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OBSERVATIONS ON THE GROWTH OF EPHEMEROPTERA IN FLUCTUATING AND CONSTANT TEMPERATURE CONDITIONS

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OBSERVATIONS ON THE GROWTH OF EPHEMEROPTERA IN FLUCTUATING AND CONSTANT TEMPERATURE CONDITIONS

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Abstract

1 The paper is in two parts, the first of which describes the life cycles of some common lotic Ephemeroptera in a small stream system in western Ireland and the second the life cycles of two species in an isothermic stream in Co. Galway.
2 Growth cycles of ten species are investigated in a normal stream. The cycle for *Caenis rivulorum* is presented for the first time. Some of the other results differ slightly from results obtained elsewhere. *Ecdyonurus venosus* has a growth pattern resembling that described by Rawlinson (1939).
3 In an isothermic stream the growth rate of *Ephemerella ignita* is altered by a difference in temperature and its growth is a function of total day-degrees.
4 The growth rate of *Baetis rhodani* is similar in the two types of stream and appears to bear little relation to temperature.
5 Observations on allometry in the final instar of *Baetis rhodani* are made, together with observations on the size of the final instar under different conditions.
It is concluded that various factors may influence final instar size in *Baetis rhodani* and the role of temperature requires further investigation.

General Introduction

The life cycles of the common lotic Ephemeroptera are well known (see Macan 1961). However, studies on these species continue in order to make comparisons of the differing rates of growth in different places. Not a lot is known about the factors which control growth in most species although temperature is thought to be responsible for some variation (Elliott 1967, Radford and Hartland-Rowe 1971, Ulfstrand 1968) and nutritional and competitive factors are also supposed to be important (Ulfstrand 1969, Radford and Hartland-Rowe 1971).

This paper on Irish ephemeropteran populations is divided into two parts the first of which describes the life cycles of ten species in a surface stream

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system whose temperature varies diurnally and seasonally. These life cycles are compared with results obtained by other workers. In the second part of the paper the life cycles of two of the species treated in the first, *Baetis rhodani* and *Ephemerella ignita,* are described in more detail from an isothermic stream in western Ireland (the Cregg River, national grid reference M. 35,35). In the interpretation of both, special attention is given to the occurrence and size of the final instar. An effort is made to compare the life cycles of both species in the two stream types using the quantitative measurement of day-degree quotas.

Part I. The cycles of some Ephemeroptera in surface waters in western Ireland

Introduction

There are now many studies on the growth patterns of British lotic Ephemeroptera (bibliography in Elliott 1967) but no comparative account has been prepared for Irish populations. The following descriptions of the growth patterns of ten species in a small stream system in western Ireland (the Altahoney system, national grid reference F. 95,05) is an attempt to contribute something on the subject.

Methods and Results

Sites of collection

The streams from which material for this study was collected make up a small system whose total catchment is 109km². The work was carried out on three stretches of the river system which differed in detrital content, substratum and slightly in temperature (Table 1). The altitude of the three sites varied between 70 and 160m above O.D. and the stream widths were between 1·5 and 15m. The substratum was of quartzite boulder clay.

Observations on temperature

Spot temperature measurements for the three sites were taken for the duration of the collections (Table 1). Comparison of these figures with measurements collected by other workers (Ulfstrand 1968, Macan 1957, Elliott 1967 and Hynes 1966) shows good agreement with the general pattern of stream temperature changes in western Europe throughout a twelve-month period. From the figures produced by Hynes (1966) for the Afon Hirnant some of the greatest variation occurs at stretches of the river which are at a relatively low altitude. This is in accordance with Macan's (1958) account of a stream temperature reaching equilibrium with the air temperature within a few km of the stream source.

In the system under consideration there is little difference between the readings at the three sites but the occasional nature of the measurements may have been responsible for this. During a later and more detailed investigation of the three sites the temperature at site I was found to be consistently higher during the summer months than at either of the other two stretches. Above site II there is a lake which maintains a steady flow of water through that stretch and through site III which is further downstream. During a dry summer, however, the stream flow is greatly reduced at site I and only a small trickle of water persists. At site I this permits the water which is almost isolated in pools to reach a comparatively high temperature.

