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Studies on Blackflies (Diptera: Simuliidae) breeding in bog streams in Upper Teesdale

by

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(Graduate Society)

... being a thesis presented in canditature
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ABSTRACT

This study, on the immature stages of the Simuliidae, was undertaken in streams draining bogs in Upper Teesdale.

There were four parts to the investigation:

Firstly, a qualitative survey of fourteen sites showed eleven of the thirty-five British species of Simuliids to be present.

Secondly, quantitative programmes showed streams to have three types of population structure: those with larvae present mainly in winter; mainly in summer; and throughout the year. Most streams were in the latter two categories, larval numbers being lower in winter at the higher altitudes. In summer 1972, absolute population estimates were obtained from two streams by removal trapping. More larvae occurred in the lower sections of the streams and, in the streams where the winter populations were low, larval numbers were larger early in summer; this was not true of the lower altitude stream.

Thirdly, cumulative frequency x size-measurement plots were made on probability paper from which the modal size-classes corresponding to the larval instars of each species could be determined. All species had seven larval instars and percentage frequency distributions for each sampling date were constructed. The detailed population biology could then be determined. Larval life was much shorter in summer at 30-40 days than in winter. Two generations were distinguished, that in winter commonly having two cohorts and that in summer often as many as four.

Fourthly, life-tables were constructed from which mortality and production estimates were determined. Mortality of complete larval cohorts ranged from 91%-98% and the production estimates from this poor habitat are amongst the lowest recorded for Simuliids, the maximum level for an equivalent cohort of S.vernum + S.brevicaule + S.monticola + S.nitidifrons being 56.9 mg. $m.^{-1}$ stream length.

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1. INTRODUCTION

The Simuliidae have a world-wide distribution and are well known in many areas as biting pests - "blackflies" and "buffalo-gnats" are common names - and as vectors of disease organisms.

Only the female flies bite but their effect on livestock after large emergences has been well documented (Rempel and Arnason, 1947; Fredeen, 1958; Anderson and Voskuil, 1963). In West and Central Africa several species, notably Simulium damnosum Theobald, are vectors of the microfilarial parasite Onchocerca volvulus which causes the disease "African river blindness". This is an important disabling disease and considerable work has been carried out on the biology of the adults and immature stages of the Simuliidae in this region (e.g. Brown, 1962; Duke et. al., 1966). A projected 20-year control programme to reduce the blackfly numbers in the basin of the River Volta, in West Africa, is about to be undertaken by the World Health Organization (Muirhead-Thomson, 1974) which underlines their medical importance in the region.

Eggs are laid in water-courses and the larvae are dependent on a water current to obtain food. They are passive filter-feeders using paired cephalic fans which are extended into the current. The body of the larva remains largely within the boundary-layer of slower-flowing water adjacent to the substratum (Hynes, 1970). After normally seven larval instars a pupa is formed from which the adult fly emerges and breaks the surface of the water.

In a survey of the bottom fauna of streams in the Scottish Highlands, Morgan and Egglishaw (1965) found simuliids made up 10.3% of the total fauna in spring and 5.5% of the total in summer when the number of all animals collected was three times greater. Other important faunal components of these hill streams were: Plecoptera, 33%; Ephemeroptera, 32%; and Chironomidae 9% in the spring samples. In summer the proportions of these groups changed with 5%; 23%; and 32% respectively. The numbers of Plecoptera were thus reduced in summer while there were increases in the numbers of Ephemeroptera, Simuliidae and, especially, Chironomidae.

Armitage et. al. (1974, and in press) have carried out surveys of the invertebrate fauna of streams in the Cow Green basin and Moor House Nature Reserve, two of the three areas studied in the present project. (The third area was the eastern slope of Cronkley Fell in the Upper Teesdale National Nature Reserve.) They found over 120 taxa to be represented and the wide range of animal types in these hill streams was similar to that described by Morgan and Egglishaw (1965) in Scotland. In this case up to 3% only of the fauna consisted of simuliids and Ephemeroptera were the most numerous animals at all times of year.

Empirical observation of the blackfly larval fauna of the bog streams in Upper Teesdale, i.e. streams up to one metre in width draining peat and blanket bog, showed them to be an important part of the animal communities living on trailing vegetation and stones. In these habitats, Simuliids will make up a greater percentage of the total fauna than the estimates given by the above authors would suggest. Their kick-samples will include animals from the gravels where simuliids do not usually occur.

The Upper Teesdale area consists of high and wet Pennine moorland and the climate is severe. In addition to extremes of temperature, animals living in the streams draining the moorland are subjected to frequent spates. Also, nutrient levels are low and the predominating potential source of food is peat particles from the constant erosion which takes place.

Previous qualitative work has been carried out on several groups of freshwater invertebrates in Upper Teesdale. A general review of this work has been prepared by Crisp (1973), including data from Nelson (1965) on aerial insects near streams; Brown et. al. (1964) on Plecoptera; and Crisp and Nelson (1965) on Ephemeroptera. Davies and Smith (1958) and Smith (1969) studied the biology of Simuliids in streams draining the western Pennine escarpment, and blackfly material for experimental and taxonomic investigation has been collected from the area (Phillipson, 1956, 1957; Davies, 1966).

The present study provided a means of examining in detail the ecology of an important component of the bog stream ecosystem. The objectives were fourfold: to conduct a qualitative survey to determine which Simuliid species were present, and where; to conduct quantitative programmes to gain insight into seasonal fluctuations in population density; to construct percentage frequency distributions for the common species to study their population biology; and, finally, to obtain mortality and production estimates for the common species in two streams at different altitudes.

The initial survey, carried out in the streams shown in Fig. 2.1, resulted in a species list for each stream and an indication of their relative abundance. Of the 35 British species of Simuliids given by Davies (1968) ten were found in the bog streams in 1971 and a further species the following year.

Quantitative programmes were of two types: those using samplers; and those which took advantage of the naturally occurring substrate. Of the former type, the polythene tape method of Williams and Obeng (1962) was employed in 1971 and another type of sampler, using Juncus stems, used in the summer of 1972 to obtain relative population estimates at one point in the streams. In a programme of the second type Potamogeton leaves were removed from a small stream where these formed the predominant substratum. In this case the population estimates were expressed in numbers of larvae per 10 Potamogeton leaves.

When absolute population estimates are necessary, as in mortality and production studies, quantitative sampling of simuliid larvae presents a considerable problem. Egglishaw (1969) has shown that high variances were obtained from a series of samples taken in riffles and the distribution of larvae will be affected by current flow at the micro-habitat level. As the current régime alters, so will the numbers of simuliids vary and their distribution is often markedly discontinuous. To overcome this effect either a large number of replicate samples must be taken, or some attempt can be made to sample the whole population of a given stretch of stream. The latter approach was taken in the present study.

Removal trapping has been used in estimating the numbers of mammals in a population (Leslie and Davis, 1939) and the method, as applied to insect populations, has been described by Southwood (1966). The slope of the regression of animal numbers in successive collections will be proportional to the total number of animals in the sample area. Zippin (1956) has given an elegant statistical treatment of removal trapping data using a method of maximum likelihood, and this was used here to gain population estimates with 95% confidence limits.

Such a method is ideally suited to work on populations of animals in small streams. Here, the narrow width ensures that the whole stream can be sampled effectively. The method, however, can only be applied to populations of animals which do not readily leave the area once the substrate has been disturbed.

Quantitative sampling showed that the simuliid larval populations in the bog streams conform to the pattern described by Maitland and Penney (1967) for headwater streams. That is, larvae were more numerous in the summer months than in winter, the populations in the Moor House streams being very small at the latter time.

In the third section of the investigation larvae of known species were measured and assigned to their respective instars. The instar categories were determined using Cassie's (1954) method of polymodal analysis on the data for all larvae of each species, and percentage frequency distributions could then be constructed. The pattern of development was similar to that described by Rubzov (1956) with a synchronised winter larval generation, sometimes divided into two cohorts, and a summer generation with overlapped cohorts. In some cases the overlap prevented the separation of these cohorts, but this was not always the case. Mortality estimates were obtained by two methods: that of Richards and Waloff (1954); and an age-distribution method similar to that used by Service (1973). This study includes the first attempt to determine the mortality of larvae in each instar in field populations of Simuliids, Neveu (1970) in France, having presented overall larval mortality estimates. The life-tables (Appendix 3) show greater losses in the early instars than in later ones and the overall mortality estimates range from 66% for S.vernum in the upper part of Moss Burn, to 100% mortality of S.monticola larvae in the lower part of Cronkley stream 2.

Production studies in freshwater biology have become increasingly important, especially after the International Biological Programme investigations. Few have been carried out in a habitat as poor as a high moorland stream. Production of the Simuliid larval populations was calculated from life-tables using the eliminated biomass method of Winberg et. al. (1971). Any errors present in the life-tables will consequently occur in the production tables. Values are given only for complete cohorts and the largest obtained was 23.7 mg dry weight m^{-1} stream length for S.vernum in the lower part of Cronkley stream 2. This constrasts markedly with the smallest cohort production value of 260 mg m^{-2} dry weight given by Ladle et. al. (1972) for Simulium (Wilhelmia) equinum L in a Dorset chalk stream. Various factors contribute to the very much lower production figures obtained from the bog streams, as will be discussed later.

2(i) DESCRIPTION OF FIELD SITES

The underlying rock of the Northern Pennines, in which Upper Teesdale is situated, is limestone with intrusions of whin sill. This is overlain by peat which supports a flora typical of high, wet moorland: Calluno-Eriophoretum; Trichophoro-Eriophoretum; Juncetum; and areas of Sphagnum spp. blanket bog from which the study streams drain. After heavy rainfall the bogs become saturated and run-off into the streams is rapid.

Qualitative work was carried out in the streams shown in Fig. 2.1. These can be divided into three areas (altitudes given in metres and feet above O.D.):

The Cronkley streams: Dufton Sike, 350 m. (1150 ft.); Cronkley Stream 1, 380 m. (1250 ft.); Cronkley Stream 2, 380 m. (1250 ft.); and Cronkley Stream 3, 325 m. (1070 ft.).

The Cow Green streams: Force Burn Foot, 490 m. (1600 ft.); Mattergill and Rowantree Sikes, both 475 m. (1560 ft.); Borderonmere Sike, 500 m. (1640 ft.); and Dubby Sike East Grain, 530 m. (1740 ft.).

The Moor House streams: Moss Burn, rising at 700 m. (2300 ft.), but sampled in 1971 at 580 m. (1900 ft.); Rough Sike, rising at 670 m. (2200 ft.), and also sampled at 580 m. (1900 ft.) and Force Burn: tributaries A and B, 700 m. (2300 ft.).

Quantitative sampling was undertaken in 1971 in Cronkley streams 2 and 3; in Dubby Sike East Grain; Moss Burn; Rough Sike; and Force Burn tributary A.

In the winter of 1971/72, Cronkley stream 3: section A, within a bog area (see Fig. 2.2), was sampled intensively. This stream is very small (at most 0.5 m. wide) and larvae almost exclusively inhabited leaves of Potamogeton sp. The leaves can be seen in Plate 1, which

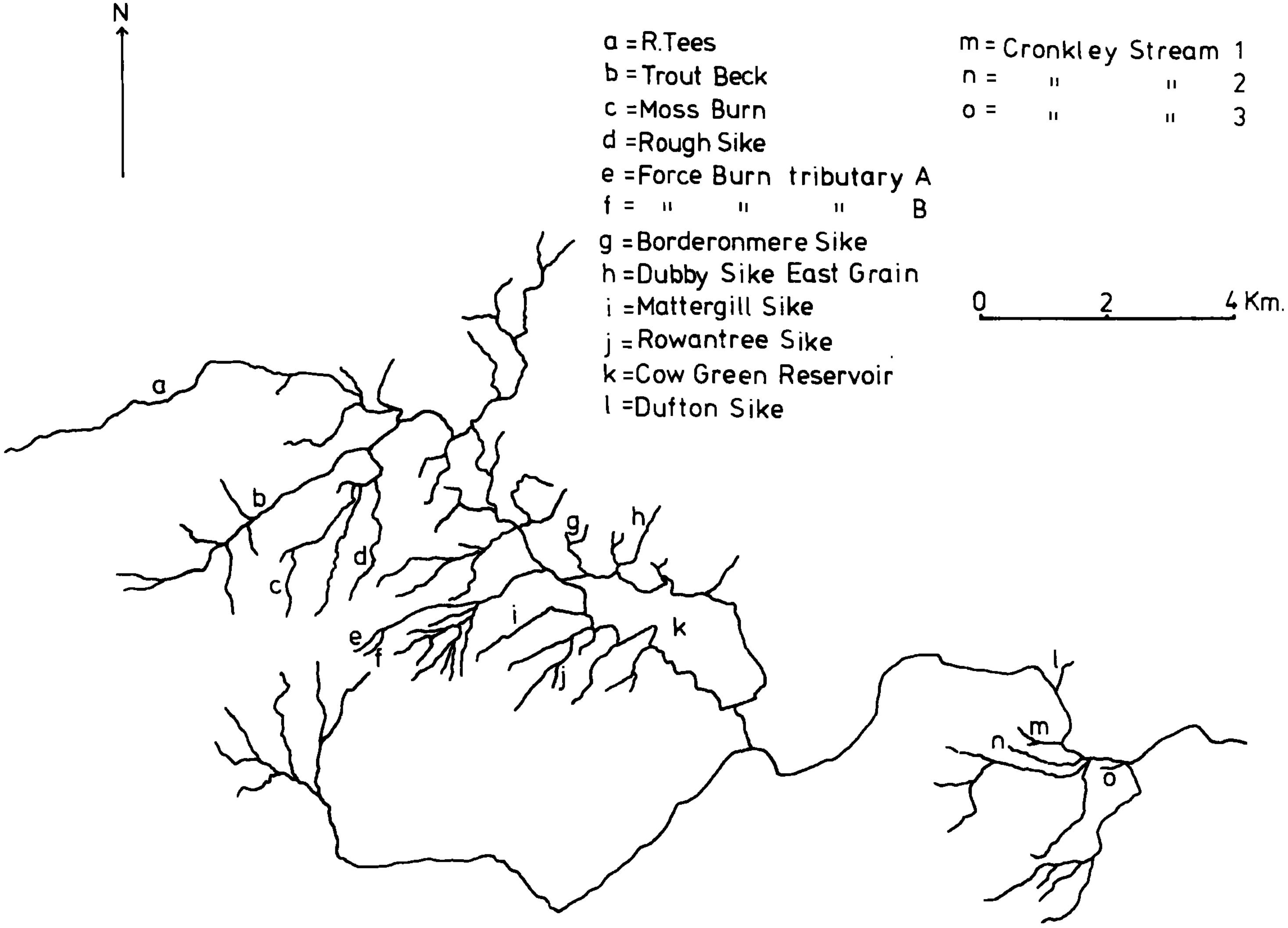


Fig. 2.1. Map of the study streams

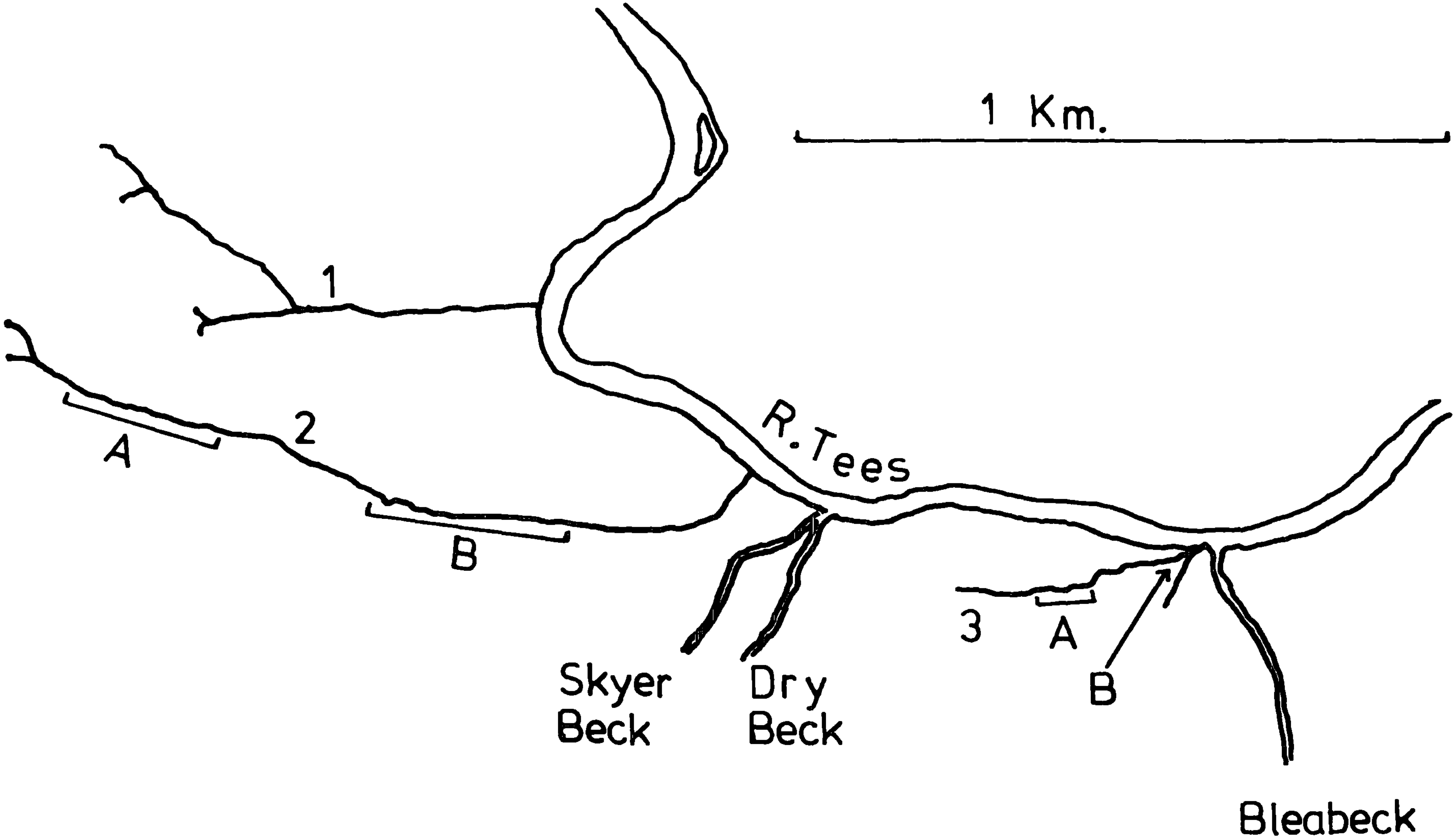


Fig. 2.2. THE CRONKLEY STREAMS

also shows the extent of the surrounding vegetation in summer. Section B (Plate 2) was more open and situated near the confluence with the Tees (Fig. 2.2).

In summer 1972 Cronkley stream 2 was divided into two sections, A and B (see Fig. 2.2). Section A (Plate 3) was characterised by its wide bed of clean stones and silt, whereas the stones downstream were covered by the moss *Drepanocladus revolvens*. As shown in Plate 4, section B was more densely overgrown and not as wide as the upper section. The following plants were identified in Cronkley stream 2: sections A and B (the first five were both trailing and rooted in the stream; the other three all trailed in from the banks): *Agrostis* sp.; *Equisetum palustre*; *Carex* sp.; *Ranunculus flammula*; *Juncus bulbosus*; *Veronica beccabunga*; *Erica tetralix*; and *Calluna vulgaris*.

Moss Burn was also studied intensively in the summer of 1972, being divided into four sections: A; B; C; and D (see Fig. 2.3). Section A (Plate 5) consisted of pools and "trickles" which were rich in peaty detritus trapped by the abundant trailing vegetation. Section B (Plate 6) ran through an area of eroding peat and the bed was quite stony. Plants identified in this section include extensive beds of *Juncus* sp., with *Ranunculus flammula* and trailing *Eriophorum* sp. As in section A there were deep pools here (over 0.5 m.) and these contained suspended peat particles, but there was no evidence of planktonic organisms.

Sections C and D of Moss Burn (Plates 7 and 8) were near the confluence with Netherhearth Sike and here the beds were of large stones which were relatively free of moss (an indication of the instability of the substrate). Rooted vegetation consisted of *Agrostis* sp. and *Equisetum palustre*, while *Juncus* sp. and *Carex* sp. trailed in from the banks.

Of the other streams Dufton Sike drained through a meadow which was stocked throughout the year and probably had a higher organic content

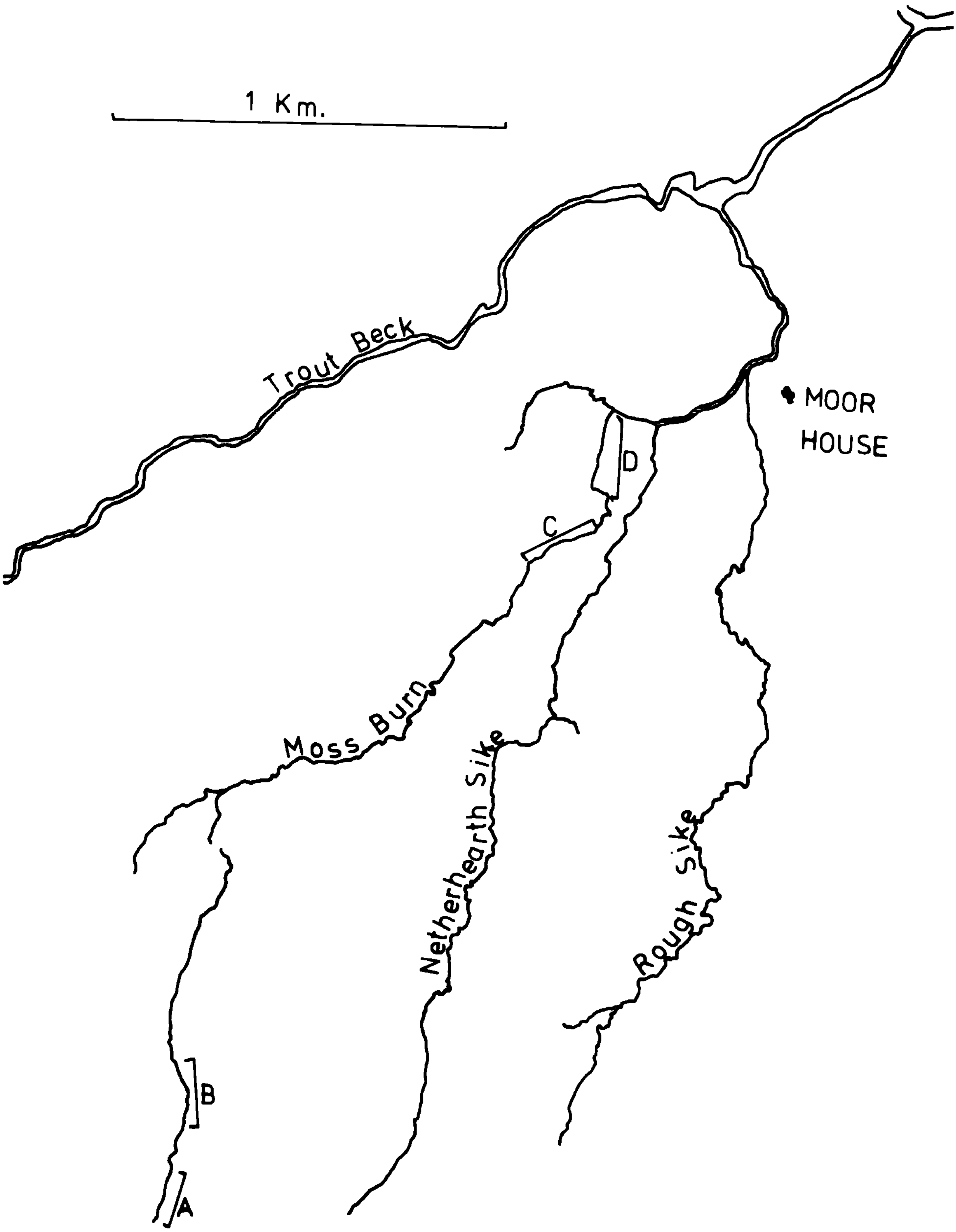


Fig.2.3. THE MOOR HOUSE STREAMS

PLATE 1

Cronkley stream 3: section A looking towards the source. The water surface is masked by *Potamogeton* leaves and the course of the stream can be traced through the dense surrounding vegetation. This is the condition of the stream in mid-summer when the stream is less than 0.5 m. wide.

PLATE 2

Cronkley stream 3: section B looking towards the source. Here the bog stream becomes wider - ca. 1 m. - near its confluence with the Tees. Sampling was carried out in the part of the stream shown in the upper half of the plate.

PLATE 3

Cronkley stream 2: section A looking downstream. The stream is ca. 1 m. wide here and follows the fell wall closely throughout the section.

PLATE 4

Cronkley stream 2: section B looking downstream. The main part of the stream, in which removal sampling was carried out, can be seen in mid-plate having passed under the fell wall which it crossed higher up. Narrower than section A it was also more densely overgrown.

PLATE 5

Moss Burn: section A looking toward the source. In this plate the "pool and trickle" nature of the stream is clearly visible, the flowing sections being ca. 0.25 m. wide.

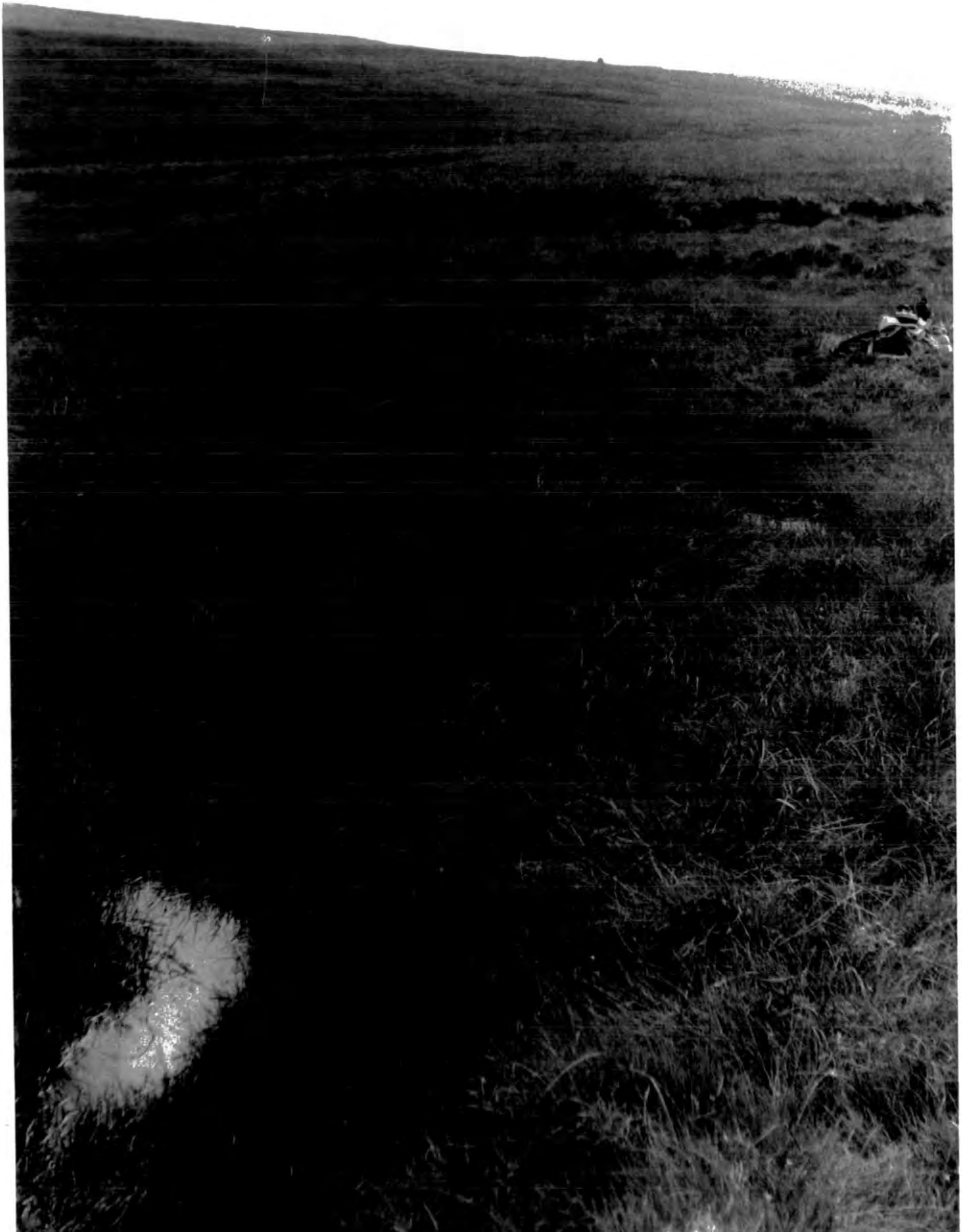


PLATE 6

Moss Burn: section B Part of section B showing the type of eroding peat area through which it flowed. Most of the section had a less stony bed and there were large beds of rooted vegetation.

PLATE 7

Moss Burn: section C looking upstream. The bed consists of large, clean stones and the width of the stream varied between 0.75 m. and 2m.

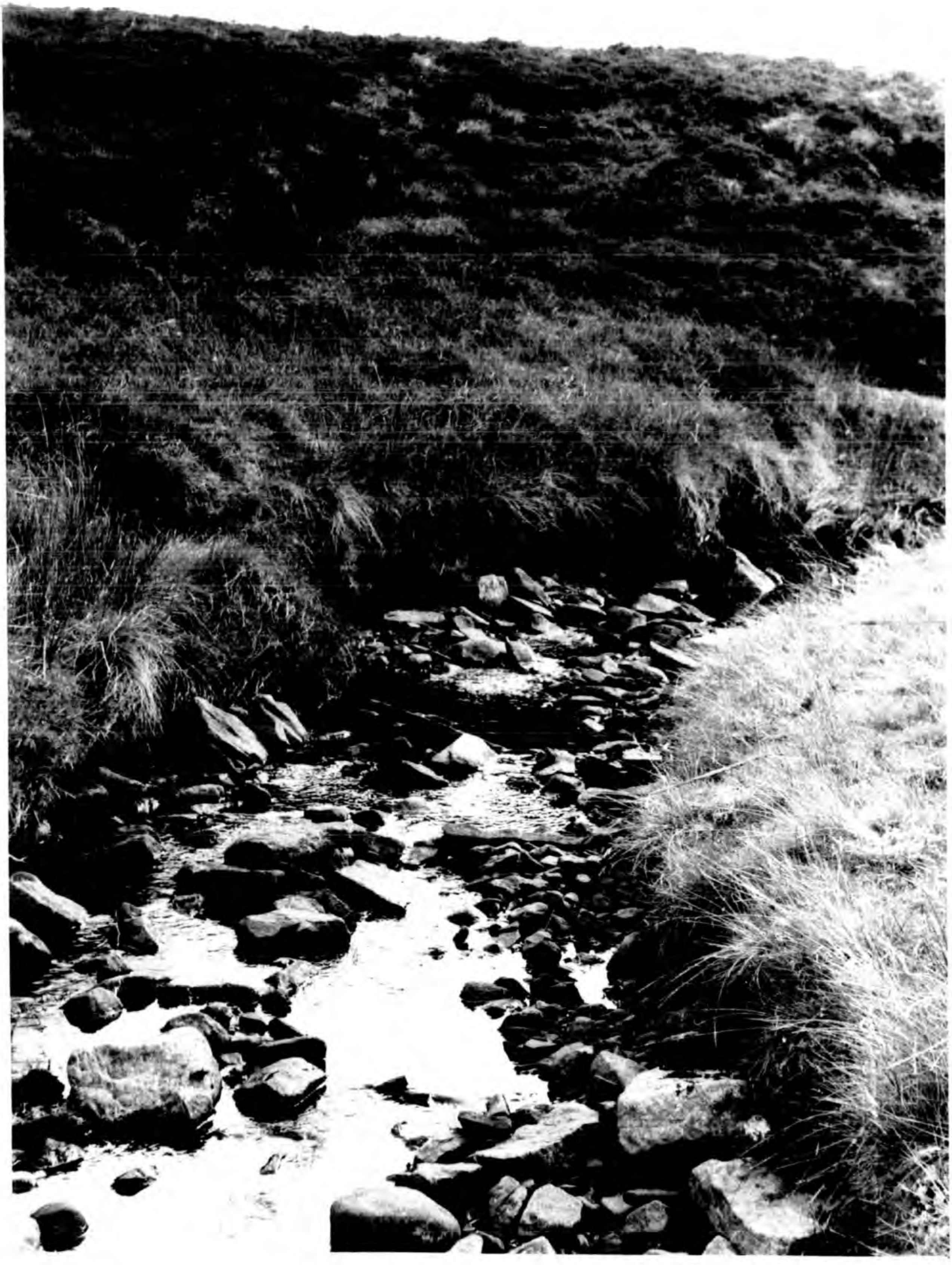


PLATE 8

Moss Burn: section D looking upstream and taken on the same day as Plate 7. The bed of the stream is similar to that in section C and banks of stones, which characterise the lower reaches and only became covered in spate, are visible. Stream width was similar to that in section C and the growth of *Juncus* is especially noticeable in this plate.

than the other streams. The Cow Green streams on the western side of the reservoir were topographically similar to the lower reaches of Moss Burn, while those of the eastern side were more like section B of the latter stream. Force Burn tributary A was also of this type, while tributary B resembled section A of Moss Burn. The latter stream dried up during summer 1971 in the region sampled.

The climate of the Moor House Nature Reserve, which contains the upper part of the Tees basin, has been compared by Manley (1936) to that of southern Iceland. The average rainfall is over 185 cms. falling on 240 days of the year, mostly in spring, autumn and winter. Sudden heavy showers can occur in summer which cause spates, a feature of the study streams. Spates increase the amount of suspended material carried downstream (Crisp, 1966; Armitage in pers. comm.) in the bog streams, and Crisp (1966) has also shown that the chemical composition of the water varies with flow-rate. In Rough Sike, another Moor House stream, he found the concentration of calcium ions to be 4.0 to 8.5 mg. $l.^{-1}$ at discharges of less than 3 l. $sec.^{-1}$, but fell to 1.0 mg. $l.^{-1}$ or less as the discharge approached 1000 l. $sec.^{-1}$. In contrast the concentration of potassium and phosphate ions rose with increasing stream discharge.

Gorham (1956) found that Trout Beck, also on the Moor House Reserve, has a pH of 7.8 in dry weather, which was reduced to pH 6.2 in wet weather. Some of this reduction will be caused by drainage through the peat, Gorham (loc. cit.) having recorded the water of some moorland pools to be as low as pH 3.7.

Spot temperature readings were taken on each sampling date and these are presented in Appendix 1. The results necessarily only give an outline of annual variations in temperature taken at approximately the same time each day. They do show that summer temperatures exceeded 15°C in all but Cronkley stream 3, section A, and the bog streams are thus "summer-warm" as defined by Edington (1966).

To obtain accurate temperature measurements in summer 1972 a "Cambridge" mercury-in-steel thermograph was set up in Moss Burn below section D. The bulb was anchored to the bed of a fast-flowing stretch by large stones and assumed to record temperature throughout the water column (Kamler, 1965, has shown water temperature to be little different between surface water and that flowing over the bed in Polish mountain streams).

After calibration, hourly temperatures were read from the chart and from these the mean daily temperature could be calculated. This record, together with the daily maximum and minimum temperatures, is presented in Fig. 2.4. Over the summer the absolute temperature range was from $5^{\circ}C$ to $25^{\circ}C$, i.e. 20 C°. As meteorological records are kept at Moor House Nature Reserve, rainfall and air temperature records have been presented from the same period (Figs. 2.5 and 2.6). Mean air temperature was calculated as $\frac{1}{2}$ (maximum + minimum), and showed a very significant correlation with mean water temperature as would be expected (r of means = +0.817 with n=62, $P < 0.001$). Rainfall, too, had a marked effect on water temperature in reducing the mean level and flattening the diel curve which usually gave a minimum value at 6.00 hours and a maximum at 17.00 hours.

Macan (1958a) studied a small, stony stream and found the largest daily temperature range to be 6.8 C° but, as Crisp and Le Cren (1970) point out, this may be because of the location of his thermograph downstream from an underground section. The latter authors found ranges $>$ 12 C° occasionally in Rough Sike, and this was true of Moss Burn in the present study where the largest daily range was 14.5 C°.

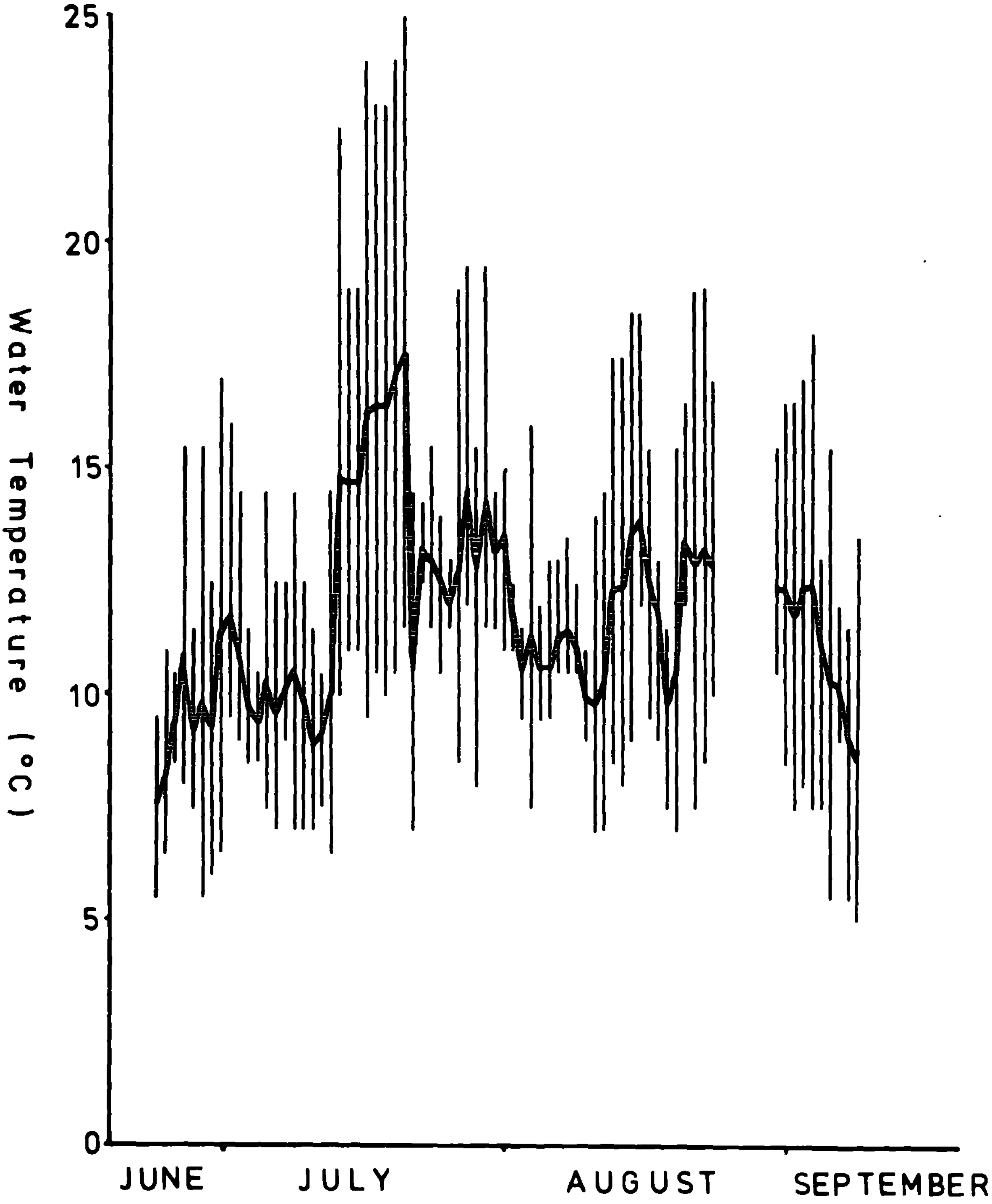


Fig. 2.4. Mean daily water temperature, with daily maximum and minimum, of Moss Burn. Summer 1972.

