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*Larval development and adult life with particular reference to ovarian maturation in certain stoneflies (Plecoptera) of the upper part of the river Wear.*

Eric Svensson

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## ABSTRACT.

The study was divided into three main sections dealing with larval life, the adults and the eggs.

The growth rates of the larvae were investigated by constructing graphs of mean body length, mean head width and mean pronotum length against time; by construction of histograms of size group frequencies for samples taken on specific dates; and by the determining of the percentage change indices of the move up of larvae from one instar to the next over specified periods of time.

These three methods of evaluating the growth rates of the larvae were used to determine the degree of retardation of growth in winter if indeed retardation occurred. They also made possible comparison of growth rates of larvae at high and low stations on the river.

Studies on the adults were directed towards investigating the effect of feeding or starving on life expectancy and towards the importance of feeding in relation to maturation of the eggs in the sub-order Filipalpia. Mature female larvae of both filipalpian species and setipalpian species were dissected together with adults to determine when maturation of the eggs was completed. Mating behaviour was observed and flight periods determined for the commonest species.

Dissections of mature female flies were carried out and egg counts were made with a view to establishing some idea of the fecundity of the commonest species. The eggs were measured and described, some were drawn and others were photographed.

LARVAL DEVELOPMENT AND ADULT LIFE WITH PARTICULAR  
REFERENCE TO OVARIAN MATURATION IN CERTAIN STONEFLIES  
(PLECOPTERA) OF THE UPPER PART OF THE RIVER WEAR.

by

Eric Svensson B.Sc. (Dunelm).

..... being a thesis presented in candidature for the  
degree of Master of Science in the University of Durham 1972.



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INTRODUCTION.

The stoneflies are now considered to be a separate order, the Plecoptera, though they were originally classified as a mere family, (family Perlidae) in the extensive order Neuroptera of Linnaeus, which also included dragonflies and mayflies. Stoneflies are considered to be primitive in many respects and retain many of the features of the fossil Protoperlaria from the lower Permian.

The Order is subdivided into two Sub-orders mainly on the basis of the structure of the mouthparts. On one hand there is the Sub-order Filipalpia with the labrum less than twice as wide as long, mandibles short and stout, and glossae as long as paraglossae. On the other hand is the Sub-order Setipalpia with the labrum more than twice as wide as long, mandibles elongated and reduced glossae.

The British records list 34 species but of these, four species namely Rhabdiopteryx anglica Kimmins, Isoperla obscura Zetterstedt., Isogenus nubecula Newman, and Chloroperla apicalis Newman, have very restricted distributions or the records are doubtful.

The eggs of certain stoneflies have been described by Rousseau (1921), Samal (1923), Wu (1923),



Needham and Claassen (1925), Percival and Whitehead(1928), Helson (1934), Kuhlreiber (1934), Miller (1939), Hynes (1941), and Brinck (1949).

Plecopteran eggs may be broadly classified into two groups based on their external morphology. The eggs of the Setipalpia are variable in shape but never round and they often possess an anchor plate or basal plate. The eggs of the Filipalpia are round or ovoid and lack an anchor plate. Another feature which is different in the two types of egg is the chorion which in the Setipalpia is composed of two layers, an outer exochorion which is hard and thick and an inner endochorion which is thin and delicate. In the Filipalpia the chorion is a single delicate membrane except in Brachyptera risi Morton, where a thick exochorion is found. Brinck (1949) also investigated the occurrence and distribution of micropyles through the chorions of the eggs of Setipalpia and the use to which these openings were put. Micropyles also exist in the case of B. risi and must exist in all stonefly eggs even if not yet observed.

The incubation periods of eggs of various species of stoneflies have been investigated by Percival and Whitehead (1928), Hynes (1941), Brinck (1949). Also Miller (1939) rearing Pteronarcys proteus Newman, found that low temperatures delayed hatching by as much as 152 days. Apart from certain setipalpiian eggs, notably Dinocras cephalotes Curtis,

with 97-112 days incubation (Hynes, 1941), the incubation required by those plecopteran eggs investigated by the above workers was remarkably closely correlated with similar observations made by Brinck (1949). In the case of Capnia nigra the eggs develop to a late stage within the body of the female requiring about 21 days to do so; the egg mass has no sticky substance, each embryo being enclosed by a thin membrane which the fully developed larvae try to penetrate as soon as the eggs contact the water (Brinck, 1949).

Brinck (1949) records that larvae of first and second instars of most plecopteran species are so remarkably similar and of such a generalised structure as to make it extremely difficult to distinguish between genera and species. Because of this uniformity of bodily structure Brinck (1949) refers to instars I and II of length 0.5-1.5 mm as nymphulae. He further states that these nymphulae often exist in a quiescent state at seasons which are adverse as regards the later stages of the species.

The growth rates of plecopteran larvae have been investigated by Brinck (1949), Hynes (1941), Svensson P.O. (1966). Both Brinck (1949) and Svensson P.O. (1966) commented on the retardation of larval growth during the winter months in hiemal developing species but Hynes (1941) found no such marked retardation of growth in British material though he did report definite retardation in the growth of larvae of Protonemura meyeri Pictet, investigated by Frost working in Ireland on the River Liffey. Temperature is generally regarded as being the most important environmental factor influencing the growth rates of stonefly larvae. Brinck (1949), for specimens from Swedish streams,

states that B.risi is apparently an unstable species as regards the hatching of the eggs or the beginning of larval growth after the quiescent period of the nymphulae. This was borne out by the fact that in two essentially similar Swedish streams one population of B. risi was definitely composite, very small larvae being taken at the same time as fully developed larvae, while the other population was very uniform indeed, all the specimens probably having hatched at the same time.

With the exception of the Perlidae it seems that all stonefly larvae complete their growth and emerge in one year though some doubt does exist in the case of Chloroperla tripunctata Scopoli, (Hynes, 1941).

In Swedish material, Brinck (1949) recognised five basic patterns of larval growth:-

- 1) Hiemal species with an obvious retardation of the mean growth rate in the winter months and having a late emergence.

- 2) Hiemal species growing during autumn and early winter and emerging in late winter.

- 3) Hiemal species where mean growth is fairly steady being only slightly affected during the winter months.

- 4) Species inhabiting springs where growth is unaffected by seasonal changes.

- 5) Aestival species growing during the warmest season of the year.

Emergence of adults of the Sub-order Filipalpia

usually takes place very close to the waters edge but in the Sub-order Setipalpia the full grown larvae of certain species walk several yards from the waters edge or ascend bridge supports or bushes for a few feet before moulting to form the adult.

Mertens (1923), Schoenemund (1924), Kuhlreiber (1934), all stated that no adult stoneflies fed and that the mouthparts were degenerate. Frison (1935) showed that feeding occurred in some members of the Sub-order Filipalpia. Newcomer (1918) stated that in California Taeniopteryx pacifica Banks, did feed as adults and that they caused damage to fruit trees by eating buds. Hynes (1942) working with Nemoura cinerea Retzius found that feeding was an important part of the life history, being necessary for mating and egg production. Also fed adults of N. cinerea lived about eight times as long on average as unfed adults, the food being lichens and Protococcales. Brinck (1949) also studied feeding of adult stoneflies both in the laboratory and in the field and confirmed Hynes' observations regarding the feeding of the adult Filipalpia being necessary for egg development.

The females of the large Setipalpia run over the water surface when ovipositing thus spreading the eggs as they become detached from the egg mass. Females of the smaller Setipalpia often fly over the water dipping the tip of the abdomen into the water releasing the eggs as they go. Masses of mature eggs of filipalpian species disintegrate on coming into contact with water and the eggs fly apart spreading widely.

Hynes (1958) recognised five main types of habitat:-

- 1) Still waters with emergent vegetation.
- 2) Stony shores of lakes.
- 3) Emergent vegetation on banks of rivers and streams.
- 4) Small streams with stony beds.
- 5) Rivers with stony beds and moss on larger stones.

Stoneflies show a tendency to select a particular type of habitat by families rather than as individual species. For example the Nemouridae tend to favour still or slow flowing water where there is much emergent vegetation (genera:- Nemoura, Nemurella). Other Nemouridae while not particularly favouring still or slow flowing water certainly do prefer habitats where there is either emergent vegetation, moss, or decaying vegetable matter (genera:- Protonemura, Amphinemura). This latter group of Nemouridae is often found in association with species of Taeniopterygidae (Taeniopteryx nebulosa (Linn) Aubert 1950 and B.risi) which also prefer situations where moss or emergent vegetation exist. The Capniidae frequent stony lake shores for preference while the Leuctridae generally favour stony streams and rivers with fast flowing water. The larger Perlidae and Perlodidae and the Chloroperlidae also occur in stony streams and rivers though larger rocky substrates are favoured by the larger species.

As can be appreciated from examination of the

wide variety of these habitats the oxygen concentration of the water will also vary considerably. Therefore the preference for a particular habitat by particular species is influenced not only by the amount of vegetation or animal life present to serve as food but also possibly indicates the level of oxygen concentration tolerated by each species. Madsen (1968) working on B. risi and Nemoura flexuosa Aubert stated that a qualitative correlation exists between the oxygen requirements of the two species and the oxygen conditions in their respective habitats; B. risi favoured habitats where good oxygen concentration prevailed and N. flexuosa showed that it could exist in a much wider range of habitats where the oxygen concentrations varied from high to low.

Hynes (1941) discussed the influence of altitude and temperature on the distribution of certain species (viz. Diura bicaudata Linné and Perlodes microcephala Pictet) and came to the conclusion that altitude itself was not a limiting factor but that, according to the bodies of water under examination, it could influence the water temperature and hence permit or preclude stonefly species according to their particular temperature thresholds. He observed that D. bicaudata had only been found in running water above 700' - 1000' but that it occurred in lakes down to 100', the suggestion being that the larger body of water would remain colder at low altitude and thus allow D. bicaudata to exist. Hynes also noticed that P. microcephala was never

found in association with D. bicaudata reaching its upper altitudinal limit where D. bicaudata reached its lower altitudinal limit i.e. Hynes proposed a lower limit temperature threshold for P. microcephala. He further suggested that all other species not extending up to the sources of streams at 2000' might also have lower limit temperature threshold.

Variation in the substrate may also account for the presence or absence of certain species of stone-flies, some preferring stable substrata others unstable, Hynes (1941) and Brinck (1949).

Hynes (1941) stated that species occurring in streams subject to drying up were all species where emergence of the adults occurred in spring and were all species having a one year life cycle. It seemed therefore that either the eggs could tolerate drought or that the very young larvae could get down into the gravel and so prevent themselves drying up. Species having a two or three year cycle e.g. Perla species and species emerging in late summer and autumn i.e. the larvae of which are half grown during the dry season, were unable to live in such places owing to the fact that large larvae cannot escape desiccation during drought. Brinck (1949) stated that drought exterminated the larvae in unshaded situations but that shade and subsoil water might alleviate these conditions.

Brinck (1949) was unable to claim any correlation between pH and distribution of stoneflies, most species

being frequently found in water of pH varying between 6.0 and 8.0. He did comment on one exception to this statement i.e. Capnia bifrons Newman, which always occurred in waters with high calcium and pH between 7.5 and pH 8.7. The pH tolerance of N. cinerea in Brinck's account was given as pH 4.5 - 9.0 an exceptionally wide range indeed.

The aims of this study are to investigate further:-

- a) The occurrence of stonefly species in the upper reaches of the River Wear.
- b) the growth and development of the larvae at different times of the year at differing levels of the river.
- c) the emergence of the adults and any observable flight periods.
- d) the maturation of the ovaries of certain of the more common species, particularly in relation to any food intake by adult females.
- e) any other feature of adult life that may have a bearing on the ability or otherwise of stoneflies to produce mature eggs.

THE LARVAE.

THE LARVAE.

SAMPLING AND LARVAL DISTRIBUTION.

I. Description of the Upper River Wear.

The particular stretch of the river (Wearhead to Witton Park), concerned in this study is shown in Fig. 1 which is derived from parts of sheets 84 and 85 of the ordnance survey, scale of 1" to 1 mile.

The river is formed by the junction of Burnhope Burn and Killhope Burn immediately above the bridge at Wearhead. The altitude at this point is 1,050 feet.

When the water level is normal the approximate width of the river is 15'-20' at Wearhead; 20-25' at Westgate; 30'-35' at Stanhope; 35' - 40' at Wolsingham; 45'-50' at Witton Park. The width of the complete river bed at all stations is considerably wider than these dimensions comprising stony stretches on each side of the main water body which only become covered during flood conditions. Also the river banks are grassy and tree lined at all stations, willow bushes occur at all stations and these provide the main resting sites for the emerging adult stoneflies.

The bed of the river is composed of large stones, mainly limestone and sandstone, set into large pebbles and coarse gritty gravel and sand. Caught up

amongst the stones a varying amount of floating debris, especially twigs and dead leaves, is found. At Wearhead this debris is always fairly fresh and not in any advanced state of decomposition but at lower stations especially at Witton Park where the rate of water flow is less, well rotted material is encountered.

The total length of the river spanned by the five main sampling stations is 40 Km. (= 24.6 miles).

II. The sampling programme and station sampled.

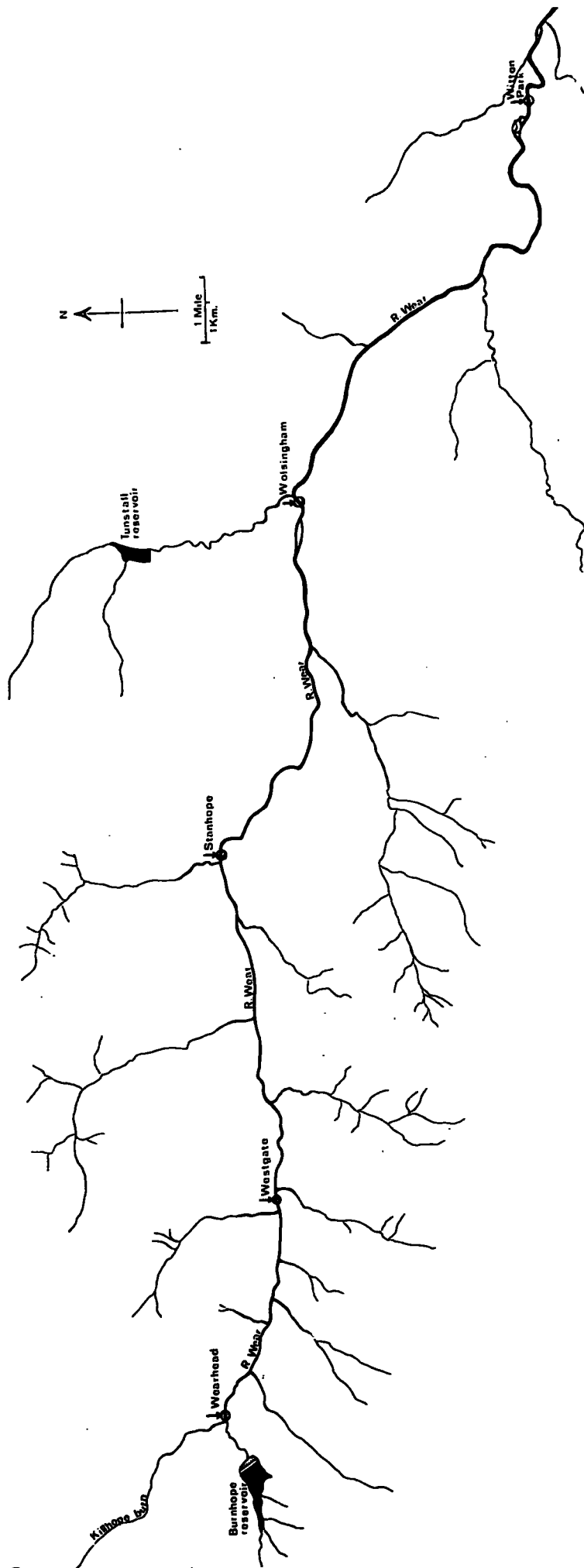
Originally five stations were chosen for sampling the plecopteran larval populations living in the water and also for sampling the adult Plecoptera under the stones and on the riverside vegetation. The five stations (fig. 1.) were chosen to be as nearly alike as possible.

They were:-

Wearhead	Map ref. 857395	Altitude 1,050 feet
Westgate	Map ref. 908381	Altitude 900 feet
Stanhope	Map ref. 991393	Altitude 700 feet
Wolsingham	Map ref. 075368	Altitude 500 feet
Witton Park	Map ref. 171308	Altitude 300 feet

Sampling of the larvae was accomplished by kicking up the stones and gravel of the river bed and collecting the dislodged cloud of sand, stones and animals and plant material in a net placed immediately downstream. Each sampling effort was of thirty seconds duration and at each station three such sample units were taken to avoid the danger of getting the wrong impression of the composition and abundance of the various larval populations in the event of taking an atypical sample. The net contents for each sampling effort were then transferred to wide mouthed jars and enough 5% formalin solution was added to kill and preserve the animals caught. These samples were subsequently sorted by hand from large shallow white enamel dishes and the plecopteran larvae were identified

Fig1 Map of the upper River Wear showing the five main sampling stations on this section



and preserved in 4% formalin solution.

Sampling of the adults was accomplished by turning over stones and capturing any exposed newly emerged adults by the use of a "pooter" or by holding a wide mouthed linen net under the branches of riverside bushes and beating them with a stout stick to dislodge the adults which were then sucked up into the "pooter" as before. Many of the adults taken were kept alive and used for feeding and ovarian maturation experiments. Others were killed and preserved immediately by first wetting them with alcohol then dropping them into 4% formalin solution. In addition other adults were collected by sweep-netting of the ground vegetation and again some were kept alive while others were killed and preserved immediately as described above.

III. Larval distribution.

1. Larval species list.

Sub-Order Filipalpia.

- Amphinemura sulcicollis (Stephens)
- Protonemura praecox (Morton)
- Protonemura meyeri (Pictet)
- Nemoura cambrica (Stephens)
- Nemoura cinerea (Retzius)
- Nemoura erratica (Claassen)
- Brachyptera risi (Morton)
- Taeniopteryx nebulosa (Linn) Aubert 1950
- Leuctra inermis (Kempny)
- Leuctra hippopus (Kempny)
- Leuctra moselyi (Morton)
- Leuctra fusca (Linné)
- Leuctra geniculata (Stephens)

Sub-Order Setipalpia.

- Chloroperla torrentium (Pictet)
- Chloroperla tripunctata (Scopoli)
- Isoperla grammatica (Poda)
- Dinocras cephalotes (Curtis)
- Perla bipunctata (Pictet)
- Diura bicaudata (Linné)
- Perlodes microcephala (Pictet)

2. Total numbers of larvae taken Nov.1966-Sept.1967.

Table 1 gives the total numbers of stonefly larvae captured at the five main sampling stations from November 1966 to September 1967. Table 1 also gives information about the distribution of each larval species in this section of the River Wear and indicates the degree of abundance of each species at high and low stations. An indication is also given that filipalpiian species in the genus *Leuctra* prefer the upper stations especially in the cases of *L. inermis* and *L. hippopus* which are hiemal developing species. *L. fusca* and to a lesser extent *L. moselyi* which are aestival developing species seem able to tolerate conditions at lower stations. *B. risi* and all setipalpiian species with the exception of *C. torrentium* seem able to tolerate lower stations at least as well if not better than upper stations.

3. Distribution of individual species.

The occurrence of each species in the upper River Wear as recorded in the present study was compared with records of Butcher et al (1937) from the River Tees, and with records of Brown, Cragg and Crisp (1964) from Moor House National Nature Reserve.

Species also recorded by Butcher are indicated by \*

Species also recorded by Brown, Cragg, and Crisp are indicated by +

TABLE I.

Total numbers of stonefly larvae captured at the five main sampling stations  
November 1966 - September 1967.

<u>SPECIES</u>	<u>WEARHEAD</u>	<u>WESTGATE</u>	<u>STANHOPE</u>	<u>WOLSINGHAM</u>	<u>WITTON PARK</u>
<i>Amphinemura sulcicollis</i>	689	397	431	321	365
<i>Protonemura praecox</i>	10	9	13	3	11
<i>Protonemura meyeri</i>	9	0	13	4	0
<i>Nemoura cambrica</i>	0	1	0	0	0
<i>Nemoura cinerea</i>	1	0	0	0	1
<i>Brachyptera risii</i>	12	4	21	13	20
<i>Taeniopteryx nebulosa</i>	1	0	1	1	0
<i>Chloroperla torrentium</i>	17	25	6	0	4
<i>Chloroperla tripunctata</i>	0	1	0	1	0
<i>Isoperla grammatica</i>	30	19	28	9	41
<i>Dinocras cephalotes</i>	0	9	3	1	40
<i>Perla bipunctata</i>	1	4	2	0	12
<i>Perlodes microcephala</i>	2	0	0	2	4
<i>Leuctra inermis</i>	464	194	42	8	3
<i>Leuctra hippopus</i>	8	0	5	1	1
<i>Leuctra moselyi</i>	46	16	8	2	1
<i>Leuctra fusca</i>	1229	269	89	135	680
<i>Diura bicaudata</i>	2	0	0	0	0

Amphinemura sulcicollis (Stephens) \*+

This species was recorded at all five main sampling stations and in addition at the following stations sampled by Miss Holborn:-

		Grid ref.
I	Cowshill	(856398)
II	St. John's Chapel	(889381)
III	Eastgate	(957395)
IV	Stanhope	(001384)
V	Witton-le-Wear	(153313)
VI	Above Bishop Auckland	(205303)
VII	Below Bishop Auckland	(211310)
VIII	Todhills Bridge	(210344)
IX	Shincliffe	(287409)
X	Durham Sands	(282434)
XI	Cocken Bridge	(280472)

It was very abundant at all upper stations but was only moderately abundant at Witton-le-Wear and Witton Park. At Bishop Auckland its numbers fell still more and by Todhill's Bridge it was only present in very small numbers. (See Table 2). It seems that the species completes development and emerges rather earlier at lower levels of the river than at the higher stations. For example the last records of 1966-67 larvae captured were:-

Wearhead - one full grown larva on 18/6/67

Witton Park - thirteen full grown larvae on 28/5/67

This indication is further reinforced when records of the capture of the first adults are examined:-

Wearhead - Six adult males and two adult females on 21/5/67.

TABLE 2.

Relative abundance of *Amphinemura sulciollis*

larvae at selected stations on The River Wear

STATION	DISTANCE FROM SOURCE K.M.	RELATIVE ABUNDANCE.												OVER ALL RELATIVE ABUNDANCE.
		1966						1967						
		XI	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	
WEARHEAD	0.0	○		○	○	+	○	○	+	×	+	○	○	○
WESTGATE	4.8	○		○	○	○	○	○	×					○
STANHOPE	13.6	○		○	○	○	○	○	+	○	○	○	○	○
WOLSHINGHAM	22.4	○		○	○	○	○	+	+					○
WITTON PARK	34.4	○		○	○	○	○	+	×	×	+	+	○	○
BISHOP AUCKLAND	40.0	○		○	○		○	×	×	+	○	+	+	○
TODHILL'S BRIDGE	48.0	+		+	+									+
DURHAM SANDS	66.4	+			×				+	+		+	+	+

KEY:-

○	○	+	×	
---	---	---	---	--

Very abundant

Fairly abundant

Scattered specimens

No specimens taken

No sample available

Witton Park - 3 adult males and 1 adult female on 7/5/67.

In spite of this discrepancy in time of completion of development and therefore of the commencement of adult life, the larvae of the next generation were captured from all levels on or about the same date:-

Cowhill	- very large numbers	- 24/7/67
Wearhead	- ten specimens	- 6/8/67
Stanhope	- fairly large numbers	- 10/7/67
Stanhope	- very large numbers	- 24/7/67
Bishop Auckland-	ten specimens	- 24/7/67

The reason for this almost simultaneous reappearance of larvae in late July remains obscure. Larvae of this species were only absent from samples for a very short time, the 1966-67 generation finishing development by late May/mid June, and the 1967/68 generation reappearing as first instars by mid July/late July. For an indication of relative abundance of larvae of this species at the various stations see Table 2.

Protonemura praecox (Morton) \*±

This species was present in small numbers at all stations as far as below Bishop Auckland, it was not taken at lower stations in 1966-67. The last fully developed larvae were taken from mid April/late April 1967. Larvae less than 3.0 mm. reappeared in samples in August 1967. Because of the small numbers of larvae it was not possible to compare times of completion of

development at high and low stations.

Protonemura meyeri (Pictet)\*+

This species was present in small numbers, however its range extended at least as far as that of P. praecox. It was recorded from samples as late as 31/5/67 and reappeared as very small larvae in late July/early August. It was not possible to compare times of completion of development at high and low stations.

Nemoura cambrica (Stephens)+

Rare. Four specimens were found a) at Witton Park on 5/2/67 measuring 2.4 mm; b) at Stanhope on 30/4/67 Measuring 3.7 mm.; c) at Westgate on 11/6/67 measuring 7.0 mm.; d) at Wearhead on 22/10/67 measuring 2.0 mm.

Nemoura cinerea (Retzius)+

Two specimens recorded a) at Witton Park 5/2/67 and b) at Wearhead 22/10/67.

Nemoura erratica (Claassen)+

One specimen recorded at Wearhead 28/1/68.

Brachyptera risi (Morton)\*+

This species was found in small numbers from Wearhead to Witton Park but was more common at the upper stations. The population was of a composite

structure, small larvae still being found when the majority of larvae taken were fully developed.

Taeniopteryx nebulosa (Linn) Aubert 1950 \*\*

Four isolated specimens were captured at widely spaced stations in the river and with considerable intervening periods of time. The records are as follows:-

at Wolsingham	5/11/66
at Stanhope	26/6/67
at Bishop Auckland	10/7/67
at Wearhead	28/1/68

Leuctra inermis (Kempny)\*\*

This species was found at all the main sampling stations but was considerably more abundant at upper stations. Larvae were taken from September 1966-June 1967, the last full grown larvae were captured at Wearhead on 11/6/67. Small larvae of body length 1.5 - 2.0 mm. reappeared in samples taken at Wearhead on 11/9/67.

Leuctra hippopus (Kempny)+

Very few specimens were taken but its distribution seemed to be much the same as that of L. inermis.

Leuctra moselyi (Morton)+

This species was only present in moderate numbers. Its period of development was from late spring to early summer. The first specimens were taken on 12/4/67 and

the last specimens were taken on 2/7/67.

Leuctra fusca (Linné)

This species was present in large numbers at all the five main sampling stations. The first larvae taken at Wearhead were captured on 30/4/67 and the 1st ones on 11/9/67. At Witton Park the dates of the respective captures were 21/5/67 and 11/9/67. The species developed from late spring to late summer/early autumn.

Leuctra geniculata (Stephens)

Rare. Found in very small numbers at Bishop Auckland.

By examining the records of the capture of larvae of the family Leuctridae obtained it was possible to see a definite succession of species throughout the year, from L. hippopus to L. inermis to L. moselyi to L. fusca. The first two named species were hiemal in their development and the other two named species were aestival in their development. L. geniculata seemed to have much the same development period as L. fúsca but the small number of specimens taken preclude any definite statement on this subject.

Chloroperla torrentium (Pictet) \*+

This species was present in small numbers from Wearhead to Bishop Auckland but was not recorded below this point. The last fully developed larvae were recorded in mid June and small larvae of the 1967-1968 generation were taken in mid October.

Chloroperla tripunctata (Scopoli)\*+

Extremely rare. Found together with C.torrentium but this species seemed to develop rather earlier and emerge rather earlier too. Twelve specimens were recorded. The species was found at Westgate, Eastgate, Stanhope, Wolsingham and Witton-le-Wear.

Isoperla grammatica (Poda)\*+

This species was found in small numbers from Wearhead to Todhills Bridge but seemed to favour the middle/lower stations. The last larvae of the 1966-67 generation were taken in late May 1967 and small larvae of the 1967-68 generation reappeared in samples taken at Stanhope on 24/7/67.

Dinocras cephalotes (Curtis)\*+

This species was taken in small numbers from Cowshill to below Bishop Auckland. It was found mainly under large stones and boulders not easily removed by the fast current. Lower stations were favoured.

Perla bipunctata (Pictet)\*+

Like D. cephalotes this species was found from Wearhead to below Bishop Auckland. Also it was found mainly under large stones and boulders. Although found together with D. cephalotes it was not as frequently captured.

Perlodes microcephala (Pictet)\*+

Larvae were taken at stations from Cowshill to Todhill's Bridge but not in large numbers and it was not as common as D. cephalotes or P. bipunctata.

Diura bicaudata (Linné)+

Two specimens only were taken, both on the same occasion on 30th April 1967 at Cowshill.

IV Proportion of each species in samples.

The relative proportion (%) of each species in the total larval population was calculated at monthly intervals to obtain a clearer picture of the succession of the commoner species throughout the year. This method of comparing the incidence of the various species of larvae was carried out first for Wearhead, then for Witton Park.

Table 3 gives percentage composition of larval samples from Wearhead. Fig. 2 shows the percentage of the three most abundant species, A. sulcicollis and L. inermis (both hiemal species) and L. fusca (an aestival species). Fig 2. indicates the degree to which these common species were able to exist together and also shows the sudden advent of a species and the equally sudden departure of a species from the water because of mass hatching and mass emergence respectively.

Table 4 gives percentage composition of larval samples from Witton Park. Fig. 3 shows the percentage of the two most abundant species A. sulcicollis (an hiemal species) and L. fusca (an aestival species). Fig.3 also shows the sudden appearance and disappearance of these species.

Figures 2 and 3 also make it possible to compare the populations at Wearhead and Witton Park. At Wearhead there were two frequently occurring hiemal species which were A. sulcicollis and L.inermis

Fig.2. Percentages of total larval population of *A.sulcicollis* *L.inermis* and *L.fusca* at Wearhead Nov.1966- Mar.1968.

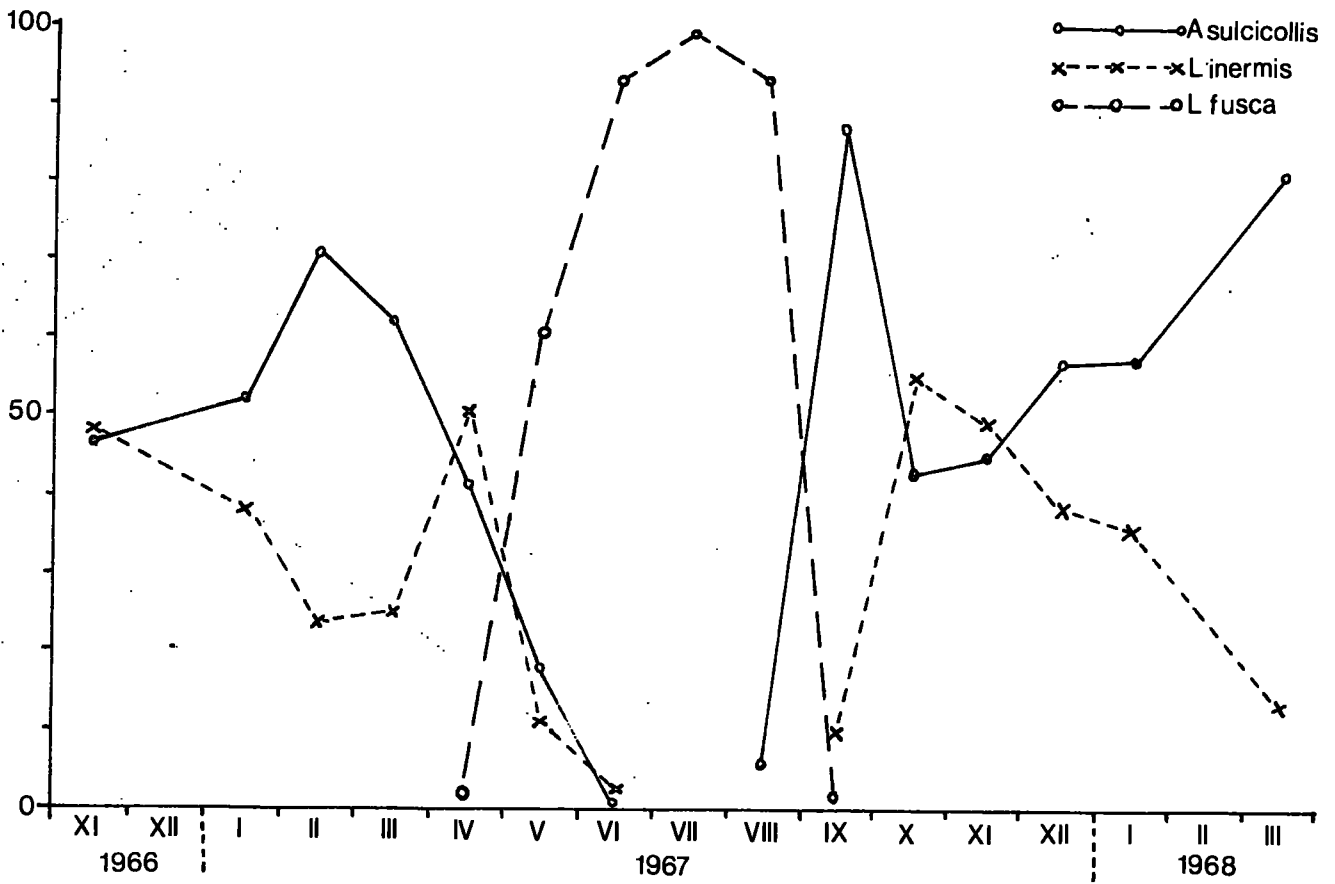


Fig.3. Percentages of total larval population of *A.sulcicollis* and *L.fusca* at Witton Park Nov.1966 - Mar.1968.