TABLE 1.—Mean readings for 5 monthly spot temperature measurements at each of three sites on a small river system in western Ireland

	Sites		
Months	I	II	III
X	8·8	9·3	9·5
XI	6·2	7·0	7·3
XII	7·2	7·5	7·5
I	6·0	6·0	6·9
II	6·5	6·7	7·1
III	6·9	7·3	7·7
IV	8·2	7·9	8·3
V	13·4	12·0	12·5
VI	18·3	18·0	18·7
VII	13·0	14·0	14·6
VIII	14·3	16·7	17·3
IX	16·8	17·2	17·3

METHODS OF COLLECTION

Hand-net samples were collected at monthly intervals throughout a twelve-month period and all Ephemeroptera were identified to species and measured to the nearest 0·1mm. The results are arranged after the methods of Macan (1961) where successive modal points of monthly length frequency histograms are joined to form a growth curve and the limits of the length frequency histograms are represented by a vertical bar to delimit the range of sizes. Where the results are insufficient to permit the calculation of growth rates by these methods the individual readings are placed on a twelve-month length diagram and the growth curves are suggested by a continuous line. Emergence data (or more accurately, flight period data) were collected from Mundie trappings, sweep netting the bankside vegetation and beating tray collections from bankside trees.

SPECIES FOUND

Comparison of the species list (Table 2) for the river system with the results obtained by other authors indicates that the fauna is composed of species normally taken at low altitude in Britain, i.e. the faunal list is more similar to that of the Ford Wood Beck (Macan 1957) than the Walla Brook (Elliott 1967). Many of the species which are listed here have been widely taken in this country and are common. Macan (1960) found that *Heptagenia lateralis* was absent from Lake District streams in which the temperature rose above 18°C and concluded this was a reason. According to Macan's calculations the temperature of the stream system in western Ireland was above the tolerable limits for this species. However, the temperature difference may be too small to be significant.

TABLE 2.—The species constitution of the Ephemeroptera in a small stony stream in western Ireland. The figures refer to the total catch over a 12-month period.

Baetis rhodani (Pict.)	1,217
Caenis rivulorum Etn.	432
Baetis muticus (L.)	409
B. scambus Etn.	398
Rhithrogena semicolorata (Curt.)	297
Ephemerella ignita (Poda)	178
Heptagenia lateralis (Curt.)	131
Paraleptophlebia submarginata (Steph.)	83
Ecdyonurus venosus (Fabr.)	47
Heptagenia sulphurea (Mull)	32
Centroptilum luteolum (Mull)	13
Paraleptophlebia cincta (Retz.)	3
	3,240

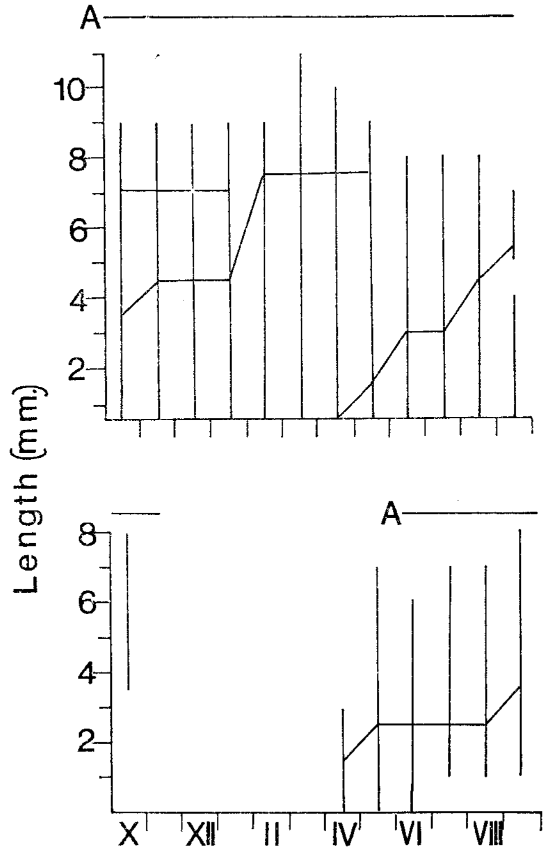
GROWTH RATES

An account of the growth of the species considered here is given in Figs. 1–7. For *Caenis rivulorum* the growth pattern is presented for the first time but the other species have been investigated by several authors permitting comparison of the results obtained here with the situation in other parts of the British Isles and Europe.

Baetis rhodani (Fig. 1) and *B. muticus* are bivoltine. The results in the present work are similar to those described by most other workers. Ulfstrand (1968) reviews the situation in *rhodani* whose life cycle is similar in different parts of Europe.

