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THE EFFECT OF TEMPERATURE ON *RHITHROGENA SEMICOLORATA* (EPHEM.)

Contents

1. Introduction

Rhithrogena semicolorata (CURTIS) has one generation per year, emerges in the early part of the summer, and grows throughout the winter. That the hatching period extends from about August to about January is deduced from the occurrence of very small nymphs, and there is some evidence of downstream migration before emergence (MACAN 1957). The temperature of the stream where these studies were made was recorded continuously (MACAN 1958) and the intention now is to try to correlate events in the life cycle and events in the temperature cycle, in the hope that this will prove a useful preliminary approach to a problem which can ultimately be solved only by experimental work.

2. Rate of growth

The increase in the average size of nymphs in successive catches is a valid measure of rate of growth only if the population of a later catch has not been augmented from eggs unhatched at the time of a former. Growth of *R. semicolorata* cannot, therefore, be measured in this way until after January, at which time, however, nymphs that have reached their full size and stopped growing introduce another source of error. Clearly some other means of finding rate of growth must be sought and it must be borne in mind that there are three unmeasured variables: the two just mentioned and the number of nymphs that have invaded the sampling area from regions above it.

After trying several, I selected the one shown in fig. 1. The numbers in each size group are expressed as percentages of the total catch and histograms for successive months are then superimposed in pairs one on the other. The earlier month is indicated by the thick line, the later by the thin one and by shading. It is then possible to assess by eye the amount of growth from the extent to which the columns of the larger size-groups are taller than they were a month before. It is indeed possible by adding together the differences between the various columns to obtain for each month a rough value, which, if of no great mathematical significance, should be useful for comparative purposes. For example the difference of 21 between February and January in fig. 1 is reached in the following way:

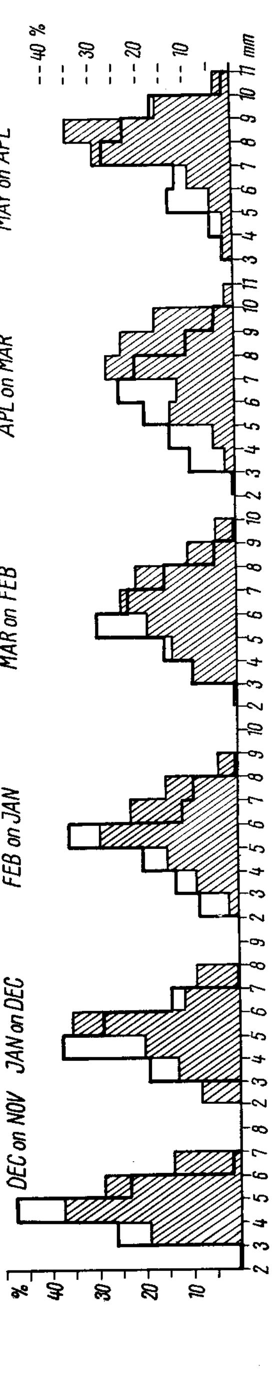

Fig. 1. Percentage of nymphs in each size group. The earlier month has a thick outline, the later has a thin one and is also shaded.

	6—7 mm	7—8 mm	8—9 mm	9—10 mm
	size groups			
Feb.	23	15	4	1 %
Jan.	12	9	1	0 %
difference	11	6	3	1/21

When all the differences are compared in this way, the following is the result:

	Dec.	Jan.	Feb.	Mar.	April
1951	—	—	16	22	21
1952	18	17	21	16	34

The month preceding the collection made in February 1952 was unusually cold, with an average temperature of 2·5° C and a maximum of 4·5° C. In the next four weeks both figures were about double. In 1951, February was warmer and March colder, temperature remaining near the same level throughout the eight weeks. This pattern is not reflected in the growth, which appears to proceed at a rather constant rate throughout the winter. There is some indication of an increase at the end of the winter and it may actually be great but masked in an average because many nymphs have ceased to grow. HARKER's (1952) statement that "a temperature level of about 6° C is required for active growth" is not true of the specimens in the stream studied. They are also different from those in the Mölle, which did not grow at all from the beginning of November to the end of February (ILLIES 1952, fig. 6).