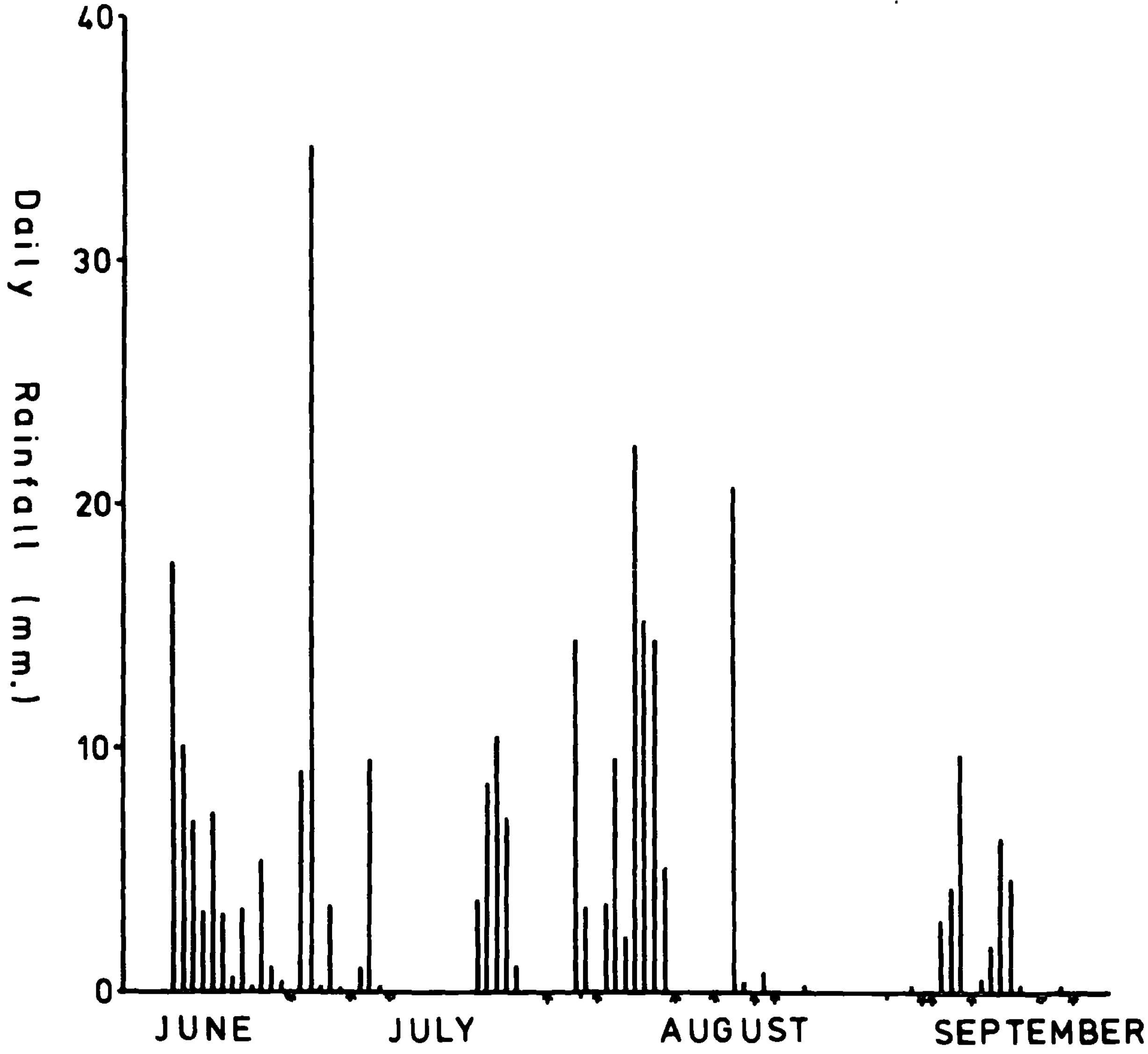


Fig. 2.5. Rainfall in mm. day^{-1} for the given months at Moor House, 1972. (Arrows indicate days for which data were not available.)

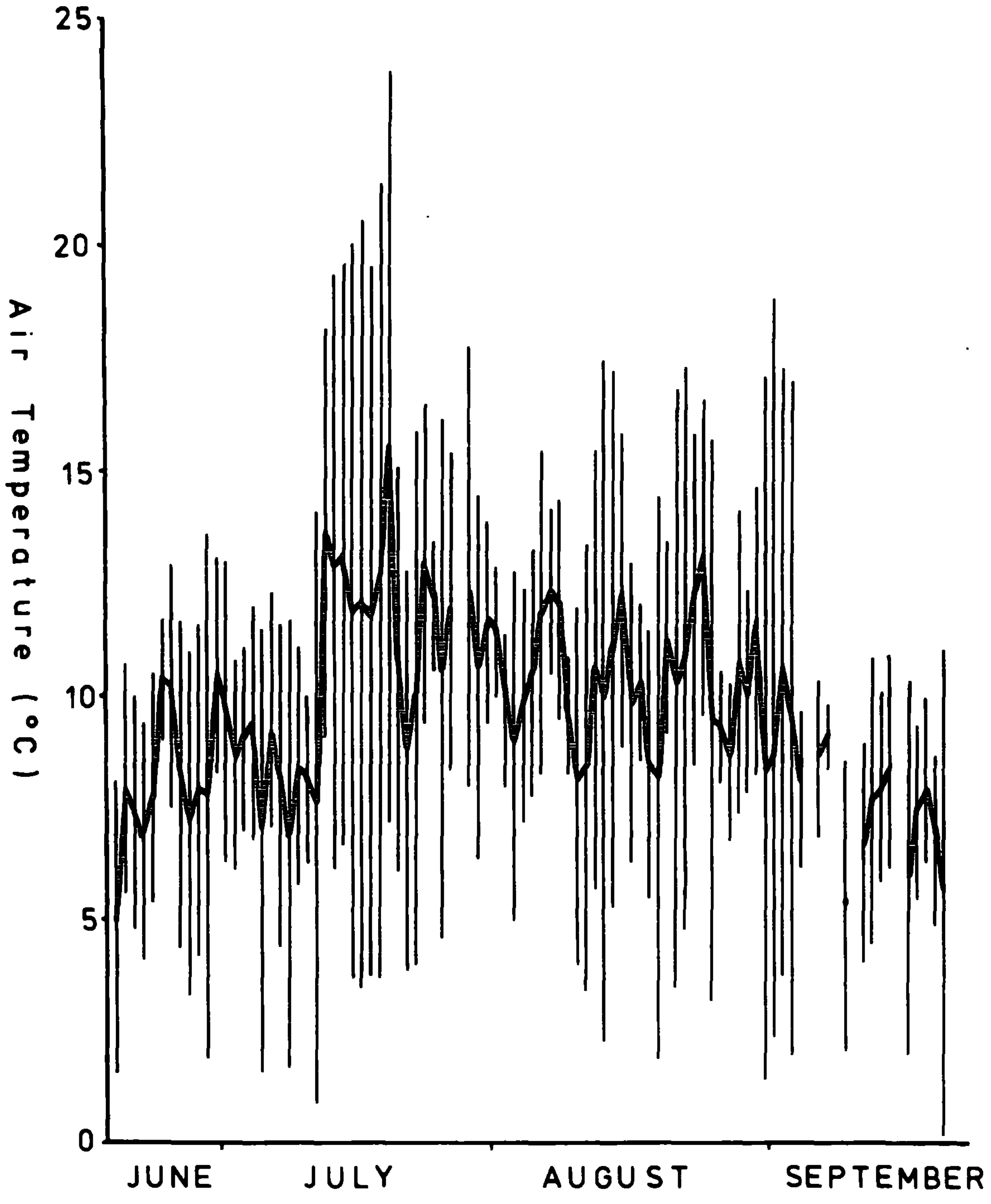


Fig. 2.6. Mean air temperature - $^1/_2$ (max.+min.) - with maximum and minimum temperatures. Moor House. Summer 1972.

2(ii) SPECIES FOUND IN THE UPPER TEESDALE STREAMS

The following species were collected in the study:

Prosimulium arvernense Grenier
Simulium (*Eusimulium*) *vernum* Macquart
Simulium (*E.*) *brevicaule* Dorier and Grenier
Simulium (*E.*) *naturale* Davies
Simulium (*E.*) *angustitarse* Lundstroem
Simulium (*E.*) *aureum* Fries.
Simulium (*Simulium*) *tuberosum* Lundstroem
Simulium (*S.*) *monticola* Friedrichs
Simulium (*S.*) *variegatum* Meigen
Simulium (*S.*) *ornatum* Meigen
Simulium (*S.*) *nitidifrons* Edwards

In addition, *Prosimulium inflatum* Davies; *Prosimulium hirtipes* Fries, and *Simulium* (*E.*) *dunfellense* Davies have been collected from streams draining from the western Pennine escarpment and Armitage et. al. (1974) have recorded *Simulium* (*S.*) *reptans* Linn. in Maize Beck, a tributary of the Tees.

3(i) SAMPLING AND TREATMENT OF QUALITATIVE COLLECTIONS

Qualitative samples from the study streams were taken by hand collecting larvae and pupae from stones and adding rooted and trailing stream vegetation. The whole was taken to the laboratory in labelled jars containing enough water to keep the collections moist. Samples were placed into enamel trays containing water and the pieces of vegetation washed well, searched, and any larvae and pupae removed to a vial of 70% alcohol. The remaining water was poured through a sieve which consisted of a polythene bottle with its base cut off and a hole cut in the lid to accept the metal gauze. This was of mesh 0.13 mm x 0.13 mm, which is adequate to retain most small larvae (Maitland and Penney, 1967) without causing excessive clogging. The sieve was dismantled and the gauze inverted in a Petri dish of 70% alcohol and the sample examined repeatedly under the binocular microscope at x25 magnification. Larvae were removed and placed into the labelled vial.

3(ii) IDENTIFICATION OF LARVAL AND PUPAL SIMULIIDAE

Identification of larvae and pupae was carried out using the keys of Davies (1966, 1968). Subsequently, S.latipes has been re-named S.vernum (Crosskey and Davies, 1972) and the latter name has been used in this study.

Examination of last instar larvae of S.vernum and S.naturale, larvae having dark pupal respiratory histoblasts, showed typical specimens and transitional types which could not be assigned to either species. Overall length measurement of typical specimens of both species from the bog streams showed there to be no size difference between the two species as Davies (1966) found. As a result of the difficulty in separating the two, both were grouped as S.vernum in this study.

It was possible to use features for the identification of larvae under a binocular microscope in the way that Obeng (1965) has done. The shape and proportion of the post-genal cleft of the species found proved to be a reliable character and descriptions are given in Davies (1966, 1968). Additionally, the cephalic apotome markings in *S.aureum*, *S.nitidifrons*, and *S.monticola* provided easy separation of these species. Body colouration of freshly-killed material showed more variation but larvae of *S.aureum* tended to be golden-brown; *S.angustitarse*, pale green; and *S.nitidifrons*, olive green. *S.monticola* larvae were usually dark grey in body colour.

Some larvae, especially the smaller instars, required more detailed study and where the larvae were too small to be identified, or were damaged, they were measured as "unidentified" larvae.

The structure of the respiratory filaments provided a reliable means of identification of pupae. In common with the larvae, pupae of *S.vernum* and *S.naturale* showed a range of characters common to both.

3(iii) DISTRIBUTION AND SEASONAL ABUNDANCE OF THE UPPER TEESDALE SIMULIIDAE

Data on the distribution and seasonal abundance of Simuliid larvae are presented in Tables 3.1-3.4. Tables 3.1-3.3 cover the streams sampled until the summer of 1972, and Table 3.4 the results of the collections carried out by removal catching at that time. The abundance categories in Tables 3.1-3.3 were devised from polythene tape samples and from general collection in the streams over similar time periods. This is necessarily an arbitrary system but treating the data seasonally gives a comparative measure of changes in population density of the various species. The seasons were divided as follows:

Spring:	March-May
Summer:	June-August
Autumn:	September-November
Winter:	December-February

Very few larvae were collected in Moss Burn and Rough Sike in the winter (Table 3.1). No collecting was undertaken in either Borderonmere Sike or Dubby Sike East Grain during winter 1971, but a search of Weelhead Sike, another Cow Green stream, at this time yielded no larvae, so the situation in the Cow Green streams may be similar to that of the Moor House ones. In both these areas large populations of larvae were present in the summer of 1971 (Tables 3.1-3.2).

Larvae were collected from the Cronkley streams throughout the year. Stream 3: section A shows the reverse situation to that found in the Moor House streams (Table 3.3) in that larval numbers were at their lowest in summer with large numbers at other times.

The removal trapping data provide more detailed records of abundance and distribution within two streams. In Moss Burn, more larvae were found in June, July and August than in September of 1972, whereas, in Cronkley stream 2, June was the month of lower numbers (Table 3.4). Larvae were more abundant in the lower sections of streams than in the upper parts, but further consideration of numbers will be given when considering the maximum likelihood population estimates in Chapter 4.

The following species were collected during this study from the fourteen sampling sites given in Tables 3.1-3.3.

<u>Prosimulium arvernense</u>. <u>P.arvernense</u> was collected at three of the sites but was always rare. Apart from the record in June 1972 from Cronkley stream 2, this species was confined to winter and spring and is known to pupate in April and May (Davies, 1968). Insufficient numbers were present to determine if this species had an egg-diapause in summer with hatching in autumn, as Davies and Smith (1958) found with the closely-related <u>P.hirtipes</u>.

Stream	Species	1971			
		Winter	Spring	Summer	Autumn
Rough Sike	*S.vernum*	+	+	+++	++
	S.brevicaule	+	0	++	+
	S.aureum	0	+	++	++
	S.nitidifrons	0	+	++	++
Moss Burn	*P.arvernense*	0	R	0	0
	S.vernum	+	+	+++	+
	S.brevicaule	+	0	+	0
	S.monticola	0	+	++	++
	S.nitidifrons	0	0	++	++
Force Burn Tributary A	*S.vernum*	—	—	+++	—
	S.brevicaule	—	—	++	—
	S.nitidifrons	—	—	+	—
Force Burn Tributary B	*S.vernum*	—	—	+	—
	S.brevicaule	—	—	+	—
	S.aureum	—	—	++	—

KEY:	—	No collection taken	
	0	Absent from collections	
	R	Rare	
	+	Occasional	Arbitrary units based on tape and general collections
	++	Common	
	+++	Abundant	

Table 3.1 Seasonal abundance of *Simulium* spp. in the Moor House streams

Stream	Species	1971		
		Spring	Summer	Autumn
Force Burn Foot	*S.variegatum*	++	—	—
Mattergill Sike	*S.vernum*	+	+	—
	S.brevicaule	+	+	—
	S.monticola	+	+	—
	S.variegatum	++	++	—
Rowan Tree Sike	*S.vernum*	+	+	—
	S.brevicaule	+	0	—
	S.monticola	++	++	—
	S.variegatum	+	0	—
Borderonmere Sike	*S.vernum*	+	+++	++
	S.brevicaule	+	++	+
	S.aureum	0	+	0
	S.monticola	0	0	R
	S.nitidifrons	0	++	++
Dubby Sike East Grain	*S.vernum*	+	+++	++
	S.brevicaule	++	+++	+
	S.nitidifrons	0	+	+

KEY:			
	—	No collection taken	
	0	Absent from collections	
	R	Rare	
	+	Occasional	Arbitrary units based on tape and general collections
	++	Common	
	+++	Abundant	

Table 3.2 Seasonal abundance of *Simulium* spp. in the Cow Green streams

Table 3.3 Seasonal abundance of *Simulium* spp. in the Cronkley streams

KEY:
— No collection taken
0 Absent from collections
R Rare
+ Occasional) Arbitrary units based on tape
++ Common) and general collections
+++ Abundant)

Stream	Species	1970	1971				1972		
		Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Dufton Sike	*S.vernum*	—	—	++	—	—	—	—	—
	S.ornatum	—	—	++	—	—	—	—	—
Cronkley Stream 1	*S.vernum*	+	+	++	+++	++	++	++	+++
	S.brevicaule	++	+	++	+	+	+	+	+
	S.angustitarse	+	0	+	+	R	+	0	+
	S.monticola	0	0	+	0	0	0	R	0
	S.nitidifrons	+	+	++	+++	+	0	+	++

(continued overleaf)

Cronkley Stream 2	P.arvernense	0	R	0	0	0	R	+	See Figure 3.4
	S.vernum	+	+	++	++	++	++	++	
	S.brevicaule	++	++	+	++	++	++	+	
	S.angustitarse	R	R	0	0	0	+	0	
	S.aureum	R	R	0	0	0	0	0	
	S.monticola	+	+++	++	+	++	++	++	
	S.nitidifrons	++	++	++	++	+++	++	++	
Cronkley Stream 3 Section A	P.arvernense	0	R	0	0	0	0	0	—
	S.vernum	+++	+++	+++	+	++	+++	+++	—
	S.brevicaule	+	++	+	0	++	+	+	—
	S.angustitarse	+	+	+	+	++	++	++	—
	S.aureum	++	+	0	0	0	0	0	—
	S.monticola	0	R	0	0	0	0	0	—
	S.nitidifrons	+	+	0	0	0	0	0	—
Cronkley Stream 3 Section B	S.vernum	+	+	++	++	++	++	—	—
	S.brevicaule	+++	++	++	+	+	++	—	—
	S.angustitarse	+	0	+	+	++	0	—	—
	S.aureum	++	0	0	++	++	0	—	—
	S.nitidifrons	+	0	0	0	++	0	—	—

Table 3.4 Monthly abundance of <u>Simulium</u> spp. from removal collections in 1972

KEY:	
0	Absent in collections
R	< 10 larvae per mean monthly collection
+	10-50 " " " " "
++	51-150 " " " " "
+++	> 151 " " " " "

Species	Month	Moss Burn				Cronkley Stream 2	
		Section A	Section B	Section C	Section D	Section A	Section B
<u>P.arvernense</u>	vi	0	0	0	0	0	R
<u>S.vernum</u>	vi	+	+++	++	+++	+	++
	vii	+	+++	++	+++	+++	+++
	viii	++	++	++	+++	+++	+++
	ix	—	+	++	++	+++	++
<u>S.brevicaule</u>	vi	+	+	+	++	+	++
	vii	+	+	+	+	++	++
	viii	+	+	+	+	++	++
	ix	—	0	R	R	++	++
<u>S.angustitarse</u>	vii	0	R	0	0	0	0
	viii	0	0	0	0	0	R

(continued overleaf)

S.aureum	vi	++	++	0	R	0	0
	vii	++	+	0	0	R	0
	viii	++	++	0	0	0	0
	ix	—	R	0	0	0	0
S.tuberosum	vi	0	0	0	0	0	R
	vii	0	0	0	0	0	R
S.monticola	vi	0	R	++	+++	0	+
	vii	0	0	++	++	+	++
	viii	R	+	++	++	+++	+++
	ix	—	0	+	++	+++	++
S.nitidifrons	vi	+	++	+	+++	R	+
	vii	+	+	+	+	++	+
	viii	+	++	+	++	++	+++
	ix	—	R	R	+	++	+++

Simulium vernum. The commonest and most adaptable species in the Upper Teesdale bog streams having been collected from thirteen sites, including such varied habitats as the grassy Force Burn: tributary B and Mattergill Sike with its bed of boulders and large stones.

S.vernum was abundant in summer 1971 in Rough Sike; Moss Burn; Borderonmere Sike; Dubby Sike East Grain; and Cronkley stream 1 and was the major component of the overwintering larval population in Cronkley stream 3: section A. It was also abundant in both streams studied in summer 1972.

S.brevicaule Collected from twelve sites and abundant in Cronkley stream:3: section B in autumn 1970 and Dubby Sike East Grain in summer 1971. Although present in all but one removal trapping site, the species was never abundant in summer 1972 though common in Cronkley stream 2. In fact, it was mostly only an occasional (i.e.) 10-50 larvae per mean monthly collection, in Moss Burn at this time (Table 3.4).

S.angustitarse Apart from an isolated specimen in Moss Burn: section B, this species was confined to the Cronkley streams. Only occasionally found in Cronkley stream 3 in autumn 1970 and most of 1971, it was common in section A in autumn 1971 and winter and spring 1972. Numerically, S.angustitarse was more important than S.aureum in the second winter here with the reverse situation in the first (Table 3.3). S.angustitarse is found in small streams with trailing vegetation (Davies, 1968) and it is probably the lesser quantities of this substrate that made the species only an occasional in the other Cronkley streams. Its absence elsewhere also suggests an altitudinal limitation.

S.aureum Found in six of the sampling sites, and, with the exception of Rough Sike, commonly found only in the headwaters where streams were small and the vegetation content high. This species typically inhabits such small, slower-flowing weedy streams in hill areas (Grenier, 1953; Davies, 1968) and with S.vernum, is the most numerous simuliid in this habitat in the bog streams.

S.tuberosum Rare in the bog streams and found only during summer 1972 in Cronkley stream 2: section B. This species is typical of rivers above the limit of cultivation (Davies, 1966).

S.monticola Present in seven sites and abundant in winter 1971 in Cronkley stream 2. Such large overwintering populations often occur in S.monticola (Davies, 1966). This species was also abundant in both sections of Cronkley stream 2 and the lowest section of Moss Burn in summer 1972.

S.variegatum Only found at the foot of streams draining into the western side of Cow Green Reservoir; Force Burn; Mattergill Sike; and Rowantree Sike. Here, the bed of the streams consists of large stones and boulders and the more stable substrate provides conditions which S.variegatum prefers (Davies, 1966).

S.ornatum Possibly common in Dufton Sike but only one sample was taken in spring 1971. Although draining a bog, this stream passes through pasture-land before joining the Tees and the richer organic material content of such a stream probably accounts for the presence of S.ornatum here.

S.nitidifrons After S.vernum and S.brevicaule the most widely distributed species in the Upper Teesdale bog streams, occurring at nine of the sampling sites. In summer 1972 S.nitidifrons was abundant in both Moss Burn: section D and Cronkley stream 2: section B (Table 3.4).

Occurrence of this species has been connected with the presence of trailing vegetation (Grenier, 1953) but it is only present in large numbers downstream from the shallow sections.

Seven *Simulium* species were found in each of Cronkley stream 2 and stream 3: section A, whilst several streams supported five species.

Table 3.4 showed there to be a similar simuliid fauna in both sections of Cronkley stream 2. In Moss Burn, however, with the change of habitat between the upper and lower sections, a succession of species occurred downstream. The results from removal catching data in August for Moss Burn: sections A, B, and D have been grouped in Table 3.5.

Species	Section A	Section B	Section D
S.vernum	++	++	+++
S.brevicaule	+	+	+
S.aureum	++	++	0
S.monticola	R	+	++
S.nitidifrons	+	++	++

Table 3.5 Abundance of *Simulium* spp. in three sections of Moss Burn in August 1972

KEY: As for Table 3.4

Being adaptable species *S.vernum* and *S.brevicaule* occurred in similar numbers in all three sections. *S.aureum* - as in the temporary Force Burn: tributary B - was common in the upper reaches where the stream was little more than a "trickle". *S.monticola*, on the other hand, showed increasing numbers toward the stonier downstream sections and was virtually absent from section A. The bed of small stones overlying peat, typical of section B, was probably important in reducing

S.monticola to the status of an occasional here. S.nitidifrons showed a similar preference for the downstream sections but was common in section B where vegetation-only removal collections were taken, probably the most important factor in this case.

4(i) PROBLEMS IN QUANTITATIVE SAMPLING OF LARVAE

Any quantitative sampling programme must take into account the distribution of simuliid larvae in the streams. Most species prefer a streamline flow (Grenier, 1949; Hocking and Pickering, 1954) which aids their passive feeding method in that such currents support larger quantities of suspended material and larvae can orientate easily in the uni-directional flow.

Observation of the micro-distribution of larvae shows them to be aggregated into areas related to the complex pattern of water velocities in shallow streams. Phillipson (1957) has shown that S.monticola and S.variegatum have different current preferences and, if this applied to other species, there is a difficulty in gaining accurate population estimates unless a large number of replicates are taken. The use of replicates will overcome current differences and the effect of micro-distribution but the resulting large number of samples would be most time-consuming to process if any of the conventional area-based samplers were used. One feature of sampling larval simuliids (which has been exploited in all the methods used in the present study) is their ability to remain attached to substrates after removal from the stream (cf. Carlsson, 1962).

4(ii) POPULATION INDEX METHODS

(a) The tape method Polythene tapes were used by Williams and Obeng (1962) as a means of collecting Simuliid larvae from small streams running into the River Dee. They observed that larvae occurred mainly on trailing vegetation and the tapes are an attempt to reproduce this habitat. Tapes have the advantage of requiring a small depth of water, in contrast to the cones used by Wolfe and Peterson (1958) and Abdelnur (1968) to collect larvae, and are thus particularly suitable for sampling in small streams.

In the present study each tape (measuring 45 cm x 4 cm) was cut from heavy-duty polythene sheeting and had one end threaded through a wire loop and held by staples. Wooden pegs were hammered into the stream bed at the sampling sites and the wire loops placed over these pegs to locate each tape in the stream. The abrasive effect of spates did cause some tapes to tear but this was not a serious problem in the bog streams.

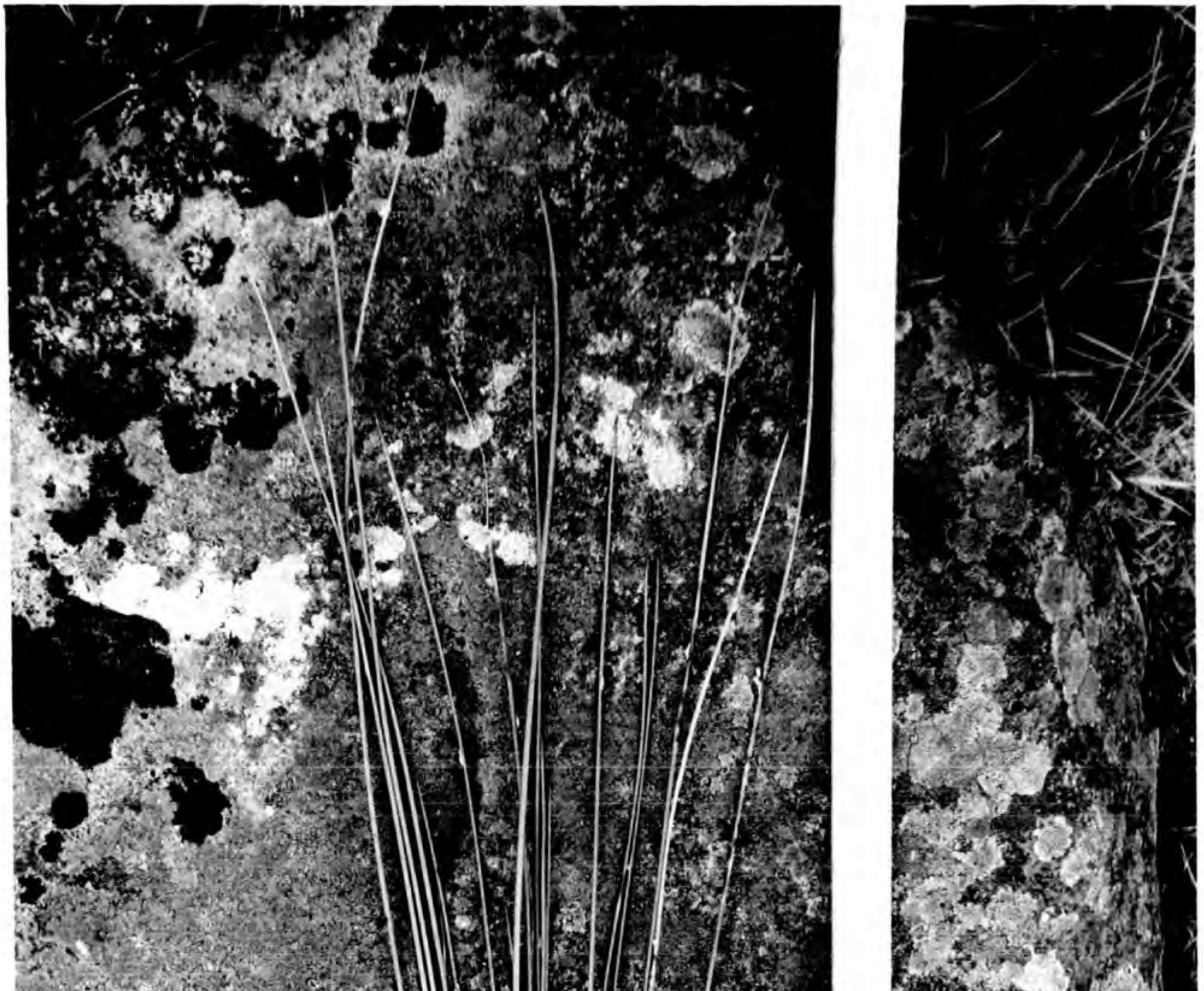
In summer 1971 five tapes were placed in Dubby Sike East Grain and three in each of Rough Sike, Moss Burn, and Force Burn: Tributary A. Five tapes were inserted in Cronkley stream 2 from xi.70 to v.72. On each sampling occasion three tapes were replaced in each stream and those taken out brought to the laboratory. The number of larvae per tape was used as the relative population index in this case.

(b) *The Juncus-sampler method* Just as Williams and Obeng (1962) had used polythene tapes to replicate trailing vegetation, the *Juncus*-samplers, devised in the present study, also did so only using material naturally occurring in the streams. Each sampler consisted of several cut stems of the rush (ca. 20) clamped by "Meccano" angle brackets (see Plate 9). As in the tape method, each sampler had a wire loop attached by which it was anchored to a peg in the stream bed.

Being cylindrical the contact area between stems was small and they presented a large surface to the current. On removal of the samplers from the stream, the *Juncus* stems were cut adjacent to the clamp and brought to the laboratory where larvae were removed. Each stem was cut into sections (ca. 10 cm. long) and the length and diameter of the sections recorded and applied to the formula $2\pi rh$. (This method was used by Harrod and Hall, 1962, to determine the surface area of stems and leaves of *Ranunculus fluitans*.) The total surface area of each sampler was thence determined from which the number of larvae

PLATE 9

A Juncus-sampler, scale provided by the width of the metre rule, i.e. 25 cm.



1000 cm^{-2} could be calculated, this area being approximately the surface area of stem exposed in each case. This was the unit used in expressing results. Three samplers were inserted in Cronkley stream 2 and three in Moss Burn, all being changed on each sampling occasion, to provide a record of population changes occurring at one point in these streams in summer 1972.

Observation while collecting in the bog streams suggests that the numbers of larvae on the samplers were high when the numbers on the surrounding substrates were high. Tapes and Juncus-samplers increase the amount of available substrate for settlement and, where there is a high population density, larvae will move on to them in large numbers. This is especially true after spates. Zahar (1951) and Phillipson (1956) have observed that larvae change their position in the stream bed during spates and, when they regain the trailing vegetation, the samplers will be colonised, especially as they provide an optimal habitat. The flow over both is streamlined which is a factor favouring blackfly larval colonisation.

Disney (1972) has shown that the number of simuliid larvae caught on artificial substrates in an African river is greater after three days than after two, and similarly, after one day. No colonisation experiments were conducted but the shortest time samplers were left in the streams in the present study was three days.

(c) Sampling from Potamogeton leaves in Cronkley stream 3 In Cronkley stream 3: section A larvae were found exclusively on Potamogeton leaves. These were well-overlapped making the expression of numbers per unit area impossible since no measure could be taken of the actual area of leaf exposed to the current. Sampling was carried out from leaves adjacent to the central "channel" and this lessened the overlapping effect as leaves were not as closely applied here.

Each leaf, having larvae and pupae on both abaxial and adaxial surfaces, was cut at the base of the petiole. Initially, twenty leaves were taken in each collection but after March, when the numbers obtained began to decrease, it was necessary to remove more than this in order to obtain sufficient larvae for the construction of frequency distributions. Numbers were expressed per ten Potamogeton leaves.

4(iii) ABSOLUTE POPULATION ESTIMATES

Absolute population estimates are required in mortality and production studies. Ladle et. al. (1972) took samples from 0.05 $m.^2$ Ranunculus using a box sampler having mapped the distribution of this plant in their 200 m. study length and monitored the change in distribution of the plant through the year. Such a method was not feasible in the much smaller bog streams: the amount of trailing vegetation is less; and large numbers of samples would be required to obtain sufficient larvae for the construction of frequency distributions.

Sampling by "catch per unit effort" has the advantage that the length of stream sampled compensates for variations in the distribution of available substrate - where this is present in large amounts the sample length will be short and, conversely, small amounts will give long sample lengths. Southwood (1966) concludes that, within a habitat, estimates based on a visual observation method using a known effort can approach the measurement of absolute population values. By repeating the standard sampling effort on three, or more, successive occasions within the sample length collections can be obtained whose numbers form a regression from which an absolute population estimate can be obtained.

Whereas Turner (1962) found difficulty in sampling a large enough proportion of a population of desert arthropods to obtain reasonable results, a small bog stream provides a very much better habitat for such a method. Here, the region in which the animals are living is delimited by the stream banks and by the length covered during sampling, so a relatively large proportion of the population is taken in the collections. The method was used in Cronkley stream 2: sections A and B, and Moss Burn: sections B, C, and D in summer 1972, and the stages used in taking removal samples were as follows:

(i) A marker peg was inserted into the bank to mark the starting point of collection.

(ii) Pieces of trailing vegetation - from plants rooted in the bed and on the banks - were collected into a jar. These were taken in as near to a random method as possible, each piece being about 10 cms long.

(iii) After 15 minutes the first collection was labelled and a peg placed in the bank to delimit the sample stretch.

(iv) The method described in (ii) above was repeated and, if necessary, sampling continued from the upper peg again if the downstream peg was reached within the 15-minute collecting period.

(v) A third collection was undertaken from the position where the second stretch ended and the same sampling effort employed for a further 15 minutes.

In Cronkley stream 2 and Moss Burn: section B, larvae were confined largely to trailing vegetation. In Moss Burn: sections C and D, where they were also numerous on the stones, the method outlined had to be modified. In this case, five minutes vegetation collection was undertaken to delimit the sample length and ten minutes collection from stones was carried out within this in each sample. With stone sampling, stones which had been used in the first collection were examined again if they were picked up in the second collection to ensure that the approach was as random as possible.

Using Zippin's (1956) method, the population estimates were calculated as follows from the numbers in the consecutive samples. Estimates were obtained for all larvae before they had been identified to species:-

(i) Firstly, T, the total catch, was obtained by adding the larval totals in each collection.

(ii) The value of $\sum_{i=1}^{k} (i-1)y$ was found

where k = the number of consecutive samples used (3), and

y = the catch on the ith occasion.

(iii) From (i) and (ii) the ratio R was obtained:

$$R = \frac{\sum_{i=1}^{k} (i-1)y}{T}$$

(iv) Now, $R = \frac{q}{p} = \frac{k\,q^k}{(1-q^k)}$ where

p = the probability of capture on a single occasion

$q = 1-p$

(v) The total population estimate, P, was now obtained

$$P = \frac{T}{(1-q^k)}$$

Zippin (loc. cit.) gives graphs of $(1-q^k)$ for various values of R and k and so the value could be read off directly and the equation solved for P.

(vi) The standard error of P was given by:

$$\text{S.E. of P} = \sqrt{\frac{P(P-T)T}{T^2 - P(P-T)\ \left[(kp)^2/_{1-p}\right]}}$$

Graphs of p for values of R and k are also given and so the equation could be solved for the standard error of P.

(vii) Two standard errors of the population estimate on either side gave the estimate with 95% confidence limits. The data from the removal collections are presented in Appendix 2 together with the population estimates. D is the index of precision (Elliott, 1971a) given as a percentage. Some factors governing the index of precision values given in Appendix 2 will be considered in Chapter 4(iv).

4(iv) ASSESSMENT OF REMOVAL CATCHING AS A MEANS OF ESTIMATING THE NUMBERS OF LARVAL SIMULIIDAE IN A BOG STREAM

Moran (1951) has outlined the theory of maximum likelihood estimation based on removal trapping. His work was based on small mammals and the method has four principal conditions which must be met. These points have been discussed by Southwood (1966) with reference to insect populations.

The points are as follows:

(i) The population must not be so large that the catching of one individual interferes with the catching of another;

(ii) The population must remain stable during the catching period;

(iii) The chance of being caught must be the same for all animals.

(iv) The trapping procedure must not lower (or increase) the likelihood of an animal being caught.

Considering these point by point:

(i) During the 45-minute collection period of the present study, natality, mortality and migration will be minimal. Observation whilst collecting suggested that very few larvae became detached and those that did retained their silk "anchor" line. In addition, disturbance of the substrate was reduced by standing on the banks of the stream where possible.

(ii) This point is mostly applicable to small mammal trapping and presented no difficulty in sampling the bog streams.

(iii) The chance of being caught was equal for all animals because the substrate on which all larval instars and pupae were known to occur was removed.

(iv) The collecting method may well have affected the likelihood of larvae being removed in successive samples. To satisfy condition (iii) it was important to remove vegetation: this consequently reduced the available habitat. Because the sampling effort in each fifteen minutes was the same, longer relative stream lengths were sampled in the second and third collections to obtain equivalent sized vegetation collections. However, it seems likely that a larger proportion of optimal habitat was removed in the first collection than in the others when sampling rooted vegetation, e.g. <u>Agrostis</u>. Such sites were on the peripheral, and downstream leaves of the plant and a large number of these would be removed in the first sample. The practice was not to select these sites but to distribute them equally between the three collections but this was difficult to carry out. An alternative, within condition (iv), would be to remove larvae and leave the vegetation <u>in situ</u> to be sampled perhaps in the second and third collection. This type of method was employed in collecting from stones. Apart from the effect on condition (iii), a larger time-interval than 15 minutes would be required and it was decided to adopt the method outlined in 4(iii). Vegetation trailing from the banks did not present such a problem since ca. 10 cm. lengths could be removed without knowing where there were optimal sites.

If more optimal sites were collected in the first sample the resulting maximum likelihood calculation would underestimate the population. Such an error would increase the index of precision from the low levels given in Appendix 2.

Assessment trials were conducted to see how the method worked in practice. On one day population estimates of adjacent stretches of Cronkley stream 2 were made. The first stretch gave an estimate of 436 ± 28 and that downstream of it 497 ± 97 with 95% confidence limits, showing the estimates to be similar. The available vegetation was more plentiful in the upstream site and this is reflected in the length of stream sampled, 18.0 metres in contrast to the 23.0 metre sample length of the downstream site.

The mean sampling length of each collection in each stream for summer 1972 is given in Table 4.1. The mean sample length and its variance were larger when vegetation samples were taken (the first three sections below) than where stones and vegetation were collected together.

Stream and Section	Mean Sample Length	Variance
Cronkley 2: Section A	19.4 m.	79.1
Cronkley 2: Section B	21.9 m.	199.9
Moss Burn: Section B	18.9 m.	86.2
Moss Burn: Section C	14.0 m.	26.9
Moss Burn: Section D	10.9 m.	17.2

The large variances in the first three streams above give an indication of the patchy distribution of vegetation along the length of the stream. If a fixed area of stream was taken on each sampling occasion the inaccuracy due to the differing distribution of substrate would be considerable.

TABLE 4.1 Length of stream sampled on the given dates in 1972.

All distances given in metres. ? = no length taken.

Date	Moss Burn			Cronkley Stream 2	
	Section B	Section C	Section D	Section A	Section B
16 vi	-	-	-	-	13.8
19 vi	-	-	-	-	10.7
26 vi	-	-	-	-	23.0
28 vi	7.0	17.3	-	-	-
29 vi	-	-	-	9.5	36.5
30 vi	-	-	11.6	-	-
3 vii	-	-	-	7.1	36.0
5 vii	?	-	5.7	-	-
6 vii	-	6.0	-	-	-
7 vii	-	-	-	12.8	5.0
11 vii	8.7	13.4	8.7	-	-
12 vii	-	-	-	-	8.4
17 vii	-	-	-	-	22.4
19 vii	-	11.2	7.7	-	-
21 vii	-	-	-	14.0	25.0
25 vii	28.7	-	-	-	-
26 vii	-	10.9	16.0	-	-
27 vii	-	-	-	14.7	38.9
2 viii	-	7.6	6.2	-	-
3 viii	-	-	-	18.2	11.1
7 viii	9.8	-	-	-	-
10 viii	-	-	11.8	15.2	9.2
14 viii	27.5	-	-	-	-
15 viii	-	19.5	8.2	-	-
16 viii	-	-	-	16.3	11.3
20 viii	21.9	-	-	-	-
21 viii	-	20.5	14.8	-	-
23 viii	-	-	-	32.5	23.4
29 viii	28.7	20.0	18.5	-	-
30 viii	-	-	-	-	21.0
3 ix	-	-	-	31.6	16.0
7 ix	-	-	-	30.8	18.7
17 ix	-	-	-	30.6	64.2
Sum of Lengths	132.3	126.4	109.2	233.3	394.6
Mean Length Sampled	18.9	14.0	10.9	19.4	21.9
Variance of Mean	86.2	26.9	17.2	79.1	199.9

The choice of three, rather than four, samples was taken after using four samples in a preliminary study on stones in Cronkley stream 1 and vegetation in Cronkley stream 2: sections A and B. The following population estimates were obtained:-

	With Three Samples	With Four Samples
Cronkley Stream 1	646 ± 113	719 ± 47
Cronkley 2: Section A	151 ± 5	154 ± 2
Cronkley 2: Section B	572 ± 17	579 ± 6

In each case, the standard error was reduced when using four rather than three samples. The population estimates in both sections of Cronkley stream 2 were little different when using three or four samples. The fourth sample was numerically 4% of the first in both sections and it was because most larvae had been removed in the first three collections that the final population estimates were similar.

