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Life Histories of Some Species of *Ecdyonurus* (Ephemeroptera) in the River Lune, North-Western England

by

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ABSTRACT

Collections were made regularly from a substratum of rounded stones in the River Lune, England, by lifting the superficial stones and sweeping a net beneath them. Three species of *Ecdyonurus* emerge one after the other from May to October. Months elapse between emergence and the capture of larvae of the new generation in the R. Lune but elsewhere, when the species occur alone, larvae abound in every month. It is concluded that the life histories are similar in the various types of water-body but that, when more than one species is numerous, small larvae do not come to the upper layers of the substratum until larger larvae of another species have vacated them.

INTRODUCTION

The River Lune, some 90 km long, flows southwards between two upland masses, the Pennine Chain in the centre of northern England and the Lake District to the west of it. The river receives much of its water from the Pennines, which are composed mainly of limestone, and some from the Lake District, from whose older rocks soft water flows.

On leaving the uplands the river enters a long alluvial plain intensively farmed, and runs swiftly over a bottom that is generally of rounded pebbles. Away from the edge the fauna is poor in species but those which can inhabit this unstable substratum are abundant. In shallow water near the margin, where the current is less swift, the fauna is more diverse, and larvae of *Ecdyonurus* are numerous (Macan 1976).

In October 1977 work was started at Gressingham, near the lower end of the alluvial plain, in connexion with a study by Dr. U. Humpesch of the rate of development of eggs of *Ecdyonurus* at different temperatures. Visits made during every one of the subsequent twelve months revealed that life histories were not the same as in some other localities. Accordingly during the summer of 1979, when Dr. Humpesch had returned to Austria, further collections were made, partly in order to arrange a programme to coincide with critical events rather than with the

fixed schedule that is unavoidable at the start of an investigation, and partly to remove any misgivings about possible misidentifications.

The intention now is to describe the life histories of three species in the R. Lune and to compare them with life histories in Ford Wood Beck and in Windermere. Ford Wook Beck is a small stony stream and in it *Ecdyonurus torrentis* is almost the only species present. Windermere is a lake and the only species found on its stony substratum is *E. dispar*.

METHODS

Collections were made with a net of coarse mesh, because one with a fine mesh did not allow the water in the fast part of the river to pass through sufficiently quickly. Larvae of *Ecdyonurus* less than 2 mm long can pass through this mesh (Macan 1958a). Each collection lasted for two minutes, during which time stones were lifted and the net thrust beneath them. Specimens that remained clinging to the stone were dislodged by swilling.

TEMPERATURE

The close relationship between temperature and rate of development has been shown by Humpesch (1980, inpress). Ideally temperature should be measured in the exact spot where the specimens were collected; in a small stream temperature changes with distance from the source and with the amount of shading, in a river it may be higher near the margins than in the middle, and in a lake on windless days in summer and winter there may be a steep gradient with increasing depth. The ideal has not been attained but the information available is sufficient to indicate important trends.

A recording thermograph was maintained in Ford Wood Beck for several years (Macan 1958b). The North West Water Authority operates a similar instrument in the R. Lune at Halton, a few km below Gressingham, and the average daily temperature there in 1977, 1978 and 1979 has been made available through the good offices of Dr. D. Cragg-Hine. The Freshwater Biological Association takes a spot reading of the temperature at the edge of Windermere every morning at about 0830 hrs.

When average weekly temperature in 1955 and 1956 in the beck and the lake are compared, little difference is evident during the first three months of the year. Thereafter the lake warms up more rapidly than the beck. The annual maximum during five years in the beck ranged from 16° to 19° C, the latter being exceptional, and in the lake between 17° and 23° C (Kipling & Roscoe 1977).

In 1978 the temperature of the R. Lune lay between 6° and 7° C during most of January and February, rising or falling only very slightly outside those limits. From early March onwards the trend was irregularly upwards. The exact temperature of the lake in January and February is unknown as there were many days on which ice prevented a measurement but it was certainly under 4° C. Then it

too rose with ups and downs similar to those in the river and a difference of about 3°C. From the beginning of May the gap began to close, and by the end of the month both had reached a peak at 18°C. In July Windermere tended to be slightly warmer than the River Lune but it was consistently a degree or two colder during the autumn cooling. The course of events was similar in 1977 and 1979, but in the fine dry summer of 1977 the river reached a higher temperature than the lake, highest average weekly temperature and highest daily temperature being 22.2° and 23.5°C in the R. Lune and 19.9° and 21.3°C in Windermere. The spring of 1979 was unusually cold, and in the R. Lune the upward trend from 7°C started about a month later than in 1978.

