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The occurrence of Heptagenia lateralis (Ephem.) in streams in the English Lake District

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Summary:
1. During the summer of 1959 the maximum temperature at 18 stations in 8 streams was measured. The range was 16 — 28⁰ C.
2. Heptagenia lateralis appeared to be limited by a maximum temperature of about 18⁰ C.
3. The egg can probably withstand higher temperature than the nymph.
4. It is known that H. lateralis grows little in winter and it is suggested that, in the warmer streams, transition from winter temperature when there is slight growth to summer temperature high enough to be lethal is so rapid that the nymphs have not time to complete development.

Zusammenfassung:
1. Während des Sommers 1959 wurden die Temperaturmaxima an 18 Stationen in 8 Flüssen gemessen. Die Schwankung war 16 — 28⁰ C.
2. Das Vorkommen von Heptagenia lateralis schien durch ein Maximum von 18⁰ C begrenzt zu sein.
3. Anscheinend können die Eier höhere Temperaturen besser vertragen als die Nymphen.
4. Es ist bekannt, daß H. lateralis im Winter nur ein geringes Wachstum aufweist, und es kann angenommen werden, daß der Übergang von winterlichen Temperaturen zu jenen hohen Sommertemperaturen, die für die Art tödlich sind, in den höher temperierten Flüssen so schnell vor sich geht, daß die Nymphe nicht Zeit genug findet, ihre Entwicklung zu vollenden.

Heptagenia lateralis (Curtis) is one of the commonest species in some small stony streams but is scarce or absent in others (3). A possible explanation came to light during the course of an analysis of stream temperature (4) and measurements to test it were made in 1959.

Methods: Ordinary maximum and minimum wall - thermometers, protected by a metal tube, were concealed at 18 stations in 8 streams and read and reset at intervals throughout the summer. They were calibrated against a good laboratory instrument. Three disappeared during the summer; one was probably washed away, one was probably and one was certainly stolen.

The weather: The summer of 1959 was ideal for a study of maximum temperature, for, although no unusually high values were recorded, fine weather persisted from May till mid - October. Rainy periods were the second and fourth weeks of June and the beginning, middle and end of July, small amounts of rain fell in the same parts of August, September was without rain until the third week and then another dry period was almost unbroken till 16 October. Visible water disappeared from much of the beds of several streams in September.

The temperature: The table shows the maximum temperatures on various dates. The difference between the highest and the lowest is 12⁰ C. On the whole

all the readings in any one stream are similar, and the maximum in May is rarely much below the highest temperature of the summer. Windermere, for whose temperature 1 m below the surface, I am indebted to Mr. W. H. M o o r e, warms up more slowly to a maximum several degrees below that which it has reached in other years. The date of the maximum in the streams varies unaccountably. Although they were at their lowest levels on 20 September, that no particularly high maxima were recorded in October shows that highest temperatures are not associated with small volume, as was noted by M a c a n (4).

Nor Moss Beck rises in a former tarn reduced to a swamp by a deepening of the outflow. Water now lies in shallow pools among which are many islands and peninsulas. The temperature was recorded close to the moss. Holbeck rises on a hillside and then flows sluggishly across a flat area just over 300 m above sea level. Smooth Beck flows out of a fishpond and Stock Ghyll rises on open moorland at an altitude of about 400 m. These four streams then flow through woods or tree - lined gorges in which the temperature drops. All the upper stations are above and the middle and lower stations in the shaded zone. Outgate, a tributary of Ford Wood Beck, rises in a moss, Dan Beck in a fishpond, but the upper station in both was at the end of a tunnel which had cooled the water. The upper station of Pull Beck was at the foot of a wooded slope. These three streams flow across open country in which the water warms up. High Wray Beck emerges from a thick bed of peat on a slope facing north and runs through a wooded gorge.

The occurrence of Heptagenia lateralis: The catches of H. l a t e r a l i s in the table include some not in M a c a n's (3) table 6 and a few made later. No regular collections have been made in Windermere but a number of specimens for taxonomic work were obtained in it in 1940.

A glance at the occurrence of H. l a t e r a l i s suggests that it is associated with low temperature, but this is not true of all the places, and the anomalies must be examined before any association can be accepted. The species is abundant in Holbeck upper, although this is one of the warmest stations. It is, however, not far above a long stretch in which the species was particularly abundant, and a tendency to spread, especially during the cold time of year, might be expected. Conditions in Stock Ghyll were similar. It was scarce in the coldest stream of all that have been studied by the writer, Whelpside Ghyll (4, p. 98), and I attributed this in an earlier paper (3, p. 338) to the steepnees of the stream. The low temperature is due to the fact that the stream rises higher up than any of the others (about 800 m). It must not be overlooked, however, that there are no trees beside most of it. In all the other streams, the low temperature with which H. l a t e r a l i s appears to be associated is due to shading by trees, and the correlation might therefore be between the insect and the vegetation not between the insect and temperature. However, the occurrence in Windermere and other lakes (2, p. 82) shows that it is not and the explanation offered of the scarcity in Whelpside Ghyll may be allowed to stand for the time being. The findings, then, suggest that the distribution is governed by temperature, a maximum temperature above 18^0 C being too warm for this species. It is not, of course, possible to establish an exact thermal deathpoint from observations of this kind, because that depends not only on the actual temperature but on the duration of exposure and the temperature at which the animal has been living previously.

