THE LIFE HISTORIES AND DRIFTING OF THE PLECOPTERA AND EPHEMEROPTERA IN A DARTMOOR STREAM

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Large numbers of Plecoptera and Ephemeroptera were taken during a recent study of invertebrate drift and the food of salmonids in a Dartmoor stream (Elliott 1965a, 1967a,b). Some of this material has now been used to determine the life histories described in this paper.

Hynes (1941, 1961) describes the life histories of many species of British Plecoptera and Macan (1961) summarizes all available studies on the life histories of British Ephemeroptera, except those of Brown (1961) and Hynes (1961). Although few comparisons have yet been made, it appears that life histories often differ from place to place and from year to year, and that much of this variation is related to temperature (Macan 1961; Pleskot 1951, 1958, 1961). More studies are therefore needed before generalizations can be made.

One of the conclusions from the work on invertebrate drift was that the density of animals in the drift varied considerably throughout the year (Elliott 1965a, 1967a). A comparison of the life history of each species with the density of nymphs in the drift has helped to explain these variations.

PHYSICAL CONDITIONS IN THE STREAM

The Walla Brook, a tributary of the East Dart, rises at an altitude of 412 m in central Dartmoor (National Grid Reference SX668806) and flows due south for about 7·0 km. The stream can be divided into three sections according to gradient, substrate and dominant plants. In section 1, the gradient is steep (fall about 3·5%) and the bottom is chiefly large stones and a small amount of gravel with bryophytes (*Fontinalis antipyretica* Hedw., *Hygrohypnum ochraceum* Turn. and *Scapania undulata* (L.) Dum. as the dominant plants. This section starts at the source and ends after about 2 km. Section 2 continues for about 3·9 km and the bottom is chiefly gravel and small stones, with *Myriophyllum spicatum* L. and *Callitriche aquatica* Sm. replacing bryophytes as the dominant plants. This change in bottom conditions is probably the result of the decreased gradient in section 2 (fall about 1%). The final 1·1 km forms section 3 where the bottom conditions are similar to section 1 and the gradient is once again steep (fall about 4%). Site 1 (SX668790) is in section 1 and site 2 (SX669786) in section 2.

Dartmoor is a large granite intrusion (sometimes referred to as a 'boss') and therefore all streams and rivers on the moor are very poor in dissolved salts. Analyses of water samples from the Walla Brook were made in June 1966 and showed calcium concentrations of 0·057 and 0·072 m-equiv/l (1·13 and 1·44 ppm) and total ions of 0·383 and 0·411 m-equiv/l at the source and site 2 respectively. Values for pH fluctuated between 6·4 and 6·8 not only at different times of the year, but also for samples taken simultaneously at different points in the stream.

Water velocity was frequently measured during each sampling period (5–7 days in each month) and the following categories were recognized according to the mean surface velocity at site 2:

(1) Major spate (over 1 m/sec) November 1963,

(2) Minor spate (0·5–1 m/sec) May, June, August and December 1963, March and May 1964.

(3) Normal (0·4–0·5 m/sec) July, September and October 1963, April and October 1964.

(4) Drought (0·1–0·4 m/sec) January, February, June to September 1964.

During each sampling period a continuous air temperature record was obtained on a thermograph situated 25 cm above the ground next to site 2. Water temperature readings were taken every 3 h at both sites. The mean air temperature and maximum and minimum air and water temperatures are given in Table 1.

Table 1. *Mean, maximum and minimum air temperatures and maximum and minimum water temperatures for each sampling period from May* 1963 *to October* 1964. (*Monthly mean, maximum and minimum air temperatures are included for January, February and March* 1963)

			Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Air temperature (°C)														
1963	Site 2	Mean	−3·9	−1·3	4·5		7·5	18·2	15·8	14·0	14·9	9·9	9·4	−1·4
		Max.	2·2	4·4	9·4		11·7	22·8	26·2	19·8	18·8	12·8	10·8	2·0
		Min.	−10·0	−8·9	−1·7		3·5	13·8	10·2	9·2	10·0	3·2	7·0	−6·5
1964	Site 2	Mean	4·7	0·3	2·5	7·7	10·6	10·6	14·6	17·7	13·2	8·7		
		Max.	6·2	5·0	9·2	12·4	11·8	13·6	19·1	22·1	20·2	11·2		
		Min.	3·5	−5·0	−1·8	3·5	9·0	7·2	4·2	10·5	−0·5	2·1		
Water temperature (°C)														
1963	Site 1	Max.					9·2	17·5	14·5	13·3	13·8	11·6	9·8	6·4
		Min.					8·4	10·8	10·1	10·2	12·2	10·2	9·5	4·8
	Site 2	Max.					9·8	17·8	14·5	13·4	13·8	11·8	10·0	6·4
		Min.					8·4	11·2	10·8	11·8	12·2	10·2	9·5	4·8
1964	Site 1	Max.	6·0	5·2	8·2	10·0	10·8	13·8	15·5	17·4	15·2	12·0	9·2	6·0
		Min.	5·0	3·0	4·5	6·8	10·3	10·3	11·8	12·7	11·5	7·6	7·4	4·5
	Site 2	Max.	6·9	5·2	8·2	10·2	11·3	13·9	15·8	17·6	15·2	12·2	9·4	6·2
		Min.	6·0	4·5	4·8	6·8	10·3	10·3	12·2	13·1	11·8	7·6	7·6	4·8

This study started in May 1963 after one of the coldest winters ever recorded on Dartmoor. Although no temperature readings were taken near the Walla Brook in the winter of 1962–63, daily readings were taken at the meteorological station in Princetown which is about 8 km south-west of site 2. The daily readings from Princetown have been used to obtain mean, maximum and minimum air temperatures for January, February and March 1963 (Table 1). The severe winter of 1962–63, as will be seen later, greatly influenced the life histories of the Plecoptera and Ephemeroptera. Therefore a brief account of the winter is included here.

December 1962 was mild with the maximum air temperature above 0° C on 29 days and a mean maximum of 5·7° C. The mean minimum air temperature was 0·9° C and there was air frost on 11 days and ground frost on 18 days. Towards the end of the month, there was a notable fall in air temperature with both ground and air frost on the last 8 days, two of which had maximum temperatures below 0° C. This cold weather continued through January 1963 and the maximum air temperature was above 0° C on only 7 days with a mean maximum of −1·7° C. The mean minimum air temperature was −6·2° C and there was both air and ground frost on every day of the month. There were heavy falls of snow in January, and although the Walla Brook was never frozen solid, local observers remembered that the surface ice was thick enough to support a tractor. Conditions slightly improved in February with the maximum air temperature above 0° C on 18 days and a mean maximum of 1·1° C. The mean minimum air temperature was −3·6° C and there was air frost on 24 days and ground frost on every day of the month. Air temperatures returned to normal in March and were comparable to those of March 1964 (Table 1). The maximum air temperature was above 0° C on every day of the month with a mean maximum of 6·9° C. The mean minimum was 2·2° C and there was air frost on 13 days. In spite of the increased air temperature, patches of snow were present on Dartmoor until the last week in May 1963. The winter of 1963–64 was mild with light falls of snow and only occasional ground frost.

Both air and water temperatures reached maximum values earlier in 1963 (June and July) than in 1964 (July and August). Although there was little difference in water temperatures at the two sites, the temperatures at site 2 were never less than those at site 1 (Table 1).

