of 93 catches, fewer than ten specimens were collected. Only 6 times did numbers exceed twenty and the highest was 76.

In this collection, made in Outgate Beck in September, numbers were high in both halves of the coarse net collection and in the phytoplankton net collection, which suggested that nymphs were abundant over a fairly large area. They were not particularly abundant in the following month. On the other occasions, the large numbers were in only one of the collections, which suggested that the nymphs aggregated in peculiar local conditions that were only rarely disturbed by the collector.

*Heptagenia lateralis* occurred at all the stations but the greatest numbers were at station 3, Sykeside and Outgate.

### *Baetis rhodani* (Pictet)

Harker (1952) was unable to work out the life-history of *B. rhodani* from her figures, which excluded specimens less than 2 mm. long. The present series of collections was no more fruitful till, in the autumn of 1951, a fine net was brought into use in addition to the coarse one. As a result, enormous numbers of tiny nymphs, which passed through the coarse net, were captured, and it is these tiny nymphs that provide the clue to the life-history of *B. rhodani*. The error of the coarse net is discussed in another publication and here it suffices to recapitulate that the two nets caught roughly equal numbers of specimens 5-6 mm. long and the coarse net caught about half the specimens 4-5 mm. long, one in six of those 3-4 mm. long, one in thirty of those 2-3 mm. long, and hardly any of those under 2 mm. long.

To elucidate the life-history we have therefore:

1. The catches in the fine net, some of which are so large that it is preferable to present the actual figures rather than histograms, which is done in table 3.

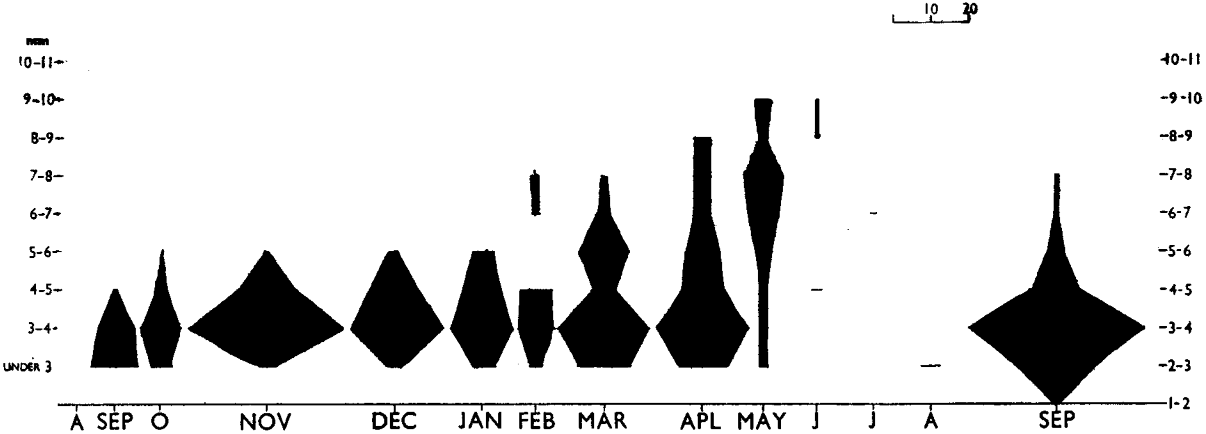

Fig. 5. Actual numbers of *Heptagenia lateralis* caught with the coarse net arranged in mm. size-groups (season 1951-2).

TABLE 3

Monthly catches with the fine net of *Baetis rhodani* arranged in size groups

| | Oct. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0-1 mm. .. | 802 | 195 | 525 | 189 | 68 | 3 | 425 | 11,023 | 6,215 | 3,435 | 3,087 | 731 | 133 | 225 |
| 1-2 mm. .. | 401 | 385 | 1,733 | 635 | 616 | 192 | 171 | 1,087 | 4,270 | 5,710 | 7,189 | 1,913 | 1,483 | 577 |
| 2-3 mm. .. | 214 | 251 | 439 | 389 | 493 | 320 | 125 | 250 | 558 | 1,619 | 971 | 780 | 1,198 | 392 |
| 3-4 mm. .. | 40 | 122 | 107 | 106 | 160 | 204 | 201 | 87 | 76 | 421 | 550 | 236 | 285 | 142 |
| 4-5 mm. .. | 7 | 59 | 56 | 47 | 68 | 122 | 268 | 33 | 64 | 253 | 290 | 12 | 187 | 65 |
| 5-6 mm. .. | 19 | 57 | 55 | 20 | 49 | 80 | 217 | 33 | 63 | 98 | 151 | 98 | 76 | 24 |
| 6-7 mm. .. | 10 | 21 | 34 | 27 | 27 | 52 | 136 | 39 | 56 | 12 | 8 | 58 | 29 | 3 |
| 7-8 mm. .. | 3 | 6 | 21 | 14 | 11 | 43 | 84 | 47 | 52 | 0 | 0 | 12 | 15 | 0 |
| 8-9 mm. .. | 2 | 4 | 9 | 8 | 15 | 34 | 19 | 0 | 0 | 0 | 0 | 2 | 9 | 0 |
| 9-10 mm. .. | 0 | 2 | 1 | 3 | 7 | 12 | 12 | 7 | 1 | 0 | 0 | 0 | 3 | 0 |
| 10-11 mm. .. | 0 | 1 | 4 | 4 | 6 | 3 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11-12 mm. .. | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

2. The catches in the coarse net which are subject to the error just mentioned but which have the advantage of extending over three years. They are presented as kite histograms in fig. 6, in which actual numbers and not percentages are used.

