Biological studies on some moorland short-palped craneflies (Tipulidae, Diptera)

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Abstract

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Moorland Tipulidae (in particular, short-palped craneflies with special reference to *Tricyphona immaculata*) have been studied on the upper Teesdale moor district of Chapel Fell (Ref. NY 863349) between September 1992 and August 1993. The lifecycles of a number of short and long-palped craneflies were recorded using a series of pit-fall traps located at fourteen sites previously selected to represent the range of vegetation present at Chapel Fell summit, 630m.

Spiracular disc size was measured in five small-palped species and frequency distribution histograms are given showing the presence of four instars in each.

Using pit-fall traps *Tricyphona immaculata* was found to emerge as an adult both in May and September. Through the collection of peat from the field and subsequent extraction of larvae *Tricyphona immaculata* was found to exist in two groups, one beginning its lifecycle in the spring, the other in the autumn. Laboratory experiments on eggs of *Tricyphona immaculata* revealed that eggs do not respond differently to long and short-day photoperiod regimes and that egg development was positively related to temperature.

Field experiments indicated species-site habitat associations. Larval densities for short-palped species are given along with adult-site occurrence for both long and short-palped species.

The two different habitats of *Sphagnum* and *Nardus* are shown to maintain different densities of three species of short-palped cranefly.

Annual variation in cranefly numbers is discussed in relation to the summer drought of 1992 after which most species showed a decline in number. Egg development in *Tipula czezeki* was found not to be influenced by short and long-day photoperiod regimes and this finding is compared to the hatching distribution found in *Tipula pagana* eggs when subjected to similar conditions. A comparative assessment on larval growth showed that the relationship of breadth and length differs between the species studied. *Molophilus ater* and *Ormosia pseudosimilis* adults are also compared physically.

Acknowledgements

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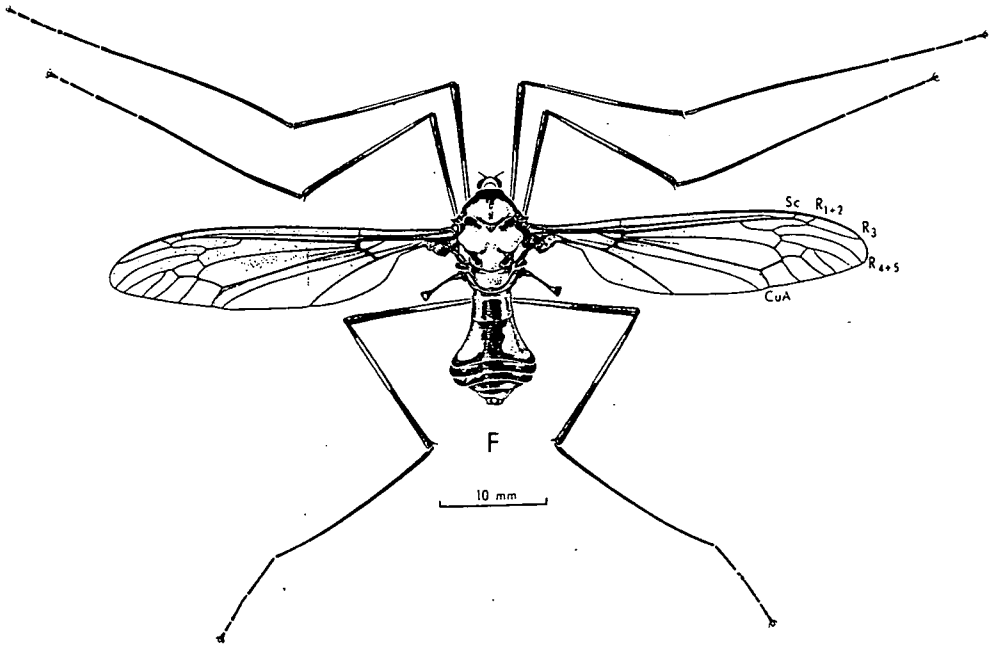
Dedicated to Ania, moja kochana zona.



Biological studies on some moorland short-palped craneflies (Tipulidae, Diptera)

By

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... being a thesis presented in candidature for the degree of Master of Science in the University of Durham, 1995.

Contents

Declaration

1) Chapter 2 The study area and sampling sites by John Coulson, 1991, Independant report.
2) Figure 3.3.2a Wet funnel extraction apparatus by Smith, 1973.
3) Figure 1, Chapter 7 The distribution of hatching of *Tipula pagana* eggs kept at 10°C under (a) light-dark; 18:6 and (b) light-dark; 6:18. From Butterfield and Coulson, 1988.

Craneflies belong to the family Tipulidae, of the insect order Diptera. Their main characteristics for identification are a V-like suture marking on their dorsal thorax, their relatively long and straight second anal vein and their long legs, hence their other common name, daddy-long-legs.

The family Tipulidae is divided into three subfamilies. The Tipulinae represent the long-palped craneflies, while the Cylindrotominae and Limoninae comprise the short-palped craneflies (Coe 1950).

The British Tipulidae comprise over 300 species and a few studies have catalogued fauna in accordance with habitat association. (Barnes 1925, Coulson 1959, 1962, Crisp and Lloyd 1954, Freeman 1968).

The description and keys to the larvae is given in Brindle (1960, 1967) and the adults in Coe (1950). I have included diagrams of different larvae perspectives to clarify identification for future work on the species studied here. See figures 3.3.3a, 4a, 4b and 4c.

Ecological investigations on craneflies have tended to concentrate on those species causing injury to pasture grasses and crops. Two notorious cranefly pests in Europe are *Tipula paludosa* Meigen and *Tipula oleracea* L. and Barnes (1925, 1937) has investigated the distribution and bionomics of *Tipula paludosa* whilst other biological aspects of *T. paludosa* and *T. oleracea* have been described by Milne et al. (1958, 1965) and Laughlin (1958, 1960, 1967).

Freeman (1964, 1967, 1968) has studied a range of tipulid species in the south of England and Butterfield (1976a and b), Coulson (1956, 1959, 1962), Hadley (1966, 1969, 1971a and b), Horobin (1971) and Coulson *et al.* (1976) have conducted work on the more common species pertaining to the Northern Pennines Moorhouse National Nature Reserve.

Prior to this work the short-palped group, although numerically larger than that of the Tipulinae, has received scant attention from ecologists. Cuthbertson (1926) described the behaviour of swarming and the work of Crisp and Lloyd (1954) identified the species habitat associations found in a patch of woodland mud.

Coulson (1959) has summarised the seasonal distribution of both long and short palped craneflies on the Moor House Nature Reserve. The work of Hadley (1969, 1971a and b), Horobin (1971) and Coulson *et al.* (1976) have all focused on the short-palped cranefly, *Molophilus ater* Meigen detailing the species biology comprehensively. *M. ater* is a small, sub-apterous (non-flying, vestigial wing) cranefly which has an adult emergence lasting roughly three weeks starting around mid-May. Hadley (1966, 1969, 1971a and b) described the life cycle, emergence biology and growth rates of the species. He also identified that most of the mortality occurred in the egg and the first instar (though to a lesser degree, being as high as 88% and 92%). As shown in section 6, cranefly populations fluctuate considerably from season to season and recovery from drought may not be immediate.

The ability of craneflies to synchronise their lifecycles with season, under different temperature regimes due to differences in site altitude, led Horobin (1971) to investigate and describe the effects of altitude on *M. ater*. By recording the average temperature at each altitude site (ranging from 430 to 820m) by using the sucrose inversion technique and observing the emergence pattern of the species at each site, Horobin postulated a temperature threshold for pupation. This temperature (around 5-6°C), below which pupation cannot occur, is thought to be responsible for both the synchronising of emergence and the delay in emergence at higher altitudes (Horobin 1971). This situation has been contrasted with that of *Tipula pagana* Meigen in that *T. pagana* may require a low temperature for pupation to occur, i.e. a low maximum temperature threshold below which the temperature must fall. It has been suggested that these temperature differences are linked with the enzyme process involved in the manufacture of pupation inhibiting hormone (Horobin 1971).

Coulson *et al.* (1976) showed how *M. ater* and *Tipula subnodicornis* Zett. maintain their lifecycles by relating the development of the animal to its existence altitude. The rate of larval growth in *M. ater* appears to be unaffected by field temperatures with only the immediate pre-pupal and pupal stages showing temperature dependency. In the autumn,

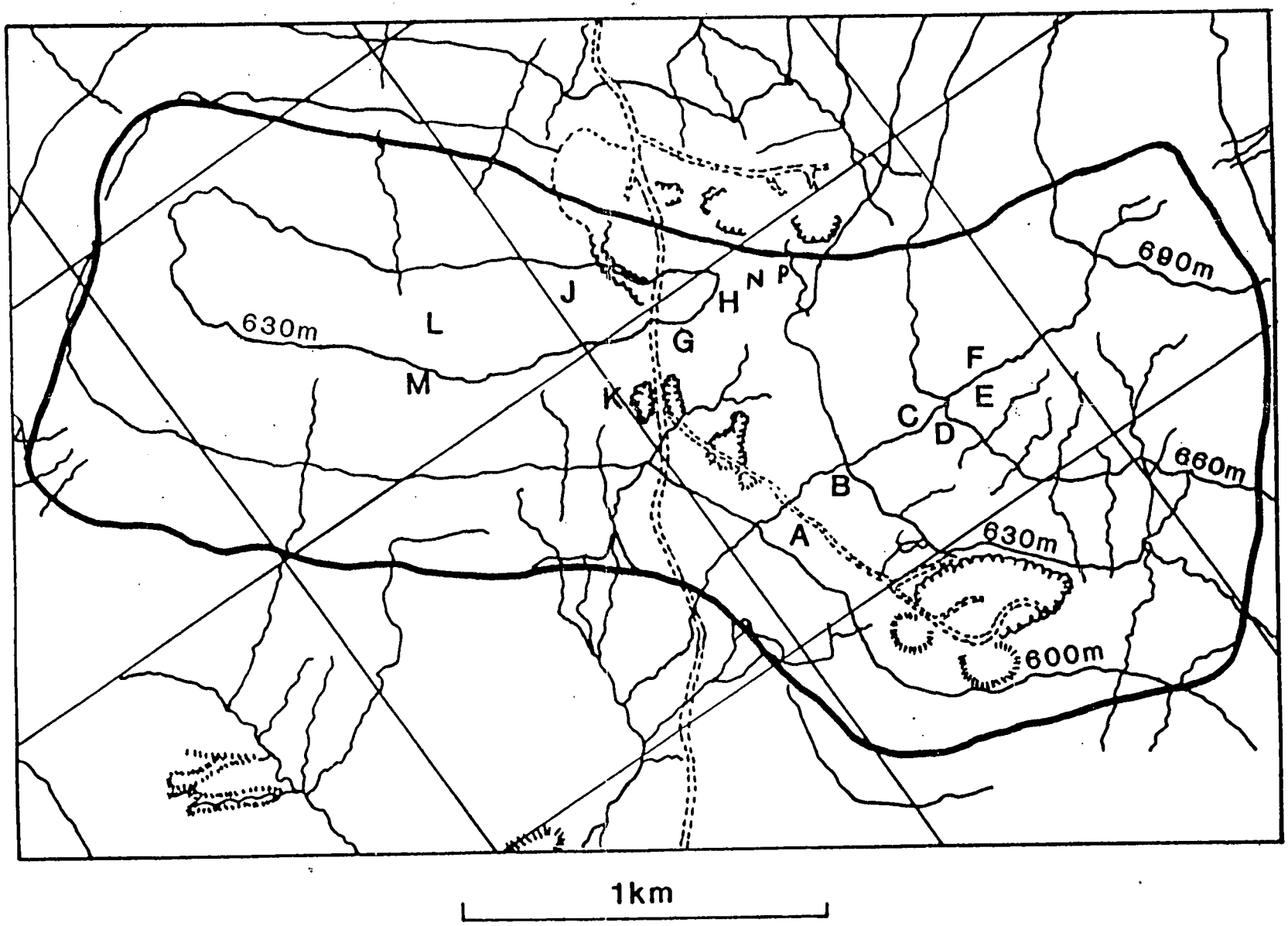
a reduced rate of development is observed in those larvae that have reached full growth. Further development is inhibited or slowed down by the short day length and this inhibition is thought to promote synchrony in development between larvae at varying stages of growth.

The development rates of *Tipula subnodicornis* egg, larvae and pupae were examined further by Butterfield (1976b). Again the annual lifecycle is maintained over a wide range of latitude and altitude by a change in the relationship between the rate of development and temperature during the larval stage. Butterfield proposed that during the larval development of *T. subnodicornis,* the relationship between development and temperature changes with a fall in the optimum temperature for development. A continuation of larval growth at the northern end of the species distribution may be allowed therefore whilst those members of the population further south are restricted in their rate of development. Thus a wider geographical range is thought to be possible.

The present study, involving a series of ecological investigations on a selected number of craneflies, was conducted on the upper Teesdale moorland district of Chapel Fell (Ref NY 863349). The work examines the lifecycle of a number of short-palped craneflies. Particular attention has been focused on *Tricyphona immaculata* Meigen, because this species is almost unique in that, unlike most other species of cranefly, *T. immaculata* has two separate adult emergences per annum. This phenomenon, previously noticed by John Coulson from collected pitfall trap data (pers. comm.), has been observed to exist in the well studied Northern Pennine Moorhouse National Nature Reserve and also on the Pennine summit of Chapel Fell.