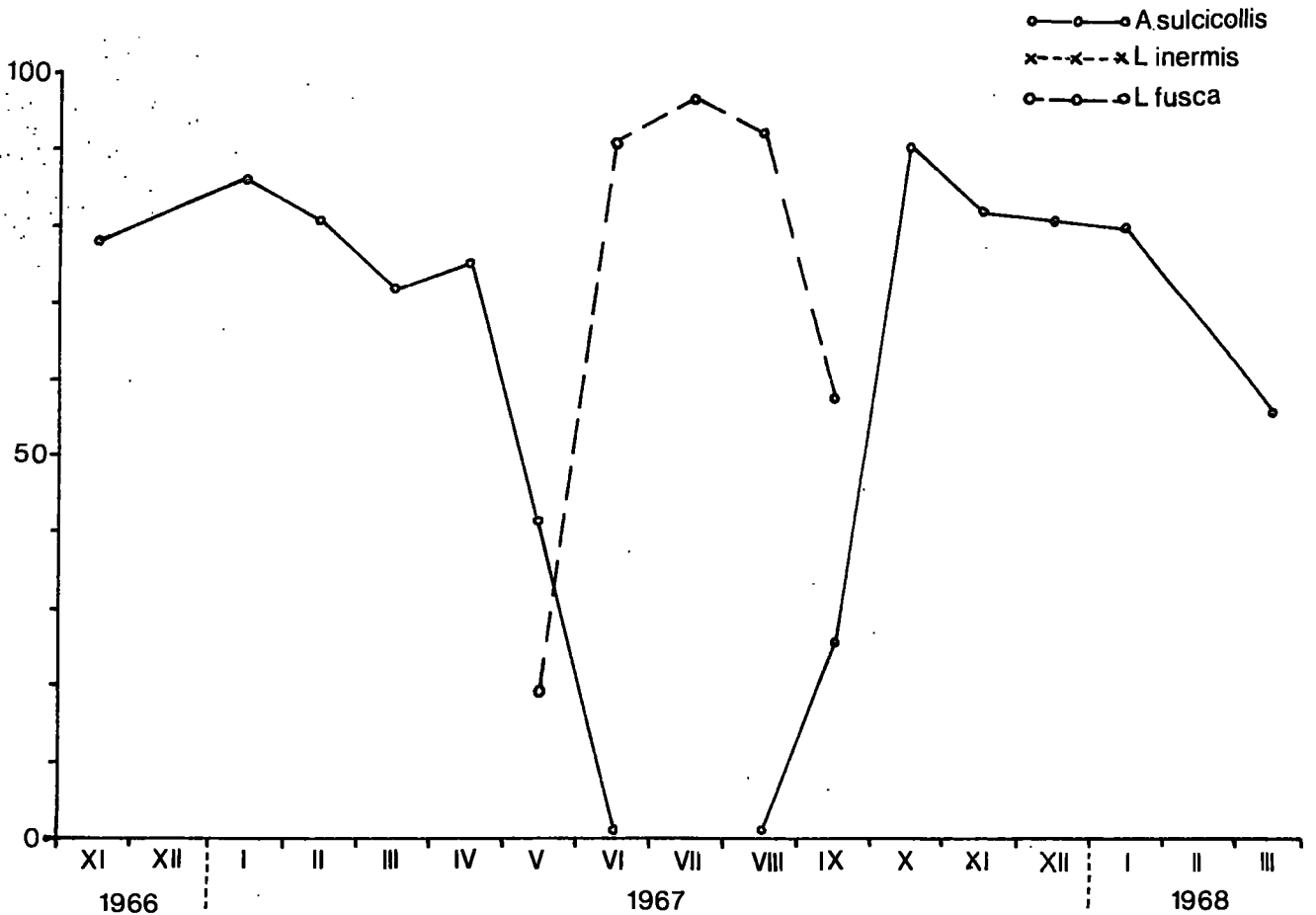


TABLE 3.

Percentage composition of larval samples - Wearhead 1966-1968.

SPECIES	1966												1967												1968		
	XI	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III										
A.sulcicollis	46.8	0	52.1	71.1	62.5	41.3	17.7	0.5	0.5	5.6	87.1	42.3	45.0	57.7	57.3	0	81.5										
L.inermis	48.1	0	38.0	23.5	25.0	50.6	10.5	1.3	-	-	9.6	55.1	49.3	38.0	35.7	0	13.0										
L.hippopus	-	0	7.0	-	-	-	0.6	-	-	-	0.6	2.1	-	0.2	-	0	-										
L.mpselyi	-	0	-	-	-	0.5	3.6	4.7	0.5	-	-	-	-	-	-	0	-										
L.fusca	-	0	-	-	-	1.7	60.7	93.2	99.1	93.9	1.2	-	-	-	-	0	-										
P.praecox	1.3	-	1.4	1.6	6.3	0.5	-	-	-	-	-	-	0.5	0.4	1.3	-	-										
P.meyeri	-	0	-	-	-	-	-	-	-	0.6	-	-	-	-	-	0	-										
B.risi	-	0	-	0.5	-	4.3	0.3	-	-	-	-	-	2.9	0.2	-	0	-										
C.torrentium	-	0	1.4	0.5	-	0.9	2.8	0.3	-	-	-	-	-	0.8	1.8	0	-										
I.grammatica	3.9	0	-	2.7	6.3	0.5	3.9	-	-	-	0.6	0.4	2.4	1.0	2.6	-	5.6										
D.cephalotes	-	0	-	-	-	-	-	-	-	-	-	-	-	0.2	-	0	-										
P.bipunctata	-	N	-	-	-	-	-	-	0.5	-	-	-	-	-	-	N	-										
P.microcephala	-	-	-	-	-	-	-	-	-	-	1.1	-	-	0.2	-	-	-										

TABLE 4.

Percentage composition of larval samples - Witton Park 1966-68.

SPECIES	1966			1967												1968		
	XI	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	
A. sulcicollis	78.3		86.8	81.2	72.7	75.3	41.9	1.1	-	0.7	25.0	90.5	82.2	81.1	80.4		55.6	
L. inermis	-		-	-	-	2.6	3.5	-	-	-	-	-	1.8	-	2.0		5.5	
L. hippopus	-		-	-	-	-	3.5	-	-	-	-	-	1.8	-	-		-	
L. moselyi	-		-	-	-	-	-	0.6	-	-	-	-	-	-	-		-	
L. fusca	-		-	-	-	-	19.4	91.6	96.8	92.9	57.1	-	-	-	-		-	
P. praecox	7.3		1.8	-	-	-	-	-	-	1.4	3.6	-	3.5	3.8	2.0		5.5	
P. meyeri	-		-	-	-	-	-	-	-	-	-	-	-	1.9	-		-	
B. risi	-		0.9	2.6	14.5	9.1	3.5	-	-	-	-	-	-	-	5.9		16.5	
C. torrentium	-		-	-	1.8	2.6	-	-	-	-	-	2.4	-	-	-		-	
I. grammatica	10.2		9.0	9.7	7.2	5.2	12.9	-	-	-	-	2.4	4.3	11.4	7.8		22.2	
D. cephalotes	2.9		0.9	4.4	1.8	2.6	-	5.6	2.8	3.6	14.3	4.8	1.8	-	-		-	
P. bipunctata	-		-	0.9	1.8	1.3	16.1	1.1	0.6	0.7	-	-	-	1.9	-		-	
P. microcephala	1.5		0.9	-	-	-	-	-	-	1.4	-	-	1.8	-	2.0		5.5	

with the former slightly more dominant whereas at Witton Park L. inermis was virtually absent leaving A. sulcicollis in a completely dominant position during the winter months. At both stations there was only one really dominant aestival species, L. fusca. At both stations larvae of L. fusca comprised over 90% of the total larval population during the months of June, July and August.

V. Mutual association of species.

The mutual association of stonefly larvae at the five main sampling stations was investigated according to the method used by Brinck (1949) in estimating the mutual association of larvae of Swedish stoneflies. The number of specimens taken at each sampling station is tabulated (see table 1) and by inspection each pair of species was allocated a degree of mutual association as follows:-

- 0 = The two species are not found at the same stations.
- 1 = The two species have one or more stations common but only scattered specimens occur there but they reach their maximum abundance at different stations.
- 2 = Both species fairly abundant at several stations but do not reach their maximum abundance in the same localities.
- 3 = Both species are restricted to and reach maximum abundance at the same station but at different times.
- 4 = Both species reach their maximum abundance at the same stations at the same time.

Species having high mutual association indices were kept together as far as possible and the data arranged in Table 5. When this had been done it was possible to discern two main groups, preferring on the one hand upper stations and on the other lower stations. There was a considerable degree of overlap of the two

Table 5. Degrees of Mutual Association of species of larvae. (for key see text page 31.).

	<i>Perla bipunctata</i>	<i>Perlodes microcephala</i>	<i>Isoperla grammatica</i>	<i>Brachyptera risi</i>	<i>Protonemura praecox</i>	<i>Protonemura meyeri</i>	<i>Chloroperla tripunctata</i>	<i>Taeniopteryx nebulosa</i>	<i>Nemoura cambrica</i>	<i>Nemoura cinerea</i>	<i>Amphinemura sulcicollis</i>	<i>Diura bicaudata</i>	<i>Chloroperla torrentium</i>	<i>Leuctra inermis</i>	<i>Leuctra hippopus</i>	<i>Leuctra moselyi</i>	<i>Leuctra fusca</i>	
I	4	3	3	3	1	1	1	1	1	1	2	1	2	2	1	2	2	<i>D. cephalotes</i>
		3	3	3	1	1	1	1	1	1	2	1	2	2	1	2	2	<i>P. bipunctata</i>
			3	3	1	1	1	1	0	1	2	1	2	2	1	2	2	<i>P. microcephala</i>
				4	2	2	1	1	1	1	2	1	2	2	1	2	2	<i>I. grammatica</i>
II					2	2	1	1	1	1	2	1	2	2	1	2	2	<i>B. risi</i>
						2	1	1	1	1	2	1	2	2	1	2	2	<i>P. praecox</i>
							1	1	0	1	2	1	2	2	1	2	2	<i>P. meyeri</i>
III								1	1	0	1	1	1	1	1	1	1	<i>C. tripunctata</i>
									1	1	1	1	1	1	1	1	1	<i>T. nebulosa</i>
										0	1	1	1	1	1	1	1	<i>N. cambrica</i>
IV											1	1	1	1	1	1	1	<i>N. cinerea</i>
												3	3	4	3	3	3	<i>A. sulcicollis</i>
													3	3	3	1	3	<i>D. bicaudata</i>
														3	3	4	3	<i>C. torrentium</i>
															3	3	3	<i>L. inermis</i>
																3	3	<i>L. hippopus</i>
																3	<i>L. moselyi</i>	

I. Species preferring lower reaches of the river.

II. Species ranging from upper to lower reaches but with some tendency to favour middle or lower stations.

III. Species so infrequent that to classify them as upper, middle or lower species proved impossible.

IV. Species preferring upper stations on the river.

associations and in addition certain rarer species could not be readily assigned to one group or the other because of their scarcity.

GROWTH AND DEVELOPMENT OF THE LARVAE.

I. Measurement methods.

Three measurements were taken in respect of each individual larva, the overall length of the body, the maximum width of the head capsule, and the length of the pronotum (prothoracic segment). In order to obtain these measurements the specimens were examined under a binocular microscope using an eyepiece graticule which had been previously calibrated against a stage micrometer slide. All measurements were taken when the individual specimens had been pressed flat either using a dissecting needle or in badly curled specimens by placing a piece of microscope slide on top of them. In all cases measurements were taken to the nearest 0.1 mm.

From the data obtained by measurement it was possible to calculate mean values for the total body length, width of head capsule and length of pronotum at intervals of three to four weeks throughout the year. Graphing of these mean values against time yielded growth curves which potentially revealed speed of growth of the various species at different times of the year.

Certain limitations of the use of the mean as the basis upon which to construct growth curves must be taken into account. For instance mean size may fail to increase or may even decrease if further hatching from eggs occurs after the main component of

the population was already some way towards completion of larval growth. Therefore it is important to take into account other evidence regarding the occurrence or otherwise of very small larvae when interpreting the growth curves.

A complementary method of interpreting the measurement data was the construction of histograms of size group frequencies of the larvae throughout the period of study. These helped to indicate the duration of the hatching periods and also indicated the relative speed at which growth occurred at different seasons and also provided a means of comparing hatching periods, total growth periods and growth rates at high and low stations.

For tables of data obtained as a result of measurements see appendix I.

II. Growth pattern of each species.

1. Amphinemura sulcicollis. Total number examined was 3,402. As stated previously this species was common at all five main sampling stations and it was possible to compare growth rates throughout the larval life from November 1966 to May/June 1967 at all five localities and also to continue this comparison from August 1967 to March 1968 in respect of Wearhead and Witton Park. Figures 4-8 inclusive show mean body length, mean head width and mean pronotum length plotted against time. All the graphs show a high degree of correlation between these dimensions. The standard deviation from these mean values was calculated and was plotted for body length on the graphs.

This gave an indication of the distribution of the individuals about the mean for body lengths and showed the population to be very compact, probably consisting of only one or two instars in each of the samples examined. In all but three samples at Wearhead the S.D. was less than  $\pm 0.5$ mm and at Witton Park all but five samples had an S.D. of less than  $\pm 0.5$ mm from the mean body length; at neither station did the S.D. exceed  $\pm 0.75$  mm in respect of any individual sample.

Histograms of size groups at frequencies of 0.5mm were constructed and these revealed that the populations of Amphinemura sulcicollis showed a strong approximation to a normal distribution (see figures 9-13 inclusive) as regards body length and were therefore capable of being regarded as uni-modal populations.

Fig. 4. Growth of larvae of *Amphinemura sulcicollis* at Wearhead Nov.66- Mar.68.

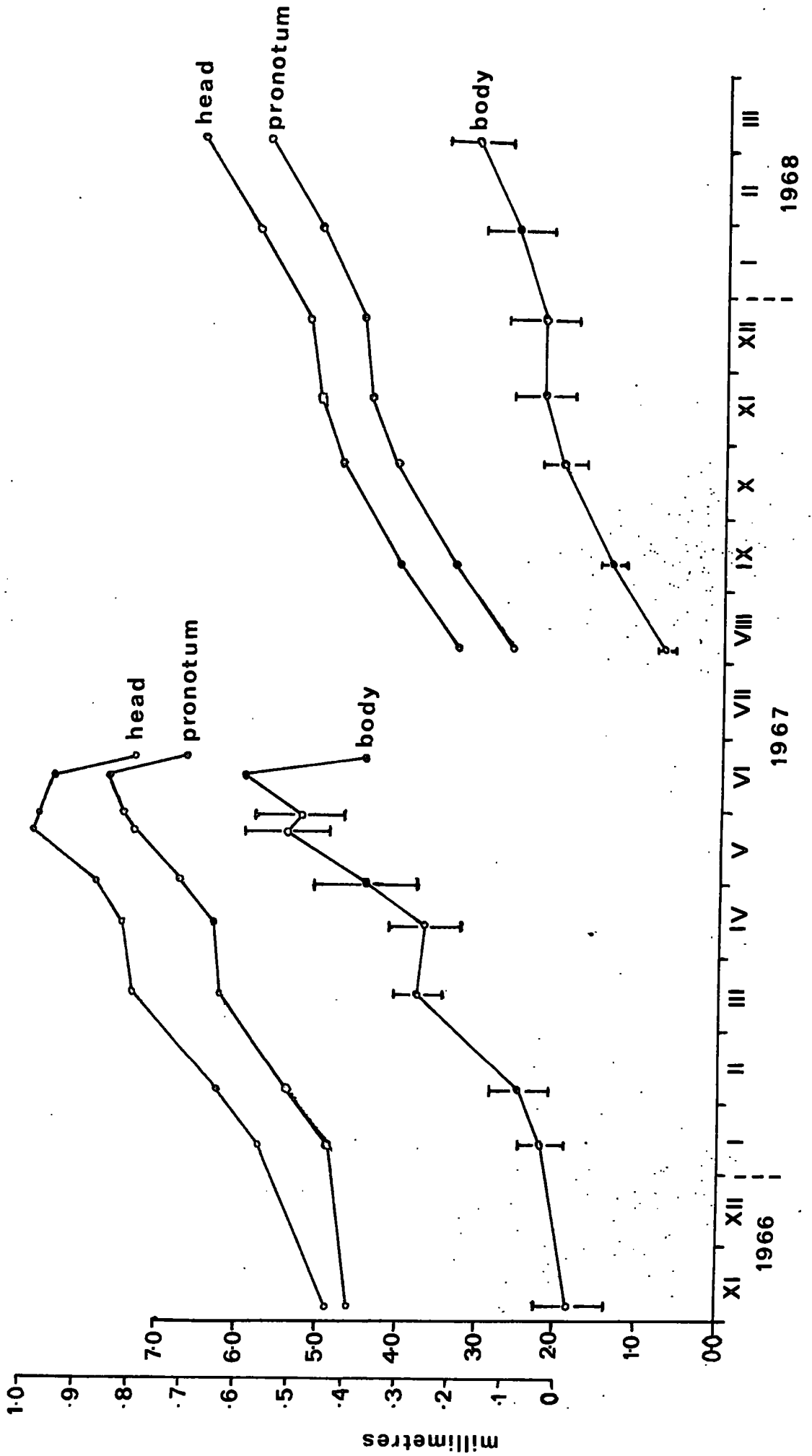


Fig.5. Growth of larvae of *Amphinemura sulcicollis* at Westgate Nov.66 - Jun.67.

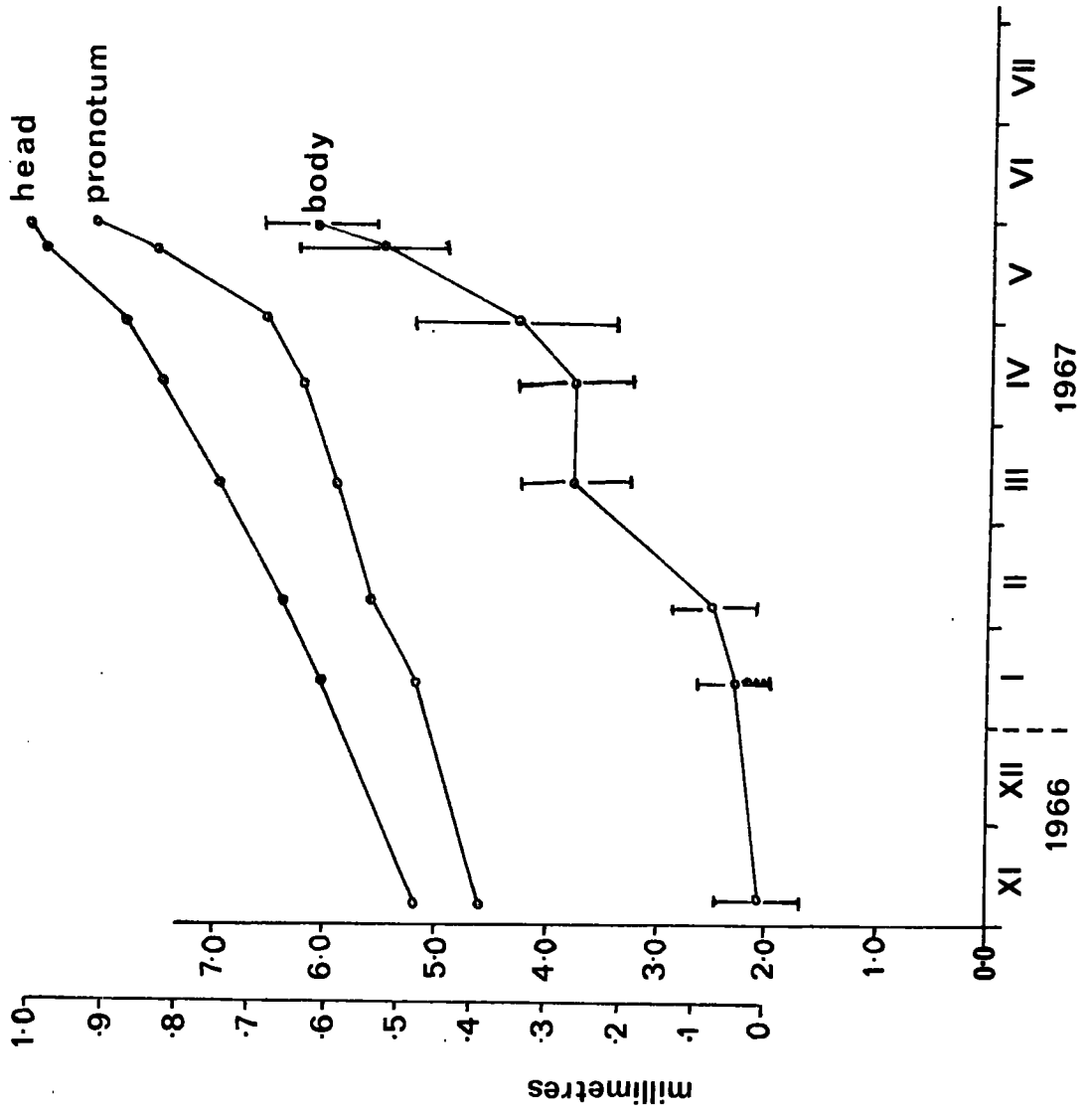


Fig.6. Growth of larvae of *Amphinemura sulcicollis* at Stanhope Nov.66. - Jun.67.

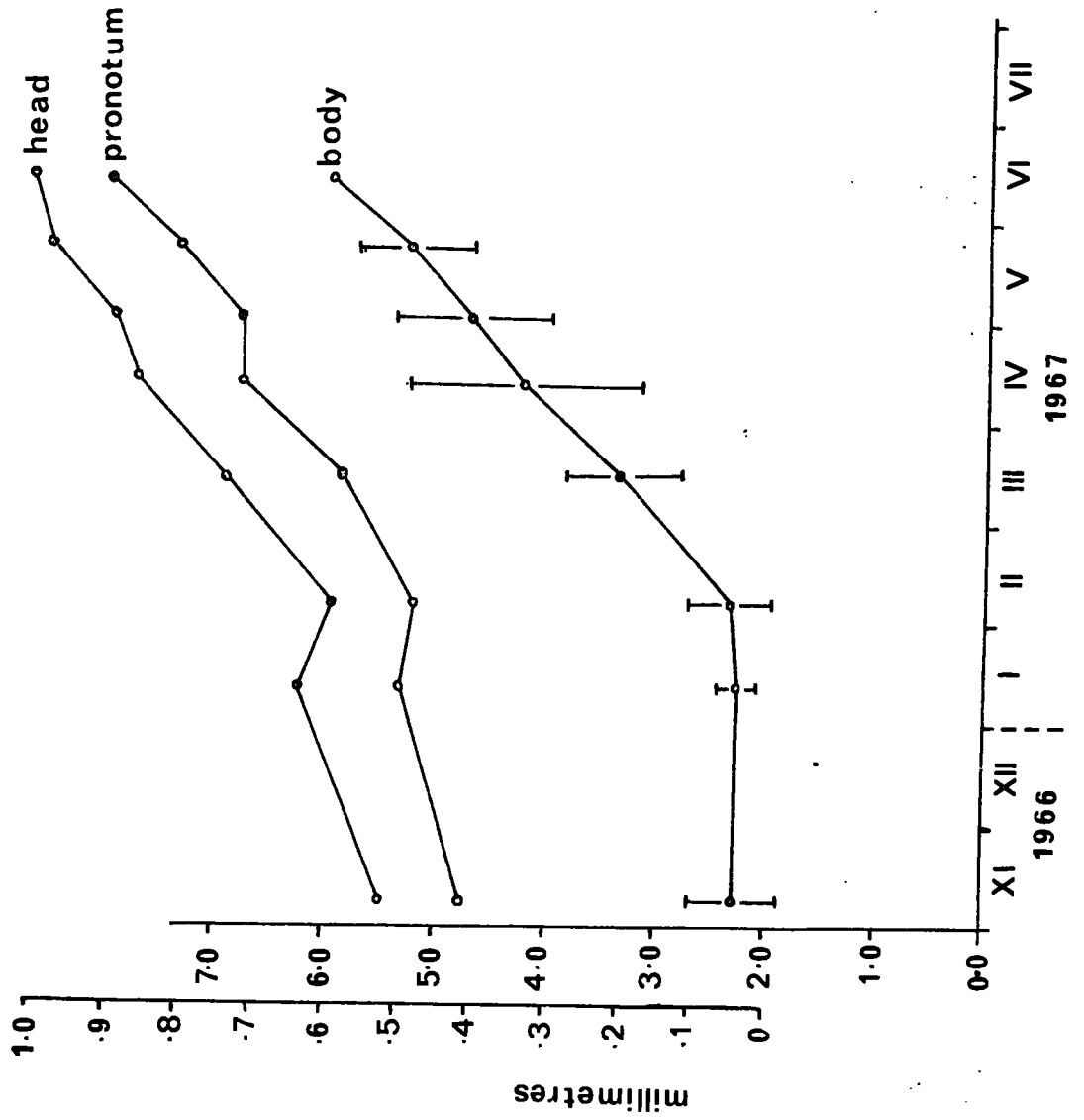


Fig. 7. Growth of larvae of *Amphinemura sulcicollis* at Wolsingham Nov.66. - Jun.67.

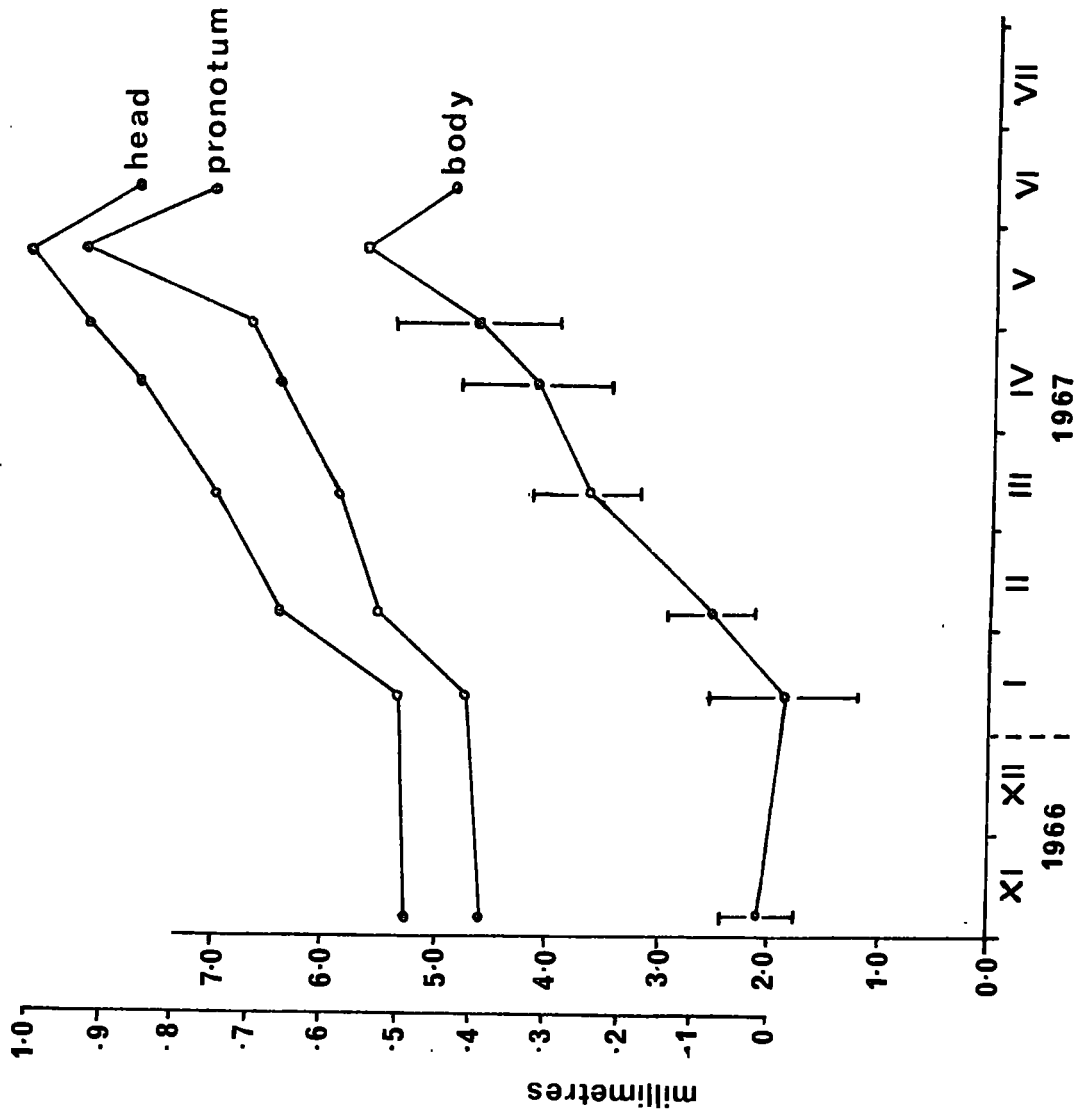


Fig. 8. Growth of larvae of *Amphinemura sulcicollis* at Witton Park Nov.66. - Mar.68.

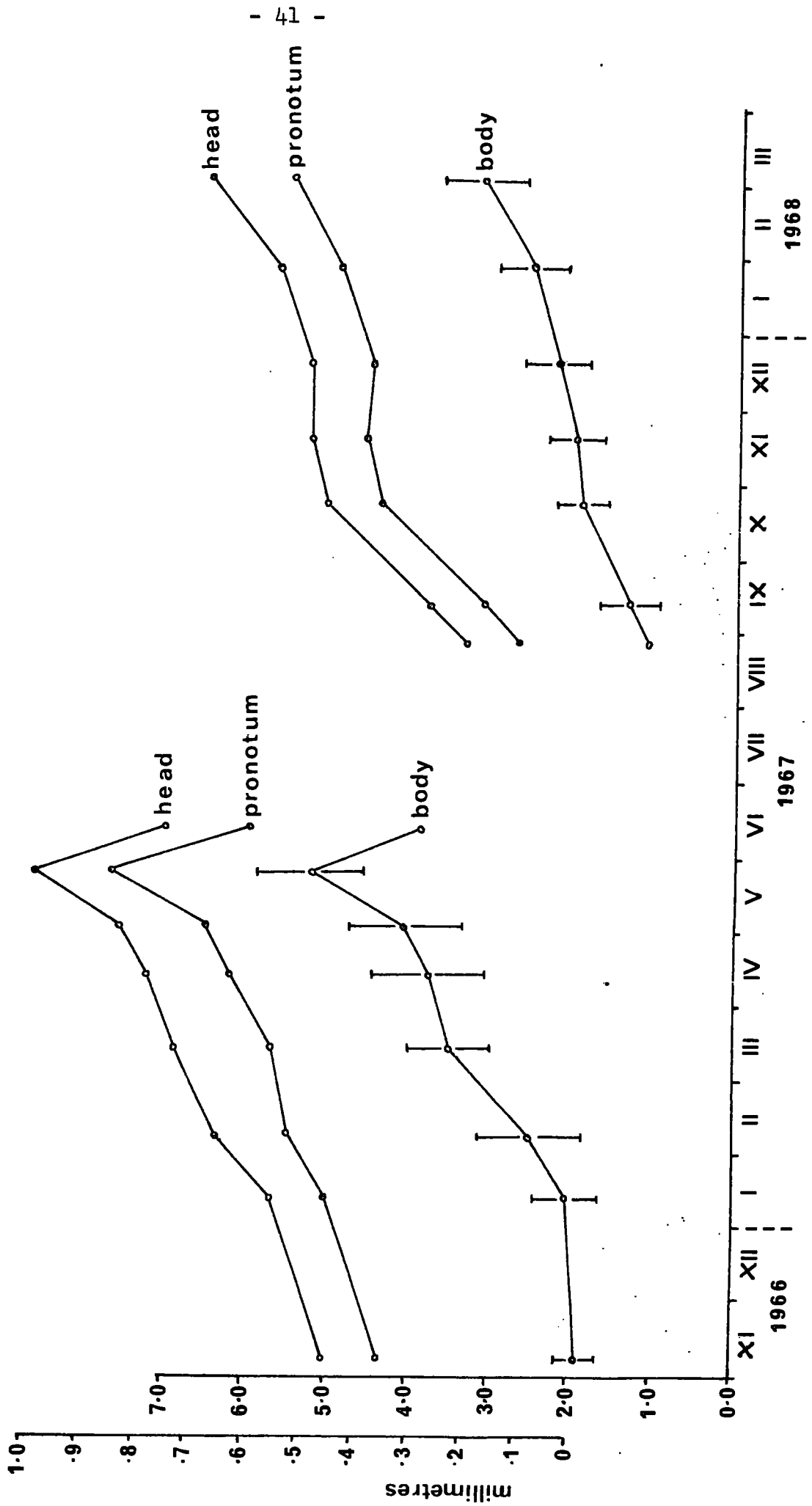


Fig.9. Distribution of size groups in samples of *A.sulcicollis* at Wearhead.