METHODS

Quantitative samples of the benthos were taken with a shovel sampler (Macan 1958a) which removes 0·05 m^2 of bottom. Although early sampling indicated a non-random distribution of the benthos, it was soon evident that the variation in the benthos across the stream was far greater than along it. Therefore four samples per month were taken in a diagonal transect across the stream at each site. Shovel samples were taken from May 1963 to August 1964 at site 1 and from May 1963 to December 1964 at site 2. Non-quantitative samples were taken with a pond net in February, March and April 1965. A double-walled net was fitted to the shovel sampler and all nets were made of nylon sifting cloth (24 meshes/cm). These nets retained small nymphs (1–2 mm long) of Plecoptera and Ephemeroptera but did not easily clog. All samples were preserved in 70% alcohol and hand sorted in the laboratory.

Two kinds of drift samplers were used, namely surface nets and modified high-speed plankton samplers. As these samplers have already been described in detail (Elliott 1967a), only a brief account is given here. A surface net floated on the water and had a rectangular mouth with an effective sampling area of 336 cm^2, water being sampled to a depth of 7 cm from the surface. A Watts current meter was used to determine the velocity of the water entering the net and therefore an estimate could be made of the total volume of water filtered by the net. The net of the modified plankton sampler was enclosed in a metal cylinder and a flow-meter in the rear of the tube recorded directly the volume of water passing through the net. Iron rods secured the sampler in the mid-water region and the circular mouth had an effective sampling aperture of 78·5 cm^2. The nets of both drift samplers were made of nylon sifting cloth with a mesh of 440 μ (15·5 meshes/cm). Sampling was carried out for 24 h at each site and the nets were emptied every 3 h. Of the two types of drift sampler, only the surface nets could be used in shallow water such as site 1 where the average depth of water rarely exceeded 15 cm. Both types of drift sampler were used at site 2 where the average depth was rarely below 25 cm. Drift samples were taken from May 1963 to August 1964 at site 1 and from May 1963 to October 1964 at site 2.

Although all sizes of Plecoptera and Ephemeroptera were taken in the drift, the large nymphs were often predominant. Since a combination of drift and bottom samples would have produced a bias towards the larger nymphs, the nymphs taken in the drift were not used to determine the life histories.

Emerging imagines were frequently taken in the drift samples and therefore it was possible to determine the emergence period of most species. The flight period was known from catches with a sweep net and a bilateral insect trap. The latter was a small version of that used by Roos (1957) and caught insects flying above the surface of the water at site 2.

LIFE HISTORIES AND DRIFTING

Table 2 includes all the species of Plecoptera and Ephemeroptera ever taken from the Walla Brook. It is apparent that the last four species of Plecoptera and the last six species of Ephemeroptera were not present in sufficient numbers for life histories to be described. The life histories of the remaining twelve species are illustrated by Figs. 1–12.

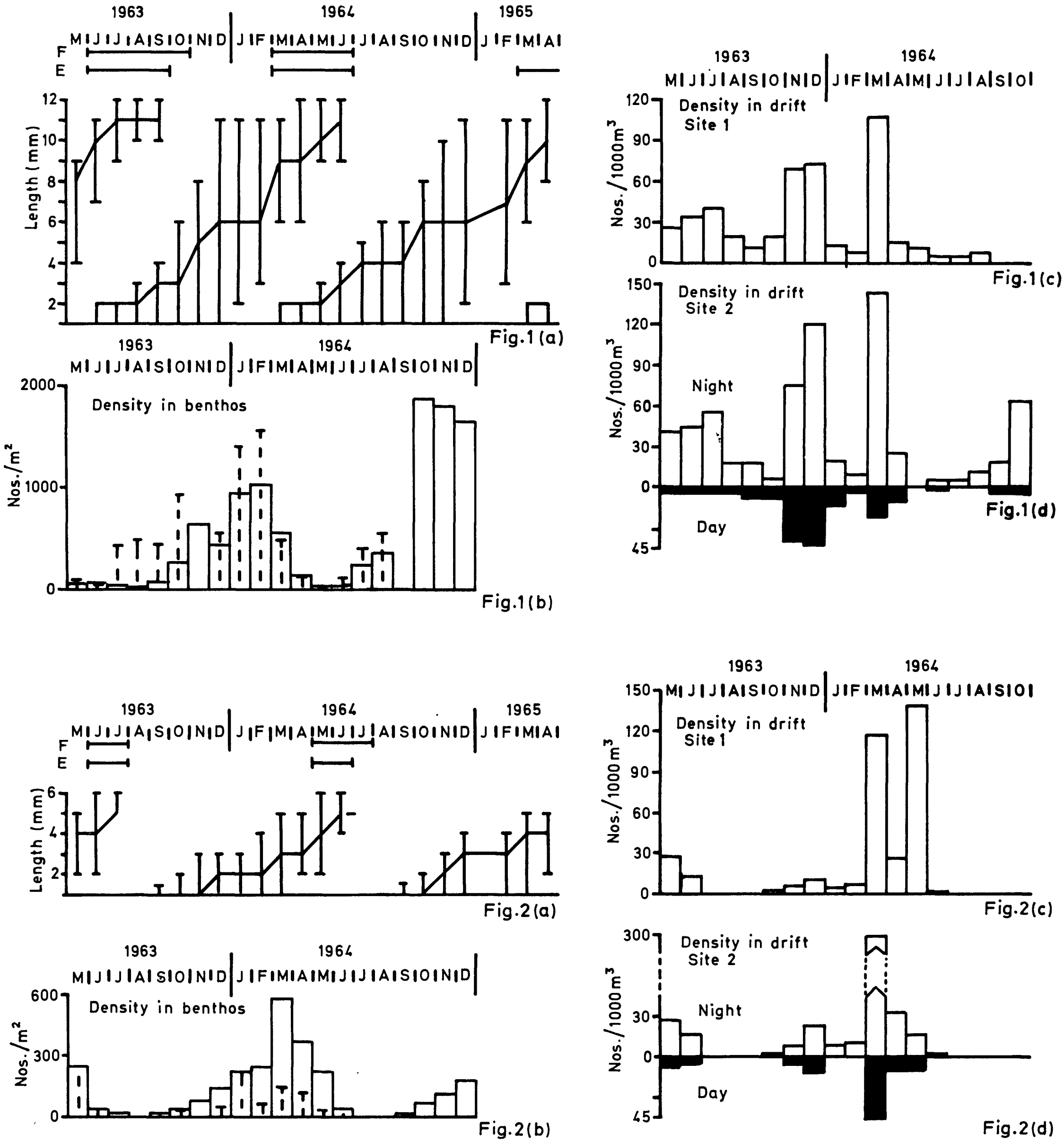
Table 2. *Total numbers of Plecoptera and Ephemeroptera taken with a shovel sampler and pond net at sites* 1 *and* 2 (Heptagenia lateralis *and* Caenis rivulorum *were only found near the junction of the Walla Brook with the East Dart and were never taken at sites* 1 *and* 2)

Plecoptera		Ephemeroptera	
Protonemura meyeri (Pictet)	3562	*Baëtis rhodani* (Pictet)	4680
Amphinemura sulcicollis (Stephens)	2243	*Ephemerella ignita* (Poda)	1928
Isoperla grammatica (Poda)	1971	*Baëtis scambus* Eaton	1362
Leuctra inermis Kempny	1153	*B. niger* (L.)	423
Chloroperla torrentium (Pictet)	852	*Ecdyonurus venosus* (Fabricius)	168
Perlodes microcephala (Pictet)	758	*Paraleptophlebia submarginata* (Stephens)	15
Leuctra hippopus Kempny	348	*Baëtis pumilus* (Burmeister)	12
Dinocras cephalotes (Curtis)	47	*Leptophlebia vespertina* (L.)	8
Brachyptera risi (Morton)	12	*Rhithrogena semicolorata* (Curtis)	1
Nemoura cambrica Stephens	3	*Heptagenia lateralis* (Curtis)	–
Leuctra fusca (Linné)	3	*Caenis rivulorum* Eaton	–