(FIG. 1)

(FIG. 2)



FIGS. 1–2—Life cycles of (1) *Baetis rhodani* (above) and (2) *B. scambus* (below). A marks the occurrence of adults in this and subsequent figures (to Fig. 7).

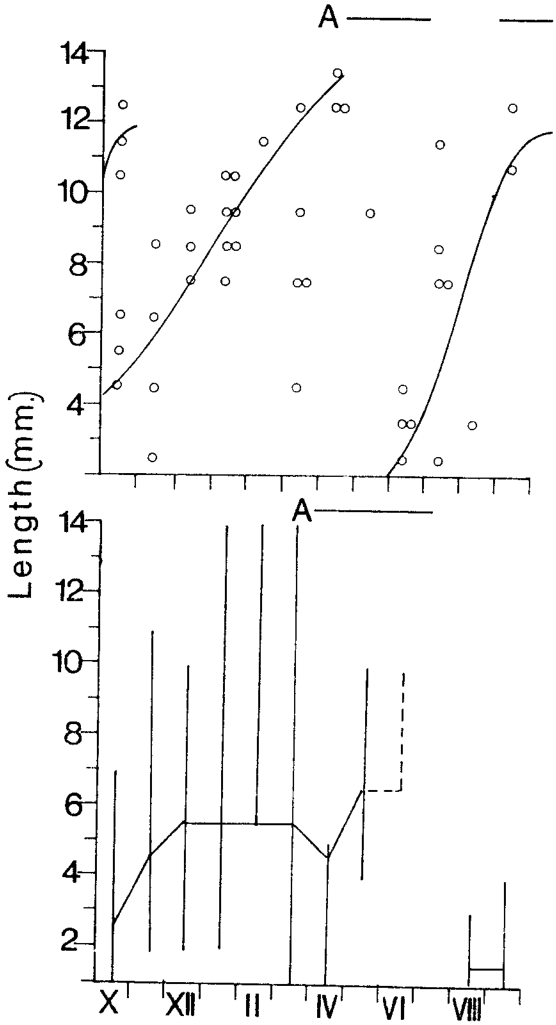
Pleskot (1958) has described *Baetis bioculatus* as having two quick summer generations and Elliott (1967) reports a similar cycle in *scambus*. In western Ireland *scambus* appears to be univoltine (Fig. 2); either that or the second generation is poorly represented. The presence of very small nymphs of *scambus* was recorded for a short period only.

Ecdyonurus venosus has been described as having two types of life cycle (Rawlinson 1939 and Elliott 1967). The species was poorly represented in the stream system examined but a second generation (quick growing summer generation) appeared to be present (Fig. 3) thus confirming Rawlinson's type of cycle.

The life cycle of *Rhithrogena semicolorata* has been investigated by a number of authors and the results from the west of Ireland (Fig. 4) display some variation from the typical patern, chiefly in that there is a fall in the position of the modal point from March to April. A noteworthy point in the present work is the size of the final instars, as indicated by the vertical range lines. Harker (1952) indicates a final instar size of 14mm and Macan (1957) a final instar size of less than 12mm. Hynes (1966) reports a final instar size of less than 10mm. In the present work at the beginning of emergence the largest nymphs were over 13mm long, but later only smaller ones could be found and the last to emerge were between 9 and 10mm long. The size difference may be the result of the emergence of smaller individuals as the

(FIG. 3)

(FIG. 4)



FIGS. 3–4—Life cycles of (3) *Ecdyonurus penosus* (above) and (4) *Rithrogena semicolorata* (below).

hatch progresses, a phenomenon reported as widespread in the Ephemeroptera (Coleman and Hynes 1970) (see also part II).