LIFE HISTORIES IN THE RIVER LUNE

The data obtained in 1979 are presented in Fig. 1. The scales are not all the same and attention is, therefore, directed to Table 1, which shows the numbers caught.

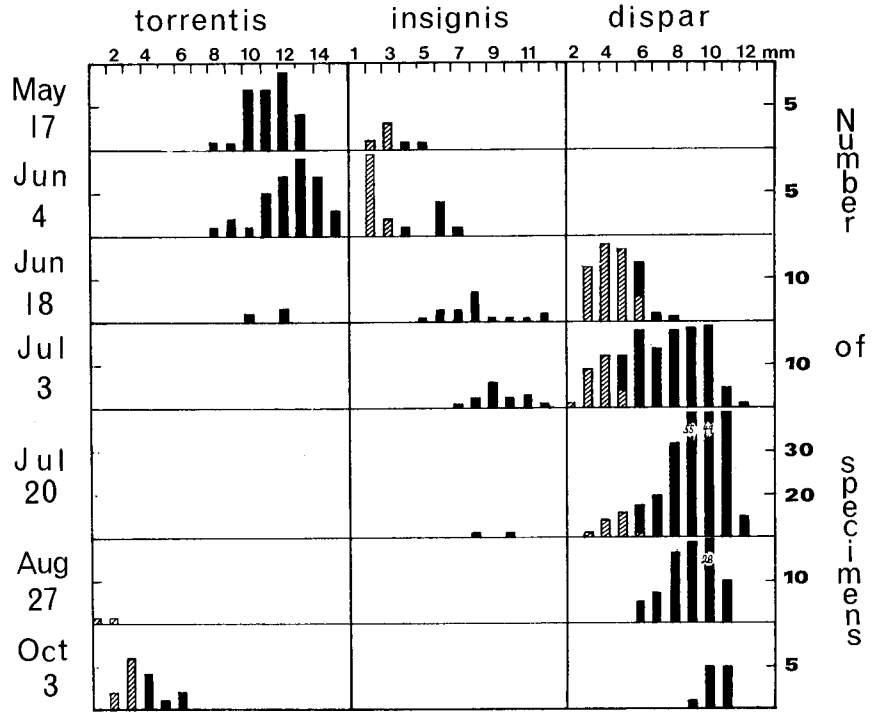

Fig. 1. *Ecdyonurus* in the River Lune at Gressingham in 1979: numbers in each size-class. The specimens in the column headed 2, for example, were between 2 and 3 mm long and so on.

The small larvae which could not be indentified with certainty are indicated by the diagonal shading, and have been allocated to the species to which they are most likely to belong. The largest larvae of *E. torrentis*, having been measured carefully in 1978, were measured by eye in order to avoid excessive handling before they were transferred to dishes with flowing water in order that identification might be confirmed from the subimagines and imagines.

Table 1. *Ecdyonurus* in the River Lune at Gressingham in 1979: numbers caught in two minutes in a net with a coarse mesh.

	17 May	4 June	18 June	3 July	20 July	27 Aug.	2 Oct.
torrentis	29	35	5	0	0	0	7
			6				
insignis	2	3	19	8	2	0	0
			19	15			
dispar	0	0	9	138	223	82	11
			2	107			
sp. indet.	4	25	56	23	21	2	8
			130	26			
venosus	0	0	5	0	2	0	0
			2	0			

A generation of *E. torrentis* came to an end in June. Collections in 1977 and 1978 had shown this species to be present from the autumn onwards, growing slowly in winter and more rapidly in spring. There was a generation of *E. dispar* during the summer, and one of *E. insignis* between these two species. *E. venosus* was also recorded but numbers were too small for any conclusions about life history (Table 1).