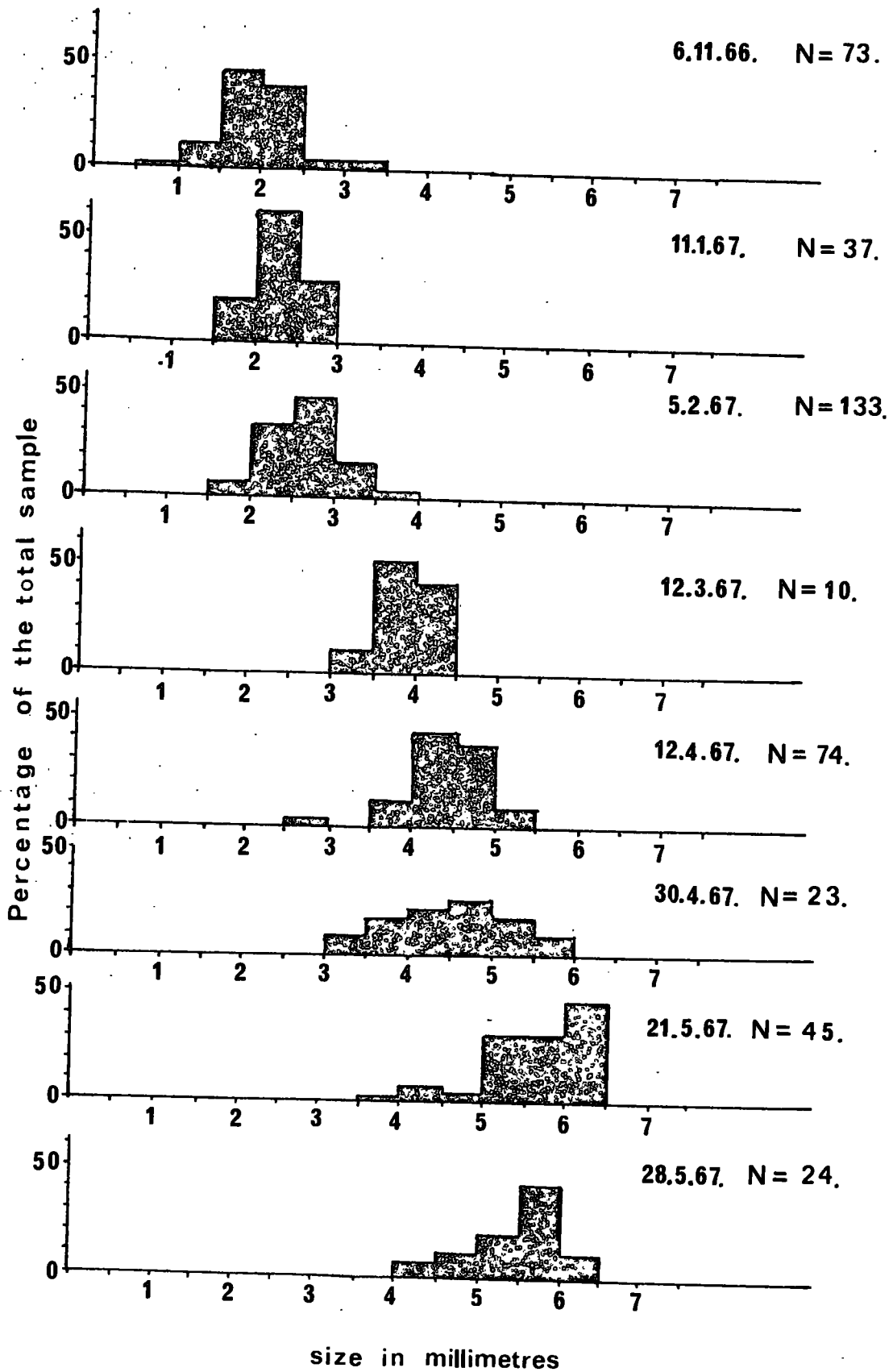


Fig.10. Distribution of size groups in samples of *A.sulcicollis* at Westgate.

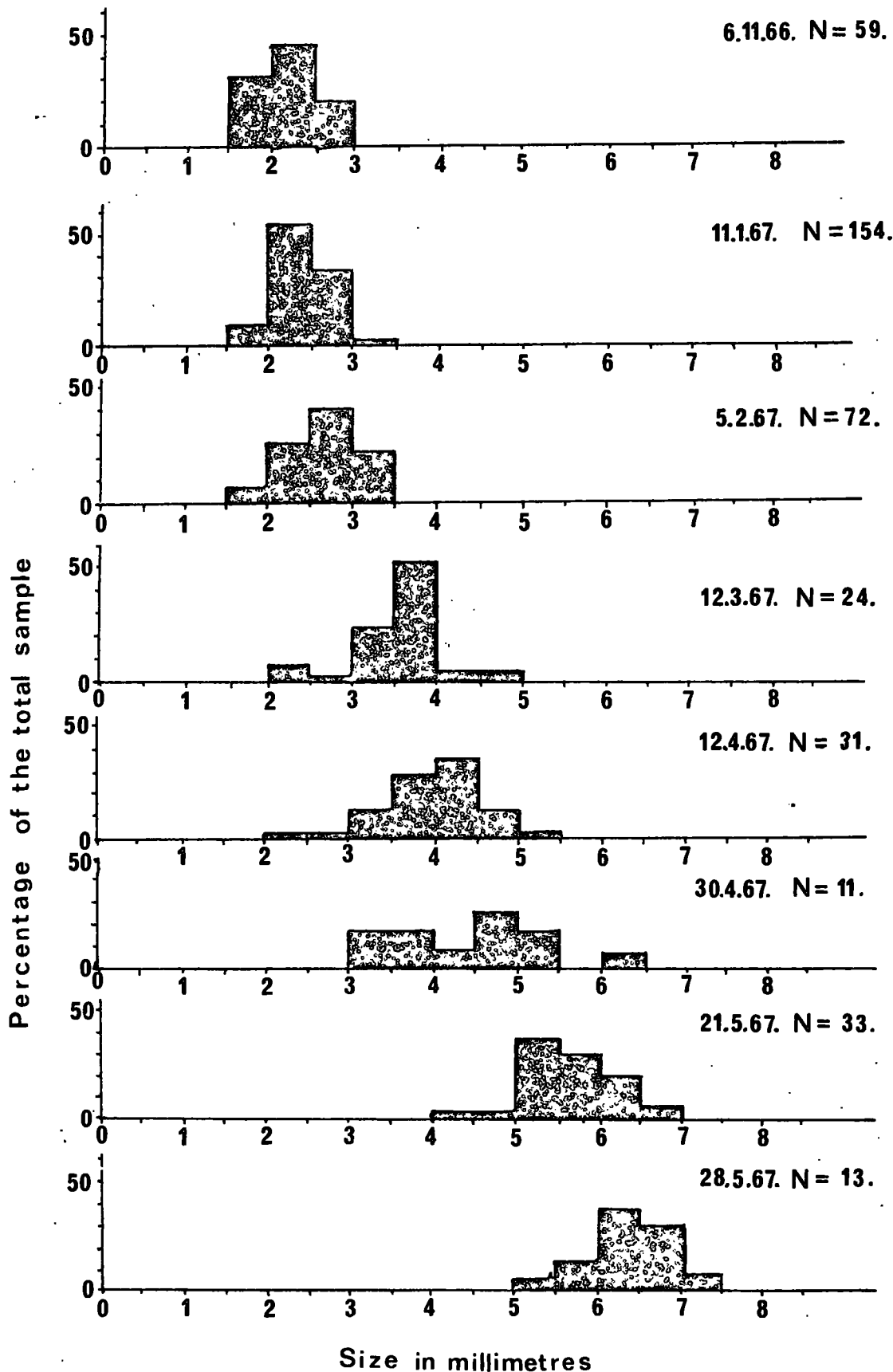


Fig.11. Distribution of size groups in samples of *A.sulcicollis* at Stanhope.

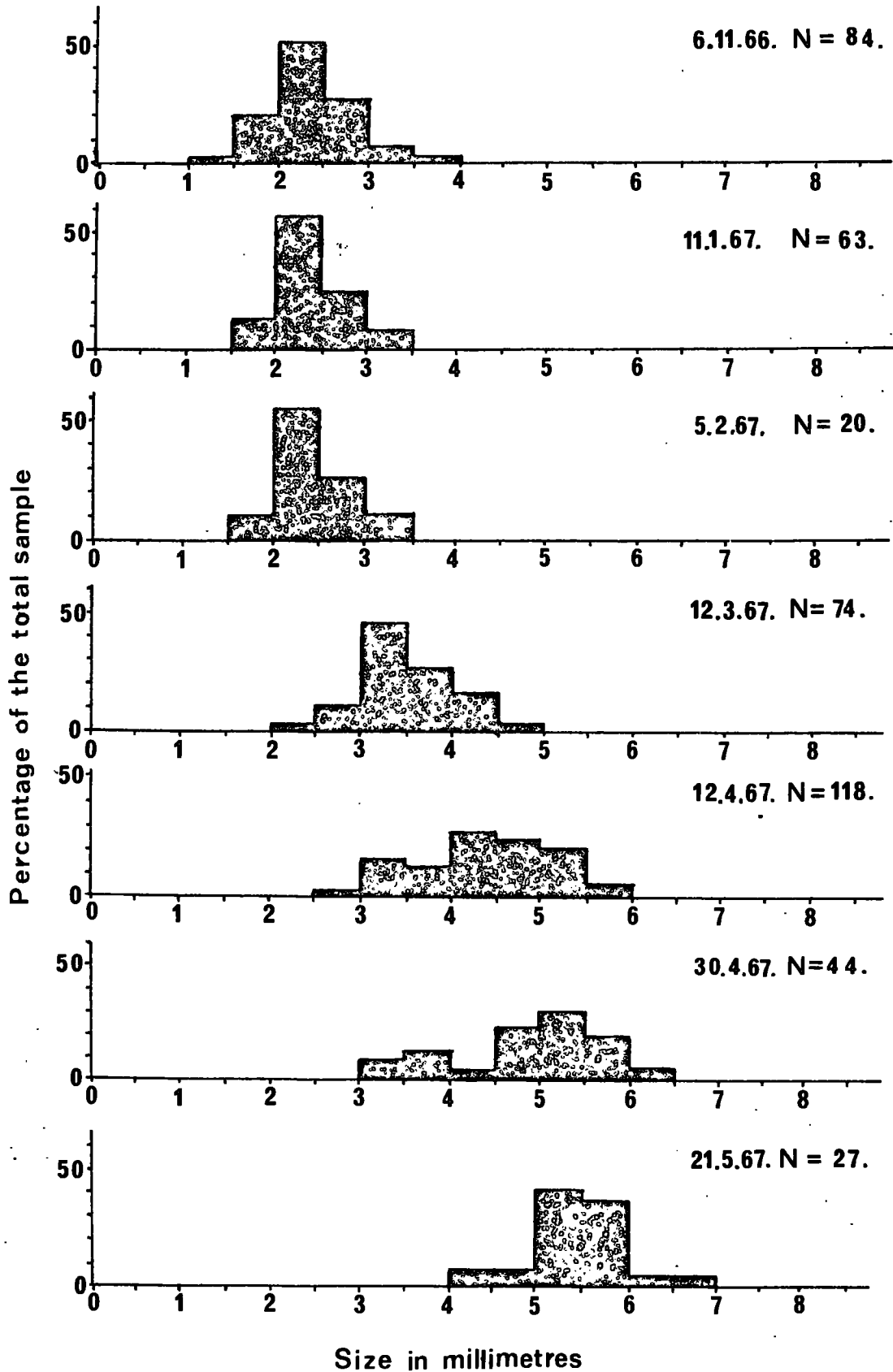


Fig.12. Distribution of size groups of *A. sulcicollis* in samples at Wolsingham.

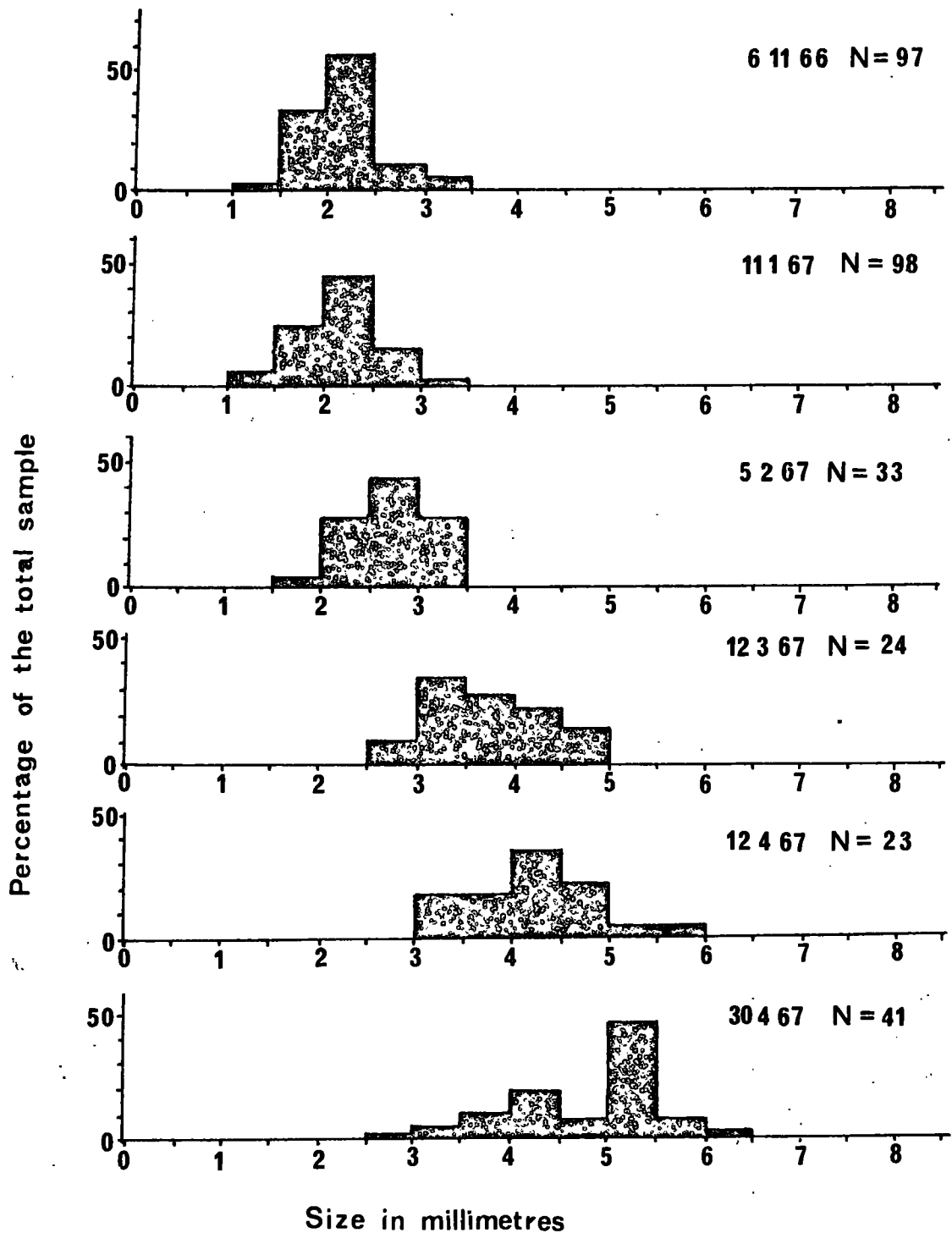
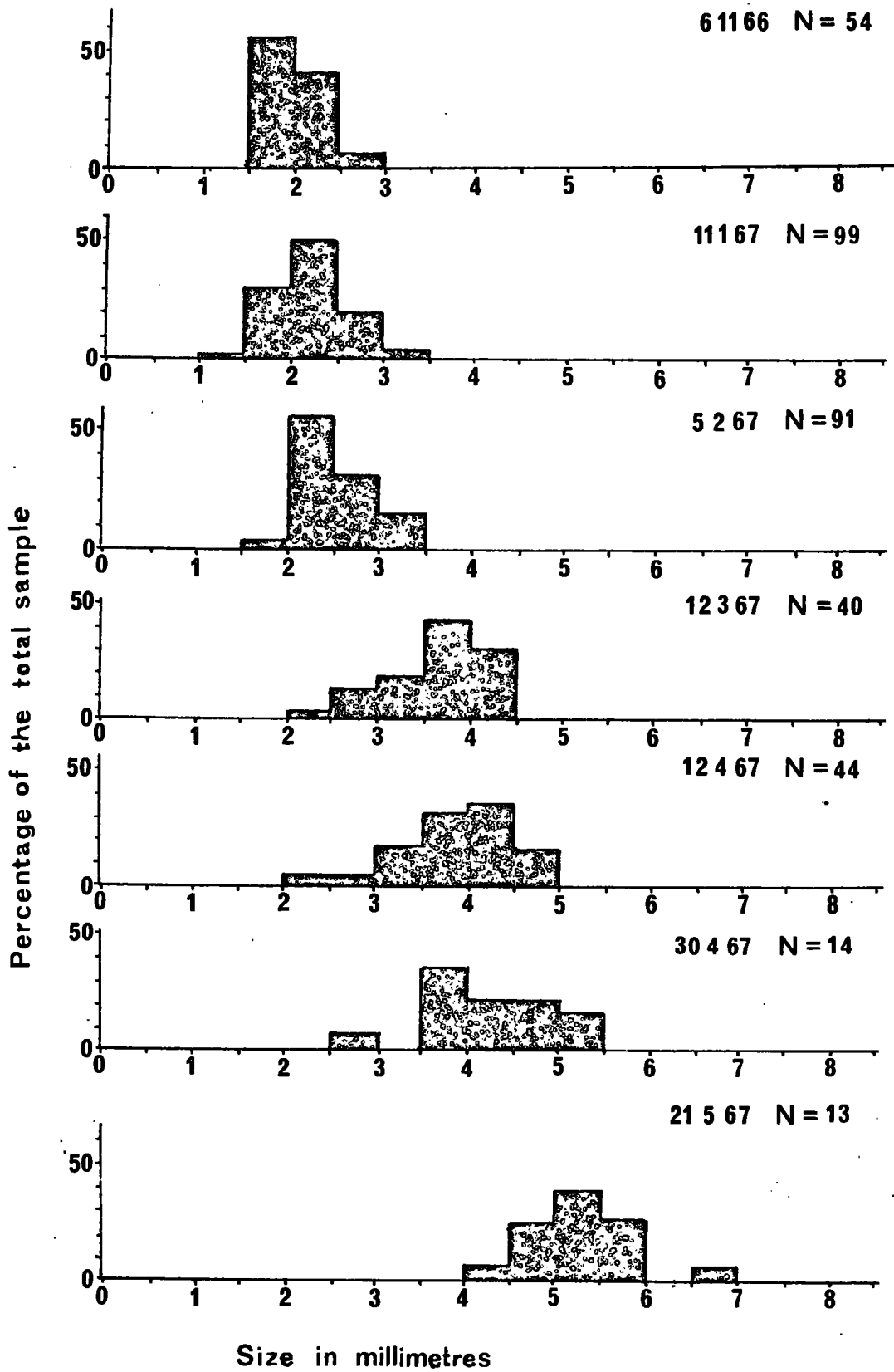


Fig.13. Distribution of size groups in samples of *A. sulcicollis* at Witton Park.



Both the graphical method and the histogram method of interpreting the data seemed to indicate that growth of the larvae was retarded during the winter months. This retardation seemed to occur at Wearhead and Witton Park almost equally.

When mean values for body length of larvae captured at Wearhead and Witton Park were compared it was noticed that the larvae from Wearhead were consistently larger throughout the larval life. The relevant data is compared in Table 6.

Table 6. Comparison of mean body length of larvae of *Amphinemura sulcicollis* at Wearhead and Witton Park.

<u>Date.</u>	<u>Wearhead.</u>	<u>Witton Park.</u>
6/11/66	1.83 (73 larvae)	1.92 (54 larvae)
11/1/67	2.23 (37 larvae)	2.08 (99 larvae)
5/2/67	2.54 (133 larvae)	2.50 (91 larvae)
12/3/67	3.82 (10 larvae)	3.51 (40 larvae)
12/4/67	3.78 (74 larvae)	3.75 (44 larvae)
30/4/67	4.40 (23 larvae)	4.09 (14 larvae)
21/5/67	5.41 (45 larvae)	5.20 (13 larvae)

The mean values for body length of larvae of *A. sulcicollis* at Wearhead and Witton Park were compared statistically to see if the observed differences were significant or not. First the Standard Error of the difference between the means was calculated according to the formula:-

$$\text{S.E. of the difference between two means, } \sigma_d = \sqrt{\left(\frac{\sigma_1^2}{n_1} + \frac{\sigma_2^2}{n_2}\right)}$$

The resulting values were then used to calculate a value for  $t$  and these calculated values were then compared with values for  $t$  from tables at the level of  $p = 0.05$ .

By this process the means for body length of A. sulcicollis at Wearhead were seen to be significantly different from the values for specimens at Witton Park on only two of the sample dates, 11/1/67 and 12/3/67. Differences in the means for body length were not significant on 6/11/66, 5/2/67, 12/4/67, 30/4/67 or 21/5/67. It was therefore concluded that the observed differences in the means between samples of A. sulcicollis at Wearhead and Witton Park were probably caused by the irregular size of the samples on the two dates when significant differences were recorded, and that in fact the two sets of samples were representative of a single homogeneous population.

The total period of time required for the growth of the larvae to full size was from late July to mid May, almost exactly ten months. From hatching in late July it took the larvae of Amphinemura sulcicollis till early February of the following year to attain a mean size equal to half the mean size of full grown larvae i.e. 6 months or 60% of the time spent as larvae was needed to reach half size. From early February the growth rate accelerated so that

the rest of the growth was completed by mid May i.e.  $3\frac{1}{2}$ -4 months or 40% of the time spent as larvae were needed to complete the second half of larval growth in order that the first adults could emerge in mid May.

2. Protonemura praecox. Total number examined was 101. The small number of larvae available made it difficult to assess the growth of Protonemura praecox though it was possible to construct a rough growth curve by plotting mean body length against time (see figure 14). From this and by inspection of the data available it seemed that growth remained fairly constant during the whole period of larval life and winter temperatures had no retarding effect on the rate of growth. Emergence took place in late February/early March. The total time taken for the completion of larval growth was eight months from early July/early March.

3. Protonemura meyeri. Total number examined was 76. As in the case of Protonemura praecox only a small number of larvae was available and therefore only a rough growth curve could be constructed from the available data. (See figure 15.) Again as in the case of Protonemura praecox there seemed to be little or no retardation of growth during winter and emergence

Fig.14. Growth of larvae of *Protonemura praecox*, June 66 – April 67.

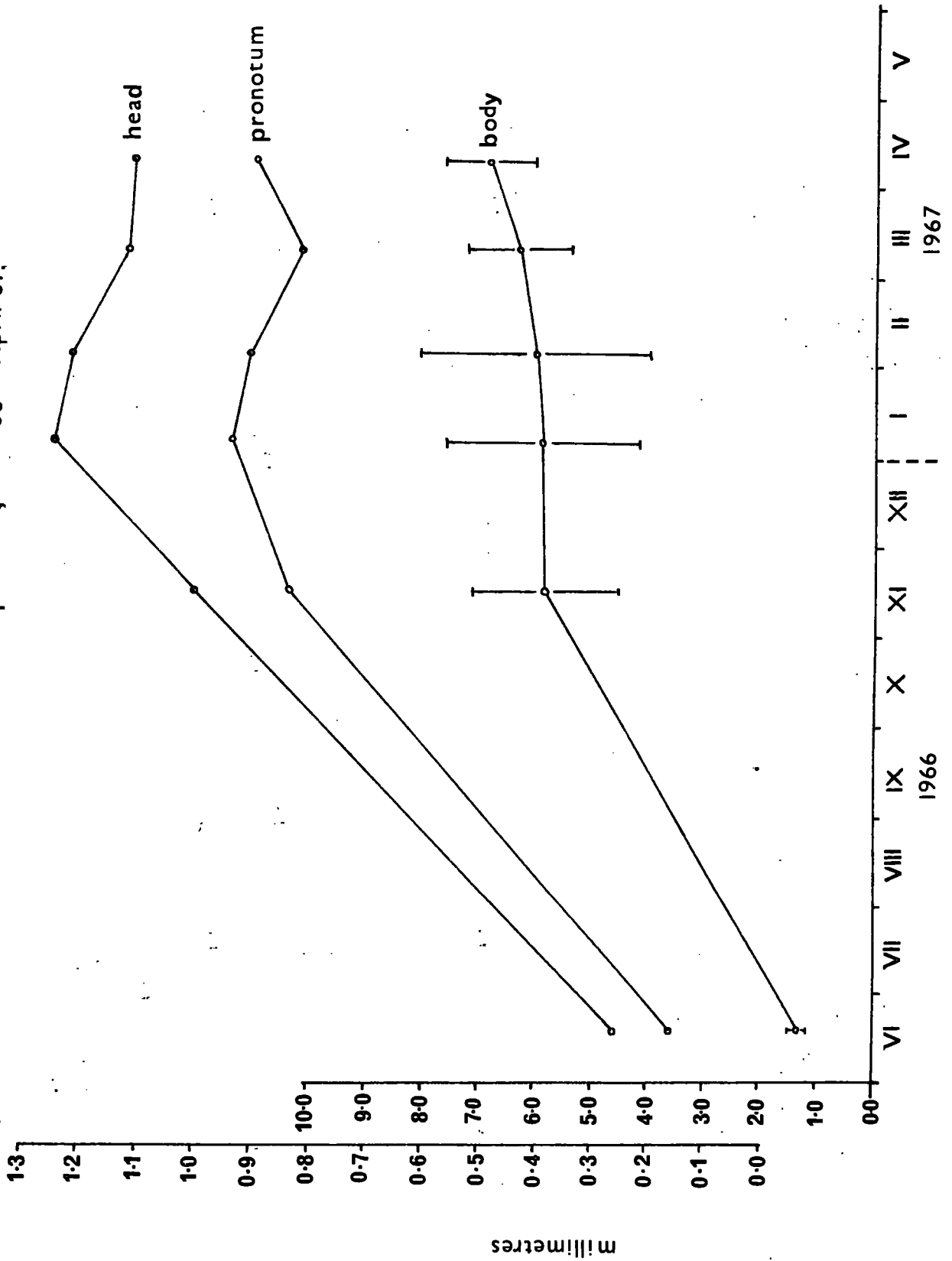


Fig. 15. Growth of larvae of *Protonemura meyeri*, June 66 - April 67.

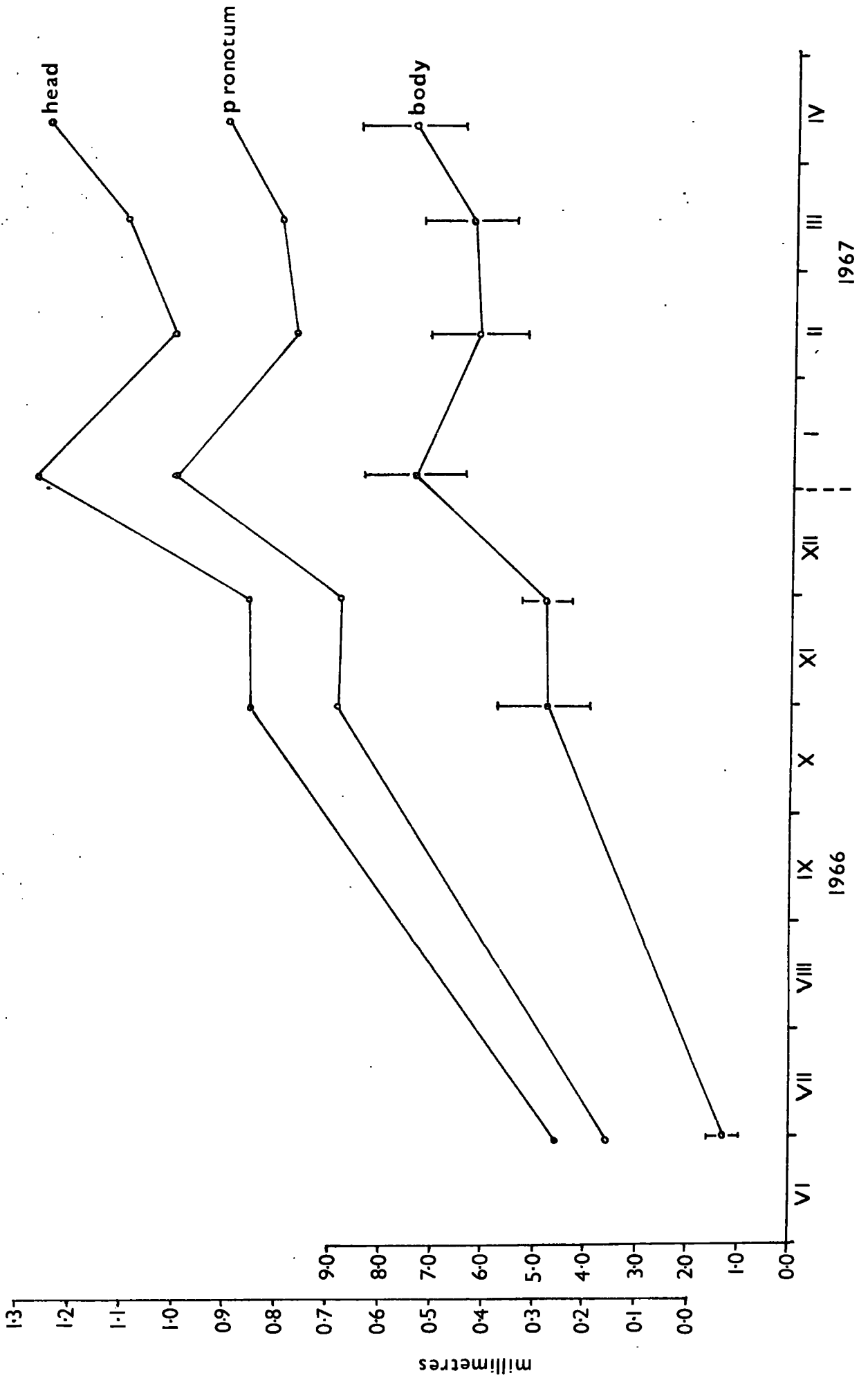
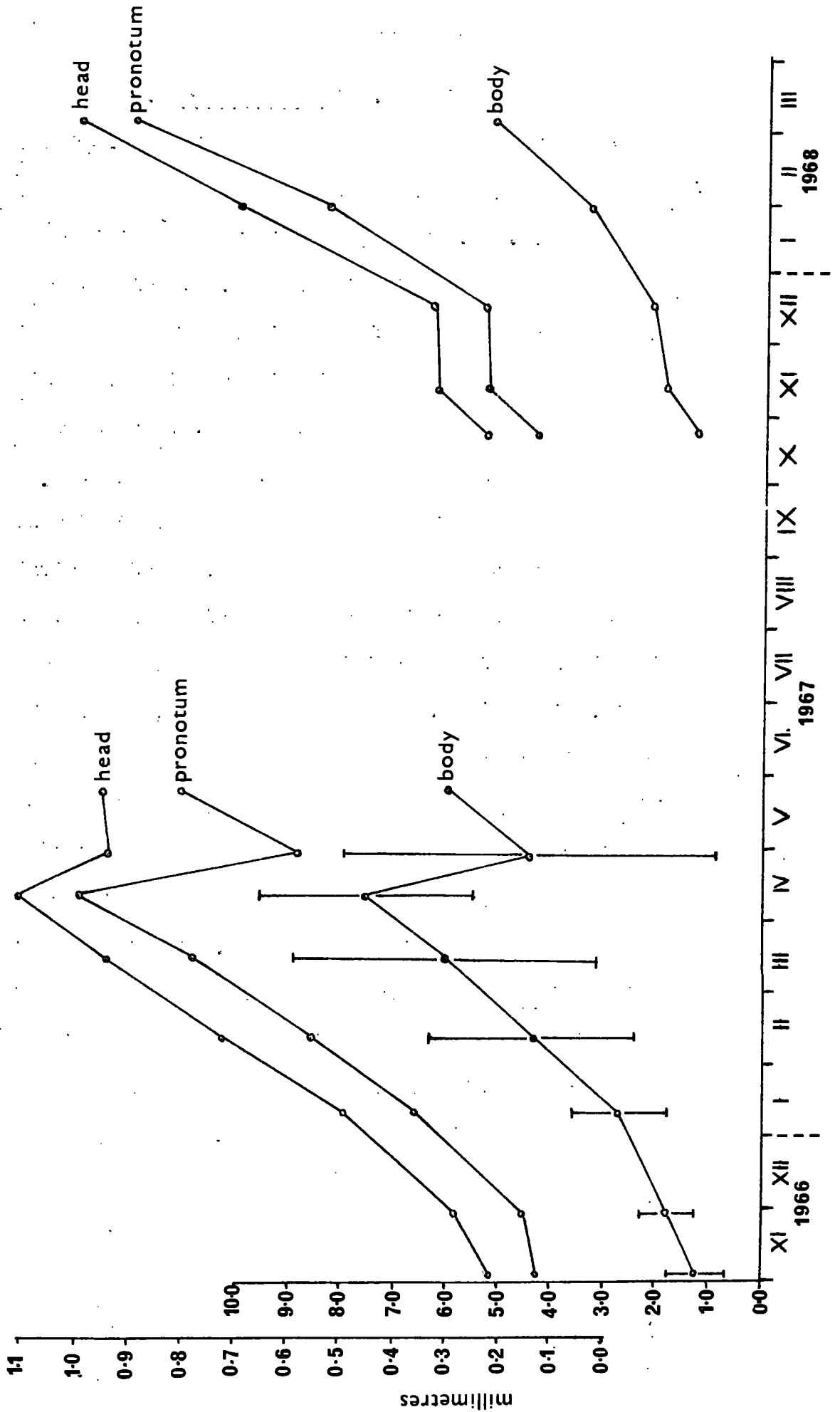


Fig.16. Growth of larvae of *Brachyptera risi* Nov.1966 - Mar.1968.



certainly do not remain in the river bed and join the next year's crop. Therefore this species seems to be unstable with regard to either hatching of the eggs or to the onset of larval growth. (cf. Brinck, 1949).