3. The lengths of adult specimens caught in an emergence trap, which, as will be seen presently, provide confirmation of a hypothesis at a point where confirmation is welcome. They are in table 4.

TABLE 4

Numbers of adult *Baetis rhodani* caught in 1952 in the emergence trap at station 1

| April | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|
| 21st 1 | 8th 0 | 1st 1 | 2nd 15 | 4th 2 | 4th 0 | 5th 0 | 2nd 0 | 1st 0 |
| | 11th 0 | 3rd 3 | 7th 11 | 7th 6 | 7th 0 | 8th 0 | 8th 0 | 15th 0 |
| | 14th 1 | 4th 0 | 12th 3 | 11th 1 | 9th 0 | 16th 0 | 20th 2 | 20th 0 |
| | 19th 0 | 8th 7 | 16th 3 | 14th 1 | 15th 1 | 19th 1 | | 26th 0 |
| | 27th 3 | 13th 7 | 20th 2 | 19th 1 | 23rd 3 | 29th 3 | | |
| | | 17th 5 | 26th 9 | 24th 12 | 29th 1 | | | |
| | | 22nd 3 | 31st 14 | 31st 6 | | | | |
| | | 29th 24 | | | | | | |
| 1 | 4 | 50 | 57 | 29 | 5 | 4 | 2 | 0. |

All through the winter there are large numbers of nymphs 0-1 mm. long, but how far this is due to hatching and how far to failure of the nymphs to grow cannot be determined for certain. Numbers in the higher size groups suggest that little growth is taking place, but the sudden increase in tiny ones in January is likely to be due to a sudden burst of hatching. In March there is a small increase in the numbers of nymphs in the higher size groups, presumably due to growth (table 3). The shape of the kite histogram in this month in both 1951 and 1952 is waisted (fig. 6) and it seems reasonable to postulate that the larger ones are the nymphs that hatched in the previous autumn and the smaller ones those that hatched in mid-winter. We shall follow the fate of these two groups and therefore the first thing to do is to devise for them some name that is not cumbersome. Autumn nymphs and winter nymphs seem convenient terms, and these may be shortened to "an" and "wn." Anticipating the possibility that we may want to follow the next generation, let us call them "an 1" and "wn 1." The populations are very similar in 1951 and 1952, unexpectedly since 1951 was a colder year, but in 1950 the an 1 group is poorly represented (fig. 6). Whether this might be due to the long dry summer of the year before is a matter of speculation.

April is a critical month in this analysis. First the scarcity of the smallest nymphs (table 3) suggests that a generation has come to an end and it may, therefore, be assumed that any later increase in numbers will be due to the hatching of this season's eggs. We are thus provided with a point of departure that was not available to Harker. Secondly adults appear for the first time (table 4), which, together with the more tapering shape of the kite histogram (fig. 6) indicates that an 1 is beginning to emerge.