3. *Start of emergence*

Some nymphs are full-grown in January or February but emergence does not start until May when there is generally a week or two of small catches preceding big ones late in the month or early in June (fig. 2).

If time of emergence were governed entirely by temperature, it should vary considerably from year to year and from place to place, as indeed in some

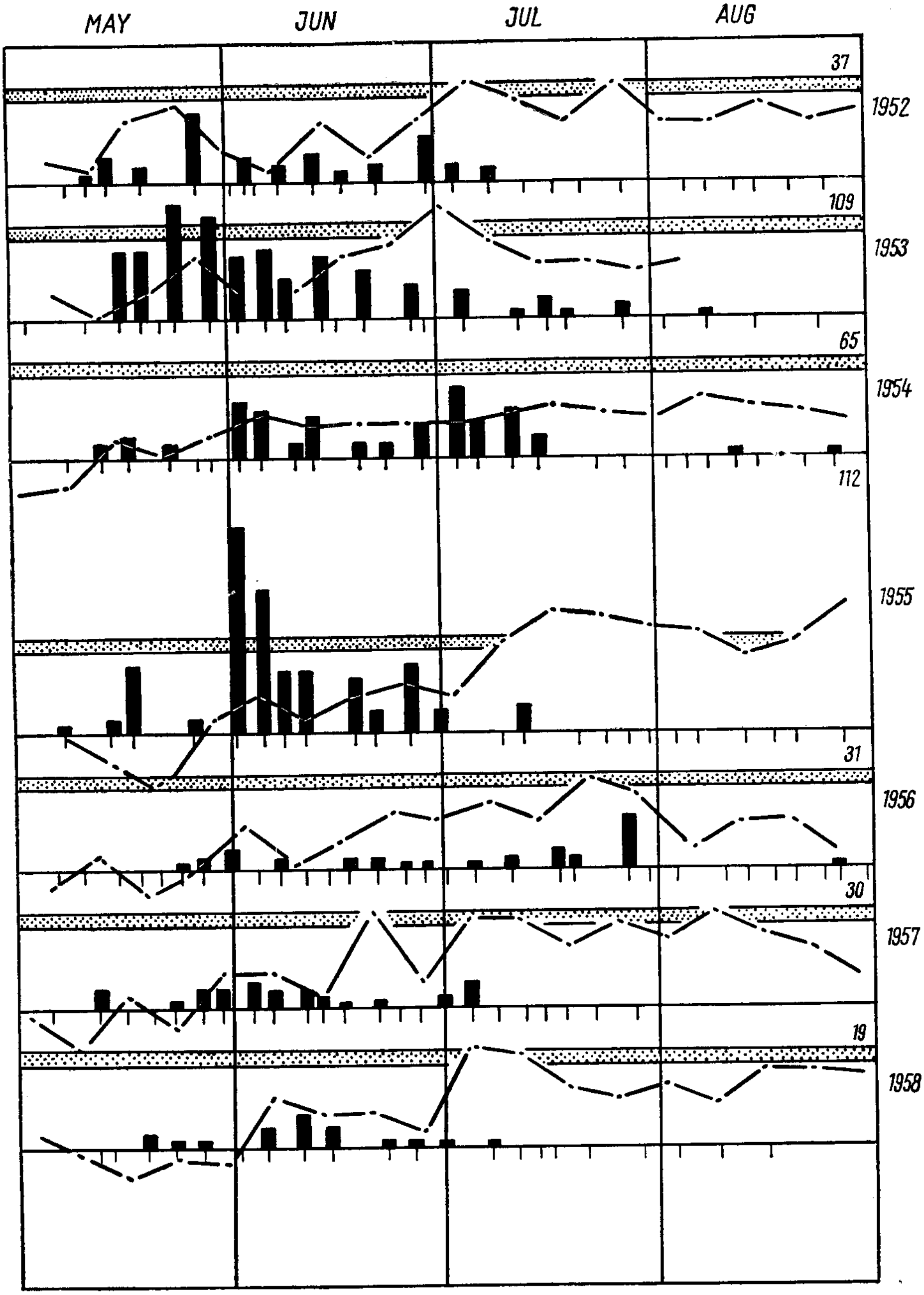

Fig. 2. The histogram shows the number of adults taken in an emergence trap. The small vertical lines indicate when the trap was visited. The figure at the right-hand side gives the total for the year. Scale: the last four catches in 1958 are each one nymph.
The graph shows the average weekly air temperature. Scale: the histogram baseline is 10° C, the two lines enclosing the dots 16 and 17° C.