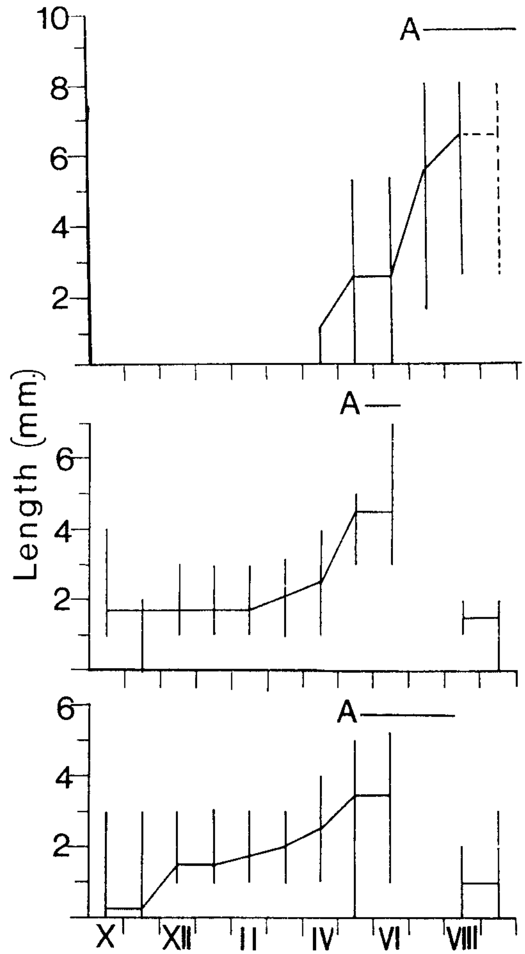
Heptagenia lateralis displays a growth pattern which resembles that described for the species by Hynes (1961), i.e. slow, steady growth throughout the year, with a quiescent period from January to March. This pattern differs from the situation described by Macan (1957) in which growth is from March to May, the majority of individuals remaining the same size for the rest of the year.

H. sulphurea was taken in too small numbers to permit a detailed assessment of its life history. Ulfstrand (1968) describes the species as very variable but having bursts of growth in the spring and early autumn and these features of its development are present in the Irish populations.

(FIG. 5)

(FIG. 6)

(FIG. 7)



FIGS. 5–7—Life cycles of (5) *Ephemerella ignita* (above), (6) *Paralepto-phlebia submarginata* and (7) *Caenis rivulorum* (below).

The life cycle of *Ephemerella ignita* has been described by a number of workers and displays some variation; in the present work an earlier start to nymphal growth is suggested (Fig. 5) than that recorded in the Walla Brook by Elliott (1967).

The life cycle of *Paraleptophlebia submarginata* has been described by Macan (1957) whose results were based on few specimens. Macan concluded that growth is rapid after August until January when there is a slowing down until March or April. The western Ireland population was also composed of few individuals and the growth pattern (Fig. 6) is consequently irregular. However, growth would appear to be stationary for the greater part of the year with a burst of development beginning in February.

Caenis rivulorum (Fig. 7) is a slow grower according to Hynes' classification (1961). Its development continues throughout the winter and the generation type is most similar to that of *Heptagenia lateralis*—the S3 type.

Discussion

The above account of the life cycles of some common Ephemeroptera confirms the observation of other workers that they display great similarity from place to place. The most widespread difference in detail from the results of other workers are, slightly earlier development than in, for example, the Walla Brook populations (Elliott 1967) (for example, *Ephemerella ignita*) and a shorter duration of the smaller nymphs of several species (for example *Baetis scambus*). Macan (1957), in comparing the emergence of *Rhithrogena semicolorata* in different temperature regimes concludes that lower temperature results in longer duration of emergence. Temperature conditions are assumed to be responsible for the comparatively short duration of the smaller instars in the Ephemeroptera. The comparatively short duration of a stage of development is also assumed to be responsible for greater synchrony resulting in a unimodal length-frequency histogram pattern in *Baetis scambus*.

Part II. The life histories of two ephemeropteran species in an isothermic stream

Introduction

The life histories of *Ephemerella ignita* and *Baetis rhodani* have been investigated by several workers and display little variation in different conditions in the British Isles (see for example Macan 1961 and Elliott 1967). Regulating factors in Ephemeropteran life cycles generally are difficult to identify although temperature is thought to play some part (Macan 1961, Pleskot 1951, 1958 and 1961). Work carried out on the populations of an isothermic stream in western Ireland has enabled an evaluation of temperature on the life cycles of both *Baetis rhodani* and *Ephemerella ignita* which are abundant in the area.

METHODS AND RESULTS

SITES OF COLLECTION

Warm subterranean waters are a feature of the north Clare limestones where their average temperature varies between 10 and 11°C (Tratman 1969). The stream in question occurs in neighbouring Co. Galway where it rises from a subterranean source and flows to join the Corrib system. Over a twelve-month period samples were taken within 30m of the stream source whose substratum is composed of loose limestone rocks. Downstream for a distance of 1km large stretches of the river bed consist of marl which would discourage upstream migration of Ephemeroptera so that the isothermic populations remain isolated.