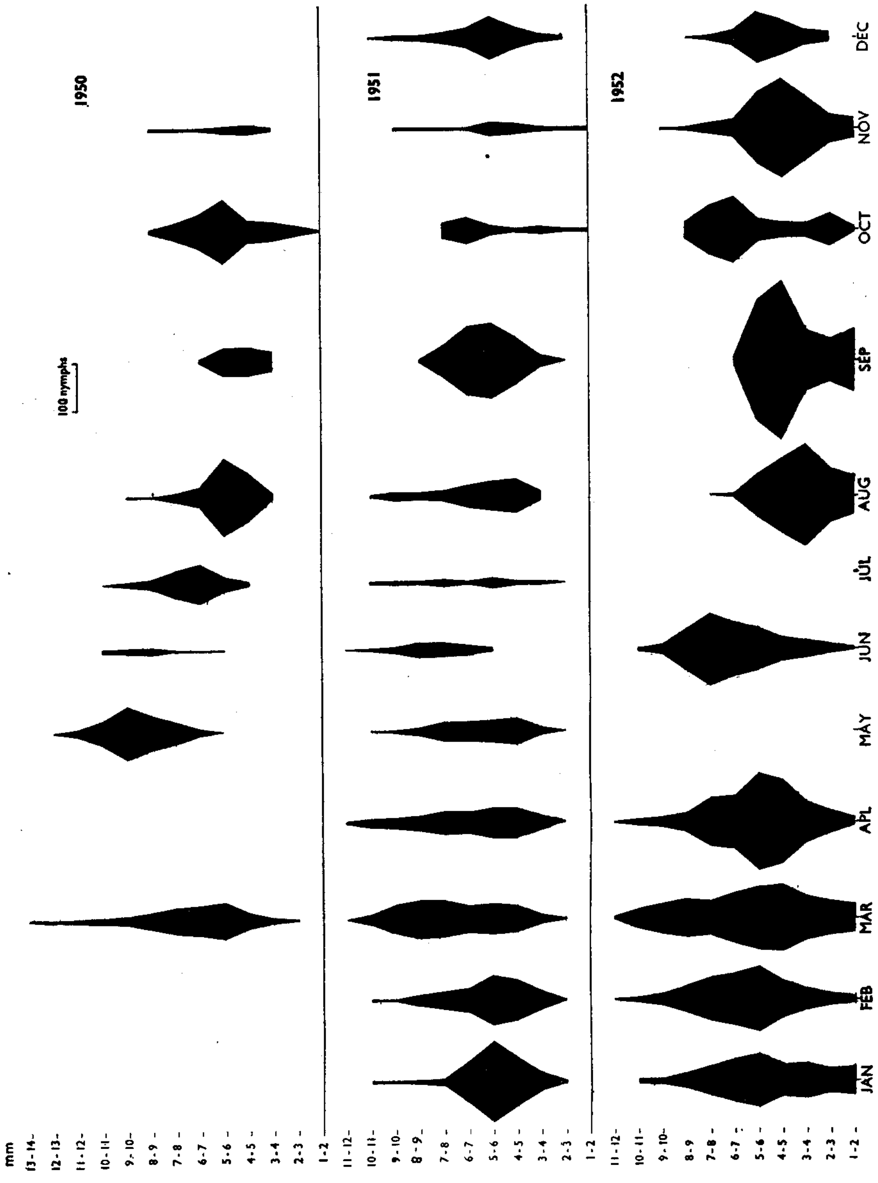

Fig. 6. Actual numbers of *Baetis rhodani* caught in the coarse net arranged in mm. size-groups.

In May the size-group 4-5 mm. contains the most nymphs (table 3), whereas in April the maximum was in the 2-3 mm. size-group. If all the May figures are pushed back two size-groups they correspond remarkably closely with those of April, except at the top, where there are fewer nymphs owing to emergence and at the bottom, where there are more owing to the hatching of eggs laid by the an 1 adults. Evidently an increase of 2 mm. in length has been general during the month between the two collections. The new generation, progeny of an 1, may be called an 2, and therefore in May there is an 2 beginning, wn 1 approaching maturity and an 1 finishing.

In June the number of specimens less than 1 mm. long reaches the astonishing total of 11,023 (table 3), but nymphs large enough to be caught by the coarse net are fewer than in any other month in 1950 and 1951 (fig. 6). Presumably the last of the nymphs from last year's eggs have nearly all emerged and the new generation is still small. 1952 appears to be a little behind the other two years, though it is difficult to be certain because nymphs were always more abundant.

In this year, the only one when adult and fine-net data are available, the histogram in fig. 6 suggests that in June an 1 has almost finished emerging but wn 1 has scarcely started. The adult catches (table 4) indicate that it started just about the time when the nymphal collections were being made, and continued vigorously till the end of the first week in July, after which there was a decrease in numbers. Presumably, therefore, some time in July, probably towards the end, perhaps later, the emergence of specimens originating the year before finishes.

Is there any check on this suggestion that up to late July the specimens emerging are what have been called the an 1 and wn 1 generations? I think that the sizes of the adults (table 5) provide such a check. It was first noticed in 1952 that the specimens emerging in summer were small. In 1953 more attention was paid to this phenomenon and on July 20 an entry in the notes runs: "One imago 6 mm. long, the first small one I have seen this summer," but it was not until the following year that a record of lengths was kept all through the season. In 1954 (table 5) small ones first appeared in mid-July, though it was not until mid-August that the larger ones disappeared. In 1955 the separation was much more clear cut and complete within a week. It seems a reasonable hypothesis that the big adults, 8.5-10.5 mm. in length, come from big nymphs that have overwintered and therefore lived long, and that the small ones, 5.5-8 mm. in length, come from nymphs that have grown up within the summer, maturing in a shorter time and perhaps growing faster. If this is accepted, the figures mean that the overwintering generation comes to an end in late July or early August and the summer generation begins emerging in July. This was the conclusion reached from the study of the nymphs and so the study of the size of the adults provides a pleasing confirmation of a story that did contain a certain number of assumptions.