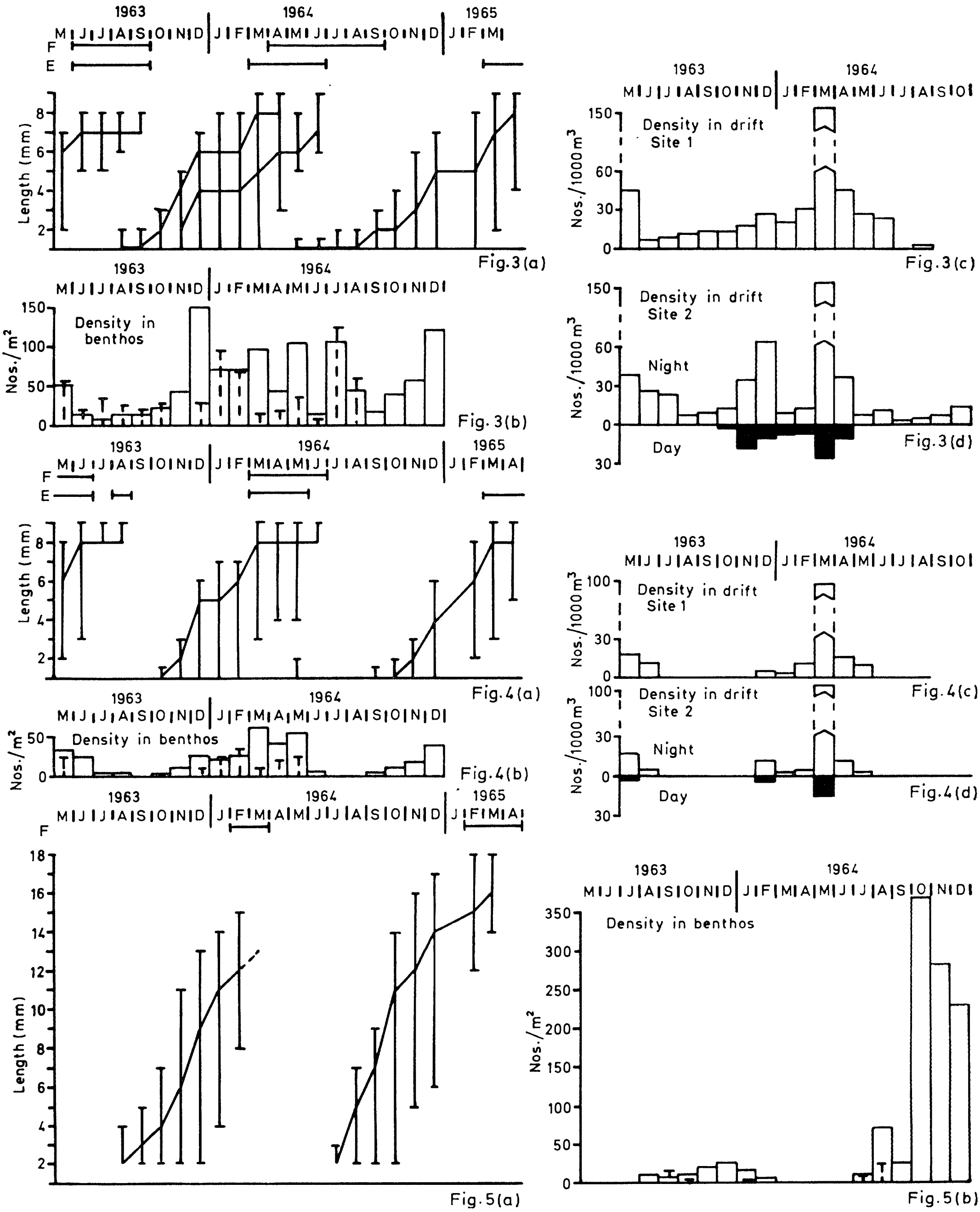
The method of illustrating each life history is based on that used by Macan (1961). The top horizontal line (F) indicates the flight period of the imagines and the next line (E) represents the period when emerging imagines were taken in the drift samples. In each month the vertical line indicates the size range of the nymphs, and the modes for each month have been joined to give some indication of major periods of growth. The mode represents the size attained by the greatest number of nymphs and is preferable to the mean for reasons given by Macan (1958b, 1961). Measurements were from front of labrum to tip of abdomen and the number of nymphs measured for each life history is given in Table 2.

Figs. 1–12 also show the numbers of each species per square metre at site 1 (vertical broken lines) and site 2 (columns).

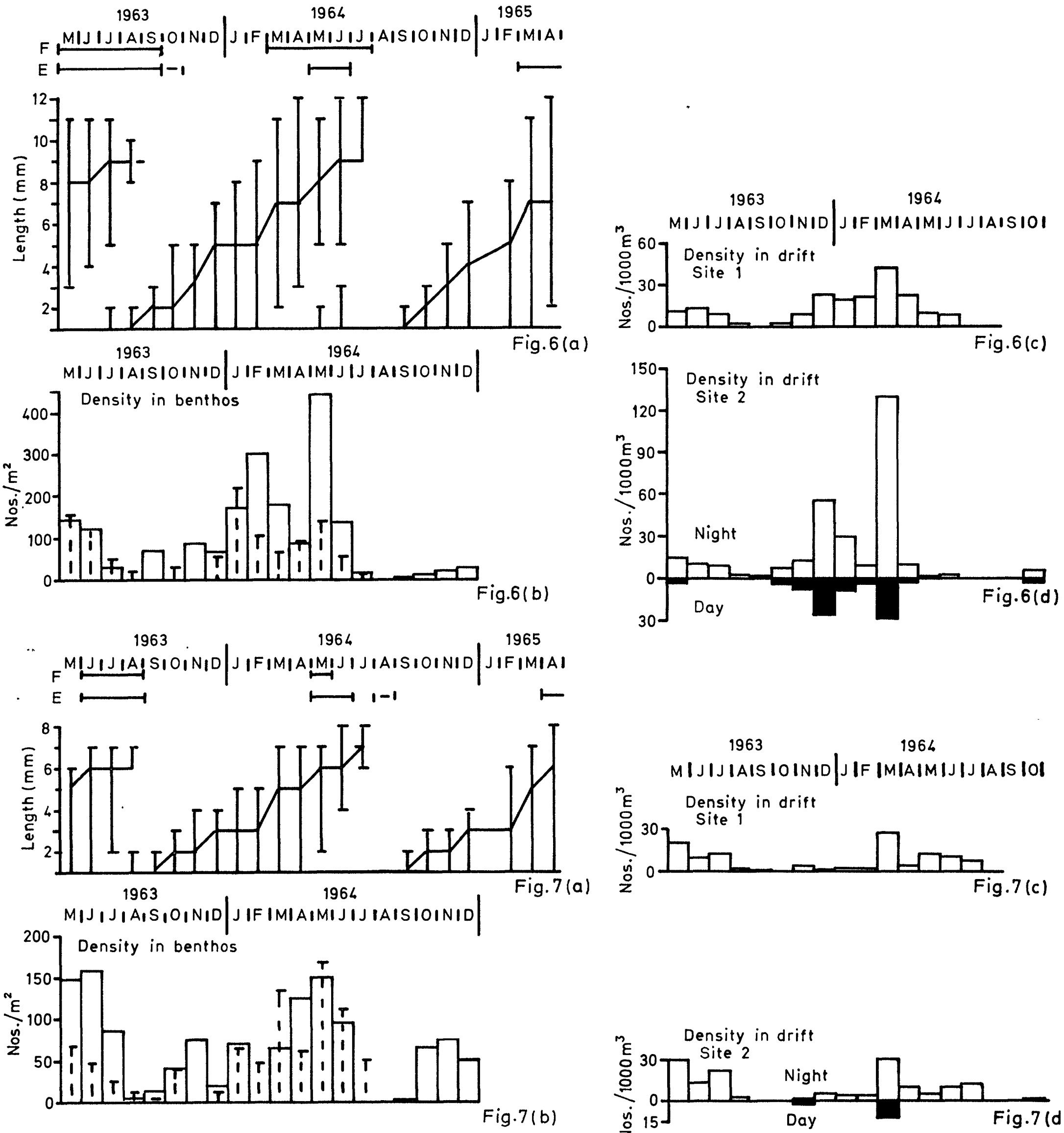
Work on invertebrate drift has shown that rate of flow is one of the chief factors which determines the number of animals drifting past a sampling point (Elliott 1967a). Therefore, in seeking the other factors which affect the number of animals in the drift, it is important to compare numbers per unit volume of water rather than numbers per unit time. Comparisons are further complicated by the nocturnal increase in the number of animals in the drift and therefore the mean density of each species in the drift has been worked out separately for day and for night. Day values are always low and are only given for site 2. It is therefore more important to consider the nocturnal density of each species in