METHODS OF COLLECTION

Samples were taken at approximately monthly intervals by disturbing the substratum of areas of $1m^2$ and collecting all material so dislodged in a handnet (25 threads/cm). The insects were killed by immersion in alcohol and sorted under a dissecting microscope. The two species considered here were arranged in monthly length-frequency histograms and the modal points and spread of these were employed in the construction of growth curves after the methods of Macan (1961). Britt (1953) has shown that injured nymphs that are preserved differ in size from live material; here it was assumed that all specimens were contracted (or extended) by a constant proportion as all had been killed in the same way (Britt *l.c.* gives a correction of 4·18% for total length measurements of uninjured, preserved *Ephemera simulans* Walk). Nymphs which were obviously distorted however were counted and discarded. Final instar nymphs, identified on wing pad development, were measured to the nearest 0·1mm (Tables 3–4). Similar samples were collected from the stream in which temperature fluctuated diurnally and seasonally (see Figs. 1 and 5) and a number of spot collections of summer final instars were made on various substrata and at different altitudes for comparative purposes.

INTERPRETATION OF RESULTS

The life cycle of *Ephemerella ignita* in an isothermic stream is interpreted from the data presented in Fig. 8. The raw data in the form of length-frequency histograms are shown in Fig. 8b. In Fig. 8a (in which the raw data are transformed to a conventional diagram representing the growth cycle) the cycle is similar to but of longer duration than that in a surface stream (compare with Fig. 5). *Baetis rhodani* has two generations annually (Fig. 9) and its growth rates appear to be similar to cycles investigated elsewhere (compare with Fig. 1).

An interesting feature of the life cycle of *Ephemerella ignita* is the cyclical pattern of final instar sizes (Table 3). There is evidence that this phenomenon has been recorded elsewhere: Britt (1962) noted a relationship between the length and egg number of *Ephemera simulans* Walk. and reported a decrease in the number of eggs laid per individual as a hatch progressed. Coleman and Hynes (1970) report a reduction in instar as a hatch progresses as widespread. The situation in *Baetis rhodani* (Table 4) is discussed below.

(a)

(b)