Further trials on the use of more samples were undertaken subsequently in Cronkley stream 2. Five removal collections were taken in both sections A and B and the following numbers were obtained in summer 1973:

	With First 3 Samples	With all 5 Samples
Cronkley 2: Section A	380 ± 14	413 ± 7
Cronkley 2: Section B	5173 ± 399	4920 ± 148

As with the previous trials the more samples used the more accurate the population estimate. This greater accuracy was lost in using a 3 x 15-minute collecting programme. In an intensive field-season however the time saved in field-, and laboratory, work was considered worthwhile at the expense of the decrease in accuracy. Further sources of error are shown in Appendix 2. The large value of D obtained from Cronkley stream 2: section B on 29.vi results from the second sample being larger than the first. On 29.viii in Moss Burn: section D the third sample was larger than the second and this resulted in the value of 14% for the index of precision here.

4(v) RESULTS OF QUANTITATIVE SAMPLING

A graph of the numbers of larvae collected per tape from Cronkley stream 2 is presented in Fig. 4.1. Peaks occurred in the winter of both 1970/71 and 1971/72, the former being the larger, but the largest numbers were found during the summer. A noticeable decline in the populations occurred in May of both years and, as will be seen in Chapter 5, this coincided with pupation and emergence of the over-wintering generations of the species present.

The data presented in Fig. 4.2 are rather inadequate in the case of Moss Burn and Force Burn: tributary A but, in both, it can be seen that the population density, on occasion, exceeded 40 larvae per tape. In Rough Sike, where the winter generation was very poorly represented, the maximum numbers of larvae were collected in July with a smaller peak in August which is similar to the pattern from the Juncus-samples in Moss Burn during summer 1972 (Fig. 4.3). The results from the Cow Green stream, Dubby Sike East Grain, were more like the Juncus-sampler results from Cronkley stream 2 with increasing numbers to a peak in August. It was mentioned in Chapter 3 that very few larvae were found in winter in a neighbouring Cow Green stream but no information was available from Dubby Sike in winter. It does seem, however, that an early summer peak in numbers occurs after a poorly represented winter generation.

S.vernum was the dominant species in Cronkley stream 3: section A and the graph of numbers per 10 Potamogeton leaves (Fig. 4.4) shows the winter peak tailing off toward May just as the populations in Cronkley stream 2 did.

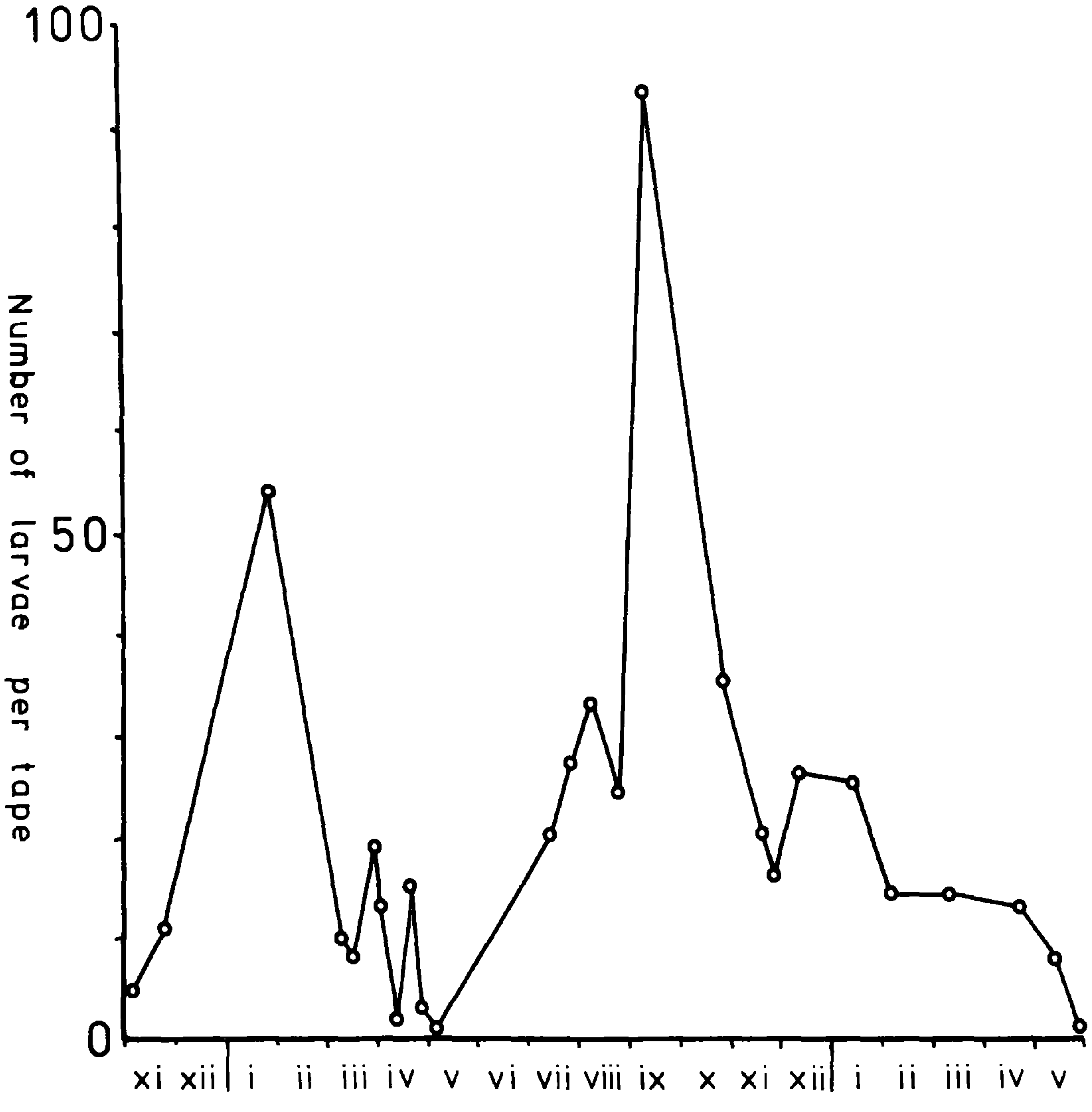


Fig. 4.1. Numbers of larvae per tape collected in Cronkley Stream 2. (All spp.)

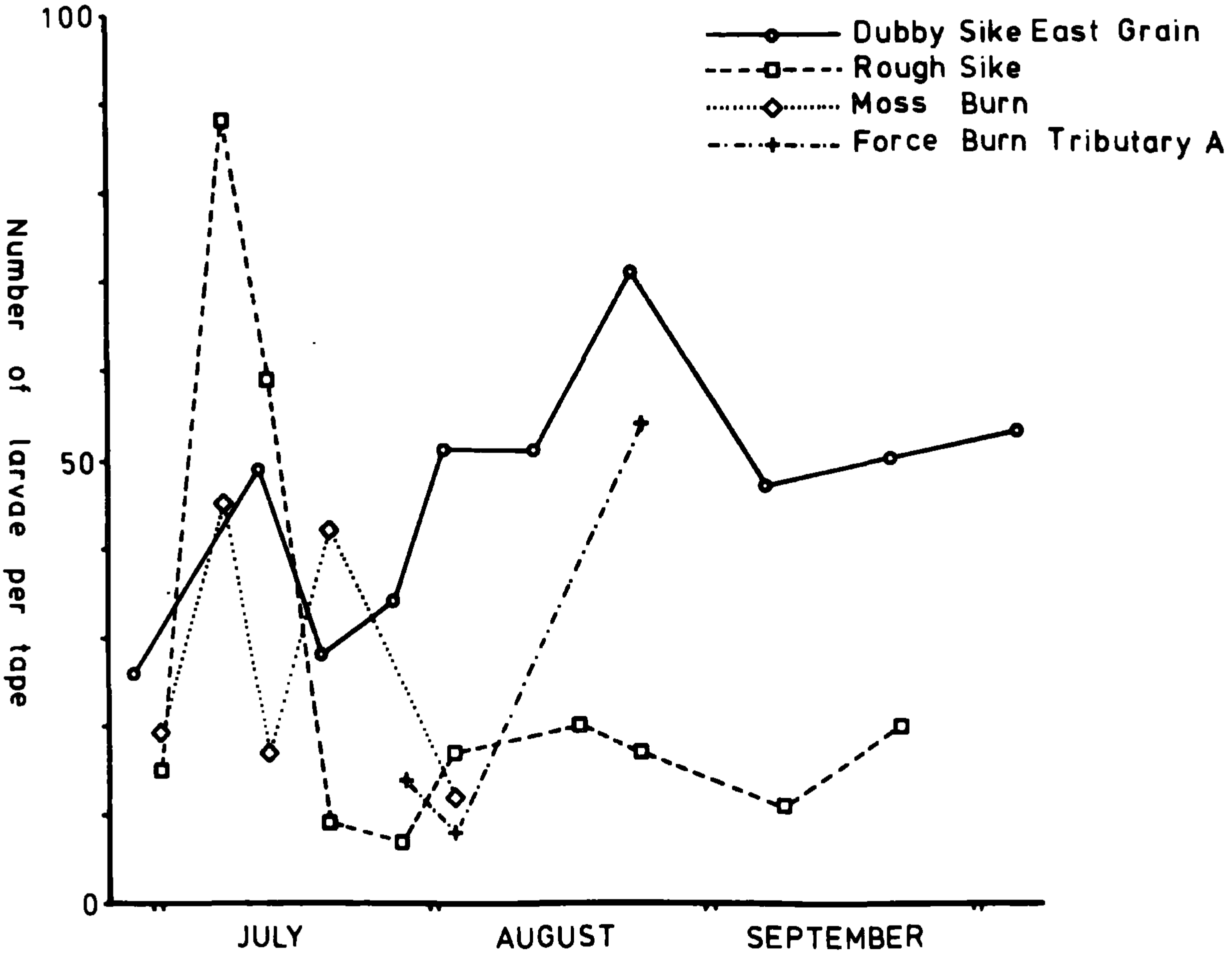


Fig 4.2. Number of larvae per tape collected from four streams (all spp.)

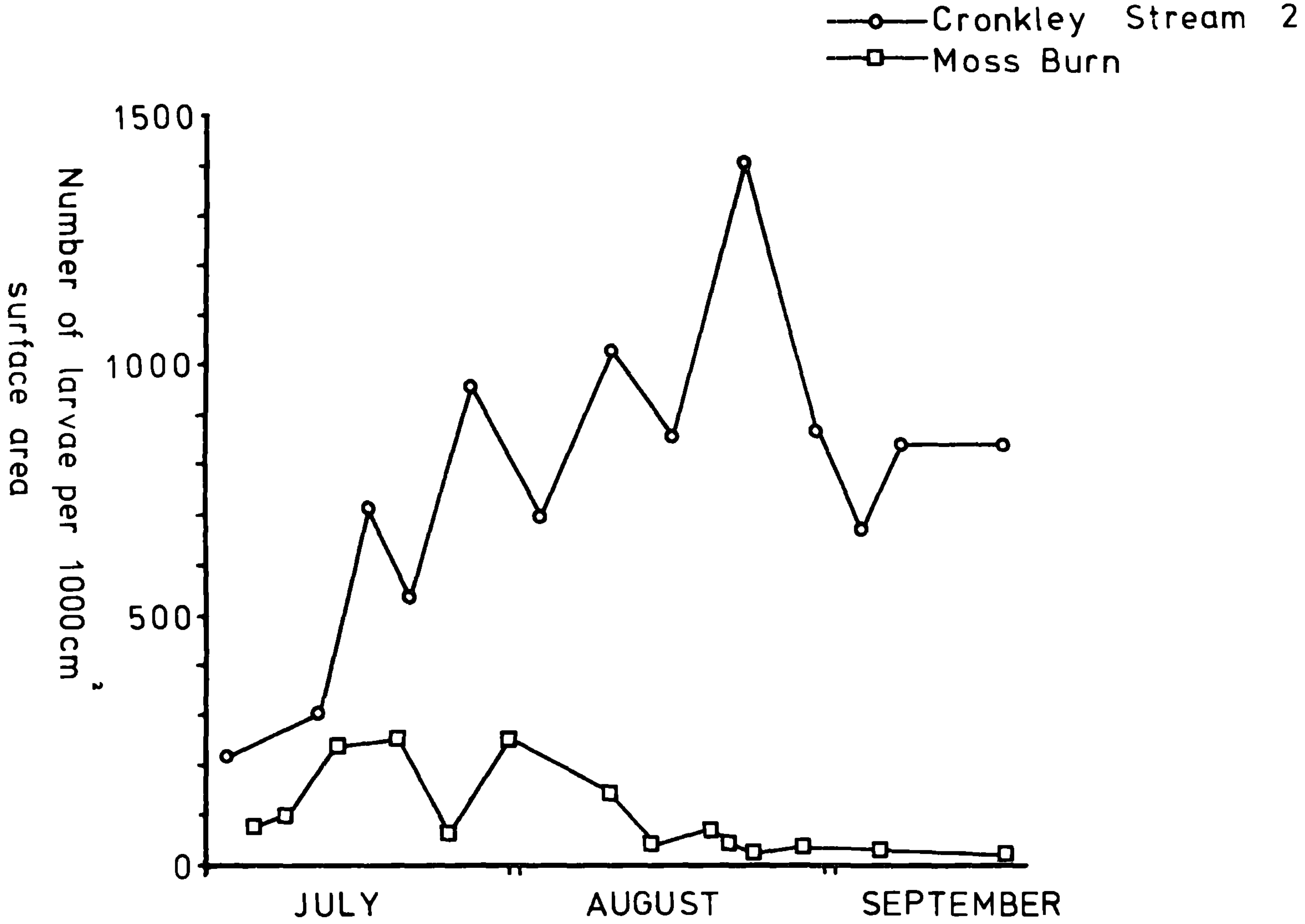


Fig. 4.3. Number of larvae per 1000 cm² surface area of *Juncus* in Cronkley Stream 2 and Moss Burn.

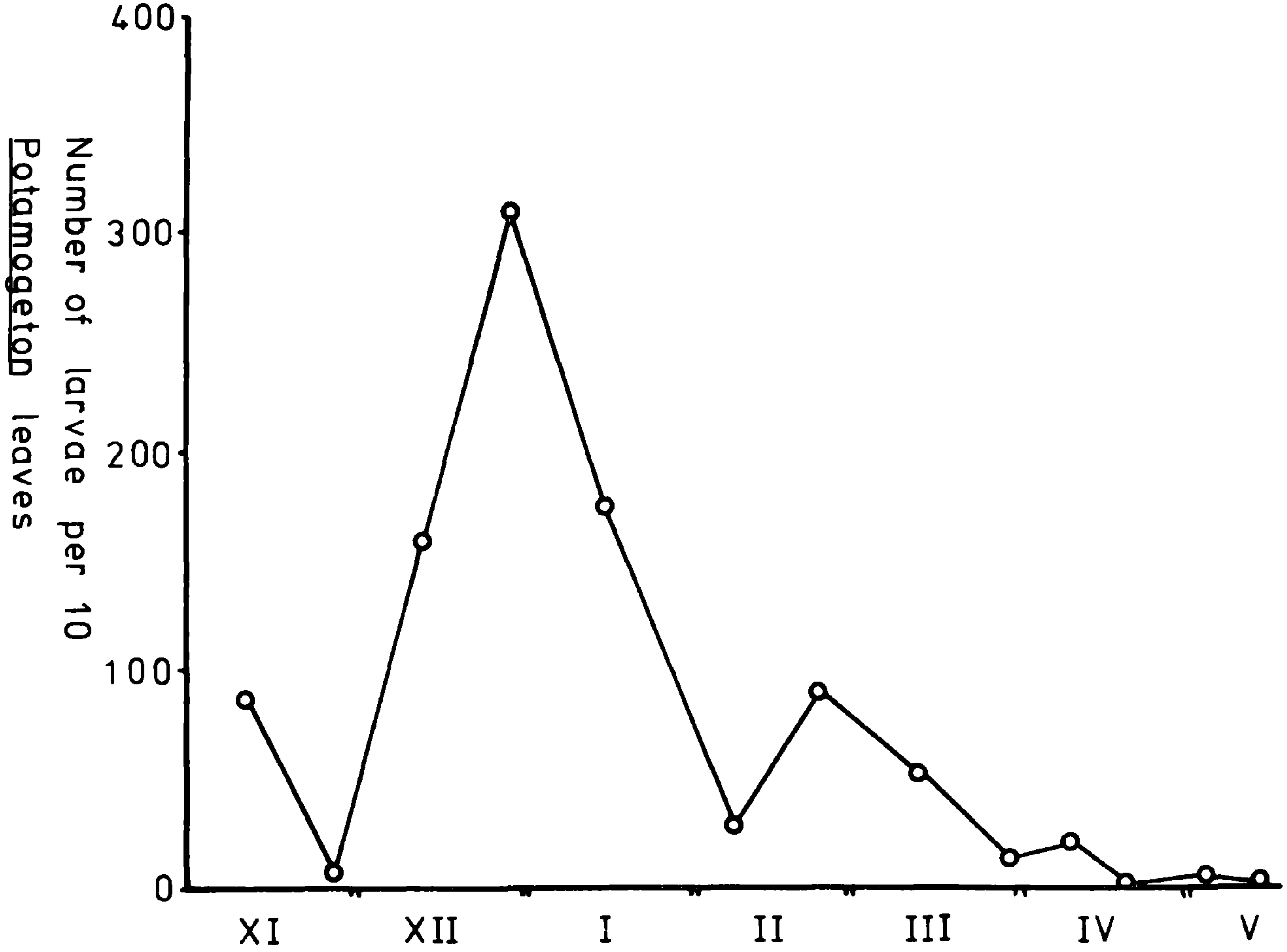


Fig. 4.4. Number of S.vernum larvae per 10 Potamogeton leaves collected in Cronkley Stream 3 : Section A. XI - V = November - May 1971/72

Ladle et. al. (1972) found the same pattern of falling numbers in spring in the case of *S.ornatum* and *S.equinum* in Bere Stream, Dorset, though here it was earlier in March and April. The same authors showed that larvae were more numerous in summer than winter in this stream, although Harrod (1964b) discovered the reverse of this situation in another southern chalk stream. Neveu (1972, 1973a) has concluded that this pattern is connected with altitude: in upland streams the populations are largest in summer and the reverse is true in lowland streams. As altitude will have an effect on climate this may well be the general case but other factors, such as the volume of the water body, will also have their effect. For example, Armitage (in personal communication) has reported larger winter populations of simuliids in the Tees near Cow Green, which is a large body of water at altitude. The fact that small streams can have much reduced flows in summer also plays a part in affecting numbers as was the case of Cronkley stream 3: section A and the stream studied by Ladle and Esmat (1973). The disparity between Ladle et. al. (1972) and Harrod (1964b) also shows that altitude is not the only factor affecting the pattern of seasonal abundance, both streams being low-lying.

Graphs of the maximum likelihood population estimates are presented in Figs. 4.5 and 4.6.

Numbers of larvae dropped in Moss Burn: section B from 918 ± 204 on 28.vi. to 212 ± 10 on 7.viii, after which they rose to 1049 ± 28 (see Fig. 4.5). Little variation in numbers on successive sampling dates was found in section C, the highest value recorded being 505 ± 72 on 2.viii which had decreased to 214 ± 19 by 15.viii. After a peak of 1129 ± 130 on 30.vi. the population density remained similar until the peak of 1680 ± 218 on 2.viii in Section D (Fig. 4.5) at the time of the similar peak in section C. Numbers thence decreased

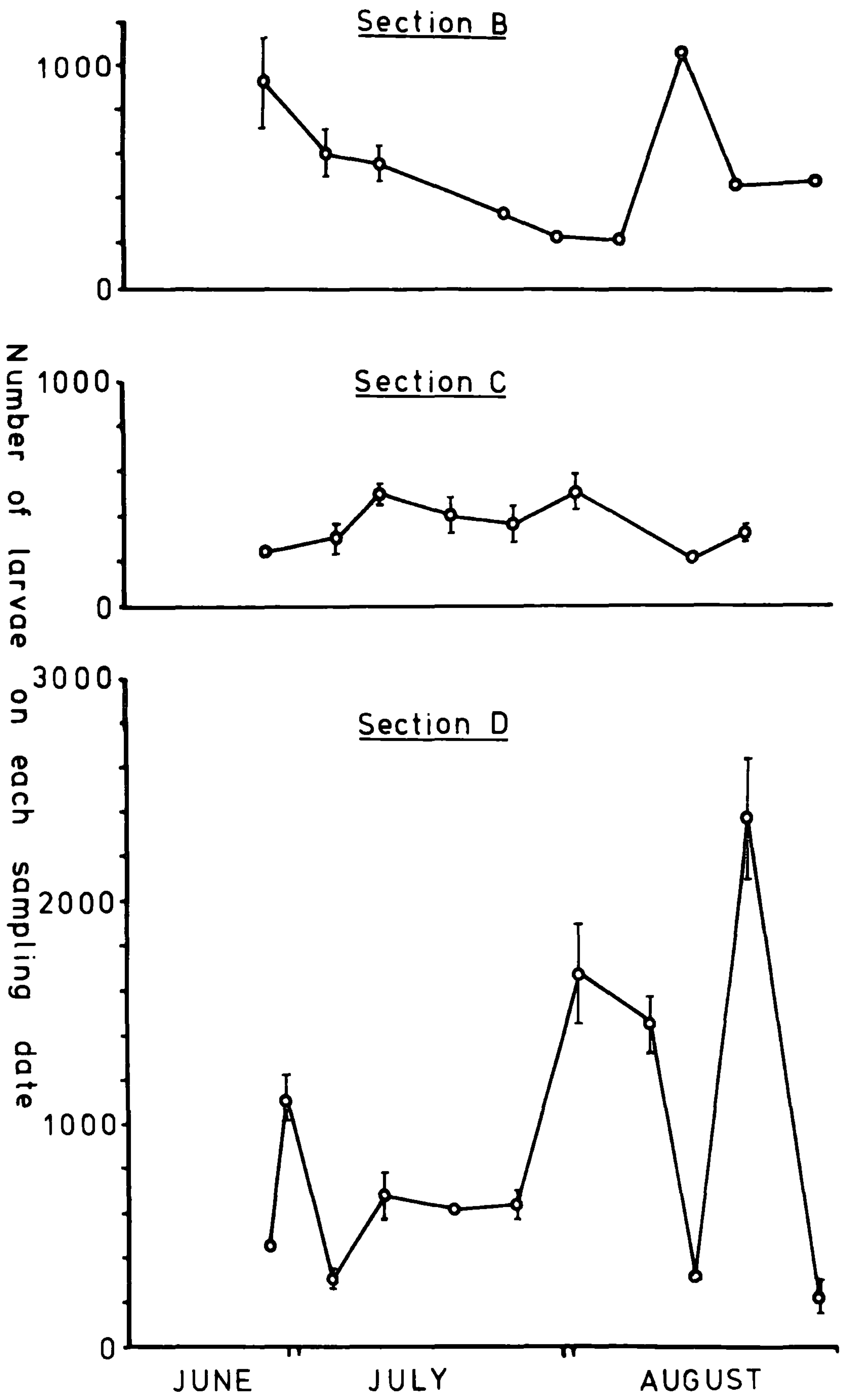


Fig. 4.5. Population estimates (with 95% confidence limits) for larvae in three sections of Moss Burn.

igs. 4.5 & 4.6. Confidence limits not given for some results where values were too small to be included.)

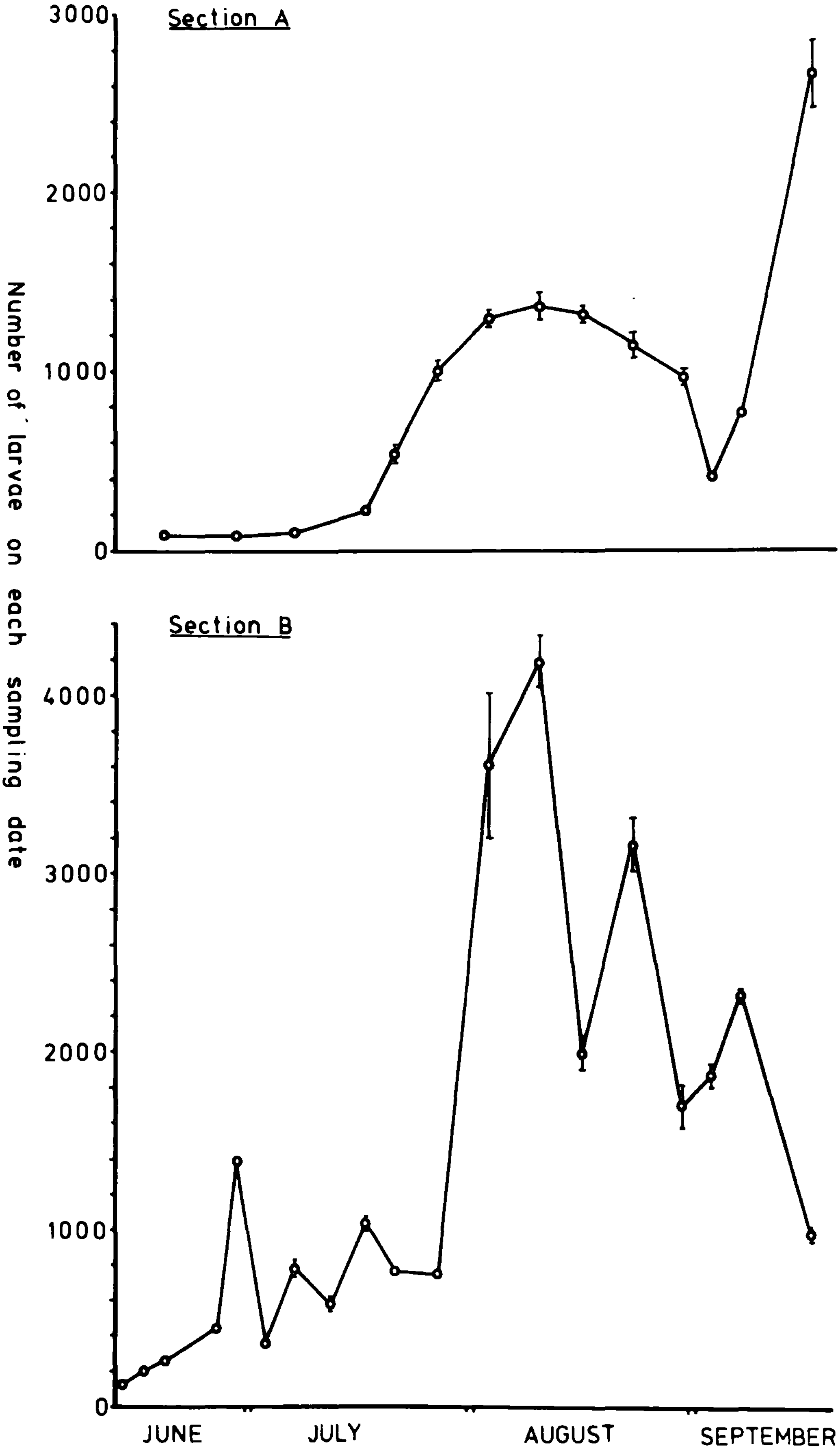


Fig. 4.6. Population estimates (with 95% confidence limits) for larvae in Cronkley Stream 2 Sections A and B.

with the exception of the estimate of 2377 ± 271 on 21.viii. which did not correspond with a large number of larvae on the Juncus-samplers and remains a suspect result.

Comparison of sections B, C, and D in Fig. 4.5 shows that changes in population numbers differ markedly between the uppermost and lowest stretches. There was a decrease in population density in the former at a time when numbers were increasing lower down and the 14.viii maximum in section B corresponded with a fall-off in numbers in section D.

On average more larvae were collected from section D than section B which, in turn, supported larger populations than section C. Quite why there was such a large disparity between the adjacent downstream sites is not known. More vegetation was available in section D (see Table 4.1) which may account for the difference but reference to Plates 7 and 8 show that the substrate and flow conditions were generally similar between the two.

Both sections of Cronkley stream 2 (Fig. 4.6) showed increases in numbers through July with consistently large estimates in section A throughout August. There was a marked peak at this time in section B with a population of 4199 ± 145 on 10.viii. after which numbers decreased, although there were peaks of 3174 ± 151 and 2332 ± 40 on 23.viii. and 7.ix. respectively. Section A, in contrast, had a sharp increase in numbers in early September with the highest estimate obtained in this section of 2682 ± 188 on 17.ix. A similar increase at this time was shown from the tape records (Fig. 4.1) in September 1971.

As in Moss Burn, more larvae were collected from the lower, than the upper, section. Further discussion of the seasonal patterns and the species composition of the quantitative data will be given in Chapter 8(i). To gain information on the detailed population biology of the species present larvae were measured and frequency distributions constructed (Chapter 5).

4(vi) COMPARISON OF REMOVAL TRAPPING ESTIMATES AND JUNCUS-SAMPLER RESULTS

Juncus-samplers provide an estimate of relative population changes occurring at one point in the stream. Even allowing for small differences in the length of time these samplers were exposed in the stream the large changes in population which take place during the summer will be mirrored by the numbers of larvae obtained on the samplers. The *Juncus*-samplers were replaced on the same days as removal collections were made in Cronkley stream 2: section B. Plotting the estimated total population from the removal collections and the numbers of larvae 1000 cm^{-2} from the *Juncus*-samplers should indicate whether the changes in population obtained from removal trapping correspond with population changes occurring at one place in the stream. From the regression $b = 2.48$ and $S.E.^{b} = 0.97$ and 't' is therefore 2.56. With n-2 degrees of freedom = 11, $P < 0.05$ thus the pattern of numbers is not significantly different. It is therefore probable that the changes in population seen in successive removal trappings are the result of actual changes in numbers in the stream rather than differences in the vegetation sampled in adjacent sites; or that the *Juncus*-samplers reflect the same population changes as the removal estimates.

5(i) A. SEPARATION OF LARVAL INSTARS

From measurement of Lepidoptera larvae, Dyar (1890) concluded that a geometrical progression of head-capsule width occurred in successive instars. This has become known as Dyar's growth rule and the ratio of size increase between instars is about 1.4:1. There are known to be many exceptions to it however (Imms, 1957). The principle has been used in separating larval instars but doubt over its general acceptability makes one cautious of its use in this case.

Smith (1969) carried out a polymodal analysis of head-capsule widths in Prosimulium hirtipes and was able to distinguish eight larval instars. The mean growth index of 1.3 shows agreement with the growth rule for this species. Several studies have been carried out on other species and conflicting conclusions have been drawn with regard to the number of larval instars. In his pioneering study, Puri (1925) reared Simulium aureum and S.erythrocephalum DeGeer and pupation occurred after the sixth moult. Terterjan (1957) also concluded six instars to occur in Odagmia kiritshenkoi Rubz. after biometric analysis and Harrod (1964a) found the same number of instars in S.nitidifrons but with non-compliance with Dyar's growth rule.

Evidence that Simulium spp. larvae show agreement with the growth rule has been provided by Johnson and Pengelley (1970) after overall length and cephalic apotome measurement of S.rugglesi Nicholson and Mickel showed seven instars in this species. No morphological adaptations such as the increasing lateral protruberances in later instars (V-VII) of S.damnosum Theobald (Grenier and Feraud, 1960) occur in the species studied but first instar larvae could be distinguished by the presence of the "egg-burster" on the apotome and last-instar larvae had dark, air-filled pupal respiratory filaments inside the pre-pupal cuticle.

Having identified larvae, measurements were taken for use in polymodal analysis. Larvae could then be assigned to their various instars.

5(i) B. MEASUREMENT OF LARVAE

The reliability of various measurements of blackfly larvae has been examined by Terterjan (1957). He emphasised that sclerotised cuticle has a minimum growth between moults and maximum growth directly after a moult. In contrast, the soft body will grow throughout the instar.

To provide good instar separation it is therefore important to measure sclerotised rather than soft body parts as has been well illustrated by Edmondson (1971) with respect to the chironomid <u>Chironomus tentans</u>.

In the present study the width of the cephalic apotome (frons-clypeus) was determined for <u>S.vernum</u> in Cronkley stream 3: section A, and <u>S.nitidifrons</u> in Cronkley stream 2 (up to 15.v.72). The method of measurement is that given by Smith (1969). Larvae of known species were decapitated and the heads transferred from 70% alcohol to a staining block containing glycerol. Individual heads were aligned in a "strip" of glycerol on a slide and each arranged with the cephalic apotome uppermost. The slide was placed on the stage of a microscope having an eyepiece graticule giving 89 divisions per millimetre and, by movement of the stage, the rows of heads were scanned and the maximum width of each cephalic apotome taken and noted.

Unfortunately, cephalic apotome width measurement proved too time-consuming for use on larvae collected in the summer 1972 sampling programme. Another disadvantage of the method is that . heads would be difficult to match with their respective bodies when drying larvae before weighing. Overall length - from the anterior tip of the head (without cephalic fans) to the posterior tip of the abdomen - was employed even though the instar separation will be necessarily less accurate. An eyepiece graticule having 10 divisions per millimetre was used in a binocular microscope and lengths recorded to 0.1 mm. Any larvae which had become contracted presented a problem in that they had to be gently extended before measurement. As this group comprised less than 1% of the total number of larvae it was decided this was not an important source of error.

5(ii) LARVAL INSTAR GROUPINGS

Cassie (1954) published a method of analysing polymodal biological material using probability paper and his method was used in the present study. The advantage of the method is that it allows one to read off the mean and standard deviation of each modal class directly. The steps are as follows:

(i) Data for each species in each stream were pooled so that the total number of larvae in each size class (divisions in the case of cephalic apotome width measurements and 0.1 mm intervals in the case of overall lengths) for the season were obtained.

(ii) These values were converted to percentages of the whole and cumulative percentages determined. The cumulative percentages were plotted on the probability scale against the size category on the other axis.

(iii) Inflexions in the resulting curve were noted and the data between inflexions re-calculated as cumulative percentages of each modal class.

(iv) Replotting this new data resulted in a series of straight lines and the mean of each class was where each line crossed the 50%

TABLE 5.1 Mean cephalic apotome widths for S.vernum in Cronkley Stream 3 Section A, and S.nitidifrons in Cronkley Stream 2

Mean width in divisions (89 divisions = 1 mm) with one standard deviation

	S.vernum in Cronkley Stream 3: Section A		S.nitidifrons in Cronkley Stream 2	
Instar	Mean Cephalic Apotome Width (divisions) ± 1 S.D.	Ratio of Means	Mean Cephalic Apotome Width (divisions) 1 S.D.	Ratio of Means
II	9.0 ± 1.2	-	10.6 ± 0.6	-
III	13.7 ± 1.6	1.52	14.7 ± 1.9	1.38
IV	19.3 ± 2.2	1.41	19.6 ± 2.4	1.33
V	25.5 ± 2.5	1.32	26.0 ± 2.2	1.32
VI	32.8 ± 3.2	1.29	34.2 ± 3.2	1.32
VII	41.7 ± 3.7	1.27	43.2 ± 4.2	1.26

TABLE 5.2 Mean overall lengths of S.vernum instars in 3 streams.

Mean length in divisions (1 division = 0.1mm) with one standard deviation

	Moss Burn Section B		Moss Burn Section D		Cronkley Stream 2 Section A	
Instar	Mean Overall Length (Divisions) ± 1 S.D.	Ratio of Means	Mean Overall Length (Divisions) ± 1 S.D.	Ratio of Means	Mean Overall Length (Divisions) ± 1 S.D.	Ratio of Means
II	11.8 ± 1.1	-	11.8 ± 1.2	-	11.8 ± 1.3	-
III	16.5 ± 2.3	1.40	17.3 ± 2.0	1.47	17.0 ± 2.6	1.44
IV	24.3 ± 2.7	1.47	23.9 ± 3.1	1.38	24.5 ± 2.7	1.44
V	34.2 ± 4.0	1.41	34.3 ± 4.6	1.44	34.4 ± 3.6	1.40
VI	46.7 ± 5.6	1.37	47.4 ± 6.1	1.38	47.3 ± 4.6	1.38
VII	61.6 ± 4.8	1.32	61.3 ± 4.6	1.29	64.2 ± 4.9	1.36

TABLE 5.3 Mean overall lengths of S.brevicaule instars in Cronkley Stream 2 Section A, and S.aureum instars in Moss Burn Section B. Mean length in divisions (1 division = 0.1 mm) with one standard deviation

	S.brevicaule		S.aureum	
Instar	Mean Overall Length (Divisions) ± 1 S.D.	Ratio of Means	Mean Overall Length (Divisions) ± 1 S.D.	Ratio of Means
II	11.0 ± 0.7	-	10.7 ± 1.2	-
III	15.3 ± 1.7	1.39	15.7 ± 2.0	1.47
IV	22.3 ± 3.4	1.46	24.6 ± 3.1	1.57
V	32.0 ± 4.3	1.44	33.4 ± 3.9	1.36
VI	45.3 ± 4.5	1.42	44.5 ± 4.1	1.33
VII	61.2 ± 6.4	1.35	56.2 ± 6.7	1.26

TABLE 5.4 Mean overall lengths of S.monticola instars in two streams. Mean length in divisions (1 division = 0.1 mm) with one standard deviation

	Moss Burn Section D		Cronkley Stream 2 Section A	
Instar	Mean Overall Length (Divisions) 1 S.D.	Ratio of Means	Mean Overall Length (Divisions) 1 S.D.	Ratio of Means
II	10.0 ± 1.3	-	10.3 ± 1.2	-
III	14.4 ± 2.2	1.44	14.9 ± 2.6	1.45
IV	22.7 ± 2.7	1.58	21.8 ± 3.5	1.46
V	31.0 ± 3.5	1.37	30.5 ± 3.6	1.40
VI	43.8 ± 4.8	1.41	43.0 ± 5.2	1.41
VII	58.1 ± 4.8	1.33	57.5 ± 4.7	1.34

TABLE 5.5 Mean overall lengths of S.nitidifrons instars in two streams.

Mean length in divisions (1 division = 0.1 mm) with one standard deviation

	Moss Burn: Section D		Cronkley Stream 2: Section A	
Instar	Mean Overall Length (Divisions) ± 1 S.D.	Ratio of Means	Mean Overall Length (Divisions) ± 1 S.D.	Ratio of Means
II	11.0 ± 2.0	-	12.0 ± 1.8	-
III	18.9 ± 2.9	1.72	18.3 ± 3.3	1.53
IV	27.5 ± 3.7	1.46	27.7 ± 3.8	1.51
V	40.4 ± 5.1	1.47	39.5 ± 4.8	1.43
VI	52.5 ± 6.2	1.30	54.0 ± 5.0	1.37
VII	66.0 ± 3.3	1.26	68.6 ± 4.9	1.27

TABLE 5.6 Mean size ranges of larval instars of S.angustitarse in Cronkley stream 3 Section A

Instar	Mean Range (mm)
II	1.00 - 1.25
III	2.25 - 2.50
IV	3.25 - 3.50
V	4.00 - 4.25
VI	5.75 - 6.00
VII	7.00 - 7.25

probability level. The standard deviation either side of this mean is where the line crossed the 15.83% and 84.17% probabilities respectively. The results are given in Tables 5.1-5.5. Larvae of S.angustitarse in Cronkley stream 3: section A were placed into size-ranges and the mean size-range of each instar is given in Table 5.6.

In all species polymodal analysis showed seven larval instars to be present in contrast to Puri's (1925) finding of six with S.aureum and Harrod's (1964a) of six with S.nitidifrons. The ratio between means was not constant between instars and Smith (1969) also observed this effect with ratios of 1.20; 1.29; 1.48; 1.39; 1.28; 1.29; and 1.17 respectively in P.hirtipes. The mean ratios in the present study were 1.32 and 1.36 for S.nitidifrons cephalic apotome width and S.vernum apotome width respectively. Length measurement mean ratios varied from 1.39 for S.vernum in Moss Burn: sections B and D, to 1.44 for S.nitidifrons in Moss Burn: section D. These overall ratios show there is thus compliance with Dyar's growth rule in all species.