As a means of comparing the life history of *T. immaculata* to other similarly sized short-palped craneflies, I have investigated other species in an attempt to characterise the biological differences of *T. immaculata*. Observations made under field and laboratory conditions have been made and these findings are now presented and discussed.

Map 1. Chapel Fell study area



2 The study area and sampling sites

2.1 Location and physiography

Chapel Fell (also known as Langdon Common (Ref NY 863349-map 1)) is on the watershed between the drainage areas of the River Tees and the River Wear. The area used in this study is bisected by the 630m contour. It is an area of Pennine moorland lying approximately 10km east of the Moorhouse National Nature Reserve.

The whole area is above the treeline with the summit just over 700 m. The area is exposed to wind and is subject to an appreciable amount of rain. The climate, like that of Moorhouse, is similar to that of southern Iceland at sea-level (Manley 1936, 1943). The annual rainfall is three times that of Durham City but the duration of the rainfall is almost ten times greater because much of the extra precipitation falls as drizzle (Moorhouse weather station.).

Table 2.1 Estimated average monthly rainfall for the Northern Pennines. Based on six years records; monthly totals may be up to 10% in error.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ins. and fractions	6.5	6	5.75	4	3.75	4	6	7	4.5	7.5	6.5	8.5

From Manley 1943.

As a consequence, there is frequent cloud cover and a reduced amount of solar radiation reaches the ground (Manley 1943).

In most years, the peat is waterlogged in at least 10 months of the year, but exceptionally a long, warm, dry summer, such as that of 1989, occurs and greatly affects the invertebrate populations.

2.2 The study sites

Twelve sites (A-M excluding I), previously chosen to represent the diversity of vegetation were used to portray species habitat associations. Having gained this information, sites showing greatest species densities were concentrated on and used as a

reliable source of material. Two extra sites, N and P, were added in 1992 to provide additional site coverage.

The vegetation is *Calluneto-Eriophoretum* (McVean & Ratcliffe 1962) and is restricted to blanket bog, but in many places it is replaced by a more extensive *Eriophorum vaginatum*. In places, erosion of the blanket bog has led to the formation of peat hags, areas of bare peat and islands of vegetation in places where erosion has not removed the primary peat. The blanket bog depth is dissected by streams and these are edged with alluvial deposits which contain a high mineral content. These areas support a grassland dominated by *Nardus stricta* and *Festuca ovina*. Grasslands also occur on areas where peat has been prevented from accumulating or has been subject to drift of soils or bed-rock. Human activity, arising from quarrying or road building, has also produced small grassland areas. Areas of shallow peat or with peaty gleys are often dominated by *Juncus squarrosus* with tufts of *Festuca ovina* and *Deschampsia flexuosa* forming the *Juncetum squarrosi* sub-alpium community (Eddy, Welch & Rawes 1968).

The area is managed as a grouse moor by the Raby Estate. Sheep graze extensively on Chapel Fell and they show a preference for the areas with grasses rather than those of heather.

2.3 Description of sites

Site A. Organic content of soil 27%

Dominant plants: Grasses and *Juncus squarrosus*.

This site is on a well drained mineral soil where the grasses *Agrostis tenuis*, *Anthoxanthum odoratum*, *Deschampsia flexuosa* and *Festuca ovina* are common. *Juncus squarrosus* has the highest single species cover (25%) and the herb *Galium saxatile* is also abundant.

Site B. Organic content of soil 99%

Dominant plant: *Eriophorum vaginatum*.

A deep peat area dominated by cotton grass *Eriophorum vaginatum*, with the grass *Deschampsia flexuosa* and bilberry *Vaccinium myrtillus* well represented.

Site C. Organic content of soil 33%

Dominant plants: Grasses.

A small mineral alluvial site forming a narrow strip about 5m wide adjacent to a stream. Tussocks of *Nardus stricta* and *Deschamsia flexuosa* dominate with *Anthoxanthum odoratum* and *Festuca ovina* also attaining a high cover. Small clumps of *Juncus effusus* are present nearby.

Site D. Organic content of soil 89%

Dominant plants: *Eriophorum vaginatum*, *Deschamsia flexuosa*.

A shallow peaty site with hummocks of *Vaccinium myrtillus*, *Empetrum nigrum* and *Vaccinium vitis-idaea* interspersed with *Eriophorum vaginatum*, *Deschamsia flexuosa* and small amount of *Eriophorum vaginatum*, *Deschamsia flexuosa* and small amounts of *Eriophorum angustifolium*.

Site E. Organic content of soil 97%

Dominant plant: *Eriophorum vaginatum*.

A typical blanket bog area on an almost level site dominated by *Eriophorum vaginatum* and with heather *Calluna vulgaris* attaining a high cover (30%).

Site F. Organic content of soil 44%

Dominant plant: *Nardus stricta*.

An alluvial grassland site forming a strip 5m wide alongside a stream and adjacent to blanket bog. The organic content is intermediate between that of sites A and C and the peat sites e.g. sites B, G, and H. The pit fall traps were within an area dominated by *Nardus stricta*, Within a few metres of the traps and away from the stream, there is a transition to a narrow strip of *Nardus* grassland with *Vaccinium myrtillus*, *Calluna vulgaris* and *Eriophorum vaginatum* co-dominant before reaching a *Calluna* dominated community on the blanket peat.

Site G. Organic content of soil 96%

Dominant plants: *Eriophorum vaginatum*, *Calluna vulgaris*.

A blanket peat site where *Eriophorum* and ericaceous species are abundant and the grass *Deschampsia flexuosa* attains a moderate cover (21%).

Site H. Organic content of soil 97%

Dominant plant: *Calluna vulgaris*.

A level site where the peat has eroded to form hags and islands of vegetation. Heather *Calluna vulgaris* is the dominant plant, although the two species of cotton grasses, *Eriophorum vaginatum* and *E. angustifolium* jointly have a similar cover to the *Calluna*. *Erica tetralix* is abundant (12% cover).

Site J. Organic content of soil 99%

Dominant plant: *Eriophorum vaginatum*

A peat site with *Eriophorum vaginatum* dominant and *Calluna vulgaris* sub-dominant. The *Eriophorum vaginatum* hummocks alternate with wetter, sparsely vegetated hollows which contain *E. angustifolium* and bog asphodel *Narthecium ossifragum*. There is a small amount of *Vaccinium myrtillus* towards one end of the line of traps.

Site K. Organic content of soil 99%

Dominant plants: *Eriophorum vaginatum* and *Deschampsia flexuosa*.

A peat site, similar to site B, where *Eriophorum vaginatum* and *Deschampsia flexuosa* are co-dominant and *Eriophorum angustifolium* is abundant (19% cover)

Site L. Organic content of soil 61%

Dominant plants: *Festuca ovina*, *Nardus stricta*.

A grassland site with a relatively high organic content. Tussocks of *Nardus stricta* alternate with *Festuca ovina* and other grasses. *Galium saxatile* (18%) and *Juncus squarrosus* (13%) are frequent.

Site M. Organic content of soil 98%

Dominant plant: *Juncus squarrosus*.

A peat site with a high cover (48%) of *Juncus squarrosus* interspersed with *Deschampsia flexuosa* and smaller quantities of *Festuca ovina* and *Eriophorum vaginatum*.

Sites N & P

These sites are similar to site H.

2.4 Climate 1989-1992

In the north of England, the late spring and summer of both 1989 and 1990 were warm with an above average temperature, whilst the 1988-89 and 1989-90 winters were relatively mild. Both years had below average spring and summer rainfall in Durham but in the Pennines the two years differed in that in 1989 there was little rainfall from mid-May until August whereas in 1990, two weather fronts caused appreciable rainfall in the western parts of County Durham. As a result, 1990, unlike 1989, did not have the long period (over 3 months), where evaporation of water from the soil exceeded rainfall. Data collected at Moorhouse from 1952 to 1980, at a similar altitude (600m) to the Chapel Fell site, showed only two of 29 years when similar conditions occurred. Above average summer temperatures in the uplands are usually associated with low rainfall, since high pressure systems are associated with both events. Drying out of blanket bog is an infrequent occurrence. A high watertable throughout the year is a characteristic of blanket bog conditions and it is evident that the 1989 condition were exceptional, representing an event which occurred only about once in 15 years.

The latter part of 1990 was characterised by at least average rainfall in most months and the peat soils at Chapel Fell remained very wet until May and early June when some drying out occurred. Heavy rain in the second half of June restored the wet soil conditions and only slight drying out occurred in late July and August. (Coulson pers. comm.)

2.5 Water content of the soil

Five samples of soil, 0-5cm deep, were taken at each site in the last week of July in 1989, 1990, 1991. They were dried at 80°C to determine the water content and the results are given in Table 2.5 as the ratio of water to the dry content. The values obtained in 1989 (average 3.9 for peat site) are comparable with those from Moor House (10km away) in 1956 (average 3.5).

Table 2.5 The water content of soil samples (average from 5 soil cores) taken 0-5cm deep on each of 12 of the 14 study sites in July 1989-1991. The results are expressed as water/dry weight. Note sites A, C, F, and L are mineral soils, the remainder peat soils. In the case of peat soils the dry weight is almost all organic matierial.

Date	Site													
	A	B	C	D	E	F	G	H	J	K	L	M	N	P
25.7.89	1.6	5.6	0.6	4.6	4.0	0.7	4.1	2.4	4.6	4.6	1.0	2.2	--	--
23.7.90	2.4	7.2	2.0	6.8	5.1	2.1	6.4	5.1	7.4	6.9	1.4	4.9	--	--
24.7.91	0.7	6.5	0.9	5.2	5.8	1.3	5.3	4.9	5.3	6.2	1.6	4.2	--	--

Chapter 3

The lifecycle of *Tricyphona immaculata* Meigen.

3.1.1 Introduction

Prior to this study, it had been observed that *Tricyphona immaculata* had an emergence pattern unlike that of most other craneflies in that it exhibited two separate periods of emergence in the year. The first emergence occurred in the spring between mid-May and ended within four weeks in mid-June. The second emergence occurred after a gap of about 3 months, with adults appearing in mid-September (Coulson 1959).

The first objective was to establish the exact emergence pattern of *Tricyphona immaculata* to confirm that adults emerge on two separate occasions. Once established a comparative approach could then be used to identify why *Tricyphona immaculata* emerges only in May/June and September when other similar sized short-palped craneflies such as *Limnophila meigen,* Verr. and *Erioptera trivialis* Mg. have a much longer duration of emergence (starting approximately the same time as *Tricyphona immaculata,* towards the end of May) and make full use of the warmer and relatively dryer months of summer. It was thought that the avoidance of summer emergence by *Tricyphona immaculata* might be beneficial to the species. This was based on the idea that by concentrating the number of adults into two emergences, outside the unfavourable desiccating time span of summer, the percentage of successful matings would be optimised.

Two hypotheses were formulated to explain biannual emergence in *Tricyphona immaculata.*

1) Either there is one population of *Tricyphona immaculata* going through two generations a year, one passing rapidly through instar development over the 2.5 months in summer and then the other going through a much slower development sequence from egg to adult over the autumn and winter months.

2) Or there are two annual overlapping populations, one emerging in the spring and one emerging in the autumn and each taking twelve months to complete its development.

Possible developmental rates for each of the proposed predicaments are shown in the Figures 3.1a and 3.1b for the two population condition and the one population case respectively.

The essential questions are therefore;

a) Is biannual emergence caused by two populations or by one?

b) How long are the developmental stages?

To answer these two questions, the length of time that the lifecycle took and the span of time of each lifecycle stage had to be detected.

3.2 Studies On The Egg Stage.

3.2.1 Introduction.

The consideration given to the ecological problem of maintaining a lifecycle over a wide temperature range has provoked much work. Mani (1962), Jordan (1962), Pearsall (1953), Reay (1964), Welch (1965) and Whittaker (1965, 1971) have all produced information relating the ecology of various high altitude species to their occurrence altitudes. However the factors behind the control of emergence synchronisation have been given less attention. Previous studies on cranefly eggs, such as that by Butterfield and Coulson (1988) have concentrated on the response of eggs to the environmental aspects of temperature and photoperiod. Such work has illustrated that even at this early stage of the lifecycle, a high degree of development control is maintained and that even when the species covers a wide geographical range individual adaptations exist to produce a synchronous emergence.

Possible Rates Of Development Between January And December.