species it does (PLESKOT 1951, 1953). MACAN (1958, p. 100) calculates that it should be three to four weeks earlier in Ford Wood Beck after a warm season than after a cold one. That of *R. semicolorata* is not, and a glance at fig. 2 is sufficient to show that the emergence of this species (histogram) is too regular to be governed entirely by temperature (line). Nevertheless, the peak is in May in 1952 and 1953 when that month was warm, and not till June in 1955 when it was cold. In 1954 and 1956, both years with rather uniformly cool summers, the first peak was not very distinct and there was a second one, in July. Temperature, therefore, would seem not to be without influence on emergence but it is probably but one factor in a complex, resolution of which cannot be achieved by the present method of associating field data.

4. End of emergence

The line in fig. 2 shows the average air temperature each week, the histogram baseline being 10° C and the two lines between which the dots are being 16 and 17° C. In 1954 emergence went on until late August, and it will be noted that the temperature never reached 16° C. 1956 and 1953 were similar except that in each there was one week in which temperature rose above 16° C. In the remaining years emergence came to an end when the average temperature rose above 16° C and remained above it for two successive weeks. Average water temperature tends to be the same as average air temperature but to lag behind it (MACAN 1958) and therefore water temperature does not reach a level which air temperature attains for a short period only. It appears, therefore, that mature nymphs are killed at an average temperature of about 16° C. HARKER's (1952) finding that emergence lasted longer in a stream that was probably colder than the author's confirms his conclusion, which is similar to that of IDE (1935). PLESKOT (1953) believes that the decreased concentration of oxygen associated with high temperature may be more important than the temperature itself. The actual lethal threshold, which depends on the temperature reached, on how long the animal was exposed to it, and on the temperature at which the animal was living previously, cannot be determined from these field data.

5. Hatching of eggs

According to IDE (1935) nymphs that hatch too soon, as well as those that do not emerge soon enough, are killed by lethally high temperature. The time of hatching of eggs of *Rhithrogena* was not established in the present investigation with sufficient accuracy to justify a statement.

6. Discussion

A study of PLESKOT's (1951) paper makes anyone who has studied only one stream aware that his conclusions must be cautious, but it is safe to draw attention to two unknown quantities that have come to light during the present study. The first is the temperature that the eggs can tolerate and the question of whether their hatching is determined by external or intrinsic factors, and the other is the stimulus that starts emergence. Taxonomic uncertainties preclude any precise statement about the geographical range of *R. semicolorata*, but obviously it could thrive in a stream appreciably higher or farther north than the one studied. Southwards its range may be curtailed by the temperature that the eggs can tolerate. If, however, emergence is inflexibly related to a factor or combination of factors in which temperature is not important, temperature could restrict range by reaching a lethal level before the stimulus to emerge came into play. Another consequence of such a condition would be a life history less variable than that of a species whose emergence depended more on temperature. Such a species could have two generations in water that was warm in winter and cool in summer, but only one either where a long winter did not permit time for more, or where warmth in summer was excessive. Survival under the last conditions would require eggs which were more tolerant of high temperature than nymphs and which remained unhatched while conditions were unfavourable.

7. *Summary*

1. *Rhithrogena semicolorata* has one generation per year, the adults starting to emerge in May and the eggs to hatch in August.
2. Growth proceeds steadily throughout the winter apparently little influenced by temperature.
3. The peak of emergence is both later and less distinct in colder years, but happens annually nearer the same date than it would if temperature were the sole controlling factor.
4. Emergence comes to an end when the average air temperature reaches about 16° C and remains at or above that level for two weeks or more. In years when this does not happen, a few adults appear as late as the end of August.

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