Reverting now to the nymphs, and especially to fig. 6, we expect to find a new generation, an 2, coming on in August and the foremost ones emerging at, however, a smaller size than their parents. The kite histogram for 1952 bears out this expectation precisely, though in the other two years there are still some large nymphs, presumably wn 1 stragglers; their numbers are greatest in 1951, which was colder during the first half than the other two years. Emergence continues till early November and the upper bulge at the top of the October kite histogram (fig. 6) is probably caused by wn 2, the lower by the first of the nymphs that will overwinter.

The smallest nymphs have been somewhat neglected in this analysis and it is desirable therefore to go back to May, when they first appear, and discuss them further (table 3). Interpretation of exactly what happens to them is extremely difficult because such colossal numbers apparently perish and a vast bulge in the lowest size groups does not pass on to the higher ones. In fact the study of the tiny nymphs rather than contributing to what has gone before depends on it before any interpretation is possible. An 1 and wn 1 eggs presumably hatch from May to August; it is not possible to make out when one comes to an end and the other begins, nor is it obvious why there were so many tiny nymphs in June. The first an 1 eggs hatch to give rise to an 2 nymphs in early May and the generation has completed development by the end of July, that is in about three months. If all nymphs take three months to complete development in summer, the August-September nymphs are the an 2 and the October-November nymphs the wn 2 generation. Do the an 2 eggs hatch in the autumn and the wn 2 eggs in the winter to give next year's an 1 and wn 1 generations respectively? Perhaps they do, for the kite histograms suggest that there is the same sequence of events each year, but, until more is known about why the smallest nymphs are to be found in every month, it will not be possible to say exactly what happens·

The an 1 and wn 1 adults were more numerous than those of the an 2 and wn 2 generations (table 4), though the reverse might be expected because the quick summer generation has a shorter time in which to be eaten by predators or perish in other ways. There are three possible explanations:

1. Conditions in 1952 were unfavourable for the quick summer generation.

2. Not all the eggs of the overwintered adults hatch soon, with the result that the nymphs do not mature till the following year; in other words only part of the population achieves the quick summer generation.

3. Error is due to the fact that all the adult collections were made in one place.

There was nothing obviously unfavourable about 1952, but, until more is known about *Baetis rhodani*, the first possibility cannot be discarded. The plausibility of the second possibility remains imponderable, but the third can be examined. Table 6 shows the percentage of large nymphs at station 1 in the different months each year, large nymphs being arbitrarily defined as those over 6 mm. long in the first six months of the year and over 5 mm. long in the second. In one or more of the months May to September inclusive in all three years, at least 63% of all the large nymphs found at the five stations were taken at station 1, the lowermost. These figures suggest that some time in the summer, early in 1951 and late in 1952, though why is obscure, there is a congregation at station 1. During the rest of the year there was only twice more than 40% at station 1, and the figures seem to indicate a certain amount of moving about, though their exact significance is hard to assess. What is clear, however, is that any statement about the size of an adult population based on a trap at one point may be widely erroneous.

TABLE 5

Lengths of adult *Baetis rhodani* caught in the emergence trap

| 1954 mm. | 5 | 5.5 | 6 | 6.5 | 7 | 7.5 | 8 | 8.5 | 9 | 9.5 | 10 | 10.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| May .. .. | – | – | – | – | – | – | – | 3 | 3 | 3 | – | – |
| June .. .. | – | – | – | – | – | – | – | 1 | 2 | 3 | 3 | 2 |
| July | | | | | | | | | | | | |
| 4th, 7th .. | – | – | – | – | – | – | – | 2 | 3 | – | – | – |
| 12th .. | – | – | – | 1 | – | 2 | – | 4 | 4 | – | – | – |
| 16th .. | – | – | – | – | – | – | – | 6 | 3 | 1 | 5 | – |
| 24th .. | – | – | – | – | – | – | 2 | 3 | 3 | – | – | – |
| August | | | | | | | | | | | | |
| 2nd, 5th, 8th | – | – | – | 1 | 2 | 4 | 10 | 2 | 2 | – | – | – |
| 12th .. | – | – | 2 | 1 | 1 | 1 | – | – | – | – | – | – |
| 15th, 22nd, 26th, 29th | 2 | 7 | 5 | 1 | 2 | – | – | – | – | – | – | – |
| 1955 | | | | | | | | | | | | |
| May .. .. | – | – | – | – | – | – | – | – | 1 | 1 | 1 | – |
| June .. .. | – | – | – | – | – | – | – | – | – | 2 | – | – |
| July | | | | | | | | | | | | |
| 21st, 25th .. | – | – | – | – | – | – | 12 | – | – | 7 | – | – |
| 28th .. | – | – | – | 1 | 3 | 2 | 6 | – | 2 | – | – | – |
| 31st .. | – | – | 10 | 8 | 6 | – | – | – | – | – | – | – |
| August .. | – | – | – | 7 | 5 | 15 | 1 | – | – | – | – | – |
| September .. | – | – | – | – | 6 | 1 | 2 | – | – | – | – | – |
| October .. | – | – | 7 | 1 | 10 | – | – | – | – | – | – | – |