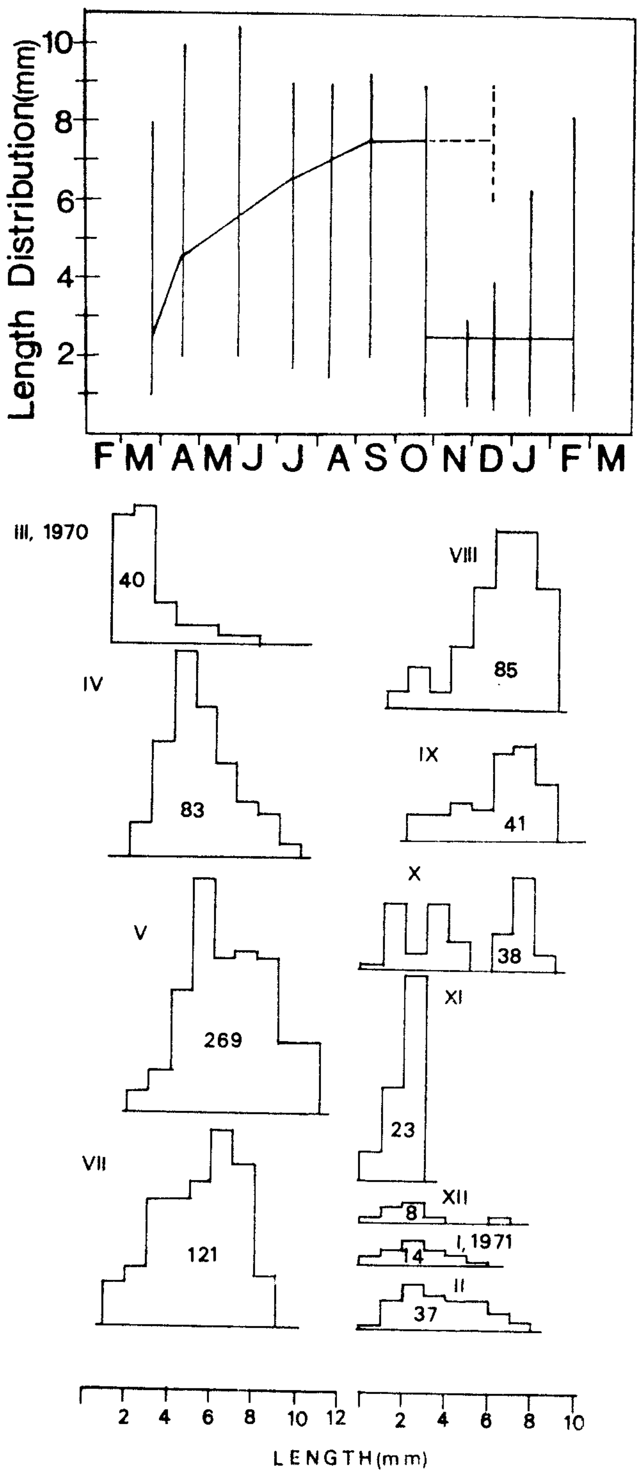


FIG. 8—The life cycle of *Ephemerella ignita* in an isothermic stream. 8a—Growth determined by the methods of Macan (1961); 8b—Histograms showing the raw data on which the results in 8a are based.

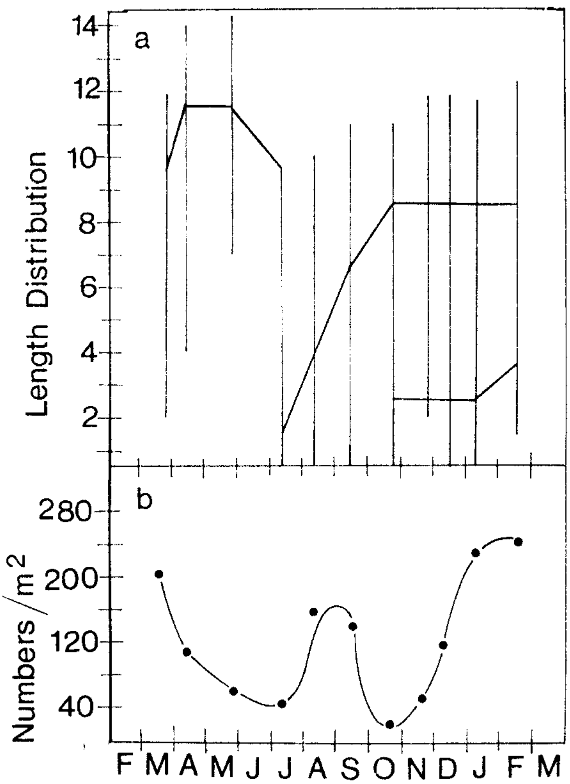


FIG. 9—The life cycle of *Baetis rhodani* in an isothermic stream. Conventions are as for Fig. 8 a

The growth cycles of the two Ephemeroptera measured in a normal stream were similar to those reported by other workers whose papers have been referred to above. Miller (1941) used a day-degrees method to predict emergence times and the method was employed in the present study to

TABLE 3.—Length (mm) of the final instar of *Ephemerella ignita* during a 12-month period in an isothermic stream

Date	Number examined	Mean	Range	Standard deviation
iv	10	8·3	7·2– 9·7	0·64
v	51	8·6	6·2–10·0	0·60
vii	48	7·3	5·5– 8·9	0·43
viii	37	7·3	5·8– 8·6	0·83
ix	21	7·4	6·0– 8·4	1·80
x	11	7·2	6·4– 8·1	0·40
xi	–			
xii	1	6·1	not calculated	

TABLE 4.—Length (mm) of the final instar of *Baetis rhodani* during a 12-month period in an isothermic stream

iii	31	9·4	7·8–11·3	1·17	
iv	163	11·6	9·2–13·1	1·15	——S
v	28	11·1	9·8–14·0	0·91	
vii	6	8·7	7·2– 9·5	0·72	——S
viii	67	8·6	7·0– 9·4	0·92	
ix	81	8·3	6·0–10·9	0·30	
x	40	9·4	8·0–10·7	0·72	——S
xi	10	9·3	8·7–11·0	2·20	
xii	6	9·9	8·2–11·2	1·00	
i	26	9·9	9·1–11·7	0·23	
iii (above)	31	9·4	7·8–11·3	1·17	

——S successive samples differ significantly in size

estimate the maximum number of day-degrees required for development of the Ephemeroptera on the basis of the growth curves. The point at which the line begins to rise is noted (for *Baetis rhodani* these points are July and January and for *Ephemerella ignita* March) as is the point at which growth levels off (for *Baetis rhodani* April and for *Ephemerella ignita* September) and the average daily temperature for the intervening period is multiplied by the number of days (in the case of the normal stream the mean monthly air temperature was used because it had been shown to be in close agreement with the temperature of the stream). In Table 5 there is close agreement between the day-degree quotas of *Ephemerella ignita* in two stream types and a temperature control of the growth cycle of this species is proposed (i.e. the addition of biomass in an individual occurs at a rate which is directly controlled by temperature). *Baetis rhodani*, on the other hand, completes its development at temperatures of wide variation.