5. Leuctra inermis. Total number examined was 1007. This species was only really abundant at upper stations and the growth curve which was constructed, (fig. 18), was derived from the combined data obtained by measuring larvae captured at Wearhead and Westgate. This combination of samples proved advisable because of the irregularity of the size of the samples taken as regards Leuctra inermis, thus making it difficult to construct adequate separate growth curves for the two stations. The composition of the populations of Leuctra inermis at different times of the year was also investigated by preparing histograms showing the percentage frequency of different size groups. (see fig. 19). From the use of both of these techniques it was possible to see a definite retardation of the rate of growth during November, December and January. The larvae became full grown and began to emerge in late April/early May. The first small larvae of the next generation were captured in late August/early September. The total time needed for the completion of larval growth was eight months.

Fig.18. Growth of larvae of *Leuctra inermis* at Wearhead and Westgate Nov.1966 - Mar.1968.

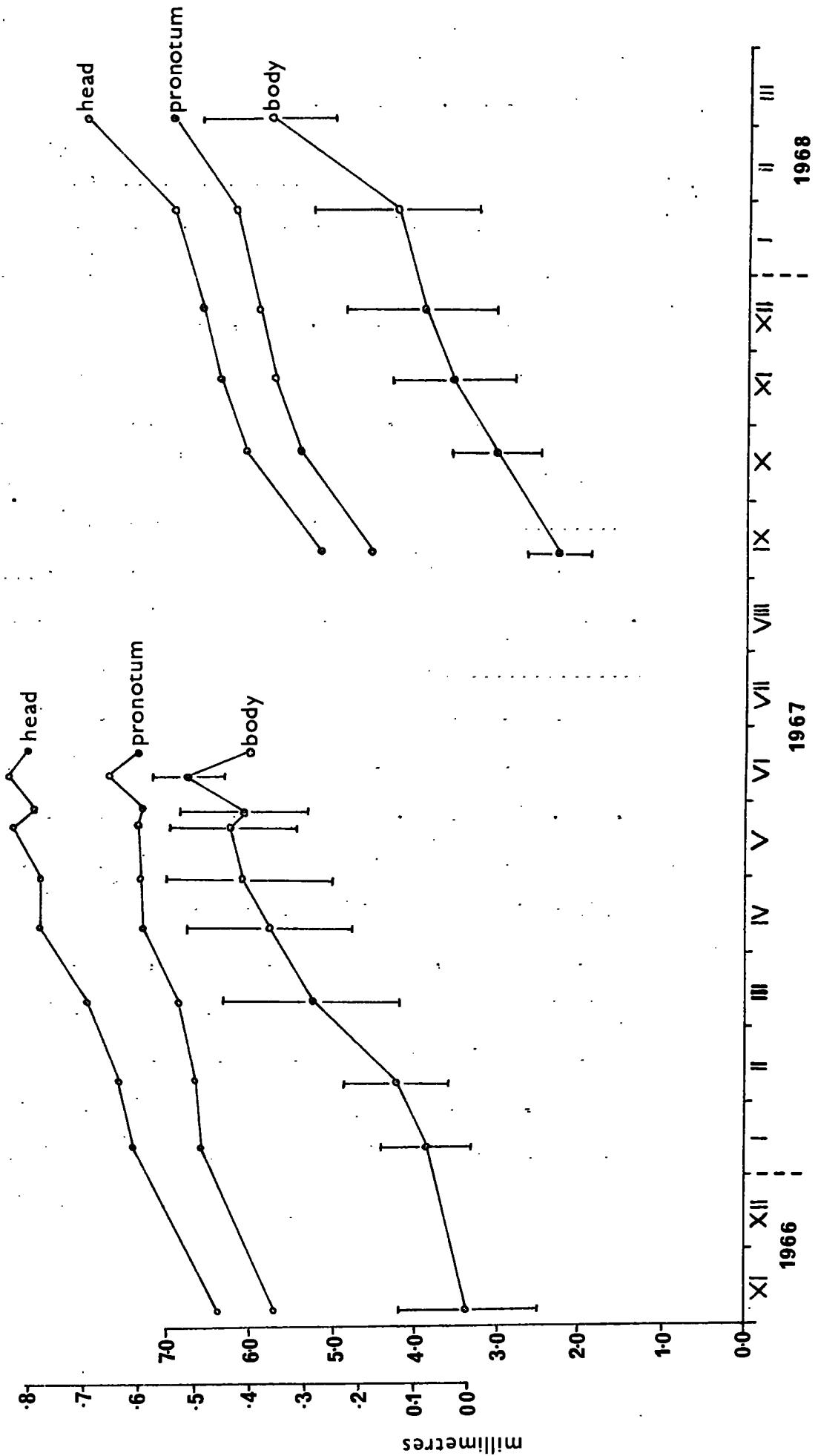


Fig.19. Distribution of size groups of samples of *Leuctra inermis* larvae at Wearhead and Westgate.

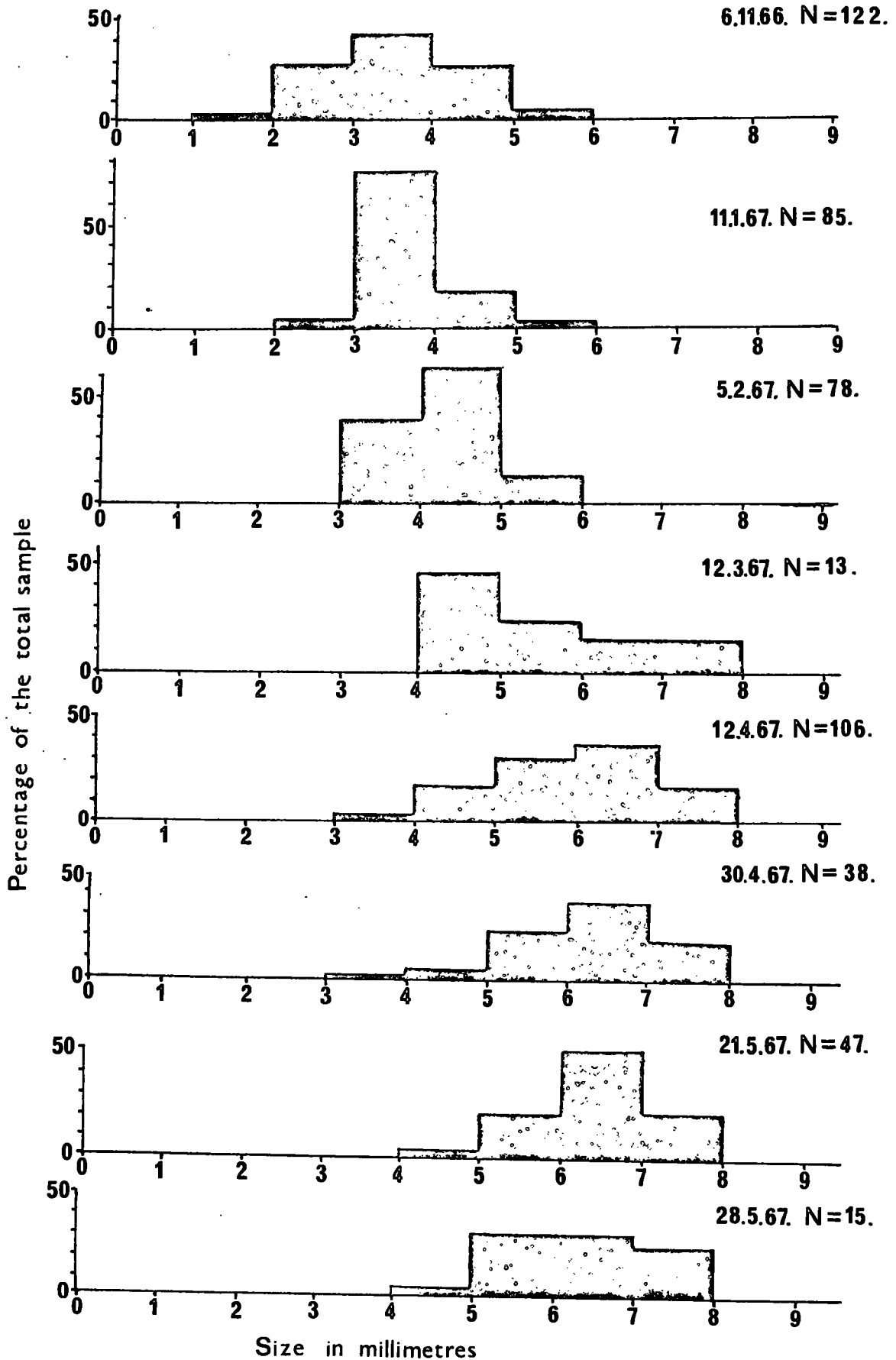
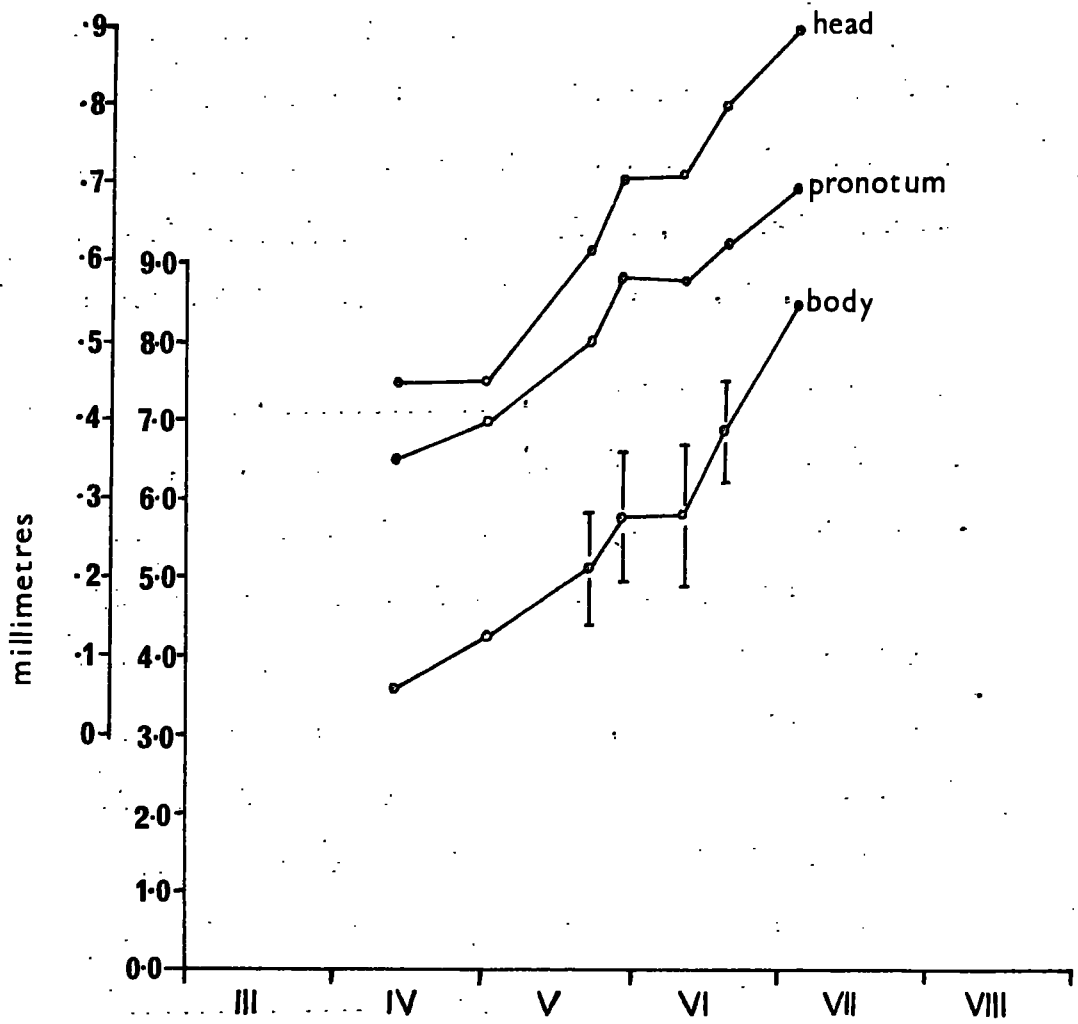


Fig.20. Growth of larvae of *Leuctra moselyi* 1967.



There is a definite size difference between fully mature male and female larvae, the females being the larger and this size difference no doubt explains the greater length of growth period for female larvae as opposed to male larvae. This difference in the sexes as regards size is shown in the histograms of size frequencies (figs. 21 and 22). At first these histograms were seen to be uni-modal when only small larvae were present but by early July the histograms became polymodal as male larvae reached maximum size in large numbers and as female larvae became noticeably larger.

Larvae of Leuctra fusca continued to be taken in samples till mid September and in view of the time from capture of first small larvae to emergence of first adults this indicated a fairly long hatching period for the eggs and therefore this should be reflected in the degree of overlap of records of larval captures and captures of adults. This was so, (see fig. 28).

Graphs of mean body length for specimens captured at Wearhead and Witton Park (figs. 23 and 24) revealed that growth was continuous and even as would be expected for a species which is aestival in its larval development.

There was some indication that larval life began earlier at Wearhead than at Witton Park, for example at Wearhead 119 larvae were captured on 21/5/67 while at Witton Park on the same day only 6 larvae

Fig.21. Distribution of size groups of larvae of *Leuctra fusca* in samples at Wearhead.

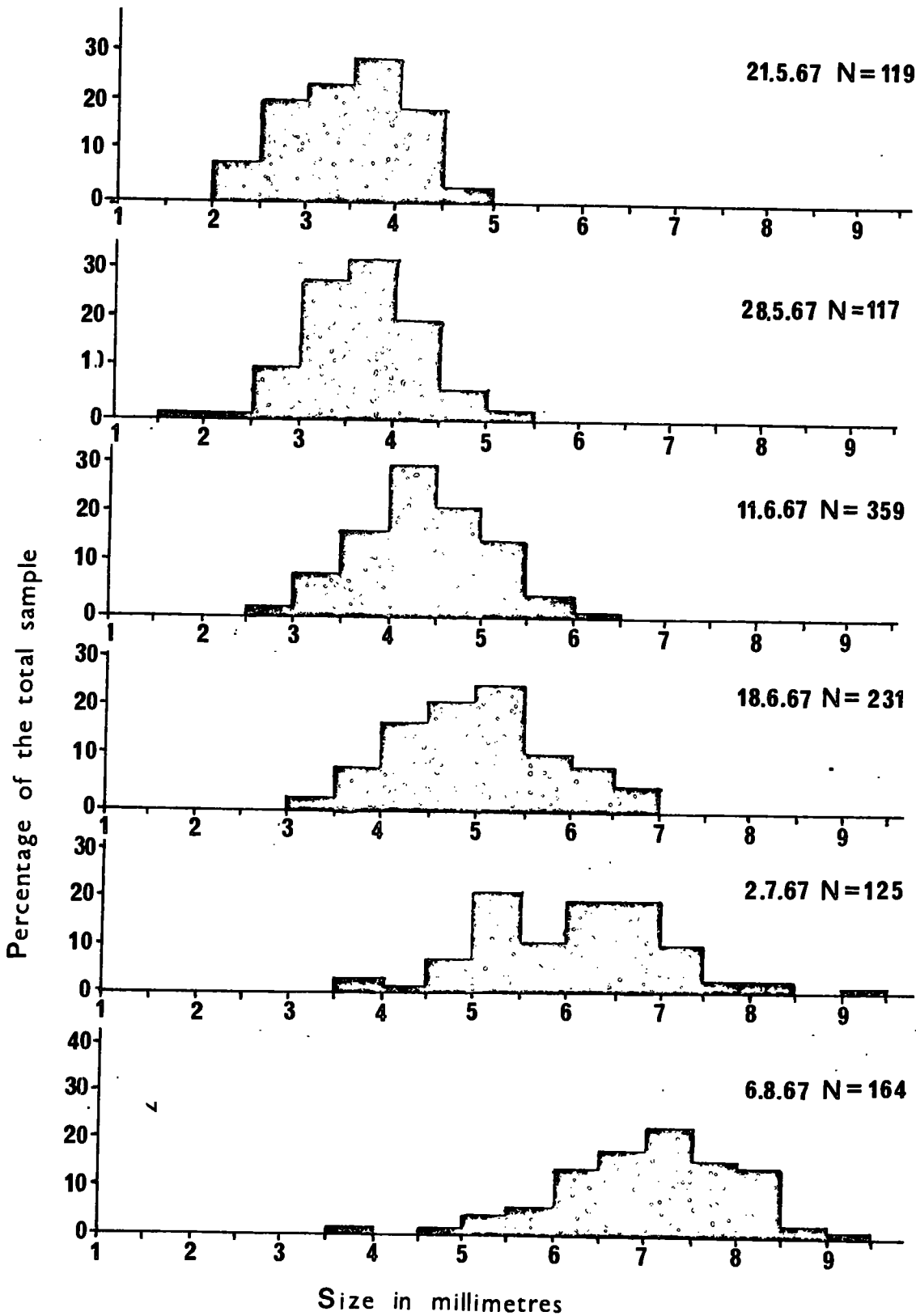


Fig. 22. Distribution of size groups in samples of *Leuctra fusca* at Witton Park.

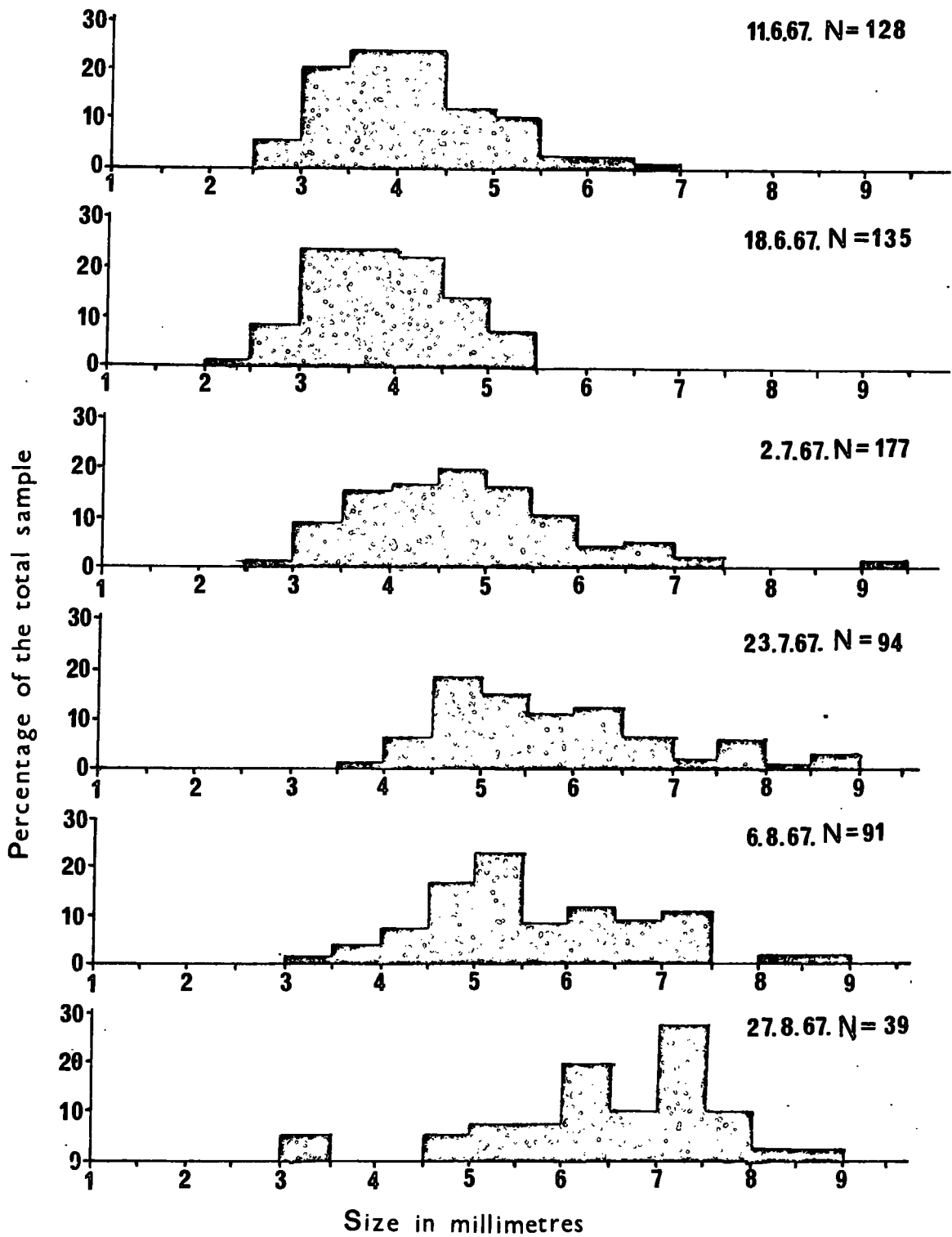


Fig. 23. Growth of larvae of *Leuctra fusca* at Wearhead 1967.

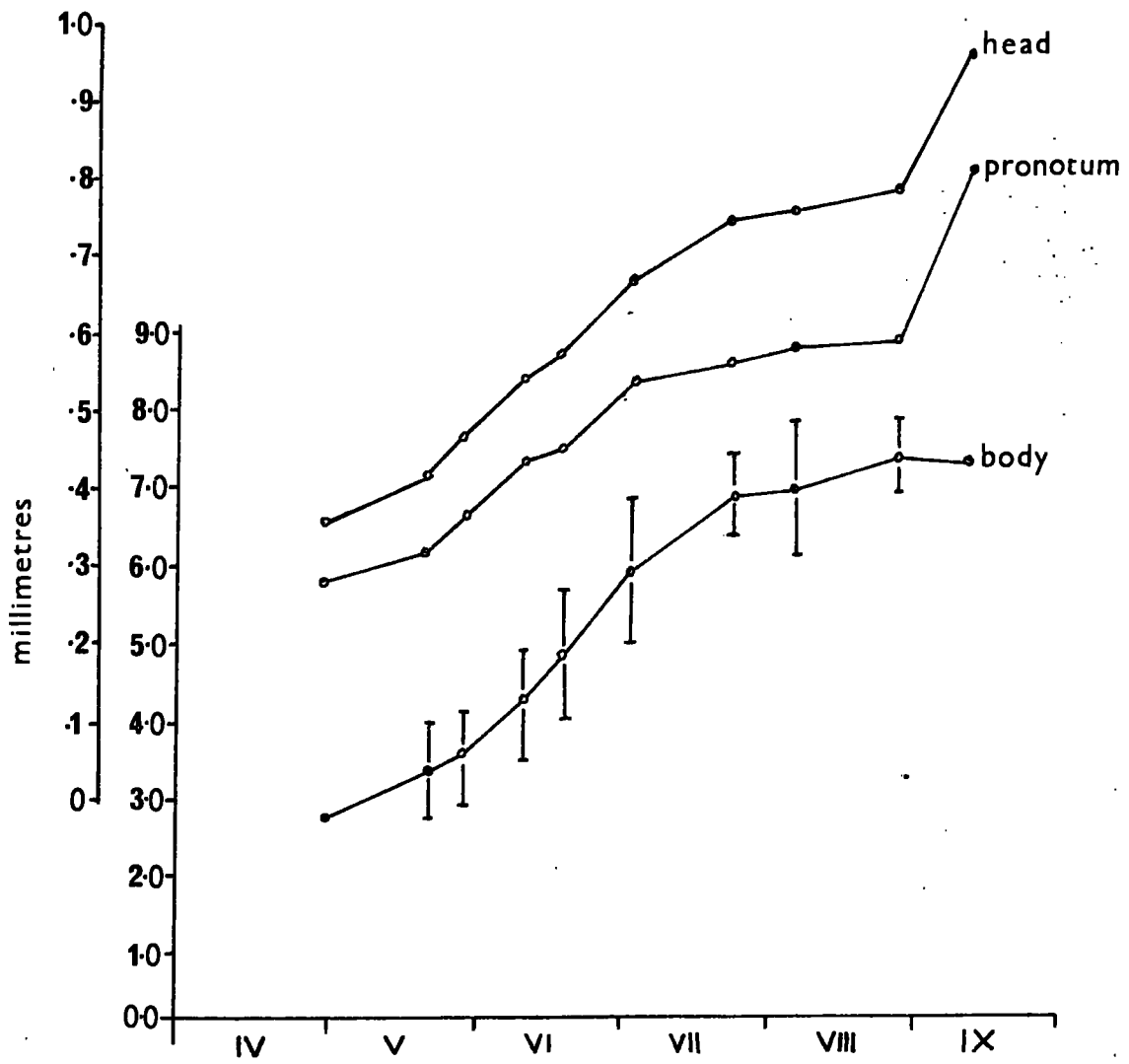
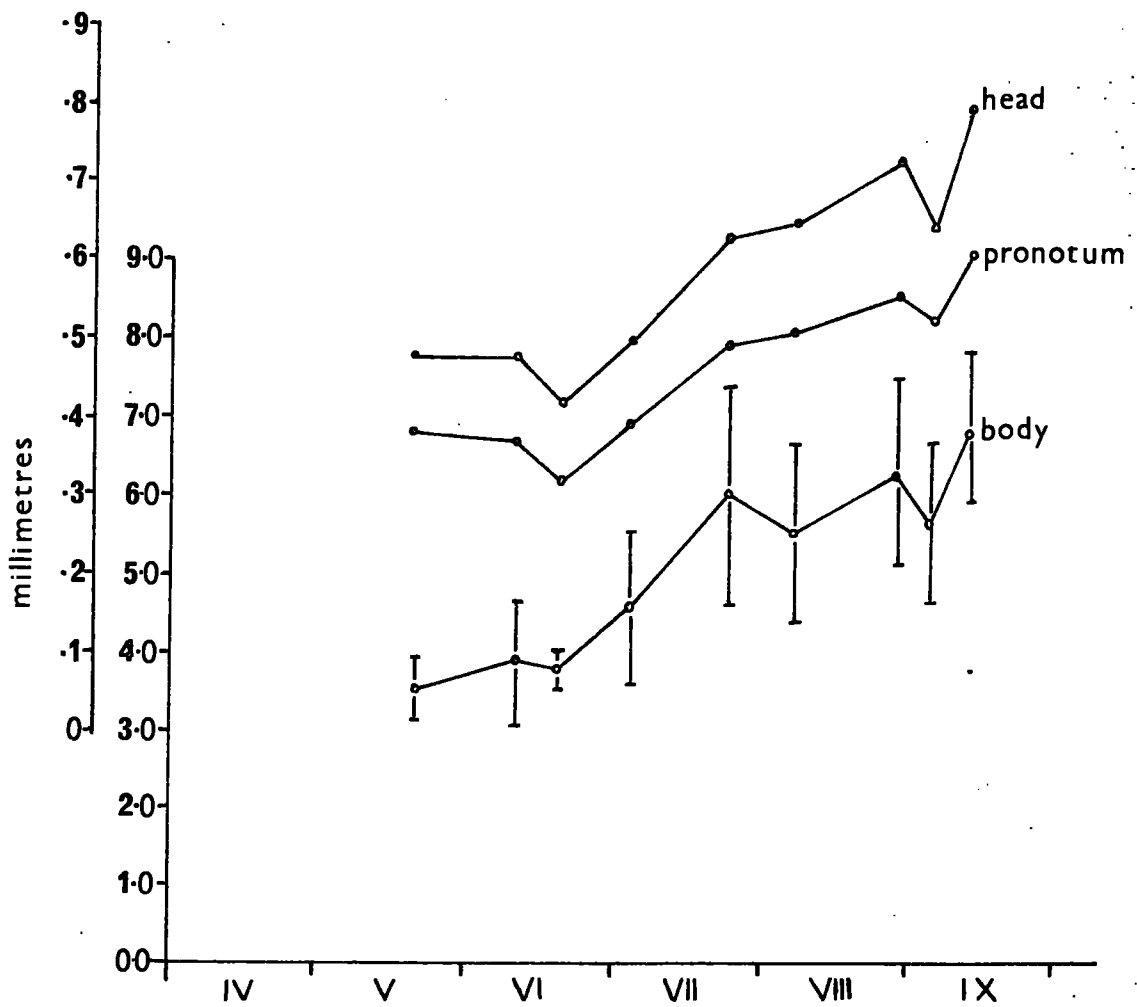


Fig.24. Growth of larvae of *Leuctra fusca* at Witton Park 1967.



were captured. The numerical discrepancy is too great to be attributable to the relative abundance of the species at high and low stations on the river because by 11/6/67 the numbers of larvae captured were 359 at Wearhead and 128 at Witton Park, a ratio of only 3:1 not 20:1 as in the case of the figures for 21/5/67.

No small larvae were captured in autumn or winter thus indicating that hatching is delayed till the following spring or if it does occur in autumn, the newly hatched larvae (the nymphulae of Brinck, 1949) lie dormant in the gravel and do not commence active growth till the spring.

When graphs of mean body length for Wearhead and Witton Park were compared (figs. 23 and 24) it was seen that larvae at Wearhead were consistently larger than larvae at Witton Park. The relevant data are compared in Table 7.

Table 7. Comparison of mean body length of larvae of Leuctra fusca at Wearhead and Witton Park.

<u>Date.</u>	<u>Wearhead.</u>	<u>Witton Park.</u>
21/3/67	3.30 mm (119 larvae)	3.5 mm (6 larvae)
28/5/67	3.50 mm (117 larvae)	Flood conditions.
11/6/67	4.21 mm (359 larvae)	3.93 mm (128 larvae)
18/6/67	4.79 mm (231 larvae)	3.80 mm (135 larvae)
2/7/67	5.95 mm (125 larvae)	4.64 mm (177 larvae)
23/7/67	6.86 mm (103 larvae)	6.07 mm (83 larvae)
6/8/67	6.95 mm (164 larvae)	5.53 mm (91 larvae)
27/8/67	7.36 mm (5 larvae)	6.35 mm (39 larvae)

As in the case of A. sulcicollis the mean values for body length of larvae of L. fusca at Wearhead and Witton Park were compared statistically to see if the observed differences were significant or not. Again the Standard Error of the difference between the means was calculated and the values used to calculate values for t. These values were compared with values for t from tables at the level of  $p = 0.05$ . Samples taken on 11/6/67, 18/6/67, 2/7/67, 23/7/67 and 6/8/67 were examined in this way.

In all cases the means for body length of specimens taken at Wearhead were seen to be significantly different from the values for specimens at Witton Park, i.e. on identical sample dates those larvae taken at Wearhead were significantly and consistently larger than those larvae taken at Witton Park. Furthermore since in all cases the samples were numerically large these differences could not be attributable to varying sample size. In all probability these differences in mean body length reflect an earlier start to active larval growth at Wearhead as opposed to Witton Park as previously suggested.