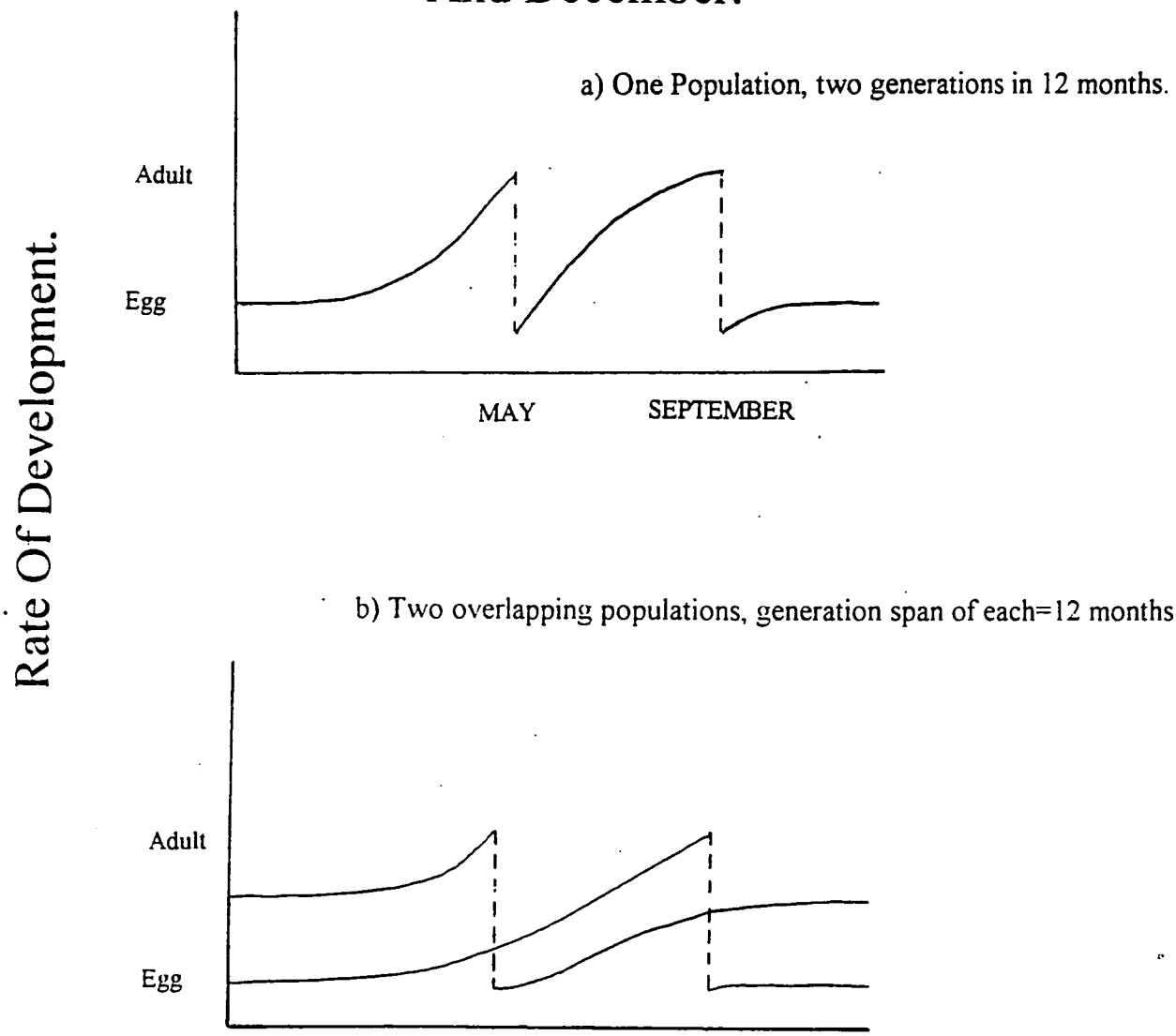


Figure 3.1a + b. Hypothesised development rates for *T. immaculata* larvae.

The study by Butterfield and Coulson (1988) on the rate of development in the over wintering eggs of *Tipula pagana* illustrated that eggs of this univoltine species possess the ability to control their development rate through a diapause. Long day length (light-dark 18:6) at 10°C both increased development rate and increased the degree of hatching synchrony (last few days before hatching only). A reduction in temperature to 5 or 1°C also increased hatching synchrony when the eggs were returned to 10°C.

Eggs that are laid by the autumn emerging adults of *Tipula pagana* take far longer to develop at 10°C than those of spring and summer emerging craneflies. The development duration variance of these eggs is also higher. The variability over the emergence dates is suggested by Tauber *et al.* (1986) to be an adaptation against adverse conditions during the egg and first instar stage. It appears therefore that eggs of *Tipula pagana* are adapted to prolong their development, with short day length extending the delay.

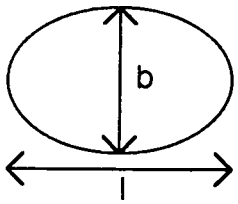
Egg diapause has been reported by Pritchard (1983) to occur in three other species with over wintering eggs; *Tipula czizeki* (deJong), *Tipula staegeri* (Neilson) and *Tipula luteipennis* (Meigen). Although Laughlin (1967) and Freeman (1967) offer no supporting evidence to support the contention, my own studies in section 7 clarifies the situation with *Tipula czizeki*.

The purpose of the following study was to assess the effect of temperature and photoperiod on the egg development rate. This laboratory experiment could then be applied to the field observations.

3.2.2 Egg Biometrics

Egg Volume

Appropriate measurements were taken of *Tricyphona immaculata* eggs to enable estimation of egg volume and a comparison with egg dimensions from another short-palped cranefly *Molophilus ater*, Meigen. Ten eggs, chosen at random, were measured as below:



Volume=4/3* π*l/2*b^2/4

Table 3.2.2.a

Volume of ten eggs of *Tricyphona immaculata* taken from 3 females

Length (mm)	Breadth (mm)	Volume (mm^3)
0.51	0.26	0.018
0.51	0.23	0.014
0.46	0.25	0.015
0.51	0.23	0.014
0.48	0.21	0.011
0.47	0.25	0.015
0.47	0.21	0.010
0.43	0.21	0.009
0.48	0.24	0.014
0.51	0.21	0.012

Volume = 1.33*3.14 *length/2 *$breadth^2$/4 mm^3

Volume $\bar{X}$ =0.0138mm^3.

S.D. =0.00239mm^3

The mean volume of egg with S.D. is 0.0138mm $\pm$ 0.0024mm.

Hadley (1966) found the linear dimension of *Molophilus ater* eggs to be; mean length 0.221mm $\pm$ 0.9mm, mean breadth 0.134mm $\pm$ 0.2mm. The calculated mean volume for *Molophilus ater* eggs is therefore 0.00117mm^3. *Tricyphona immaculata* eggs are therefore 11.8 times as large as those of *Molophilus ater.*

3.2.3 Egg Development.

a) The Effect Of Temperature.

Introduction.

The purpose of this experiment was to determine whether or not the eggs of *Tricyphona immaculata* have a development rate which is directly related to the temperature they are subject to in their immediate environment. This would identify the time spent in the egg stage of development.

Culture methods.

Adults of *Tricyphona immaculata* were taken from the field site of Chapel Fell and immediately paired and transferred back to the department in a small screw cap container containing damp filter paper. All females were given a period of 24h for coupling, fertilisation and oviposition of eggs at a temperature of 10°C on a L:D; 18:6 photoperiod regime.

The filter papers containing the eggs were then removed, enclosed within Petri dishes (8.8cm by 1.3cm in depth) and kept in a series of constant temperature cabinets at 5°, 8°, 10°, 15°, 20° and 25°C until the eggs hatched. The eggs were inspected daily. At each temperature both the number of larvae hatched and the date of emergence were noted.
Eggs from adults emerging in the spring were all maintained on a long photoperiod regime of L:D; 18:6. Eggs from autumn adults where then subjected to two photoperiod regimes L:D; 18:6 and L:D; 6:18, under a similar range of temperatures.
Hatching success was recorded by dividing the number of emerged larvae by the number of eggs. As temperature batches were composed of eggs from mixed females, the percentage of infertile eggs was assumed to be constant as all batches contained the same number of eggs from each female. Eggs from all females were divided across the full range of temperatures. Development rate was determined by dividing the number of days to hatching by 100.

Results

Larval hatch rate for *Tricyphona immaculata*

The percentage hatch rates, for each temperature regime, are given below. All eggs were laid in September.

$$\% \text{ Larval Hatching} = \frac{\text{No. of emerged larvae.}}{\text{No. of eggs.}} * 100$$

Table 3.2.3a Showing percentage hatching success with temperature for *Tricyphona immaculata*

Temperature °C	No. larvae	No. eggs	Percentage hatch success ±95% con. limits.
*5	28	41	68±14.4
5	42	65	65±11.7
*8	32	40	80±12.5
8	39	43	91±8.8
*10	42	50	84±10.2
10	21	80	26±9.7
15	27	39	69±14.7
20	50	70	71±10.6
25	0	25	0

* These batches are all from the same female on the same date and are therefore strictly comparable. The percentage of unfertilised eggs within the temperature divisions is therefore assumed equal. All other batches are made up of eggs from 6 females with an equal division of eggs.

The second batch of eggs maintained at 10°C consisted of a large proportion of pearly white eggs and it is believed that this colour dissimilarity from the normal brown indicated infertility.

Figure 3.2.3a Shows the percentage larval hatching rate for related eggs under five different temperatures.

Effect Of Temperature On Development Rate.

Table 3.2.3b Development rates for *Tricyphona immaculata* eggs laid in September.

Temperature. °C	No. of days to hatching.	Development rate 100/days	No. eggs
*5	44	2.27	41
5	45	2.22	65
*8	25	4	40
8	26	3.84	43
*10	20	5	50
10	19	5.26	80
15	13	7.69	39
*20	10	10	70
25	--	--	25

-- = no resulting larvae.

* These batches are all from the same female.

The number of days required for development falls from 44 days at 5°C to 10 days at 20°C. No larvae hatched from those eggs incubated at 25°C and it is assumed that all eggs at this temperature died due to heat stress and not desiccation as all filter papers were ensured moist each day.

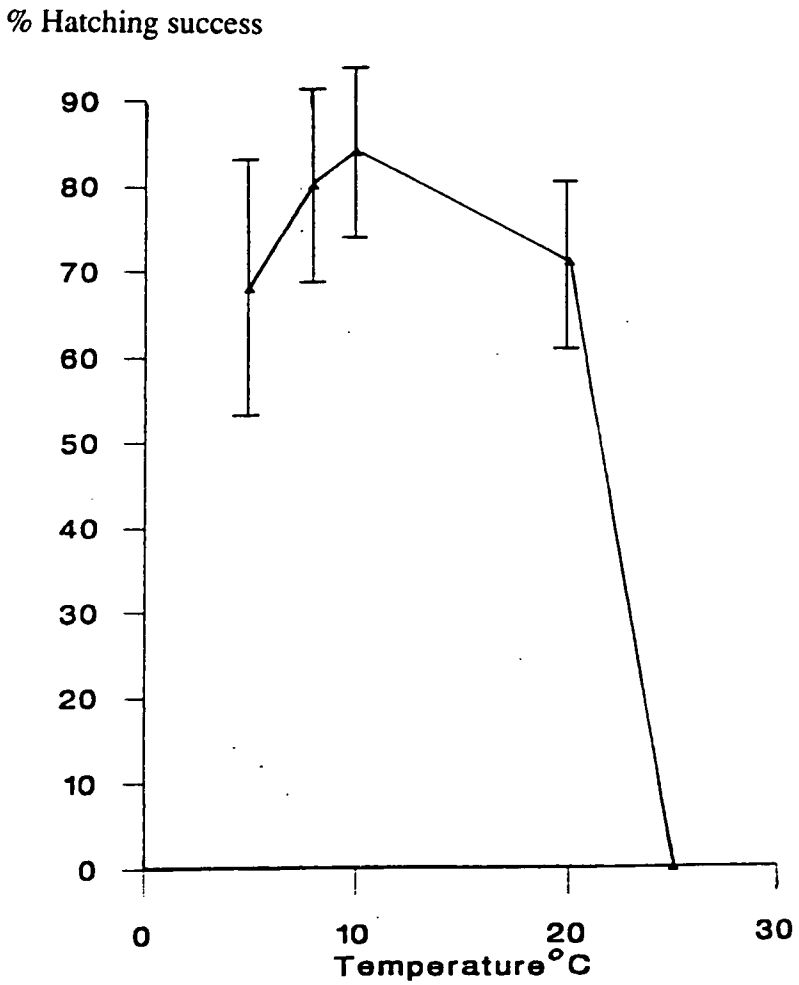


Figure 3.2.3a Percentage larval hatching success for eggs deposited from a single female maintained under four different temperatures 5, 8, 10, 20 and 25°C on a photoperiod regime of LAD; 18:6

Table 3.2.3c Development rates for *T. immaculata* eggs laid in May.

Temperature. °C	No. of days to hatching	Development rate 100/days	No. of eggs
5	44	2.27	40
8	26	3.84	40
10	22	4.54	40
15	14	7.14	40
20	11	9.09	40
25	--	--	40

Figure 3.2.3b compares the development rates of spring and autumn eggs under constant temperatures. Development is clearly related to temperature, the warmer the eggs the faster the cellular activity. The linear equation for autumn eggs is: $y=-0.24+0.52x$, $r^2=0.996$, S.E. of slope=0.0125. The linear equation for the spring eggs is: $y=0.072+0.45x$, $r^2=0.997$, S.E. of slope=0.0146 (where y is the percentage development per day and x is the temperature in °C). After comparing the slopes of the two regressions using the standard errors of the two slopes it is be concluded that the development rates of spring and autumn eggs are not significantly different. ($t=3.64$, n.s: d.f.=6, $P>0.01$)

Figure 3.2.3c shows the average number of days required for hatching in spring eggs and the development rate of those eggs, expressed as 100/days to hatch plotted against temperature. The linear equation for the relationship between egg development rate and temperature, between 5°C and 20°C is: $y= -0.20 + 0.52x$, $r^2 =0.997$ (where y is the percentage development per day and x is the temperature in °C).

