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THE LIFE-CYCLE OF *Chloëon dipterum* L. (EPHEMEROPTERA : BAETIDAE)

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In spite of the abundance of *Chloëon dipterum* L. in still water habitats in the south of England, there is no published information on the pattern of growth of the larvae of this mayfly. Eaton (1883) claimed that *Chloëon* in general was double brooded, while Harris (1952) states that *C. dipterum* completes one generation each year.

During the course of a study on the feeding habits of *C. dipterum,* carried out in S.E. Leicestershire during 1957-1959, samples of larvae were collected at two to four week intervals from several ponds. Every larva in these samples was measured and the life-cycle was deduced from the changes in the mean size and the size composition of the samples. The results of some laboratory experiments on the growth and emergence of *C. dipterum* that have a bearing upon the interpretation of the life-cycle are discussed.

Materials and Methods

Samples of larvae were collected by means of a phytoplankton net, which was of sufficiently fine mesh to capture the smallest larvae (Macan, 1957). At least one hundred larvae were taken whenever this was possible within a practicable collecting time. Each larva was measured under a binocular microscope to the nearest millimetre, while still wet, from the front margin of the head to the base of the caudal cerci. Larvae were returned alive to the precise place from which they had been collected and throughout the whole series collections were always made at the same place in each pond. A record was kept of the occurrence of larvae nearing metamorphosis which were easily recognisable by the large size and dark colour of the wingbuds.

The National Grid References of the ponds are given below:—

Baggrave	—O.S.1947, 2½ ins./mile.		Sheet 43/60, 696086.
Whites Barn	— ,,	,,	Sheet 43/70, 708074.
Quenby Willows	— ,,	,,	Sheet 43/70, 709052.
Fludes Lane	— ,,	,,	Sheet 43/60, 642002.

These are all small field ponds undergoing a wide seasonal fluctuation in temperature, being covered with ice for four to six weeks in the winter and reaching 22-23° C. in the surface layers in the summer. Dense populations of *C. dipterum* larvae were present which probably contributed a major part of the biomass of the animal production in the habitats.

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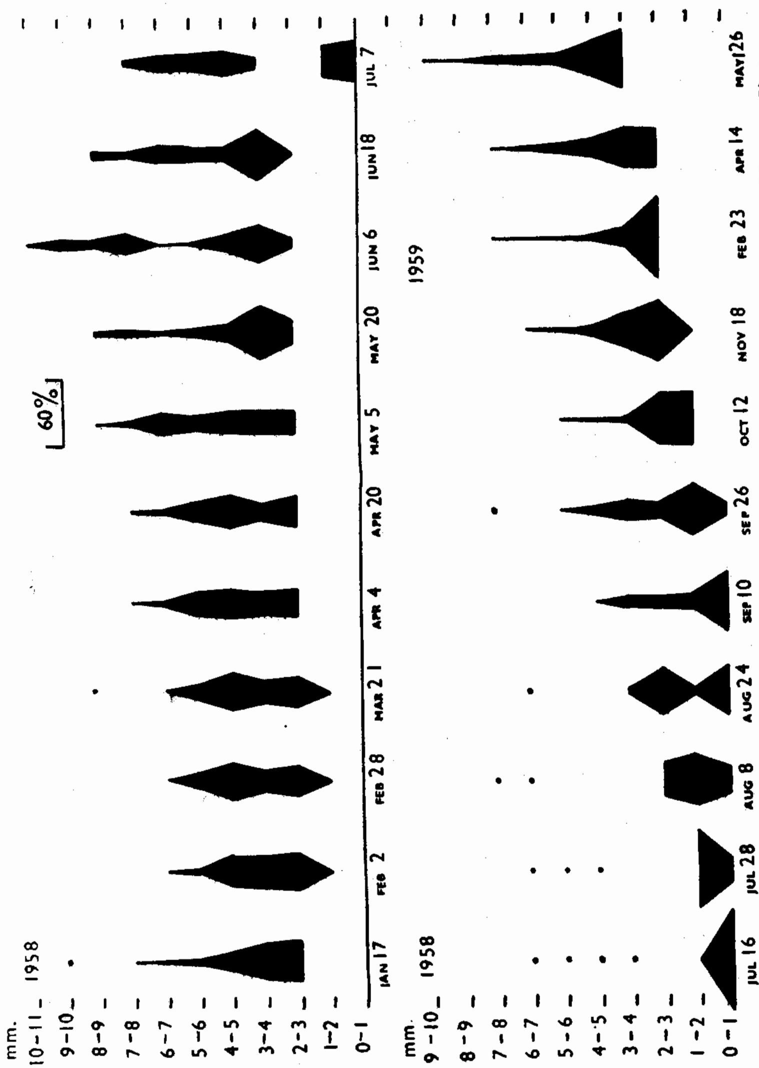

Fig. 1.—Percentage composition in millimetre size groups of collections of *Chloëon dipterum* from Baggrave pond, S.E. Leicestershire, 1958-9. Isolated values of less than 1 per cent. are indicated by dots.