TABLE 5.—The total number of day-degrees required for development of *Baetis rhodani* and *Ephemerella ignita* in a normal and an isothermic stream

Baetis rhodani	Winter generation	Autumn generation
Normal stream	1194	2209
Isothermic stream	890	1010
Ephemerella ignita		
Isothermic stream	1730	
Normal stream	1802	

CONSIDERATION OF THE CYCLE IN *Ephemerella ignita*

The cyclical nature of growth in *Ephemerella ignita* remains to be explained. On each sampling date the banks of the upper Cregg River were sweep-netted. Although final instars of *Ephemerella* were frequent in the benthic population few adults were captured until September and October when, on both sampling dates, a large number of sub-imagos and adults were taken.

The period of egg incubation can be calculated in two ways for *Ephemerella*:
a, the annual number of day-degrees in a normal (surface) stream has been calculated at 3,835; subtracting the total required for nymphal growth (1802, (Table 5) leaves 2,033).
b, if the total number of day-degrees is calculated from the end of July, at which time adults appear (Fig. 5) to April, when the first nymphs make their appearance in the benthos the figure is 2,260.

For the isothermic stream the total number of day-degrees from mid-September to mid-May are 2,563, or 2,391 from mid-October to the period of maximum numbers in the benthos. Although there is some discrepancy between the calculated cumulative temperature required for ovidevelopment and the observed cumulative temperature of maximum hatch to highest nymphal density the higher calculated figure for the former and lower for the latter are close and cumulative temperature is suggested to explain the frequency of nymphs in May.

A possible reason for the cyclical nature of growth in *Ephemerella* is summer and autumn air temperature which permit oviposition. Otherwise the cycle is similar to that in a normal stream (Fig. 5), the persistence of nymphs being longer and the rate of development slower.

THE FINAL INSTAR OF *Baetis rhodani*

Macan (1950) has noted size differences of from 7 to 11mm in length of the final instar of *Baetis rhodani* which is the most variable of the British Ephemeroptera. Macan (1957) and Elliott (1967) found imagines of the summer generation to be smaller than the winter emerging generation and similar findings were made in the present work.

The volume of final instars of various sizes was measured after the methods of Welch (1948) and the results presented in Fig. 10 show that instars of various sizes conform to the cube law. Various skeletal features of the final instar plotted against total length indicate that increase in length is allometric (Fig. 11). The selected anatomical features are those chosen for *Leptophloebia cupida* (Say) by Clifford (1970). It is thus assumed that measurements of variability apply equally to the anatomical parts examined.

A bivoltine cycle for *Baetis rhodani* in an isothermic stream is supported by numerical occurrence of the final instars (Table 4). According to calculations presented in Table 4 there are three significantly different size ranges annually. Two of these (April-May) and (October-February) correspond to summer and winter growing nymphs (Fig. 9); the intermediates (July-September) are either the later nymps of the winter cohort or the forerunners

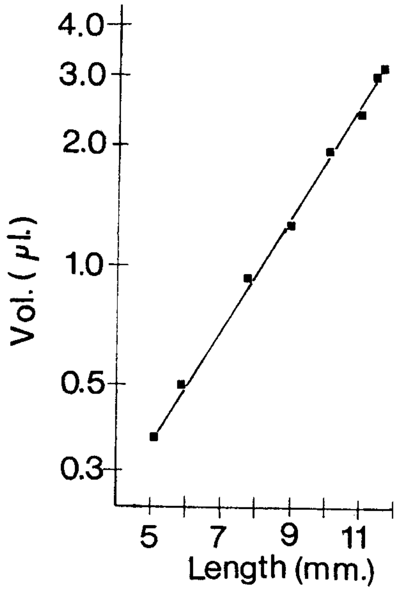


Fig. 10—The volume of final instars of various sizes of *Baetis rhodani* plotted against body length.