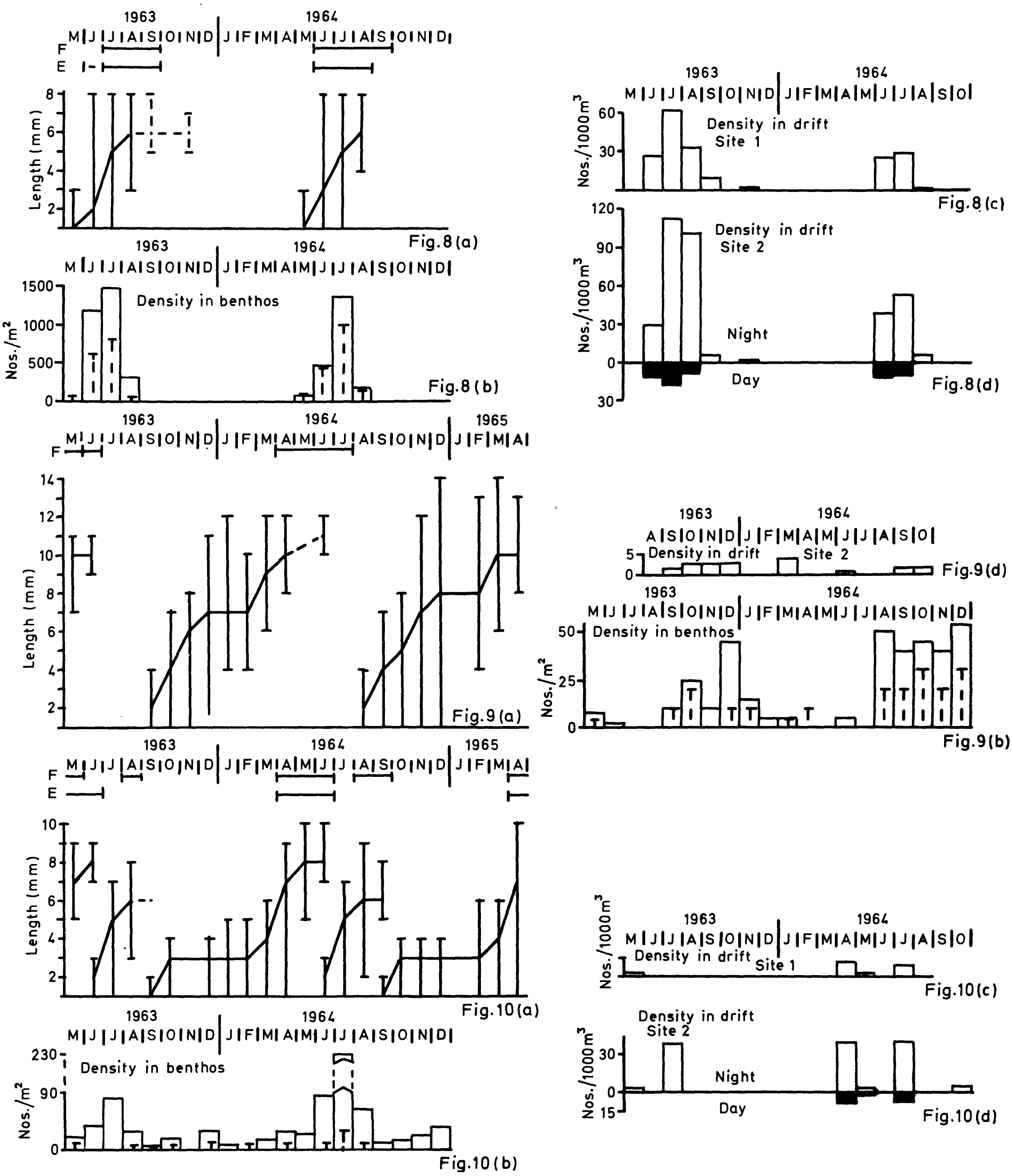
FIGS. 1 and 2. *Protonemura meyeri* (Fig. 1) and *Amphinemura sulcicollis* (Fig. 2). In each life-history diagram (Figs. 1a and 2a), the mode and size range of nymphs are shown for each month, also the flight period (F) and the emergence period (E). The density of nymphs in the benthos (Figs. 1b and 2b) is given as numbers/m² at site 1 (vertical broken lines) and site 2 (columns). The mean density of nymphs in the drift at site 1 (Figs. 1c and 2c) and at site 2 (Figs. 1d and 2d) is given as numbers/1000 m³ during the day and at night.



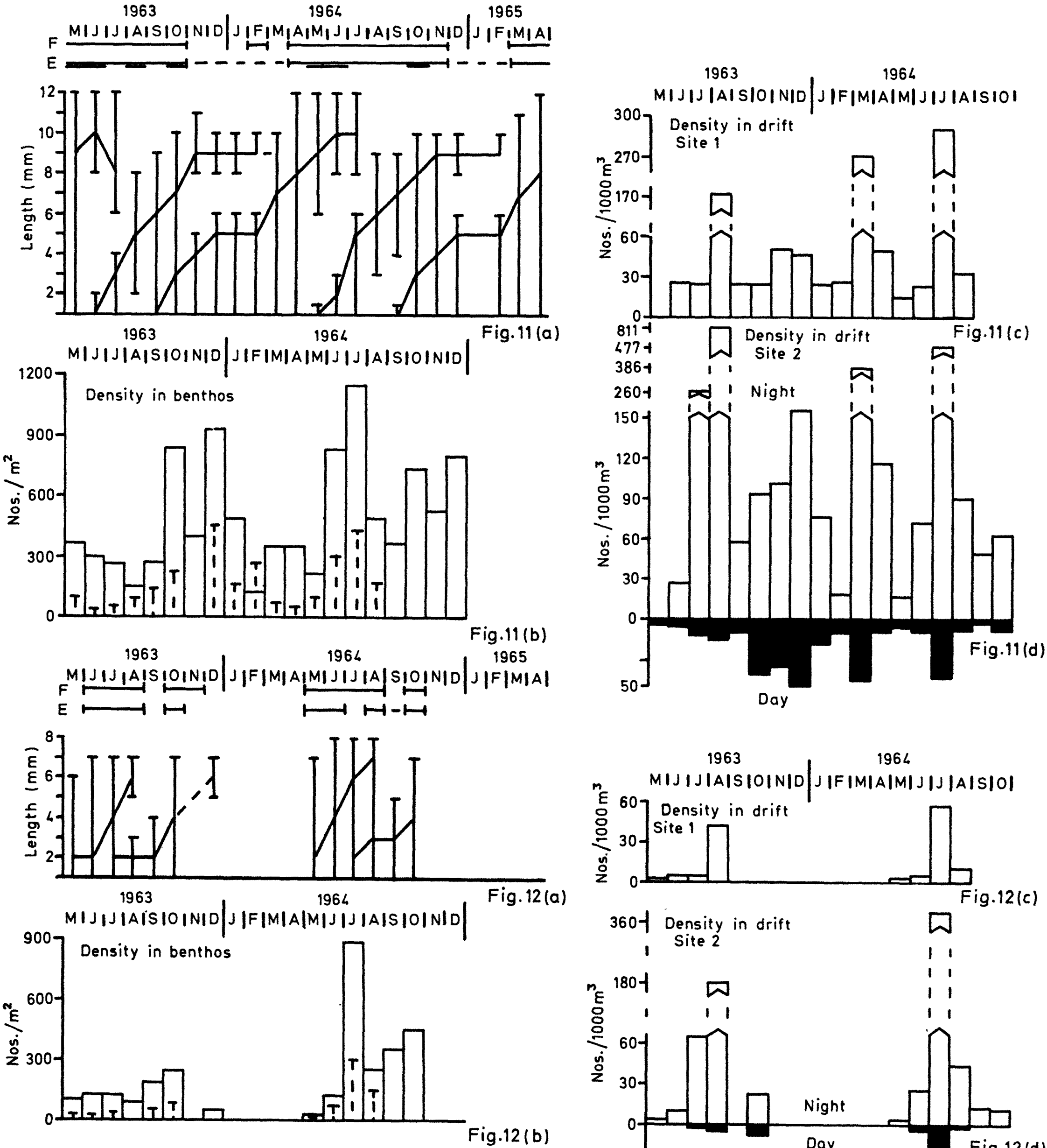
FIGS. 3–5. *Leuctra inermis* (Fig. 3), *L. hippopus* (Fig. 4) and *Perlodes microcephala* (Fig. 5). Conventions as in Fig. 1.