The rate of egg development is therefore positively related to temperature.

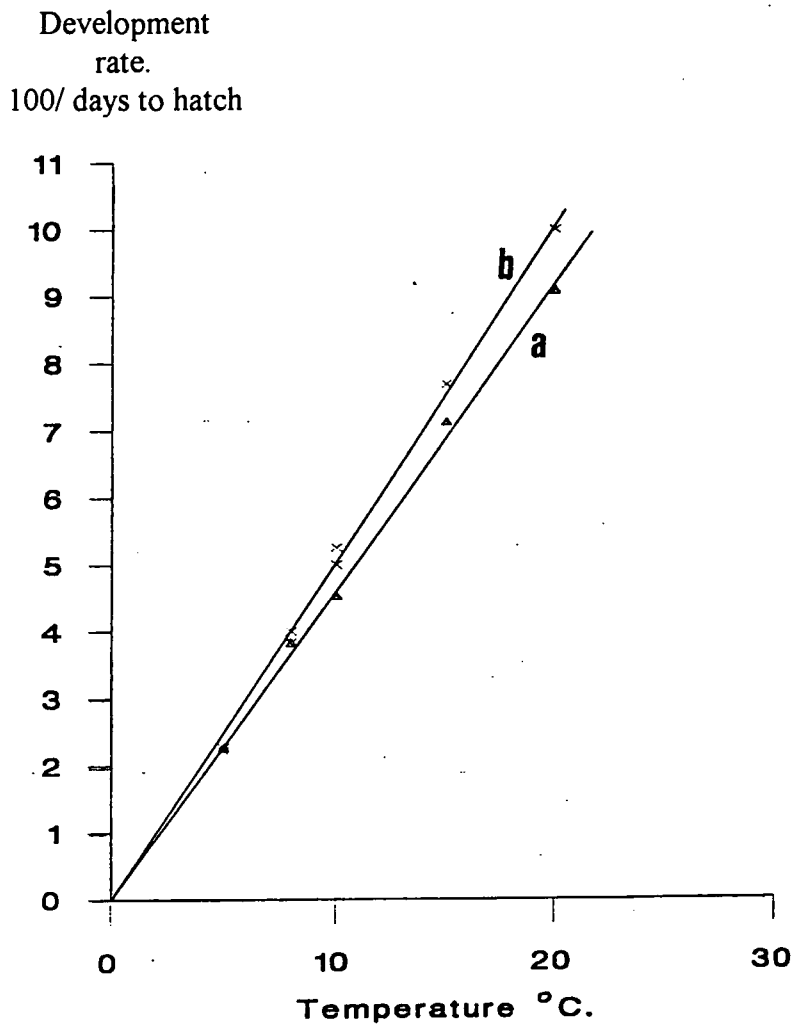


Figure 3.2.3b. Rate of egg development for batches of *Tricyphona immaculata* eggs maintained under a photoperiod of L:D; 18:6 at temperatures of 5,8,10,15, 20 and 25°C. a) development rate of spring eggs. b) development rate of autumn eggs.

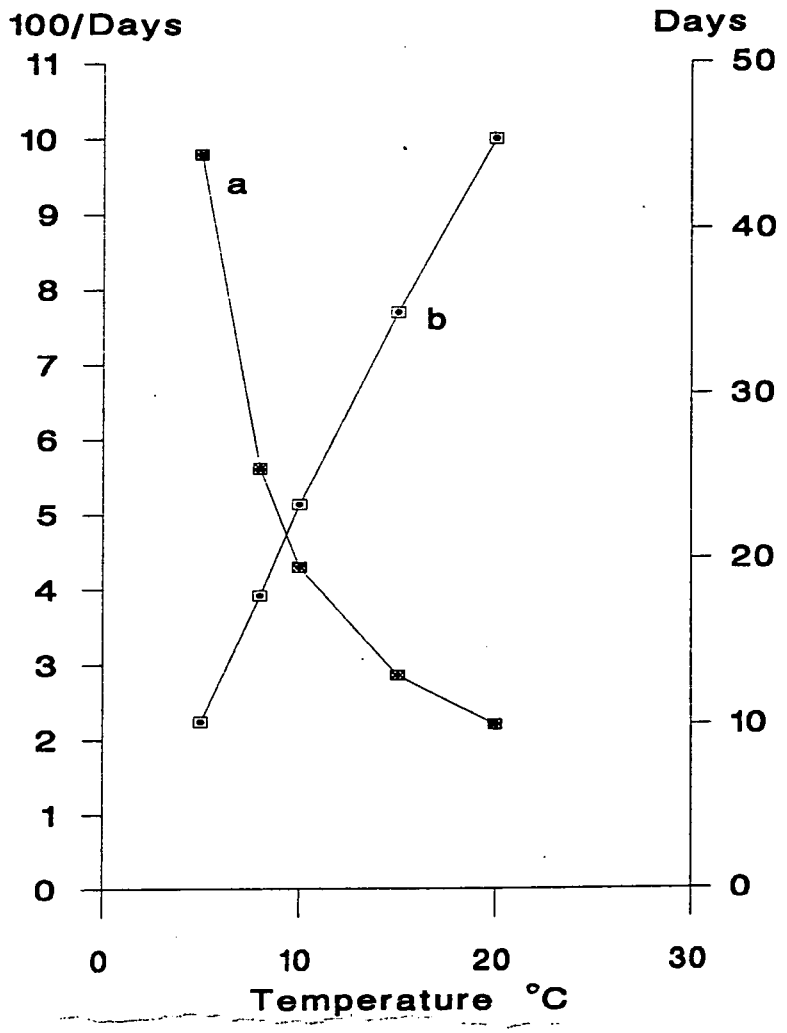


Figure 3.2.3c a) The number of days for *Tricyphona immaculata* eggs (laid in the spring) to hatch plotted against temperature. b) The rate of development of eggs plotted against temperature.

3.2.4 The Effect Of Photoperiod

Results

Table 3.2.4 Showing development rate of *Tricyphona immaculata* eggs under long and short photoperiods.

Temperature °C	Photoperiod regime	Number of days	Development rate	No. eggs hatching
10°C	L:D;18h:6h	23	4.34	6
10°C	L:D;6h:18h	23	4.34	8

The development rate was highly synchronous having a spread of less than 24 hours. Egg development was not influenced by photoperiod regime.

3.3 Studies On The Larval Stage

3.3.1 Introduction

The larvae, once hatched, were transferred to a new Petri dish containing a small amount of upper ground peat (top 20mm of ground peat) lying on a thin layer of agar jelly. The purpose of the agar was to act as a water holding substrate base of a gelatinous consistency sufficient to allow the larvae to burrow if they so desired.

These cultures were set up at the range of temperatures 5, 8, 10, 15 and 20°C. The intention was to observe the rate the larvae progressed through their instars in accordance with the temperature they were subject to.

Unfortunately attempt to cultivate failed and I believe the reasons behind the failure were;

a) The vulnerability of the small first instar to desiccation.
b) Larvae crawling out of the peat and becoming 'lost' in the agar base or container walls.

This failure served to focus my efforts on the events in the field.

Beginning in September 1992, regular visits (varying from once a fortnight to twice a week depending on the time of cranefly season) were made to the field sites on Chapel Fell and on each trip peat was collected and returned to the department for larval extraction. Hadley (1971) describes the larval ecology of *Molophilus ater* using similar procedures outlined below. Unlike Hadley's work, I was faced with the prospect of finding my species in various stages of development (if two overlapping populations exist) and so the approach to interpretation of extracted material required much forethought. The aim of this section is thus to explain the process of obtaining larvae from the field and to present the findings from 12 months field work.

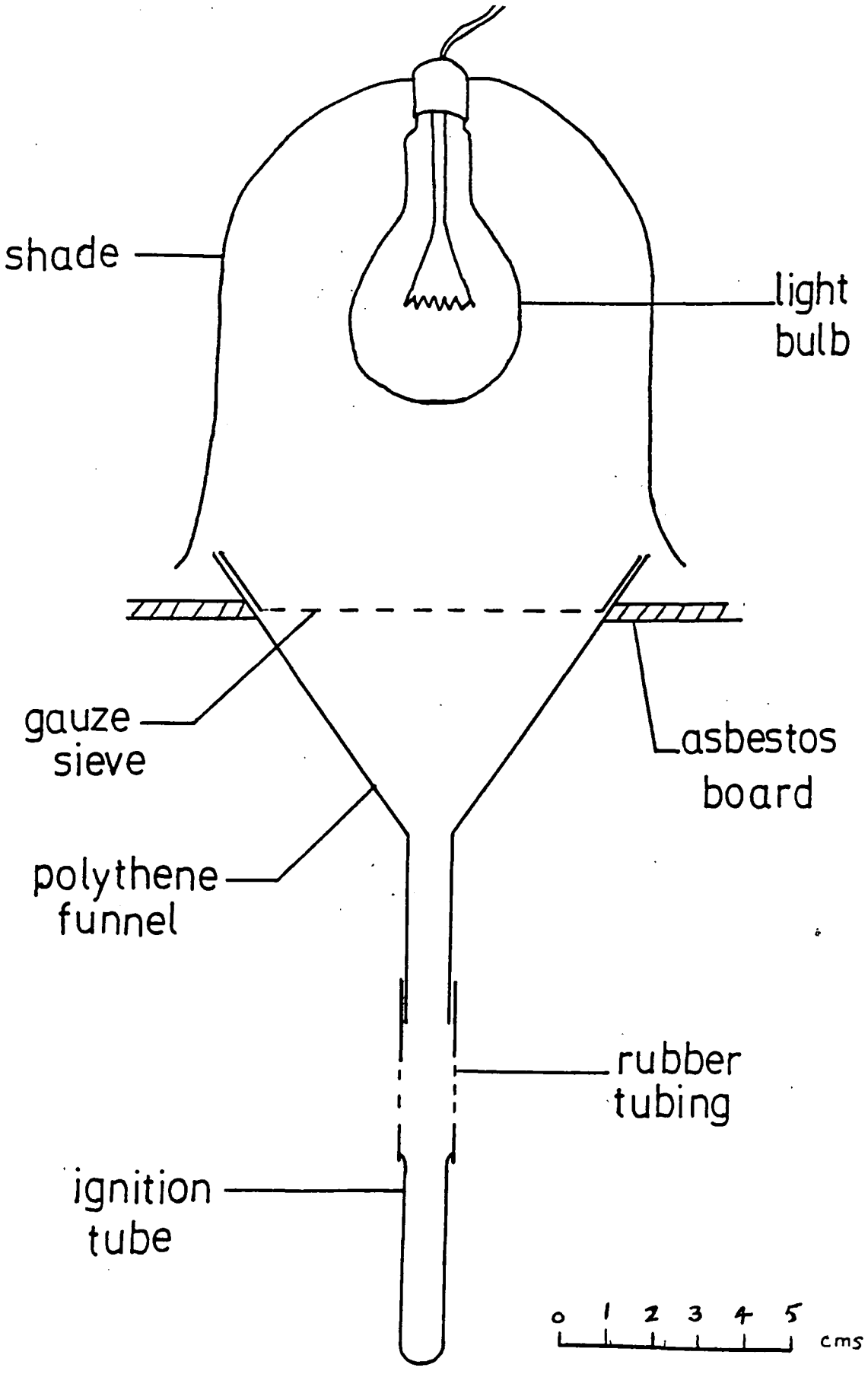
3.3.2 Methods Of Obtaining Larvae

The method of extraction that I employed was that of the wet funnel technique. Figure 3.3.2a (after Smith 1973) shows the apparatus involved in the operation developed by O'Connor (1955, 1962) and previous work by Hadley (1966) and Horobin (1971) has demonstrated the techniques efficiency.

In this method of larval extraction peat is immersed in water towards the very top of the funnel; and rested on a gauze sieve. It seems advantageous to break the peat up slightly to aid the penetration of water, so easing the movement of larvae also.

Over the next two and a half hours the intensity of the bulb (of 60W) is increased gradually from low to high and after this period the intensity remains at this level for a further half an hour. The larvae move down the temperature gradient, through the soil

Figure 3.3.2a Wet funnel extraction apparatus



and sieve and fall through the water to be collected in an ignition tube fitted to the funnel base by rubber tubing.

Stress must be placed on the importance of using a thin layer of substrate in each funnel. Several authors such as Dinaburg (1942) and Peachey (1962) have drawn attention to the importance of not overloading the funnel with substrate. The 6cm deep cores brought back from the field were first divided into two 3cm lengths and each was then broken and extracted in a separate funnel.

25 soil cores were taken at each site and processed collectively.

Other Methods Of Obtaining Larvae

Several other methods have been devised for the extraction of larvae. The petrol floatation method, originally devised by Salt & Hollick (1944), was used to good effect by Horobin (1971). The wetting of the larval cuticle involves using a light hydrocarbon liquid, immiscible with water, which wets the waxes on the insect cuticle and so raises the insect to the surface hydrocarbon layer from which it can be recovered.

Horobin calculated the petrol extraction process to have an efficiency of 92%. Although higher than the estimated efficiency of the wet funnel extraction process (between 63% and 89% for *Molophilus ater*, Hadley 1971) Although not tested, the method is reported as being unpleasant, potentially dangerous and time consuming. As a consequence it was not utilised in this study.