Results

The pattern of growth observed in all four ponds was the same, in that one main generation was completed in 1958. The results obtained from Baggrave pond will be described in detail and the numbers of larvae occurring in each size group in the samples are expressed as percentages in figure 1. Larvae of under 1 mm. were present for a period of only ten to eleven weeks in the summer (Fig. 1) and in the absence of any evidence of delayed hatching of eggs as found by Macan (1957) in the case of *Baetis rhodani* Pictet the growth of *C. dipterum* from autumn to early summer may be expressed by comparing the mean lengths of successive samples (Fig. 2b).

The results indicate that one generation of *C. dipterum* emerged in Baggrave pond in 1958. The population of over-wintering larvae made little growth from January until the beginning of May, when the proportion of larger larvae increased sharply and the average size continued to increase rapidly until by the 16th July all but a few of the individuals had emerged. On the 7th July larvae of less than 1 mm. appeared in the collections for the first time and continued to do so until the end of September. The last few survivors of the overwintered generation were collected at the end of August. A single larva of 7 mm. taken on the 26th September probably belonged to this generation, but it is also possible that it had hatched from an egg laid at the beginning of the 1958 oviposition period. This larva showed none of the characteristics of imminent emergence and as no exuviae or adults were observed after the end of August it is unlikely that any larvae hatched from eggs laid in 1958 reached the adult state in that year. In the absence of data on the hatching of the eggs of *C. dipterum* it may be tentatively assumed that at the temperatures prevailing in the ponds studied the incubation period of the eggs was about 14 days, the time recorded by Degrange (1955) for *Chloëon simile* Eaton at 12° C. In this case the emergence period of *C. dipterum* probably began and ended about two weeks before the dates on which larvae of 0-1 mm. were collected for the first and last times, i.e. from 23rd June to 12th September (Fig. 2a).

The new generation grew rapidly in the autumn, but between the middle of November and the middle of April 1959 growth was slight; in fact there was a decrease in mean size. On the 26th May there were relatively more large larvae present than in the collection made on 20th May 1958, a difference that was probably due to the generally higher temperatures in the early part of 1959 compared with 1958 (Fig. 2a).

In Quenby Willows and Fludes Lane ponds larvae of less than 1 mm. were not present until 16th July, a fortnight later than in the other ponds. In Whites Barn pond, where higher maximum temperatures were reached than in the other ponds, the newly hatched 1958 generation grew more rapidly so that there was an overlap between the sizes of the old and new generations. Thus, at the end of July and the beginning of August (Table 1), large larvae were collected that may have belonged to either generation and it is possible that a few larvae of the new generation emerged and laid eggs that hatched in September, giving rise to the large numbers of 0-1 mm. larvae collected on 9th September.

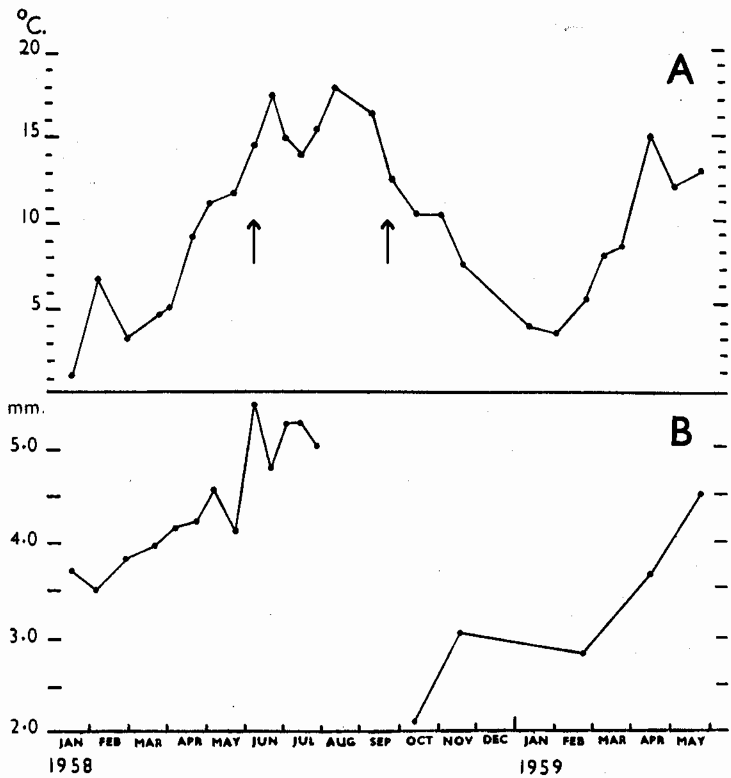

Fig. 2a.—The fluctuation in temperature 6 ins. beneath the surface of Baggrave pond, 1958-9. (The dates between which adults were probably emerging are indicated by arrows.)

Fig. 2b.—The mean size of samples of *Chloëon dipterum* collected in Baggrave pond, 1958-9.

TABLE 1.