TABLE 6

Number of large nymphs of *Baetis rhodani* at station 1 expressed as percentage of number at all five stations

| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1950 | – | – | 26 | – | – | – | 88 | 68 | 90 | 24 | 8 | – |
| 1951 | 14 | 8 | 19 | 29 | 63 | 78 | 47 | 46 | 29 | 28 | 40 | 40 |
| 1952 | 49 | 20 | 26 | 23 | 26 | 37 | 69 | 44 | 39 | 29 | 33 | 42 |

*Baetis pumilus* (Burmeister)

Small specimens of this species passed through the coarse net as did those of *B. rhodani* and, therefore, the fine-net catches are the most important ones for the elucidation of the life-history. The results with this net are presented in fig. 7, in which actual numbers in each size-group each month are shown.

The first collection was made in October, 1951, and a glance at the figure suggests that a new generation of nymphs has just hatched, for most are in the 1-2 mm. size-group and the biggest only 3-4 mm. long. During the next two months there is some growth. In January there is less evidence of growth, but there is an influx of tiny ones, presumably from eggs that have

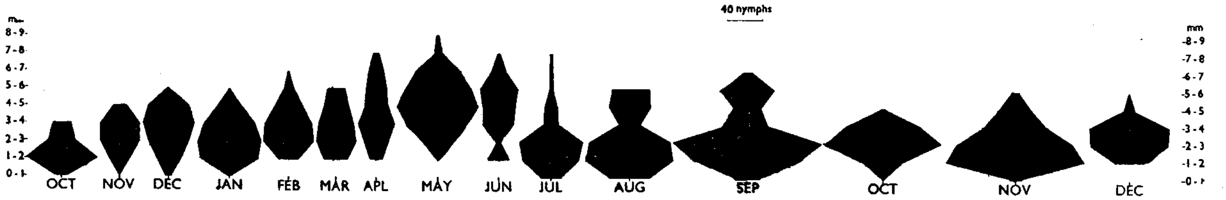

Fig. 7. Actual numbers of *Baetis pumilus* caught in the fine net arranged in mm. size-groups.

just hatched. Growth continues and by April the largest specimens are 7-8 mm. long. Emergence of this overwintering generation starts in May (table 7) and, to judge from fig. 7, goes on till July.

TABLE 7

Number of *Baetis pumilus* caught in the emergence trap at station 1 in 1952

| | | | |
|---|---|---|---|
| Apr. | 21st | 0 | |
| May | 8th | 0 | |
| | 11th | 3 | |
| | 14th | 0 | |
| | 19th | 0 | |
| | 27th | 2 | Total 5 |
| June | 1st | 0 | |
| | 3rd | 2 | |
| | 8th | 3 | |
| | 13th | 0 | |
| | 17th | 1 | |
| | 22nd | 0 | |
| | 29th | 9 | Total 15 |
| July | 2nd | 8 | |
| | 7th | 11 | |
| | 12th | 5 | |
| | 16th | 1 | |
| | 20th | 1 | |
| | 26th | 3 | |
| | 31st | 2 | Total 31 |
| Aug. | 4th | 1 | |
| | 7th | 1 | |
| | 11th | 0 | |
| | 14th | 0 | |
| | 19th | 1 | |
| | 24th | 2 | |
| | 31st | 6 | Total 11 |
| Sept. | 4th | 2 | |
| | 7th | 5 | |
| | 9th | 5 | |
| | 15th | 7 | |
| | 23rd | 4 | |
| | 29th | 3 | Total 26 |
| Oct. | 5th | 0 | |
| | 8th | 1 | |
| | 16th | 0 | |
| | 19th | 0 | |
| | 29th | 0 | Total 1 |
| Nov. | 2nd | 0 | |
| | 20th | 0 | |
| Dec. | 1st | 0 | |
| | 15th | 0 | |
| | 20th | 0 | |
| | 26th | 0 | Total 0 |

In June the number of nymphs 1-2 mm. long, at a minimum in May, goes up again and specimens in the 0-1 mm. size-group were taken in the shovel sampler at this time; there can be little doubt that these are the progeny of the overwintering generation that started laying eggs about a month previously. In July the figure is tadpole-shaped and, if the interpretation so far is correct, the new nymphs constitute the body, the stragglers of the overwintering generation the tail. In August the figure is hour-glass shaped, in other words there are two distinct size groups with modes at 1-2 mm. and 4-5 mm. respectively. There can be very few, if any, overwintering nymphs as late as this and probably every specimen derives from an egg laid the same summer. The upper bulge must be the tadpole's body of July, and the lower bulge must be made up of nymphs that have hatched since then. These two size-groups may represent nymphs that hatched in autumn and in winter, though there is no direct evidence apart from the appearance of many small nymphs in January already mentioned. A similar explanation of a waisted figure in the life-history of *B. rhodani* was put forward.