Mechanical methods such as washing soil samples though a series of graded sieves have been used to good effect in quantitative studies. Large *Tipula* sp. larvae were successfully obtained using this method by Coulson (1962) and Freeman (1967) but the method is not suitable for use on relatively small organisms as the process is too coarse. Like the petrol flotation method it is again time consuming.

Barnes (1941) and Milne, Coggins & Laughlin (1958) developed other methods for extracting *Tipula* sp. but both have major disadvantages, and again, were not considered appropriate for this study.

3.3.3 Procedure for determination of instar stage

Introduction

Before larvae can be assigned to an instar stage, a histogram of growth stages must be made. *Tricyphona immaculata* instar determination was done by measuring the maximum diameter of the spiracular disc in larvae. By continuing to record the maximum diameter of this respiratory structure, a histogram of growth was constructed which then enabled the accurate determination of instar stage.

After killing the extracted larvae by quick immersion in boiling water, the larvae were then preserved in 70% alcohol and labelled with date and site for later inspection.

Figure 3.3.3a gives various perspectives from *Tricyphona immaculata*. The larvae are whitish or yellowish and are distinguished by the form of the anal segment which possesses four elongated anal palpillae. The cuticle is covered with short pubescence and the length of *Tricyphona immaculata* (fourth instar) is around 15mm. It occurs in marshy soil, Sphagnum bogs and in acid marshes (Brindle 1967). Of the three species of *Tricyphona* described by Brindle (1967), *Tricyphona immaculata* is reported to be the most common.

Hadley (1966) makes extensive remarks on the various procedures for insect instar determination and the information he presents in his thesis is condensed below.

Dyar (1890) observed that the head capsule width of lepidopterous larvae increases in a geometric progression of increments at each moult by a factor of approximately 1.4 on average. Many other cuticle structures, such as the spiracular disc, were then observed to show such stepwise growth jumps (e.g. Kettle, 1948; Hale, 1965).

Work, such as that by Calvert (1929), Forbes (1934) and Beck (1950), drew caution to the simplistic view of growth progression by giving evidence that rates of growth could

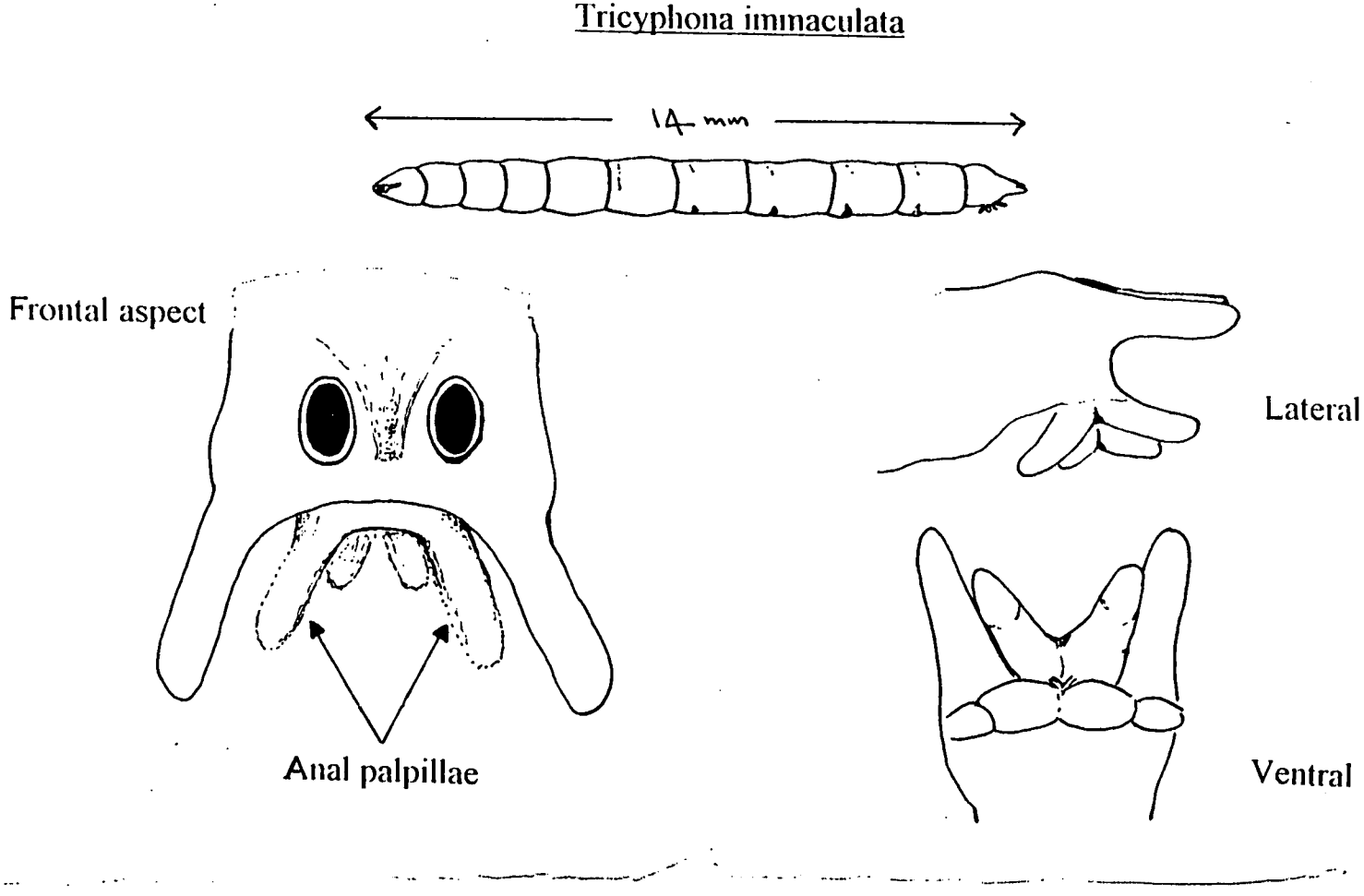


Figure 3.3.3a Various perspectives of *Tricyphona immaculata* in its larval phase. Spiracular disc diameter between 12µm and 104µm.

and did differ between instar stages. The rate of growth increase between the first and second and the rate of growth increase between the third and fourth being larger than that for any other moult.

Most evidence available, regarding the number of instars affiliated with a lifecycle, is restricted almost entirely to the Tipulinae. Coulson (1956) measuring spiracular discs in six species of cranefly, found the larval phase to comprise 4 instar stages. Work by Hennig (1950) and Brauns (1954) support this.

Apart from the work by Hadley (1966) on *Molophilus ater* there have been no related investigations on any other member of the tribe *Eriopterini.*
In sections 4.3 and 4.5 the histograms of larval spiracular disc diameters along with emergence information for *Erioptera trivialis* and *Ormosia psuedosimilis* are given.

As time was a limiting factor in this study, due to the number of species covered and the broadness of the investigation, only the spiracular disc was used as a means of instar determination. However, it soon became apparent that this characteristic was a credible means of evaluation.

Method of measuring spiracular disc

To facilitate the examination of larvae, the author found it beneficial to first preserve the specimens in alcohol for it produced rigidity and made handling specimens easier. The animals were then placed vertically on the side of a Petri dish with the posterior spiracular lobes pointing upwards for viewing. All measurements were made with ×100 and ×400 magnitude using a graticule.

Results

The frequency distributions of *Tricyphona immaculata* spiracular disc diameters are shown in Figure 3.3.3a. the distribution clearly shows 4 defined size groups ranging from a first instar spiracular disc diameter of 0.0125mm to a fourth instar of spiracular disc diameter 0.104mm. This indicates that *Tricyphona immaculata* has 4 larval instars.

Table 3.3.3a Compares the mean instar disc diameters of *Tricyphona immaculata* larvae and shows the rate of increase between each stadium

	Instars			
Maximum diameter of spiracular disc	**1**	**2**	**3**	**4**
Number measured	12	9	25	37
Mean (μ)	12.0	25.0	54.1	104.2
Standard deviation	0	0	5.3	5.5
Rate of increase	2.08	2.16	1.92	

Figure 3.3.3b shows the logarithmic transformation of the data and the linear relationship demonstrates the geometric progression.

The straight line produced by plotting the logarithm of the mean spiracular disc diameter for each instar against the instar number 1-4 is supportive of Dyar's rule.

3.3.4 Instar occurrence between September 1992 and August 1993.

Introduction

In order to determine the progress of *Tricyphona immaculata* as it develops through its larval stages the question must be asked "What is the duration of time spent in each larval instar". The sum of these separate time growth increments will give a strong

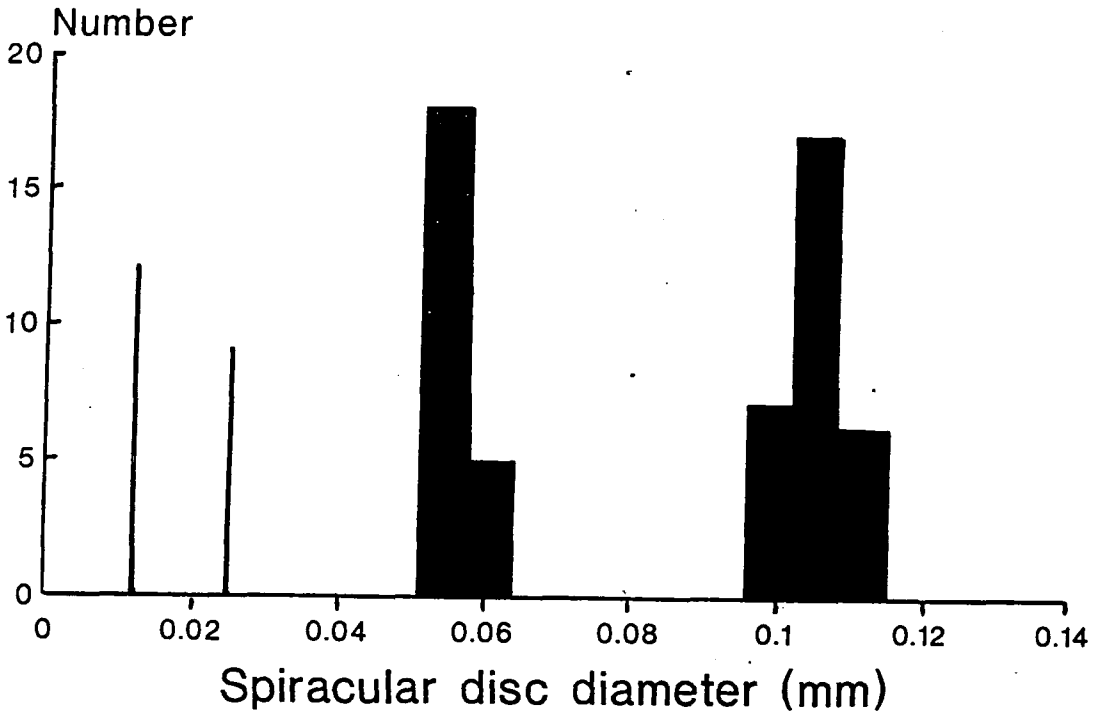


Figure 3.3.3a Maximum diameter of spiracle disc of *Tricyphona immaculata* larvae. Frequency distribution histogram showing presence of 4 larval instars.

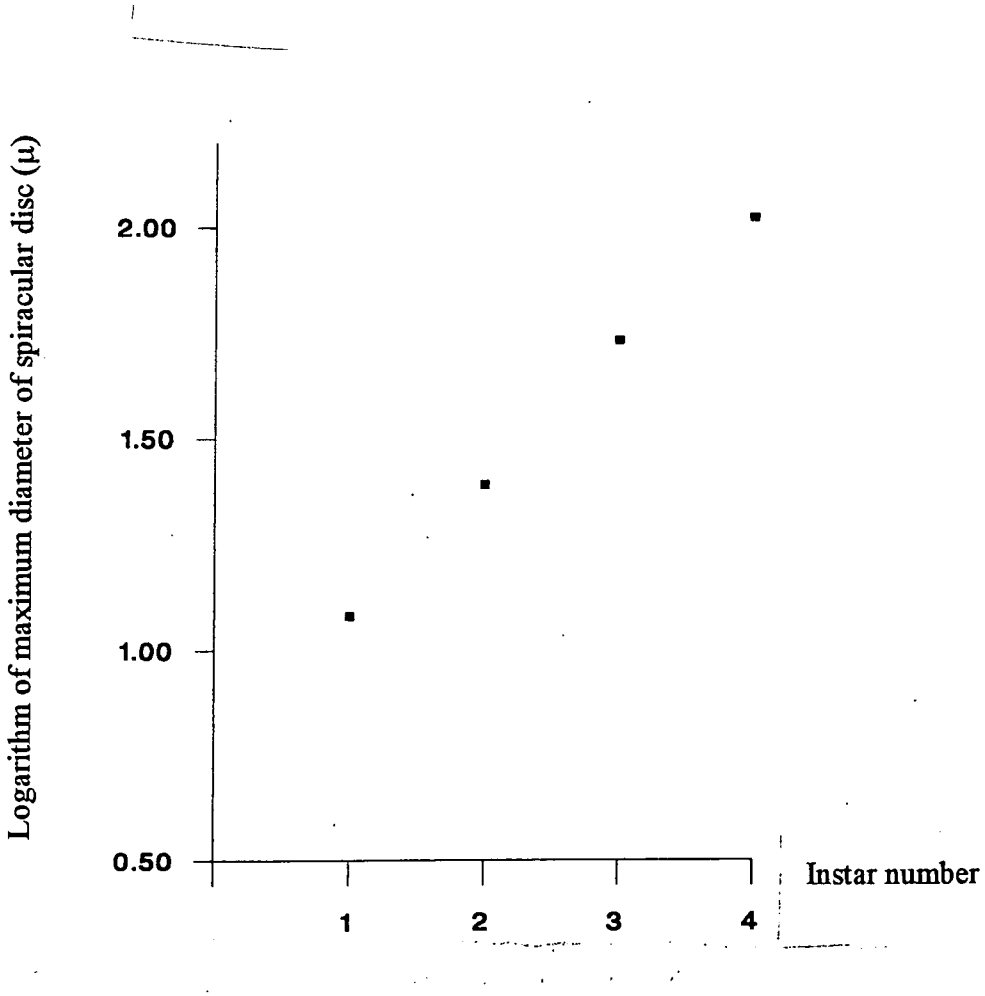


Figure 3.3.3b The logarithm of the mean maximum diameter of the spiracular disc in each of the four instars (μm) for *Tricyphona immaculata*. The linearity suggests that an intermediate instar has not been missed.

indication as to whether two generations a year are possible or only one. As discussed in section 3.1, if the biannual emergence is caused by two overlapping populations, then it would be expected that these two populations would overlap throughout the course of their development. The sampling of larvae from the field was intented to establish when each instar occurred and, if neccessary, assign larvae of different instar (occuring at the same time) to either the autumn or spring emerging population. Care was taken to segregate larval instars with the correct population. The starting point for this process was based on the knowledge that larvae belonging to those adults emerging in May will be in the first instar stage from May-June onwards. Similarly, those eggs laid in September will give rise to first instars shortly afterwards.