Using the mean and standard deviation obtained for each species larvae were assigned to their respective instars. Larvae between instar distributions were considered to be in the instar nearest to their apotome width or overall length. From the percentage instar composition, frequency histograms were prepared for each species in each stream and these are given in Figures 5.3-5.13.

5(iii) USE OF INDIVIDUAL REMOVAL SAMPLES AS SUB-SAMPLES OF THE WHOLE

The three consecutive samples in each removal collection should be sub-samples of the whole from the point of view of the proportion of each instar present. With the large summer collections it would be advantageous if individual samples could be used in place of the whole collection on occasions. In order to examine whether this conclusion was valid larvae from two early collections - Moss Burn: section D on 30.vi.72 and Cronkley stream 2: section B on 26.vi.72 - were identified and the instar distribution of the first sample compared with the sum of the other two (Tables 5.7 and 5.8). The slope, b, of the resulting regression line, when divided by the standard error of the slope, S.E.^{b}, will give a value of 't' which can be looked up in tables, entering with n-2 degrees of freedom.

On the basis of the levels of probability presented in Table 5.9 it was decided that the first removal collection only could be used as a sub-sample of the whole when samples were large. The result for *S.nitidifrons* in Cronkley stream 2: section B when $P < 0.3$ shows that inaccuracy occurs when using small samples.

To further substantiate the assumption that the first sample would be representative of the collection as a whole the same method was applied to the collection of 2.viii.72 in Moss Burn: section D. Here there were small larvae of *S.monticola* and *S.nitidifrons* and the results confirmed the previous findings with non-significant differences between samples 1 and 2+3. The data are presented in Tables 5.10 and 5.11.

5(iv) SIZE DIFFERENCES IN WINTER AND SUMMER LARVAE

A decrease in the size of last instar simuliid larvae in summer has been noted by Grenier (1949); for pupae by Zahar (1951); and for adults by Edwards (1920); Davies (1957) and Neveu (1973b) and the same feature occurs in other groups, e.g. working on the stonefly *Capnia bifrons* Khoo (1964) found adults decreasing in size with the onset of summer.

The overall length of *S.vernum* larvae with black pupal respiratory histoblasts were arranged into a winter group (March-May) and a summer group (July-October) for Cronkley stream 2 in 1971/72 (Table 5.12).

TABLE 5.7 Numbers of larvae in each instar of the given species from the collection of 30.vi.72 in Moss Burn Section D.

	S.vernum		S.brevicaule		S.monticola		S.nitidifrons	
Sample / Instar	1	2+3	1	2+3	1	2+3	1	2+3
II	8	2	1	1	3	7	4	6
III	54	59	24	23	9	8	35	41
IV	28	41	29	30	61	67	38	31
V	28	42	1	4	27	18	2	1
VI	15	32	1	0	3	1	1	2
VII	5	0	0	1	0	0	0	0

TABLE 5.8 Numbers of larvae in each instar of the given species from the collection of 26.vi.72 in Cronkley stream 2 Section B.

	S.vernum		S.brevicaule		S.nitidifrons	
Sample / Instar	1	2+3	1	2+3	1	2+3
II	4	6	14	6	7	5
III	23	16	14	8	11	6
IV	30	19	50	25	8	2
V	10	14	15	9	2	1
VI	6	7	4	5	0	0
VII	6	8	10	5	0	0

With a null hypothesis of no difference in size between winter and summer larvae $\chi^2 = 33.51$, which, with 11 degrees of freedom, gives $P < 0.001$. It is thus seen that summer larvae are very significantly smaller than winter larvae in this species.

Known last instar larvae of S.vernum were analysed from Cronkley stream 3: section A to see if there was a decrease in size of larvae which pupated in March compared to those which pupated in May as Neveu (1973b) found for imagines over this period (Table 5.13). These data have been presented in graphical form (Figs. 5.1 and 5.2) where standard deviations given in Table 5.13 have not been included. For the 1971 population, r (of means) = -0.98 $P < 0.001$ and for the 1972 population r (of means) = -0.86 $P < 0.01$ showing, in both years, a significant decrease in mean cephalic apootome width, and therefore size, toward summer.

The same approach was used for S.vernum and S.brevicaule in Cronkley stream 2 and the data are presented in Tables 5.14 and 5.15. When r of the given means was calculated the values obtained were -0.21, $P > 0.1$ with S.vernum and r = -0.84, $P < 0.02$ with S.brevicaule showing no significant reduction in the size of S.vernum larvae but a significant one in the case of S.brevicaule. Any decrease which occurs will be masked by taking overall length as the size measurement instead of cephalic apotome width.

Comparison with mean overall length of last instars in Tables 5.2 and 5.3 shows that the larvae of both S.vernum and S.brevicaule were larger in winter than in summer 1972, confirming the result in Table 5.12. The mean size of winter larvae 1971/72 were 7.4 mm and 7.3 mm for S.vernum and S.brevicaule respectively, and 6.4 mm and 6.1 mm for the same species in summer.

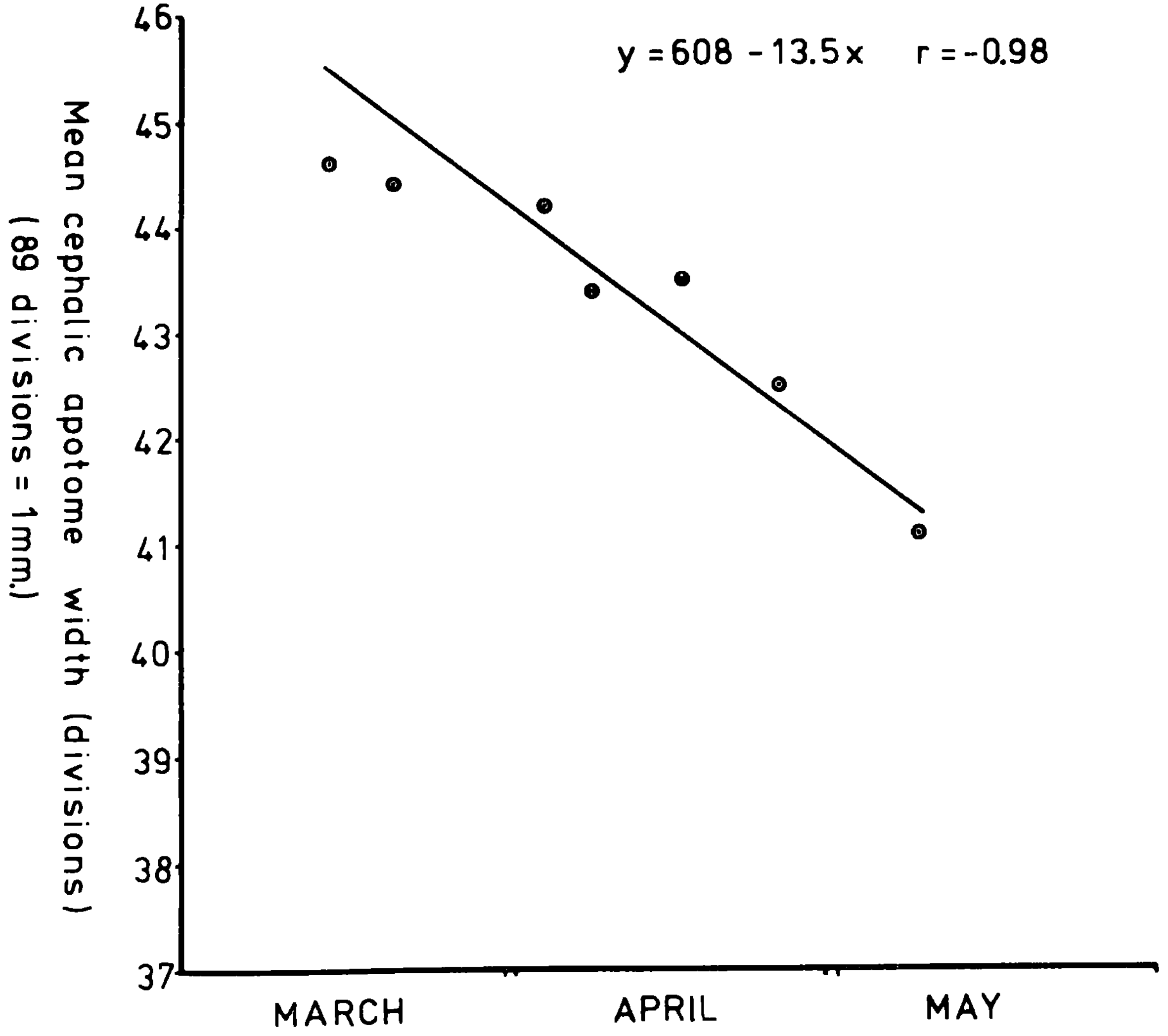


Fig. 5.1. mean cephalic apotome width of *S.vernum* final instar larvae with successive samples in Cronkley Stream 3 : Section A. 1971.

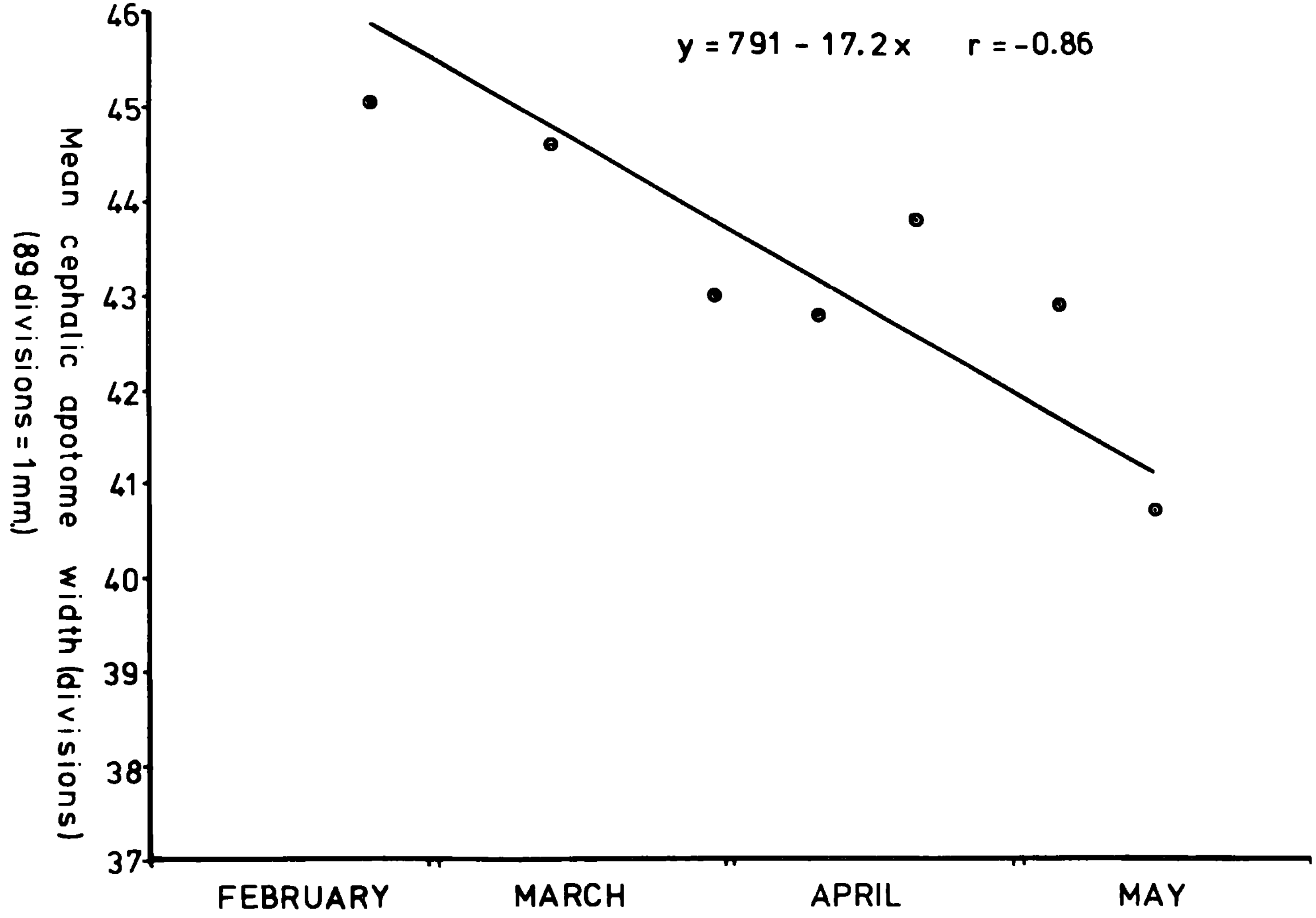


Fig. 5.2. mean cephalic apotome width of <u>S.vernum</u> final instar larvae with successive samples in Cronkley Stream 3 : Section A. 1972.

TABLE 5.9 Tables of b, $S.E^b$, t and P for the species given in Tables 5.7 and 5.8

Moss Burn Section D 30.vi.72	Slope b	Standard Error of Slope $S.E^b$	t	Degrees of Freedom n-2	Probability P
S.vernum	1.2086	0.2575	4.6810	4	< 0.01
S.brevicaule	0.9765	0.0555	17.5702	4	< 0.001
S.monticola	1.0664	0.1320	8.0758	3	< 0.01
S.nitidifrons	0.9539	0.1442	6.6146	3	< 0.01
Cronkley Stream 2 Section B 26.vi.72					
S.vernum	0.4686	0.0899	5.2112	4	< 0.01
S.brevicaule	0.4654	0.0396	11.7427	4	< 0.001
S.nitidifrons	0.5000	0.2781	1.7975	2	< 0.3

TABLE 5.10 Numbers of larvae in each instar of the given species from the collection of 2.viii.72 in Moss Burn Section D

	S.vernum		*S.monticola*		*S.nitidifrons*	
Instar \ Sample	1	2+3	1	2+3	1	2+3
II	4	7	43	52	24	17
III	11	7	15	22	36	24
IV	5	7	5	5	1	6
V	24	99	5	4	8	2
VI	39	97	1	8	0	4
VII	18	31	0	0	0	2

TABLE 5.11 Tables of b, S.E.^{b}, t and P for the species given in Table 5. .

Moss Burn Section D	Slope b	Standard Error of b S.E.^{b}	t	Degrees of Freedom n-2	Probability P
S.vernum	3.0383	0.7370	4.1223	4	$<$ 0.02
S.monticola	1.1623	0.1223	9.4977	3	$<$ 0.01
S.nitidifrons	0.5784	0.0914	6.3271	4	$<$ 0.01

TABLE 5.12 Number of winter and summer final instar larvae in 0.25 mm size-classes for S.vernum in Cronkley Stream 2

Size-Class in mm	Winter Larvae	Summer Larvae
5.75 - 6.00	0	1
6.00 - 6.25	0	1
6.25 - 6.50	1	2
6.50 - 6.75	4	6
6.75 - 7.00	10	2
7.00 - 7.25	6	3
7.25 - 7.50	15	0
7.50 - 7.75	12	0
7.75 - 8.00	5	0
8.00 - 8.25	5	0
8.25 - 8.50	1	0

5(v) LARVAL INSTAR FREQUENCY DISTRIBUTIONS IN THE STUDY STREAMS 1970-72

As has been mentioned in Chapter 3, the Moor House streams are characterised by the virtual absence of winter generations, whereas the Cronkley streams all support sizeable generations at this time. Any consideration of the winter generation of simuliid larvae in Upper Teesdale will therefore be confined to the Cronkley streams.

In Cronkley stream 3: section A, where larval numbers were much reduced in summer development of S.vernum was more advanced in autumn 1970 than in 1971. Larvae were in the third and fourth instars by 13.x in the former case, whereas instars II and III predominated in the latter on 11.xi.71 (see Fig. 5.3). Reference to the frequency distributions shows growth of S.vernum to be more rapid through the winter than that of S.angustitarse in this stream. This difference in "phase" is similar to that found by Obeng (1967) in S.reptans and S.variegatum. The same author found S.angustitarse in an overwintering generation but virtually absent during the summer in hill streams in North Wales. Ladle and Esmat (1973) studied a small stream in southern England where S.vernum was present during winter but not summer, and postulated that the reduced water level - with its effect on current speed - was responsible for the much lower numbers in summer. A similar reason could be forwarded in the present study: from depth measurements (Appendix 1) the mean summer depth in 1971 was 1.9 cm above minimum and mean winter depth in 1971/72 was 4.2 cm above minimum. In the southern stream the second commonest species represented was S.ornatum (Ladle and Esmat, loc cit).

The frequency histograms (Fig. 5.3) show pupation of S.vernum to begin at about the same time in both years studied: 10.iii.71 and 13.iii.72. S.angustitarse in the latter year pupated later than S.vernum in the same year, the first pupae being present on 10.iv.72.

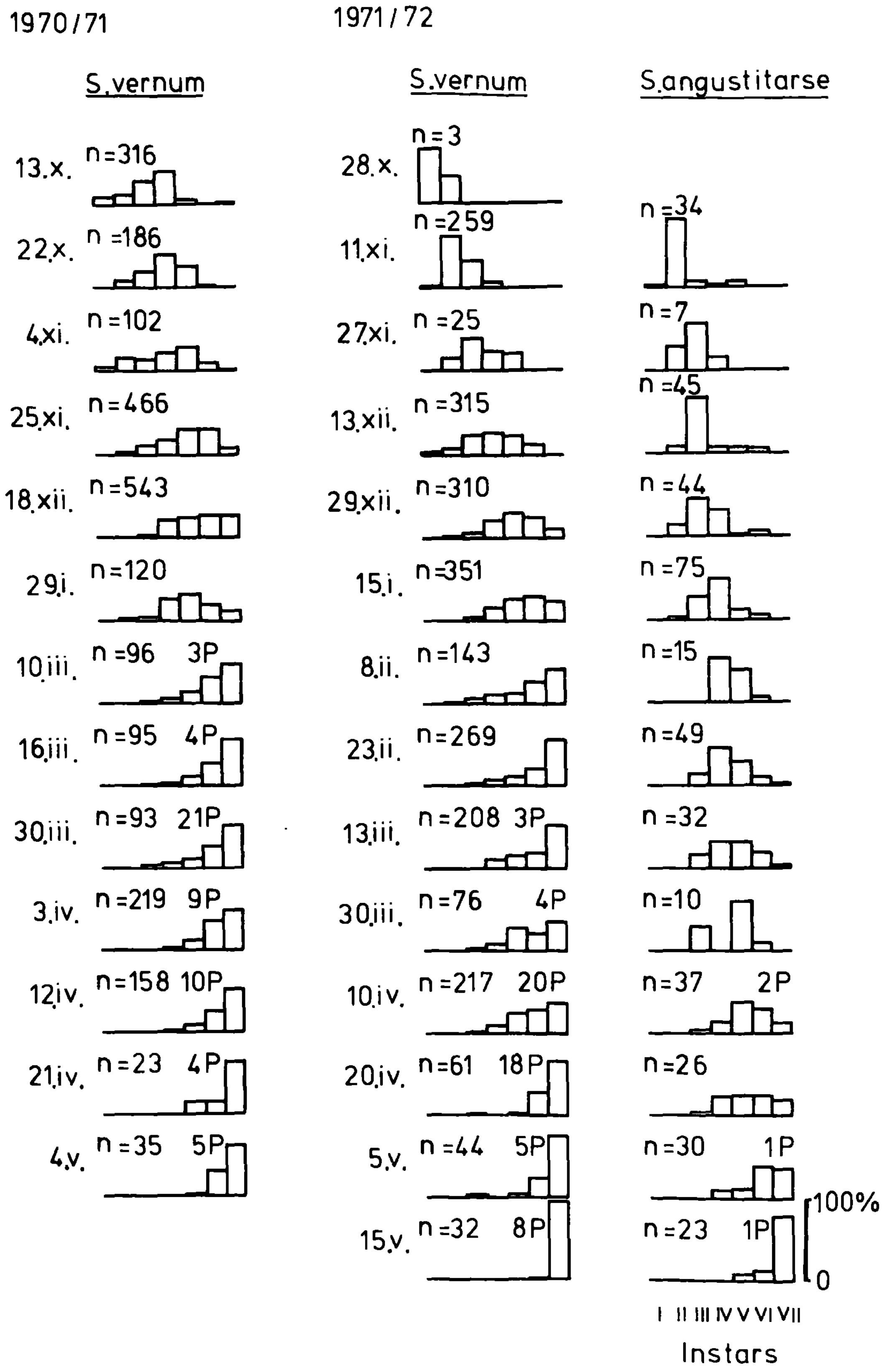


Fig. 5.3. Percentage instar frequency distributions for S.vernum and S.angustitarse in Cronkley Stream 3 : Section A.
n=number of larvae in sample.
P= " " pupae " "

TABLE 5.13 Mean cephalic apotome width in divisions (89 divisions = 1 mm) with one standard deviation of S.vernum final instar larvae in Cronkley Stream 3 Section A on the given dates.

Date	Number of Larvae	Mean Cephalic Apotome Width (Divs.)	S.D.
10.iii.71	5	44.6	2.3
16.iii.71	11	44.4	1.8
30.iii.71	6	43.7	1.7
3. iv.71	18	42.9	1.5
12. iv.71	16	43.0	1.4
21. iv.71	1	42.0	-
4. v.71	9	40.6	1.6
23. ii.72	19	45.1	1.8
13.iii.72	26	44.6	0.8
30.iii.72	6	43.0	2.2
10. iv.72	17	42.8	1.0
20. iv.72	9	43.8	2.6
5. v.72	8	42.9	1.2
15. v.72	13	40.7	1.4

TABLE 5.14 Mean overall length in mm with one standard deviation of S.vernum final instar larvae in Cronkley Stream 2 on the given dates.

Date	Number of Larvae	Mean Overall Length (mm)	S.D.
23. ii.72	6	7.4	0.3
30.iii.72	1	6.9	-
10. iv.72	21	7.4	0.4
20. iv.72	12	7.6	0.3
28. iv.72	9	7.3	0.5
5. v.72	3	7.4	-
15. v.72	6	6.8	0.3

TABLE 5.15 Mean overall length in mm. with one standard deviation of S.brevicaule final instars in Cronkley Stream 2

Date	Number of Larvae	Mean Overall Length (mm)	S.D.
23.ii.72	4	7.7	-
10.iv.72	7	7.5	0.3
20.iv.72	20	7.5	0.3
28.iv.72	10	7.5	0.5
5. v.72	17	7.0	0.5
15. v.72	14	7.1	0.3

Reference to Fig. 5.4 shows *S.vernum* to pupate later in Cronkley stream 2 with the first record on 5.v.72 and the pattern of development is less synchronised here as can be seen from the frequency distributions for 20.x.71 to 23.ii.72. The same is true for *S.brevicaule* (Fig. 5.4) where first pupae were obtained on 20.iv.72 after 47% of larvae were present as final instars on 13.xii.71. Histograms for 29.xii.71 to 13.iii.72 suggest the occurrence of a second hatch in this species. Evidence of a second hatch is also found in winter 1971/72 for *S.nitidifrons* in Cronkley stream 2 (Fig. 5.6) whilst over 50% of larvae of *S.monticola* were present as instar III and 35% as instar IV on 8.ii.72, showing that the mid-winter hatches of eggs were possibly most important in this species (Fig. 5.5).

Overwintering generations of *S.brevicaule*, *S.nitidifrons* and probably *S.vernum* therefore have two cohorts - the first from eggs hatching in October and the second from batches of eggs which at least partially overwinter. Winter larvae of *S.monticola*, on the other hand, are predominantly from this source although the larvae of instars II, III and IV collected in Cronkley stream 2 on 18.xii.70 may result from a slow-developing late-autumn hatch. Pupation of the winter generation continues over at least a month in most cases and the presence of the second winter cohort may contribute to this. The slowest winter development was that shown by *S.nitidifrons* in Cronkley stream 1, which did not produce pupae until June 1971, not included on figure 71% of larvae being in instars III and IV on 13.x.70 (Fig. 5.6). Data from the summer frequency distributions have been summarised in Fig. 5.13.

In Cronkley stream 2, 1971, two summer cohorts of both *S.vernum* and *S.nitidifrons* were distinguished each extending over a long period: the first cohort of *S.vernum* hatching in late-June and pupating in

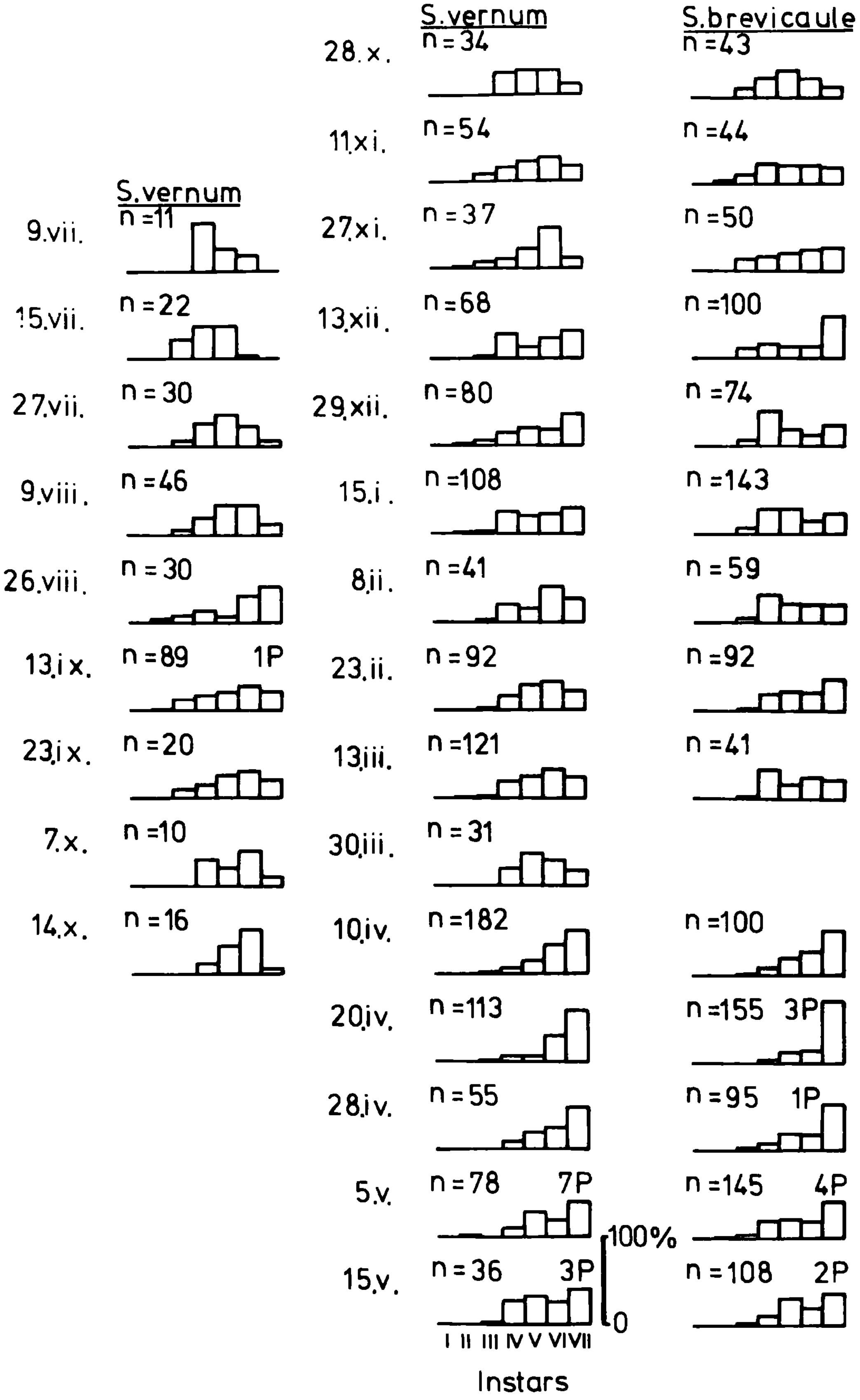


Fig. 5.4. Percentage instar frequency distributions for S.vernum and S.brevicaule in Cronkley Stream 2. July 1971-May 1972. n = number of larvae in sample. P = no. of pupae.

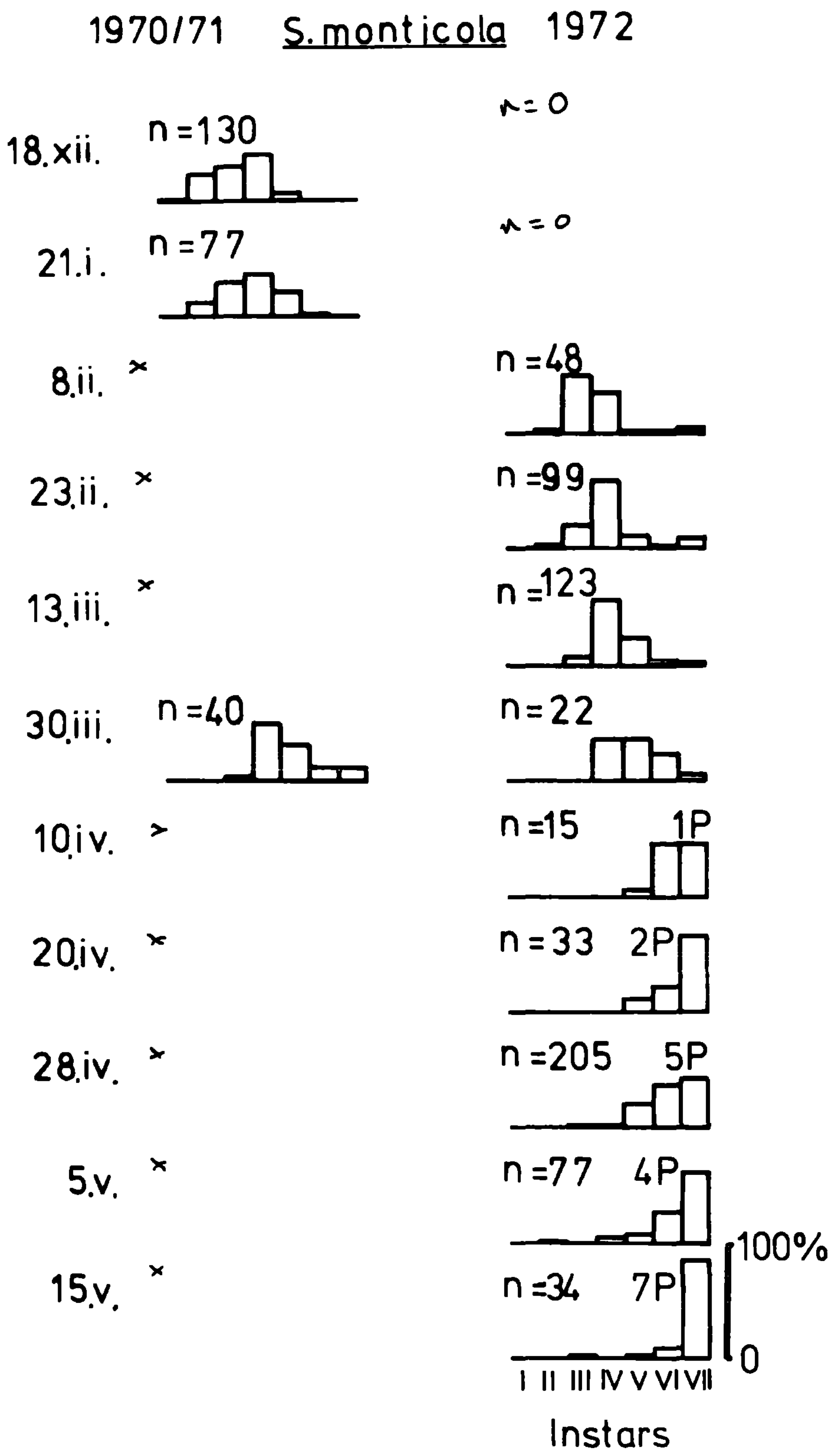


Fig. 5.5. Percentage instar frequency distributions for two winter generations of S.monticola in Cronkley Stream 2.

n = number of larvae in sample

P = " " pupae " "

× = no samples taken on these dates in 1971

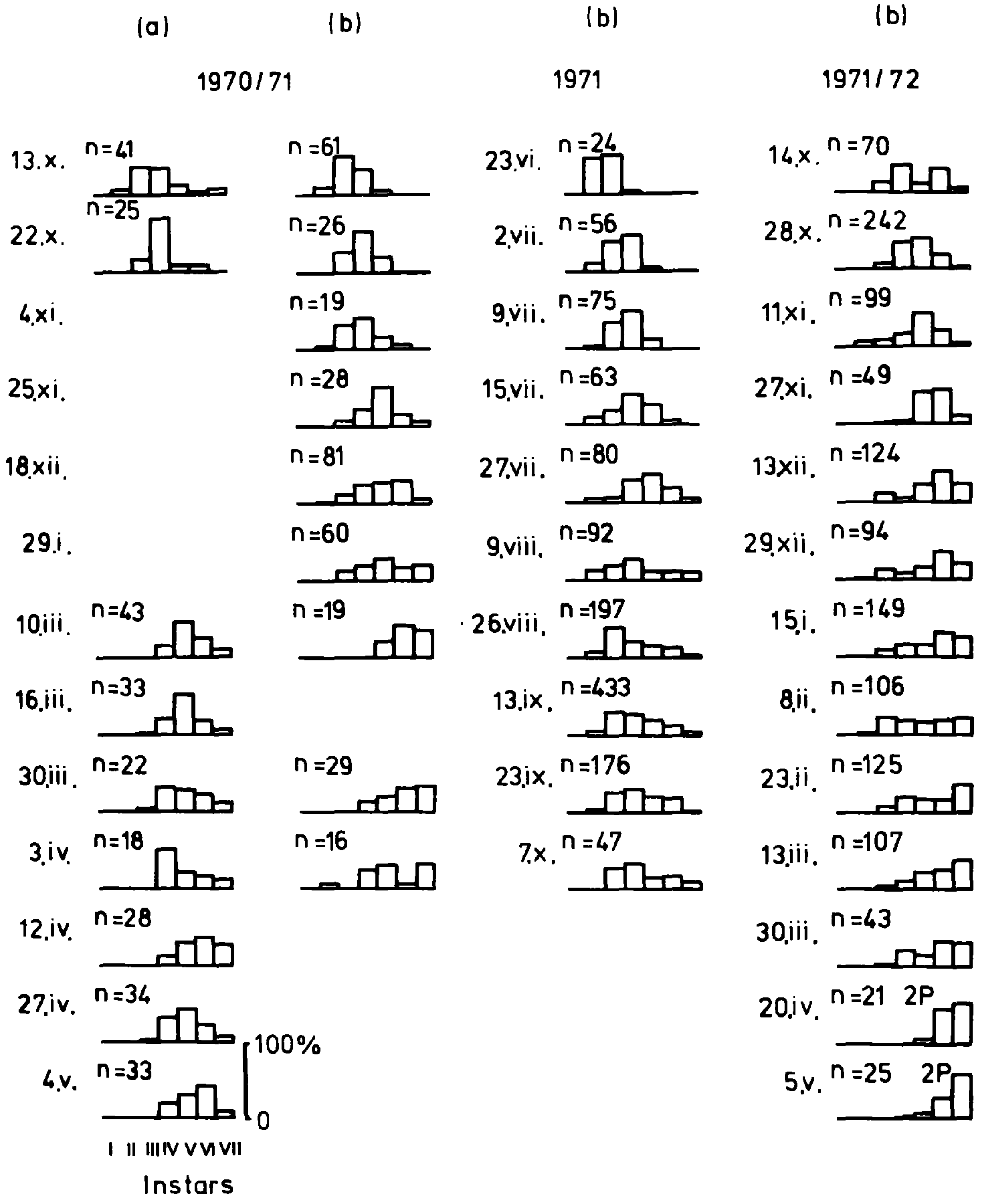


Fig. 5.6. Percentage instar frequency distributions for <u>S.nitidifrons</u> in: (a) Cronkley Stream 1 in winter 1970/71; and (b) Cronkley Stream 2 in winter 1970/71, summer 1971; and winter 1971/72.

n = number of larvae in sample

P = " " pupae " "

late-August which is considerably longer than the duration of cohorts obtained from the more detailed study in summer 1972.

Section A, 1972, of the same stream presented confusing frequency histograms (see Fig. 5.7). A first cohort of *S.vernum* probably pupated in late-July but further recognition of cohorts in this species - or of *S.brevicaule* throughout the summer - was difficult. The first cohorts of *S.monticola* and *S.nitidifrons* in this section appeared in mid-July with the overwintering generation beginning to appear in early-September as in the case of *S.brevicaule*.

All species in section B of Cronkley stream 2 (Fig. 5.8) were still present as the winter generation at the onset of removal collection in mid-June. As with section A, it was difficult to differentiate cohorts in *S.vernum* and *S.brevicaule* but there appeared to be at least two summer cohorts in each case. The first summer cohort of *S.monticola* hatched in late-June: early-July, pupating in late-July : early-August, and the second hatched in early-:mid-August with pupation in late-August : early-September. The first summer cohort of *S.nitidifrons* did not appear until mid-: late-July and pupated in mid- : late-August, with the second hatching in mid-August. In all species the winter generation hatched in early-September.

Both Dubby Sike East Grain and Force Burn tributary A were not sampled sufficiently often to accurately determine cohorts, but it seems there were two of *S.vernum* and *S.brevicaule* in Dubby Sike and of *S.vernum* in Force Burn (Fig. 5.9).

Two cohorts of *S.vernum* could be distinguished in Moss Burn, 1971, (see Fig. 5.9) hatching in ?late-June and late-July : early-August giving pupation in mid-:late-July and ?late-August respectively.