Percentage composition in milimetre size groups of samples of *Chloëon dipterum* collected at Whites Barn pond, 1958.
(Results expressed to nearest one per cent.)

Date	n	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
18.6.58	54	0	0	0	7	24	22	21	15	7	4
3.7.58	223	79	0	0	0	2	4	6	5	2	2
15.7.58	138	60	26	2	0	0	0	1	7	3	1
28.7.58	261	27	46	12	4	4	2	1	1	1	0
11.8.58	133	15	33	46	1	2	1	1	1	0	0
24.8.58	191	14	16	58	9	2	0	0	0	0	0
10.9.58	853	77	8	5	7	2	1	0	0	0	0
26.9.58	495	13	49	7	17	10	4	0	0	0	0

n = total number of larvae in sample.

Regulation of the life-cycle

Present in many of the samples collected from all the habitats in the winter were large larvae of 6 to 9 mm., a size at which emergence took place in the summer. In many of these larvae the wingbuds were well developed in January but none was ever found in which the darkening in colour which precedes metamorphosis had taken place. Larvae transferred to aquaria at the beginning of January and kept at room temperature 16-18° C.) emerged in the middle of February. It is likely that insufficiently high temperature is the factor preventing fully grown larvae from achieving complete physiological maturity and emerging in the winter.

A distinction between the temperature requirements for general growth and the onset of the processes leading to emergence may also explain the fact that the largest larvae disappear at the beginning of the emergence period and are not replaced, although smaller larvae are still abundant. It appears that emergence takes place at a smaller size as the summer progresses and this may be due to the larvae that were already large in the winter continuing to grow in the absence of a suitable temperature for emergence and reaching a greater size than the larvae completing their growth in the spring and early summer under temperature conditions that induce full maturity at the smallest possible size. The precise way in which such a temperature stimulus acts is unknown. Larvae may need to experience a certain threshold temperature or the effect of temperature may be cumulative so that emergence depends both upon the temperature and the time of exposure. Larvae collected in the spring and kept at 10° C. emerged successfully and in view of this it is surprising that the emergence period does not extend further into the autumn in the field as temperatures remain above this level until October. Illies (1952) found that the temperature requirements for growth of several species of mayfly larvae were greater in the late summer and autumn than in the spring. This may also be the case for the emergence of *C. dipterum* and would have the value of restricting the emergence of adults to the season when air temperatures are high enough to allow successful flight and mating activity, and the onset of temperatures low enough to prevent the hatching of the eggs is not imminent.

Moon (1938) found that a spring increase in the growth rate of *Leptophlebia marginata* (L.) and *L. vespertina* (L.) in Lake Windermere was accompanied by an increase in the amount of algae in the gut and suggested that the amount of algal food available was an important factor regulating the seasonal pattern of growth in these species. Studies on the food of *C. dipterum* (Brown, 1959 and 1961) showed that there was a synchronous increase of the growth rate and of the quantity of algae in the gut in the spring but the quantity of food available could not have been the factor limiting growth in the winter because the maximum production of algae took place in the ponds in January and February. Temperature appeared to be the limiting factor controlling the growth of larval *C. dipterum* in small ponds, although in other habitats it is possible that qualitative and quantitive changes in the composition of the food play an important part.

Discussion

It is probable that the life history of many species of Ephemeroptera is regulated so that unfavourable environmental conditions are avoided by the interpolation of resting periods in the egg or larval stages. Macan (1957) discusses the examples of *Ephemerella ignita* Poda and *Rhithrogena semicolorata* (Curtis) which undergo what is probably a diapause in the egg and larval stages respectively. The life cycle of *C. dipterum* lacks any true diapause for although larvae full grown in the winter may not emerge for several months they do so soon after being transferred to a higher temperature.

C. dipterum completed one main generation in S.E. Leicestershire in 1958, but as a result of an advancement of emergence due to higher temperatures in 1959 it is probable that a far larger proportion of adults emerged in late August from eggs that had been laid in late May of that year. The species is known to be viviparous in the southern part of its range (Joly, 1877, and discussion in Eaton, 1883) and it is reasonable to assume that as many generations are completed as the temperature conditions allow. The plasticity of the lifecycle and the direct dependence of the rate of development upon temperature may be regarded as part of the adaptation of this species to life in small temporary bodies of water.

Summary

1. The life cycle of *C. dipterum* in four ponds in S.E. Leicestershire was deduced by measuring samples of larvae collected at 2-4 weekly intervals over a period of eighteen months beginning in January 1958.

2. One main generation emerged from June to September in 1958. Small larvae were not collected before the beginning of July or after the end of September, there was thus no evidence of delayed hatching of eggs.
3. Emergence took place about a fortnight earlier in 1959 in correlation with the higher temperatures, with the probable result that a considerably larger second generation of imagines was produced at the end of the summer.
4. It is suggested that temperature is the factor limiting the growth of *C. dipterum*. The life cycle is a temperature labile one lacking a true diapause and adapted to the rapid completion of numerous generations in small temporary bodies of water.

Acknowledgments

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