In 1979 cold weather persisted for an unusually long time. In 1978, when temperature was closer to the long-term average, *E. torrentis* was emerging in May and none was taken on 2 June, on which date small larvae attributed to *E. dispar* were taken for the first time. Total numbers of *E. dispar* were lower in 1978, and *E. insignis* was not taken in sufficient numbers for a distinct generation to be evident. Apart from these differences the sequence of events in the two years was similar.

COMPARISON WITH PREVIOUS OBSERVATIONS

No previous study of *E. insignis* in Britain has been discovered. It was not recorded in the Coquet, another river draining the uplands of northern England (Wise 1976). In that river the life histories of *E. torrentis* and *E. dispar* were almost the same as in the R. Lune, the main differences being that *E. dispar* was found during a shorter period (Table 2). In contrast, where either was the only or almost the only species present, its larvae were abundant in every month of the year.

E. dispar. In Windermere (Macan & Maudsley 1968, fig. 2) larvae grew all through the winter and some had reached full size by May or June, though during these

Table 2. Summary of some differences between *E. torrentis* and *E. dispar* in Ford Wood Beck (FWB), River Lune, River Coquet (1) highest station (335 m above sea level), (2) lowest station (15 m), and Windermere.

Species	Locality	Emergence period total	main	Length of largest larvae	First appearance of small larvae in large numbers
torrentis	FWB	May-Sept.	June, July	13-14 mm	August
	Lune 1978	May	May	15-16 mm	September
	1979	May-June	May-June		September
	Coquet (1)	Apr.-May	May	14-15 mm	September
	(2)	Apr.-May	April	15-16 mm	September
dispar	Windermere	June-Oct.		15-16 mm	September
	Lune	July-Oct.		11-12 mm	June
	Coquet (1)	July-Aug.	Aug.	9-10 mm	July
	(2)	June-Aug.	July	11-12 mm	June

months specimens of all sizes were still present. Observations on emergence were not made but Kimmins (1972), who collected around Windermere during the war, records a flight period from June to October. In June the number of small nymphs increased, and Macan & Maudsley (1968) interpret this to be the appearance of a second generation. However, the findings of Humpesch (1980, in press) on rate of development of eggs and larvae at different temperatures show that these small larvae could not have come from eggs laid the same year; they could only have come from eggs laid late during the previous season when the temperature was falling to a level at which development was slow. It is possible that eggs laid by the earliest adults give rise to a quick summer generation emerging late in the season, but most of the population achieves one generation in a year.

The course of events in the R. Lune was similar to that in Windermere except that no larvae were captured during the winter. Small nymphs, assumed to be those of *E. dispar* because no other species was present in later collections when larvae had reached a size at which they could be identified, were captured for the first time on 18 June (Fig. 1). Two weeks later, on 3 July, there were a large number of nymphs of all sizes, some fully grown. On 20 July the catch in two minutes was larger still, but a higher proportion of specimens was nearing full size. From June onwards the distribution of sizes is similar in the river and in the lake, except that there are fewer small specimens in the Lune.

The larvae that were numerous on 18 June could not have been small enough to be missed by the collector on 4 June; that is clear from the findings of Humpesch (in press). They were probably in the substratum at a depth where the technique of lifting the superficial stones did not reach them. The river is long but such collections as were made further upstream produced no evidence that the sudden appearance at Gressingham was due to downstream migration. Collections made at some distance from the margin showed that there had been no inshore migration from the central region of the river.

If then the larvae which suddenly appeared in the catches in mid June had previously been developing elsewhere, it would seem that the life history of *E.*

dispar in the Lune and in Windermere is similar, except that growth in the river in winter and spring is slower with a consequent shortening of the flight period.

Now must be sought an explanation of why the larvae remained so long away from the superficial stones. They may seek refuge from floods deep in the substratum, but March, April and May are the months when floods are least likely to occur. Some less transient factor must have been the cause. The explanation favoured is that the larvae are prevented from colonising the superficial stones by the larger larvae of *E. torrentis*.

E. torrentis. In Ford Wood Beck, a small stony stream, larvae grew throughout the winter (Macan 1957, fig. 4). Adults were caught in a trap from May to September, though the main period of emergence was June and July. Large numbers of small larvae appeared in August. Life history in the Lune was similar except that emergence was earlier and the termination of it more abrupt, and followed by a period when no larvae were taken, the first small ones not appearing until September.