Section A of Moss Burn, 1972 (Fig. 5.10) showed an early cohort pupating in late-June : early-July in both *S.vernum* and *S.aureum*. A

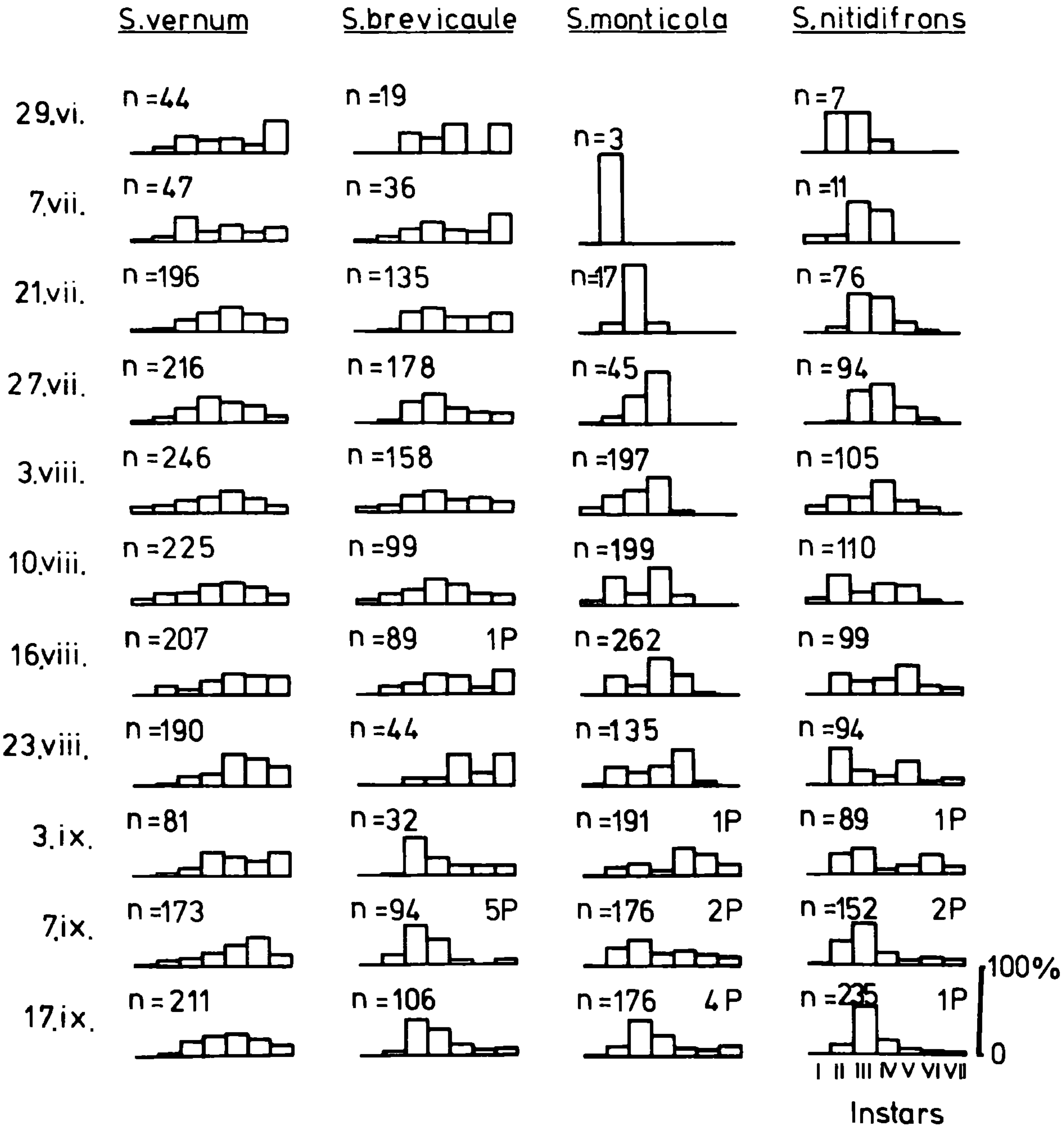


Fig. 5.7. Percentage instar frequency distributions for S.vernum; S.brevicaule; S.monticola; and S.nitidifrons in Cronkley Stream 2: Section A. Summer 1972.

n = number of larvae in sample

P = " " pupae " "

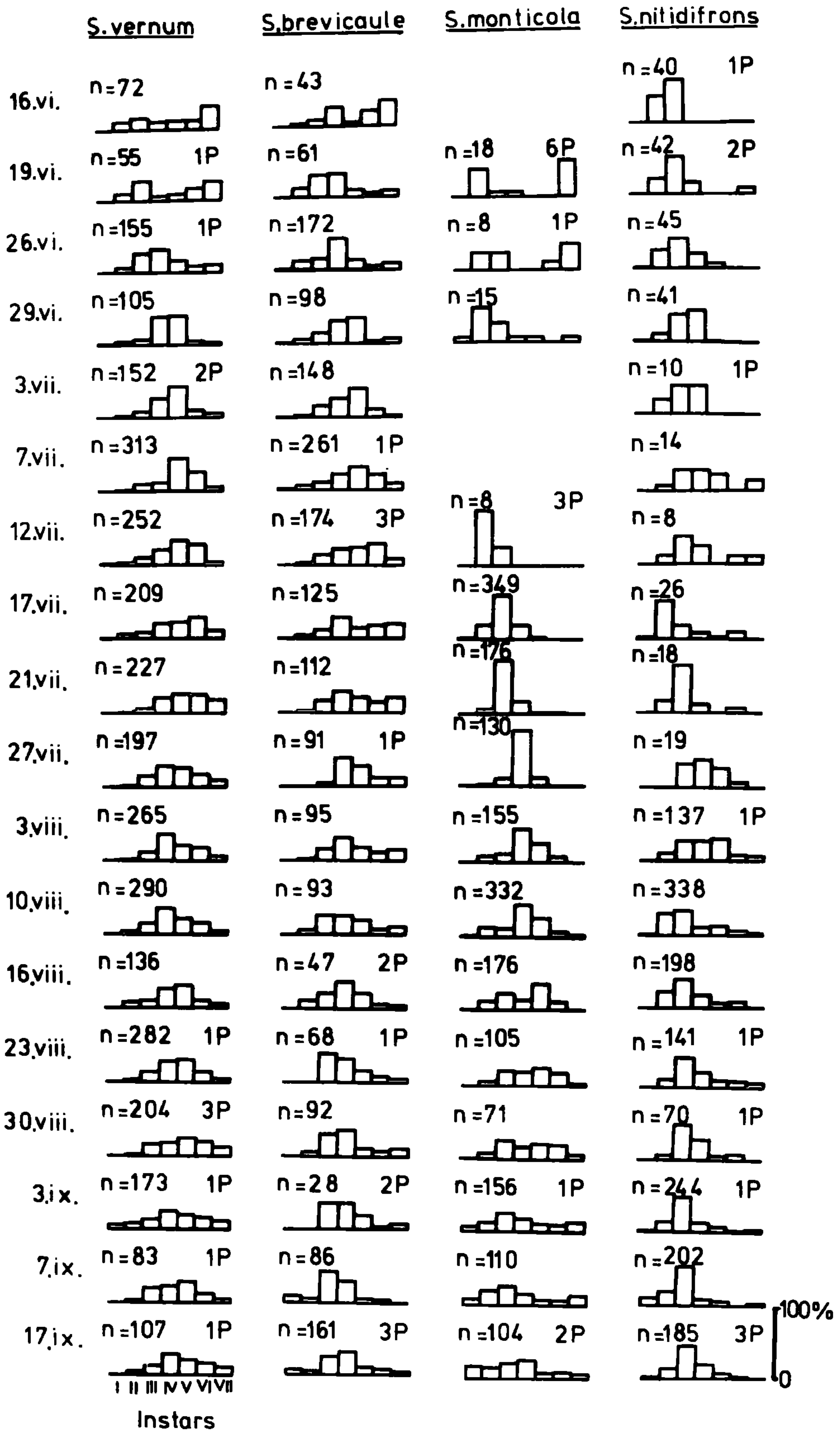


Fig. 5.8. Percentage instar frequency distributions for S.vernum; S.brevicaule; S.monticola; and S.nitidifrons in Cronkley Stream 2 : Section B Summer 1972.

n = number of larvae in sample

P = " " pupae " "

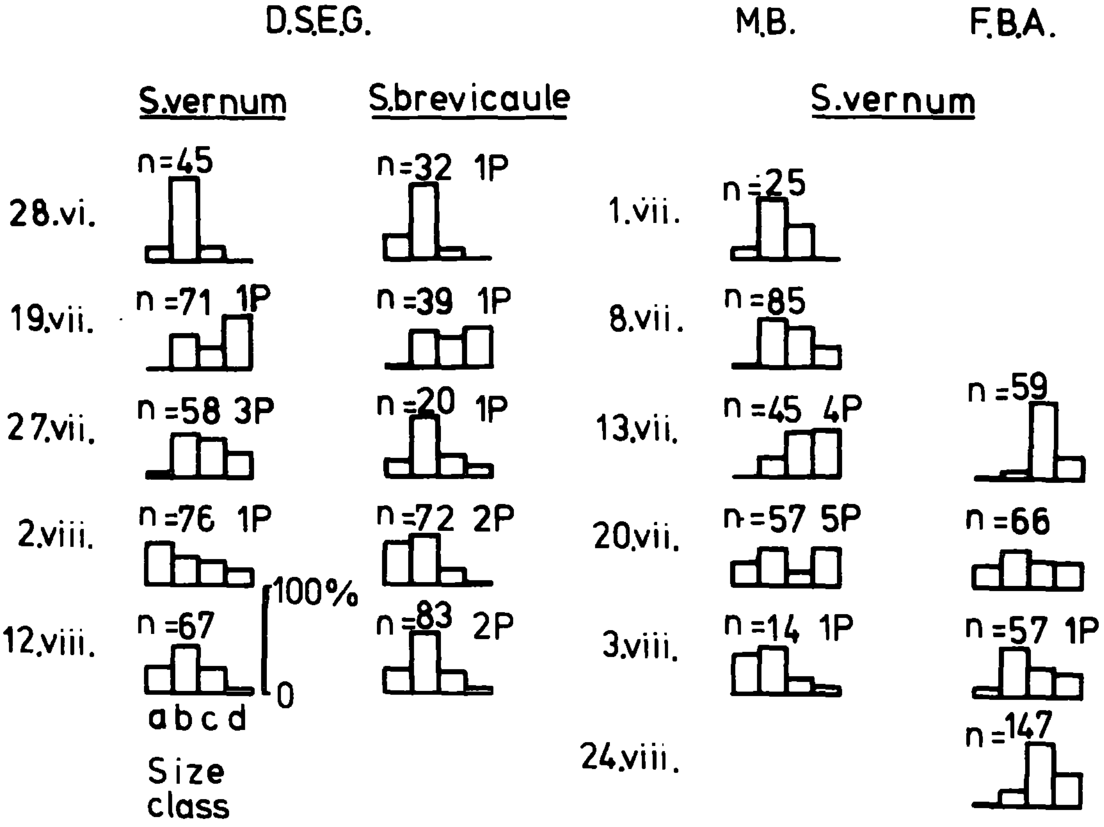


Fig. 5.9. Percentage size-class frequency distributions for S.vernum in Moss Burn (M.B.); Force Burn Tributary A (F.B.A.); and Dubby Sike East Grain (D.S.E.G.) and for S.brevicaule in the latter stream. Summer 1971.

n = number of larvae in sample

P = " " pupae " "

a = < 2.0 mm. ; b = 2.0 - 3.5 mm. ; c = 3.6 - 5.5 mm. ;

d = > 5.5 mm.

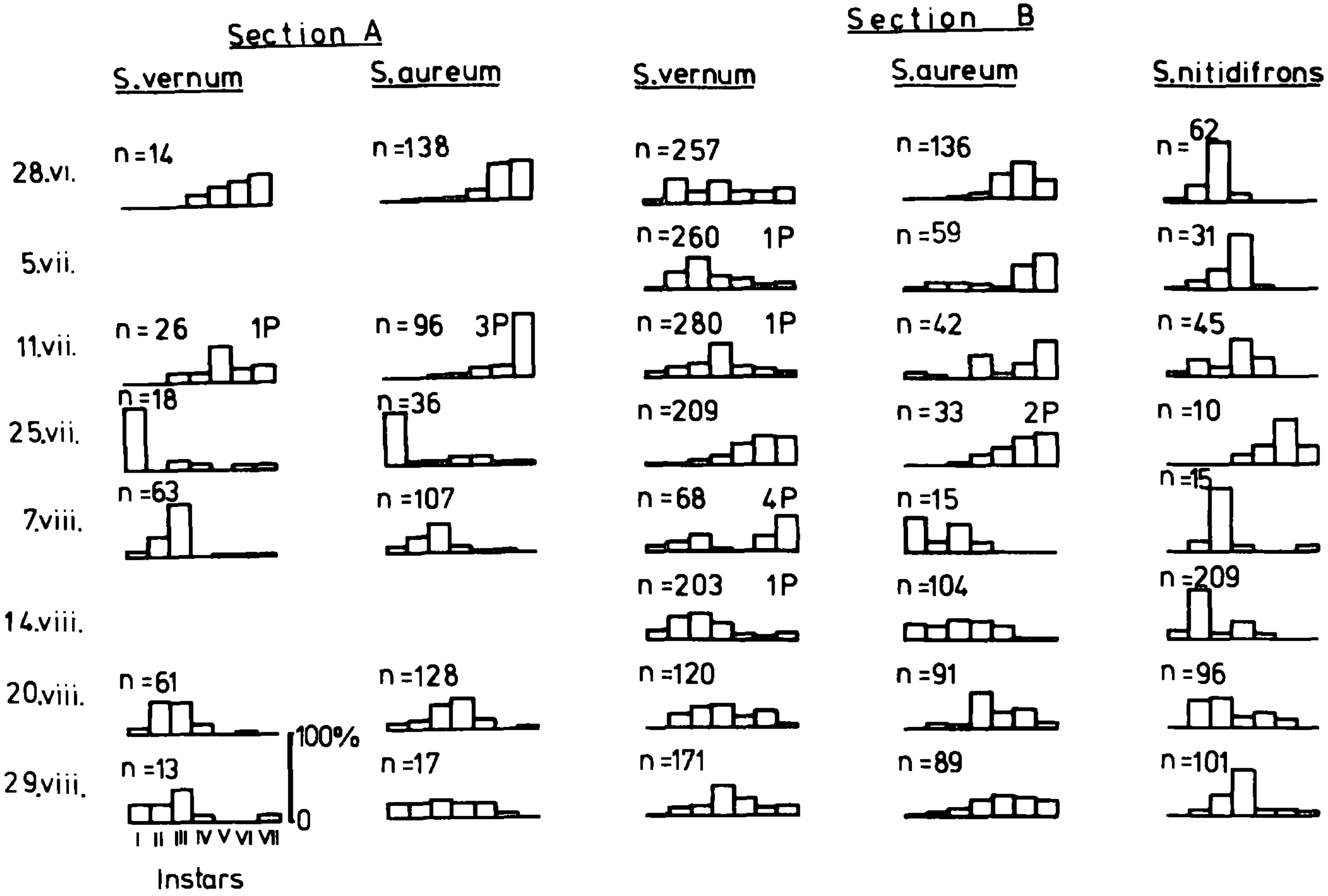


Fig. 5.10. Percentage instar frequency distributions for S.vernum and S.aureum in Moss Burn : Sections A and B and S.nitidifrons in the latter section. Summer 1972.
n = number of larvae in sample
P = " " pupae " "

second cohort of both hatched in late-July with S.vernum pupating in ?late-August and S.aureum ?early-September. A third summer cohort of each hatched in late-August.

In section B, the first cohort of S.vernum and S.aureum appeared at the same time as those in section A. However, a second cohort (Fig. 5.10) hatched in early-July here pupating in late-July in S.aureum and into early-August in S.vernum. Both species had a third cohort hatching in early-August. S.nitidifrons showed a different pattern, with two summer cohorts in Moss Burn: section B. The first produced last-instar larvae in late-July : early-August and the second in ?mid-September after hatching in mid-August.

Three summer cohorts of S.vernum and four of S.monticola could be distinguished in Moss Burn: section C, and the same pattern was found in section D, with the addition of an early-September hatch (Figs. 5.11 and 5.12). S.brevicaule and S.nitidifrons each had three cohorts in summer 1972 in section D of Moss Burn and their duration has been summarised, with all other frequency histogram material in Fig. 5.13.

Reference to the frequency histograms, and the life-tables in Appendix 3, shows different cohorts to have varying numerical importance which will, consequently, affect production. (In the life-tables a further cohort of S.vernum in section D of Moss Burn has been distinguished but this has not been included in Fig. 5.13.)

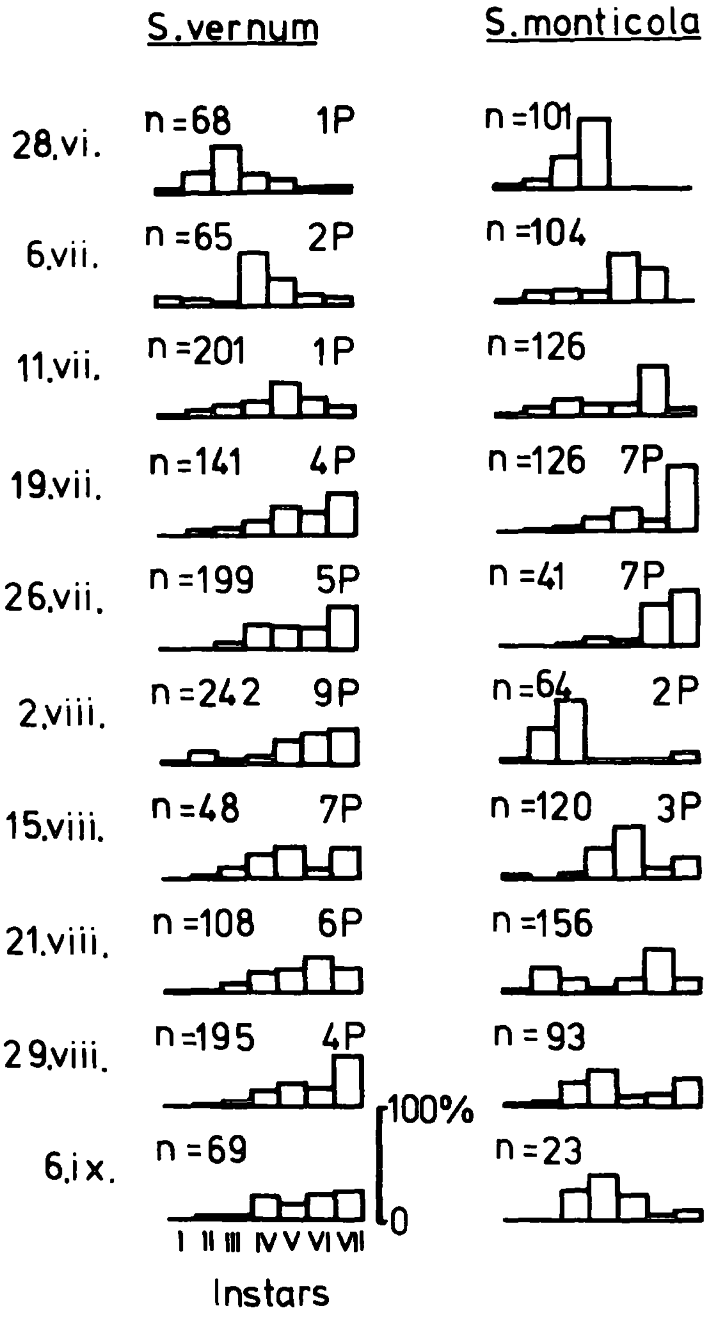


Fig. 5.11. Percentage instar frequency distributions for S.vernum and S.monticola in Moss Burn: Section C. Summer 1972.
n = number of larvae in sample. P = no. of pupae.

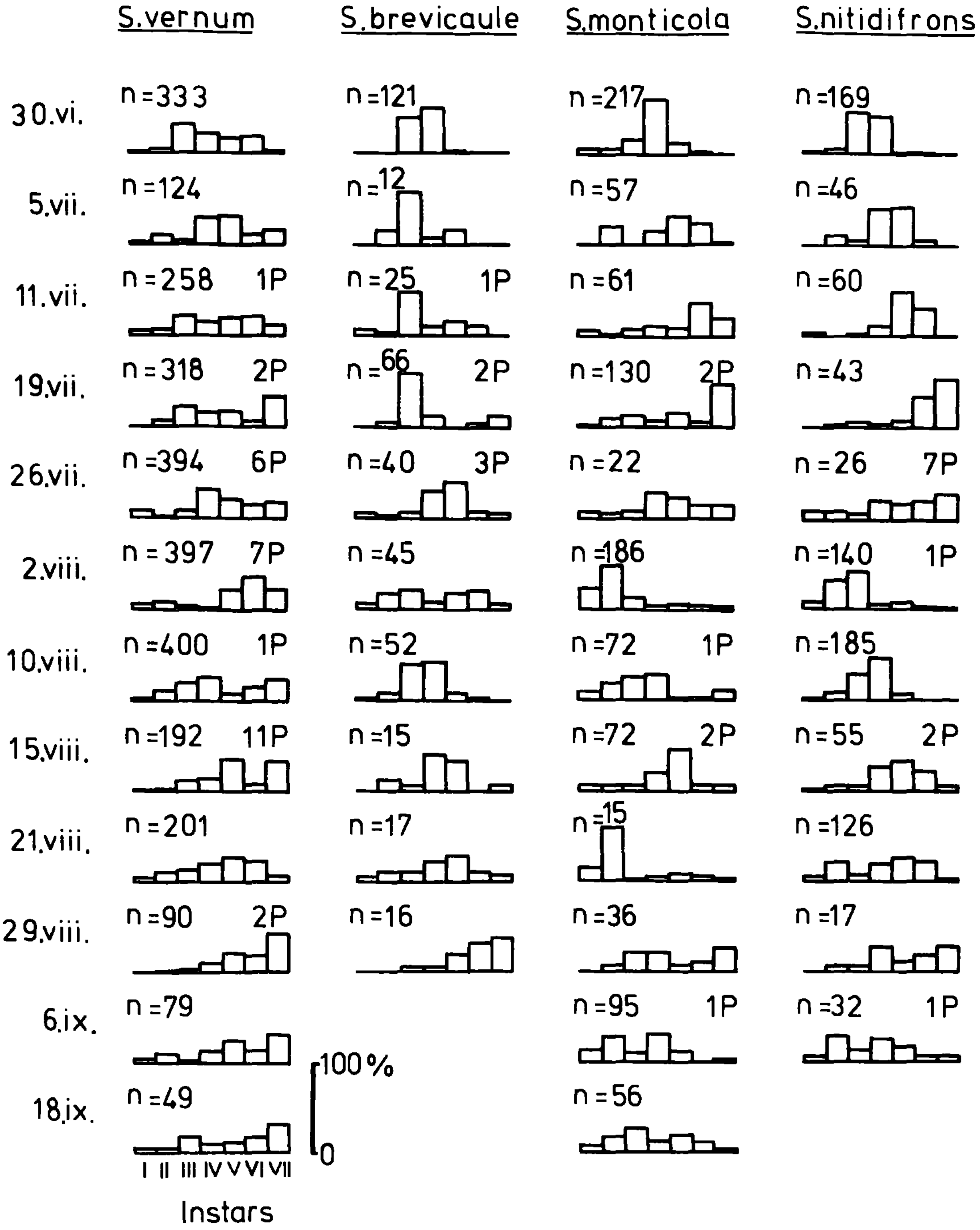
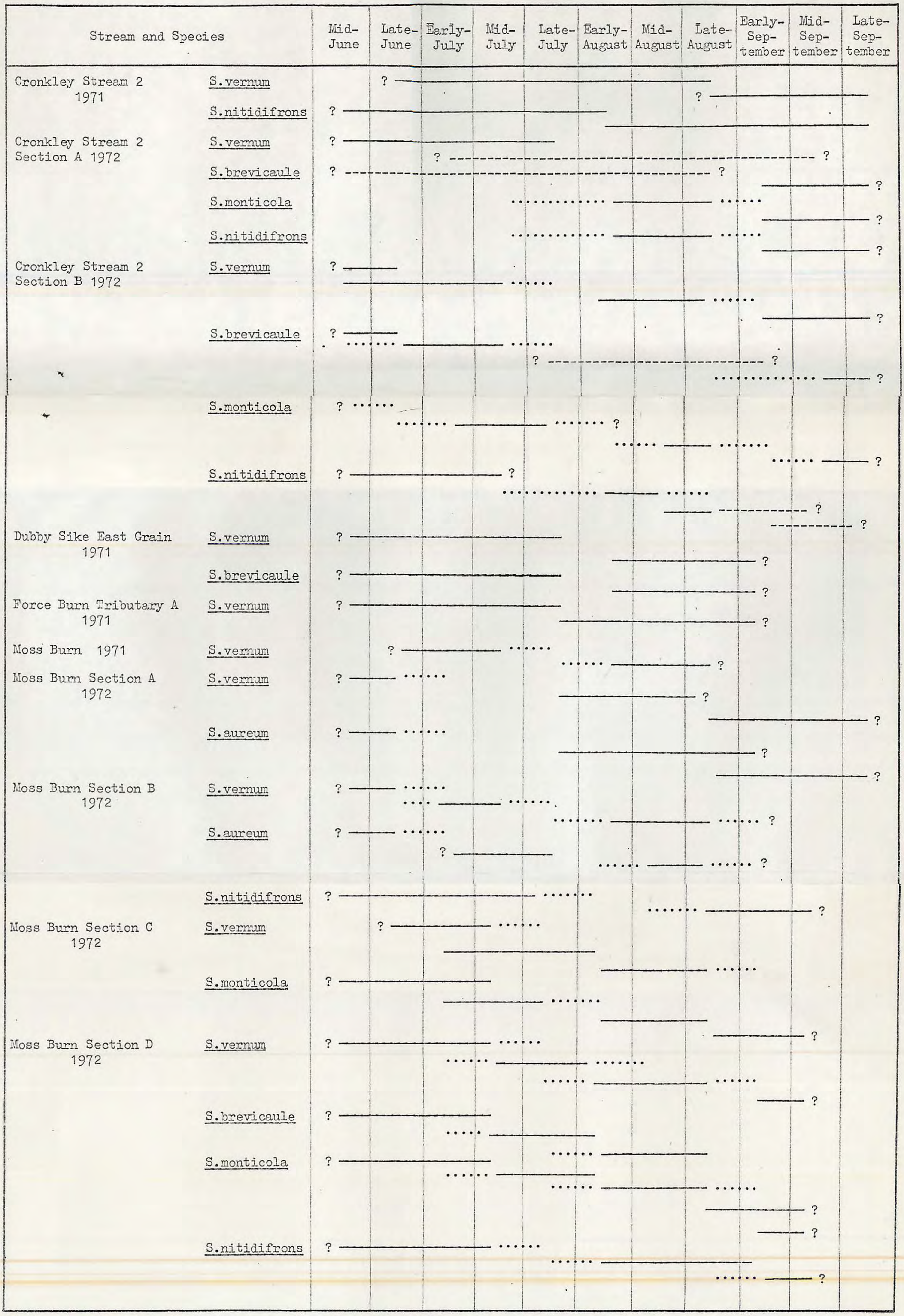


Fig. 5.12. Percentage instar frequency distributions for S.vernum; S.brevicaule; S.monticola; and S.nitidifrons in Moss Burn: Section D. Summer 1972. n = number of larvae in sample. P = no of pupae.

FIG. 5.13 The Duration of Cohorts of the Given Species in the Study Streams

? = Unknown start or end of cohort; ——— = duration of cohort; .... = extensions of each cohort so marked (i.e. first and last appearance of larvae in this cohort.)

---- = no cohorts differentiated;



6(i) THE CALCULATION OF MORTALITY: PROBLEMS AND METHOD

Calculating the mortality of larval Simuliidae presents two basic problems.

The first is that all instars must be represented in the collections in the proportions in which they actually occur in the field - in the early instars this is difficult to achieve and probably not the case with present methods. Although Obeng (1967) has reported seeing first-instar larvae moving downstream, Rubzov (1939) believes this not to be the general case. Rühm (1970), working on Boophthora erythrocephala De Geer found that first instars stayed close to the oviposition site where they spun silk threads but it was the second instars that began to move away. If Rühm's (loc. cit) findings apply in the present study (and observation would tend to support this) first-instar larvae will be under-represented in many collections. Another factor is that, even with the careful sorting method, larvae may have been missed especially when the silt content of collections was high. The short duration of the early instars (see Chapter 6(ii)) also means that they will be inadequately sampled because of the time interval between collecting trips.

The second basic problem in calculating mortality in this case is that no account has been taken of immigration and emigration. Ball et. al. (1963) have shown that simuliid larvae, marked with P^{32}, can move upstream, but this movement is not as marked as the downstream movement which has been reported by many authors, e.g. Elliott (1967); Waters (1972). The mortality estimates will therefore be affected by movement of larvae into, and out of, the sample stretches for which no estimates have been obtained.

The method used to obtain the number of larvae in each instar was that of Southwood and Jepson (1962) which has subsequently been used by Service (1973) to calculate mortality in Anopheles gambiae.

The method as applied here can be outlined as follows.

(i) The percentage instar composition was determined for each sample and, from the maximum likelihood estimate, the number of larvae in each instar on each sampling occasion was calculated.

(ii) The estimates for each instar were plotted against collecting date for the various species.

(iii) The resulting graphs were divided into the cohorts given in Chapter 5 and the area under each section of the graph determined by counting the squares for the given instar, species, and cohort.

(iv) The "instar-day" (iD) totals were entered into life tables (see Appendix 3).

By dividing the "instar-day" totals by the duration (D) of the instars one obtains the estimate (i) of the number of larvae in each instar. As Southwood (1966) points out, this number will be at the median developmental stage of each instar.

6(ii) CALCULATION OF LARVAL INSTAR DURATION

Gabbutt (1959) and Whittaker (1963) have shown a method whereby instar duration can be determined graphically. A mean length measurement of each collection is plotted against sampling date in days. By marking the known instar lengths on the length axis the values can be projected to the time axis and the duration of each instar determined.

In the present study, the overlapping cohorts make this graphical approach very much more difficult. The various cohorts can be separated (Fig. 5.13) and, by reference to the raw data, mean overall lengths of the larvae comprising a cohort marked out on each occasion. For named species and streams these data are presented in Table 6.1. Calculation of the correlation coefficient, r, of the mean overall lengths with time show the relationship to approach linearity (data when converted to logarithms give a better value of r showing the values to follow a shallow exponential curve). This regression cannot extend to the early instars or to the final instars approaching pupation, but the approximately linear relationship does hold for the overall length ranges covering most instars (no data were obtained for S.brevicaule).

Assuming that the relationship is linear, the duration of each instar will correspond to the length through which it grows (i.e.) the early instars grow through a smaller length range than later ones and will therefore require less time to do so as the animals are growing at a steady rate. Information on the overall length range of instars has been presented in Chapter 5 (Tables 5.2-5.5) where the mean overall length ± 1 S.D. are given for all species Since two standard deviations either side of the mean overall length of each instar will represent the length through which 94% of larvae will have grown for each instar, this value will correspond to the duration of each stage. The length values have been presented in Table 6.2 and, to simplify procedure, a mean range is given for each instar irrespective of species or stream, even though some of the differences are large. Measurement of known first instar larvae (with "egg burster" on the cephalic apotome) gave a mean overall length of 6.8 ± 0.6 divisions (1 division = 0.1 mm) for 189 larvae and this value was also incorporated in Table 6.2. The total of mean ranges gives a value of 87.3 so, to use the ratio obtained between instars, each mean range value must be multiplied by $^{30}/87.3$ or $^{40}/87.3$ to give the 30-, and 40-day durations (Table 6.3) indicated by the frequency distributions (Chapter 5).

Because the development of each cohort varied with respect to time the 30-, and 40-day durations - values of D for the calculation of numbers from the iD (instar-day) total - were obtained so that the

TABLE 6.1 Mean overall length of larvae in cohorts on the given days for different species and streams. r is the correlation coefficient and lengths are given in divisions (1 division = 0.1 mm)

Species, Stream and Section	Day	Number of Larvae for Mean	Mean Overall Length of Larvae in Cohort on given day in Divisions (1 div = 0.1 mm)	Correlation Coefficient r
S.aureum Moss Burn: Section B	1	76	23.4	
	7	85	34.0	
	16	66	44.1	r = +0.992
S.vernum Moss Burn: Section B	1	236	24.2	
	7	255	27.6	
	21	206	43.4	
	34	41	56.8	r = +0.997
S.nitidifrons Cohort 1. Moss Burn: Section B	1	57	19.2	
	8	28	25.1	
	14	33	30.1	
	28	12	53.9	r = +0.983
S.nitidifrons Cohort 2. Moss Burn Section B	1	128	11.1	
	7	59	15.6	
	16	85	25.7	
	36	7	44.3	r = +0.999
S.vernum Moss Burn: Section D	1	4	11.5	
	8	41	17.2	
	16	236	22.2	
	21	132	28.7	
	27	137	35.9	
	35	73	50.2	
	43	18	54.7	r = +0.986
S.monticola Cohort 1. Moss Burn: Section D	1	142	12.4	
	9	59	17.9	
	14	14	27.1	
	20	54	37.6	
	28	16	50.1	
	36	3	54.3	r = +0.987

/continued overleaf

S.monticola Cohort 2. Moss Burn: Section D	1	171	10.9	
	9	19	17.9	
	17	42	25.6	
	29	16	39.9	r = +0.997
S.nitidifrons Cronkley Stream 2: Section B	1	14	11.8	
	5	15	17.3	
	11	18	28.6	
	18	77	39.7	
	25	73	47.1	
	31	17	54.8	
	38	9	65.8	r = +0.997

TABLE 6.2 Four standard deviations (2± from mean) for overall length for the given instars of species in the given streams. The values tabulated will be the range of overall length in divisions (1 division = 0.1 mm) through which 94% of larvae will have grown.

Instar Species and Collection	I	II	III	IV	V	VI	VII
All species and collections	2.3	-	-	-	-	-	-
S.vernum							
Moss Burn : Section B	–	4.6	9.4	11.0	16.4	22.4	19.6
Moss Burn : Section D	–	5.0	8.0	12.6	19.2	25.0	18.2
Cronkley 2 : Section A	–	5.0	10.6	11.2	14.4	18.6	20.2
S.brevicaule							
Cronkley 2 : Section A	–	2.0	7.2	13.2	17.0	18.4	26.0
S.aureum							
Moss Burn : Section B	–	5.2	8.0	12.6	16.0	16.0	27.0
S.monticola							
Moss Burn : Section D	–	6.0	8.2	10.6	13.6	18.4	19.4
Cronkley 2 : Section A	–	4.8	10.8	13.4	14.6	21.0	19.0
S.nitidifrons							
Moss Burn : Section D	–	8.0	11.6	14.4	20.0	25.4	13.4
Cronkley 2 : Section A	–	7.0	12.8	15.0	19.2	19.6	19.2
Mean range of overall lengths	2.3	5.3	9.6	12.7	16.7	20.5	20.2

Data from Tables 5.2 - 5.5.

TABLE 6.3 Calculation of instar duration - to 30-, and 40-day totals from mean range of 4 x S.D. of instar lengths in divisions (1 division = 0.1 mm)

Instar	Mean Range of 4 S.D.s of Instar Length (Divs.)	Instar duration (days) for totals of: 30-days	40-days
I	2.3	0.8	1.1
II	5.3	1.8	2.4
III	9.6	3.3	4.4
IV	12.7	4.4	5.8
V	16.7	5.7	7.7
VI	20.5	7.0	9.4
VII	20.2	7.0	9.3
Σ	87.3	30.0	40.1

real value of i (the number of larvae) will lie between the two estimates. This will also affect the production estimates which are similarly expressed in two ranges corresponding to a 30-day or 40-day development. Some cohorts, e.g. those of S.nitidifrons in Cronkley stream 2: section A (Fig. 5.7) may have instar durations larger than those given for 40-day development but the majority of cohorts are within the two time ranges. Macan (1958b) and Hynes (1961) have both remarked that with constant recruitment into the population as a result of hatching any mean overall length measurement of a generation will be adversely affected. It was felt that with the separation into fairly clear cohorts, which the populations used afforded, this was an acceptable source of error. Inadequate numbers of first and second instar larvae were obtained to gain insight into their duration and it was assumed - without justification - that they also showed the linear relationship with respect to time shown by the other instars. If the durations of these instars were larger than assumed, the numbers given in the life-tables would be further reduced.

There is no reference in the literature to duration of instars in the Simuliidae though there is some on larval generation time. Puri (1925) recorded larval development in S.aureum and S.erythrocephalum as taking four to five weeks with moults every four to seven days. Under ideal conditions Wu (1931) recorded S.vittatum as having a larval duration of 13-17 days and Becker (1973) has shown experimentally that 50% of larvae of this species pupated after 7.4 days at 17°C (126 degree-days) but at 27°C only 112 degree days were necessary to enable 50% of larvae to pupate. Constant high temperatures with optimal food conditions are thus shown to be important in giving rapid development.

Fredeen (1964) has experimentally demonstrated that S.vittatum and S.venustum Say larvae, fed entirely on bacteria, will reach pupation from the first instar after 22 days when the concentration of food was high (0.22 ml. packed volume of bacteria per aquarium twice weekly) but with more dilute suspensions the larval duration is considerably larger.

Doby et. al. (1959) conducted experiments on rearing blackflies from eggs in the laboratory and their larval durations ranged from 15 to 55 days, which may well have been a function of thermal sum, since the experiments were conducted at laboratory temperatures.

From the histograms presented by Ladle et. al. (1972) it would seem that larval duration in the Dorset stream was similar at 30 to 40 days than was the case in the present study.

6(iii) LIFE-TABLES FOR MOSS BURN AND CRONKLEY STREAM 2

In the life-tables (Appendix 3) the number of larvae (i) in each instar was calculated by dividing iD by D. The value dx is that used by Morris and Miller (1954) to denote the number of individuals dying in a stage - in this case between the median developmental age of one instar and that of the succeeding one. Thompson (1928) made the important distinction between real and apparent mortality: translated to the present study apparent mortality would be represented by $\frac{dx}{i}$ for each instar, whereas real mortality (given in the life-tables as a percentage) is calculated by the proportion each dx is of the largest larval total or $\frac{dx}{i\ max}$. The real mortality column can be summed to give the mortality of each cohort and these are also given in the life-tables. In cases where the number of larvae in one instar are larger than in the preceding instar dx will be negative and the percentage this is of the total has been loosely called "recruitment". This is used in this definition only here; it is not connected with natality.

In the life-tables it is clear that there is an under-representation of early instars - in only four cohorts were there sufficient first-instar larvae to express the mortality from the first to the second instar. The first cohorts of S.vernum; S.brevicaule; and S.monticola in Cronkley stream 2: section B showed "recruitment" to be greater than mortality and these represent the large larvae of the winter generation. The first cohort of S.aureum larvae also showed "recruitment" to be greater than mortality in Moss Burn: section B and here the first cohort results from a hatch early in the season so that the early instars of this cohort were not collected. Other cohorts with greater "recruitment" were the ?mid-:late-June to mid-:late-July and early-July to early-August cohorts of S.vernum in Moss Burn: section C and of the same species in section D from ?mid-June to mid-:late-July and early-:mid-July to early-:mid-August.

In considering the mortality data (Table 6.4) it is also important to distinguish the cohorts which were not followed through at the end of the season. Here the number of larvae which have reached later instars will be small and the mortality estimates artificially high,

TABLE 6.4 Cohort Mortality from Information in the Life-Tables (Appendix 3)

Stream	Species	Mortality in Successive Cohorts	"Recruitment" in in Successive Cohorts	Resultant Mortality (%)	Instar Range over which Mortality Occurred
Moss Burn: Section B	S.vernum	77	17	60	IV-VII *
		68-70	2-3	66-67	II-VII
		98-99	-	98-99	II-VII *
	S.aureum				*
		102-103	10-11	91-93	I-VII
Moss Burn Section C	S.vernum				*
					*
		72-73	8	64-65	II-VII
Moss Burn Section D	S.vernum	25-26	5-6	19-21	V-VII *
					*
					*
		95	-	95	I-VII
	S.brevicaule	84-85	1-2	83	III-VII *
		94-95	1	93-94	III-VII
		95	-	95	III-VII
	S.monticola	64-66	32-33	32-33	IV-VII *
			3-4	84-85	II-VII
		98-99	1	97-98	I-VII
	S.nitidifrons	72	-	72	IV-VII *
		97-98	-	97-98	II-VII
Cronkley Stream 2: Section A	S.vernum	57-58	-	57-58	V-VII
	S.brevicaule	58-59	7	51-52	IV-VII
		93-94	-	93-94	III-V *
	S.monticola	119-120	23-24	96	II-VII
		59	-	59	III-IV *
	S.nitidifrons	97	-	97	II-VII
		90-92	-	90-92	II-V *
Cronkley Stream 2: Section B	S.vernum				*
		82	-	82	V-VII
		86-87	-	86-87	IV-VII
		95	-	95	III-VII *
	S.brevicaule				*
		82	-	82	IV-VII
		84	-	84	IV-VII
	S.monticola				*
		116-117	17	99-100	II-VII
		92	-	92	IV-VII
		55-57	-	55-57	I-IV *
	S.nitidifrons	97-99	-	97-99	III-VI
		94	-	94	III-VII
		91-92	-	91-92	III-V *

* Incomplete cohorts which cannot be used in comparison.

since many more larvae will have yet to grow through to pupation. It is only valid to consider those cohorts which can be followed from hatching to the onset of pupation.

When considering the life-tables (Appendix 3) for populations of larvae which have passed through a complete cohort, real mortality is seen to be greatest during the younger stages. As these are probably also underestimated this trend is probably more pronounced than it appears in the present study. Survivorship curves have not been prepared but the life-tables show that they would conform to a "type III" curve of Deevey (1947) or a "type IV" curve of Slobodkin (1962).

Considering individual cohorts, mortality in Moss Burn: section B was low - 66-67% instars II-VII for S.vernum and 91-93% mortality instars I-VII in S.aureum. Mortality of S.vernum in Moss Burn: section C was similarly low - 64-65% instars II-VII but "recruitment" occurred here as it did in earlier cohorts. This was also the case with this species in section D of Moss Burn until the late-July to late-August cohort where the mortality of instars I-VII was 95% (with 66-68% contributed by instars II-VII which compares with the result from Moss Burn: section B). In section D, S.brevicaule showed higher mortality for the two main summer cohorts of 93-94% and 95% respectively from instar III-VII. The early-:mid-July to early-August cohort of S.monticola had a mortality of 84-85% instars II-VII but the later one was higher at 97-98% instars I-VII, much being contributed by a heavy instar II mortality (see Appendix 3). In section D of Moss Burn S.nitidifrons showed 97-98% loss from instars II-VII.

Of the species in Moss Burn, mortality was lowest in S.aureum in section B and in S.vernum in all three sections studied. The highest losses were recorded in S.brevicaule and S.nitidifrons in section D.