8. Chloroperla torrentium. Total number examined was 90. This species was present in small numbers at all five main stations but seemed to be more frequent at the upper stations. The larvae hatched from the eggs in late summer and developed throughout the autumn, winter and spring until emergence in mid May. A growth curve was constructed by plotting mean body length against time though it must be emphasised that the accuracy of this graph is impaired by the low number of specimens used. (See fig. 25).

9. Isoperla grammatica. Total number examined was 405. This species was present in fair numbers at all five stations. Very small larvae were captured in late July and growth was fairly steady until the months of November, December and January when there was a definite retardation of growth. Growth recommenced in February and gained momentum until emergence in late May/early June. A graph of mean body length against time was constructed using all available specimens and this showed the retardation of growth mentioned above. (See fig. 26). This type of growth corresponds to that of a hiemal species showing a retardation of growth in winter followed by late emergence as recognised by Brinck (1949).

Fig. 25. Growth of larvae of *Chloroperla torrentium* Nov. 1966 - Jan. 1968.

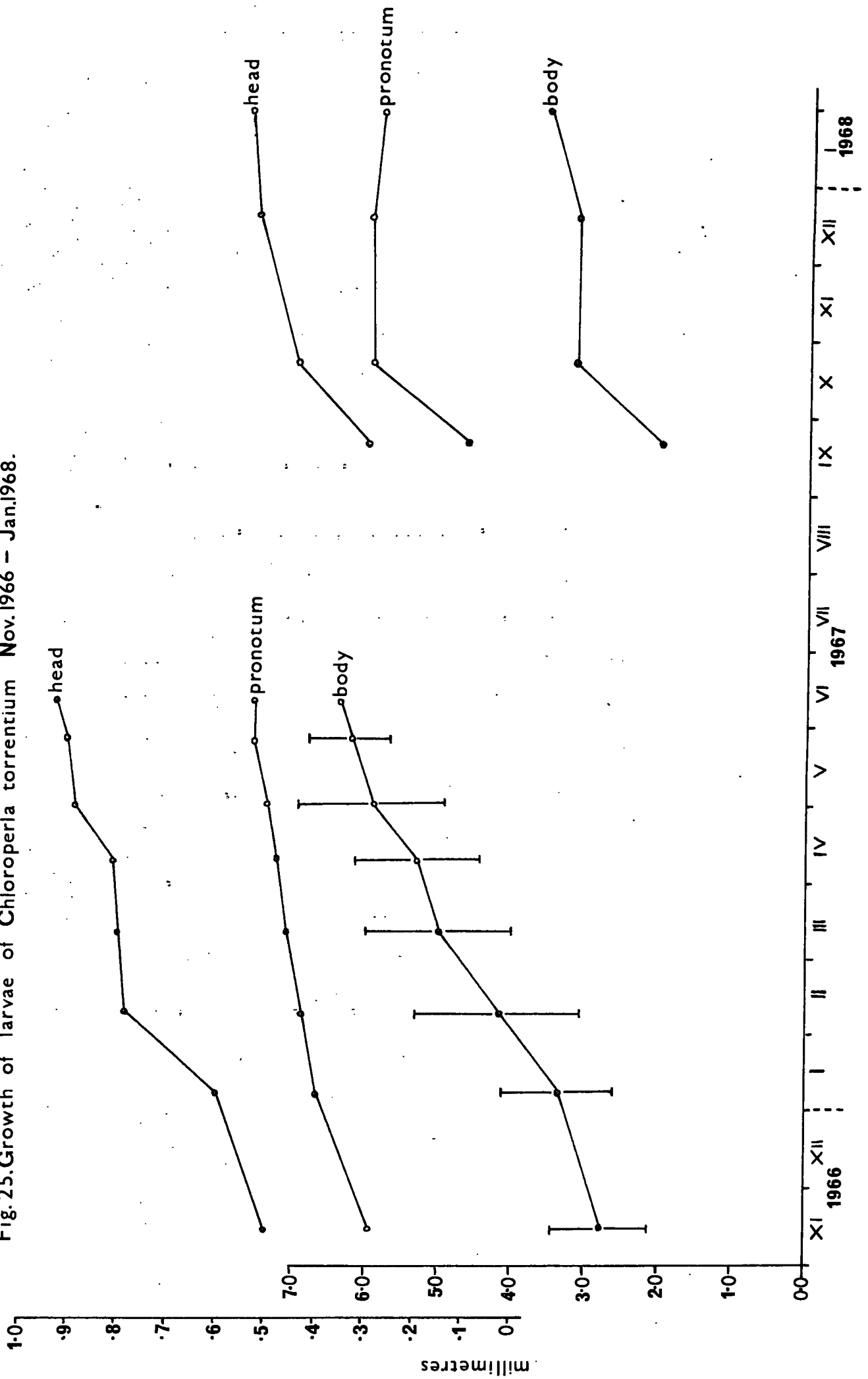
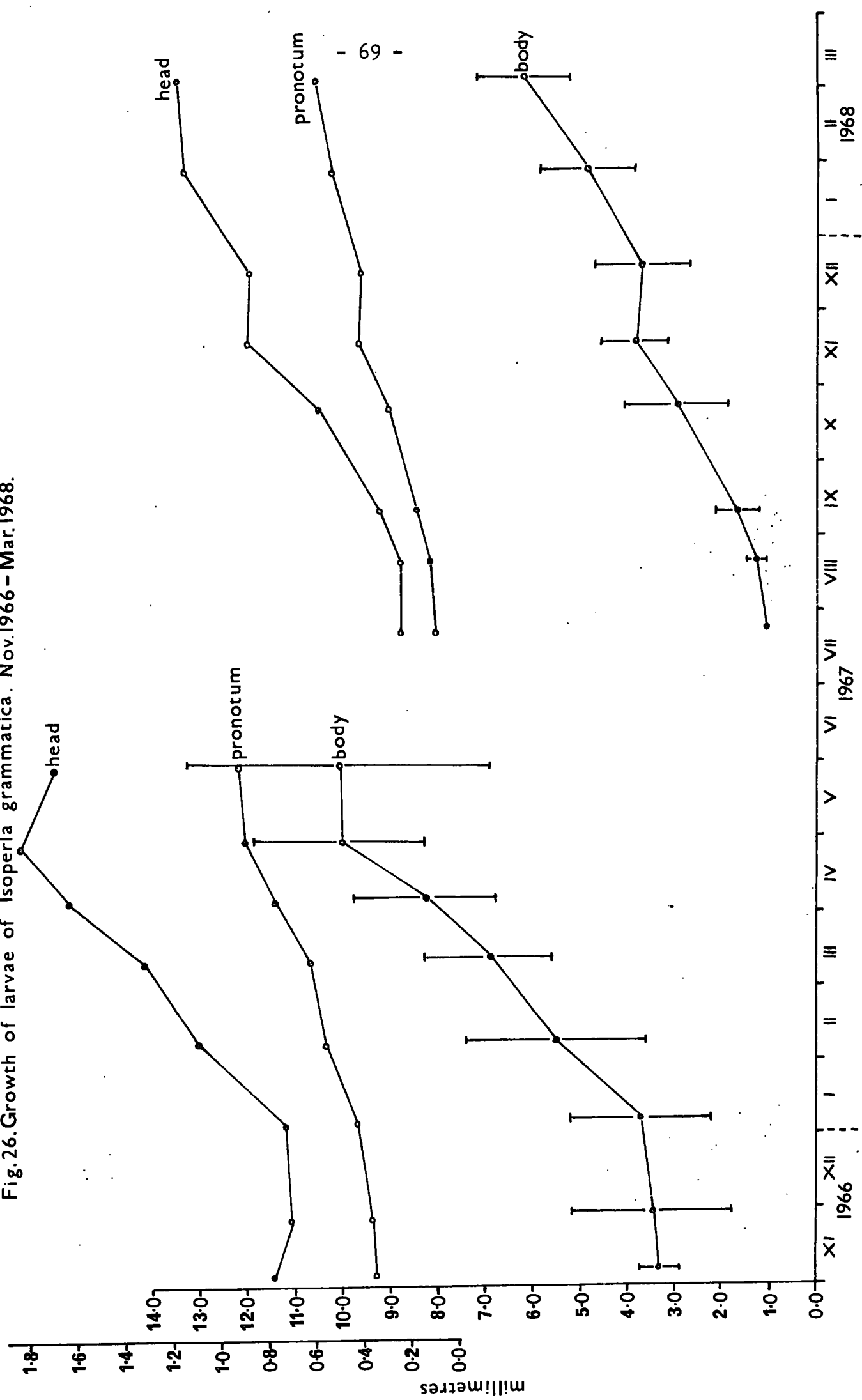


Fig. 26. Growth of larvae of *Isoperla grammatica*. Nov. 1966 - Mar. 1968.



10. Dinocras cephalotes. Total number examined was 100. This species was found in small numbers over the whole stretch of the river. Because of the fact that it takes three years to complete its larval development, larvae captured were of very mixed ages and therefore it was only possible to observe tendencies of growth. No definite pattern of growth could be arrived at with certainty without observation of specimens over a long time in the laboratory and this proved impossible. However a possible reconstruction of a growth curve was arrived at by inspection of the larvae and segregation into Year I, Year II, and Year III categories. The mean body lengths of the various small groups were plotted against a three year time axis and this rather tentative growth curve seemed to indicate a fairly steady growth rate over the whole of the larval life. There was certainly nothing in this scatter diagram (fig. 27) to suggest any retardation of growth during the colder months of the winter. Third year male and female larvae differed considerably in size so the graph was drawn so as to take account of this fact.



III. The percentage change index method of  
assesing growth rates.

1. Explanation.

A further technique was used to investigate the growth rates of the most abundant species. This method may be called the "percentage change index" method and was originally devised by Smith (1969), M.Sc. thesis, to investigate the rate of growth of certain species of Simuliidae (Diptera), where the number of larval instars was definitely known and where individual instars could be readily identified.

To determine the "percentage change index" for the growth rate of a particular species it is necessary to take two samples from the species population with a definite time interval between the two samples.

Suppose two samples were taken from a hypothetical population with an intervening time interval of 100 days.

Let sample one consist of 50 individuals, 20 at instar I, 20 at instar II, and 10 at instar III.

Let sample two consist also of 50 individuals, 20 at instar II, 15 at instar III and 15 at instar IV.

For each sample express the number in each individual instar stage as a percentage of the total sample. Then the percentage change upwards of larvae to later instar stages between sample one and sample two may be calculated as follows in Table 8

TABLE 8.

Method of calculating % change index.

Larval Stage.	% of Sample 1.	% of Sample 2.	% Difference + or -	% moved up.
Instar IV	30%	30%	+ 30	(30 - 30)% moved up = 0% moved up.
Instar III	20%	30%	+ 10	(40 - 10)% moved up = 30% moved up.
Instar II	40%	40%	0%	(40 - 0)% moved up = 40% moved up.
Instar I	40%	0%	- 40%	40% moved up = 40% moved up.
<p>∴ 11% of population changed instar stage every 10 days.</p> <p>Total % moved up = 110%</p> <p>Time interval = 100 days.</p>				

by comparing the percentage of the samples at each instar stage and noting the percentage differences which in turn indicate the percentage moved up from I to II, II to III etc..

Since the time interval is known the total percentage move up of the larvae may be converted into percentage move up per week/per ten days/ per month etc. Several percentage change indices may be calculated for different periods of larval life and comparison will yield information regarding changing growth rates.

It is important to remember that there are certain limitations of the application of the percentage change index. For example if eggs are still hatching during the time interval between taking sample one and sample two it would have the effect of reducing the change index. Therefore before applying this method to the study of growth rates of insect larvae it is important to wait until egg hatching can be reasonably expected to have ceased.

## 2. Application.

The application of the technique to the evaluation of growth rates of stonefly larvae was made difficult by the fact that not only are the instars very numerous but also the morphological distinction between one instar and the next is so fine as to make it extremely difficult to recognise the instars in each sample with speed and accuracy.

Therefore the specimens were graded according to body length to facilitate the operation of the technique.

The method was used as a further tool in the investigation of the growth rates of the more common species. This was done particularly with a view to checking whether the apparent retardation of growth of certain hiemal species during the winter, (as indicated by histograms and graphs of mean body length), was real or just an artefact.

The growth rate of the most abundant hiemal species, A. sulcicollis was investigated using the "percentage change index" method, the data being obtained from further samples taken in the winter and spring 1969-70. It was judged from previous data obtained in 1966, 1967 and 1968 that all new hatching from eggs had been completed by the middle of October. Accordingly the samples were taken at intervals of approximately two months beginning at this time. Four samples were taken in all at Wearhead on 16/10/69; 27/12/69; 14/3/70; 20/5/70. It was intended to obtain samples on the same dates at Witton Park but because of flood conditions it was only possible to get a good sample on 16/10/69 and 27/12/69. This enabled a comparison to be made between growth rates at Wearhead and Witton Park for the autumn/winter 1969 only. It was therefore decided to use the original sample data from 1966/67 to investigate growth rate at Witton Park by means of the percentage change index.

All samples were grouped into  $\frac{1}{2}$  m.m. size frequencies and the number falling into each group was expressed as a percentage of the total sample number. Using the procedure outlined in table 8 the mean weekly percentage of larvae that had moved up from one size group to the next was calculated between successive sample dates, (for detailed calculations see table XVI - XXII in Appendix II). The mean weekly percentage change indices obtained are compared in table 9, which shows that a similar pattern of growth occurred at both stations viz. a slow growth rate throughout autumn and winter followed by an extremely rapid rate of growth from March until emergence in late May.

TABLE 9.

% change indices for *Amphinemura sulcicollis* at  
Wearhead and Witton Park.

<u>Period of growth.</u>	<u>Station.</u>	<u>% change index.</u>
6/11/66 - 11/1 /67	Witton Park	4.6%
11/1/67 - 5/2/67	Witton Park	16.7%
5/2/67 - 12/3/67	Witton Park	44.8%
16/10/69- 27/12/69	Witton Park	11.3%
16/10/69- 27/12/69	Wearhead	5.8%
27/12/69- 14/3/70	Wearhead	7.0%
14/3/69 - 20/5/70	Wearhead	55.8%

The percentage change index was used to evaluate the growth rate of larvae of L. inermis. Because of fluctuating numbers in the samples, data from samples taken at Wearhead and at Westgate were combined. The dates of the samples used were 6/11/66, 5/2/67 and 12/7/67. The periods of growth reviewed were therefore:-

6/11/66 - 5/2/67 (91 days or 13 weeks).

5/2/67 - 12/4/67 (66 days or 9.4 weeks).

The calculations of the respective percentage change indices are shown in tables XXIII and XXIV in appendix II and they reveal that in the spring of 1967 the growth rate of L. inermis larvae was more than doubled when compared with the growth rate during the colder winter months of November, December 1966 and January of 1967.

Both the species dealt with above, A. sulcicollis and L. inermis are species having an hiemal larval development followed by an emergence in late spring.

One species having a typically aestival larval development and which occurred in sufficient numbers to enable its growth rate to be investigated by the percentage change index method was L. fusca. However because its appearance in the samples at Wearhead was not synchronised with its appearance in the samples at Witton Park (See Page 60 and table XI and XII appendix I), it was impractical to try to compare growth rates over identical periods of time. Growth rates were therefore compared for early and late larval life at Wearhead and

then similar comparisons were made of the samples taken at Witton Park but using different sample dates and different periods of time.

The growth periods for which percentage change indices were worked out at Wearhead were:-

- a) 21/5/67 - 18/6/67 (28 days or 4 weeks).
- b) 18/6/67 - 6/8/67 (49 days or 7 weeks).

The calculation of the respective percentage change indices are shown in tables XXV and XXVI in appendix II.

The growth periods for which percentage change indices were worked out at Witton Park were:-

- a) 11/6/67 - 2/7/67 (21 days or 3 weeks).
- b) 2/7/67 - 6/8/67 (35 days or 5 weeks).

The calculations of the respective percentage change indices are shown in tables XXVII and XXVIII in appendix II.

Both in the case of the larval populations of L.fusca at Wearhead and the larval population at Witton Park the percentage change indices for early and late larval life showed a tailing off of growth rate as time progressed. The percentage change indices for the late larval life would no doubt be depressed by the occurrence in the samples of mature larvae awaiting a suitable moment to emerge having virtually completed growth.

Upon further comparison of the percentage change indices for larval populations of L.fusca at Wearhead and at Witton Park (see table 10) it can be

seen that the values obtained were higher at all times at Wearhead, possibly indicating an increased growth rate at the upper station as compared with the lower one. It must be remembered however that the two populations were not synchronised in their development, specimens appearing earlier in samples taken at Wearhead and equally emerging and therefore disappearing earlier too, a fact which precluded exact comparison by means of the percentage change index method. The final percentage change indices and the periods of time for which they were calculated with respect to Wearhead and Witton Park are given in table 10.

TABLE 10.

Percentage change indices for larval populations of *L.fusca* at Wearhead and Witton Park.

<u>Station.</u>	<u>Time interval</u>	<u>% change upwards</u> <u>per week.</u>
Wearhead	21/5/67 - 18/6/67	78.3%
Wearhead	18/6/67 - 6/8/67	60.6%
Witton Park	11/6/67 - 2/7/67	44.0%
Witton Park	2/7/67 - 6/8/67	31.2%

Lack of sufficiently large samples of larvae of other species prevented the further application of the percentage change index to the study of their growth rates.

IV. Observation of emergence and incidence of moulting in Perla bipunctata.

The following observation of the emergence of a female specimen of Perla bipunctata was made by Mr. R.A. Dobson, a student under my supervision, on 22nd January 1970 and is included here with his permission.

Larvae of Dinocras cephalotes and Perla bipunctata were kept in shallow pie dishes in aerated water mainly with a view to observing the incidence of moulting. The temperature in the laboratory was well above that obtaining in the river, 15°C as opposed to 2° - 7°C. Also the larvae were regularly fed on chopped earthworms or mayfly larvae. Both these factors, high temperature and regular food supply may have induced this relatively early moult and emergence.

However the main reason for inclusion of this event in this account is because emergence took place during the day. This is a direct refutation of Hynes' observations. He stated that "Perla bipunctata seems only to emerge at night. No specimens have been observed emerging during the day either in the field or under laboratory conditions".

The detailed record is as follows:-

Emergence began at 11 a.m.

A larva of P. bipunctata was seen to have crawled out of the water onto the edge of the pie dish. It was placed back into the water and it immediately

crawled out again. It remained stationary on the lip of the dish. Rhythmical contractions of the body were observed and the cuticle split along the dorsal mid line in the thoracic region. Total time from beginning of contractions to complete emergence was 17 minutes. The insect was pale yellow to green in colour and the wings were white. After two hours the wings were dry and the body had become much darker.

Four specimens of P. bipunctata were observed in an attempt to discover the time interval between moults. Each specimen was marked with a distinctive spot of nail varnish so that they would not be confused one with another. These marks were renewed after moulting. The results were as follows:-

Specimen I. Molted on 16/11/69 then on 8/1/70.

Time interval between moults 53 days.

Specimen II. Molted on 23/11/69 then on 12/1/70

then died in moult 5/3/70.

Time interval between moults

a) 50 days

b) 52 days

Specimen III. Molted on 30/11/69 then emerged on

22/1/70.

Time interval between moults 52 days.

Specimen IV. Molted on 18/12/69 then on 6/2/70.

Time interval between moults 50 days.

Therefore the average observed time interval between moults from the above observations is 51.4 days i.e. 7 moults per year assuming a constant growth rate, or 17 - 18 moults during a larval life of  $2\frac{1}{2}$  years, (this allows for the fairly extensive incubation period for the eggs).

DISCUSSION OF LARVAL LIFE.

Twenty species of stonefly larvae were taken in samples from the section of the River Wear, Wearhead to Witton Park and when it is noted that the British list for the Order Plecoptera comprises only 34 species of which four species are extremely rare or doubtful records it may be assumed that in this particular area conditions favour the establishment and maintenance of stonefly colonies.

Records of the occurrence of species from the River Wear were compared with those of Butcher et al (1937) from the River Tees and with those of Brown, Cragg and Crisp (1964) from streams on the Moor House Nature Reserve. Twelve of the twenty species recorded in the present study were recorded from the River Tees by Butcher (1937) while eighteen species out of the twenty were recorded from the Moor House National Nature Reserve by Brown, Cragg and Crisp (1964).

Records of numbers of each species taken in samples at the five main sampling stations seemed to indicate a falling off in the density of populations from high to low levels of the river. This reduction in population density varied from species to species and was most marked in L. inermis, L. moselyi, and C. torrentium, and to a lesser degree in A. sulcicollis (see table 1.) One species D. bicaudata reached its lower limit at Wearhead two specimens only being taken.

This latter observation would seem to confirm Hynes' (1941) view that D. bicaudata has an upper temperature threshold preventing its colonisation of lower levels of rivers below about 1000' above sea level. The larger Perlidae i.e. P. bipunctata and D. cephalotes were taken in rather larger numbers at lower levels than at high levels of the river. This would seem to agree with the observations of Hynes (1941) and Brinck (1949) who both stated that variation in the substrate might also account for the presence or absence of certain species of stoneflies, some preferring stable substrata others unstable. Both P. bipunctata and D. cephalotes prefer habitats with rather large boulders which resist movement under flood conditions and these conditions obtained to a greater degree at Witton Park than at Wearhead.

Studies of the growth rates of the most abundant species revealed a tendency for growth to be retarded during the months of November, December and January in those species which were hiemal in their development with emergence as adults occurring in late spring. Brinck (1949) and Svensson P.O. (1966) observed similar retardations of growth in Swedish stoneflies with this pattern of development though Hynes (1941) did not recognise growth retardation in British material. Species showing marked retardation of growth were A. sulcicollis (see figs. 4 - 13 inclusive and table 9 and tables XVI - XXII inclusive in Appendix II and Leuctra inermis (see figs. 16 and 19 and tables XXIII

and XXIV on Appendix II). Other species showing retardation of growth were P. praecox (fig. 14), P. meyeri (fig. 15), I. grammatica (fig. 26).

No obvious retardation of growth was evident in the development of C. torrentium, B. risi or D. cephalotes.

Species having an aestival growth pattern, as expected, developed steadily over the whole larval period e.g. L. moselyi (fig. 20) and L. fusca (figs. 21 - 24 inclusive and tables 19 - 22 inclusive). These observations support Hynes (1941) and Brinck (1949).

It was noticed in A. sulcicollis and L. fusca that the mean body length was greater at Wearhead than at the lower level of Witton Park, (see table 6 and 7). The observed discrepancies in the case of A. sulcicollis were subsequently shown to be statistically non-significant except in two instances and it was concluded that in these two instances the significance of the differences in the means was probably reflecting the large disparity in the sample sizes under review and that the larval population of A. sulcicollis was homogeneous as regards mean body length at both high and low stations.

In the case of L. fusca the observed discrepancies in mean body length at Wearhead and Witton Park were shown to be statistically significant. The reason for the disparity in mean size remains unresolved but may in part be explained by the fact that the periods of larval development were slightly out of phase at high and low stations, hatching of the eggs and the beginning of larval growth seeming to occur slightly earlier at Wearhead than

at Witton Park.

B. risi was found to be unstable with regard to hatching of the eggs and/or the beginning of larval growth. Brinck (1949). This resulted in a composite population that was easily recognised from histograms of body length arranged in size frequencies of 0.5 m.m. (see fig. 17). The composite nature of populations of B. risi seems to result from inherent instability of the species with regard to hatching of the eggs, or the beginning of larval growth subsequent to hatching or to both events. The instability does not seem able to be ascribed to prolonged low temperatures as in springs or cold trickles since composite populations occur in quite normal streams and rivers side by side with quite uniform populations in essentially similar streams, (Brinck, 1949).

Khoo (1968) investigating the phenomenon of diapause in stoneflies observed that the eggs of B. risi had a very long incubation period and a very long hatching period. The long incubation was found to be caused by the occurrence of diapause at the stage just after the formation of the germinal disc. The long hatching period was caused by the irregular termination of diapause. Furthermore the inception and termination of diapause did not seem to be stimulated by the immediate environmental conditions. These irregularities in the length of incubation and hatching periods result in the development of composite populations as regards size.

This composite nature of the population of B. risi made it extremely difficult to construct any

accurate picture of the growth pattern of individuals of the species since the criterion of mean body length was greatly affected by the continued presence in the samples throughout the developmental period of extremely small specimens. A further point is the fact that these small specimens do not carry on growing and do not join the larval populations of the succeeding year i.e. these late developers die having failed to complete their full larval development in the one year, and do not linger on to finish developing after another year of larval life. In other words the observed composite nature of the samples of B.risi is not caused by the larval development extending over two years.

The growth rates of the most common species, A.sulcicollis, L. inermis and L. fusca were further examined by means of a technique referred to as the "percentage change index" (Smith M.Sc. thesis 1969). This technique was applied to measurement data obtained from samples taken from high and low levels of the River Wear for A. sulcicollis, and L. fusca, so that it was possible to make an attempt to compare growth rates at high and low levels for these two species.

In the case of A. sulcicollis it was impossible to obtain samples from both Wearhead and Witton Park for identical periods except in one or two instances. However between 16/10/69 and 27/12/69 the growth rate at Witton Park, as indicated by the percentage change index was almost exactly double that obtaining at Wearhead, (see table 9). This would seem

to indicate that the retardation of growth occasioned by the low temperatures of the Winter months affected specimens in the higher reaches of the river markedly before those living at Witton Park. At the same time a tremendous increase in the growth rate of specimens was seen to occur in spring at both Wearhead and Witton Park (see table 9).

Similarly larvae of L. inermis in samples taken at Wearhead and Westgate were retarded in their growth during the winter and then spurted dramatically in early spring.

Both these hiemal developing species revealed an interrupted growth during the colder months of Winter. This phenomenon was noted by Brinck (1949) and Svensson P.O. (1966) in Swedish material but was not recognised by Hynes (1941) in British material. Examination of graphs of mean body length for P. meyeri, C. torrentium and A. sulcicollis given by Hynes (1941) reveal that no samples were taken in January 1940. Therefore following sampling in mid December 1939 no further samples were taken till mid-February a fact which may have camouflaged some of the retardation of growth in the populations of the above species. It is significant that Hynes draws attention to retardation of growth in P. meyeri in the River Liffey, Ireland as investigated by Frost W.E. during the winter of 1929 - 1930.

The growth rates of L. fusca at Wearhead and Witton Park were calculated using the percentage change index

method. At both stations growth was slow in the first part of larval life. Although the periods of time investigated could not be synchronised at Wearhead and Witton Park there was an indication that the rate of growth was considerably faster at Wearhead than at Witton Park (see table 10). This may partly explain why mean body length of specimens at Wearhead was consistently greater than mean body length of specimens at Witton Park (see table 7).

A tentative estimate of the number of instars for P. bipunctata was advanced on the basis of records of time intervals between moults of four specimens kept in captivity in the laboratory; 17 - 18 moults during a larval life of  $2\frac{1}{2}$  years allowing for a fairly extensive incubation period for the eggs. Little however is definitely known regarding the number of instars and there certainly seems to be no set number characteristic of the Plecoptera; e.g. Nemoura sp. - 22 (Wu, 1923), D. cephalotes - 33 for females, fewer for males (Schoenemund, 1925), P. abdominalis Burm. - 22 (Samal, 1923).

The growth rate of D. cephalotes was estimated by measuring all available larvae, assigning them to year 1, 2, or 3 categories and plotting their body lengths against a three year time axis. Growth was slow but steady throughout year 1 accelerated somewhat in year 2 and then revealed a divergence of growth rates of male and female specimens in year 3. Overall however no obvious growth retardation was recognised during winter.

THE ADULTS.

THE ADULTS.

ADULT LIFE WITH PARTICULAR REFERENCE TO OVARIAN MATURATION.

1. Sampling and species recorded.

The adult stoneflies were sampled at the same stations as the larvae, and special emphasis was laid on collections at Wearhead and Witton Park so as to enable a comparison to be made between emergence and flight periods at upper and lower stations on the River Wear. The methods used to capture the adults were to use a large sweep net through the vegetation and herbage of the river bank, to beat resting insects from trees and bushes into the net held beneath the branches and also to collect from stones at the waters edge using a "pooter".

Altogether fifteen species were taken in the adult stage and of these only nine species were taken in sufficient numbers for it to be possible to delimit their respective flight periods.

The fifteen species captured were as in the list given on the following page.

Of the fifteen species taken as adults only one, Nemurella picteti Klapalek, was not recorded from larval samples.

List of species taken as adults.

Leuctra geniculata

Leuctra inermis

Leuctra hippopus

Leuctra moselyi

Leuctra fusca

Amphinemura sulcicollis

Protonemura praecox

Protonemura meyeri

Nemoura erratica

Nemurella picteti

Isoperla grammatica

Chloroperla torrentium

Dinocras cephalotes

Perla bipunctata

Perlodes microcephala

II. Flight periods and degree of overlap  
with larval records.

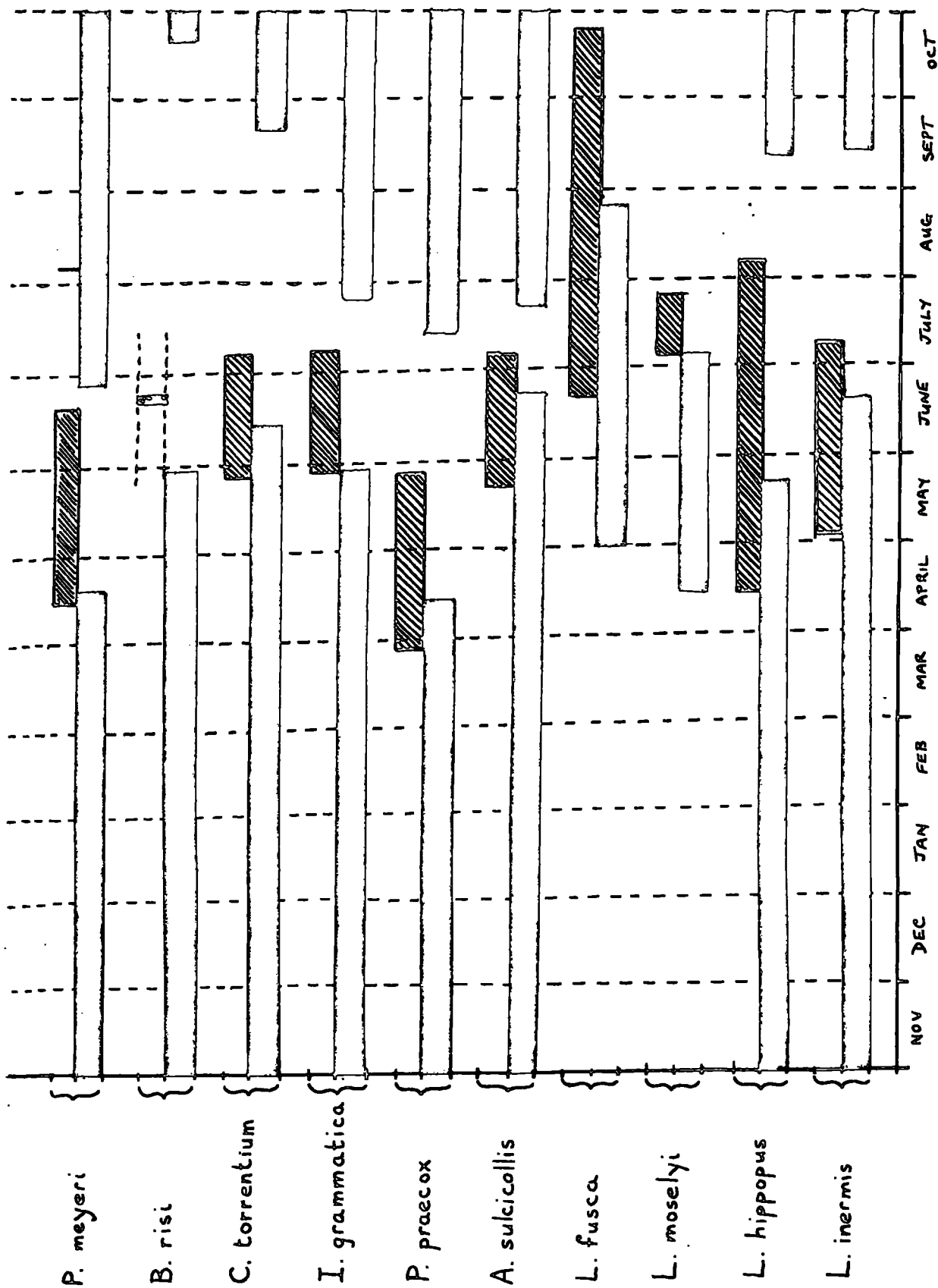
When a table was constructed to show the flight periods and also the duration of larval life some indication of the degree of overlap of the two phases in the life history of certain species was obtained. (see fig. 28).

This overlap or co-existence of larvae and adults varied in extent from species to species. Figure 28 shows that the overlap was very pronounced in L. fusca, (late June - late August); L. inermis (early May - mid June); L. hippopus (early April - late May); and A. sulcicollis (late May - late June).