FIGS. 6 and 7. *Isoperla grammatica* (Fig. 6) and *Chloroperla torrentium* (Fig. 7). Conventions as in Fig. 1.



FIGS. 8–10. *Ephemerella ignita* (Fig. 8), *Ecdyonurus venosus* (Fig. 9) and *Baëtis niger* (Fig. 10). Conventions as in Fig. 1.



FIGS. 11 and 12. *Baëtis rhodani* (Fig. 11) and *B. scambus* (Fig. 12). Conventions as in Fig. 1.

the drift and how it varies in different months. Densities are given as numbers per 1000 m^3 of water passing through the drift samplers at sites 1 and 2 (c and d in Figs. 1–12).

Interpretation of life histories

All the species described in Figs. 1–12 were univoltine except the three *Baëtis* spp. The univoltine species all had an overwintering generation except *Ephemerella ignita* which was confined to the summer months.

From November 1963 to April 1964 there was no distinct mode for each monthly sample of *Leuctra inermis* and instead two size groups were predominant (Fig. 3a). It is concluded that there were two peaks in hatching and the nymphs from the first hatch were always larger than the nymphs from the second hatch. The long flight period of *Isoperla grammatica* in 1964 indicates that emergence started at least 2 months before the first imagines were taken in the drift samples (Fig. 6a). (Some adults of this species had a two-branched instead of a simple R 2+3 in the forewing and therefore this key character is not always reliable in separating *Isoperla* from the other genera of the Perlodidae (Hynes 1958).) Emerging imagines of *Perlodes microcephala* and *Ecdyonurus venosus* were never taken in the drift samples and therefore only the flight period was known (Figs. 5a and 9a).

Baëtis niger and *B. rhodani* were bivoltine with a slow-growing overwintering generation and a fast-growing summer generation (Figs. 10a and 11a). The winter generation of *B. niger* emerged from April to June and the summer generation in August and September. Emerging imagines of *B. rhodani* were taken in every month, but the intensity of emergence varied considerably throughout the year. In Fig. 11(a) the double line indicates months when over fifty emerging imagines were taken at one or both sites, whilst the broken line indicates months when less than fifteen imagines were taken at each site in 24 h. Very few imagines emerged from November 1963 to March 1964 and from December 1964 to February 1965, and large numbers emerged in May, June and October of both years and in August 1963. Macan (1961) notes that full-grown nymphs in early winter were either fast-growing nymphs of the winter generation or stragglers from the summer generation. In the Walla Brook, the full-grown nymphs in winter were definitely from the summer generation and a few stragglers were present from November 1963 to February 1964 and from December 1964 to February 1965. Therefore the emergence period of the summer generation was far longer (August to February) than that of the winter generation (March to July). Imagines of the summer generation were usually smaller (6–8 mm) than those of the winter generation (8–9·5 mm) as found by Macan (1957). *B. scambus* was also bivoltine, but the two generations were confined to the summer months (Fig. 12a). The first summer generation emerged from June to August in 1963 and from May to August in 1964, whereas the second summer generation emerged in October of both years.

In all species, very small nymphs (1 mm size group) were present for a longer time than the flight period of the imagines (Figs. 1–12). This was probably due to the delayed hatching of some eggs, as has been observed in Plectoptera (Hynes 1961) and Ephemeroptera (Illies 1959). Small nymphs of *Protonemura meyeri*, *Amphinemura sulcicollis*, *Leuctra inermis*, *Isoperla grammatica*, *Chloroperla torrentium*, and the winter generations of *Baëtis niger* and *B. rhodani* were present for a long time, whereas those of *Leuctra hippopus*, *Ecdyonurus venosus*, and the summer generations of *Baëtis niger* and *B. rhodani* were only present for a short time. One-millimetre nymphs of *Perlodes microcephala* were never found but if the nymphs were 2 mm long on hatching, there was a period of delayed hatching which lasted 5 months in 1963 and 4 months in 1964 (Fig. 5a). In all species, the density of nymphs in the benthos gradually increased while small nymphs were being added to the population and maximum density usually occurred towards the end of the hatching period. Far greater numbers of *Baëtis niger* were involved in the summer generation than in the winter generation and the density of nymphs in the benthos reached a maximum in July of both years (Fig. 10b). Although small nymphs of *B. rhodani* were being added to the population during the long hatching periods, the presence of large nymphs of the previous generation masked the gradual increase in numbers which was seen in other species. Small nymphs of *B. scambus* were taken from May to October and the density of nymphs in the benthos gradually increased to a peak in July followed by a second peak in October (Fig. 12b). Therefore the periods of delayed hatching were probably from May to July for the first summer generation and from July to October for the second summer generation.

Mortality factors

Variations in water velocity appeared to have little effect on numbers in the benthos, but the numbers of *Protonemura meyeri*, *Isoperla grammatica* and *Chloroperla torrentium* decreased after the severe spate of November 1963. Small nymphs of *Leuctra hippopus* and *Isoperla granmmatica* were present in the benthos during May and June 1964 but disappeared in July and August, whilst the numbers of *Leuctra inermis* were considerably reduced (Figs. 3a, 3b, 4a, 4b, 6a and 6b). Water temperatures were not unduly high during the summer of 1964, so they would not account for the high mortality. June to September was a period of drought and by July everything in the Walla Brook, including the invertebrates, was covered with a layer of silt. This could have killed the small nymphs either directly or indirectly. There is no apparent reason why other species of Plecoptera and Ephemeroptera were unaffected by these drought conditions.