The method used by Hadley (1966) to calculate the duration of instars was that of Gabbutt (1959). By plotting the mean value for the maximum width of head capsule (as a measure of percentage instar composition) against the sampling date of those larvae, he was able to average out the growth stage of the species *Molophilus ater* and follow its development accordingly.

The sigmoid curve that he obtained from July to November reflected the change in the mean maximum width of head capsule. By superimposing the mean maximum head capsule measurement, previously obtained for each of the four instars, the moulting rate was demonstrated graphically and although limited by the 'random' sampling dates used it still indicated successfully the overall larval development.

The purpose of this investigation was to observe when each instar occurred in the field. Analysis would then identify the number of populations involved in the system and the duration of each instar existence.

Methods

For this study, sampling began in early September 1992 and the collection of peat for larval extraction continued until October 1993.

In section 8, the site habitats associated with *Tricyphona immaculata* are detailed. For the purpose of this experiment the three sites showing 'richest' abundance of *Tricyphona immaculata* larvae were used as sample sites. These were sites B, J and K.

Each month 25 soil cores were taken from each of the three main sites and the number of individuals collected of each instar, per month, are representative of these three sites only. All larvae were grouped according to what instar they were. This was determined by measuring the spiracular disc of the individual and then referring this against the standard instar histogram. See section 3.3.3 and figure 3.3.3a

Results

Table 3.3.4a Occurrence of *Tricyphona immaculata* instars from September 1992 to August 1993 showing the total monthly abundance of each instar in 75 soil cores (3×25) from sites B, J and K.

Months	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
No. 1st instars	--	2	1	1	1	--	--	--	--	1	--	--
No. 2nd instars	--	--	--	--	2	3	--	--	--	--	5	2
No. 3rd instars	9	--	--	--	--	--	1	2	8	--	1	5
No. 4th instars	2	3	7	4	4	4	7	1	--	1	1	--

This information is represented graphically in figure 3.3.4a

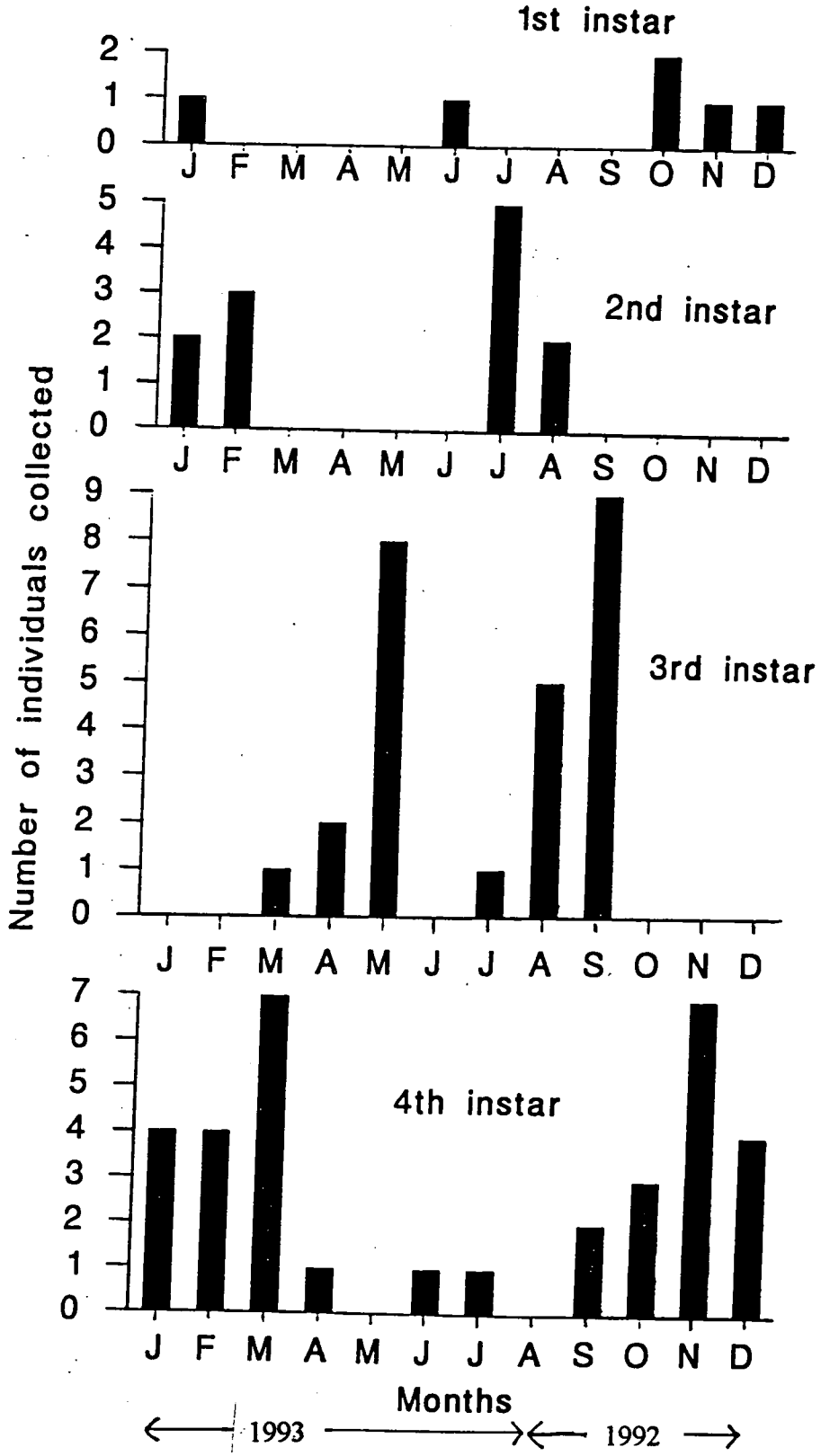


Figure 3.3.4a *Tricyphona immaculata* instar frequencies with month. Chapel Fell, September 1992-August 1993. Number of individuals collected per month representative of 75 (3×25) soil cores taken from 3 sites B, K and J.

Taking each instar in turn; 1st instars occur between October and January and in the month of June. 2nd instars occur in the months January to Febuary and July to August 3rd instars occur in the months March to May and July to September. 4th instars occur in the months September to April and in June to July.

Table 3.3.4b Separation of autumn and spring populations. Average instar stage with month September 1992-August 1993.

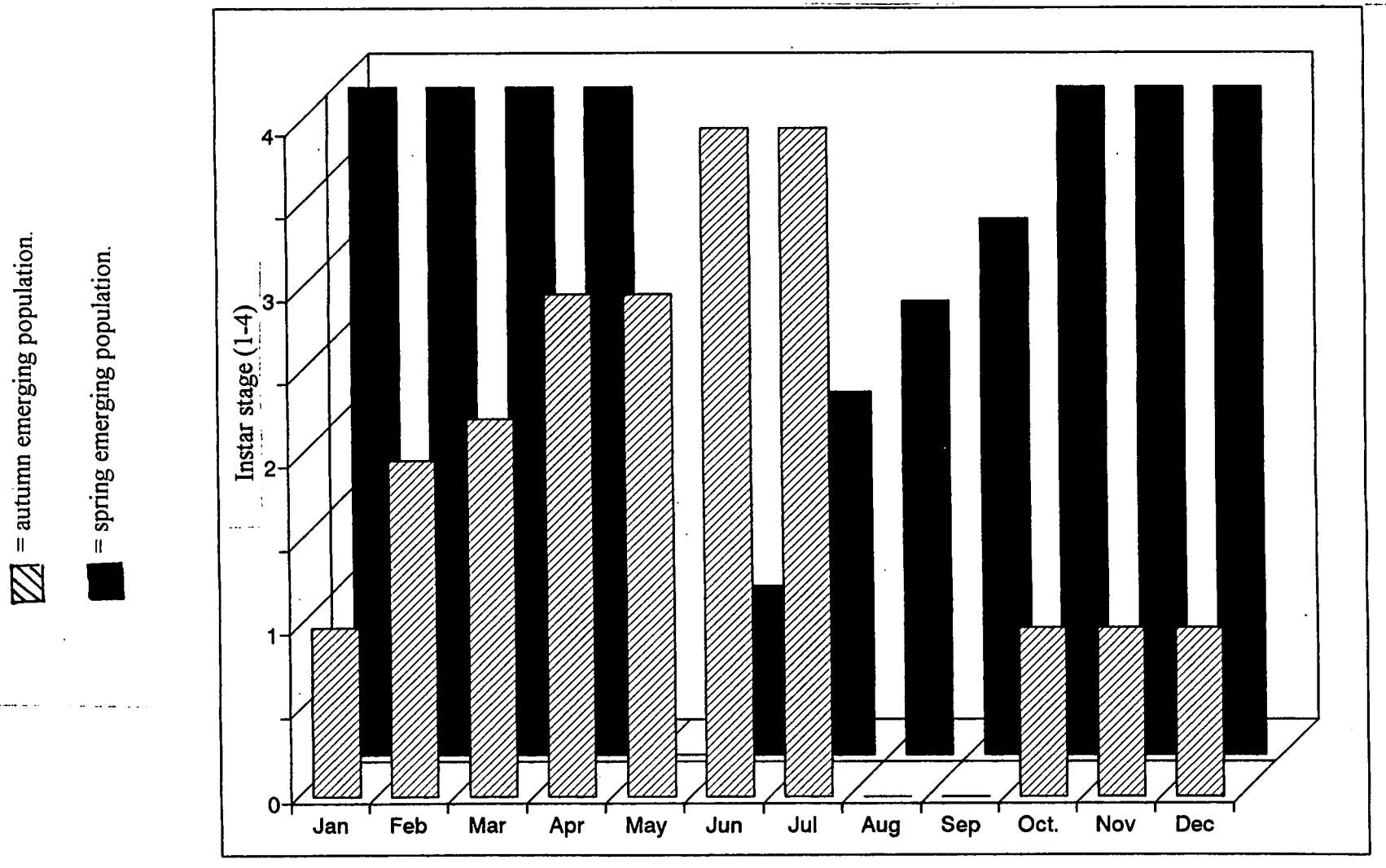
Date	Spring population average instar stage	Autumn population average instar stage
September	3.2	0
October	4	1
November	4	1
December	4	1
January	4	1
February	4	2
March	4	2.25
April	4	3
May	0	3
June	1	4
July	2.16	4
August	2.71	0

This information is represented graphically in figure 3.3.4b.

3.3.5 Larval Growth

Only a handful of studies have been made on Tipulidae larval growth in the field. Coulson (1962) produced a growth curve for *Tipula subnodicornis* which showed that the larval growth rate decreased during the winter and that by March they had obtained

Figure 3.3.4b *Tricyphona immaculata* average instar stage with month. Adults emerge late May and late August and first instars appear in June and October.



maximum weight and so were apparently fully developed. The growth curve for *M. ater* shows a rapid rate of growth acceleration from hatching in June to the onset of winter at which point growth increments where small. Growth, as mentioned previously, accelerates in the spring time until pupation occurs in May, Hadley (1966). Thus *Molophilus ater*, unlike *Tipula subnodicornis*, increased its growth rate with the arrival of spring.

Smith (1973) followed up Hadley's (1966) work after it was noticed that the variance in the larval weight was increasing as growth progressed throughout the spring period. He suggested that one section of the population was responsible for the increase in mean weight whilst some of the population were already fully developed. Smith discovered that *Molophilus ater* are still feeding and developing over the spring period and also that over his culture period of 24 January -24 March, 1972, the mean weight gains of females and males differed significantly. Females gaining an average 0.39 ± 0.04mg compared with a male gain of only 0.26 ± 0.02mg. The increase in variance of larval weight can therefore be explained by a difference in sex growth rate tailored to maximise female fecundity (Horobin 1971).