The least overlap of the larval and adult phases in the life history was observed in L. moselyi where the last larvae and the first adults were taken on the same day, 2/7/67 i.e. no overlap observed; I. grammatica where again the last larvae and the first adults were taken on the same day 28/5/67 i.e. no overlap observed; C. torrentium (late May - early June); P. praecox (late March - mid April); P. meyeri (slight overlap in mid April).

In the case of B. risi adults were only taken on one sample date 18/6/67 and then only two specimens so that it was quite impossible to give any degree of overlap.

Fig. 28. Showing duration of larval life, (□), and observed flight periods, (▨), of the commonest stoneflies, (Plecoptera).



In the cases of species exhibiting a long period of overlap it may be that this is caused by one or more of the following occurrences:-

- a) the eggs being laid by each adult on more than one occasion and the eggs having a constant incubation period and the larvae a constant larval life span.
- b) the eggs, (if laid on a single occasion) having variable incubation periods and the larvae a constant larval life span.
- c) the eggs being laid on a single occasion and having a fixed incubation period but the larval life span being variable.
- d) the eggs being laid on more than one occasion, and having variable incubation periods and the larval life being variable.

All the above sets of circumstances would result in a large degree of overlap of larval and adult phases, by causing an extension of the period necessary for all the larvae to emerge as adults.

### III. Mating behaviour.

Mating behaviour was observed mainly in L. fusca but incidental observations of matings were made in A. sulcicollis and D. cephalotes.

In the case of L. fusca the female remained stationary except for a regular rhythmic twitching and opening and closing of the genital aperture. The abdomen was curved downwards so that the tip of the abdomen was not sheltered by the wings as is usual. The male ran in a very excited manner and grasped the female from above the wings and at the same time his abdomen was curved to one side and round the female's body so that the tips of the two insects' abdomens were in the correct position for sperm transfer. They remained like this for about 2 - 3 minutes in one instance and for 5 - 7 minutes in another. The female made normal movements in the meantime i.e. crawling up away from gravity and also towards shade and away from light, carrying the male on her back. No spermpacket was seen to be transferred. The female reproductive opening remained open after mating and there seemed to be a slight distension of the abdomen here, (possibly a sperm packet internally).

Mating was observed in a tube lacking food and also in a tube with food (Pleurococcus). Feeding was also observed in the latter tube but whether prior

to or after mating or both was not determined.

The general pattern of events observed in the mating of A. sulcicollis and D. cephalotes was the same as has been described above for L. fusca. However the degree of excitation of the insects seemed greater in D. cephalotes so much so that the males often mounted the females the wrong way round in their haste, also the females seemed to make greater efforts to run away from the males especially when pursued by more than one male.

When the ripe eggs were fertilised they were extruded from the female genital opening in a consolidated mass. This was carried around for some hours and was prevented from touching the substrate over which the female was crawling by the upward curving of the abdomen. This curvature of the abdomen was so pronounced as to give the impression that the egg mass had been transferred to the dorsal surface.

When laid egg masses were allowed to come in contact with water they separated into individual eggs. This separation was often quite violent and this undoubtedly aids dispersal of the eggs.

As a prelude to mating male insects were observed to drum on the substrate with the sternum of the eighth abdominal segment. This was seen in D. cephalotes in a male kept in a plastic box approxi-

mately 10" x 4" x 3" deep together with two other males and one female. In this case the drumming was against the side of the box and was clearly audible several feet away. The duration of the drumming was about 2 - 3 seconds only and was a continuous evenly spaced series of blows with no discernible rhythm.

Drumming was also observed in one specimen of I. grammatica which was contained in a 3" x 1" specimen tube covered by a piece of nylon stocking and containing a strip of crumpled paper. This time the drumming was audible across the room and had a rhythmic quality d-d-d-dum, d-d-d-dum, d-d-d-dum etc. The duration of each drumming sequence was approximately 10 seconds. This specimen lived in captivity for 26 days when given 1% sucrose solution to drink and drumming occurred almost every day, appearing to coincide with feeding time.

#### IV. Feeding and length of adult life.

##### 1. Previous work.

Until comparatively recently it was generally believed that no adult stoneflies fed and that the mouthparts were degenerate, (Mertens, 1923; Schoenemund, 1924; Kuhlreiber, 1934). However it was shown that feeding did occur in some species of the Sub-order Filipalpia, (Frison, 1935). Also Newcomer (1918) stated that in California Taeniopteryx pacifica, Banks, fed as adults and caused damage to fruit tree buds. More recently feeding of adult stoneflies has been investigated by Hynes (1942) working on Nemoura cinerea and in this species feeding was found to be an important prerequisite for mating and successful development of the eggs by the female. Feeding was also found to extend the life of adults as much as eight times that of unfed specimens in N. cinerea. Brinck (1949) also studied feeding of adult stoneflies both in the laboratory and in the field and confirmed Hynes' observations regarding the feeding of the adult Filipalpia being necessary for egg development. Brinck also suggests that the necessity to feed may account in part for the scarcity of the Filipalpia in high mountainous districts in Sweden where there are no woods or thickets where food may be found near the banks of the streams, the main foods being lichens and unicellular algae belonging to the genus Pleurococcus (Hynes, 1942; Brinck, 1949).

2. Experimental work on feeding and length of  
adult life.

Experiments were carried out with the more common species in an attempt to determine the degree to which availability of food influenced the length of adult life. The most used species were Amphinemura sulcicollis which emerged in late Spring and Leuctra fusca which emerged in Summer, though observations were made on several other species during the course of the experiments.

In all the experiments the flies were confined in tubes 3" x 1" containing a small strip of crumpled paper for refuge and covered by a small piece of nylon stocking held by an elastic band.

Liquid food or water was supplied by placing small balls of cotton wool soaked in the appropriate liquids on top of the nylon mesh. This had the advantage of preventing condensation on the side of the tube which might trap the insects by their sticking to the sides.

Solid food could be included in the tube together with the crumpled paper.

Three stoneflies were kept in each tube and several tubes were used for each of the experimental conditions. The tubes were inspected daily and fresh food and water were supplied as appropriate. Flies

which received food were given either 1% sucrose solution on the cotton wool balls or were given pieces of sycamore bark on which there was Pleurococcus as well as small pieces of lichens. All the specimens were given water on the cotton wool balls. As flies died they were removed and preserved in 4% formaldehyde after wetting in alcohol. The day of death (i.e. day after capture) was recorded in all cases and tables were compiled from these records to see if there was any correlation between length of life and availability of food and water.

The experiments were repeated two or three times during the flight period of the commonest species, L. fusca.

Table 11 summarises the effect of sucrose and water versus water only on survival in A. sulcicollis. The full data for this experiment on A. sulcicollis are given in table XXIX in appendix III and this shows a very heavy mortality rate in all specimens, fed and unfed, male and female on day one suggesting that a high proportion of the specimens suffered some serious injury as a result of capture. It was for this reason that in summarising the results it was decided to ignore the deaths of flies taking place on days one and two after capture. The results were summarised in two ways, a) by the ~~of the~~ maximum observed number of days survival, b) the mean number of days survival ignoring

those specimens dying in the first two days.

Table 11.

Summary of effect of sucrose and water versus water  
only on survival of adults of A. sulcicollis.

Diet	Maximum observed survival in days.		
	Males.	Females	All specimens
Water only	12	4	12
1% sucrose solution	15	26	26

Diet	Mean survival in days.		
	Males	Females	All specimens
Water only	8.33	4.00	5.44
1% sucrose solution	19.00	17.40	18.43



Data obtained from the several experiments on L. fusca were summarised in table 12, the full data from all experiments are given in table XXX in appendix III. As in the case of A. sulcicollis, unfed specimens died very much quicker than fed specimens. Again the results were summarised in two ways (see table 12) and again data regarding specimens dying on days one and two of the experiment were disregarded when working out the mean number of days survival.

A further experiment was carried out with specimens of L. fusca captured at Wearhead and Witton Park on the same occasion to see if there was any difference in the survival rates of fed flies at high and low positions on the river. Table 13 summarises the data obtained and with the exception of one female specimen from Wearhead which survived 20 days under the experimental conditions, survival rates of specimens taken at Wearhead and Witton Park were very closely related. The full results of this experiment are given in table XXXI in appendix III.

In addition to the experiments carried out on A. sulcicollis and L. fusca other observations were made on the survival of the less numerous species under various dietary conditions. These observations are summarised in table 14. It is interesting to note the length of life achieved by such members of

Table 12.

Summary of the effect of various diets on the survival  
of adults of L. fusca.

Diet	Maximum observed survival in days.		
	<u>Males.</u>	<u>Females.</u>	<u>All specimens.</u>
Water only	10	10	10
1% Sucrose solution.	24	27	27
Pleurococcus and water	15	20	20
Diet	Mean survival in days.		
	<u>Males.</u>	<u>Females.</u>	<u>All specimens.</u>
Water only	5.46	6.21	5.69
1% Sucrose Solution.	12.82	11.72	12.47
Pleurococcus and water	8.42	9.31	8.72

Table 13.

Summary of survival rates of adult L. fusca at a) Wearhead  
and b) Witton Park..

Station.	Maximum observed survival in days.		
	<u>Males.</u>	<u>Females.</u>	<u>All specimens.</u>
Wearhead	14	20	20
Witton Park	15	12	15
	Mean survival in days.		
Wearhead	8.56	10.11	9.11
Witton Park	8.20	7.75	8.07

- 104-  
TABLE 14.

Observed maximum survival in days of the rarer species of  
stoneflies under various dietary conditions.

<u>Species.</u>	<u>Diet.</u>	<u>Days survival.</u>	
		<u>Males.</u>	<u>Females.</u>
L. inermis	Water only	16	13
L. inermis	1% sucrose solution	29	27
L. inermis	Pleurococcus + water	24	33
L. moselyi	1% sucrose solution	11	7
L. hippopus	Water only	11	17
L. hippopus	Pleurococcus + water	-	11
L. geniculata	Water only	9	10
P. praecox	Pleurococcus + water	-	18
P. praecox	Water only	-	3
P. meyeri	1% sucrose solution	1	1
N. erratica	Pleurococcus + water	13	-
N. cambrica	Pleurococcus + water	-	1
N. picteti	1% sucrose solution	-	4
B. risi	1% sucrose solution	-	4
I. grammatica	1% sucrose solution	26	22
C. torrentium	1% sucrose solution	17	16
C. torrentium	Water only	13	4
Ø. microcephala	Water only	14	5

the sub-order Setipalpia as I grammatica and C. torrentium when liquid food was made available to them, (see table 14). In both cases the length of time survived would seem to indicate that in the event of liquid food (e.g. nectar, honeydew on leaves) being available these species seem to be able to utilise it to prolong adult life.

V. Correlation between feeding, length of life and degree of ovarian maturation.

In an attempt to investigate the influence of feeding and length of time required to mature the eggs, female stoneflies of known age in days after emergence were dissected and the size of the eggs was measured using an eyepiece graticule. Some of the flies had been fed on Pleurococcus or 1% sucrose solution while others had been given water only. Any difference in the degree of development of the eggs was noted.

The main species used in these investigations were A. sulcicollis, L. inermis and L. fusca but observations were made in several other species as well.

In the case of A. sulcicollis a preliminary experiment revealed that if a sample of adult females were to be divided into five groups, each group being given water to drink and Pleurococcus on sycamore bark as food, and then the specimens killed in groups on days 0, 2, 4, 6 and 8 after emergence, two things could be seen when dissections were performed. Firstly there was a definite increase in egg dimensions with time and secondly greater numbers of eggs were ripened causing the ovaries to increase in size so as to eventually project forwards into the thoracic region, (see table 15).

Table 15.

Summary of preliminary investigation into feeding and maturation of eggs in females of A.sulcicollis(Experiment I).

<u>Days after emergence.</u>	<u>Size of largest eggs present.</u>	<u>Extent of Ovaries.</u>
0	175 $\mu$ x 175 $\mu$	Abdomen half filled
2	240 $\mu$ x 200 $\mu$	Abdomen filled
4	240 $\mu$ x 200 $\mu$ )	Ovary filled abdomen
6	240 $\mu$ x 200 $\mu$ )	and projected forward
8	240 $\mu$ x 200 $\mu$ )	into thoracic region.

It was noticed that even in newly emerged specimens there tended to be a few large eggs present but that the size of the ovary remained small. It was therefore decided to record not only the size of the largest eggs present but also to assign the ovary of each dissected specimen to a size class in the following five point scale in all future experiments:-

1. rudimentary (extends  $\frac{1}{4}$  length of abdomen)
2. poorly developed (extends  $\frac{1}{2}$  length of abdomen)
3. well developed (almost fills abdomen)
4. very well developed (fills abdomen and extends forwards into thorax).
5. collapsed (abdomen empty, often telescoped and most eggs laid).

Experiment II was carried out using A. sulcicollis The number of specimens used was 62 and the date of capture was 2/7/67. Again the flies were divided into more or less equal batches and were killed after 0,2,4,5,6 and 7 days.

The female flies were dissected and the size of the largest eggs present was measured and the size of the ovary relative to the size of the abdomen was recorded on the five point scale mentioned above. The results of this experiment are summarised in table 16 and are given in full in table XXXII in appendix III. Table 16 shows that in A. sulcicollis the maturation of the eggs is a fairly rapid process taking place within the first two or three days. Indeed the possibility of the eggs being ripe or nearly so at the time of emergence was entertained. However dissections of mature larvae to investigate the state of the ovary just before emergence revealed that while the ovaries were well formed they were of small size. Also the eggs were in easily recognisable ovarioles and the size of the largest eggs present was  $30\ \mu \times 30\ \mu$  i.e. about  $\frac{1}{5}$  of the final size. Another point of difference between the larvae and the adults was the relatively large amount of fat body in the larvae compared to that present in the adults.

Table 16.

Summary of development of ovaries and eggs in fed specimens of A. sulcicollis (Experiment II).

Days after emergence	Mean size of largest eggs,	Number of flies with ovaries various stages on 5point scale.					Total No. specimens.
		1.	2.	3.	4.	5.	
0	174 $\mu$ x 151 $\mu$	-	4	2	-	-	6
2	193 $\mu$ x 186 $\mu$	-	2	5	1	-	8
4	200 $\mu$ x 200 $\mu$	-	-	8	2	-	10
5	204 $\mu$ x 198 $\mu$	-	1	14	-	1	16
6	202 $\mu$ x 201 $\mu$	-	-	6	2	10	18
7	207 $\mu$ x 200 $\mu$	-	-	2	2	-	4

Similar investigations were carried out on the maturation of the ovaries with other species, notably with L. fusca which emerges in summer. Some of the flies were fed on 1% sucrose solution while others were given water only. Specimens were not killed off at specific time intervals, but were allowed to remain in the tubes until their death when they were removed and preserved till such time as they could be dissected. The preservative used was 4% formalin.

When dissected the extent of the ovary and the dimensions of the largest eggs were recorded together with the length of life in days.

The specimens used in these investigations were captured on several separate occasions throughout the flight period and all the results were pooled. This was necessary because of the samples being predominantly composed of male specimens, a fact which could not be determined in the field. The full data are given in tables XXXII and XXXIV in appendix III.

Table 17.

Summary of development of ovaries and eggs in unfed specimens of L. fusca.

Days after emergence	Mean size of largest eggs. $\mu$ x $\mu$	Number of flies with ovaries at various stages on 5-point scale.					Total No. of specimens
		1.	2.	3.	4.	5.	
1	137 x 122	-	10	-	-	-	10
3	112 x 106	1	1	-	-	2	4
4	140 x 127	-	-	1	-	-	1
5	112 x 84	4	-	2	-	-	6
6	168 x 147	-	-	2	-	1	3
7	125 x 115	4	-	4	-	1	9
8	159 x 159	-	2	1	-	-	3
9	168 x 168	-	-	1	-	-	1
10	126 x 119	-	-	2	-	-	2

Table 18.

Summary of development of ovaries and eggs in fed specimens of *L. fusca*

Days after emergence	Mean size of largest eggs. $\mu \times \mu$	Number of flies with ovaries at various stages on 5-point scale.					Total No. of specimens
		1.	2.	3.	4.	5.	
1	105 x 96	7	-	5	-	-	12
2	159 x140	-	-	3	-	4	7
3	173 x145	-	-	3	-	-	3
4	172 x143	-	-	4	-	1	5
5	175 x154	-	-	2	-	-	2
6	168 x140	-	-	1	-	-	1
7	161 x140	-	-	2	-	1	3
8	196 x168	-	-	1	1	1	3
9	154 x140	-	-	-	1	1	2
11	175 x147	-	-	2	-	-	2
12	189 x161	-	-	-	1	2	3
13	168 x140	-	-	-	-	2	2
14	168 x140	-	-	-	-	9	9
15	None found	-	-	-	-	2	2
16	None found	-	-	-	-	2	2
17	168 x140	-	-	-	-	1	1
19	None found	-	-	-	-	1	1
20	168 x140	-	-	-	-	1	1
27	None found	-	-	-	-	1	1

Table 17 and 18 show the following phenomena:-

- 1) There was a tendency for eggs to be laid in the specimen tubes by adult females of *L. fusca* whether they were fed or not.
- 2) Maturation of some of the eggs was still possible in unfed female *L. fusca* though specimens with undersized eggs were found throughout the experiments.

- 3) Maturation of the eggs was accomplished in all but a few specimens of L. fusca that were fed, and this maturation of the eggs was very rapid occurring within two or three days after emergence (c.f. similar observations on A. sulcicollis).
- 4) Many specimens of L. fusca laid the eggs in the specimen tube (35.5% of fed specimens and 10.2% of unfed specimens). If it can be assumed that distension of the abdomen with ripe eggs is a stimulus to lay then these figures indicate once more that feeding after emergence was a significant factor in the development of mature eggs.

Again the possibility of eggs being ripened before emergence was investigated by dissection of mature larvae of L. fusca which were captured during August i.e. right in the middle of the emergence period.

The average size of eggs found in these mature female larvae was  $15\mu \times 15\mu$  which represents less than  $\frac{1}{10}$  of the size of the largest eggs found in female adults. Therefore as in the case of A. sulcicollis it seems as though the actual ripening of the eggs takes place in the first two or three days after emergence though the ovaries are well formed in mature larvae and eggs are clearly seen in the ovarioles.

As can be seen from the experiments carried out on A. sulcicollis and L. fusca, the main work with regard to the maturation of the eggs of captive adult stoneflies was carried out on species belonging to the

sub-order Filipalpia because of the ease of capture and subsequent feeding and accommodation.

Adult setipalpiian stoneflies were difficult to keep alive for any length of time and were much rarer and therefore harder to catch in sufficient numbers, both factors making it impractical to try to imitate the experiments carried out on filipalpiian species. In any case the desirability of repeating the experiments with setipalpiian species was in question in view of the generally accepted opinion of other workers (Hynes, 1941; Brinck, 1949) that these species either emerged with well developed ovaries or matured them quickly without feeding. In isolated cases however certain of the smaller species of the sub-order Setipalpia were kept alive for fairly long periods when given 1% sucrose solution e.g. I. grammatica - 22 days for one female specimen e.g. C. torrentium - 16 days for one female specimen.

However their inability to consume solid food must severely limit the possibility of any significant feeding occurring after emergence. Therefore it was assumed that in the case of the Setipalpia the development of the ovaries and the ripening of the eggs must be accomplished to a great degree before emergence, the final energy source for their maturation after emergence being any available fat body laid down during the larval life.

To test this assumption mature female larvae of all available species of stoneflies belonging to the sub-order Setipalpia were dissected to investigate the egg size as compared with the egg size found in adult female flies.

In I. grammatica mature female larvae that were dissected showed well developed eggs. The largest measured  $250\mu \times 170\mu$  i.e. about  $\frac{2}{3}$  of the fully developed eggs found in adult female flies.

One mature larva of P. bipunctata captured 30/4/67 had the abdomen full of eggs. The maximum egg size in this specimen was recorded as  $504\mu \times 364\mu$ , virtually the same dimensions as were recorded from dissected adult female flies. In this specimen 28 eggs were fully developed and shelled and were dark brown in colour. A further 2,000 eggs were estimated as being virtually of full size but were obviously not completely mature being a light tawny colour and still largely confined in the lower ends of the ovarioles. Many individual ovarioles could be separated and were seen to contain chains of eggs ranging from minute undeveloped eggs at the distal end to almost full sized eggs at the proximal end.

Female larvae of D. cephalotes were also dissected and it was found that eggs were not only developed in the final instars but they were present in specimens which were one or two moults from final emergence. Specimens captured on February 6th 1971 were dissected and cream coloured eggs were found which were about half the size of eggs taken from adult female flies. These eggs were unshelled and were contained in recognisable ovarioles. Also there was a substantial amount of fat body overlying the ovary. Specimens captured in late April/early May were also dissected and this time fully mature, dark brown shelled eggs were found packing the posterior half of the abdomen with the anterior part of the abdominal cavity

filled with eggs of a lighter colour but still very well developed and of mature size,

Similarly female larvae of P. microcephala were dissected and again mature eggs were found in quantity packing the posterior part of the abdomen, with other eggs which were not so well developed being found in the anterior part of the abdominal cavity.

To complete the investigation full grown larvae of C. torrentium were dissected and again eggs were found at an advanced stage of development the largest observed being  $330\mu \times 250\mu$  i.e. having virtually the same dimensions as eggs found in mature adult flies.

All these observations therefore indicate that the assumption, that in setipalpi species eggs must necessarily be developed in the later larval stages, is correct. This is undoubtedly due to the inability to feed, and therefore the inability to obtain the necessary energy needed to mature the eggs.

THE EGGS.

SECTION III.

THE EGGS.

The number of eggs developed by fully mature females was investigated by dissecting and counting the ripe eggs contained in the ovaries. Several specimens of each species were dissected and the egg count range recorded, the mean number of eggs per count worked out for the species and this latter statistic was taken as an indication of the potential fecundity. In addition the dimensions of the largest eggs present in each specimen were measured using a microscope and a micrometer eyepiece.

Adult females of setipalpiian species were in very short supply, only two specimens of D. cephalotes and three specimens of P. bipunctata being available for dissection. In the case of D. cephalotes one specimen was gravid and a very high egg count was made and the other laid one large egg mass which was collected and counted. One specimen of P. bipunctata, which had laid some eggs already, had eggs filling only the hind third of the abdomen and therefore had only a very low egg count, another specimen which was kept alive for five days laid two egg masses of 164 and 168 respectively with a twenty four hour interval, while the third specimen proved to be completely devoid of eggs having laid them prior to capture.

Egg counts in I. grammatica and C. torrentium were low and this was attributed to the relatively large

eggs produced by these two fairly small species.

The eggs of the species of the sub-order Setipalpia that were examined were of variable size and shape but none were round. Those of I. grammatica, C. torrentium, D. Cephalotes and P. bipunctata were all oval in general shape while those of P. microcephala were tetrahedral. All the setipalpiian eggs examined had adhesive bodies.

The eggs of the filipalpiian species examined were round in general shape with the exception of those of B. risi which were oval. Again with the exception of B. risi all the filipalpiian eggs were white or cream; eggs of B. risi were light brown. None of the filipalpiian eggs had adhesive bodies on the eggs but the whole of the outer membrane was covered in some sticky secretion which served to stick the eggs together in clumps as they were extruded by the females and this enabled the eggs to be carried in masses on the tip of the dorsally recurved abdomen. When these egg masses come into contact with water they broke up scattering the eggs. In all filipalpiian eggs there was a considerable space between the egg and the surrounding delicate membrane. Drawings and photographs of the eggs of certain species of stoneflies are given in figs. 29 - 33.

Details of the eggs of each species examined now follow:-

1) Amphinemura sulcicollis.

Egg counts 295; 400; 300; 270; 490; 220; 350; 305; 470; 190; 210.

Maximum egg count:- 490.

Range of egg counts: - 190 - 490.

Mean egg count = 318.

The eggs were round, white and with a large space between the egg and the membrane. There were no adhesive bodies.

Size of egg was  $160\mu \times 133\mu$

Size of egg and membrane  $200\mu \times 200\mu$

2) Protonemura meyeri.

Egg counts:- 395; 269; 317; 178; (317 was a laid egg mass).

Maximum egg count:- 395.

Range of egg counts: - 178 - 395.

Mean egg count = 290.

The eggs were round, white and had no adhesive bodies.

Size of egg  $140\mu \times 140\mu$

Size of egg and membrane  $200\mu \times 200\mu$

3) Protonemura praecox.

Egg counts:- 934 only one specimen available.

The eggs were almost round, cream and had no adhesive bodies.

Size of egg  $140\mu \times 140\mu$

Size of egg and membrane  $196\mu \times 168\mu$

4) Nemurella picteti.

Egg count:- 713 only one specimen available.

The eggs were round, white and had no adhesive bodies.

Size of egg  $230\mu \times 230\mu$

5) Leuctra inermis.

Egg counts:- 256; 367; 265; 170; 97; 69;

Maximum egg count:- 367.

Range of egg counts: - 69 - 367.

Mean egg count = 204.

The eggs were almost round, white and had no adhesive bodies.

Size of eggs  $196\mu \times 168\mu$

6) Leuctra hippopus.

Egg counts:- 310; 294; 275; 75 (75 was a laid egg mass).

Maximum egg count:- 310.

Range of egg counts:- 75 - 310.

Mean egg count = 239

The eggs were almost round, white and had no adhesive bodies.

Size of eggs  $196\mu \times 168\mu$

7) Leuctra fusca.

Egg counts:- 1020; 585; 380; (585 was a laid egg mass)

Maximum egg count:- 1020.

Range of egg counts 380 - 1020.

Mean egg count = 662

The eggs were round, white and had no adhesive bodies.

Size of eggs  $196\mu \times 168\mu$

8) Leuctra geniculata.

Only one female specimen was available and was found to contain only a very few eggs. Size of eggs present

$168\mu \times 140\mu$

9) Brachyptera risi.

Egg counts:- 492; 200.

Maximum egg count:- 492.

Range of egg counts 200- 492.

Mean egg count = 346

The eggs were oval, light brown and had no adhesive bodies.

Size of eggs:-  $266\mu \times 196\mu$

10) Isoperla grammatica.

Egg counts:- 205; 165; 115; 146; 199; 74.

Maximum egg count:- 205.

Range of egg counts 74 - 205.

Mean egg count = 151

The eggs were oval, brown and adhesive bodies were present and were concentrated on an adhesive anchor plate connected to the main egg body by a narrow neck of tissue.

Size of eggs:-  $330\mu \times 266\mu$

11) Chloroperla torrentium.

Egg counts;- 189; 90; 58; 86; 53; 40; 35; 22;

Maximum egg count:- 189.

Range of egg counts 22 - 189.

Mean egg count = 72

The eggs were oval, yellowish brown, and adhesive bodies were present on an anchor plate at one end of the egg.

Size of egg  $330\mu \times 252\mu$

12) Dinocras cephalotes.

Egg counts:- 2,535; 938 (938 was a laid egg mass).

Maximum egg count:- 2, 535.

Range of egg counts 938 - 2535.

Mean egg count = 1737

The eggs were oval, dark brown and adhesive bodies were present on a distinct anchor plate connected to the main egg body by a neck of tissue at one end.

Size of eggs  $476\mu \times 336\mu$

13) Perla bipunctata.

Egg counts:- 194; 332 (332 consisted of 164 and 168 laid egg masses).

Maximum egg count:- 332 obviously not an indication of the potential of this species taking into account the size of the mature female flies and the size of the eggs which are roughly the same size as those of Dinocras cephalotes. The abdomen was  $\frac{1}{3}$  filled suggesting previous egg laying had already taken place. The eggs were oval and very slender compared with those of D. cephalotes, with a tendency to be pointed at the opposite end to the adhesive disc. The eggs were brown in colour.

Size of eggs  $532\mu \times 280\mu$

14) Perlodes microcephala.

Egg counts:- 1224; 1017; 814; 1269.

Maximum egg counts:- 1269.

Range of egg counts 814 - 1269.

Mean egg count = 1081.

The eggs were dark brown, almost black with a very hard shell. They were tetrahedral in shape with adhesive bodies present on an opalescent basal disc on one of the faces of the tetrahedron. The shape of the eggs permitted very efficient packing of the eggs into the abdomen leaving very little space between them.

Size of eggs:-  $448\mu$  high x  $420\mu$  side of base.

All data relating to numbers of eggs and size of eggs of the foregoing species are summarised in table 19.