Comparison of the emergence of adults from the Lune and from Ford Wood Beck, and from the Lune in 1978 and 1979, shows that it was earlier when the temperature was higher. That temperature may not be the only factor is indicated by Harker's (1952) record of emergence in March from a stream which was certainly not warmer and probably colder than the Lune (Harker 1953).

The absence of larvae from the summer collections in the Lune and their later appearance in that river compared with Ford Wood Beck can be explained in the same way as the absence of *E. dispar* in winter: as long as large larvae of the other species are present the smaller larvae of *E. torrentis* cannot colonise the stones at the surface, and while they remain in the deeper layers their growth is retarded. The eggs of *E. torrentis* from the R. Lune hatch in 18-48 days at a mean temperature of 15°C (Humpesch 1980) and, therefore, larvae must have been present for some time before they appeared in the collections.

DISCUSSION

If the interpretation based on the field data is correct, the life history of both species is similar except that, at the same temperature, *E. torrentis* emerges earlier than *E. dispar* and its eggs hatch earlier. This would account for the way in which the two species divide the Lune between them in the manner observed. The life history of *E. dispar* appears to be more complicated than that of *E. torrentis* because it lays more of its eggs in the autumn and, therefore, some small larvae do not occur in the collections until the following summer. Why *E. torrentis* emerges earlier is a question that cannot be answered until more observations have been made. Humpesch (1980) finds that there is a slight tendency for the eggs of *E. torrentis* to develop more quickly at a given temperature, but he could not make a direct comparison between the two species in the Lune because in that river there is some delayed hatching of the eggs of *E. dispar;* the time between the first and last hatching of a batch of eggs is long. In an extensive investigation of five species

from different localities he did not observe this phenomenon again; he found that the rate of development was related to temperature and that the period over which a batch of eggs hatched was short, except at the lowest temperatures. Similar observations on the rate of larval development of species other than *E. dispar* (Humpesch in press) and on the factors which induce emergence must be awaited before further comment can be made.

SIZE OF LARVAE AT TIME OF EMERGENCE

There are differences from place to place but little except speculation about the cause is possible. The full-grown larvae of *E. torrentis* were larger in the R. Lune than in Ford Wood Beck (Table 2) and larger again in the Lancashire stream, where Harker (1952) records specimens up to 19 mm long. The Lancashire stream at the point where collections were made is possibly the coldest, for it is the highest but, as temperature was measured only once a month, it is impossible to be more precise. Unexpectedly the earliest emergence was recorded here. Food may be an important factor. The Lancashire stream runs through cultivated land and Harker (1952) records a heavy growth of blue-green algae in May. Wise (1980) records earlier emergence and larger size at the lowest station in the R. Coquet (Table 2); the average temperature in May was higher in the lower reaches, but the data presented are scanty, consisting only of a maximum and minimum for each month (details in a further publication are promised).

The small size of full-grown *E. dispar* in the R. Lune compared with Windermere could be due to the fact that the larvae are prevented from reaching the surface layers, where algae grow, during the spring, the time when algal growth is luxuriant.

Genetic strains may be different in each locality, a possibility supported by the observation of Humpesch (1980) that there is delayed hatching of the eggs of *E. dispar* in the R. Lune and in no other locality investigated by him. This, however, would not affect the main hypothesis that the absence of either species from the collections when larger larvae of the other are numerous is due to some kind of reciprocal interference.

SUMMARY

In the Lune, a large river by British standards, larvae of *E. torrentis* appear in the autumn, grow through the winter and emerge in early summer. Larvae were not caught again until September. A generation of *E. dispar* is found during summer and autumn, and a small generation of *E. insignis* is interposed between them. In the absence of other species, larvae of *E. torrentis* in a small stony stream and of *E. dispar* in a lake are numerous in every month. A hypothesis is put forward that, in the presence of large larvae of another species, smaller ones are confined to the deeper parts of the substratum and do not colonise the stones at the surface until the larger larvae have emerged. While confined to the deeper regions, the larvae grow less rapidly than when at the surface.

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