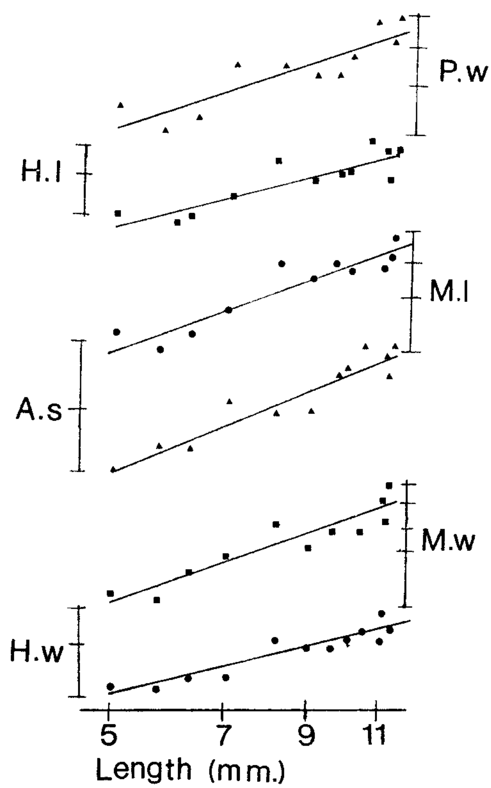


Fig. 11—Various skeletal dimensions plotted against body length of the final instar of *Baetis rhodani*: P.w., pronotum width; H.l., head length; M.l., mesonotum length; A.s., width of second abdominal segment; M.w., mesonotum width; H.w., head width.

of the summer growers or possibly a mixture of the two. Elliott (1967) suggests there is an overlap in the winter and summer cohorts of *rhodani* and the two cohorts are represented in the figures for March, as indicated by the wide range of nymphal lengths.

The most obvious cause of size difference in the final instar is the cohort type (whether the animals are winter or summer growers) (Fig. 9a) and the second the type of substratum (Table 6). There is also an altitudinal size factor (Table 7).

TABLE 6.—Length (mm) of the final nymphal instar of *Baetis rhodani* occurring on different substrata at different times of the year

	Number examined	Mean length	Range	Coef. of variability
From a normal stream flowing over quartzite				
September generation	38	6·9	5·6– 7·9	10·60
April generation	37	8·5	7·1– 9·7	8·12 (δ=0·69)
From an isothermic stream flowing over limestone				
September generation	81	8·3	6·0–10·9	3·62 (δ=0·09)
April generation	163	11·6	9·2–13·1	9·91

A comparison of the April generation (normal stream) with the September generation (isothermic stream)

Difference in means	0·2
Standard error of difference	0·12
Not significant	

TABLE 7.—Variations in the length (mm) of the final instar of *Baetis rhodani* (summer generation) at different altitudes (m above sea level) on:

Altitude	Number measured	Mean length	Range
Shale			
60	30	7·6	6·5–8·2
100	11	6·4	5·6–7·0
130	31	5·7	4·9–6·4
Old Red Sandstone			
140	22	7·4	5·3–9·6
260	8	6·7	6·1–7·4

Discussion

From the foregoing it is suggested that growth in *Baetis rhodani* is not regulated by day-degree quotas alone. In Table 5 growth is apparently independent of temperature, within the temperature range examined, and other factors may have regulatory value. The identification of these factors is difficult in the present circumstances because a number of variables are involved but the following generalisations are made about the life cycle of the species in the two types of stream investigated.

1 Two generations per year develop simultaneously in both types of stream.
2 The instars developing during the winter in either stream type are larger than those which develop in the summer and early autumn.
3 In normal types of stream the size of the final instar is secondarily modified by certain abiotic factors. An example is given in Table 6 where, at higher altitudes the final instar of the summer growing generation attains a smaller mean length; the inference of this being that in poorer trophic conditions growth of *Baetis rhodani* is to a smaller size (poor trophic conditions have been associated with the upper reaches of streams by a number of authors notably Macan (1957) and Minshall and Kuehne (1969)). In Table 4 it can be seen that the final instars of the September generation from an isothermic stream do not differ significantly in size from those of the April generation in a normal stream. However, as stated in point 2 above, the summer generation of both groups attain a smaller size than the winter stadia. It is therefore concluded that the size of the final nymphal instar in *Baetis rhodani* is seasonally determined—whether genetically or environmentally is not known—and there is much secondary environmental variation.

Acknowledgements

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Postscript

Additional information on the fauna of the Cregg River is contained in Fahy, E. (1972) The Life Cycles of some Invertebrates in an Isothermic stream in Western Ireland. *Scient. Proc. R. Dubl. Soc.* (A) **4** (23), 331–341. 1 Plate.