Fig. 29. Egg of *Nemurella picteti* (photomicrograph) x 500  
(slightly retouched outer membrane)

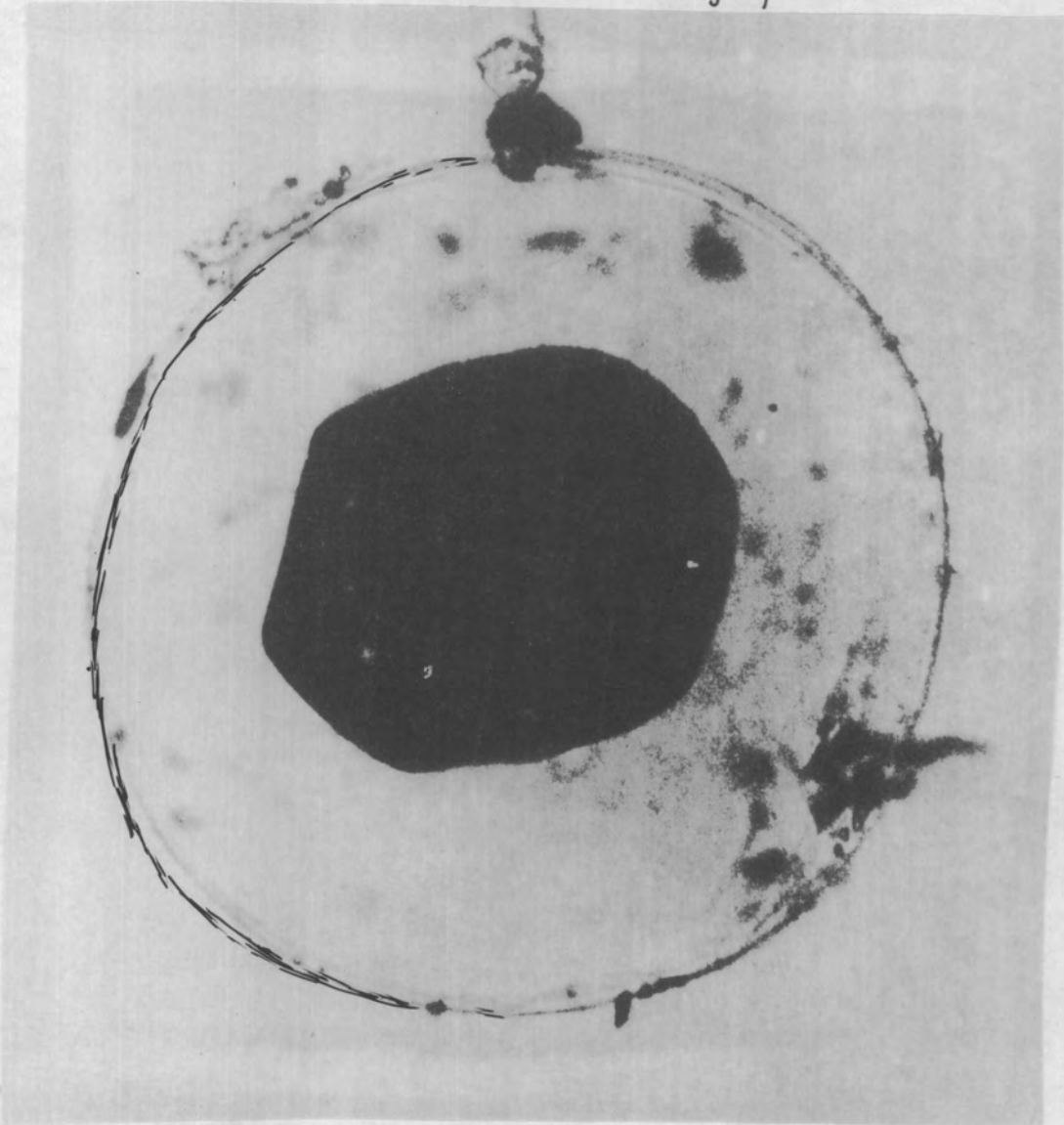
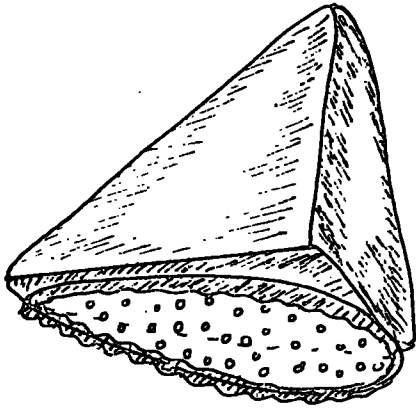
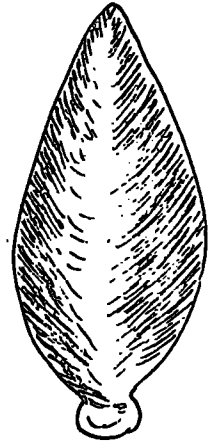


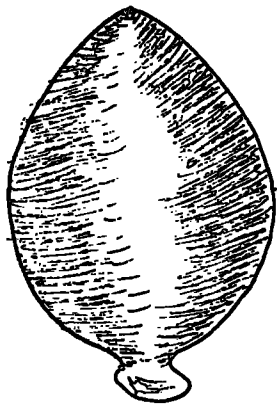
Fig. 30. Drawings of eggs of setipalpians stoneflies



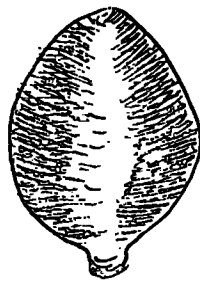
*Perlodes microcephala* × 100



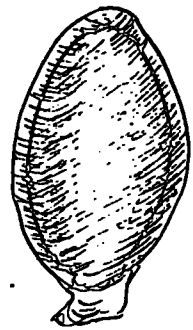
*Perla bipunctata* × 100



*Dinocras cephalotes* × 100



*Isoperla grammatica* × 100



*Chloroperla torrentium* × 100

Fig. 31. Immature egg of *D. cephalotes* (photomicrograph) x 200

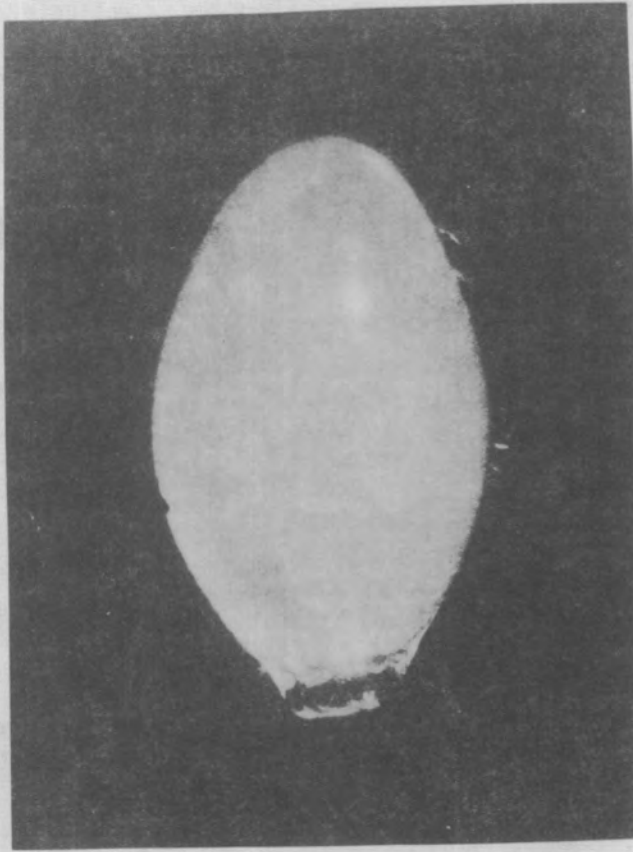
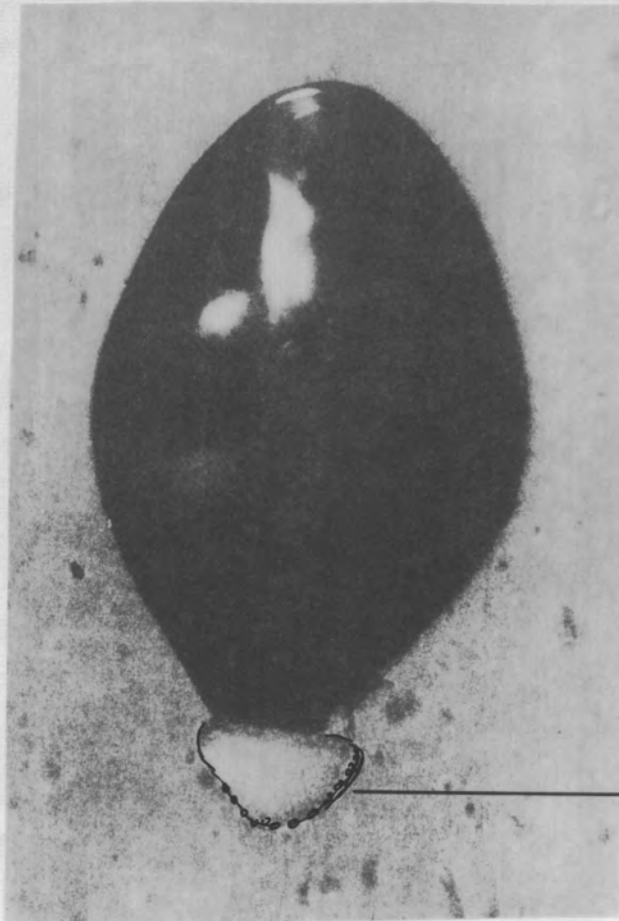
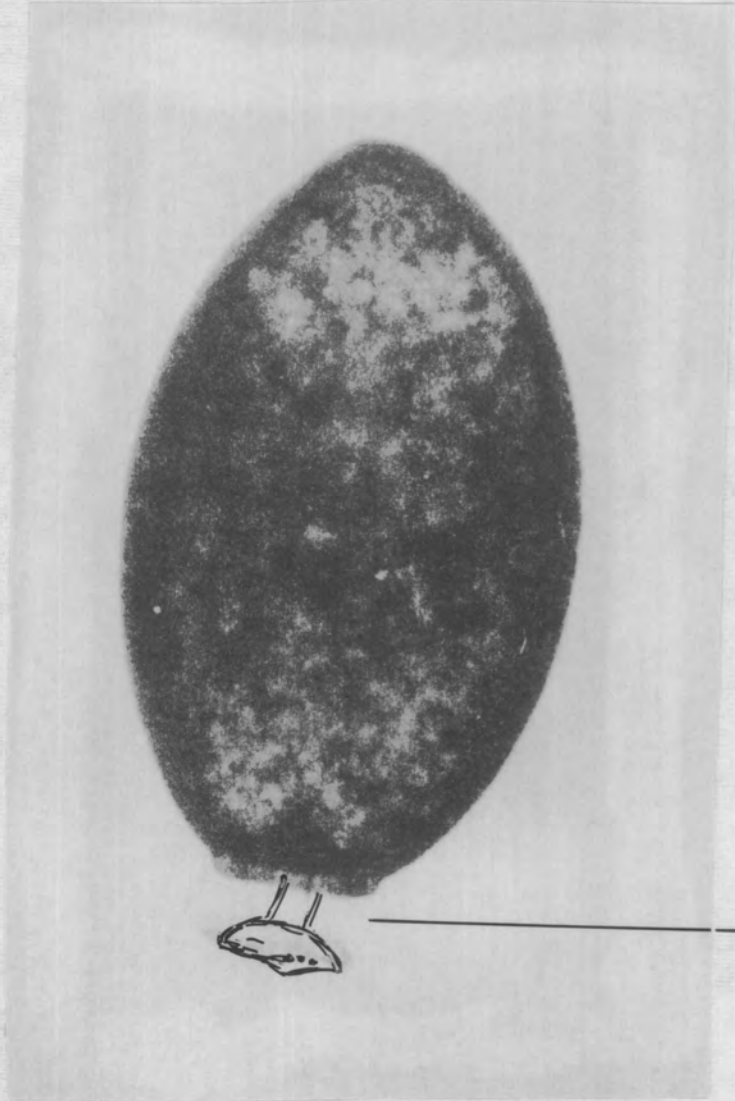


Fig. 32. Mature egg of *D. cephalotes* (photomicrograph) x 200



Anchor plate retouched  
to show adhesive bodies

Fig 33. Mature egg of *P. bipunctata* (photomicrograph) x 200



retouched to show  
anchor plate.

Table 19.

Summary of data relating to numbers of eggs and egg size in  
the commonest stoneflies.

Species.	Egg Numbers		No. of counts	Typical dimensions ( $\mu$ ) of fully ripe eggs.
	Range of counts	Mean egg No.		
A. sulcicollis	190 - 490	318	11	240 x 200
P. meyeri	178 - 395	290	5	200 x 200
P. praecox	934 (1 specimen)	-	1	196 x 168
N. picteti	713 (1 specimen)	-	1	230 x 230
L. inermis	69 - 367	204	6	196 x 168
L. hippopus	75 - 310	239	4	196 x 168
L. fusca	380 - 1020	662	3	196 x 168
L. geniculata	(1 specimen with only few ripe eggs)			168 x 140
B. risi	200 - 492	346	2	266 x 196
I. grammatica	74 - 205	151	6	330 x 266
C. torrentium	22 - 189	72	8	330 x 252
D. cephalotes	938 - 2535	21737	2	476 x 336
P. bipunctata	194 - 332	263	2	532 x 280
P. microcephala	814 - 1269	1081	4	448 (high) x 420 (base)

Discussion of adult life, feeding and egg maturation.

Mertens (1923), Schoenemund (1924), and Kuhlreiber (1934) all stated that no adult stoneflies fed and that the reason for this was the fact that the mouthparts were degenerate. While these statements are true for the larger setipalpians species, they are certainly not true for the smaller filipalpians species. In these the mouthparts are quite well developed and functional, Newcomer (1918), Frison (1935), Hynes (1941 and 1942), Brinck (1949).

Hynes (1942) working with N. cinerea was able to show that feeding prolonged the lives of both male and female specimens by a factor of 8x the life expectancy of starved flies given water only. Whether the flies were allowed to mate or not had no significant effect on the length of life. Brinck (1949) was able to confirm Hynes' view that feeding not only prolonged the life of filipalpians species but that it was essential for the maturation of the eggs. Brinck also observed feeding in the field by the following species:- B. risi, T. nebulosa, Capnia bifrons, C. nigra, L. fusca, L. hippopus, L. nigra, N. borealis, N. cinerea, N. erratica, and Nemurella picteti. This study has substantiated the work of Hynes and Brinck: experiments on A. sulcicollis and L. fusca showed that feeding prolonged the life of both male and female adults but to a lesser degree than was observed by Hynes (1942) for N. cinerea. The eggs of fed specimens also matured satisfactorily and very rapidly while those of starved

specimens did not mature satisfactorily. Maturation of the eggs was not completely halted by lack of food, some eggs managing to grow possibly using fat body as the necessary energy source though the ovary itself remained very small.

It is generally agreed that the Setipalpia do not feed as adults because of the degenerate state of the mandibles though Brinck (1949) observed that the degeneracy of the mandibles of setipalpiian species was graded, the larger Perlidae and Perlodidae having only membranous rudiments with only slightly indicated or no teeth, while Isoperla and Chloroperla although having distinctly reduced mandibles still possess definite teeth slightly chitinised in Isoperla and more heavily in Chloroperla. Brinck further records food in the gut of specimens of C. burmeisteri, a Swedish species. No observations of solid food in the guts of any setipalpiian species have been made in this study but specimens of I. grammatica and C. torrentium were shown to be able to utilise liquid food (1% sucrose solution) and so prolong their lives. Presumably small quantities of dissolved food e.g. honey dew from aphids or nectar, will be available from time to time in the wild and use of such food might well prolong life and increase the incidence of mating in the smaller setipalpiian species. Maturation of the eggs of such species would not be helped in this way however as dissections of mature female larvae showed that the eggs were almost fully developed before emergence. Brinck (1949) dissected newly emerged adult females and he also noted fully developed eggs.

Since the members of the sub-order Filipalpia have been shown to need food in order to successfully mature the eggs, Brinck speculated that species emerging in winter would be setipalpians rather than filipalpians. This however was not so, all species emerging in winter being filipalpians even though food sources were very scarce indeed in the Swedish winter. Examination of the emergence and flight periods of British material reveals a similar pattern i.e. only filipalpians species emerge in winter, the Setipalpia emerging in spring.

Ulfstrand (1968) gave flight periods for Swedish stoneflies and as might be expected the general tendency when compared with observations on British material is for the flight periods to be somewhat later in the year because of the much more prolonged and severe winter. This applies mainly to those species having an hiemal development followed by emergence in late spring.

- e.g. A. sulcicollis - late May - early July - this study:  
early July - early August - Swedish material (Ulfstrand 1968)
- e.g. P. meyeri - late May - early July - this study:  
early June - late July - Swedish material (Ulfstrand 1968)
- e.g. I. grammatica. - late May - early July - this study:  
mid June - mid September - Swedish material (Ulfstrand 1968)

Aestival developing species are not so markedly displaced in their flight periods by the differing climatic conditions in Sweden and Britain.

e.g. L. fusca. - late June - late October - this study:  
mid July - November - Swedish material  
(Ulfstrand 1968).

SUMMARY.

1. It has been established that retardation of growth rate occurs during the winter months in at least some stonefly larvae, notably A. sulcicollis, L. inermis and I. grammatica. This retardation occurred at both high and low levels of the river, but was more marked at the upper stations.
2. The growth rate of larvae of the larger stoneflies belonging to the family Perlidae which have a three year development seems unaffected during winter.
3. Larval populations of B. risi sampled in early spring were shown to be markedly bimodal as regards body length indicating the composite nature of the population with regard to size.
4. Succession of species of the genus Leuctra throughout the year was shown with regard to four species, namely L. hippopus; L. inermis; L. moselyi and L. fusca in that order.
5. Emergence of the smaller filipalpiian species was accomplished on stones at the waters edge but the larger Setipalpia were often observed emerging some distance from the water e.g. I. grammatica in bushes and D. cephalotes on breakwaters etc.
6. Well defined ovaries and eggs were demonstrated in mature final larvae of A. sulcicollis though the maximum egg size observed in these larvae was only about  $\frac{1}{5}$  of the size of mature eggs found in adult female flies.

7. Experiments with adult flies revealed a marked prolongation of life with feeding in both A. sulcicollis and L. fusca. Certain other species also showed the tendency towards a longer life if given food.
8. Certain species of adult Setipalpia seemed able to utilise liquid food.
9. Maturation of the eggs of A. sulcicollis and L. fusca was seen to be encouraged by feeding and although not entirely prevented by absence of food, seriously impaired in starved specimens.
10. The process of egg maturation was seen to be very rapid occurring in the first two or three days of adult life.
11. In filipalpiian species almost all the eggs were laid in a single egg mass. In the larger setipalpiian species more than one laying was observed and dissections of adult females often revealed two distinct bodies of eggs, a hindmost fully mature batch in front of which were many paler often unshelled eggs obviously not ready for laying.
12. Mature female final larvae of setipalpiian species were dissected and were seen to contain many fully mature eggs and many almost mature eggs, i.e. the eggs were developed to full size in the larvae and merely needed fertilisation, following the emergence of the adults, before being laid.

13. Mating behaviour was observed in both filipalpian and setipalpian species and followed the same general pattern, namely, pursuit of the female by the male; mounting on the female's back and clasping round the wings and thorax by the male; a downward curving of the male abdomen round that of the female so as to place male and female genitalia in the correct position for exchange of sperm; and final separation.
14. The eggs of 14 species were described and a comparison was made between those of filipalpian and setipalpian species for size and structure.
15. Egg counts were made for the various species by dissecting mature female flies, or by collecting laid egg masses from the walls of the tubes in which female flies were confined during experiments.

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APPENDIX I.

Tables giving data of measurements of stonefly larvae.

TABLE I.

*Amphinemura sulcicollis* captured at Wearhead (Total No. = 1197).

Date	No. of larvae N	Body Length			Head Width			Pronotum Length		
		$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.
6/11/66	73	1.83	0.198	0.445	0.43	0.011	0.105	0.39	0.005	0.070
11/1/67	37	2.23	0.088	0.297	0.56	0.016	0.127	0.43	0.008	0.088
5/2/67	133	2.54	0.097	0.3.2	0.64	0.008	0.089	0.51	0.007	0.083
12/3/67	10	3.82	0.074	0.272	0.80	0.040	0.200	0.64	0.024	0.155
12/4/67	74	3.78	0.225	0.474	0.82	0.112	0.106	0.65	0.003	0.051
30/4/67	23	4.40	0.509	0.713	0.87	0.004	0.059	0.71	0.011	0.106
21/5/67	45	5.41	0.305	0.552	0.99	0.015	0.123	0.80	0.010	0.098
28/5/67	24	5.30	0.330	0.575	0.98	0.010	0.101	0.82	0.012	0.108
11/6/67	2	6.00	-	-	0.95	-	-	0.85	-	-
18/6/67	1	4.40	-	-	0.80	-	-	0.70	-	-
6/8/67	10	0.69	0.003	0.054	0.20	-	-	0.10	-	-
11/9/67	155	1.38	0.037	0.191	0.313	0.003	0.052	0.21	0.004	0.060
22/10/67	99	2.04	0.093	0.305	0.424	0.005	0.069	0.32	0.094	0.031
17/11/67	94	2.32	0.126	0.355	0.47	0.005	0.069	0.37	0.005	0.072
17/12/67	243	2.32	0.175	0.418	0.49	0.005	0.069	0.39	0.006	0.076
28/1/68	130	2.69	0.156	0.395	0.59	0.010	0.102	0.47	0.007	0.084
3/3/68	44	3.27	0.131	0.362	0.69	0.004	0.066	0.57	0.004	0.065

TABLE II.

Amphinemura sulciollis captured at Westgate (Total No. = 397)

Date	No. of larvae N.	Body Length		Head Width		Pronotum Length				
		$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.
6/11/66	59	2.13	0.182	0.43	0.48	0.003	0.05	0.39	0.003	0.05
11/1/67	154	2.32	0.104	0.32	0.61	0.010	0.100	0.48	0.008	0.09
5/2/67	72	2.57	0.181	0.43	0.66	0.013	0.11	0.54	0.004	0.06
12/3/67	24	3.85	0.280	0.53	0.75	0.009	0.095	0.59	0.007	0.08
12/4/67	31	3.75	0.339	0.58	0.83	0.001	0.03	0.64	0.001	0.03
30/4/67	11	4.32	0.883	0.94	0.88	0.014	0.12	0.69	0.012	0.11
21/5/67	33	5.52	0.308	0.56	0.99	0.007	0.08	0.84	0.010	0.10
28/5/67	13	6.15	0.299	0.55	1.07	0.010	0.100	0.92	0.010	0.10

TABLE III.

Amphinemura sulcicollis captured at Stanhope (Total No. = 431).

date	No. of larvae N.	Body Length		Head Width		Pronotum Length				
		$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.
6/11/66	84	2.29	0.012	0.11	0.64	0.010	0.10	0.50	0.003	0.05
5/2/67	20	2.32	0.151	0.39	0.59	0.012	0.11	0.48	0.007	0.08
12/3/67	74	3.37	0.250	0.50	0.74	0.005	0.07	0.58	0.003	0.05
12/4/67	118	4.26	1.199	1.100	0.86	0.045	0.21	0.72	0.029	0.17
30/4/67	44	4.71	0.600	0.78	0.89	0.009	0.096	0.72	0.010	0.10
21/5/67	27	5.28	0.264	0.51	0.98	0.002	0.045	0.80	0.005	0.07
11/6/67	1	6.0	-	-	1.0	-	-	0.9	-	-

TABLE IV.

Amphinemura sulcicollis captured at Wolsingham (Total No. = 321).

Date	No. of larvae N.	Body Length		Head Width		Pronotum Length				
		$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.
6/11/66	97	2.11	0.113	0.34	0.49	0.008	0.09	0.39	0.004	0.07
11/1/67	98	1.86	0.519	0.72	0.50	0.039	0.20	0.41	0.027	0.17
5/2/67	33	2.56	0.126	0.36	0.66	0.009	0.10	0.53	0.007	0.08
12/3/67	24	3.61	0.262	0.51	0.75	0.006	0.08	0.58	0.009	0.09
12/4/67	23	4.11	0.379	0.62	0.85	0.014	0.12	0.66	0.019	0.14
30/4/67	41	4.64	0.591	0.77	0.92	0.012	0.11	0.70	0.010	0.10
21/5/67	3	5.70	-	-	1.00	-	-	0.93	-	-
11/6/67	2	4.80	-	-	0.85	-	-	0.75	-	-

TABLE V.  
*Amphinemura sulcirostris* captured at Witton Park (Total No. = 543).

Date	No. of larvae N	Body Length		Head Width		Pronotum Length				
		$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.
6/11/66	54	1.92	0.072	0.268	0.45	0.004	0.062	0.35	0.004	0.064
11/1/67	99	2.08	0.166	0.407	0.55	0.008	0.089	0.45	0.006	0.078
5/2/67	91	2.50	0.417	0.645	0.65	0.029	0.169	0.52	0.001	0.028
12/3/67	40	3.51	0.273	0.523	0.73	0.007	0.083	0.55	0.006	0.079
12/4/67	44	3.75	0.403	0.634	0.78	0.017	0.132	0.63	0.014	0.119
30/4/67	14	4.09	0.492	0.702	0.83	0.014	0.119	0.67	0.007	0.083
21/5/67	13	5.20	0.354	0.595	0.99	0.011	0.106	0.85	0.010	0.099
11/6/67	2	3.85	-	-	0.75	-	-	0.60	-	-
27/8/67	1	1.1	-	-	0.2	-	-	0.1	-	-
11/9/67	7	1.34	0.107	0.328	0.27	0.003	0.053	0.17	0.003	0.057
22/10/67	38	1.98	0.080	0.283	0.46	0.003	0.055	0.36	0.003	0.057
17/11/67	46	2.09	0.108	0.329	0.49	0.006	0.076	0.39	0.006	0.077
17/12/67	43	2.26	0.101	0.318	0.48	0.004	0.063	0.38	0.004	0.063
28/1/68	41	2.58	0.127	0.357	0.55	0.005	0.068	0.44	0.004	0.063
3/3/68	10	3.16	0.250	0.500	0.68	0.009	0.096	0.53	0.004	0.063

TABLE VI.

*Protonemura praecox*. All available larvae (Total No. = 104).

Date	No. of larvae N	Body Length			Head Width			Pronotum Length		
		$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.
28/6 + 1/7/66	10	1.31	0.025	0.050	0.26	0.004	0.020	0.16	0.024	0.155
6/11 + 29/11/66	17	5.93	1.585	1.259	1.09	0.026	0.161	0.84	0.022	0.148
3/1 + 11/1/67	10	5.99	2.937	1.714	1.25	0.042	0.205	0.94	0.032	0.179
5/2 + 12/2/67	10	6.06	4.152	2.037	1.22	0.080	0.283	0.91	0.053	0.230
12/3/67	5	6.40	0.956	0.978	1.12	0.022	0.147	0.82	0.018	0.133
12/4/67	4	6.95	0.583	0.763	1.18	0.002	0.044	0.90	0.100	0.100
10/7 + 24/7/67	7	1.55	0.171	0.131	0.27	0.003	0.017	0.17	0.002	0.014
8/8/67	17	1.80	0.279	0.529	0.31	0.010	0.10	0.24	0.008	0.091
20/8 + 27/8/67	5	2.22	0.282	0.531	0.50	0.016	0.040	0.38	0.010	0.100
7, 11, 18/9/67	9	2.84	0.351	0.552	0.54	0.014	0.037	0.41	0.011	0.105
24/10/67	3	4.27	-	-	0.83	-	-	0.63	-	-
17/11/67	3	2.73	-	-	0.50	-	-	0.37	-	-
17/12/67	2	7.60	-	-	1.30	-	-	0.95	-	-
28/1/67	2	7.00	-	-	1.20	-	-	0.95	-	-

TABLE VII

Protonemura meyeri. All available larvae. (Total No. = 75).

Date	No. of larvae N	Body Length			Head Width			Pronotum Length		
		$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.
28/6 + 1/7/66	11	1.32	0.06	0.245	0.26	0.004	0.063	0.16	0.003	0.055
26/10 + 2/11/66	11	4.84	1.04	1.02	0.86	0.030	0.173	0.69	0.030	0.173
29/11/66	9	4.80	0.233	0.483	0.86	0.005	0.071	0.68	0.001	0.032
3/1/67	7	7.48	1.128	1.062	1.27	0.037	0.192	1.01	0.036	0.189
12/3/67	8	6.19	0.806	0.898	1.01	0.026	0.161	0.77	0.024	0.155
14/3/67	2	6.30	-	-	1.10	-	-	0.80	-	-
3/4 + 17/4/67	13	7.51	1.024	1.012	1.25	0.039	0.198	0.91	0.015	0.123
6/8/67	1	2.4	-	-	0.50	-	-	0.40	-	-
18/9/67	2	1.70	-	-	0.35	-	-	0.25	-	-
17/12/67	6	4.43	1.090	1.044	0.90	0.023	0.152	0.63	0.010	0.100
28/1/68	3	4.77	-	-	0.83	-	-	0.60	-	-
3/3/68	2	6.55	-	-	1.2	-	-	0.90	-	-

TABLE VIII.

Brachyptera risi. All available larvae. (Total No. = 456).

Date	No. of larvae N	Body Length			Head Width			Pronotum Length		
		$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.
2/11/66	28	1.27	0.338	0.581	0.22	0.004	0.063	0.13	0.002	0.045
29/11/66	151	1.80	0.253	0.503	0.29	0.012	0.110	0.15	0.011	0.105
3/1 + 11/1/67	55	2.72	0.743	0.862	0.50	0.039	0.197	0.36	0.028	0.166
5/2 + 12/2/67	73	4.36	3.766	1.941	0.73	0.100	0.316	0.57	0.073	0.270
12/3 + 14/3/67	35	6.01	8.238	2.87	0.94	0.156	0.395	0.78	0.133	0.365
3/4 + 12/4/67	41	7.66	4.261	2.064	1.11	0.069	0.263	1.01	0.072	0.268
17/4 + 30/4/67	54	4.41	12.488	3.534	0.94	1.872	1.368	0.58	0.220	0.469
21/5 + 28/5/67	2	6.0	-	-	0.95	-	-	0.80	-	-
24/10/67	3	1.33	-	-	0.23	-	-	0.13	-	-
4/11 + 17/11/67	7	1.91	0.082	0.286	0.33	0.005	0.071	0.23	0.005	0.071
17/12/67	3	2.17	-	-	0.33	-	-	0.23	-	-
28/1/68	3	3.37	-	-	0.70	-	-	0.53	-	-
3/3/68	1	5.20	-	-	1.00	-	-	0.90	-	-

TABLE IX.

*Leuctra inermis* captured at Wearhead and Westgate (Total No. = 1007).

Date	No. of larvae N	Body Length			Head Width			Pronotum Length		
		$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var.	S.D.
6/11/66	122	3.40	0.591	0.769	0.45	0.011	0.104	0.35	0.007	0.084
11/1/67	85	3.86	0.329	0.574	0.61	0.029	0.170	0.49	0.011	0.105
5/2/67	78	4.24	0.487	0.698	0.63	0.013	0.114	0.50	0.009	0.094
12/3/67	13	5.28	1.404	1.185	0.69	0.010	0.100	0.52	0.005	0.072
12/4/67	106	5.79	1.112	1.055	0.78	0.014	0.118	0.60	0.014	0.118
30/4/67	38	6.13	0.941	0.970	0.78	0.009	0.095	0.60	0.021	0.145
21/5/67	47	6.29	0.487	0.698	0.83	0.007	0.084	0.61	0.008	0.089
28/5/67	15	6.05	0.568	0.754	0.79	0.006	0.083	0.59	0.007	0.084
11/6/67	7	6.80	0.143	0.378	0.83	0.007	0.084	0.66	0.006	0.083
18/6/67	1	6.0	-	-	0.80	-	-	0.60	-	-
11/9/67	17	2.31	0.155	0.394	0.27	0.003	0.055	0.18	0.003	0.055
22/10/67	129	3.16	0.337	0.581	0.41	0.005	0.072	0.31	0.005	0.072
17/11/67	103	3.60	0.543	0.737	0.46	0.009	0.094	0.36	0.008	0.089
17/12/67	158	3.93	0.839	0.911	0.50	0.012	0.110	0.39	0.010	0.100
28/1/68	81	4.31	1.095	1.046	0.55	0.020	0.139	0.43	0.014	0.118
3/3/68	7	5.80	0.534	0.730	0.70	0.003	0.055	0.56	0.003	0.055

TABLE X

Leuctra moselyi. All available larvae. (Total No. = 74)

Date	No. of larvae N	Body Length			Head Width			Pronotum Length		
		$\bar{x}$	Var	S.D.	$\bar{x}$	Var.	S.D.	$\bar{x}$	Var	S.D.
12/4/67	2	3.60	-	-	0.45	-	-	0.35	-	-
30/4/67	2	4.25	-	-	0.45	-	-	0.40	-	-
21/5/67	23	5.12	0.527	0.719	0.62	0.008	0.089	0.50	0.005	0.072
28/5/67	8	5.76	0.739	0.086	0.71	0.008	0.089	0.59	0.008	0.089
11/6/67	26	5.81	0.851	0.922	0.72	0.008	0.089	0.58	0.007	0.084
18/6/67	12	6.95	0.303	0.551	0.81	0.001	0.036	0.63	0.004	0.060
2/7/67	1	8.50	-	-	0.90	-	-	0.70	-	-

TABLE XI.

Leuctra fusca captured at Wearhead (Total No. = 1229).

Date	No. of larvae N	Body Length			Head Width			Pronotum Length		
		$\bar{x}$	Var	.S.D.	$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.
30/4/67	4	2.70	-	-	0.35	-	-	0.28	-	-
21/5/67	119	3.30	0.379	0.608	0.41	0.006	0.078	0.31	0.006	0.079
28/5/67	117	3.50	0.353	0.594	0.46	0.007	0.086	0.36	0.023	0.150
11/6/67	359	4.21	0.577	0.760	0.54	0.008	0.092	0.43	0.006	0.079
18/6/67	231	4.79	0.783	0.885	0.57	0.011	0.105	0.45	0.006	0.079
2/7/67	125	5.95	0.830	0.911	0.66	0.009	0.092	0.53	0.005	0.074
23/7/67	103	6.86	0.274	0.166	0.74	0.009	0.092	0.55	0.008	0.089
6/8/67	164	6.95	0.850	0.922	0.75	0.008	0.092	0.58	0.005	0.074
27/8/67	5	7.36	0.250	0.500	0.78	0.009	0.092	0.58	0.002	0.040
11/9/67	2	7.25	-	-	0.95	-	-	0.80	-	-

TABLE XII.

Leuctra fusca captured at Witton Park. Total No. = 675

Date	No. of larvae N	Body Length		Head Width		Pronotum Length				
		$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.
21/5/67	6	3.55	0.209	0.457	0.48	0.005	0.071	0.38	0.005	0.071
11/6/67	128	3.93	0.717	0.847	0.48	0.010	0.318	0.38	0.009	0.097
18/6/67	135	3.80	0.046	0.214	0.42	0.009	0.094	0.32	0.007	0.084
2/7/67	177	4.64	1.121	1.059	0.50	0.016	0.127	0.39	0.013	0.115
23/7/67	83	6.07	2.071	1.439	0.64	0.021	0.145	0.50	0.013	0.112
6/8/67	91	5.53	1.367	1.171	0.65	0.015	0.123	0.51	0.008	0.089
27/8/67	39	6.35	1.485	1.219	0.73	0.013	0.115	0.56	0.002	0.043
3/9/67	10	5.62	1.190	1.091	0.64	0.016	0.128	0.52	0.012	0.108
11/9/67	6	6.93	1.037	1.020	0.80	0.003	0.058	0.62	0.005	0.069

TABLE XIII.

Isoperla grammatica. All available larvae. (Total No. = 405).

Date	No. of larvae. N	Body Length			Head Width			Pronotum Length		
		$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.
26/10 + 6/11/66	49	3.38	1.38	0.37	0.781	0.05	0.23	0.35	0.01	0.10
29/11/66	29	3.51	2.94	1.72	0.71	0.09	0.30	0.37	0.02	0.16
3/1 + 11/1/67	43	3.71	2.35	1.53	0.74	0.18	0.43	0.43	0.04	0.19
5/2 + 12/2/67	49	5.54	3.63	1.90	1.09	0.07	0.26	0.57	0.02	0.13
12/3 + 14/3/67	16	6.91	1.85	1.36	1.33	0.24	0.49	0.62	0.01	0.10
3/4 + 12/4/67	53	8.38	2.29	1.51	1.65	0.08	0.28	0.78	0.02	0.15
17/4 + 30/4/67	51	10.20	3.34	1.83	1.85	0.07	0.27	0.91	0.02	0.14
21, 28, 31/5/67	28	10.10	10.29	3.21	1.71	0.38	0.62	0.92	0.08	0.28
24/7/67	2	1.1	-	-	0.25	-	-	0.10	-	-
20/8/67	5	1.34	0.02	0.14	0.28	0.02	0.13	0.12	0.002	0.04
7, 11, + 18/9/67	37	1.74	0.14	0.38	0.34	0.01	0.08	0.19	0.002	0.04
22/10 + 24/10/67	8	3.04	1.33	1.15	0.60	0.03	0.18	0.30	0.05	0.22
19/11/67	8	3.90	0.46	0.68	0.91	0.01	0.11	0.43	0.04	0.21
17/12/67	11	3.78	1.00	1.00	0.88	0.03	0.18	0.41	0.01	0.10
28/1/68	10	4.90	1.07	1.04	1.16	0.06	0.25	0.54	0.01	0.10
3/3/68	6	6.32	1.09	1.05	1.18	0.08	0.29	0.60	0.01	0.10

TABLE XIV.