Comparison of S.vernum and S.brevicaule in Cronkley stream 2 with the same species in Moss Burn is difficult since the maximum populations were obtained in instars IV and V in the former case. In these species, however, mortality was less in section A than in section B in both cases by a large margin (see Table 6.4). Mortality of S.monticola and S.nitidifrons were similar in section A at 96% and 97% instars II-VII respectively. Values were again higher in section B with 99-100% instars II-VII and 92% instars IV-VII for successive cohorts of S.monticola and 97-99% instars III-VI and 94% instars III-VII for S.nitidifrons.

Unless "recruitment" was greater than mortality, "recruitment" was rarely found in populations of S.vernum, and not at all in the cohorts of S.nitidifrons studied. This feature occurred in the early instars of S.monticola and the later ones of S.brevicaule. "Recruitment" is a function of several factors and will be discussed in Chapter 8.

6(iv) APPLICATION OF RICHARDS AND WALOFF'S METHOD OF CALCULATING MORTALITY

Richards and Waloff's (1954) method of calculating mortality was developed from a study on Chorthippus sp. where the population consisted of a clear cohort and the appearance of successive instars was clearly differentiated. The method was used in the present study to provide a comparative estimate to one obtained by the life-table method outlined above. The main summer generation of S.vernum in Cronkley stream 2: section A was used and the steps taken as follows.

(i) The percentage species composition of the samples was calculated for each collecting date (Table 6.5).

(ii) "Unidentified" larvae were assigned to the various instar groupings by "proportional representation" and the populations of S.vernum separated into their respective instars (Table 6.6).

(iii) The numbers of S.vernum per 100 metres were calculated (taken as a length for comparative purposes) and from the corrected percentage of S.vernum per sample (including "unidentified" larvae) the number of this species per 100 metres calculated (Table 6.7).

(iv) The percentage instar composition (from Table 6.6) was used to calculate the number of S.vernum larvae in each instar per 100 metres (Table 6.8), and the accumulated total numbers could then be obtained (Table 6.9).

(v) The mortality of each instar is given from the projection of the post-peak accumulated totals regression back to the time of first appearance of each instar. This was impossible to determine in the present study and as a result the projection was taken at day 0 when day 1 was the peak of numbers in each case. The resulting numbers were converted to fractions of 1000 first instars and a life-table constructed (Table 6.10).

(vi) The number (dx) dying at each stage was calculated by subtraction and the % real mortality obtained.

Using Richards and Waloff's method, mortality of instars I-VII of S.vernum in Cronkley stream 2 section A is 89% with instars V-VII contributing 41%. Even though the life-table method gives mortality from the median developmental age of each instar, the loss of 57-58% for instars V-VII in this case is markedly different.

6(v) COMMENTS ON THE MORTALITY ESTIMATES

Because of the likely underestimation of early instars, particularly of the firsts, it would seem that larval mortality is usually larger than the values given in Table 6.4. This will be mortality in the sense it was used in this study to include larvae

TABLE 6.5 Species composition of samples 29.vi.72 - 17.ix.72 - numbers of larvae in each species

Date	n.	*S.vernum*	*S.brevicaule*	*S.aureum*	*S.monticola*	*S.nitidifrons*	*Unidentified*
29.6.72	71	44	19	-	1	7	-
7.7.72	99	44	35	2	3	11	4
21.7.72	422	192	133	-	17	76	4
27.7.72	534	208	173	1	44	92	16
3.8.72	706	209	134	-	167	89	107
10.8.72	633	192	85	-	170	94	92
16.8.72	655	189	81	-	237	90	58
23.8.72	463	185	44	-	129	91	14
3.9.72	394	80	31	-	183	86	14
17.9.72	736	201	100	-	168	230	37

TABLE 6.6 Numbers of *S.vernum* in each instar (including assigned 'unidentified' larvae)

Date	Instar I	Instar II	Instar III	Instar IV	Instar V	Instar VI	Instar VII
29.6.72	0	3	8	6	7	4	16
7.7.72	2	3	13	6	9	6	8
21.7.72	2	6	28	41	55	36	28
27.7.72	2	11	35	59	52	39	18
3.8.72	18	22	37	44	62	43	20
10.8.72	13	23	24	47	52	43	23
16.8.72	0	21	12	34	50	48	42
23.8.72	0	4	19	24	65	54	24
3.9.72	0	2	7	21	17	13	21
17.9.72	3	9	37	44	50	39	29

Tables 6.6 - 6.10 refer to the populations of *S.vernum* in Cronkley stream 2: section A.

TABLE 6.7 Calculation of numbers of S.vernum per 100 m. stream length sampled

Date	Predicted total No. larvae/sample	Length of stream sampled (metres)	No. of larvae per 100 m. stream	corrected % age S.vernum/sample	No. of S.vernum/100 m.
29.6.72	82	9.5	863	62.0	535
7.7.72	116	12.8	906	47.5	430
21.7.72	539	14.0	3850	46.4	1786
27.7.72	1015	14.7	6905	40.4	2787
3.8.72	1304	18.2	7165	34.8	2489
10.8.72	1372	15.2	9026	35.5	3204
16.8.72	1332	16.3	8172	31.6	2582
23.8.72	1155	32.5	3553	41.0	1457
7.9.72	862	31.6	1373	20.6	283

TABLE 6.8 Numbers of S. vernum in each instar per 100 m. stream length

Date	Instar I	Instar II	Instar III	Instar IV	Instar V	Instar VI	Instar VII
29.6.72	0	35	98	73	85	49	195
7.7.72	18	28	119	55	82	55	73
21.7.72	18	55	255	373	502	328	255
27.7.72	25	142	452	761	672	504	231
3.8.72	182	222	374	446	627	436	202
10.8.72	186	327	343	670	739	612	327
16.8.72	0	261	150	423	625	599	524
23.8.72	0	31	146	184	498	414	184
3.9.72	0	7	24	74	59	45	74

TABLE 6.9 Accumulated total numbers of S.vernum larvae, i.c. VII; VII + VI; VII + VI + V, etc.

Date	I+	II+	III+	IV+	V+	VI+	VII
29.6.72	535	535	500	402	329	244	195
7.7.72	430	412	384	265	210	128	73
21.7.72	1786	1768	1713	1458	1085	583	255
27.7.72	2787	2762	2620	2168	1407	735	231
3.8.72	2489	2307	2085	1711	1265	638	202
10.8.72	3204	3018	2691	2348	1678	939	327
16.8.72	2582	2582	2321	2171	1748	1123	524
23.8.72	1457	1457	1426	1280	1096	598	184
3.9.72	283	283	276	252	178	119	74

TABLE 6.10 S.vernum life-table showing mortality during larval stages adjusted to give 1000 instar I larvae.

lx = number alive at onset of instar
dx = number dying during that instar

Instar	lx	dx	% Real Mortality
I	1000	30	3
II	970	111	11
III	859	91	9
IV	768	246	25
V	522	212	21
VI	310	196	20
VII	114	-	-

moving away from the study area in addition to those which die. The value of 89% mortality instars I-VII obtained from Richards and Waloff's method will also be subject to inaccuracy due to the non-collection of early instars and especially so considering the frequency distributions for S.vernum in Cronkley stream 2: section A. This result also gives a survivorship curve conforming to type II of Slobodkin (1962) with an arithmetic decrease in numbers with time, which is contradictory to the other life-tables and probably results from the inaccuracy of this application of the method. Projection of the post-peak accumulated totals to the first appearance of each instar would substantially alter the shape of the curve and difficulty in doing that in the present study led to the abandonment of the method.

Laboratory experiments by Hall and Harrod (1963) on S.nitidifrons showed that, under these conditions, the greatest mortality occurred in the early instars, 52.7% of first instars dying, mainly in the process of ecdysis. This provides experimental evidence of the inaccuracy of the application of Richards and Waloff's method used here.

7(i) CALCULATION OF PRODUCTION :METHODS

There is a growing literature on the production of freshwater animals as its importance in quantitative ecology has become recognised.

Production has been defined by Ivlev (1945) as "the sum of all organic matter added to the stock of a product (or other defined organic unit) in a unit of time" and it was in this sense that the word production was used in this study.

Allen (1951), developing ideas put forward by Ricker (1946) and Allen (1949),, devised a graphical method for estimating production. For one generation, numbers of animals per sample stretch are plotted against the mean weight of animals for the successive population estimates. Assuming growth and mortality to be logarithmic, Ladle et. al. (1972) fitted an Allen curve to their populations of simuliids in a Dorset stream and the production of each generation is represented by the area under the graph. Neess and Dugdale (1959) developed the mathematics of Allen's method and their analysis was used by Neveu (1970) in calculating the production of Simuliid larvae in a French hill stream.

Neveu (loc. cit.) also used a method devised by Waters (1966), which was modified (Waters, 1969) using Ricker's (1968) suggested International Biological Programme nomenclature, and was given as:

$P = G \langle B \rangle$ where P = production;
G = instantaneous growth rate; and
$\langle B \rangle$ = mean standing biomass

Having obtained life-tables it was decided that the methods outlined above would not give as accurate a production estimate as the method of Winberg et. al. (1971), based on Boysen-Jensen (1919) where:

$P = B_E + (B_t - B_o)$ where P = production;
B_E = elimination biomass; and
$B_t - B_o$ = biomass increase of population after time t.

In order to apply this method, the mean weight of each instar of each species was calculated (see 7(ii)). Multiplying i from the life-tables by the mean instar weight, m, will give the total weight of larvae in each instar class. Thus B_t of the equation will be given by im for instar VII and B_o by im for instar I. As the values of i were calculated for the median developmental age of each instar, $B_t - B_o$ will give an underestimate of the total larval biomass increase. The production estimates have been set out in Appendix 4 where it can be seen B_E has been calculated from d_x of the life-tables and i_{dx} which is the mean weight of eliminated larvae. No measure of m_{dx} has been obtained so it was given as the mean of im values for successive instars. By summation of $d_x m$ the value of B_E is obtained and the production figures obtained from Winberg's equation.

The same 30-day and 40-day durations of the life-tables were used in presenting the production figures so two values were obtained in each case. The mean length of stream for each cohort was obtained from Table 4.1 and thus the production per metre stream length given in each case and this has been summarised in Table 7.2. Only complete cohorts (those not marked with an asterisk in Table 6.4) were used in obtaining production estimates.

Tables used in calculating production are given in Appendix 4.

7(ii) DETERMINATION OF LARVAL WEIGHT

The method of drying larvae was that given by Ladle et. al. (1972). Larvae, which had been preserved in 70% alcohol were separated into instars by taking overall length measurements, having already been sorted into species.

Known numbers of each species and instar were placed in foil boats in crystallising dishes and dried in an oven at 105°C for 24 hours. In addition, two batches of 100 first-instar larvae of unknown species were similarly treated. After removal from the oven the foil boats were transferred to a desiccator and the dried larvae subsequently weighed on an electro-micro-balance. Care was taken between weighings to ensure the lid of the desiccator was closed.

After obtaining the dry weight of the larvae in this way the mean weight of each instar could be calculated for the four species. As a check against the absorption of atmospheric moisture, the balance arm was left unclamped when weighing some larvae and, though the deflection of the galvanometer needle was not large, the effect could be noticed. This was more obvious in the case of the smaller instars where the most sensitive scale was used. All weighings were completed before movement of the needle in this way.

Ladle et.al. (1972) have produced a correction factor of 1.4 for conversion of preserved dry material to fresh dry weights and this is given in Table 7.1. Graphs of the mean weight of each instar against length are plotted in Fig . 7.1 , and these show for all species the same type of length-weight curve to that given by Ladle et. al. (1972) for their species. Even after applying a correction of 1.4, however, larvae from the bog streams - although of different species - were lighter per length category than those from the southern stream.

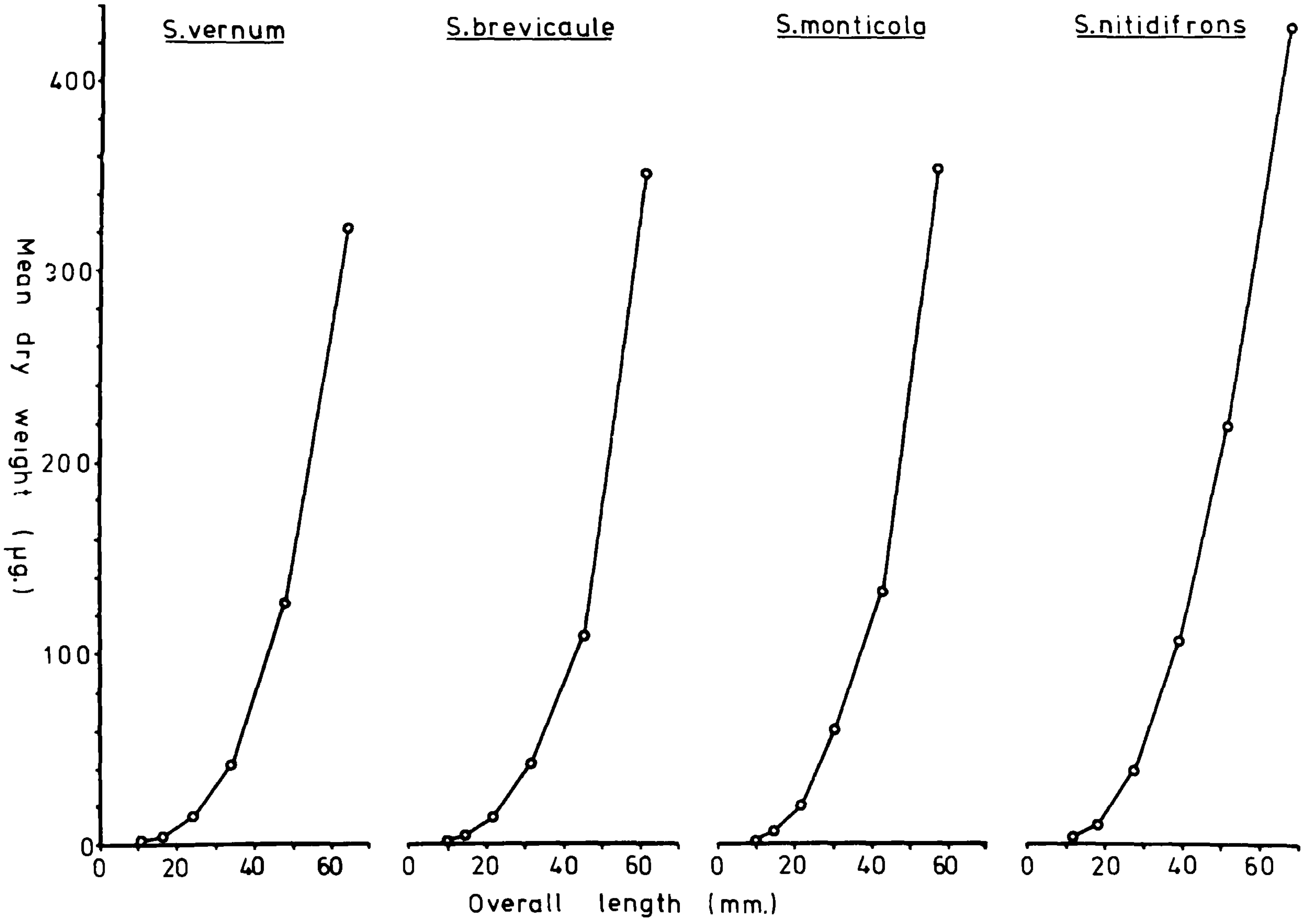


Fig. 7.1. Length - weight relationship for four species

Table 7.1 Mean Weight of Each Instar with Correction of Ladle et al (1972)

Instar	Number of Larvae in Sample	Mean Weight (µg)	Corrected Mean Weight (µg)
Unknown spp			
I	200	0.5	0.7
S.vernum			
II	53	1	1
III	117	3	4
IV	132	11	15
V	123	30	42
VI	85	90	126
VII	82	231	323
S.brevicaule			
II	19	1	1
III	75	3	4
IV	59	10	14
V	63	30	42
VI	67	77	108
VII	45	251	351
S.monticola			
II	41	1	1
III	49	4	6
IV	72	15	21
V	79	43	60
VI	79	95	133
VII	51	253	354
S.nitidifrons			
II	53	2	3
III	72	7	10
IV	51	27	38
V	76	76	106
VI	43	156	218
VII	44	305	427

7(iii) COMMENTS ON THE PRODUCTION ESTIMATES

Comparing all four species in Cronkley stream 2, production of larvae was greater in each case in section B than in section A per metre stream length in equivalent cohorts. This was also true when considering *S.vernum* in section D of Moss Burn in comparison with the same species in section C. Although not a comparable cohort in terms of time, it is interesting to note that the production of *S.vernum* in section B was nearly as large as in section D.

In terms of the production of complete cohorts, *S.vernum* was the most important species in both streams studied. *S.nitidifrons* was also important in section D of Moss Burn. Of the cohorts where "recruitment" was greater than mortality, the early-July to early-August population of *S.vernum* and the early-:mid-July to early-:mid-August cohort of the same species in Moss Burn: sections C and D respectively, were more important numerically than the cohorts for which production estimates were obtained. With these exceptions, therefore, the production values given in Table 7.2 contain the largest production figures obtained in the present study.

Considering Moss Burn: section D and Cronkley stream 2: section B the following production estimates for all species were obtained for cohorts hatching in late-July and early-August:

Moss Burn: section D 9.7 — 13.2 mg. $m.^{-1}$
Cronkley stream 2: section B 42.5 — 56.9 mg. $m.^{-1}$

Turnover ratios have not been calculated in this study because of the difficulty of obtaining mean biomass estimates. The largest production estimate of 56.9 mg. $m.^{-1}$ assuming 30-day development of all species is very low, even compared to the lowest value of Ladle et. al. (1972) for *S.equinum* alone of 260 mg. $m.^{-2}$. This comparison is made assuming the Pennine stream to be ca. 1m. wide

Table 7.2 Production Values for Four Species in Moss Burn and Cronkley Stream 2

Stream	Species	Cohort	Production (mg m^{-1})
Moss Burn Section B	S.vernum	Late-June : Early-July — Late-July : Early-August	3.3 - 4.4
Moss Burn Section C	S.vernum	Late-July : Early-August — Late-August : Early-September	1.4 - 1.8
Moss Burn Section D	S.vernum	Late-July : Early-August — Late-August	4.3 - 5.9
	S.brevicaule	Early- Mid-July — Early-August	0.8 - 1.1
		Late-July : Early-August — Late-August	0.4 - 0.6
	S.monticola	Early- Mid-July — Early-August	0.9 - 1.3
		Late-July : Early-August — Late-August : Early-September	0.9 - 1.2
	S.nitidifrons	Late-July : Early-August — Early-September	4.1 - 5.5
Cronkley Stream 2 Section A	S.vernum	Whole Summer	8.7 - 11.7
	S.brevicaule	Main Summer Generation	5.0 - 6.7
	S.monticola	Mid- Late-July : Early August— Late-August : Early September	3.4 - 4.6
	S.nitidifrons	Mid- Late-July : Early-August— Late-August : Early-September	3.1 - 4.1
Cronkley Stream 2 Section B	S.vernum	Mid-June — Mid- Late-July	3.0 - 4.0
		Early-August — Late-August : Early-September	17.6 - 23.7
	S.brevicaule	Mid- Late-June — Mid- Late-July	2.1 - 2.8
		? Late-July — ? Late-September	4.0 - 5.3
	S.monticola	Late-June : Early-July — Late-July : ?Early-August	0.2 - 0.3
		Early- Mid-August — Late-August : Early-September	11.4 - 15.2
	S.nitidifrons	?Mid-June — ?Mid-July	0.4 - 0.6
		Mid- Late-July : Early-August Mid- Late-August	9.5 - 12.7

8. DISCUSSION

(i) The population biology of Upper Teesdale Simuliidae

Few egg-masses were found during the present study, seven being collected in June 1972 and twenty-three in September of that year from Cronkley stream 2: section B. There is no way of identifying these as being from a certain species but Davies and Peterson (1956) have concluded that only the *Simulium* sub-genus lay eggs in masses, the others either laying in a film while hovering, or by dipping the abdomen into the water to allow eggs to be washed off. Oviposition was never observed but it seems probable that other methods than the formation of egg-masses were employed, there being so few found.

Egg-diapause has been demonstrated by Davies and Smith (1958) in *Prosimulium hirtipes* which did not hatch in a west Pennine stream until autumn when temperatures were at more favourable low levels. Insufficient numbers of the closely-related *P.arvernense* were obtained to determine if this species showed a similar pattern, but none were collected in the Upper Teesdale streams in summer in this study.

The absence of *S.vernum* and *S.angustitarse* larvae in Cronkley stream 3: section A was not a result of egg-diapause in these species since both were found in summer in other Cronkley streams. Plate 1 shows that this stream is well-shaded in summer and Zahar (1951) believed this to limit population numbers in Scottish streams he studied. Since Zahar's paper, Hughes (1966) has stated that he collected large populations of blackfly larvae from shaded waters in Africa, so this may be a factor influencing only temperate populations. Working in the south of England, Ladle and Esmat (1973) have described a similar reduced summer population to that found in the Pennine streams and ascribe this to the reduced water-levels of summer. Reference to Appendix 1 shows a similar reduction in water-level here, and this will diminish current-flow and cause the *Potamogeton* leaves to form more closely-applied mats.

The frequency histograms (Chapter 5) show *S.vernum*, *S.brevicaule* and *S.nitidifrons* to have a second winter generation hatch in January and February in Cronkley stream 2; hatching of *S.monticola* taking place principally at this time in both 1971 and 1972.

Such a mid-winter hatch could have resulted from eggs laid at this time (Neveu, 1973a) found adults in mid-winter near a Pyrenean stream) but no pupation occurred before March in the bog streams studied. Female flies would thus have had to undergo an upstream flight from a lower site where pupation may have begun earlier. This seems an unlikely explanation, especially when the hostile climate of the region is considered. If the eggs producing the second winter cohort were in diapause until this time it is difficult to visualise what could cause the state to be broken in mid-winter. A more credible explanation is that these eggs were in that condition described by Mansingh (1971); Mansingh et. al. (1972) as oligopause (i.e. a state between diapause and quiescence). Davies (1961) and Peterson (1970) have both described hatching of some eggs in winter months in Canadian *Prosimulium* spp. but why some eggs should hatch quickly and others only after a period of time is not known. This would merit further investigation.

Prolonged hatching of eggs in other seasons has been reported by Grenier (1949); Fredeen et. al. (1951); and Davies (1961) and the phenomenon is known to occur in other freshwater insect groups, e.g. Ephemeroptera and Plecoptera. Hynes (1970) regards this as an "insurance" against the rigours of the stream environment. Continuous hatching of the eggs of *S.vernum* and *S.brevicaule* would produce the type of confusing frequency histograms found for Cronkley stream 2:

section B in the summer of 1972. Certainly, in Cronkley stream 2, the winter generations were well synchronised when compared to the summer ones.

The timing of the first summer cohort in the study streams was affected by the presence, or virtual absence, of an overwintering generation. (Cohort being used here to describe a temporally discreet larval population represented in the frequency distributions.) In Moss Burn: section D the summer generation consisted of four cohorts in *S.vernum* and *S.monticola* (with a possible fifth in the latter) and three in *S.brevicaule* and *S.nitidifrons*. The last cohorts of *S.vernum* and *S.monticola* appear at the same time here as the presumed winter generations in Cronkley stream 2. It thus seems probable that some larvae hatch from eggs to produce "winter" larvae in Moss Burn. It is not known whether other eggs undergo a diapause through the winter as the collections suggest but the larvae which hatch from the very small winter generations in this stream. As such they cannot be considered summer cohorts which means all species in section D have three summer cohorts. This is also true of *S.vernum* and *S.aureum* in section B of Moss Burn.

There were fewer cohorts of *S.monticola* and *S.nitidifrons* in Cronkley stream 2 than in the lowest part of Moss Burn (*S.vernum* and *S.brevicaule* being impossible to differentiate into cohorts). The first cohort of all species appeared later here than in the Moor House stream, where larvae hatched from presumed diapause eggs, because larvae were hatching from eggs laid by the emerged overwintering generation.

Several workers have studied the life-histories of the same black-fly species as those in the present study. Obeng (1967) found larvae and pupae of *S.latipes* (*S.vernum*) occurring throughout summer in a Welsh mountain stream, whereas Zahar (1951) and Maitland and Penney (1967) considered it to be bivoltine as a result of their work in Scotland. Where the conditions for development are advantageous it would seem to be an opportunistic species and Davies (1968) describes "irregular" hatches throughout the summer. The same author describes S.brevicaule as having pupae from February to September, so this species appears similarly opportunistic.

Maitland and Penney (1967) concluded that S.monticola was a bivoltine species, while Obeng (1967) found three generations of this species in Wales. Both authors agree that S.nitidifrons had three generations a year.

This study on the bog streams shows that most species are at least bivoltine with a winter generation (sometimes very poorly represented) and a summer generation consisting of several cohorts. If a summer cohort hatches from eggs laid by flies which emerged from an earlier summer cohort then each will have generation status. While this remains a possibility it is not easy to furnish evidence that this did occur.

The majority of the streams studied conform to the pattern described by Maitland and Penney (1967) for headwater streams, larvae being more numerous in summer than in winter. Rivers tend to show the reverse of this pattern (Neveu, 1973a), and Armitage (in personal communication) has found this to be the case in the Tees. The exceptions to this pattern (Cronkley stream 3: section A and Force Burn: tributary B) resulted from changes in the suitability of the habitat.

A downstream species succession can be seen in Moss Burn (Table 3.5). Longitudinal zonation of benthic invertebrate species has been described in several studies on running-water systems, e.g. Dodds and Hisaw (1925); Ide (1935); Macan (1957); and Maitland (1966). When the streams are sampled further down other species will occur, e.g.

S.variegatum in the lower sections of three Cow Green streams (Table 3.2) and *S.reptans* in Maize Beck. Some species, e.g. *S.aureum* and *S.monticola* have definite habitat preferences, probably because of choice of oviposition sites by females, but this seems not to be the case with *S.vernum* and *S.brevicaule* which are both widely distributed.

Graphs to show changes in the species composition through summer 1972 are presented in Figs. 8.1-8.4. The values plotted were obtained by multiplying the population estimates (from removal trapping) by the percentage species composition. Reference to the frequency distributions in Chapter 5 shows that peaks correspond, for the most part, with hatches of larvae. Increases in numbers could also be obtained when conditions for collecting were optimal, e.g. after a period of settled weather, and this effect will influence all quantitative studies in such a habitat.

These graphs complement the data presented in Table 3.4. In section B of Moss Burn (Fig. 8.1) numbers of all species decreased through July and early-August at a time when they were increasing in section D of this stream (Fig. 8.2).

Populations of all species in Cronkley stream 2: section A built up steadily until mid-August (Fig. 8.3), after which numbers here declined until mid-September. There is no evidence from the frequency distributions (Fig. 5.7) to suggest that this increase was due to hatching of eggs on a large scale except, perhaps, in *S.brevicaule* and this emphasises the importance of determining population structure in detail before interpreting quantitative data. It seems possible that the upper part of Cronkley stream 2: section A sampled in June and early-July was not able to support such large populations of larvae for some reason as the more downstream parts sampled in late-July and August.

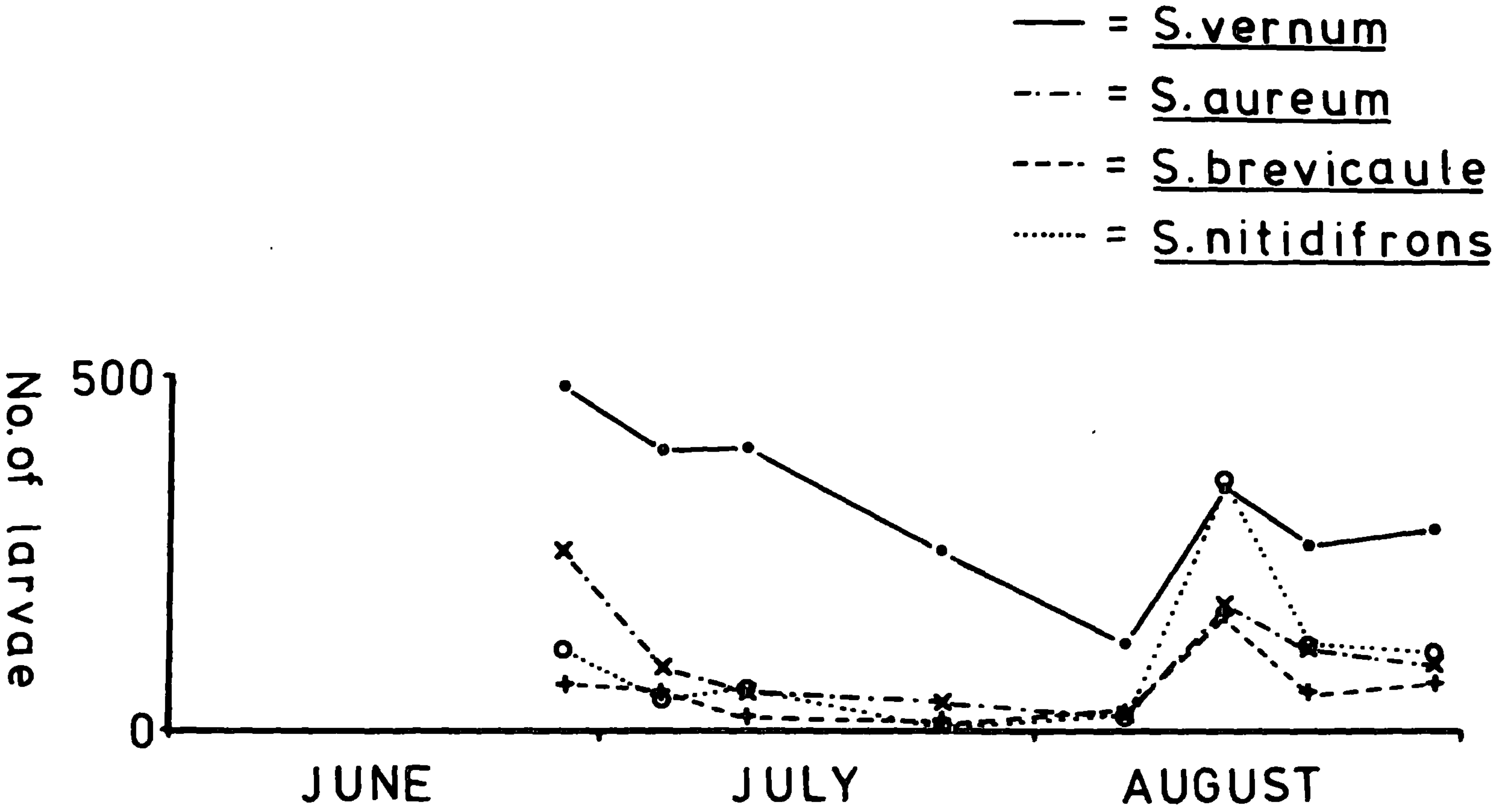


Fig. 8.1. Species composition of larvae in Moss Burn : section B. Summer 1972.

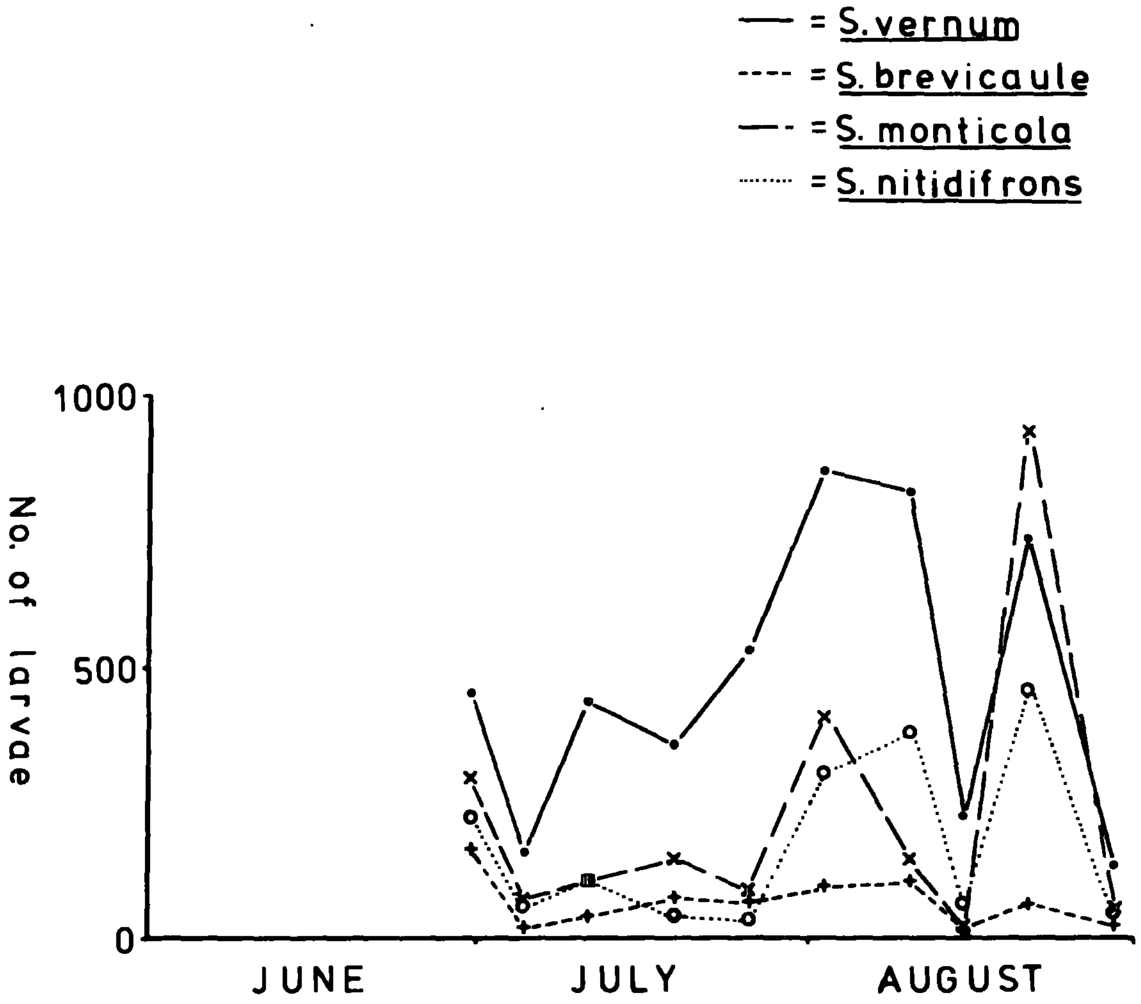


Fig. 8.2. Species composition of larvae in Moss Burn : section D. Summer 1972.

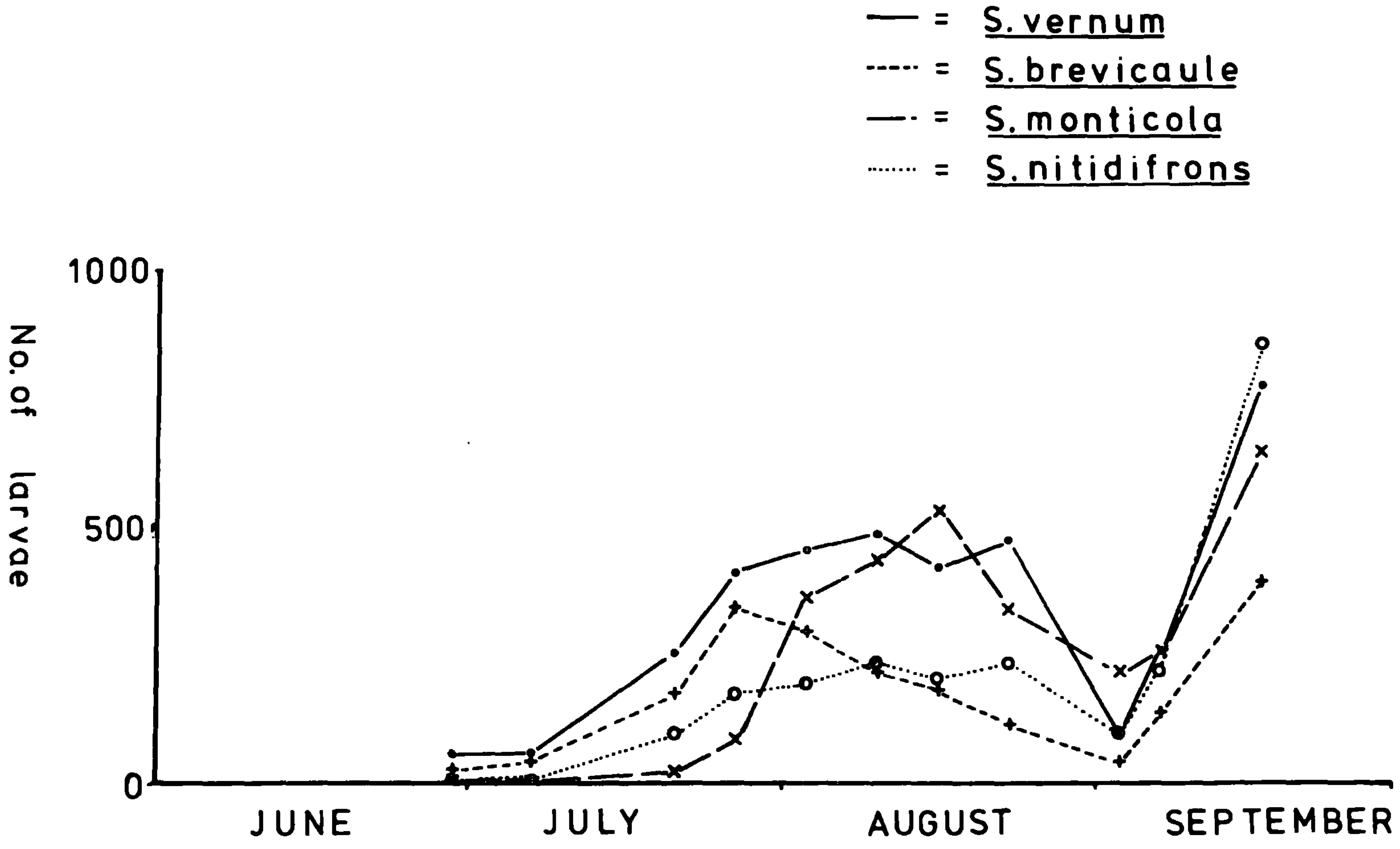


Fig. 8.3. Species composition of larvae in Cronkley stream 2 : section A. Summer 1972.

Just as the population structure was different between sections B and D of Moss Burn, Cronkley stream 2: section B proved more conducive to larval life than section A, as shown by the higher populations collected here (Fig. 8.4). Unlike Moss Burn, however, the relative abundance of the species here were similar between sections. It is interesting to note that the species of the Eusimulium sub-genus showed peaks of numbers before those of the Simulium sub-genus. A similar delay occurred in Cronkley stream 3: section A, where the development of S.angustitarse followed that of S.vernum (see Fig. 5.3). In the former case the pattern is consistent and, as vegetation sampling only was carried out here, changes in substrate type in adjacent samples do not provide an explanation.

Becker (1973) has demonstrated that, in S.vittatum, a lower thermal sum is required for 50% pupation in high rather than in lower temperatures, i.e. growth is more efficient at these higher temperatures. In the bog streams the water temperature will be very much lower in winter than in summer, as reference to Appendix 1 indicates. Apart from its direct effect on the slow development of larvae, this will indirectly affect other factors in development, e.g. the availability of suitable nutrients with the reduced activity of organisms bringing about the break-down. Whereas development of a larval cohort takes 30-40 days in summer, in winter it takes at least three times the longest summer estimate.