The important point about the August figure is, however, that, if the top bulge represents the tadpole's head of the July figure, and there does not seem to be any other explanation, the nymphs have increased their lengths by 3 mm. in the month, which is a faster rate of growth than in any species so far considered.

Very few adult *B. pumilus* have been caught in later years and therefore there are no measurements of adults comparable with those of *B. rhodani*, but work on cast nymphal skins (Macan, 1950) shows that the specimens of late summer are not as big as those emerging earlier.

The September figure resembles the August one except that the mode of each bulge is 1 mm. larger. It is unlikely, however, that growth in this month has been so much slower than in the month before and, therefore, the top bulge in September is probably derived from nymphs that were small in August. It is likely then that the September adults are the wn 2 generation, the August ones the an 2 generation, which means that *B. pumilus* has a life-history like that of *B. rhodani* except that it is shorter owing to quicker growth of the summer nymphs.

TABLE 8

Numbers of *Baetis pumilus* caught with the coarse net in ten minutes

| | | St. 1 | St. 2 | St. 3 | Ss | Og | Total |
|---|---|---|---|---|---|---|---|
| 1950 | March | 16 | 21 | 25 | 28 | 10 | 100 |
| | May | — | 9 | 16 | 49 | 8 | 82 |
| | June | 26 | 9 | 39 | 0 | 0 | 74 |
| | July | 37 | 13 | 0 | 0 | 1 | 52 |
| | August | 15 | 1 | 1 | 9 | 1 | 27 |
| | September | 22 | 4 | 2 | 2 | 0 | 30 |
| | October | 1 | 5 | 20 | 1 | 0 | 27 |
| | November | 3 | 0 | 7 | 4 | 0 | 14 |
| 1951 | January | 4 | 6 | 17 | 0 | 0 | 27 |
| | February | 7 | 8 | 20 | 2 | 5 | 42 |
| | March | 30 | 17 | 34 | 5 | 0 | 86 |
| | April | 53 | 35 | 37 | 1 | 3 | 129 |
| | May | 120 | 11 | 44 | 3 | 7 | 185 |
| | June | 25 | 0 | 0 | 0 | 0 | 25 |
| | July | 2 | 2 | 27 | 0 | 2 | 33 |
| | August | 17 | 18 | 12 | 2 | 26 | 75 |
| | September | 3 | 1 | 0 | 0 | 0 | 4 |
| | October | 0 | 0 | 0 | 0 | 1 | 1 |
| | November | 0 | 5 | 3 | 0 | 2 | 10 |
| | December | 6 | 1 | 2 | 0 | 1 | 10 |
| 1952 | January | 28 | 9 | 7 | 1 | 6 | 51 |
| | February | 22 | 1 | 10 | 0 | 2 | 35 |
| | March | 12 | 11 | 34 | 4 | 8 | 69 |
| | April | 61 | 31 | 49 | 7 | 20 | 168 |
| | June | 36 | 26 | 31 | 34 | 57 | 184 |
| | August | 10 | 3 | 16 | 12 | 41 | 82 |
| | September | 28 | 6 | 13 | 11 | 76 | 134 |
| | October | 5 | 4 | 3 | 0 | 5 | 17 |
| | November | 14 | 8 | 11 | 4 | 12 | 49 |
| | December | 8 | 0 | 0 | 1 | 2 | 11 |

In October the population consists entirely of nymphs that will overwinter. Whether there is any migration upstream or down is hard to make out. Table 8 shows the catches at each station each month and it will be seen that in July, 1950, and June, 1951, there was a concentration of specimens at station 1 that could have been derived from populations higher upstream earlier in the year, Sykeside and station 3 in the former and station 3 in the latter. On the other hand the drop in numbers at the higher stations could have been due to emergence and the rise at station 1 due to the capture of nymphs that earlier had been small enough to pass through the net. In 1952 there was less concentration at station 1 and a good population persisted in Outgate Beck from April to September.

What does appear probable from table 8 is that in different years generations are successful in different places; the overwintering generation was particularly numerous in Sykeside in 1950, at station 3 in 1951, and station 1 in 1952. The summer generation was usually widespread but was abundant in 1950 at station 1, and in 1952 in Outgate Beck where the overwintering generation had also done well. No explanation is offered.

Enormous numbers of tiny nymphs were not caught with the fine net, in which respect the two species stand in marked contrast. It is likely that the very young nymphs seek refuge between the smaller stones or in the gravel whence they will not be swept into the net of a collector turning over the larger stones, because the shovel sampler took significantly more of the smallest ones than the net. Catches with the two instruments as comparable as possible in time and place were:

| Length in mm. .. | 0-1 | 1-2 | 2-3 | 3-4 | 4-5 | 5-6 | 6-7 | 7-8 | Total |
|---|---|---|---|---|---|---|---|---|---|
| Twelve shovel samples | 6 | 205 | 95 | 14 | 6 | 1 | 0 | 0 | 327 |
| Six net samples .. | 22 | 155 | 177 | 106 | 13 | 4 | 0 | 1 | 478 |

According to Harris (1952, p. 63) and also Percival and Whitehead (1928) *B. pumilus* crawls down into the water to lay her eggs, but according to Gillies (1950) she flies over the surface of the water and dips the tip of the abdomen, behaviour that has been noticed also by the writer in Ford Wood Beck. *Baetis rhodani* has often been found on a stone picked from the stream and the egg mass, of which a good illustration is given by Clegg (1952, pl. 37), has a characteristic shape.