The severe winter of 1962–63 appeared to affect the life histories of most species of Plecoptera and Ephemeroptera in the Walla Brook. The numbers of *Protonemura meyeri* were lower after the severe winter than in other years, but enough imagines emerged to ensure large numbers in the next generation (Fig. 1b). Full-grown nymphs of *Perlodes microcephala* were smaller in size and fewer in numbers in the 1963–64 generation than in the 1964–65 generation (Figs. 5a and 5b). The low numbers in the 1963–64 generation were probably due to a high mortality of nymphs in the 1962–63 generation which coincided with the severe winter. In May, June and July fewer nymphs of *Baëtis rhodani* were taken in the bottom samples in 1963 than in 1964 (Fig. 11b) and this suggests a high mortality in the the severe winter. The winter mortality of nymphs appeared to be high in only these three species. Although winter mortality was low in all other species, the emergence of *Protonemura meyeri*, *Amphinemura sulcicollis*, *Leucra inermis*, *L. hippopus*, *Isoperla grammatica*, and *Chloroperla torrentium* was much later in 1963 than in other years (Figs. 1a, 2a, 3a, 4a, 6a and 7a). The first appearance of small nymphs of *Protonemura meyeri* and *Leuctra inermis* was much later in 1963 than in 1964, but the late-hatched specimens grew quickly and nymphs were of similar size by December of both years (Figs. 1a and 3a).

Growth and drifting

It was not possible to assess the actual growth rate of the species described in Figs. 1–12, because of the long hatching period. Changes in the mode, however, revealed periods of slow and rapid growth. Growth slowed down in winter for all species with an overwintering generation, except *Perlodes microcephala*, but the period of slow growth varied from 1 month in *Leuctra hippopus* (Fig. 4a) to 4 months in *Baëtis niger* (Fig. 10a). Although periods of rapid growth were not the same for all species, most of those with an overwintering generation grew rapidly in November, December and March and those with a summer generation grew rapidly in July and August.

The density of nymphs in the drift was high for nearly all the species which were fairly abundant in the benthos, and the only exceptions were *Perlodes microcephala* and *Ecdyonurus venosus*. These latter species were always taken in very low numbers in the drift and appeared to be less vulnerable to detachment than other species of Plecoptera and Ephemeroptera. In all other species a comparison of the density of nymphs in the drift with the life histories revealed a strong correlation between peaks in the density in the drift and periods of rapid growth (a, c and d in Figs. 1–12). These peaks were seen at night and during the day, and although in each month the nocturnal density was always greater than the diurnal density, maxima of the latter were greater than minima of the former. Although a period of rapid growth occurred just before the winter period of slow growth in *Amphinemura sulcicollis, Leuctra hippopus, Chloroperla torrentium* and *Baëtis niger*, there was only a slight increase in the density of nymphs in the drift (a, c and d in Figs. 2, 4, 7 and 10). Therefore, in some species, the density of nymphs in the drift did not greatly increase when the rapidly-growing nymphs were very small. A high density of nymphs in the drift was a reflection of the rapid growth of *Ephemerella ignita* and *Baëtis scambus* during the summer months (Figs. 8a, 8c, 8d, 12a, 12c and 12d). Nymphs of the first summer generation of *B. scambus* grew rapidly, especially in July and August, whereas those of the second generation did not grow rapidly until October and full-grown nymphs were generally smaller than those of the first generation. *B. rhodani* was by far the most numerous species in the drift and the density of nymphs in the drift increased in July, August, and October to December 1963 and March, April and July 1964 when rapid growth occurred in one or both generations (Figs. 11a, 11c, 11d).

Notes on the rarer species

The following species were all taken in low numbers in the bottom samples and therefore their life histories could not be described. *Leuctra fusca, Dinocras cephalotes, Paraleptophlebia submarginata* and *Baëtis pumilus* were all rare in the drift and benthos, and presumably were often missed by the shovel sampler because only four samples were taken at each site. Only one nymph of *Rhithrogena semicolorata* was taken in the bottom samples at sites 1 and 2, whereas three nymphs were taken in the drift samples for both January and February 1964 and twenty-eight nymphs in March. The presence of nymphs in the drift during January and February suggests that growth of this species continued through the winter as found by Macan (1957). Nymphs were more abundant near the source of the stream and therefore those taken in the drift at sites 1 and 2 in March may have been moving downstream before emergence, as found by Macan (1957). Nymphs of *Brachyptera risi, Nemoura cambrica* and *Leptophlebia vespertina* were rare in the bottom samples but not in the drift samples, where they were occasionally abundant, especially at night (Table 3). Extensive collecting with a pond net revealed that nymphs of *Brachyptera risi* were confined to the moss on the sides of very large boulders and that nymphs of *Nemoura cambrica* and *Leptophlebia vespertina* were confined to the silted bays at the sides of the stream. Therefore the absence of these species from the bottom samples was due to inadequacies in the sampling technique. As in the Afon Hirnant (Hynes 1961), small nymphs of *Brachyptera risi* were present in April but no nymphs were taken in May.

Therefore this species appears to be a cold-water stenotherm with a temperature controlled short emergence period. Emerging imagines of *B. risi* were taken in the drift at both sites in April 1964 and adults were caught in the insect trap during April and May 1964. Emerging imagines of *Leptophlebia vespertina* were taken in the insect trap during April

Table 3. Nemoura cambrica, Brachyptera risi *and* Leptophlebia vespertina—*total numbers taken in the drift at sites* 1 *and* 2

	Site 1		Site 2	
	Night	Day	Night	Day
Nemoura cambrica				
March 1964	49	15	118	32
April 1964	4	2	6	2
Brachyptera risi				
January 1964	9	0	2	0
February 1964	11	3	1	0
March 1964	93	31	42	13
April 1964	5	1	3	0
Leptophlebia vespertina				
October 1963			1	0
November 1963	27	5	79	9
December 1963	7	2	6	2
January 1964	1	0	7	4
February 1964			3	2
March 1964	101	7	320	29
April 1964	3	1	34	4
May 1964			2	0

Table 4. *Total numbers of emerging Plecoptera and Ephemeroptera taken in the night and day drift samples from May to December* 1963 *and from January to October* 1964

	1963		1964	
	Night	Day	Night	Day
Brachyptera risi			4	0
Protonemura meyeri	18	45	41	31
Amphinemura sulcicollis	11	10	20	9
Nemoura cambrica			2	1
Leuctra inermis	8	5	40	21
L. hippopus	28	25	64	21
L. fusca	19	17	2	1
Isoperla grammatica	15	23	4	2
Chloroperla torrentium	19	39	24	4
Total Plecoptera	118	164	201	90
Ephemerella ignita	7	327	2	82
Baëtis niger	0	1	3	35
B. scambus	1	79	2	86
B. rhodani	17	432	19	445
Total Ephemeroptera	25	839	26	648

and May 1964, but were never taken in the drift. Emergence probably took place close to the bank as has also been suggested for this species in a fishpond by Macan (1966).

Comparison of nocturnal and diurnal emergence

Emerging imagines of most species (see Table 4) were frequently taken in the drift samples and therefore the time of emergence was known. The large carnivores, *Perlodes* *microcephala* and *Dinocras cephalotes*, emerged on land and therefore their imagines were not taken in the drift samples. In 1964 greater numbers of emerging Plecoptera were taken at night than during the day, but in 1963 the exact opposite was seen in *Protonemura meyeri*, *Isoperla grammatica* and *Chloroperla torrentium*, with the other species showing a slight increase in emerging imagines at night (Table 4). The nocturnal increase in emerging Plecoptera is probably the typical situation and has been observed by other workers (Brinck 1949; Hynes 1941, 1958). The atypical situation in 1963 was probably connected with the late emergence of most species of Plecoptera after the severe winter. Emerging imagines of four species of Ephemeroptera were present in the drift and were always taken in greatest numbers during the day (Table 4).

DISCUSSION

Before attempting to explain why nymphs of Plecoptera and Ephemeroptera drift in lotic systems, the results of other workers will be compared with those from the Walla Brook.

Life histories

There are some notable differences between the life histories described in this paper and those described by other workers.