Tab. 1: Maximum temperatures recorded in 1959 and the number of specimens of Heptagenia lateralis and Rhithrogena semicolorata caught in ten minutes by means of a net.

Stream	Pos	Temperature °C May 19-22	May 25-30	June 4-8	June 15	June 24-30	July 3-8	July 10-15	July 23-31	Aug 16-18	Aug 27-31	Sept 8-12	Oct 9,10	Oct 19-27	max.	Heptagenia 1950 April Mar.	Heptagenia 1950 May	Rhithrogena 1954 April Mar.	Rhithrogena 1950 April Mar.	Rhithrogena 1950 May	Rhithrogena 1954 April Mar.
Nor Moss	U	—	26	—	—	28	—	27	—	—	27	17	18	—	28	0	—	—	7	—	—
Holbeck	U	22	19	19	22	22	21	22	22	—	22,5	24	—	20	24	57	28	—	19	19	—
Smooth	U	22	21	19,5	23	23	—	23	23	—	23	—	—	—	23	—	3	—	—	2	—
Ford Wood	L	13	20,5	19	—	19,5	—	17	19	—	22	20	—	—	22	0	—	—	39	—	—
Dan	M	—	—	—	—	—	—	—	—	20,5	—	—	—	—	21	—	—	—	—	—	—
Dan	U	—	18,5	—	—	19	—	19	—	—	21	—	18,6	15,5	21	—	0	1	—	23	67
Stock Ghyll	U	—	19	—	—	20	—	18,5	18,5	—	20,5	18,5	—	—	20,5	0	11	—	23	31	—
Pull	L	—	19,5	—	18	—	18	—	—	—	18	20	—	—	20	0	0	2	—	48	30
Dan	L	—	17,5	—	—	19	—	18	—	19,5	19	16,5	—	17	19,5	—	0	1	—	116	8
Smooth	L	18	17	15,5	16,5	18	—	18,5	18	—	19,5	—	—	—	19,5	—	—	—	—	—	—
Outgate		15	13	—	—	15,5	—	18	16	—	16	15	—	—	18	0	2	—	24	12	—
Holbeck	M	—	15	14	—	15	—	—	18	17	—	—	—	13	18	49	31	—	15	11	—
Stock Ghyll	L	—	—	—	—	16	—	18	16,5	—	—	—	—	14	18	43	35	—	24	26	—
Holbeck	L	15,5	14	13	15	15	15	18	15,5	15,5	—	17	—	16	18	21	21	—	53	40	—
Nor Moss	L	14	15	—	—	15	15	17	—	—	17	16,5	15,5	—	17	13	—	95	45	—	—
Pull	U	14	15	—	—	15	—	17	—	—	17	14	15,5	13	17	5	—	—	—	—	2
High Wray	L	—	17	—	—	16,5	—	17	—	—	17	14	—	—	17	—	15	—	115	146	—
High Wray	U	—	16	—	—	16	—	15,5	—	—	16	14	13	—	16	—	23	—	—	6	—
Windermere		—	—	16,5	17	18,5	19,5	—	—	20	19,5	19	—	13	20	—	—	—	—	—	—

U = upper, M = mid, L = lower.

This conclusion demands certain assumptions. H. l a t e r a l i s occurs in Windermere where maximum temperature surpasses by several degrees the limit just mentioned, though not till late in the season. It must be assumed, there-fore, that the nymphal is the critical stage and that the egg can withstand higher temperatures. Absence of the species from the warmer becks, in which the maximum does not exceed that of Windermere, is then due to failure to com-plete nymphal development before a certain temperature is reached. This could be because emergence is related to something other than temperature and the stimulus comes too late, or because development is not quick enough. The results of Pleskot (6) and Harker (1) indicate that emergence is related to tem-perature and the alternative is, therefore, more likely. H e p t a g e n i a l a t e-r a l i s grows little in winter and achieves most of its development in spring and early summer. I have no measurements other than those in Ford Wood Beck but believe that winter temperatures are similar in all streams, tending to be lowest in the exposed stretches that will be warmest in summer. All will start to warm up at about the same time, and it seems probable that some reach the lethal threshold for H. l a t e r a l i s before the nymphs have had time to complete development.

Macan (5) shows that emergence of R h i t h r o g e n a s e m i c o l o r a t a comes to an end when average temperature rises and remains at or above 16 — 17° C and suggests that this is due to death of any remaining nymphs, but it is impossible to determine the actual lethal temperature from these figures. The data in table 1 do not give a precise value either but it is obviously several de-grees above that of H. l a t e r a l i s. This species grows less in winter than R. s e m i c o l o r a t a (1, 3) and its temperature range is evidently shorter at both ends. This accounts for its more restricted distribution. On the other hand it possesses the ability to live in still water, which R. s e m i c o l o r a t a does not.

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