Having calculated the instar period occurrence of *Tricyphona immaculata* a general picture was developed showing larval instar progression over the duration of one lifecycle. It was then decided to investigate larval growth to gain a clearer insight into the populations separate development. Particular interest was focused on the developmental stage of spring larvae entering pupation as this stage of larval growth may determine whether the individual emerges in spring time or the autumn. It was considered that larvae almost ready for pupation may be subject to a 'cut off' point by a diapause and that this diapause would act on the point of growth that the individual had reached. Therefore in so doing, larvae from the autumn population that had different growth rates would be separated into emerging at different times. The larger in the spring time and the smaller, with growth remaining, in the autumn.

Practical details

Over the course of my work from September 1992 until August 1993, measurements were taken of all larval weights, lengths and breadths. Weightings were taken on a sensitive electro-micro balance (accurate to 0.001mg) after excess water had been removed by rolling them on filter paper. The length and breadth measurements were taken using an Olympus binocular microscope with a graticule eyepiece. An average instar weight was firstly determined before assigning larvae to their own population. The monthly growth data for *Tricyphona immaculata* is represented by only those measurements taken of length as this was found to give the clearest distinction between the four instars. Variance for weight being two large for third and fourth instars and breadth increments for all instars being too small.

Results

Table 3.3.5a

Average weight for instars of *Tricyphona immaculata*

Instar	Average weight (grams) $\pm$ S.D. (no. indivs.)
1	$0.75*10^{-3} \pm 0.00$ (4)
2	$2.0*10^{-3} \pm 0.00$(4)
3	$2.09*10^{-3} \pm 0.716*10^{-3}$ (18)
4	$4.77*10^{-3} \pm 2.70*10^{-3}$ (27)

Graph 3.3.5a shows the average weight for each larval instar with S.D.

Graph 3.3.5a *Tricyphona immaculata* average weight (and SD) with instar.

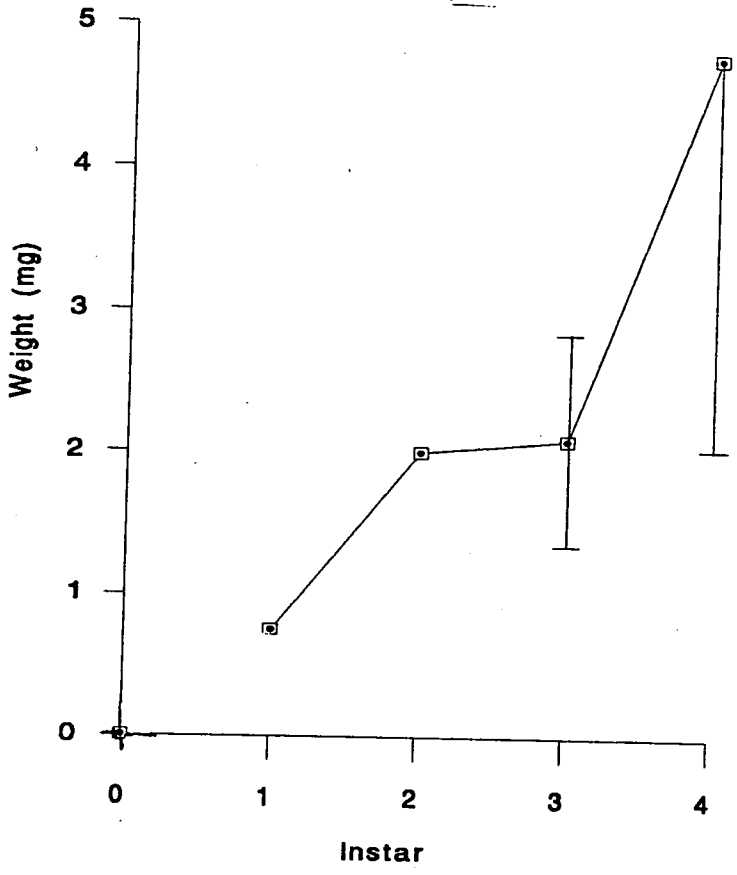


Table 3.3.5b

Tricyphona immaculata. Average length of each instar (mm)

Instar	Average length (mm) ± S.D. (no. indivs.)
1	2.77 ± 0.42 (12)
2	4.15 ± 0.91 (6)
3	8.32 ± 1.58 (19)
4	10.43 ± 1.82 (29)

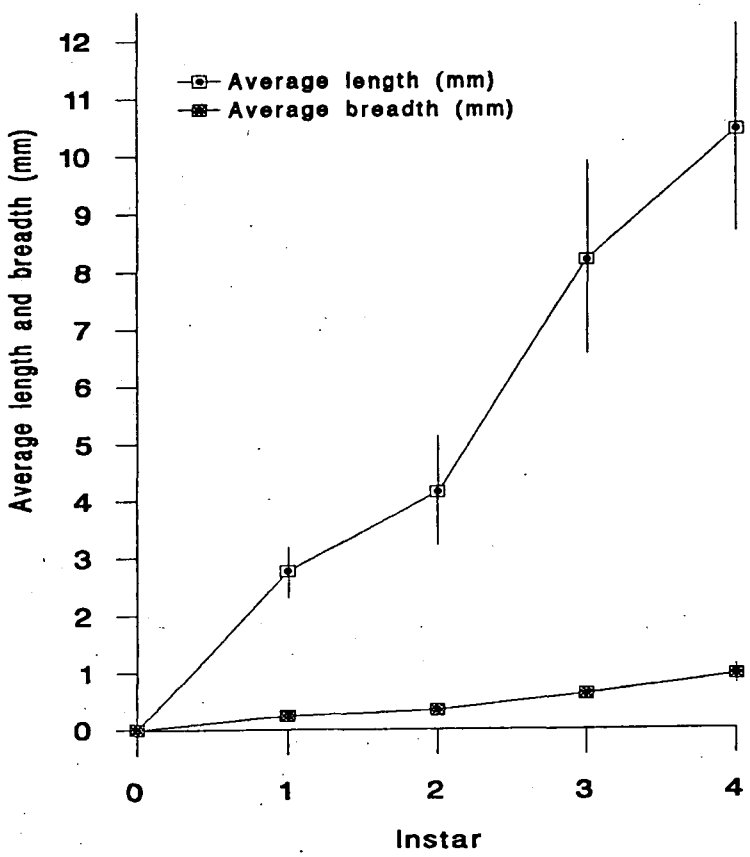
Table 3.3.5c

Tricyphona immaculata. Average breadth of each instar (mm)

Instar	Average breadth (mm) ± S.D. (no. indivs.)
1	0.24 ± 0.043 (12)
2	0.34 ± 0.072 (6)
3	0.62 ± 0.13 (18)
4	0.95 ± 0.17 (27)

All variables increase in variance with instar.

Graph 3.3.5b shows *Tricyphona immaculata* instar growth in larval length and breadth.



Graph 3.3.5b *Tricyphona immaculata* average larval length (and SD) and breadth with instar number.

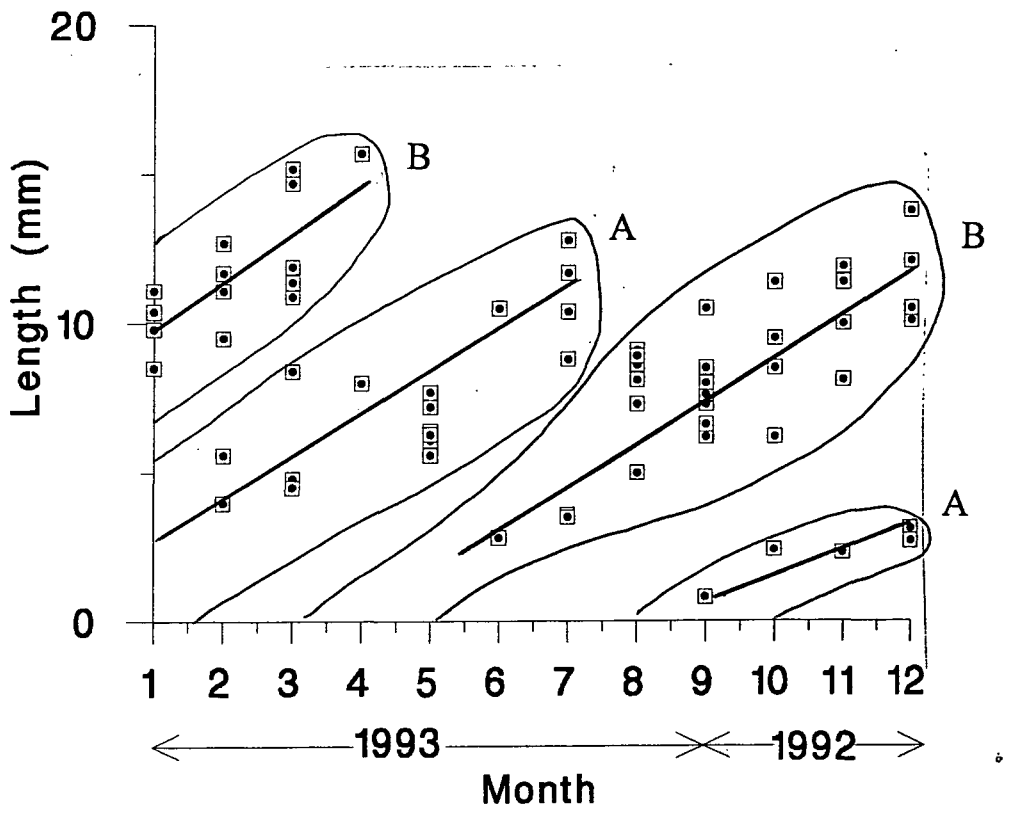
Table 3.3.5d. *Tricyphona immaculata* larval lengths by month of collection. Chapel Fell September 1992-August 1993

Month	Larval lengths recorded. (mm)
September	7.6, 6.2, 8.1, 6.6, 7.3, 7.8, 8.5, 7.6, 8.0, 10.5, 6.6
October	2.4, 3.2, 11.4, 9.5, 8.5
November	2.3, 10.0, 10.0, 11.9, 8.1, 10.0, 11.4, 10.0
December	3.1, 13.8, 10.1, 12.1, 10.5
January	2.7, 4.1, 3.8, 8.5, 9.8, 11.1, 10.4
February	12.7, 11.7, 9.5, 11.1, 4.0, 5.6, 5.2
March	7.9, 9.7, 10.9, 14.7, 11.9, 11.4, 8.4, 15.2
April	6.3, 15.7, 8.0
May	7.2, 6.2, 6.4, 6.4, 6.1, 7.7, 5.6, 6.3,
June	2.8, 10.5
July	12.8, 10.5, 3.6, 3.5, 8.8, 4.1, 3.9
August	9.0, 9.1, 6.8, 8.1, 8.6, 5.0, 8.9

These data are represented in graph 3.3.5c

3.3.6 Larval growth discussion

It is regretted that *Tricyphona immaculata* did not occur to the abundance of *Erioptera trivialis* and *Limnophila meigeni*. The only growth data collected of analytical value was that of *Tricyphona immaculata* instar length variation. Measurements taken on weight showed huge standard deviation values in the fourth instar overlapping greatly with those of the third instar stage. From graph 3.3.5a it can be seen that there is little change in average weight between the second and third instar. This may be due to the very small



Graph 3.3.5c *Tricyphona immaculata* larval lengths by month of collection with suggested generations A and B. Chapel Fell 1992-1993

number of second instars collected (4) and that the average weight produced from weighing these four together is inaccurate with no indication of weight variation. Likewise the four individuals weighed to represent the average weight of the first instar are of negligible value to the overall graph and serious interpretation can only be given to the third and fourth instars.

From information given in the introduction to larval growth the increased variation in weight may be attributable to developing sex-size dimorphism. Females being towards the top end of weight deviation and males towards the lower.

A second question must be asked and that is: are some larvae, laid in spring, taking longer than twelve months to develop (so emerging in autumn). To develop this idea further, using length as the clearest indicator for larval growth (in terms of size and not spiracular disc diameter), larval lengths were plotted against their month of collection and the pattern, although inconclusive, does show the following trend. The average length for a *Tricyphona immaculata* 4th instar is 10.4mm. On graph 3.3.5c, individuals above this length can be seen occurring every month with the exceptions of May and August, the two months before emergence takes place. If it is predicted that adults emerging in September may have come from a subsidiary pool of larvae left out of the June emergence, then we may predict two conditions for the theories acceptance. Firstly, that those larvae will have reached sufficient size immediately prior to pupation that was not quite attained in May and secondly; that these larvae will have originated from eggs laid by spring emerging adults as were those that pupated just prior to spring. So creating a second, perhaps minor, emergence 3 months from the first major wave and 15 months from when the eggs where first laid.

The picture that emerges from graph 3.3.5c, however, is in contrast to the theory just proposed. It appears that all eggs laid in the spring time reach average fourth instar length by December and that thereafter there is no merger in length with larvae from eggs laid in September. After December, three individual larvae were under 10mm in length yet still within the 4th instar length boundary. Over the three months of January, February and March these three recordings can be reasonably assigned to the spring emerging population. It is doubted that the future of such small larvae can be established

from further work based solely on field observation. With the discrimination of small, spring born larvae and rapidly growing autumn born larvae becoming unclear around April-May, laboratory techniques seem essential to keep the two separate under appropriate field conditions. Observations could then be made on emergence timing and triggering of pupation, by photoperiod setting, may enhance understanding further. From this study it is proposed that both populations have a life cycle of 12 months duration.