Nymphs of *Amphinemura sulcicollis* were absent in August 1963 and 1964 (Fig. 2a) and therefore there was no overlap of generations as found in the Afon Hirnant (Hynes 1961). In both years the flight period of *A. sulcicollis* was shorter than that observed for this species in both the Lake District and the Afon Hirnant (Hynes 1941, 1961), whereas the flight period of *Leuctra inermis* continued into September (Fig. 3a) and was therefore longer than that observed by Hynes (1941, 1961). Only in 1963 did emergence of *L. inermis* follow that of *L. hippopus*, and in 1964 and 1965 there was no succession of species as observed in the Afon Hirnant (Hynes 1961). In the Afon Hirnant small nymphs of *Protonemura meyeri* were present for a much longer period (all months except June) than in the Walla Brook, whereas small nymphs of *Chloroperla torrentium* were present for a longer period in the Walla Brook (August to April) than in the Afon Hirnant.

Ecdyonurus venosus was clearly univoltine (Fig. 9a) with no fast-growing summer generation as seen in the river Alyn (Rawlinson 1939). *Ephemerella ignita* spends the winter in the egg stage, and the start of hatching varies considerably from one area to another. Small nymphs were first taken in late May or early June in a Lake District stream (Macan 1957), in March in the Afon Hirnant (Hynes 1961), and in May in the Walla Brook. Although nymphs of *E. ignita* were not taken from the benthos after August, forty nymphs were taken in the drift samples in September 1963 and fourteen nymphs in the November spate. The latter nymphs were present long after the flight period and their emergence may have been inhibited by falling water temperatures.

The life histories of *Baëtis niger* and *B. scambus* have not been described by other workers and therefore no direct comparisons can be made. *B. niger* was not found in the Afon Hirnant (Hynes 1961) nor in the stream studied by Macan (1957), and in the Walla Brook nymphs only occurred where there were rooted plants, a relationship also noted by Macan (1961). *B. bioculatus* is closely related to *B. scambus* and also has two quick summer generations (Pleskot 1958).

The effect of the severe winter

The late emergence of many species after the severe winter of 1963 was similar to the situation in Scandinavia where the emergence of many species of Plecoptera was progressively later as the severity of the winter increased from south to north (Brinck 1949). In both the Walla Brook and Scandinavia, the growth of nymphs was retarded presumably by the very low temperatures and ice during the severe winter, and therefore development took longer with a later emergence. Pleskot (1951, 1958, 1961) compared the flight periods of Ephemeroptera from Austrian streams and found that some species emerged later in cold streams than in warm streams.

Because of the severe winter, full-grown nymphs of *Protonemura meyeri, Leuctra hippopus, Isoperla grammatica* and *Chloroperla torrentium* were present in the Walla Brook until late in the summer of 1963 and were apparently unaffected by the high water temperatures. Therefore their absence in other summers was not due to the lethal effect of high water temperature as found for *Iron pleuralis* in the warmer parts of a Canadian river (Ide 1935), *Heptagenia lateralis* in the Lake District (Macan 1960), and *Brachyptera risi* in the Afon Hirnant (Hynes 1961).

Drifting

There is very little information on the drifting of Plecoptera. A few nymphs of *Nemoura* spp., *Neoperla nipponensis, Alloperla* sp., *Nogiperla* sp., *Kaminuria* sp. and *Paragnetina tinctipennis* were taken in drift samples from the Takisawa Brook, Japan (Tanaka 1960). Although the drift samples were taken for only 10-min periods in May and 5-min periods in August, they did show that the number of Plecoptera in the drift increased at night. Müller (1966) found a similar increase for Plecoptera in Breitenbach, Germany, but did not name the species in the drift. In the Walla Brook, the density of Plecoptera in the drift always increased at night.

A large number of Ephemeroptera species have been recorded in the drift and these are now listed under countries. The number increased at night for all the following species.

Japan: *Ephemera japonica, Ephemerella* spp., *Epeorus* spp. (*E. uenoi, E. aesculus, E. latifolium, E. curvatulus*), *Ecdyonurus* spp. (*E. yoshidae, E. kibunensis, E. tobiironis*), *Paraleptophlebia chocorata, Baëtis* sp., *Baëtiella* sp., *Ameletus* sp. (Tanaka 1960).

U.S.A.: *Baëtis vagans* (Waters 1962).

Sweden: *Ephemerella ignita, Ameletus inopinatus, Baëtis* spp. (Södergren 1963), *B. vernus* (Müller 1966).

U.S.S.R.: *Ephemerella ignita, E. taeniata, Chitonophora mucronata* (Levanidova & Levanidov 1965).

Norway: *Baëtis subalpinus* (Elliott 1965b).

Germany: *Ephemera danica, Epeorus assimilis, Ecdyonurus venosus, Rhithrogena semicolorata, Chitonophora krieghoffi, Habroleptoides modesta, Baëtis rhodani, B. vernus* (Müller 1966).

England (Walla Brook): *Ephemerella ignita, Ecdyonurus venosus, Rhithrogena semicolorata, Leptophlebia vespertina, Paraleptophlebia submarginata, Baëtis rhodani, B. niger, B. scambus, B. pumilus*.

Therefore the drifting of Plecoptera and Ephemeroptera is a normal feature of lotic systems and the numbers in the drift vary considerably from day to night and also with rate of flow (Elliott 1965a, 1967a). The relationship between these variables is shown by the following equation. Let the mean density of nymphs in the drift be D_1 individuals/m^3 at night and D_2 individuals/m^3 during the day. If the volume of water passing through the drift sampler is V m^3/h and the length of the night is T h, then the number of nymphs (N) caught in the drift sampler in 24 h is given by the equation:

$$N = (VT \, . \, D_1) + [V(24-T) \, . \, D_2]$$
$$= V[T \, . \, D_1 + (24-T)D_2].$$

While T, D_1 and D_2 remain constant, N is directly proportional to V and the latter varies with the mean water velocity at the mouth of the sampler. The size of T varies from a minimum in the summer to a maximum in the winter and therefore N can vary when V, D_1 and D_2 are constant. Therefore two physical factors (water velocity and night length) can affect the size of N and these factors alone may be responsible for differences in N at different times of the year and in different streams. Therefore in seeking other factors which affect the number of nymphs in the drift, it is important to compare D_1 and D_2, which are given in Figs. 1–12 as numbers per 1000 m^3 of water passing through the drift sampler

$$D_1 = \frac{\text{total catch during night}}{VT} \times 1000$$

and

$$D_2 = \frac{\text{total catch during day}}{V(24-T)} \times 1000$$

The daily and seasonal fluctuations of D_1 and D_2 are determined by a complex of factors, including the density of nymphs in the benthos, the stage in the life history, the activity and behaviour of the nymphs, and the water velocity to which the nymphs are exposed.

The density of nymphs in the drift depends to some extent on the density of nymphs in the benthos but there is no direct relationship between these two variables (see Figs. 1–12) and a small proportion of the benthos (under 0·01%) is in the drift at any instant in time (Elliott 1965b, 1967a). In the Walla Brook, the stage in the life history appears to be one of the most important factors which determine the density of nymphs in the drift and there was a strong correlation between periods of rapid growth and increases in both D_1 and D_2, except when the nymphs were very small. D_1 is always greater than D_2 and this is probably due to daily variations in the activity and behaviour of the nymphs.

Very little is known about the daily activity pattern of nymphs of Plecoptera and Ephemeroptera. Müller (1966) has assumed that the daily fluctuations of numbers in the drift follow the activity pattern of nymphs in the benthos and although this assumption may be correct, it is supported by very little evidence. Upstream migration of *Ecdyonurus torrentis* occurred at night in a Lancashire stream (Harker 1953) and *Baëtis* sp. were more active at night in the Hampshire Avon (Moon 1940). Various samplers in lakes have taken more nymphs of Ephemeroptera at night than during the day (Moon 1940; Mundie 1959; Pieczynski 1964) and there was a nocturnal increase in the activity of *Povilla adusta* from Lake Victoria (Hartland-Rowe 1958).