### *Paraleptophlebia submarginata* (Stephens)

This is a univoltine species with emergence in May and June. Tiny nymphs are found in August and growth is fairly rapid thereafter until about January when there is a slowing down until March or April (fig. 8).

Other members of the family that have been studied have a similar life-history, except that the eggs of *Habroleptoides modesta* (Hagen) (Pleskot, 1953) develop more quickly, and those of *Leptophlebia marginata* (Linn.) and *L. vespertina* (Linn.) (Moon, 1938) more slowly. *Habrophlebia lauta* McLachlan flies later in the year than any of these but otherwise has a life-history like that of *Habroleptoides modesta* (Pleskot, 1953).

The numbers of *P. submarginata* taken were too small to justify any further conclusions.

*Ephemerella ignita* (Poda)

This species is also univoltine but has a life-history unlike that of any other species in the stream; nymphs appear in summer, grow rapidly and then disappear (fig. 9). Presumably the greater part of the year is spent in the egg stage though this remains to be confirmed. In all three years the course of events was as in 1951 except that in the other two a few nymphs were recorded in September and, when a shovel sampler was used, very small nymphs were caught late in May.

Pentelow (Butcher, Longwell and Pentelow, 1937, pp. 139 and 144) records an identical life-history in the Tees and points out that nymphs are found during a longer period in the more calcareous Wharfe (Percival and Whitehead, 1930). Later observers have recorded similar observations, and Sawyer (1953) has identified *E. ignita* on various waters in every month of the year, but, as none has provided either more details or an explanation, there seems no value in a list of references.

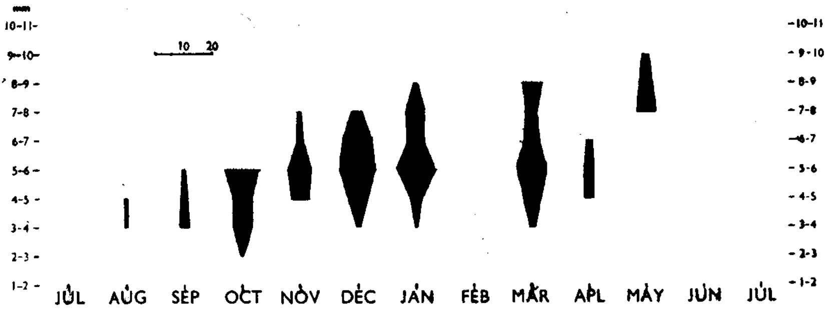

Fig. 8. Actual numbers of *Paraleptophlebia submarginata* caught with the coarse net arranged in mm. size-groups (season 1951-2).

Both Harris (1952, p. 64) and Sawyer (1950) record that this species flies upstream before egg laying. Oviposition in Ford Wood Beck has not been observed but any upstream migration seems unlikely because most of the nymphs occur at station 1. Upstream flight over a stony stream is perhaps not to be expected since Sawyer's observations are that the females lay eggs in broken water and suggest that the flight upstream may continue only till broken water is found.

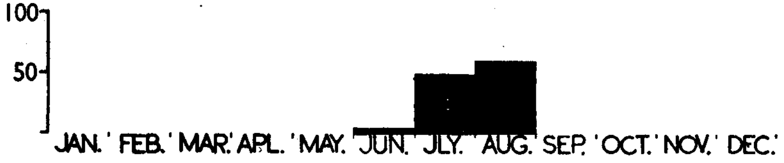

Fig. 9. Total number of *Ephemerella ignita* caught with the coarse net in 1951.

## DISCUSSION

Of these seven, only one, *Ephemerella ignita*, is a true summer species, growing during the warmest time of the year and lying dormant for the rest. All the others grow in autumn and spring, if not throughout the winter, and *Rhithrogena semicolorata*, *Heptagenia lateralis* and *Paraleptophlebia submarginata* have a period of inactivity during the middle of the summer; the stream therefore is inhabited mainly by cold-water species. In the stream studied by Harker, the period of inactivity was shorter, probably because the stream did not get so warm, and was curtailed at both ends, adults emerging later and eggs hatching earlier. It is possible that an advancement of the date of hatching could lead to a situation where conditions permitted the completion of a quick summer generation.

This variation in the life-history in two different streams raises several questions and it is worth noting comparable observations; no experimental work has been done and it is not possible at present to do more than speculate about the causes, but it may serve a useful purpose to examine the hypotheses of other workers.