Reference to the thermograph records enables one to obtain thermal sum estimates for some complete summer cohorts. Thus the late-July hatching cohorts of S.monticola and S.nitidifrons in Moss Burn: section D required 348.9 degree-days above $0^{o}C$ for their development to pupation. (Calculated as the sum of mean daily temperatures using $12.6^{o}C$ mean temperature for the gap in records from 23.viii to 29.viii.) With the

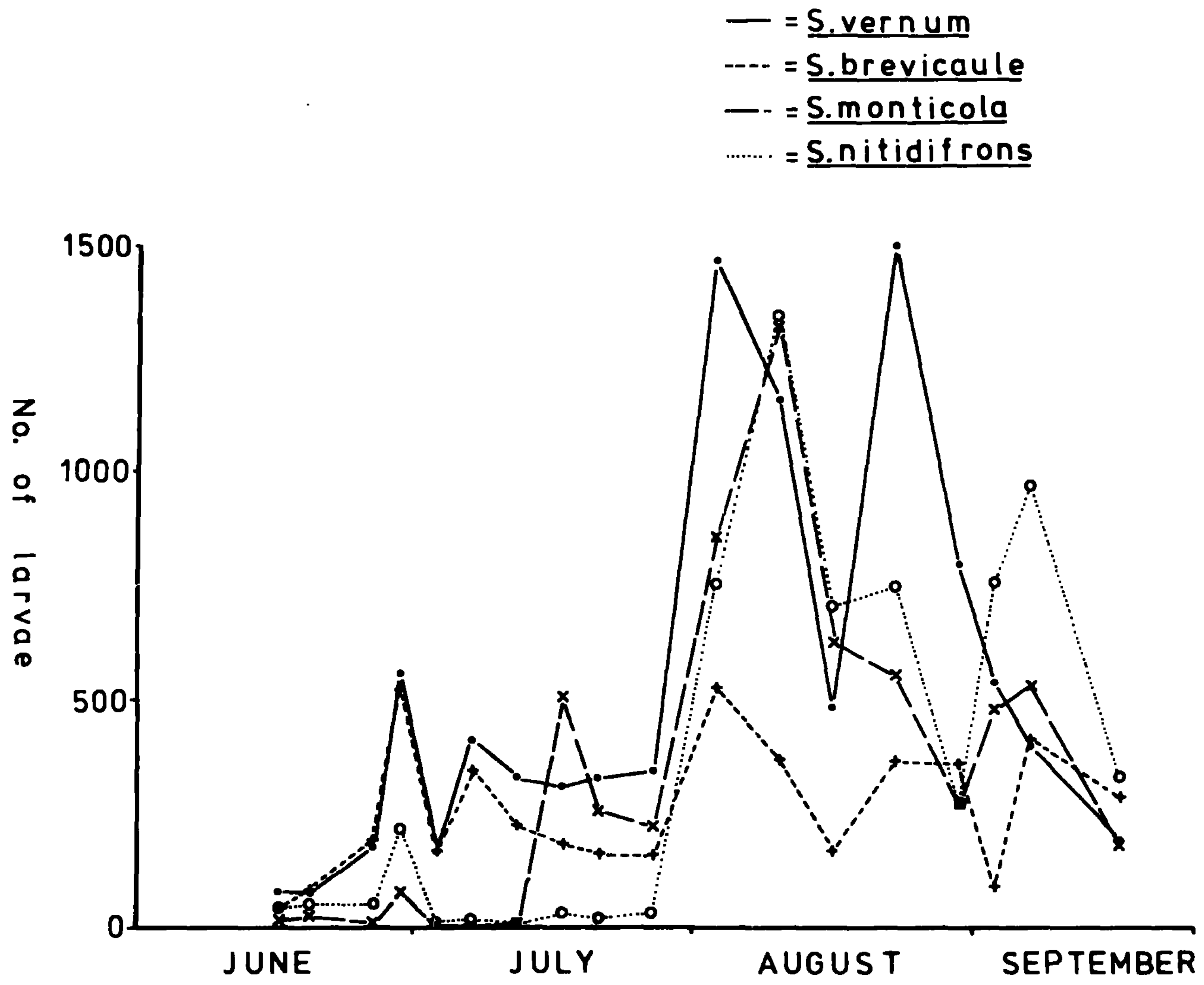


Fig. 8.4. Species composition of larvae in Cronkley stream 2 : section B. Summer 1972.

mean daily temperature over this period at 10°C this is a considerably higher requirement than the 126 degree-days at 17°C recorded by Becker (loc. cit.) for S.vittatum. In the latter case the duration was only 7.4 days for 50% pupation, so the field population in Upper Teesdale is growing at a much slower rate.

Fredeen (1964) has demonstrated that S.vittatum and S.venustum fed entirely on bacterial suspensions grow at differing rates in different concentrations at the same temperature. When the concentration of bacteria was high the growth of larvae was rapid and, when it was reduced, growth was consequently much slower. Food availability, in addition to temperature, is therefore an important factor in controlling the growth of populations in the field.

Simuliid larvae, being passive filter-feeders, are dependent on particles carried by the current. Carlsson (1962) therefore suggested that the gut contents would correspond to the suspended fine matter in the current. Where the proportions of certain types of particle were high in the current one would expect the simuliids to be largely feeding on this fraction. The diet of larvae has therefore been described as particles of animal and plant material (Jones, 1949; Egglishaw, 1964); diatoms and desmids (Badcock, 1949); bacteria (Fredeen, 1964); and, occasionally, chironomids (Badcock, 1949; Serra-Tosio, 1967), but these are probably taken by browsing over the substrate. Burton (1973) has recently described the African S.hargreavesi Gibbons actively feeding on filamentous algae.

Where the amount of suspended material is large, simuliid larval populations are often correspondingly large, and this is particularly true of lake and reservoir outlets (Müller, 1955; Ulfstrand, 1968b), and the presence of lakes along the length of rivers has been postulated by Carlsson (1968) to be a reason for the abundance of animals these contain. No such feature was present in this study but some large pools, relative to the stream size, were found in sections A and B of Moss Burn. Examination of the water from these pools showed only peat particles to be present in suspension and they were of little influence on increased food availability.

The presence of peat is known to have a suppressant effect on the growth of some diatoms (Round, 1953; Douglas, 1958) and the latter were probably of little importance as a food source in the bog streams. Growths of filamentous algae did occur in the lower sections of the bog streams and their breakdown may have contributed to the larval diet. Peat particles were the predominating organic material in the current and formed the major suspended potential food available to the larvae in the study streams. Working on the River Duddon in the Lake District, Minshall and Kuehne (1969) concluded that faunal differences between the upper and lower stretches could be explained on the basis of the type, and nutritive value, of the detritus. Coarse detritus, low in nutritive value and difficult to digest could preclude many invertebrates from the upper basin (equivalent to the region of the study streams). Recently, Madsen (1972) has shown that Plecoptera feeding on the organic layer covering stones assimilate bacteria and fungi which grow on the trapped detritus material which may in itself be of low nutritive value. Fredeen (1960) has demonstrated that simuliid larvae, fed entirely on bacterial suspensions in the laboratory, can show a similar development time to the same species under field conditions. The surface coating of peat particles may be of great importance in the nutrition of larvae in the Upper Teesdale streams and, as fungal hyphae are much more common in Pennine peat than bacteria (Latter et. al. 1967), the fungal component is potentially the major food source in the study streams.

Another factor limiting population numbers is settlement area. Schwoerbel (1972) found that in a stream of 50 cms depth (deeper than all those studied), at the maximum population density of Simuliids, only 4% of the available current volume is exploited. He went on to suggest that, at the greatest settlement density ($>$ 12 larvae cm^{-2}), it is not the food supply but the settlement area that controls numbers, and this has also been suggested by Anderson and Dicke (1960).

In the study streams the amount of suspended material was large, though probably of low quality, and the amount of available substrate varied from collection to collection. Observations by the author suggest that substrate availability was never limiting, so the settlement area hypothesis of Schwoerbel (1972) was probably not applicable here. It may explain some differences in the population estimates however. Although a standard sampling effort was employed in removal trapping, areas where vegetation was abundant probably provided more optimal sites per sampling stretch than areas where vegetation was sparse. Thus the early-August collections in Cronkley stream 2: section B were from areas of abundant vegetation (see Table 4.1) and the population estimates at this time were coincidentally high.

It has been discussed that the increase in numbers of larvae in Cronkley stream 2: section A may be due to sampling areas increasingly suitable for larval settlement. Table 4.1 shows that the sample lengths were generally smaller in section A than in section B of this stream, so the amount of available substrate appeared greater upstream. The stream narrows toward the lower section, however, and therefore a greater length will be sampled for the same effort here. It is noticeable, however, that the population estimates are very much larger downstream (see Figs. 4.8 and 4.9) and the increase in current flow with the stream narrowing may have an important effect here.

Ulfstrand (1968a), working on a Lapland stream, found that blackfly larvae showed a strong over-representation in shallow water compared to other groups and he put this down to the preferred streamlined flow régime likely in these conditions. Subsequently, Egglishaw (1969) has found the reverse of this situation in a Scottish stream with greater numbers in deeper water. That current flow is a most important determinant of the distribution of simuliid larvae has been demonstrated by Phillipson (1956, 1957) and it is probably current speed at the microhabitat level, combined with the suitability of the substrate, which governs the differences in the results of the two workers. No information on the effect of normal water depth was gained in the present study, but large numbers of larvae were able to thrive in section A of Moss Burn in regions where the maximum depth could not have exceeded 1 cm.

(ii) Mortality and production of Upper Teesdale Simuliidae

The mortality estimates obtained in the present study range from 91-93% instars I-VII for S.vernum in section B of Moss Burn, to 97-98% instars I-VII for S.monticola in Moss Burn: section D.

In Appendix 3 it can be seen that some incomplete cohorts almost certainly show a higher mortality than the values given above, e.g. all those of S.nitidifrons; others probably show a lower value, e.g. S.vernum in Moss Burn: section B. Neveu (1970) has given some low mortality values for larvae in a Pyrenean stream: 86% mortality occurring in S.ornatum sampled from mosses while "spring-summer" larvae inhabiting the benthos give values as high as 96%. The same author includes mortality estimates for S.monticola + S.dorieri Doby et Rault, which showed a loss of 95% on mosses, 94% on vegetation, and 93% in the benthos but these results, being from different years, make comparison impossible.

As mentioned in Chapter 6, mortality in the present study includes immigration into, and emigration from, the study stretch, and this probably has an important effect on the frequency distributions, notably in Moss Burn: section D. In the second and third cohorts of S.vernum it can be seen that "recruitment" was greater than mortality and this was also true of the first two summer cohorts of this species in section C of Moss Burn. Reference to the life-tables in Appendix 3 shows much of this "recruitment" was of later instars. This could have been the result of inaccuracies in the method of calculating the numbers of larvae in each instar, but it is more likely that they have moved into the study areas by downstream movement in the drift. As the instar-day totals included several samples, the effect of favourable smaller areas giving bias can be ruled out as the cause of the increased numbers of later instars.

The phenomenon of downstream movement may also have important consequences for other life-stages and, though no estimates were obtained in the present study, consideration of the subject is important in explaining events occurring in the life-histories of the different species.

Waters (1972) in his excellent review of work on drifting of stream insects described drifting as "a temporary event in the life of many members of the bottom fauna or other substrate-oriented populations". Anderson and Lemkuhl (1968) showed a five-fold increase in the drift-rate of invertebrates in an Oregon stream after freshets and, in the case of simuliids, Yakuba (1959) concluded that it was the rate of increase in flow, rather than the increase itself, which caused large migrations. This is of major importance when considering the nature of the bog streams which are subject to large and rapid increases in current-flow after rain. An attempt to obtain data on the drift-rate of simuliids in the lower part of Moss Burn was thwarted by the nets used becoming clogged with the large quantities of peat in the current (cf. Crisp, 1966).

The rainfall records from Moor House meteorological station provide information on when spates occurred in Moss Burn in summer 1972 (Fig. 2.5). Reference to Figs. 4.5 and 5.12 will then provide information on how the simuliid larval populations changed with the greatly increased flow at these times.

The frequency histograms for Moss Burn: section D show that there was no apparent differential effect on separate instars, and the only decrease in population estimates attributable to spates was that of 5.vii, a collection made the day after the largest level recorded during the summer.

In addition to the increase in flow, sudden decreases also cause mass migrations of larvae, as has been demonstrated in the United States by Tarshis and Neil (1970). Here, spillway doors were accidentally closed and the blackfly larval population spun large quantities of silk, which formed "ropes" and they were thus carried from the area by the diminishing current. When a stream dries up, as Force Burn: tributary B did in the present study, larvae must migrate downstream; move into the sediments or become desiccated. No other stream dried up but reductions in water-level after a prolonged dry spell, in reducing current flow, may cause larvae to move into more optimal conditions.

Sprules (1947) found simuliids, and Trichoptera, to be less affected by spates than Plecoptera, Ephemeroptera, and chironomids in Algonquin Park on the Canadian Shield. This is doubtless due to the more effective anchoring mechanisms of the former groups which are dependent on a strong current to obtain food. Much will depend on the composition of the benthos and Elliott and Minshall (1968) point out that, in a Lake District stream, the composition of the drift was generally similar to the total benthos, though Plecoptera and Ephemeroptera showed a higher proportion in the drift and Diptera a lower value. In his study on a European stream Müller (1970) showed that simuliids accounted for 26% of the drift and were the second most important component to the Ephemeroptera. The simuliids there would certainly have been important numerically in the benthos.

Elliott (1971b), having artificially induced drift, found simuliids were not significantly different to dead invertebrates in their drifting at modal water velocities $\geqslant$ 19 cm sec^{-1} but, at lower velocities, larvae were readily able to return to the substrate. No flow readings were taken in Cronkley stream 2 but in Moss Burn current flow ranged from 21 cm sec^{-1} to 88 cm sec^{-1} (by OTT flow-meter) over a period of two months in a typical riffle so, in the light of Elliott's (loc. cit.) findings, larvae, once dislodged, would be carried into the pool areas. They would have to regain fast-flowing stretches by some upstream migration (Elliott, 1971c) or move over the substrate to the next suitable downstream region.

In the upper sections of Moss Burn, where the flow will be much less, smaller levels of drifting would be expected in comparison with the lower sections. This will contribute to the lower levels of mortality in the upper sections of Moss Burn. If simuliid larvae are carried in the drift the silk thread they spin trails in the current, and Elliott (1971b) points out that this is likely to be less successful on a stony bottom with few macrophytes than a region where vegetation is plentiful. This furnishes another explanation for the lower mortality estimates obtained from the upper reaches of Moss Burn, where trailing plant growth was much more abundant.

Experiments by Reisen and Prins (1972) have shown that, with the exception of Ephemerella sp., drifting animals did not respond in a density-dependent fashion to benthic population increases. In contrast Müller (1966), Dimond (1967) and Ulfstrand (1968b) have regarded drifting as being a means of reducing population pressure which is distinctly density-related. Given the very small populations of Simuliid larvae occurring in the Upper Teesdale bog streams "behavioural" drift, which would occur at high population densities, would be relatively unimportant when compared with "accidental" or "catastrophic" drift, which occurs at times of spate.

An important way in which drift affects the mortality of Simuliidae is in acting on different life-stages. Thus, Yakuba (1959) postulated there was an increase in migratory activity with increase in the age of larvae, which has subsequently been disputed by Küreck (1969). Maitland and Penney (1967) demonstrated movement to pupation sites in last-instar larvae which would make dislodgement of this instar easier than earlier stages. This may contribute to the "recruitment" of later instars of S.vernum in Moss Burn: sections C and D. It is not as important in other sections since the larvae were sampled from vegetation where pupation takes place in situ.

When egg masses are placed into aerator-stirred aquaria first instar larvae, on hatching, produce masses of silk which forms into dense nets on which many of the larvae attach. If this pattern was replicated in the field it would tend to verify Yakuba's (1959) suggestion that early instar larvae stay close to the oviposition site and only later stages undergo active migrations. This is most difficult to investigate in the field since the mesh-size of net required would rapidly become clogged.

In studying the simuliid fauna of an area one is dealing with indigenous individuals; some which have drifted from upstream; and a much lower number (7-10% of downstream movement for all animals according to Elliott, 1971c) that have moved from downstream sites. Differences in the structure of the frequency distributions will be due to these sources as well as the causes of mortality outlined by Clark et. al. (1967), viz: ageing; low vitality; accidents; physico-chemical conditions; and natural enemies.

There is an extensive literature on parasites and predators of blackfly larvae and this can be outlined here. In the present study no evidence was found of protozoan infections (Zahar, 1951; Maurand, 1967; Maitland and Penney, 1967) or of nematode parasitism (Zahar, 1951). This may well be an altitude effect as mermithids are known to occur in larvae from the River Eden. Of the potential predators Hydracarina (Munchberg, 1956) are common components of the study streams fauna and have been seen to attack larval chironomids in the laboratory. Other potential predators are Plecoptera and Ephemeroptera nymphs and larval Trichoptera (cf. Jones, 1949; Maitland and Penney, 1967).

With the high levels of mortality in the younger stages one would expect production levels to be low. Reference to the life-tables in Appendix 3 shows that the number of final instar larvae collected per mean sample length often did not exceed twenty. As there were very few pupae in the collections, and taking into account the unknown pupal mortality, the number of flies emerging must have been very small. (2.8% of S.vernum were present as pupae in collections from section C and 1.1% from section D which were easily the largest numbers of pupae found in summer 1972 samples). Because of the limitations of the data no detailed consideration of the mortality estimates can be made.

As has been mentioned in the text errors incurred in the construction of the life-tables will be carried through to the production data. Some of this error will be caused by the under-representation of smaller instars and another error is in the method of determining the duration of final instar larvae. In the former case small larvae are so light relative to the later instars (Fig. 7.1) that even their considerable numbers are probably not as important as the possible over-estimation of final instar larval numbers.

Waters and Crawford (1973) have shown in a population of the mayfly *Ephemerella subvaria* that the removal summation method of calculating production (≡ Winberg et. al.'s method) gave a result in excess of the Allen curve and instantaneous growth methods; the results of the latter two being similar. The method thus tends to over-estimate production but this is compensated for by using the 30-day to 40-day durations in determining larval numbers. The frequency histograms for *S.monticola* and *S.nitidifrons* in Cronkley stream 2: section A show that here (Fig. 5.7) larval life might extend over a longer period than the maximum value used which will thus lead to overestimation of the real production in this area.

Although the development time was similar the larvae of *S.ornatum* and *S.equinum* studied by Ladle et. al. (1972) had a greater weight per body length unit. As a result one can conclude that the reserves of these larvae are somewhat greater than those of the bog streams which may have importance in egg production and therefore increased natality.

Factors which reduce mortality of larvae will increase the levels of production. In several production studies higher levels have been found where there is an increased supply of food (Hall et. al., 1970; Hughes, 1972; Maitland and Hudspith, 1974). Egglishaw (1968) has shown that streams with a high calcium concentration have more rapid breakdown of plant material and increased alkalinity has been put forward by Armitage (1958) as an important cause of increased production. In comparing two streams in America, Slack (1955) found the greater biomass in the one having stable physical conditions as animals will be less readily displaced here.

With their abundance of peat particles, low alkalinity and great instability the bog streams will provide a most unfavourable habitat for large production levels to be reached. One would expect a site below a reservoir outlet, or lake outlet, where particulate matter is abundant and the flow regulated to be the optimal site for the production of simuliids. Ulfstrand (1968b) studied such a site in Lapland and published the astonishing production figure of 3 g. wet weight cm.$^{-2}$ day^{-1} from a standing crop of not less than 125 g. m^{-2} wet weight. Assuming dry weight in Diptera larvae to be 25% of wet weight the production of blackfly larvae in the Lapland stream was some 400 times the maximum value per day recorded in the present study streams.

More comparable production figures to those obtained here have been presented by Neveu (1970) for the simuliid larvae in the Lissuraga in the Pyrenees. His measurements were in biovolume and so a correction was necessary in order to express his data in dry weight units. This is presented in Appendix 5.

Thus the annual production of simuliid larvae at the 175 m. O.D. station on the Lissuraga were <u>S.ornatum</u> 116 mg. m.$^{-2}$; <u>S.monticola</u> + <u>S.dorieri</u>, 70 mg. m.$^{-2}$; and <u>S.brevicaule</u>, 32 mg. m.$^{-2}$. Without the six incomplete cohorts in Cronkley stream 2: section B the maximum summer production of all species was 64.6 mg. m.$^{-1}$. The winter generation, being numerically smaller, would not give as large a production estimate as this and the annual figure would be a little below the 218 mg. m.$^{-2}$ recorded by Neveu (loc. cit.). The production figures for the Upper

Teesdale streams are far closer to the values in the French stream than those published by Ladle et. al. (1972) for the lowland Bere Stream in Dorset. There the annual production was much larger at 6.09 g. dry weight m^{-2}.

In their study of an American stream, in which allochthonous material was not important, Nelson and Scott (1962) were able to give dry weight production estimates for the trophic levels. They found that the ratio of primary : secondary : tertiary production was 216:8:1, which indicates the amount plants must produce to sustain the higher levels. The dominant plant in their study stream was Podostemon, an angiosperm, and this will certainly have broken down more rapidly, and released greater nutrient levels, than the dominant peat of the Upper Teesdale bog streams. In the present study the plant:herbivore ratio would certainly be larger than that given by Nelson and Scott (loc. cit.). The growths of filamentous algae which occurred in both streams would increase the available food material in the summer months but the scouring effect of spates caused their removal. In the upper reaches of Moss Burn trailing vegetation was abundant and because of this the potential increase in nutrients in these sections may have contributed to the production of larvae here.

Neveu (1970) has provided an illustration of how blackfly larval production can vary from season to season. At his 75 m. O.D. station, total net production for 1968 was 432 mg. $m.^{-2}$, whereas in 1967, at the same site, it was ohly 171 mg. $m.^{-2}$. Insufficient data are available for comparison of the simuliid populations between 1971 and 1972 in Upper Teesdale, but observation while collecting would suggest that larvae were more numerous in the latter year but not greatly so. The production figures obtained in the present study are thus not atypically low.

SUMMARY

1. A study of the larvae and pupae of the Simuliidae in the bog streams of Upper Teesdale was made from 1970 to 1972. The region was divided into three areas: Cronkley at ca. 350 m. (1150 ft.) above O.D.; Cow Green at ca. 500 m. (1640 ft.); and Moor House at ca. 580 m. (1900 ft.).

2. Of the 35 British species of simuliid, eleven were collected from the study streams and four more species are known to occur within the immediate area.

3. The climate of Upper Teesdale is briefly described and air temperature and rainfall data for summer 1972 at Moor House meteorological station are presented. A mercury-in-steel thermograph recorded water temperature in Moss Burn at this time and over three months the range of temperatures recorded extended over 20 C^{o}; the largest daily range being 14.5 C^{o}.

4. Substrate preferences of S.aureum and S.monticola lead to a zonation of these species in Moss Burn where a considerable change in habitat occurred along the length of the stream. This probably resulted from the choice of oviposition sites by the female flies of these species. S.vernum and S.brevicaule, by showing no obvious substrate preference, were able to exploit most streams.

5. A new method of gaining relative population estimates of simuliids is described. Originally, a polythene tape collecting method was employed but samplers using cut stems of Juncus were developed and used in the second year. This is a material which occurs naturally in the study streams and the surface area of the stems can easily be

calculated - small sections being cylindrical - to provide a comparative basis for estimating changes in population density.

6. The pattern of seasonal abundance of simuliid larvae varied between the Cronkley and Moor House streams. All had larger summer than winter populations (except Cronkley stream 3: section A which had excessive shading and reduced water-flow at this time). The Moor House streams had very poorly represented winter populations and the situation in the Cow Green streams was probably similar.

7. In summer 1972, larval numbers were larger in the early part of the season in Moss Burn, in contrast to the pattern in Cronkley stream 2 where summer numbers were at their lowest at this time. This effect is influenced by whether the streams supported a large winter generation or not.

8. A removal trapping technique was used to obtain absolute population estimates in summer 1972. Three fifteen-minute samples were taken using a standard sampling effort and the length of stream covered will therefore vary with the amount of suitable substrate present. The number of larvae in the three successive samples was determined and the population estimate obtained from these by a maximum likelihood statistical method.

9. The removal trapping technique is assessed and comparison with the *Juncus*-sampler results in Cronkley stream 2 made. The regression of these sets of data shows there to be no significant difference between the distributions and it is therefore probable that the changes in population seen in successive removal collections are the result of actual changes in numbers of larvae in the stream.

10. In both streams studied intensively in summer 1972, more larvae were found in the downstream, than in the upstream, sites. Moss Burn: section C provided an exception to this pattern, having fewer larvae than section B of the same stream.

11. The first of the three removal collections is shown to have the same instar composition as the other two and can therefore be used as a sub-sample of the whole. This was of considerable importance when larval numbers were high.

12. Larvae were originally measured by taking the width of the cephalic apotome. This afforded good separation into instars, each instar corresponding to a modal size-class. A probability paper method was used to find the mean and standard deviation of each modal class and, therefore of each instar. When the large numbers of larvae collected in summer 1972 were measured, overall lengths were taken which do not give such a good separation of modal classes. This afforded a considerable saving in time, however.

13. All species studied in detail had seven larval instars and there was conformity with Dyar's growth rule. Mean growth ratios were from 1.32 for <u>S.nitidifrons</u> cephalic apotome width measurement in Cronkley stream 2 to 1.44 for <u>S.nitidifrons</u> overall length measurement in Moss Burn: section D.

14. Overwintering larvae of <u>S.vernum</u> from Cronkley stream 3: section A were smaller : - as measured by mean cephalic apotome width - with the onset of spring. It has also been shown that last instar larvae of <u>S.vernum</u> were significantly smaller in summer than in winter in Cronkley stream 2.

15. After larvae had been assigned to their respective instars percentage frequency histograms were constructed to show growth through the instars and a picture of the number of generations and cohorts built up. The number of pupae found in each collection was entered on the histograms to show when pupation was taking place, so that the population biology of the Upper Teesdale Simuliidae was known in detail. The duration of larval life was 30-40 days in summer and up to 150 days for the same species in winter.

16. The winter generation, where present, often had a mid-winter hatching cohort and, in the case of S.monticola in Cronkley stream 2, this was numerically the more important. It seems most unlikely that the eggs hatching to give this cohort are in diapause until mid-winter and a more likely condition is that described as oligopause.

17. The summer generation of all species was marked by the presence of a minimum of two cohorts, in some cases up to four being found.

18. Peat particles form the predominant suspended organic material in the bog streams and will thus be the major food source of the bog stream simuliids. It is probably the microorganisms which the peat contains, rather than the particles themselves, which are important in nutrition. Other factors, in addition to food supply, which govern the growth of simuliid larvae are temperature and settlement area neither of which will be limiting in the summer.

19. It is demonstrated that growth in overall length is approximately linear with respect to time. The duration of each instar will therefore correspond to the length through which it has to grow and, using the previously obtained dimensions, it was possible to construct instar

durations giving larval development times of 30-, and 40-days to correspond with the field populations.

20. The instar durations were used in an "age-distribution" method of calculating the number of larvae in each instar of each species in the population. These figures were entered in life-tables from which mortality could be determined. Larval mortality for complete cohorts ranged from 91-93% to 97-98% in the present study, although higher percentages did occur in several incomplete cohorts. The largest mortality was recorded in the younger instars.

21. The mean dry weight of each instar in each species was determined and growth in weight found to show an exponential increase with overall length and, therefore, time.

22. From the mean dry weights and the number of larvae in each instar, production was calculated using an eliminated biomass method. The largest estimate obtained, for an equivalent cohort of four species in the lower part of Cronkley stream 2 was 56.9 mg. $m.^{-1}$ which is amongst the lowest recorded production estimates for Simuliids. The production values found in the present study were slightly below those for a Pyrenean mountain stream but much below those recorded from a Southern English chalk stream, and very much below the levels attained by a simuliid larval population in a lake outlet in Lapland.

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APPENDIX 1

Spot Temperature and Depth Measurements for the Study Streams on the Dates shown. Depth is given in cms above the Minimum Value Recorded and Temperature in °C from a Mercury Thermometer

Date	Cronkley Stream 2		Cronkley Stream 3		
	t°C	Depth (cms)	t°C A	t°C B	Depth (cms)
13.10.70	8.6	-		10.5	-
22.10.70	7.0	-	8.1	8.1	-
4.11.70	7.2	-	7.8	7.8	-
25.11.70	7.4	-	6.8	6.4	-
18.12.70	7.0	-	7.0	7.0	-
29. 1.71	6.0	5.0	5.1	5.0	5.5
10. 3.71	5.2	3.0	3.8	4.0	4.5
16. 3.71	5.3	2.5	5.2	4.5	3.5
30. 3.71	8.0	3.5	7.2	8.0	4.5
3. 4.71	5.8	3.0	6.0	5.2	3.0
12. 4.71	8.0	1.5	7.2	8.2	1.5
21. 4.71	10.9	1.0	8.0	13.0	0.5
27. 4.71	8.0	3.5	7.4	8.4	3.5
4. 5.71	10.5	2.0	7.5	13.0	1.0
20. 5.71	9.3	1.0	7.5	9.6	0.5
28. 5.71	9.4	1.0	7.4	9.6	1.0
8. 6.71	8.6	0.5	7.9	9.7	0.5
16. 6.71	9.3	1.0	7.5	10.9	2.0
23. 6.71	11.5	2.0	11.1	12.4	5.5
2. 7.71	16.9	1.5	9.6	20.2	2.5
9. 7.71	13.4	1.0	8.3	14.4	1.5
15. 7.71	13.9	0.5	8.5	15.0	1.0
27. 7.71	14.7	1.5	10.8	17.6	2.5
9. 8.71	12.9	2.5	10.4	14.6	4.5
26. 8.71	12.6	2.0	9.0	13.8	2.0
13. 9.71	10.4	1.5	8.7	11.1	1.5
23. 9.71	10.6	1.0	8.5	11.4	1.0
7.10.71	13.1	0.5	9.1	13.7	0.0
14.10.71	5.3	0.5	7.3	5.0	0.5
28.10.71	7.3	3.0	7.5	7.1	1.5
11.11.71	5.9	2.5	6.4	6.0	2.5
27.11.71	6.6	5.5	6.5	6.4	6.5
13.12.71	5.9	1.0	6.2	5.7	1.5
29.12.71	4.0	1.5	5.7	3.7	1.5
15. 1.72	5.5	5.0	5.2	4.3	5.5
8. 2.72	5.8	5.0	4.2	3.9	6.0
23. 2.72	5.4	3.0	4.4	3.7	4.0
13. 3.72	4.6	2.5	4.0	2.9	4.0
30. 3.72	5.7	4.0	4.4	4.3	-
10. 4.72	7.5	5.5	8.3	8.4	6.5
20. 4.72	9.2	3.0	6.8	8.3	3.0
5. 5.72	7.4	1.5	6.9	8.1	4.0
15. 5.72	6.8	2.5	6.9	7.0	5.5
23. 5.72	9.6	2.5	-	-	-
28.5.72	7.1	4.5	7.8	7.7	6.5
31. 5.72	9.3	5.5			
6. 6.72	9.9	5.0			
13. 6.72	8.6	4.0			
16. 6.72	11.1	3.5			
19. 6.72	8.5	4.0			

t°C A = temperature in section A
t°C B = temperature in section B
Depth taken at B.

(continued overleaf)

29. 6.72	8.5	3.5
3. 7.72	9.3	2.5
7. 7.72	10.7	2.5
12. 7.72	11.4	2.5
17. 7.72	15.5	1.0
21. 7.72	10.9	2.0
27. 7.72	13.9	2.0
3. 8.72	10.7	1.0
10. 8.72	12.4	2.5
16. 8.72	12.9	1.5
23. 8.72	12.9	0.0
30. 8.72	12.0	0.0
3. 9.72	-	0.0
7. 9.72	12.0	0.5
17. 9.72	8.6	0.5
29. 3.73	6.1	2.5
31. 7.73	17.2	-

Date	Borderon Mere Sike		Dubby Sike E. Grain	
	t°C	Depth (cms)	t°C	Depth (cms)
2.6.71	18.5	-	14.5	-
4.6.72	13.6	-	12.0	-
14.6.71	9.7	-	-	-
22.6.71	10.6	11.5	10.6	5.5
28.6.71	12.0	10.0	10.9	5.0
5.7.71	18.6	3.0	17.2	0.5
12.7.71	19.6	0.0	16.8	0.0
19.7.71	13.1	0.0	12.0	0.0
27.7.71	14.9	2.0	13.5	1.5
2.8.71	15.4	2.0	13.8	1.5
12.8.71	12.7	1.0	11.8	1.5
23.8.71	14.6	1.0	13.2	1.0
7.9.71	15.9	1.5	14.7	1.5

Date	Rough Sike		Nether Hearth Sike		Moss Burn	
	t°C	Depth (cms)	t°C	Depth (cms)	t°C	Depth (cms)
1.12.70	2.4	-	-	-	2.8	-
15.4.71	11.2	-	-	-	-	-
19.5.71	9.9	-	11.3	-	-	-
26.5.71	17.2	-	17.7	-	-	-
1.7.71	18.3	-	20.6	-	19.7	-
8.7.71	22.4	-	22.4	-	22.3	-
13.7.71	17.1	-	17.3	-	17.6	-
20.7.71	12.6	-	13.4	-	13.8	-
28.7.71	15.5	-	16.8	-	16.4	-
3.8.71	14.4	0.5	14.8	2.0	14.2	2.5
17.8.71	12.8	2.5	11.5	2.5	12.0	3.5
24.8.71	14.8	0.0	14.9	0.0	15.0	0.0
9.9.71	14.4	2.5	13.6	0.5	14.2	0.5
22.9.71	-	0.0	-	0.0	-	-

APPENDIX 2

Removal Sampling Data for each Sample on the Date Shown

T = Total number of larvae in all three samples
R = Conversion ratio
P = Population estimate
D = Percentage index of precision

Table 1: Moss Burn Section B
Table 2: Moss Burn Section C
Table 3: Moss Burn Section D
Table 4: Cronkley 2 Section A
Table 5: Cronkley 2 Section B

TABLE 1

Stream and Station	Date	Collections 1	2	3	T	R	P	± 2 S.E.	% D
Moss Burn Section B	28.6.72	251	175	134	560	0.79	918	± 204	11%
	5.7.72	206	120	92	418	0.73	589	± 103	9%
	11.7.72	201	107	91	399	0.72	546	± 75	7%
	25.7.72	181	67	42	290	0.52	322	± 22	3%
	31.7.72	146	53	14	213	0.38	224	± 11	3%
	7.8.72	136	46	19	201	0.42	212	± 10	2%
	14.8.72	634	300	63	997	0.43	1049	± 28	1%
	20.8.72	344	75	28	447	0.29	456	± 8	1%
	29.8.72	316	67	55	438	0.40	461	± 16	2%

TABLE 2

Stream and Station	Date	Collections 1	2	3	T	R	P	± 2 S.E.	% D
Moss Burn Section C	28.6.72	137	26	46	209	0.56	238	± 26	5%
	6.7.72	109	69	42	220	0.70	297	± 74	12%
	11.7.72	242	68	95	405	0.64	494	± 45	5%
	19.7.72	145	117	48	310	0.69	408	± 71	9%
	26.7.72	136	74	58	268	0.71	367	± 83	11%
	2.8.72	167	139	63	369	0.72	505	± 72	7%
	15.8.72	123	41	29	193	0.51	214	± 19	5%
	21.8.72	173	94	30	297	0.52	330	± 24	4%

TABLE 3

Stream and Station	Date	Collections			T	R	P	± 2 S.E.	% D
		1	2	3					
Moss Burn Section D	28.6.72	346	76	19	441	0.26	450	± 8	1%
	30.6.72	409	351	121	881	0.67	1129	± 130	6%
	5.7.72	142	78	38	258	0.60	307	± 39	7%
	11.7.72	198	92	118	408	0.80	680	± 104	8%
	19.7.72	356	137	74	567	0.50	625	± 30	2%
	26.7.72	275	145	100	520	0.66	650	± 67	5%
	2.8.72	339	262	222	823	0.86	1680	± 218	6%
	10.8.72	387	362	185	934	0.78	1459	± 125	4%
	15.8.72	167	69	47	283	0.58	329	± 29	5%
	21.8.72	615	365	375	1355	0.82	2377	± 271	6%
	29.8.72	87	34	43	164	0.73	231	± 64	14%

TABLE 4

Stream and Station	Date	Collections			T	R	P	± 2 S.E	% D
		1	2	3					
Cronkley Stream 2 Section A	19.6.72	86	2	2	90	0.06	90	-	-
	29.6.72	45	23	7	75	0.49	82	± 10	6%
	7.7.72	79	20	11	110	0.38	116	± 8	3%
	17.7.72	142	42	23	207	0.43	223	± 17	4%
	21.7.72	254	134	70	458	0.60	539	± 47	4%
	27.7.72	521	225	137	883	0.57	1015	± 52	3%
	3.8.72	703	302	156	1161	0.53	1304	± 55	2%
	10.8.72	643	407	130	1180	0.57	1372	± 78	3%
	16.8.72	644	386	142	1172	0.57	1332	± 46	2%
	23.8.72	485	347	127	959	0.63	1155	± 72	3%
	30.8.72	535	240	111	886	0.52	984	± 41	2%
	3.9.72	303	99	19	421	0.33	434	± 10	1%
	7.9.72	616	144	76	836	0.35	862	± 14	1%
	17.9.72	760	705	332	1797	0.76	2682	± 188	4%

TABLE 5

Stream and Station	Date	Collections			T	R	P	± 2 S.E	% D
		1	2	3					
Cronkley Stream 2 Section B	13.6.72	74	29	7	110	0.39	116	± 8	3%
	16.6.72	151	24	14	189	0.28	193	± 5	1%
	19.6.72	181	42	14	237	0.30	244	± 8	2%
	26.6.72	234	113	45	392	0.52	436	± 28	3%
	29.6.72	275	511	86	872	0.78	1384	± 703	25%
	3.7.72	208	68	46	322	0.50	358	± 28	4%
	7.7.72	402	170	108	680	0.57	782	± 52	3%
	12.7.72	269	181	55	505	0.58	580	± 36	3%
	17.7.72	745	181	78	1004	0.34	1035	± 16	1%
	21.7.72	547	117	80	744	0.37	775	± 17	1%
	27.7.72	437	214	61	712	0.47	766	± 24	2%
	3.8.72	912	681	509	2102	0.81	3624	± 406	6%
	10.8.72	1732	1052	575	3359	0.66	4199	± 145	2%
	16.8.72	843	579	236	1658	0.63	1998	± 95	2%
	23.8.72	1215	611	523	2349	0.71	3174	± 151	2%
	30.8.72	738	437	226	1401	0.63	1709	± 116	3%
	3.9.72	1038	623	92	1753	0.46	1884	± 65	2%
	7.9.72	1439	570	183	2192	0.43	2332	± 40	1%
	17.9.72	592	290	54	936	0.43	996	± 26	1%

APPENDIX 3

Life-tables for Upper Teesdale Simuliidae

iD = "instar-Day" total

D = duration of each instar

i = number of larvae at median developmental age of each instar

dx = number of larvae dying between median developmental age of one instar and that of the succeeding instar

S.vernum MOSS BURN, SECTION B

? → Late-June:Early-July

Instar	iD	D	i	dx	% Real Mortality
IV	699	4.4	159	97	61
V	355	5.7	62	25	16
VI	260	7.0	37	-27	-17
VII	447	7.0	64	-	-
IV	699	5.8	121	75	62
V	355	7.7	46	18	15
VI	260	9.4	28	-20	-17
VII	447	9.3	48	-	-

77% Mortality - 17% "Recruitment" Instars IV-VII

Late-June:Early-July → Late-July:Early-August

Instar	iD	D	i	dx	% Real Mortality
I	440	0.8	550	-254	-
II	1448	1.8	804	240	30
III	1860	3.3	564	84	10
IV	2112	4.4	480	221	27
V	1479	5.7	259	10	1
VI	1745	7.0	249	-20	-2
VII	1886	7.0	269	-	-
I	440	1.1	400	-203	-
II	1448	2.4	603	180	30
III	1860	4.4	423	59	10
IV	2112	5.8	364	172	29
V	1479	7.7	192	6	1
VI	1745	9.4	186	-17	-3
VII	1886	9.3	203	-	-

68-70% Mortality - 2-3% "Recruitment" Instars II-VII

Early-:Mid-August → Early-:?Mid-September

Instar	iD	D	i	dx	% Real Mortality
I	365	0.8	456	-106	-
II	1011	1.8	562	177	31
III	1270	3.3	385	165	29
IV	966	4.4	220	140	25
V	456	5.7	80	33	6
VI	329	7.0	47	38	7
VII	63	7.0	9	-	-
I	365	1.1	332	-89	-
II	1011	2.4	421	132	31
III	1270	4.4	289	122	29
IV	966	5.8	167	108	26
V	456	7.7	59	24	6
VI	329	9.4	35	28	7
VII	63	9.3	7	-	-

98-99% Mortality Instars II-VII

__S.aureum__ MOSS BURN: SECTION B

? → Late-June:Early-July

Instar	iD	D	i	dx
I	46	0.8	58	25
II	60	1.8	33	18
III	50	3.3	15	-50
IV	284	4.4	65	-2
V	383	5.7	67	-51
VI	827	7.0	118	-12
VII	909	7.0	130	-
I	46	1.1	42	17
II	60	2.4	25	14
III	50	4.4	11	-38
IV	284	5.8	49	-1
V	383	7.7	50	-38
VI	827	9.4	88	-10
VII	909	9.3	98	-