Although most species of Plecoptera and Ephemeroptera show a strong negative phototaxis until just before emergence, a few species are known to be positively phototactic. In the Plecoptera, *Nemoura* (*Protonemura*) *fumosa* does not avoid light (Kühtreiber 1934) and *N. cinerea* and *N. picteti* have been seen on the tops of stones in the afternoon and evening (Brinck 1949). Nymphs of *Baëtis harrisoni* showed a strong positive phototaxis in a South African stream (Hughes 1966) and nymphs of *Paracloëon* sp. were day active in a Brazilian stream (Sattler in Müller 1966).

In both field and laboratory experiments the nocturnal increase in numbers in the drift was suppressed by an artificial light with an intensity of 0·5 ft-candles or more (as measured at the surface of the water), whereas permanent darkness did not affect the basic pattern and the numbers in the drift still increased at a time corresponding to the normal night (Elliott 1965a, 1967a; Müller 1965, 1966). Therefore the nymphs appear to possess an inherent activity pattern together with a strong negative phototaxis, but the activity and behaviour of most species has yet to be studied. Although little is known about the nocturnal movements of the nymphs, both Hynes (1941) and Brinck (1949) conclude that some Plecoptera move on to the tops of stones at night in order to feed on the algae, and nymphs of both Plecoptera and Ephemeroptera have been seen on the upper surfaces of stones at night (Hubault 1927; Elliott 1965a, 1967a). Nymphs of *Paraleptophlebia* sp. were under the stones during the day but moved on to the upper surface at night and fed on algae (Chapman & Demory 1963). Therefore the nocturnal movements are probably associated with foraging.

From the work in the Walla Brook it was concluded that drifting was a passive process and therefore all the nymphs in the drift were swept off the bottom (Elliott 1967a). The nymphs are under the stones during the day and therefore they are not exposed to the current, except when near the edge of a stone. The activity of the nymphs probably increases at night, and these nocturnal movements are associated with foraging over both upper and lower surfaces of stones. Therefore more nymphs are in a position to be detached at night, and the detachment of a nymph will depend on the strength of the current, the tenacity of the nymph and the jostling between nymphs.

As all measurements of water velocity in the Walla Brook were at least 5 cm above the bottom, it was impossible to determine the water velocity to which the nymphs were actually exposed. Ambühl (1959) found that the water velocity in a tank was considerably reduced near the surface of a 'stone' made of plaster of Paris. The thickness of this layer of comparatively still water was about the same as the height of most aquatic invertebrates, and therefore a nymph on the top of a stone would be exposed to a very low water velocity. However, it cannot be assumed that a similar phenomenon exists in streams, because flow is more turbulent and stones do not have the smooth surfaces of the experimental 'stones'. Dorier & Vaillant (1954) placed various species in an experimental trough and gradually increased the water velocity. They recorded the water velocity at which each species was swept away and the large variation in their results was probably a reflection of the tenacity of the different species. Therefore the tenacity of a nymph probably varies considerably from one species to another and this may explain why some species are rare in the drift, e.g. *Perlodes microcephala* and *Ecdyonurus venosus*, whereas other species are abundant in the drift, even at low current speeds, e.g. *Baëtis* spp. and *Ephemerella ignita* during the summer drought of 1964 (water velocity 0·1 m/sec at a point 5 cm from the bottom).

The increased drifting at times of rapid growth may be due to increased competition between nymphs for food and space with some nymphs being pushed off, or near to, the edge of the stones. Although several studies have dealt with the food of Plecoptera and Ephemeroptera, little is known about the times of feeding or the food requirements at different stages in the life history. Although all the causes of drifting are not yet known, it is apparent that they are intimately connected with the activity, behaviour and feeding of the nymphs.

ACKNOWLEDGMENTS

I wish to thank Dr T. T. Macan for all his help in the preparation of this paper, and Professor L. A. Harvey for reading the manuscript.

SUMMARY

1. Monthly samples of invertebrate drift and benthos were taken from the Walla Brook, a small stream on Dartmoor (south-west England). A shovel sampler and pond net were used for the bottom samples, and both surface nets and modified plankton samplers for the drift samples. The drift samplers are briefly described. Both drift samplers and an insect trap provided information on the imagines.

2. The physical and chemical conditions in the Walla Brook are described. This study started after one of the coldest winters ever recorded on Dartmoor and the climate of January and February 1963 was very severe.

3. Life histories are described for the following species: Plecoptera: *Protonemura meyeri*, *Amphinemura sulcicollis*, *Leuctra inermis*, *L. hippopus*, *Perlodes microcephala*, *Isoperla grammatica* and *Chloroperla terrentium*. Ephemeroptera: *Ephemerella ignita*, *Ecdyonurus venosus*, *Baëtis niger*, *B. rhodani* and *B. scambus*.

Notes are given on the following species: Plecoptera: *Nemoura cambrica*, *Leuctra fusca*, *Brachyptera risi* and *Dinocras cephalotes*. Ephemeroptera: *Leptophlebia vespertina*, *Paraleptophlebia submarginata*, *Rhithrogena semicolorata*, *Heptagenia lateralis*, *Caenis rivulorum* and *Baëtis pumilus*.

4. All species of Plecoptera and Ephemeroptera, except *Ephemerella ignita* and *Baëtis scambus*, had an overwintering generation and this was followed by a fast-growing generation in *B. niger* and *B. rhodani*. The generations of *Ephemeraella ignita* and *Baëtis scambus* were confined to the summer months.

5. In all species there was a period of delayed hatching during which the density of nymphs in the benthos usually increased. A severe spate in November 1963 reduced the numbers of *Protonemura meyeri*, *Isoperla grammatica* and *Chloroperla torrentium*, and there was a high mortality of small nymphs of *Leuctra inermis*, *L. hippopus* and *Isoperla grammatica* during the summer drought of 1964.

6. During the severe winter of 1962–63 there appeared to be a high mortality of nymphs in only three species (*Protonemura meyeri*, *Perlodes microcephala* and *Baëtis rhodani*). The emergence of *Protonemura meyeri*, *Amphinemura sulcicollis*, *Leuctra inermis*, *L. hippopus*, *Isoperla grammatica* and *Chloroperla torrentium* was much later in 1963 than in a normal year, and this appeared to be due to a marked retardation in growth rate by the very low winter temperatures.

7. Growth of all species, except *Perlodes microcephala* and possibly *Rhithrogena semicolorata*, slowed down considerably during a normal winter. Although periods of rapid growth were not the same for all species, most species with an overwintering generation grew rapidly in November, December and March and those with a summer generation grew rapidly in July and August.

8. *Perlodes microcephala* and *Ecdyonurus venosus* were the only species which were taken in the drift in very low numbers relative to their numbers in the benthos. In nearly all species the density of nymphs in the drift increased during periods of rapid growth, except when the nymphs were very small. The density of nymphs in the drift was always greater at night than during the day.

9. The results of other workers are discussed. The number of nymphs (N) taken in a drift sampler in 24 h is given by the equation: $N = V\ [T\,.\,D_1 + (24-T)D_2]$ where the volume of water passing through the sampler = Vm^3/h, length of night = T h, mean density of nymphs in the drift = D_1 individuals/m^3 at night and D_2 individuals/m^3 during the day. The various factors which affect D_1 and D_2 are discussed. It is concluded

that the density of nymphs in the drift reflects both the number of nymphs moving over the exposed parts of stones and aquatic plants, and the extent of the competition between nymphs for food and space. More nymphs are on the tops of stones at night and competition appears to be greatest between rapidly-growing nymphs.

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(*Received* 25 *October* 1966)