Brinck (1949, pp. 142-4) shows that the emergence of many species of Plecoptera is progressively later in colder zones in Sweden. Nearly all the species emerge in the first half of the year, lay eggs and die. The eggs hatch after a fairly short time but the nymphulae that emerge from them do not grow during the high temperatures of summer and show no increase in size till the autumn. Growth is slowed down by the low temperature of midwinter and therefore specimens take longer to develop in the north than in the south and emerge later. The significant part of this life-history is the nymphula, which can tolerate quite high temperatures but which does not grow until the waters become cold in autumn.

Ide (1935) observed that *Iron pleuralis* in a Canadian river emerged from mid-April to mid-August near the spring, but only from mid-May to mid-June lower down. His explanation of the restricted emergence period in the lower warmer parts of the river is a very simple one. He postulates that, for a period during the summer, temperature is high enough to kill all but eggs. These take a long time to develop and any that hatch too soon give rise to nymphs doomed to succumb to a lethal temperature. This will mean that the first adult will appear later in the following year than in parts of the river that are colder in summer. The emergence period cannot go on as long because any nymph that has not emerged by a certain time will be killed by high temperature. Ide also points out that, in a stream with little annual temperature fluctuation, the breeding period will be restricted by a winter air temperature too low for the adults to mate.

Pleskot (1953) describes how *Habroleptoides modesta*, a common European species that does not occur in Britain, has a flight period restricted to early summer, though small nymphs are present all through the summer. She argues that summer temperatures cannot therefore be lethal but suggests that at them there is not enough oxygen for nymphs that, about to metamorphose, are in a critical stage when transference of oxygen from medium to tissues is difficult. It is oxygen lack at high temperatures that restricts emergence to early summer.

There are thus two possible explanations of the curtailment of the emergence period at its latter end—a direct temperature effect according to Ide and an indirect temperature effect according to Pleskot. Both may be right; only experiment can show. There are also two possible explanations of what prevents nymphs appearing earlier in summer than they do. Again Ide postulates a direct temperature effect, but the hatching of the egg may be determined by something within it and it could be a stage, like the plecopteran nymphula, that will not develop further until conditions are favourable. Ide mentions heredity but says little about it; it seems likely that mortality among nymphs that have come out of the egg too soon or have failed to complete development in time becomes reduced quite soon because selection produces a strain with a life-history adapted to the local conditions. It is clear, for example, that *Rhithrogena* avoides emergence of adults too early by what is probably a diapause, for some nymphs are full grown in mid-winter but none emerge before May. Whatever causes the kind of life-history under discussion and its variation from place to place, there is little doubt that it is ultimately due to temperatures that reach an unfavourably high level in summer.

## SUMMARY

1. Collections were made every month for three years in a small stony stream in the Lake District.

2. *Rhithrogena semicolorata* emerges mainly in late May and June, the new generation begins to appear in August, September or October and growth proceeds throughout the winter, development being completed in one season. Tiny nymphs are found up to January, which is thought to be due to delayed hatching of eggs, a phenomenon of considerable importance in the calculation of growth rate and productivity. In a stream studied by Harker, which was probably colder, emergence went on longer, eggs hatched sooner, and nymphs grew bigger. Most eggs are perhaps laid in the swiftest reach of the stream, from where the nymphs move upstream and down. They tend to move downstream before emergence.

3. *Ecdyonurus torrentis* has a life-history similar except that emergence takes place throughout the summer. This species is most plentiful at the lower end of the stream.

4. *Heptagenia lateralis* is also univoltine but it grows less in winter and emerges later than *Rhithrogena semicolorata.* It is most abundant in the upper parts of the stream. In the stream studied by Harker it differed in exactly the same way as *Rhithrogena semicolorata.*

5. *Baetis rhodani* has a long overwintering and a quick summer generation, the former emerging from April to July, the latter from July to November. It seems likely that each can be divided into two according to whether the members or their parents emerged from the egg in autumn or in mid-winter, though it is not possible to be certain of this until more is known about delayed hatching of eggs and what causes them to hatch ultimately. The

adults of the summer generation are smaller than the others. There was a concentration of nymphs at the lower end of the beck some time during each of the three summers.

6. *Baetis pumilus* has a similar life-history, but the emergence period is shorter.

7. *Paraleptophlebia submarginata* adults appear in May and June, tiny nymphs in August, and growth slows down in the middle of the winter.

8. *Ephemerella ignita* nymphs are found only in June, July, August and occasionally September, and the species is thought to spend the rest of the year dormant in the egg stage.

9. *Rhithrogena semicolorata*, *Heptagenia lateralis* and *Paraleptophlebia submarginata* have a resting period in the summer, probably spent in the egg stage. It seems likely that it tides over a period of unfavourably high temperature. The theories of other workers are discussed. Temperature may have a direct lethal effect, or oxygen may be deficient in the warm waters of summer. However temperature exerts its influence originally, it seems likely that natural selection soon produces a strain adapted to local conditions.

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