"Recruitment" > Mortality

Early-:Mid-August → Late-August:?Early-September

Instar	iD	D	i	dx	% Real Mortality
I	265	0.8	331	187	56
II	259	1.8	144	34	10
III	364	3.3	110	-34	-10
IV	635	4.4	144	72	22
V	409	5.7	72	25	8
VI	328	7.0	47	22	7
VII	175	7.0	25	-	-
I	265	1.1	241	133	55
II	259	2.4	108	25	10
III	364	4.4	83	-26	-11
IV	635	5.8	109	56	23
V	409	7.7	53	18	7
VI	328	9.4	35	16	7
VII	175	9.3	19	-	-

102-103% Mortality - 10-11% "Recruitment" Instars I-VII

S.vernum MOSS BURN: SECTION C

?Mid-:Late-June → Mid-:Late-July

Instar	iD	D	i	dx
II	83	1.8	46	2
III	146	3.3	44	-64
IV	475	4.4	108	-16
V	704	5.7	124	70
VI	377	7.0	54	-75
VII	905	7.0	129	-
II	83	2.4	35	2
III	146	4.4	33	-49
IV	475	5.8	82	-9
V	704	7.7	91	51
VI	377	9.4	40	-57
VII	905	9.3	97	-

"Recruitment" > Mortality

Early-July → Early-August

Instar	iD	D	i	dx
I	124	0.8	155	53
II	183	1.8	102	-13
III	380	3.3	115	-81
IV	864	4.4	196	-29
V	1285	5.7	225	20
VI	1434	7.0	205	-24
VII	1605	7.0	229	-
I	124	1.1	113	37
II	183	2.4	76	-10
III	380	4.4	86	-63
IV	864	5.8	149	-18
V	1285	7.7	167	14
VI	1434	9.4	153	-20
VII	1605	9.3	173	-

"Recruitment" > Mortality

Late-July:Early-August → Late-August:Early-September

Instar	iD	D	i	dx	% Real Mortality
I	54	0.8	68	-171	-
II	430	1.8	239	145	61
III	311	3.3	94	1	0
IV	410	4.4	93	16	7
V	439	5.7	77	12	5
VI	458	7.0	65	-18	-8
VII	584	7.0	83	-	-
I	54	1.1	49	-130	-
II	430	2.4	179	108	60
III	311	4.4	71	0	0
IV	410	5.8	71	14	8
V	439	7.7	57	8	4
VI	458	9.4	49	-14	-8
VII	584	9.3	63	-	-

72-73% Mortality - 8% "Recruitment" Instars II-VII

<u>S.vernum</u> MOSS BURN: SECTION D

? → Early-July

Instar	iD	D	i	dx	% Real Mortality
V	298	5.7	52	13	25
VI	274	7.0	39	-3	-6
VII	291	7.0	42	-	-
V	298	7.7	39	10	26
VI	274	9.4	29	-2	-5
VII	291	9.3	31	-	-

25-26% Mortality - 5-6% "Recruitment" Instars V-VII

?Mid-June → Mid-:Late-July

Instar	iD	D	i	dx
III	476	3.3	144	-12
IV	685	4.4	156	-5
V	919	5.7	161	55
VI	743	7.0	106	-91
VII	1377	7.0	197	-
III	476	4.4	108	-10
IV	685	5.8	118	-1
V	919	7.7	119	40
VI	743	9.4	79	-69
VII	1377	9.3	148	-

"Recruitment" > Mortality

Early-:Mid-July → Early-:Mid-August

Instar	iD	D	i	dx
I	237	0.8	296	-16
II	562	1.8	312	-144
III	1458	3.3	456	14
IV	1945	4.4	442	20
V	2403	5.7	422	-89
VI	3575	7.0	511	50
VII	3224	7.0	461	-
I	237	1.1	215	-19
II	562	2.4	234	-97
III	1458	4.4	331	-4
IV	1945	5.8	335	23
V	2403	7.7	312	-68
VI	3575	9.4	380	33
VII	3224	9.3	347	-

"Recruitment" > Mortality

Late-July:Early-August → Late-August

Instar	iD	D	i	dx	% Real Mortality
I	1094	0.8	1368	403	29
II	1737	1.8	965	371	27
III	1961	3.3	594	44	3
IV	2419	4.4	550	135	10
V	2363	5.7	415	220	16
VI	1367	7.0	195	131	10
VII	447	7.0	64	-	-
I	1094	1.1	995	271	27
II	1737	2.4	724	278	28
III	1961	4.4	446	29	3
IV	2419	5.8	417	110	11
V	2363	7.7	307	162	16
VI	1367	9.4	145	97	10
VII	447	9.3	48	-	-

95% Mortality Instars I-VII

S.brevicaule

MOSS BURN: SECTION D

? → Mid-July

Instar	iD	D	i	dx	% Real Mortality
III	227	3.3	69	11	16
IV	253	4.4	58	42	61
V	89	5.7	16	5	7
VI	78	7.0	11	-1	-1
VII	83	7.0	12	-	-
III	227	4.4	52	8	15
IV	253	5.8	44	32	62
V	89	7.7	12	4	8
VI	78	9.4	8	-1	-2
VII	83	9.3	9	-	

84-85% Mortality - 1-2% "Recruitment" Instars III-VII

Early-:Mid-July → Early-August

Instar	iD	D	i	dx	% Real Mortality
I	37	0.8	46	8	-
II	68	1.8	38	-121	-
III	526	3.3	159	101	64
IV	256	4.4	58	-1	-1
V	339	5.7	59	32	20
VI	191	7.0	27	18	11
VII	65	7.0	9	-	-
I	37	1.1	34	6	-
II	68	2.4	28	-92	-
III	526	4.4	120	76	63
IV	256	5.8	44	0	0
V	339	7.7	44	24	20
VI	191	9.4	20	13	11
VII	65	9.3	7	-	-

94-95% Mortality - 1% "Recruitment" Instars III-VII

Late-July:Early-August → Late-August

Instar	iD	D	i	dx	% Real Mortality
I	99	0.8	124	0	-
II	223	1.8	124	-29	-
III	504	3.3	153	43	28
IV	484	4.4	110	78	51
V	180	5.7	32	20	13
VI	87	7.0	12	5	3
VII	50	7.0	7	-	-
I	99	1.1	90	-3	-
II	223	2.4	93	-22	-
III	504	4.4	115	32	28
IV	484	5.8	83	60	52
V	180	7.7	23	14	12
VI	87	9.4	9	4	3
VII	50	9.3	5	-	-

95% Mortality Instars III-VII

S.monticola MOSS BURN: SECTION D

?Mid-June → Mid-July

Instar	iD	D	i	dx	% Real Mortality
III	152	3.3	46	-89	-
IV	596	4.4	135	87	64
V	271	5.7	48	-11	-8
VI	413	7.0	59	-33	-24
VII	641	7.0	92	-	
III	152	4.4	35	-68	-
IV	596	5.8	103	68	66
V	271	7.7	35	-9	-9
VI	413	9.4	44	-25	-24
VII	641	9.3	69	-	-

64-66% Mortality - 32-33% "Recruitment" Instars IV-VII

Early-:Mid-July → Early-August

Instar	iD	D	i	dx	% Real Mortality
I	101	0.8	126	-12	-
II	249	1.8	138	80	58
III	191	3.3	58	12	9
IV	204	4.4	46	-6	-4
V	296	5.7	52	24	17
VI	195	7.0	28	6	4
VII	153	7.0	22	-	-
I	101	1.1	92	-12	-
II	249	2.4	104	61	59
III	191	4.4	43	8	8
IV	204	5.8	35	-3	-3
V	296	7.7	38	17	16
VI	195	9.4	21	5	5
VII	153	9.3	16	-	-

88% Mortality - 3-4% "Recruitment" Instars II-VII

Late-July:Early-August → Late-August:Early-September

Instar	iD	D	i	dx	% Real Mortality
I	795	0.8	994	82	8
II	1641	1.8	912	697	70
III	711	3.3	215	97	10
IV	521	4.4	118	76	8
V	237	5.7	42	32	3
VI	72	7.0	10	-6	-1
VII	115	7.0	16	-	-
I	795	1.1	723	39	5
II	1641	2.4	684	522	72
III	711	4.4	162	72	10
IV	521	5.8	90	59	8
V	237	7.7	31	23	3
VI	72	9.4	8	-4	-1
VII	115	9.3	12	-	-

98-99% Mortality - 1% "Recruitment" Instars I-VII

S.nitidifrons MOSS BURN: SECTION D

?Mid-June → Mid-:Late-July

Instar	iD	D	i	dx	% Real Mortality
I	53	0.8	66	-1	-
II	120	1.8	67	-40	-
III	354	3.3	107	-28	-
IV	593	4.4	135	5	4
V	741	5.7	130	64	47
VI	462	7.0	66	28	21
VII	268	7.0	38	-	-
I	53	1.1	48	-2	-
II	120	2.4	50	-30	-
III	354	4.4	80	-22	-
IV	593	5.8	102	6	6
V	741	7.7	96	47	46
VI	462	9.4	49	20	20
VII	268	9.3	29	-	-

72% Mortality Instars IV-VII

Late-July:Early-August → Early-September

Instar	iD	D	i	dx	% Real Mortality
I	424	0.8	530	-334	-
II	1555	1.8	864	349	40
III	1701	3.3	515	140	16
IV	1651	4.4	375	190	22
V	1057	5.7	185	72	8
VI	788	7.0	113	96	11
VII	117	7.0	17	-	-
I	424	1.1	385	-263	-
II	1555	2.4	648	261	40
III	1701	4.4	387	102	16
IV	1651	5.8	285	148	23
V	1057	7.7	137	53	8
VI	788	9.4	84	71	11
VII	117	9.3	13	-	-

97-98% Mortality Instars II-VII

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CRONKLEY STREAM 2: SECTION A

Total for Summer

Instar	iD	D	i	dx	% Real Mortality
I	541	0.8	676	-95	-
II	1387	1.8	771	-74	-
III	2790	3.3	845	-126	-
IV	4271	4.4	971	-69	-
V	5926	5.7	1040	354	34
VI	4803	7.0	686	246	24
VII	3081	7.0	440	-	-
I	541	1.1	492	-86	-
II	1387	2.4	578	-56	-
III	2790	4.4	634	-102	-
IV	4271	5.8	736	-34	-
V	5926	7.7	770	259	34
VI	4803	9.4	511	180	23
VII	3081	9.3	331	-	-

57-58% Mortality Instars V-VII

S.brevicaule CRONKLEY STREAM 2: SECTION A

Main Summer Generation

Instar	iD	D	i	dx	% Real Mortality
I	270	0.8	338	16	-
II	579	1.8	322	-205	-
III	1739	3.3	527	-2	-
IV	2327	4.4	529	204	39
V	1852	5.7	325	102	19
VI	1563	7.0	223	-37	-7
VII	1821	7.0	260	-	-
I	270	1.1	245	4	-
II	579	2.4	241	-154	-
III	1739	4.4	395	-6	-
IV	2327	5.8	401	160	40
V	1852	7.7	241	75	19
VI	1563	9.4	166	-30	-7
VII	1821	9.3	196	-	-

58-59% Mortality - 7% "Recruitment" Instars IV-VII

Early-September → ?

Instar	iD	D	i	dx	% Real Mortality
II	48	1.8	27	-67	-
III	311	3.3	94	46	49
IV	213	4.4	48	42	45
V	35	5.7	6	-	-
II	48	2.4	20	-51	-
III	311	4.4	71	34	48
IV	213	5.8	37	32	45
V	35	7.7	5	-	-

93-94% Mortality Instars III-V

S.monticola CRONKLEY STREAM 2: SECTION A

Mid-:Late-July:Early-August ⟶ Late-August:Early-September

Instar	iD	D	i	dx	% Real Mortality
I	443	0.8	554	-1053	-
II	2893	1.8	1607	949	59
III	2170	3.3	658	-366	-23
IV	4505	4.4	1024	484	30
V	3080	5.7	540	421	26
VI	834	7.0	119	60	4
VII	416	7.0	59	-	-
I	443	1.1	403	-802	-
II	2893	2.4	1205	712	59
III	2170	4.4	493	-284	-24
IV	4505	5.8	777	377	31
V	3080	7.7	400	311	26
VI	834	9.4	89	44	4
VII	416	9.3	45	-	-

119-120% Mortality - 23-24% "Recruitment" Instars II-VII

Early-September ⟶ ?

Instar	iD	D	i	dx	% Real Mortality
II	413	1.8	229	-12	-
III	795	3.3	241	143	59
IV	430	4.4	98	-	-
II	413	2.4	172	-9	-
III	795	4.4	181	107	59
IV	430	5.8	74	-	-

59% Mortality Instars III-IV

S.nitidifrons CRONKLEY STREAM 2: SECTION A

Mid-:Late-July:Early-August ⟶ Late-August:Early-September

Instar	iD	D	i	dx	% Real Mortality
I	206	0.8	258	-919	-
II	2119	1.8	1177	637	54
III	1782	3.3	540	41	3
IV	2197	4.4	499	185	16
V	1787	5.7	314	218	19
VI	669	7.0	96	58	5
VII	267	7.0	38	-	-
I	206	1.1	187	-696	-
II	2119	2.4	883	478	54
III	1782	4.4	405	26	3
IV	2197	5.8	379	147	17
V	1787	7.7	232	161	18
VI	669	9.4	71	42	5
VII	267	9.3	29	-	-

97% Mortality Instars II-VII

Early-September ⟶ ?

Instar	iD	D	i	dx	% Real Mortality
I	5	0.8	6	-91	-
II	174	1.8	97	2	2
III	312	3.3	95	75	77
IV	90	4.4	20	11	11
V	50	5.7	9	-	-
I	5	1.1	5	-68	-
II	174	2.4	73	2	3
III	312	4.4	71	55	75
IV	90	5.8	16	10	14
V	50	7.7	6	-	

90-92% Mortality Instars II-V

S.vernum CRONKLEY STREAM 2: SECTION B

? → Late-June

Instar	iD	D	i	dx
IV	23	4.4	5	0
V	30	5.7	5	-43
VI	339	7.0	48	-17
VII	457	7.0	65	-
IV	23	5.8	4	0
V	30	7.7	4	-32
VI	339	9.4	36	-13
VII	457	9.3	49	

"Recruitment" > Mortality

Mid-June → Mid-:Late-July

Instar	iD	D	i	dx	% Real Mortality
I	19	0.8	24	-108	-
II	237	1.8	132	-36	-
III	554	3.3	168	-177	-
IV	1520	4.4	345	-141	-
V	2772	5.7	486	204	42
VI	1971	7.0	282	196	40
VII	604	7.0	86	-	-
I	19	1.1	17	-82	-
II	237	2.4	99	-27	-
III	554	4.4	126	-136	-
IV	1520	5.8	262	-98	-
V	2772	7.7	360	150	42
VI	1971	9.4	210	145	40
VII	604	9.3	65	-	-

82% Mortality Instars V-VII

Early-August → Late-August:Early-September

Instar	iD	D	i	dx	% Real Mortality
I	23	0.8	29	-812	-
II	1514	1.8	841	-1040	-
III	6208	3.3	1881	-1108	-
IV	13152	4.4	2989	1001	33
V	11330	5.7	1988	1006	34
VI	6875	7.0	982	582	19
VII	2802	7.0	400	-	-
I	23	1.1	21	-610	-
II	1514	2.4	631	-780	-
III	6208	4.4	1411	-857	-
IV	13152	5.8	2268	797	35
V	11330	7.7	1471	740	33
VI	6875	9.4	731	430	19
VII	2802	9.3	301	-	-

86-87% Mortality Instars IV-VII

Early-September → ?

Instar	iD	D	i	dx	% Real Mortality
I	110	0.8	138	-55	-
II	348	1.8	193	-325	-
III	1709	3.3	518	220	42
IV	1311	4.4	298	60	12
V	1356	5.7	238	174	34
VI	450	7.0	64	37	7
VII	191	7.0	27	-	-
I	110	1.1	100	-45	-
II	348	2.4	145	-243	-
III	1709	4.4	388	162	42
IV	1311	5.8	226	50	13
V	1356	7.7	176	128	33
VI	450	9.4	48	27	7
VII	191	9.3	21	-	-

95% Mortality Instars III-VII

<u>S.brevicaule</u> CRONKLEY STREAM 2: SECTION B

? → Late-June

Instar	iD	D	i	dx
V	20	5.7	4	-18
VI	151	7.0	22	-24
VII	323	7.0	46	-
V	20	7.7	3	-13
VI	151	9.4	16	-19
VII	323	9.3	35	-

"Recruitment" > Mortality

Mid-:Late-June → Mid-:Late-July

Instar	iD	D	i	dx	% Real Mortality
I	58	0.8	73	-215	-
II	518	1.8	288	-19	-
III	1012	3.3	307	-181	-
IV	2145	4.4	488	132	27
V	2032	5.7	356	219	45
VI	959	7.0	137	47	10
VII	632	7.0	90	-	-
I	58	1.1	53	-163	-
II	518	2.4	216	-14	-
III	1012	4.4	230	-140	-
IV	2145	5.8	370	106	29
V	2032	7.7	264	162	44
VI	959	9.4	102	34	9
VII	632	9.3	68	-	-

82% Mortality Instars IV-VII

? Late-July ⟶ ? Early-September

Instar	iD	D	i	dx	% Real Mortality
II	536	1.8	298	-773	-
III	3534	3.3	1071	-20	-
IV	4800	4.4	1091	645	59
V	2544	5.7	446	250	23
VI	1370	7.0	196	23	2
VII	1209	7.0	173	-	-
II	536	2.4	223	-580	-
III	3534	4.4	803	-25	-
IV	4800	5.8	828	498	60
V	2544	7.7	330	184	22
VI	1370	9.4	146	16	2
VII	1209	9.3	130	-	-

84% Mortality Instars IV-VII

S.monticola CRONKLEY STREAM 2: SECTION B

? → Mid-:Late-June

Instar	iD	D	i	dx
VI	9	7.0	1	-33
VII	239	7.0	34	-
VI	9	9.4	1	-25
VII	239	9.3	26	-

"Recruitment" > Mortality

Late-June:Early-July → Late-July:?Early-August

Instar	iD	D	i	dx	% Real Mortality
I	5	0.8	6	-285	-
II	524	1.8	291	229	79
III	206	3.3	62	-50	-17
IV	494	4.4	112	101	35
V	61	5.7	11	6	2
VI	38	7.0	5	3	1
VII	11	7.0	2	-	-
I	5	1.1	5	-213	-
II	524	2.4	218	171	78
III	206	4.4	47	-38	-17
IV	494	5.8	85	77	35
V	61	7.7	8	4	2
VI	38	9.4	4	3	1
VII	11	9.3	1	-	-

116-117% Mortality - 17% "Recruitment" Instars II-VII

Early-:Mid-August → Late-August:Early-September

Instar	iD	D	i	dx	% Real Mortality
I	169	0.8	211	-1422	-
II	2940	1.8	1633	-116	-
III	5771	3.3	1749	-334	-
IV	9164	4.4	2083	799	38
V	7321	5.7	1284	848	41
VI	3055	7.0	436	264	13
VII	1202	7.0	172	-	-
I	169	1.1	154	-1071	-
II	2940	2.4	1225	-87	-
III	5771	4.4	1312	-268	-
IV	9164	5.8	1580	629	40
V	7321	7.7	951	626	40
VI	3055	9.4	325	196	12
VII	1202	9.3	129	-	

92% Mortality Instars IV-VII

Early-:Mid-September → ?

Instar	iD	D	i	dx	% Real Mortality
I	562	0.8	703	47	7
II	1181	1.8	656	130	18
III	1735	3.3	526	222	32
IV	1336	4.4	304	-	-
I	562	1.1	511	19	4
II	1181	2.4	492	98	19
III	1735	4.4	394	164	32
IV	1336	5.8	230	-	-

55-57% Mortality Instars I-IV

S.nitidifrons CRONKLEY STREAM 2: SECTION B

?Mid-June → ?Mid-July

Instar	iD	D	i	dx	% Real Mortality
II	262	1.8	146	-56	-
III	668	3.3	202	93	46
IV	481	4.4	109	98	49
V	63	5.7	11	8	4
VI	20	7.0	3	-	-
II	262	2.4	109	-43	-
III	668	4.4	152	69	45
IV	481	5.8	83	75	49
V	63	7.7	8	5	3
VI	20	9.4	3	-	-

97-99% Mortality Instars III-VI

Mid-:Late-July:Early-August → Mid-:Late-August

Instar	iD	D	i	dx	% Real Mortality
I	346	0.8	433	-2459	-
II	5206	1.8	2892	-102	-
III	9892	3.3	2994	1969	66
IV	4512	4.4	1025	424	14
V	3426	5.7	601	300	10
VI	2109	7.0	301	128	4
VII	1214	7.0	173	-	-
I	346	1.1	315	-1854	-
II	5206	2.4	2169	- 79	-
III	9892	4.4	2248	1470	65
IV	4512	5.8	778	333	15
V	3426	7.7	445	221	10
VI	2109	9.4	224	93	4
VII	1214	9.3	131	-	

94% Mortality Instars III-VII

Early-September → ?

Instar	iD	D	i	dx	% Real Mortality
I	823	0.8	1029	109	-
II	1656	1.8	920	-729	-
III	5441	3.3	1649	1297	79
IV	1548	4.4	352	207	13
V	824	5.7	145	-	-
I	823	1.1	748	58	-
II	1656	2.4	690	-547	-
III	5441	4.4	1237	970	78
IV	1548	5.8	267	160	13
V	824	7.7	107	-	-

91-92% Mortality Instars III-V

APPENDIX 4

Production Data for Complete Cohorts of the Given Species in Moss Burn and Cronkley Stream 2

i = number of larvae in each instar

m = mean weight of each instar (μg.)

d_x = number of larvae dying between median development times of instars

m^{dx} = $\frac{m_{II}-m_{I}}{2}$ etc.

$d_x m$ = eliminated biomass for "between-instar" classes

$B_t - B_o$ = change in biomass of population from median developmental age of first instars to median developmental age of seventh

B_E = $\sum d_x m$

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MOSS BURN: SECTION B

Late-June:Early-July → Late-July:Early-August

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	550	0.7	385	-	-	-
II	804	1	↓	240	3	720
III	564	4		84	10	840
IV	480	15		221	29	6409
V	259	42		10	84	840
VI	249	126		-	-	-
VII	269	323	86887	-	-	-

B_t-B_o = 86502 µg B_E = 8809 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	400	0.7	280	-	-	-
II	603	1	↓	180	3	540
III	423	4		59	10	590
IV	364	15		172	29	4988
V	192	42		6	84	504
VI	186	126		-	-	-
VII	203	323	65569	-	-	-

B_t-B_o = 65289 µg B_E = 6622 µg

Production = 71911 µg — 95311 µg in a mean sample length of 21.6 m.

= 3.3 mg — 4.4 mg m^{-1} dry weight production

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MOSS BURN: SECTION C

Late-July:Early-August → Late-August:Early-September

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	68	0.7	48	-	-	-
II	239	1	|	145	3	435
III	94	4	|	1	10	10
IV	93	15	|	16	29	464
V	77	42	|	12	84	1008
VI	65	126	↓	-	-	-
VII	83	323	26809	-	-	-

$B_t-B_o = 26761\ \mu g$ $B_E = 1917\ \mu g$

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	49	0.7	34	-	-	-
II	179	1	|	108	3	324
III	71	4	|	-	-	-
IV	71	15	|	14	29	406
V	57	42	|	8	84	672
VI	49	126	↓	-	-	-
VII	63	323	20349	-	-	-

$B_t-B_o = 20315\ \mu g$ $B_E = 1402\ \mu g$

Production = 21717 μg — 28678 μg in a mean sample length of 15.7 m.

= 1.4 mg — 1.8 mg m^{-1} dry weight production

<u>S.vernum</u> MOSS BURN: SECTION D

Late-July:Early-August → Late-August

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	1368	0.7	958	403	0.9	363
II	965	1	↓	371	3	1113
III	594	4		44	10	440
IV	550	15		135	29	3915
V	415	42		220	84	18480
VI	195	126		131	225	29475
VII	64	323	20672	-	-	-

$B_t - B_o = 19714\ \mu g$ $B_E = 53786\ \mu g$

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	995	0.7	697	271	0.9	244
II	724	1	↓	275	3	92
III	446	4		29	10	290
IV	417	15		110	29	3190
V	307	42		162	84	13608
VI	145	126		97	225	21825
VII	48	323	15504	-	-	-

$B_t - B_o = 14807\ \mu g$ $B_E = 39249\ \mu g$

Production = 54056 μg — 73500 μg in a mean sample length of 12.6 m.

= 4.3 mg — 5.9 mg m^{-1} dry weight production

S.brevicaule MOSS BURN: SECTION D

Early-:Mid-July → Early-August

Instar	i	m	im	d_x	m^{dx}	d_xm
I	46	0.7	32	-	-	-
II	38	1	↓	-	-	-
III	159	4		101	9	909
IV	58	14		-	-	-
V	59	42		32	75	2400
VI	27	108		18	230	4140
VII	9	351	3159	-	-	-

$B_t - B_o = 3127$ µg $B_E = 7449$ µg

Instar	i	m	im	d_x	m^{dx}	d_xm
I	34	0.7	24	-	-	-
II	28	1	↓	-	-	-
III	120	4		76	9	684
IV	44	14		-	-	-
V	44	42		24	75	1800
VI	20	108		13	230	2990
VII	7	351	2457	-	-	-

$B_t - B_o = 2433$ µg $B_E = 5474$ µg

Production = 7907 µg — 10576 µg in a mean sample length of 9.4 m.

= 0.8 mg — 1.1 mg m^{-1} dry weight production

<u>S.brevicaule</u> MOSS BURN: SECTION D

Late-July:Early-August → Late-August

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	124	0.7	87	-	-	-
II	124	1		-	-	-
III	153	4		43	9	387
IV	110	14		78	28	2184
V	32	42		20	75	1500
VI	12	108	↓	5	230	1150
VII	7	351	2457	-	-	-

B_t-B_o = 2370µg B_E = 5221 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	90	0.7	63	-	-	-
II	93	1		-	-	-
III	115	4		32	9	288
IV	83	14		60	28	1680
V	23	42		14	75	1050
VI	9	108	↓	4	230	920
VII	5	351	1755	-	-	-

B_t-B_o = 1692 µg B_E = 3938 µg

Production = 5630 µg — 7591 µg in a mean sample length of 12.6 m.

= 0.4 mg — 0.6 mg m^{-1} dry weight production

S.monticola MOSS BURN: SECTION D

Early-:Mid-July → Early-August

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	126	0.7	88	-	-	-
II	138	1	↓	80	4	320
III	58	6		12	14	168
IV	46	21		-	-	-
V	52	60		24	97	2328
VI	28	133		6	244	1464
VII	22	354	7788	-	-	-

$B_t - B_o = 7700\ \mu g$ $B_E = 4280\ \mu g$

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	92	0.7	64	-	-	-
II	104	1	↓	61	4	244
III	43	6		8	14	112
IV	35	21		-	-	-
V	38	60		17	97	1649
VI	21	133		5	244	1220
VII	16	354	5664	-	-	-

$B_t - B_o = 5600\ \mu g$ $B_E = 3225\ \mu g$

Production = 8825 μg — 11980 μg in a mean sample length of 9.4 m.

= 0.9 mg — 1.3 mg m^{-1} dry weight production

<u>S.monticola</u> MOSS BURN: SECTION D

Late-July:Early-August → Late-August:Early-September

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	994	0.7	696	82	0.9	74
II	912	1		697	4	2788
III	215	6		97	14	1358
IV	118	21		76	41	3116
V	42	60		32	97	3104
VI	10	133	↓	-	-	-
VII	16	354	5664	-	-	-

$B_t - B_o$ = 4968 μg B_E = 10440 μg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	723	0.7	506	39	0.9	35
II	684	1		522	4	2088
III	162	6		72	14	1008
IV	90	21		59	41	2419
V	31	60		23	97	2231
VI	8	133	↓	-	-	-
VII	12	354	4248	-	-	-

$B_t - B_o$ = 3742 μg B_E = 7781 μg

Production = 11523 μg — 15408 μg in a mean sample length of 12.6 m.

= 0.9 mg — 1.2 mg m^{-1} dry weight production

<u>S.nitidifrons</u>   MOSS BURN: SECTION D

Late-July:Early-August → Early-September

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	530	0.7	371	-	-	-
II	864	3	↓	349	7	2443
III	515	10	↓	140	24	3360
IV	375	38	↓	190	72	13680
V	185	106	↓	72	162	11664
VI	113	218	↓	96	323	31008
VII	17	427	7259	-	-	-

$B_t - B_o$ = 6888 μg B_E = 62155 μg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	385	0.7	270	-	-	-
II	648	3	↓	261	7	1827
III	387	10	↓	102	24	2448
IV	285	38	↓	148	72	10656
V	137	106	↓	53	162	8586
VI	84	218	↓	71	323	22933
VII	13	427	5551	-	-	-

$B_t - B_o$ = 5281 μg B_E = 46450 μg

Production = 51731 μg — 69043 μg in a stream length of 12.6 m

= 4.1 mg — 5.5 mg m^{-1} dry weight production

S.vernum CRONKLEY STREAM 2: SECTION A

Total for Summer

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	676	0.7	473	-	-	-
II	771	1		-	-	-
III	845	4		-	-	-
IV	971	15		-	-	-
V	1040	42		354	84	29736
VI	686	126	↓	246	225	55350
VII	440	323	142120	-	-	-

$B_t - B_o$ = 141647 µg B_E = 85086 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	492	0.7	344	-	-	-
II	578	1		-	-	-
III	634	4		-	-	-
IV	736	15		-	-	-
V	770	42		259	84	21756
VI	511	126	↓	180	225	40500
VII	331	323	106913	-	-	-

$B_t - B_o$ = 106569 µg B_E = 62256 µg

Production = 168825 µg — 226733 µg in a mean sample length of 19.4 m.

= 8.7 mg — 11.7 mg m^{-1} dry weight production

<u>S.brevicaule</u> CRONKLEY STREAM 2: SECTION A

Main Summer Generation

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	338	0.7	237	-	-	-
II	322	1	↓	-	-	-
III	527	4	↓	-	-	-
IV	529	14	↓	204	28	5712
V	325	42	↓	102	75	7650
VI	223	108	↓	-	-	-
VII	260	351	91260	-	-	-

$B_t - B_o$ = 91023 µg B_E = 13362 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	245	0.7	172	-	-	-
II	241	1	↓	-	-	-
III	395	4	↓	-	-	-
IV	401	14	↓	160	28	4480
V	241	42	↓	75	75	5625
VI	166	108	↓	-	-	-
VII	196	351	68796	-	-	-

$B_t - B_o$ = 68624 µg B_E = 10105 µg

Production = 78729 µg — 104385 µg in a mean sample length of 15.6 m.

= 5.0 mg — 6.7 mg m^{-1} dry weight production

S.monticola CRONKLEY STREAM 2: SECTION A

Mid-:Late-July:Early-August → Late-August:Early-September

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	554	0.7	388	-	-	-
II	1607	1		949	4	3796
III	658	6		-	-	-
IV	1024	21		484	41	19844
V	540	60		421	97	40837
VI	119	133		60	244	14640
VII	59	354	20886	-	-	-

$B_t - B_o$ = 20498 µg B_E = 79117 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	403	0.7	282	-	-	-
II	1205	1		712	4	2848
III	493	6		-	-	-
IV	777	21		377	41	15457
V	400	60		311	97	30167
VI	89	133		44	244	10736
VII	45	354	15930	-	-	-

$B_t - B_o$ = 15648 µg B_E = 59208 µg

Production = 74856 µg — 99615 µg in a mean sample length of 21.7 m.

= 3.4 mg — 4.6 mg m^{-1} dry weight production

S.nitidifrons CRONKLEY STREAM 2: SECTION A

Mid-:Late-July:Early-August → Late-August:Early-September

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	258	0.7	181	-	-	-
II	1177	3		637	7	4459
III	540	10		41	24	984
IV	499	38		185	72	13320
V	314	106		218	162	35316
VI	96	218	↓	58	323	18734
VII	38	427	16226	-	-	-

$B_t - B_o$ = 16045 µg B_E = 72813 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	187	0.7	131	-	-	-
II	883	3		478	7	3346
III	405	10		26	24	624
IV	379	38		147	72	10584
V	232	106		161	162	26082
VI	71	218	↓	42	323	13566
VII	29	427	12383	-	-	-

$B_t - B_o$ = 12252 µg B_E = 54202 µg

Production = 66454 µg — 88858 µg in a mean sample length of 21.7 m.

= 3.1 mg — 4.1 mg m^{-1} dry weight production

S.vernum CRONKLEY STREAM 2: SECTION B

Mid-June → Mid-:Late-July

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	24	0.7	17	-	-	-
II	132	1		-	-	-
III	168	4		-	-	-
IV	345	15		-	-	-
V	486	42		204	84	17136
VI	282	126	↓	196	225	44100
VII	86	323	27778	-	-	-

$B_t - B_o$ = 27761 µg B_E = 61236 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	17	0.7	12	-	-	-
II	99	1		-	-	-
III	126	4		-	-	-
IV	262	15		-	-	-
V	360	42		150	84	12500
VI	210	126	↓	145	225	32625
VII	65	323	20995	-	-	-

$B_t - B_o$ = 20983 µg B_E = 45225 µg

Production = 66208 µg — 88997 µg in a mean sample length of 22.0 m.

= 3.0 mg — 4.0 mg m^{-1} dry weight production

<u>S.vernum</u> CRONKLEY STREAM 2: SECTION B

Early-August → Late-August:Early-September

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	29	0.7	20	-	-	-
II	841	1		-	-	-
III	1881	4		-	-	-
IV	2989	15		1001	29	29029
V	1988	42		1006	84	84504
VI	982	126		582	225	130950
VII	400	323	129200	-	-	-

$B_t - B_o$ = 129180 µg B_E = 244483 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	21	0.7	15	-	-	-
II	631	1		-	-	-
III	1411	4		-	-	-
IV	2268	15		797	29	23113
V	1471	42		740	84	62160
VI	731	126		430	225	96750
VII	301	323	97223	-	-	-

$B_t - B_o$ = 97208 µg B_E = 182023 µg

Production = 279231 µg — 373663 µg in a mean sample length of 15.8 m.

= 17.6 mg — 23.7 mg m^{-1} dry weight production

S.brevicaule CRONKLEY STREAM 2: SECTION B

Mid-:Late-June → Mid-:Late-July

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	73	0.7	51	-	-	-
II	288	1		-	-	-
III	307	4		-	-	-
IV	488	14		132	28	3696
V	356	42		219	75	16425
VI	137	108	↓	47	230	10810
VII	90	351	31590	-	-	-

$B_t - B_o$ = 31539 μg B_E = 30931 μg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	53	0.7	37	-	-	-
II	216	1		-	-	-
III	230	4		-	-	-
IV	370	14		106	28	2968
V	264	42		162	75	12150
VI	102	108	↓	34	230	7820
VII	68	351	23868	-	-	-

$B_t - B_o$ = 23861 μg B_E = 22938 μg

Production = 46769 μg — 62470 μg in a mean sample length of 22.0 m.

= 2.1 mg — 2.8 mg m^{-1} dry weight production

S.brevicaule CRONKLEY STREAM 2: SECTION B

? Late-July → ? Late-September

Instar	i	m	im	d_x	m^{dx}	$d_x m$
II	298	1	298	-	-	-
III	1071	4		-	-	-
IV	1091	14		645	28	18060
V	446	42		250	75	18750
VI	196	108	↓	23	230	5290
VII	173	351	60723	-	-	-

$B_t - B_o$ = 60425 µg B_E = 42100 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
II	223	1	223	-	-	-
III	803	4		-	-	-
IV	828	14		498	28	13944
V	330	42		184	75	13800
VI	146	108	↓	16	230	3680
VII	130	351	45630	-	-	-

$B_t - B_o$ = 45407 µg B_E = 31424 µg

Production = 76831 µg — 102525 µg in a mean sample length of 19.4 m.

= 4.0 mg — 5.3 mg m^{-1} dry weight production

<u>S.monticola</u> CRONKLEY STREAM 2: SECTION B

Late-June:Early-July → Late-July:?Early-August

Instar	i	m	im	d_x	m^{dx}	d_xm
I	6	0.7	4	-	-	-
II	291	1		229	4	916
III	62	6		-	-	-
IV	112	21		101	41	4141
V	11	60		6	97	582
VI	5	133	↓	3	244	732
VII	2	354	708	-	-	-

B_t-B_o = 704 µg B_E = 6371 µg

Instar	i	m	im	d_x	m^{dx}	d_xm
I	5	0.7	4	-	-	-
II	218	1		171	4	684
III	47	6		-	-	-
IV	85	21		77	41	3157
V	8	60		4	97	388
VI	4	133	↓	3	244	732
VII	1	354	354	-	-	-

B_t-B_o = 350 µg B_E = 4961 µg

Production = 5311 µg — 7075 µg in a mean sample length of 21.6 m.

= 0.2 mg — 0.3 mg m^{-1} dry weight production

S.monticola CRONKLEY STREAM 2: SECTION B

Early-:Mid-August → Late-August:Early-September

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	211	0.7	148	-	-	-
II	1633	1	│	-	-	-
III	1749	6	│	-	-	-
IV	2083	21	│	799	41	32759
V	1284	60	│	848	97	82256
VI	436	133	↓	264	244	64416
VII	172	354	60888	-	-	-

$B_t - B_o$ = 60740 µg B_E = 179431 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	154	0.7	108	-	-	-
II	1225	1	│	-	-	-
III	1312	6	│	-	-	-
IV	1580	21	│	629	41	25789
V	951	60	│	626	97	60722
VI	325	133	↓	196	244	47824
VII	129	354	45666	-	-	-

$B_t - B_o$ = 45558 µg B_E = 134335 µg

Production = 179893 µg — 240171 µg in a mean sample length of 15.8 m.

= 11.4 mg — 15.2 mg m^{-1} dry weight production

S.nitidifrons CRONKLEY STREAM 2: SECTION B

? Mid-June → ? Mid-July

Instar	i	m	im	d_x	m^{dx}	$d_x m$
II	146	3	438	-	-	-
III	202	10	↓	93	24	2232
IV	109	38		98	72	7056
V	11	106		8	162	1296
VI	3	218	654	-	-	-

$B_t - B_o$ = 216 µg B_E = 10584 µg

Instar	i	m	im	d_x	m^{dx}	$d_x m$
II	109	3	327	-	-	-
III	152	10	↓	69	24	1656
IV	83	38		75	72	5400
V	8	106		5	162	810
VI	3	218	654	-	-	-

$B_t - B_o$ = 327 µg B_E = 7866 µg

Production = 8193 µg — 10800 µg in a mean sample stretch of 19.5 m.

= 0.4 mg — 0.6 mg m^{-1} dry weight production

S.nitidifrons CRONKLEY STREAM 2: SECTION B

Mid-:Late-July:Early-August → Mid-:Late-August

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	433	0.7	303	-	-	-
II	2892	3	↓	-	-	-
III	2994	10	↓	1969	24	47256
IV	1025	38	↓	424	72	30528
V	601	106	↓	300	162	48600
VI	301	218	↓	128	323	41344
VII	173	427	73871	-	-	-

$B_t - B_o = 73568\ \mu g$ $B_E = 167728\ \mu g$

Instar	i	m	im	d_x	m^{dx}	$d_x m$
I	315	0.7	221	-	-	-
II	2169	3	↓	-	-	-
III	2248	10	↓	1470	24	35280
IV	778	38	↓	333	72	23976
V	445	106	↓	221	162	35802
VI	224	218	↓	93	323	30039
VII	131	427	55937	-	-	-

$B_t - B_o = 55716\ \mu g$ $B_E = 125097\ \mu g$

Production = 180813 µg — 241296 µg in a mean sample length of 19.0 m.

= 9.5 mg — 12.7 mg m^{-1} dry weight production

APPENDIX 5

The calculation of a conversion factor for Neveu's (1970) biovolume production data, to give results in dry weight.

(i) Using Ladle et al (1972), the weight of a larva of S.ornatum of overall length 4 mm will be 140 µg. (This length being taken as the median of overall length measurements.)

(ii) Taking the mean width of such a larva as being 0.5 mm, the volume will be given by $\pi r^2 h$, i.e. 0.79 mm^3.

(iii) By dividing this value into those given by Neveu (1970) in $mm^3 m^{-2}$ the number of larvae of this hypothetical dimension can be obtained and, by multiplying by 140 µg, the dry weight production m^{-2} can be obtained.

(iv) This conversion was used for all the species and is obviously inaccurate but it does furnish a means of comparing the production of the Pyrenean stream blackflies with those of Upper Teesdale.