*Chloroperla torrentium*. All available larvae. (Total No. = 90).

Date	No. of larvae N	Body Length			Head Width			Pronotum Length.		
		$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.	$\bar{x}$	Var	S.D.
6/11 + 29/11/66	5	2.78	0.430	0.656	0.50	0.02	0.14	0.29	0.005	0.071
3/1 + 11/1/67	3	3.37	-	-	0.60	-	-	0.40	-	-
5/2 + 12/2/67	7	4.18	1.260	1.120	0.79	0.161	0.401	0.43	0.009	0.095
12/3 + 14/3/67	9	5.02	1.042	1.021	0.80	0.006	0.077	0.46	0.001	0.032
3,12 + 17/4/67	15	5.31	0.720	0.849	0.81	0.002	0.045	0.48	0.001	0.032
30/4/67	14	5.91	1.050	1.025	0.89	0.003	0.055	0.50	0.006	0.078
21,28 + 31/5/67	23	6.18	0.296	0.544	0.91	0.042	0.205	0.53	0.062	0.249
11/6 + 13/6/67	3	6.40	-	-	0.93	-	-	0.53	-	-
18/9/67	1	2.00	-	-	0.30	-	-	0.10	-	-
22/10 + 24/10/67	2	3.25	-	-	0.45	-	-	0.30	-	-
17/12/67	4	3.20	-	-	0.53	-	-	0.30	-	-
28/1/67	4	3.60	-	-	0.55	-	-	0.28	-	-

TABLE XV.

Derived from measuring all available larvae of Dinocras cephalotes and then estimating year of growth of each individual specimen. (Total No. = 100).

Month	Year I of Larval Life			Year II of Larval Life			Year III of Larval Life		
	N	$\sum x$	$\bar{x}$	N	$\sum x$	$\bar{x}$	N	$\sum x$	$\bar{x}$
August	1	2.6	2.60	3	19.4	6.23	2	28.0	14.00
September	20	32.7	1.64	2	23.3	11.65	2	28.0	14.00
October	2	3.3	1.65	1	12.0	12.00	-	-	-
November	7	12.8	1.83	2	16.2	8.10	2	50.5	25.25
December	-	-	-	-	-	-	2	49.2	24.60
January	2	4.3	2.15	3	28.6	9.53	-	-	-
February	1	2.1	2.10	3	31.2	10.40	1	20.0	20.00
March	2	7.7	3.85	-	-	-	1	18.0	18.00
April	9	23.6	2.62	3	42.1	14.03	-	-	-
May	1	3.3	3.30	3	44.0	14.67	3	71.5	23.83
June	12	50.8	4.23	2	28.0	14.00	-	-	-
July	7	36.3	5.19	1	21.0	21.00	-	-	-

APPENDIX II.

Tables giving data for calculation of percentage change  
indices for larval growth rates.

TABLE XVI

Percentage change index for A. sulcicollis at Wearhead between

16/10/69 and 27/12/69 (72 days or 10.3 weeks).

Size Group in m.m.	% of sample in each size group.		% Difference # or -	% larvae moving up to next size group
	Sample A 16/10/69	Sample B. 27/12/69.		
3.5 - 3.9	0	1	+1	(1 - 1)% = 0%
3.0 - 3.4	3	14	+11	(12 - 11)% = 1%
2.5 - 2.9	7	27	+20	(32 - 20)% = 12%
2.0 - 2.4	64	47	-17	(15 + 17)% = 32%
1.5 - 1.9	26	11	-15	15% = 15%
<p>∴ Total % larvae moved up = 60%</p> <p>∴ Time interval in weeks = 10.3 weeks.</p> <p>∴ Mean % larvae moved up per week = 5.8%</p>				

TABLE XVIII

Percentage change index for *A. sulcicollis* at Wearhead between

27/12/69 and 14/3/70 (77 days or 11 weeks).

Size Group in m.m.	% of sample in each size group.		% Difference + or -	% larvae moving up to next size group.
	Sample A. 27/12/69	Sample B. 14/3/70.		
4.0 - 4.4	6	3	+3	(3 - 3)% = 0%
3.5 - 3.9	1	9	+8	(11 - 8)% = 3%
3.0 - 3.4	14	28	+14	(25 - 14)% = 11%
2.5 - 2.9	27	31	+4	(29 - 4)% = 25%
2.0 - 2.4	47	27	-20	(9 + 20)% = 29%
1.5 - 1.9	11	2	-9	9% = 9%
<p>Total % larvae moved up = 77%</p> <p>Time interval in weeks = 11 weeks</p> <p>∴ Mean % larvae moved up per week = 7.0%</p>				

TABLE XXIII

Percentage change index for *A. sulcicollis* at Wearhead between  
14/3/70 and 20/5/70 (67 days or 9.6 weeks)

Size Group in m.m.	% of sample in each size group.		% Difference + or -	% larvae moving up to next size group.
	Sample A. 14/3/70	Sample B. 20/5/70		
6.5 - 6.9	-	5	+5	(5 - 5)% = 0%
6.0 - 6.4	-	29	+29	(34 - 29)% = 5%
5.5 - 5.9	-	21	+21	(55 - 21)% = 34%
5.0 - 5.4	-	26	+26	(81 - 26)% = 55%
4.5 - 4.9	-	14	+14	(95 - 14)% = 81%
4.0 - 4.4	3	5	+2	(97 - 2)% = 95%
3.5 - 3.9	9	-	-9	(88 + 9)% = 97%
3.0 - 3.4	28	-	-28	(60 + 28)% = 88%
2.5 - 2.9	31	-	-31	(29 + 31)% = 60%
2.0 - 2.4	27	-	-27	(2 + 27)% = 29%
1.5 - 1.9	2	-	-2	2%

Total % of larvae moved up = 546%  
 Time interval in weeks = 9.6 weeks  
 ∴ Mean % of larvae moved up per week = 55.8%

TABLE XIX

Percentage change index for A. sulcicollis at Witton Park between  
6/11/66 and 11/1/67 (66 days or 9.4 weeks.)

Size Group in m.m.	% of sample in each size group.		% Difference + or -	% larvae moving up to next size group
	Sample A. 6/11/66.	Sample B. 11/1/67.		
3.0 - 3.4	9	3	+3	(3 - 3)% = 0%
2.5 - 2.9	6	18	+12	(15 - 12)% = 3%
2.0 - 2.4	39	49	+10	(25 - 10)% = 15%
1.5 - 1.9	55	30	-25	25% = 25%
<p>Total % of larvae moved up = 43%</p> <p>Time interval in weeks = 9.4 weeks</p> <p>∴ Mean % of larvae moved per week = 4.6%</p>				

TABLE XX

Percentage change index for *A. sulcicollis* at Witton Park between  
11/1/67 and 5/2/67 (25 days or 3.6 weeks.)

Size Group in m.m.	% of sample in each size group.		% Difference + or -	% larvae moving up to next size group
	Sample A. 11/1/67	Sample B 5/2/67		
3.0 - 3.4	3	14	+ 11	(11 - 11)% = 0%
2.5 - 2.9	18	29	+ 11	(22 - 11)% = 11%
2.0 - 2.4	49	54	+ 5	(27 - 5)% = 22%
1.5 - 1.9	30	3	- 27	27% = 27%
<p>Total % of larvae moved up = 60%</p> <p>Time interval in weeks = 3.6 weeks</p> <p>∴ Mean % of larvae moved up per week = 16.7%</p>				

TABLE XXI

Percentage change index for *A. sulcicollis* at Witton Park between

5/2/67 and 12/3/67 (35 days or 5 weeks).

Size Group in m.m.	% of sample in each group.		% Difference. + or -	% larvae moving up to next size group
	Sample A. 5/2/67	Sample B. 12/3/67		
4.5 - 4.9	-	2	+ 2	(2 - 2)% = 0%
4.0 - 4.4	-	25	+25	(27 - 25)% = 2%
3.5 - 3.9	-	40	+40	(67 - 40)% = 27%
3.0 - 3.4	14	18	+4	(71 - 4)% = 67%
2.5 - 2.9	29	12	-17	(54 + 17)% = 71%
2.0 - 2.4	54	3	-51	(3 + 51)% = 54%
1.5 - 1.9	3	-	-3	3%
Total % larvae moved up				= 224%
Time interval in weeks				= 5 weeks
∴ Mean % of larvae moved up per week =				44.8%

TABLE XXII

Percentage change index for A. sulcicollis at Witton Park between

16/10/69 and 27/12/69 (72 days or 10.3 weeks).

Size Group in m.m.	% of sample in each size group.		% Difference + or -	% of larvae moving up to next size group
	Sample A. 16/10/69	Sample B. 27/12/69		
3.0 - 3.4	-	9	+ 9	(9 - 9)% = 0%
2.5 - 2.9	-	20	+20	(29 - 20)% = 9%
2.0 - 2.4	26	61	+35	(64 - 35)% = 29%
1.5 - 1.9	60	10	-50	(14 + 50)% = 64%
1.0 - 1.4	14	-	-14	14% = 14%
<p>Total % of larvae moving up=116%</p> <p>Time interval in weeks = 10.3 weeks.</p> <p>∴ Mean % larvae moved up per week = 11.3%</p>				

TABLE XXIII

Percentage change index for *Leuctra inermis* at Wearhead and Westgate (combined data) between 6/11/66 and 5/2/67.

Size Group in m.m.	% of sample in each size group.		% Difference + or -	% larvae moving up to next size group
	Sample A. 6/11/66.	Sample B. 5/2/67.		
6.0 - 6.4	-	1	+ 1	(1 - 1)% = 0%
5.5 - 5.9	1	6	+ 5	(6 - 5)% = 1%
5.0 - 5.4	2	10	+ 8	(14 - 8)% = 6%
4.5 - 4.9	8	21	+13	(27 - 14)% = 14%
4.0 - 4.4	19	29	+10	(37 - 10)% = 27%
3.5 - 3.9	18	21	+ 3	(40 - 3)% = 37%
3.0 - 3.4	23	12	-11	(29 + 11)% = 40%
2.5 - 2.9	17	-	-17	(12 + 17)% = 29%
2.0 - 2.4	9	-	- 9	(3 + 9)% = 12%
1.5 - 1.9	3	-	-3	3%
<p>Total % larvae moved up = 169%</p> <p>Time interval in weeks = 13 weeks</p> <p>∴ Mean % larvae moved up per week = 13%</p>				

TABLE XXIV

Percentage change index for L. inermis at Wearhead and Westgate  
(combined data) between 5/2/67 and 12/4/67.

Size Group in m.m.	% of sample in each size group		% Difference + or -	% larvae moving up to next size group
	Sample A. 5/2/67	Sample B 12/4/67		
7.5 - 7.9	-	8	+ 8	(8 - 8)% = 0%
7.0 - 7.4	-	8	+ 8	(16 - 8)% = 8%
6.5 - 6.9	-	14	+14	(30 - 16)% = 16%
6.0 - 6.4	1	22	+21	(51 - 21)% = 30%
5.5 - 5.9	6	13	+ 7	(58 - 7)% = 51%
5.0 - 5.4	10	16	+ 6	(64 - 6)% = 58%
4.5 - 4.9	21	8	-13	(51 + 13)% = 64%
4.0 - 4.4	29	8	-21	(30 + 21)% = 51%
3.5 - 3.9	21	2	-19	(11 + 19)% = 30%
3.0 - 3.4	12	1	-11	11%

Total % larvae moved up	= 319%
Time interval in weeks	= 9.4 weeks
∴ Mean % larvae moved up per week	= 33.9%

TABLE XXV

Percentage change index for *L. fusca* at Wearhead between 21/5/67  
and 18/6/67 (28 days or 4 weeks).

Size Group in m.m.	% of sample in each size group.		% Difference + or -	% larvae moving up to next size group
	Sample A 21/5/67	Sample B 18/6/67		
6.5 - 6.9	-	5	+5	(5 - 5)% = 0%
6.0 - 6.4	-	8	+8	(13 - 8)% = 5%
5.5 - 5.9	-	11	+11	(24 - 11)% = 13%
5.0 - 5.4	-	25	+25	(49 - 25)% = 24%
4.5 - 4.9	2	22	+20	(69 - 20)% = 49%
4.0 - 4.4	18	18	0	(69 + 0)% = 69%
3.5 - 3.9	29	8	-21	(48 + 21)% = 69%
3.0 - 3.4	23	3	-20	(28 + 20)% = 48%
2.5 - 2.9	20	-	-20	(8 + 20)% = 28%
2.0 - 2.4	8	-	-8	8% = 8%

Total % larvae moved up	= 31.3%
Time interval in weeks	= 4 weeks
∴ Mean % larvae moved up per week	= 78.3%

TABLE XXVI

Percentage change index for *L. fusca* at Wearhead between 18/6/67 and 6/8/67 (49 days or 7 weeks).

Size Group in m.m.	% of sample in each size group		% Difference + or -	% larvae moving up to next size group.
	Sample A. 18/6/67	Sample B 6/8/67		
9.0 - 9.4	-	2	+ 2	(2 - 2)% = 0%
8.5 - 8.9	-	2	+ 2	(4 - 2)% = 2%
8.0 - 8.4	-	15	+15	(19 - 15)% = 4%
7.5 - 7.9	-	15	+15	(34 - 15)% = 19%
7.0 - 7.4	-	23	+23	(57 - 23)% = 34%
6.5 - 6.9	5	18	+13	(70 - 13)% = 57%
6.0 - 6.4	8	14	+ 6	(76 - 6)% = 70%
5.5 - 5.9	11	5	- 6	(70 + 6)% = 76%
5.0 - 5.4	25	4	-21	(49 + 21)% = 70%
4.5 - 4.9	22	1	-21	(28 + 21)% = 49%
4.0 - 4.4	18	0	-18	(10 + 18)% = 28%
3.5 - 3.9	8	1	- 7	(3 + 7)% = 10%
3.0 - 3.4	3	-	- 3	3% = 3%
Total % larvae moved up				= 422%
Time interval in weeks				= 7 weeks
∴ Mean % of larvae moved up per week =				60.6%

TABLE XXVII

Percentage change index for *L. fusca* at Witton Park between  
11/6/67 and 2/7/67 (21 days or 3 weeks).

Size Group in m.m.	% of sample in each size group.		% Difference + or -	% larvae moving up to next size group.
	Sample A. 11/6/67.	Sample B. 2/7/67.		
7.5 - 7.9	-	1	+1	(1 - 1)% = 0%
7.0 - 7.4	-	2	+2	(3 - 2)% = 1%
6.5 - 6.9	2	5	+3	(6 - 3)% = 3%
6.0 - 6.4	2	4	+2	(8 - 2)% = 6%
5.5 - 5.9	2	11	+9	(17 - 9)% = 8%
5.0 - 5.4	10	16	+6	(23 - 6)% = 17%
4.5 - 4.9	12	19	+7	(30 - 7)% = 23%
4.0 - 4.4	23	16	-7	(23 + 7)% = 30%
3.5 - 3.9	23	16	-7	(16 + 7)% = 23%
3.0 - 3.4	20	9	-11	(5 + 11)% = 16%
2.5 - 2.9	6	1	-5	5% = 5%

Total % of larvae moved up	= 132%
Time interval in weeks	= 3 weeks
∴ Mean % of larvae moved up per week	= 44.0%

TABLE XXVIII

Percentage change index for *L. fusca* at Wearhead between 2/7/67  
and 6/8/67 (35 days or 5 weeks).

Size Group in m.m.	% of sample in each size group		% Difference + or -	% of larvae moving up to next size group.
	Sample A 2/7/67	Sample B 6/8/67		
8.5 - 8.9	-	2	+ 2	(2 - 2)% = 0%
8.0 - 8.4	-	2	+ 2	(4 - 2)% = 2%
7.5 - 7.9	1	-	- 1	(3 + 1)% = 4%
7.0 - 7.4	2	11	+ 9	(12 - 9)% = 3%
6.5 - 6.9	5	10	+ 5	(17 - 5)% = 12%
6.0 - 6.4	4	12	+ 8	(25 - 8)% = 17%
5.5 - 5.9	11	9	- 2	(23 + 2)% = 25%
5.0 - 5.4	16	23	+ 7	(30 - 7)% = 23%
4.5 - 4.9	19	18	- 1	(29 + 1)% = 30%
4.0 - 4.4	16	8	- 8	(21 + 8)% = 29%
3.5 - 3.9	16	4	- 12	(9 + 12)% = 21%
3.0 - 3.4	9	1	- 8	(1 + 8)% = 9%
2.5 - 2.9	1	-	- 1	1% = 1%
Total % of larvae moved up				= 176%
Time interval in weeks				= 5 weeks
∴ Mean % of larvae moved up				= 31.2%

APPENDIX III.

Tables giving data on length of life of fed and starved adult stoneflies and on degree of ovarian maturation in each case.

TABLE XXIX.

Effect of sucrose and water versus water only on survival in A. sulcicollis.

1) Water only. (8males and 13 females = 21 stoneflies used).

<u>Days survival.</u>	<u>Males</u>	<u>Females</u>	<u>All specimens.</u>
1	4	5	9
2	1	2	3
4	1	6	7
9	1	0	1
12	1	0	1

2) Sucrose and water (14 males and 13 females = 27 stoneflies used).

<u>Days survival.</u>	<u>Males</u>	<u>Females</u>	<u>All specimens.</u>
1	3	7	10
2	2	1	3
7	1	0	1
8	1	0	1
10	0	1	1
11	1	0	1
13	2	0	2
14	1	0	1
15	3	1	4
17	0	1	1
19	0	1	1
26	0	1	1

TABLE XXX

Effect of sucrose and water, versus Pleurococcus, versus Water only on length of life of L. fusca.

1) Water only. (77 males and 35 females = 112 stoneflies used).

<u>Days survival</u>	<u>Males.</u>	<u>Females.</u>	<u>All specimens.</u>
1	11	6	17
2	3	0	3
3	6	4	10
4	15	1	16
5	18	6	24
6	5	3	8
7	11	9	20
8	4	3	7
9	3	1	4
10	1	2	3

2) Sucrose and Water. (75 males and 35 females = 110 stoneflies used).

<u>Days survival</u>	<u>Males.</u>	<u>Females.</u>	<u>All specimens.</u>
1	8	6	14
2	7	0	7
3	1	3	4
4	5	3	8
5	4	0	4
7	3	3	6
8	2	2	4
9	2	0	2
10	4	0	4
11	1	1	2
12	3	2	5
13	4	2	6
14	5	5	10
15	5	2	7
16	11	2	13
17	4	1	5
18	2	0	2
19	0	1	1
21	3	0	3
24	1	0	1
27	0	2	2

3) Pleurococcus & Water (44 males + 25 females = 69 stoneflies used).

<u>Days survival</u>	<u>Males.</u>	<u>Females.</u>	<u>All specimens.</u>
1	16	6	22
2	4	6	10
4	3	2	5
5	5	2	7
6	1	1	2
7	3	0	3
8	4	1	5
9	1	2	3
10	2	0	2
11	0	1	1
12	2	1	3
13	1	0	1
14	3	2	5
15	1	0	1
20	0	1	1

TABLE XXXI.

Comparison of survival in days of fed specimens of  
L. fusca at Wearhead and at Witton Park.

1) Wearhead. (27 males + 18 females = 45 stoneflies used).

<u>Days survival</u>	<u>Males.</u>	<u>Females.</u>	<u>All specimens.</u>
1	9	4	13
2	2	5	7
4	3	1	4
5	1	2	3
6	1	0	1
7	2	0	2
8	2	1	3
9	1	1	2
10	1	0	1
11	0	1	1
12	2	0	2
13	1	0	1
14	2	2	4
20	0	1	1

2) Witton Park (20 males + 7 females = 27 stoneflies used)

<u>Days survival</u>	<u>Males</u>	<u>Females</u>	<u>All specimens.</u>
1	7	2	9
2	2	1	3
4	0	1	1
5	4	0	4
6	0	1	1
7	1	0	1
8	2	0	2
9	0	1	1
10	1	0	1
12	0	1	1
14	1	0	1
15	1	0	1

TABLE XXXII.

Showing development of ovaries in fed *Amphinemura sulcicollis*.

DAYS AFTER EMERGENCE	N° OF FLIES	SIZE OF LARGEST EGGS μ x μ	RELATIVE STATE OF OVARIES
0	6	a 168 x 140	Poorly developed. Abdomen half filled
		b 168 x 140	Fairly well developed. More than half length of abdomen
		c 168 x 140	Poorly developed. Abdomen half filled.
		d 168 x 140	Poorly developed. Abdomen half filled.
		e 173 x 160	Poorly developed. Abdomen half filled
		f 200 x 186	Well developed. Abdomen almost full.
2	8	a 200 x 165	Well developed. Abdomen almost full.
		b 186 x 160	Poorly developed. Abdomen half filled.
		c 200 x 200	Well developed. Abdomen almost full.
		d 200 x 200	Very well developed. Ovary extends into thorax
		e 200 x 200	Well developed. Abdomen almost full.
		f 200 x 200	Well developed. Abdomen almost full.
		g 160 x 160	Poorly developed. Abdomen nearly half full.
		h 200 x 200	Well developed. Abdomen almost full.
4	10	a 200 x 187	Well developed. Abdomen almost full.
		b 200 x 213	Very well developed. Ovary extends into thorax.
		c 213 x 200	Very well developed. Ovary extends into thorax.
		d 200 x 187	Well developed. Abdomen almost full.
		e 200 x 200	Well developed. Abdomen almost full
		f 200 x 200	Well developed. Abdomen almost full
		g 200 x 200	Well developed. Abdomen almost full.
		h 200 x 200	Well developed. Abdomen almost full
		i 200 x 200	Well developed. Abdomen almost full.
		j 200 x 200	Well developed. Abdomen almost full.
5	16	a 133 x 120	Poorly developed. Abdomen less than half full
		b 200 x 200	Well developed. Abdomen almost full
		c 213 x 200	Well developed. Abdomen almost full
		d 200 x 200	Ovary reduced in size. Abdomen telescoped. Only few eggs.
		e 213 x 200	Well developed. Abdomen almost full.
		f 213 x 200	Well developed. Abdomen almost full.
		g 200 x 200	Well developed. Abdomen almost full.
		h 213 x 200	Well developed. Abdomen almost full
		i 213 x 200	Well developed. Abdomen almost full
		j 200 x 187	Well developed. Abdomen almost full
		k 213 x 200	Well developed. Abdomen almost full
		l 213 x 200	Well developed. Abdomen almost full
		m 213 x 200	Well developed. Abdomen almost full
		n 213 x 200	Well developed. Abdomen almost full
		o 213 x 200	Well developed. Abdomen almost full
		p 226 x 213	Well developed. Abdomen almost full.
6	18	a 213 x 200	Very well developed. Ovary extends into thorax
		b 200 x 200	Well developed. Abdomen almost full
		c 200 x 200	Abdomen almost empty. Only few ripe eggs left
		d 200 x 200	Abdomen almost empty. Only few ripe eggs left.
		e 200 x 200	Abdomen almost empty. Only few ripe eggs left.
		f 200 x 213	Well developed. Abdomen almost full
		g 200 x 200	Abdomen almost empty. Only few ripe eggs left.
		h 200 x 200	Abdomen almost empty. Only few ripe eggs left.
		i 200 x 200	Abdomen almost empty. Only few ripe eggs left.
		j 213 x 200	Well developed. Abdomen almost full
		k 200 x 200	Well developed. Abdomen almost full.
		l 213 x 200	Well developed. Abdomen almost full
		m 200 x 200	Abdomen telescoped. Only few ripe eggs left.
		n 200 x 200	Abdomen telescoped. Only few ripe eggs left.
		o 200 x 200	Very well developed. Ovary extends into thorax
		p 200 x 200	Abdomen telescoped. Only few ripe eggs left.
		q 200 x 200	Abdomen telescoped. Only few ripe eggs left
		r 200 x 200	Well developed. Abdomen almost full.
7	4	a 200 x 200	Well developed. Abdomen almost full
		b 213 x 200	Very well developed. Ovary extends into thorax
		c 213 x 200	Very well developed. Ovary extends into thorax
		d 200 x 200	Well developed. Abdomen almost full.

TABLE XXXIII.

Showing development of the ovaries in unfed specimens of

Leucra fusca.

DAYS AFTER EMERGENCE	N <sup>o</sup> OF FLIES	SIZE OF LARGEST EGGS. (μ)	RELATIVE STATE OF OVARIES.
1	10	a 140 x 112	Poorly developed. Less than $\frac{1}{4}$ length of abdomen.
		b 168 x 140	Poorly developed. Less than $\frac{1}{2}$ length of abdomen
		c 140 x 127	Poorly developed. Less than $\frac{1}{2}$ length of abdomen
		d 140 x 127	Poorly developed. Less than $\frac{1}{2}$ length of abdomen.
		e 112 x 112	Very poorly developed. Ovary less than $\frac{1}{4}$ length of abdomen
		f 127 x 112	Poorly developed. Less than $\frac{1}{2}$ length of abdomen
		g 127 x 112	Poorly developed. Less than $\frac{1}{2}$ length of abdomen
		h 140 x 127	Poorly developed. Less than $\frac{1}{2}$ length of abdomen
		i 140 x 127	Poorly developed. Less than $\frac{1}{2}$ length of abdomen
		j 140 x 127	Poorly developed. Less than $\frac{1}{2}$ length of abdomen.
3	4	a 140 x 127	Poorly developed. Less than $\frac{1}{2}$ length of abdomen
		b 84 x 84	Very poorly developed. Less than $\frac{1}{4}$ length of abdomen
		c None found	Abdomen empty. Eggs laid in tube perhaps.
		d None found.	Abdomen empty. Eggs laid in tube perhaps
4	1	a 140 x 127	Fairly well developed. Ovary fills abdomen.
5	6	a 168 x 140	Well developed. Ovary fills abdomen
		b 168 x 140	Well developed. Ovary fills abdomen.
		c 84 x 56	Very poorly developed. Less than $\frac{1}{4}$ length of abdomen
		d 84 x 56	Very poorly developed. Less than $\frac{1}{4}$ length of abdomen
		e 84 x 56	Very poorly developed. Less than $\frac{1}{4}$ length of abdomen
		f 84 x 56	Very poorly developed. Less than $\frac{1}{4}$ length of abdomen
6	3	a 168 x 140	Well developed. Ovary fills abdomen
		b 168 x 154	Well developed. Ovary fills abdomen.
		c None found.	Abdomen empty. Eggs laid in tube perhaps
7	9	a 196 x 182	Very well developed. Ovary fills abdomen.
		b 196 x 182	Very well developed. Ovary fills abdomen
		c 45 x 45	Very poorly developed. Ovary less than $\frac{1}{4}$ of abdomen
		d 84 x 56	Very poorly developed. Ovary less than $\frac{1}{4}$ of abdomen
		e None found.	Abdomen empty. Eggs laid in specimen tube
		f 45 x 45	Very poorly developed. Ovary less than $\frac{1}{4}$ of abdomen
		g 45 x 45	Very poorly developed. Ovary less than $\frac{1}{4}$ of abdomen
		h 196 x 182	Well developed. Abdomen almost filled
		i 196 x 182	Well developed. Abdomen almost filled.
8	3	a 168 x 168	Fairly well developed. Abdomen $\frac{1}{2}$ filled.
		b 168 x 168	Fairly well developed. Abdomen $\frac{1}{2}$ filled
		c 140 x 140	Fairly well developed. Abdomen almost full.
9	1	a 168 x 168	Well developed. Abdomen filled
10	2	a 112 x 98	Fairly well developed. Abdomen almost full
		b 140 x 140	Fairly well developed. Abdomen almost full.

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TABLE XXXIV.

Showing development of the ovaries in fed specimens of *Leucra fusca*.

DAYS AFTER EMERGENCE	N <sup>o</sup> OF FLIES	SIZE OF LARGEST EGGS.	RELATIVE STATE OF OVARIES
1	12	a 56 $\mu$ x 56 $\mu$	Poorly developed. Ovary less than $\frac{1}{2}$ length of abdomen
		b 56 $\mu$ x 56 $\mu$	Poorly developed. Ovary less than $\frac{1}{2}$ length of abdomen.
		c 56 $\mu$ x 56 $\mu$	Poorly developed. Ovary less than $\frac{1}{2}$ length of abdomen.
		d 56 $\mu$ x 56 $\mu$	Poorly developed. Ovary less than $\frac{1}{2}$ length of abdomen.
		e 140 $\mu$ x 140 $\mu$	Well developed. Ovary filled abdomen.
		f 56 $\mu$ x 56 $\mu$	Poorly developed. Ovary less than $\frac{1}{2}$ length of abdomen.
		g 84 $\mu$ x 84 $\mu$	Poorly developed. Ovary fills $\frac{1}{2}$ of abdomen.
		h 140 $\mu$ x 140 $\mu$	Well developed. Ovary filled abdomen.
		i 168 $\mu$ x 140 $\mu$	Well developed. Ovary filled abdomen.
		j 196 $\mu$ x 168 $\mu$	Well developed. Ovary filled abdomen.
		k 168 $\mu$ x 140 $\mu$	Well developed. Ovary filled abdomen.
		l 84 $\mu$ x 84 $\mu$	Poorly developed. Ovary less than $\frac{1}{2}$ length of abdomen.
2	7	a 140 $\mu$ x 140 $\mu$	Well developed. Ovary filled abdomen
		b None Found	Laid in tube. Abdomen empty
		c None Found	Laid in tube. Abdomen empty
		d 168 $\mu$ x 140 $\mu$	Well developed. Ovary filled abdomen.
		e None Found	Laid in tube. Abdomen empty
		f None Found	Laid in tube. Abdomen empty
		g 168 $\mu$ x 140 $\mu$	Well developed. Ovary filled abdomen.
3	3	a 168 $\mu$ x 140 $\mu$	Ovary well developed. Eggs being laid.
		b 182 $\mu$ x 154 $\mu$	Ovary well developed. Eggs being laid
		c 168 $\mu$ x 140 $\mu$	Ovary well developed. Eggs being laid.
4	5	a 168 $\mu$ x 140 $\mu$	Ovary well developed.
		b None Found	Laid in tube. Abdomen empty
		c 154 $\mu$ x 140 $\mu$	Ovary well developed
		d 168 $\mu$ x 140 $\mu$	Ovary well developed
		e 196 $\mu$ x 154 $\mu$	Ovary well developed
5	2	a 196 $\mu$ x 168 $\mu$	Ovary well developed. Egg mass attached.
		b 154 $\mu$ x 140 $\mu$	Ovary well developed
6	1	a 168 $\mu$ x 140 $\mu$	Ovary well developed
7	3	a 154 $\mu$ x 140 $\mu$	Ovary well developed
		b None Found	Laid in tube. Abdomen empty
		c 168 $\mu$ x 140 $\mu$	Ovary well developed.
8	3	a 196 $\mu$ x 168 $\mu$	Ovary very well developed
		b 196 $\mu$ x 168 $\mu$	Ovary well developed.
		c None Found	Laid in tube
9	2	a None Found	Laid in tube
		b 154 $\mu$ x 140 $\mu$	Ovary well developed.
11	2	a 168 $\mu$ x 140 $\mu$	Ovary well developed
		b 182 $\mu$ x 154 $\mu$	Ovary well developed
12	3	a None Found	Laid in tube
		b 196 $\mu$ x 168 $\mu$	Ovary very well developed
		c 182 $\mu$ x 154 $\mu$	Only few eggs left. Laid in tube
13	2	a 168 $\mu$ x 140 $\mu$	Only few eggs left. Laid in tube
		b 168 $\mu$ x 140 $\mu$	Only few eggs left. Laid in tube
14	9	a None Found	Laid in tube. Abdomen empty
		b None Found	Laid in tube. Abdomen empty
		c None Found	Laid in tube. Abdomen empty
		d None Found	Laid in tube. Abdomen empty
		e 168 $\mu$ x 140 $\mu$	Only few eggs left. Laid in tube
		f None Found	Laid in tube. Abdomen empty
		g None Found	Laid in tube. Abdomen empty
		h 168 $\mu$ x 140 $\mu$	Only few eggs left. Abdomen empty
		i None Found	Laid in tube. Abdomen empty.
15	2	a None Found	Laid in tube. Abdomen empty
		b None Found	Laid in tube. Abdomen empty
16	2	a None Found	Laid in tube. Abdomen empty
		b None Found	Laid in tube. Abdomen empty
17	1	a 168 $\mu$ x 140 $\mu$	Only few eggs left. Laid in tube
19	1	a None Found	Laid in tube
20	1	a 168 $\mu$ x 140 $\mu$	Only few eggs left. Laid in tube
27	1	a None Found	Laid in tube