3.4 Studies on the adult stage

3.4.1 Introduction

It has been shown in the previous section that *Tricyphona immaculata* exists as two groups, one beginning its cycle in the spring time, the other in the autumn. It has also been shown that the two groups do not appear to converge and overlap in their developments and that it seems unlikely that the life span can be shortened or lengthened from 12 months. Given this, the first hypothesis to explain biannual emergence (that of there being one population of *Tricyphona immaculata* undergoing two generations in a year) can be rejected.

To complete the documentation of the life history of *Tricyphona immaculata,* we need only to examine the biology of the adult stage, starting with the evidence for biannual emergence. The effects of altitude on spring emergence will then be looked at followed by details of the sex ratio.

The Tipulidae of Chapel Fell moorland have been listed in several invertebrate study reports from work conducted by Dr John Coulson and his workers at Durham University. Since 1989 pit falls have been laid down in mid May and collected fortnightly until late autumn after most invertebrate activity has ceased. The initial observation of *Tricyphona immaculata* biannual emergence was made by Coulson in the late 1980 and collected and examined material existed three years prior to the commencement of this study in October 1992.

The collected data allowed for an immediate review of the adult emergence of *Tricyphona immaculata* and the fortnightly pick up of pit falls was deemed sufficiently

frequent for a preliminary insight into the break between the two peaks of emergence. This being estimated to last from the end of June to the beginning of September. Data is presented here from the two years 1992-1993.

3.4.2 Methods of sampling adults

The sampling of adults was conducted using a series of pit fall traps located at fourteen sites previously selected to represent the range of vegetation sites present at Chapel Fell summit, 2000ft (630m). At each of the fourteen sites 10 pit falls were positioned in a straight line at intervals of 2m. Each pit fall consisted of a plastic jar sunk into the ground so that its rim was flush with the ground surface. A solution of weak detergent with formulin (2%) acted as a 5cm deep killing and preservation fluid. The detergent reduced surface tensions and thus prevented escape of insects. Hadley (1966) has demonstrated the accuracy of these traps in providing information on adult emergence patterns. No attempts were made to estimate density of adults because numbers were low. However, larval densities were recorded (see section 8.2.1).

3.4.3 The emergence period

3.4.3a Emergence at Chapel Fell 1992 and 1993

Results

Table 3.4.3a

Emergence information for *T. immaculata* during 1992

Period	Number of adults	
Date (day/month)	Males	Females
15/5-29/5	397	187
29/5-12/6	138	175
July	0	0
August	0	0
20/8-4/9	0	4
4/9-18/9	0	4

This is represented in graph 3.4.3a

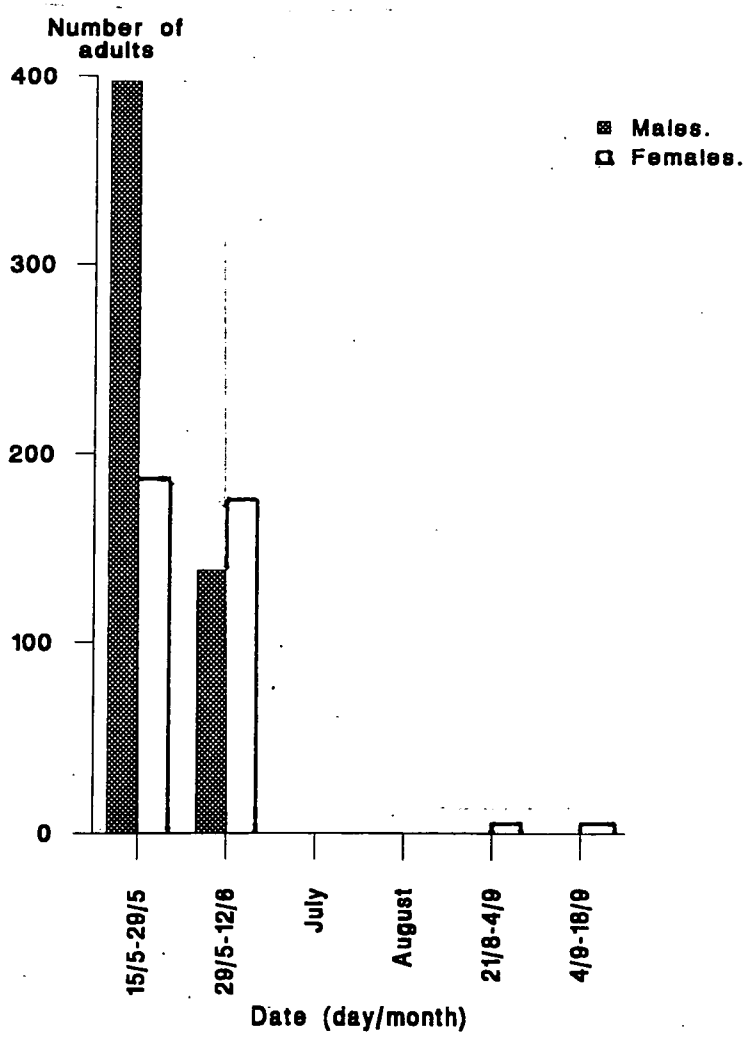
Compared with the spring, the autumn emergence was low and atypical of other years.

Table 3.4.3aii

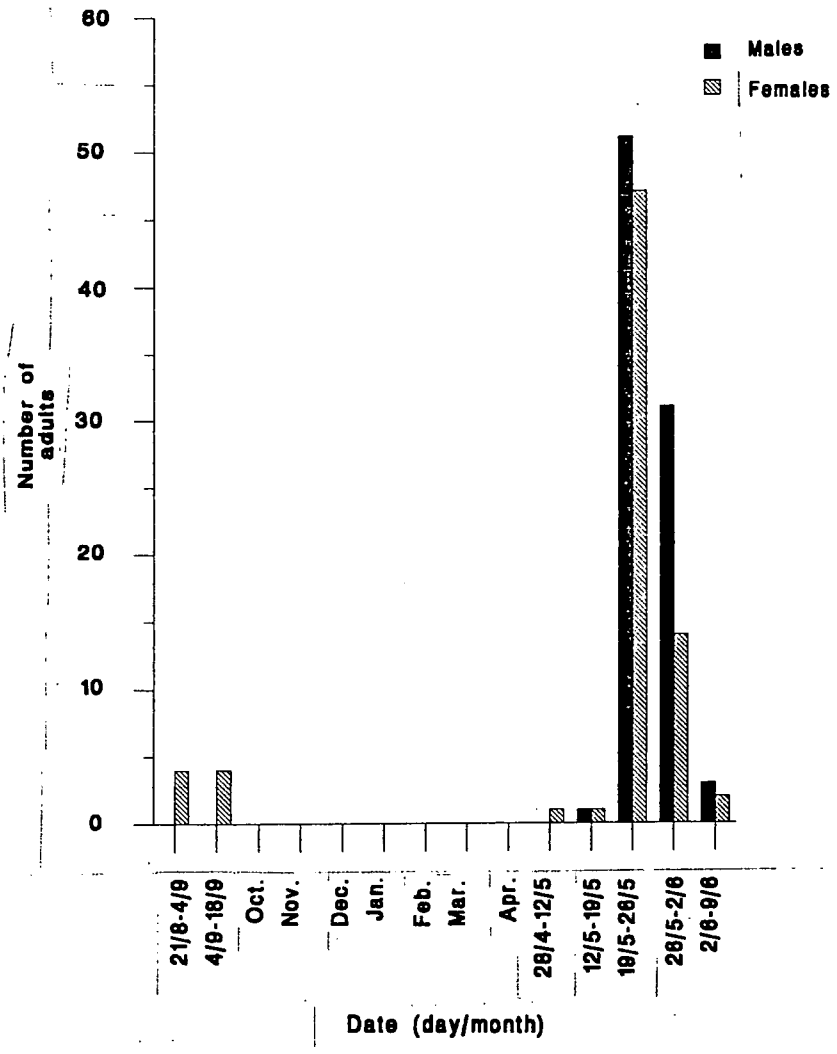
Emergence information for *Tricyphona immaculata* during the spring emergence 1993

Period	Number of adults	
Date (day/month)	Males	Females
28/4-12/5	0	1
12/5-19/5	1	1
19/5-26/5	51	47
26/5-2/6	31	14
2/6-9/6	3	2

This is represented in graph 3.4.3aii along with data from the previous September.



Graph 3.4.3a *Tricyphona immaculata* adult emergence numbers 1992



Graph 3.4.3aii *Tricyphona immaculata* adult emergence numbers from September 1992 to June 1993

3.4.3b The effect of altitude on spring emergence

The exact altitude range of *Tricyphona immaculata* is known to be from sea level to well over 660m (Coulson, pers. comm.). *Tricyphona immaculata,* like many other insects, is able to maintain and complete its life cycle over wide climatic and ecological conditions. At an altitude of 630m the first adult emergence occurred during the spring, beginning just after mid-May and ending about 3 weeks later in June. The second emergence took place during early autumn around mid-September. Both emergences are therefore synchronised. This situation of events, applying to animals living at an altitude of 630m, differs from that found at higher altitudes. On the higher slopes of Great Dun Fell, the second highest peak in the northern Pennines with a summit of 2780ft (847m) the two emergences of *Tricyphona immaculata* are closer together, the spring emergence occurring later and the autumn emergence arriving earlier. The duration of the emergence is also found to be shorter, (Downie unpublished).

Adaptations differ between craneflies in an effort to complete their life-cycles under widely different temperature regimes. Soil temperature recording on Great Dun Fell showed a decrease of 1°C for 207m rise in altitude. Although the temperature gradient varies seasonally a considerable difference in mean annual temperature of 2.4°C was found to exist between the 370m and 847m sites (Coulson *et al.* 1976). At higher altitudes *Tipula rufina* Meigen and *Pedicia rivosa* L. take twice as long to complete one generation (Coulson, 1959 and unpublished data). In other insects, the adaptation is one of rapid development with growth being completed in only three months (Davies & Smith 1958).

At higher altitudes, the emergence of both *Tipula subnodicornis* and *Molophilus ater* is delayed yet both species emerge only once a year. Adaptations exist in both species to minimise this delay and it appears that in *Molophilus ater* the rate of growth is independent of temperature. Larvae transfered from lower to higher altitude sites showed no difference in emergence timing from their original site. However, the immediate pre-pupal and pupal stages were found to be strongly temperature dependent

in both species and it is believed that this influence accounts soley for the delay in emergence (Coulson *et al.* 1976)

The purpose of this investigation was to establish the range of emergence dates of *Tricyphona immaculata* over the altitude range of 430m to 610m on the south-west slope of Chapel Fell.

Methods

The study was carried out on the south-west slope of Chapel Fell between St. John's Chapel and Chapel Fell peak. Five sites were chosen of altitudes 430m, 460m, 515m, 580m, and 610m. It was hoped, prior to the study, that all sites would be composed of similar vegetation. Unfortunately the cotton grass *Eriophorum vaginatum*, common in deep peat and an indicator vegetation for *Tricyphona immaculata* did not extend lower that sites 4 and 5. Drainage aspect and perhaps ditches influencing the water table, decomposition, flora and invertebrate fauna, Coulson, Butterfield and Henderson (1990). Site 5, the lowest site at 430m, was inorganic.

Sampling of craneflies took place over May and June 1993 using 10 plastic containers (coffee cups, 2 metres apart) placed in a straight line at each of the 5 sites. *Tricyphona immaculata* has been collected in small numbers from the top of Chapel Fell from the first week in May with a definite surge of emergence during the month's last week. It was predicted that emergence would occur slightly earlier on the lower sites. However, with such a relatively small change in altitude (only 200m altitude change of suitable habitat) and in consideration of the small density of *T. immaculata*, this difference was expected to be unnoticeable. All sites were inspected weekly. A dilute solution of 2% formulin and detergent was used as a 5cm deep killing and preservation fluid.

Table 3.4.3b The emergence dates of male and female *Tricyphona immaculata* at five altitude sites in 1993.

Site and altitude	26/5		2/6	
	M	F	M	F
1 (610m)	7	9	3	5
2 (580m)			1	3
3 (515m)			1	
4 (460m)	1	5		
5 (430m)				

3.4.3c Average sex ratio

Barnes, (1937); Hemmingsen, (1956) and Freeman, (1964) have all made studies on several adult populations of Tipulidae. Their findings of male bias populations, i.e. excess in male numbers, are discounted by Hadley (1966) on the basis that their values were estimated from studies on the total adult population and therefore the true adult sex ratio may have been distorted by mortality between males and females (Hadley, 1966).

Hadley (1966), unlike Coulson with *Tipula paludosa*, was not able to determine the sex ratio of *Molophilus ater* by sexing pupal cases throughout the emergence period owing to the small size of pupal case in *Molophilus ater*. The method employed by Hadley to determine the sex ratio of *Molophilus ater* was that of taking daily vacuum suction readings from emergence traps. Using this technique he obtained a significant sex ratios difference from unity, ($X^2 = 264$, d.f.=1, $P<0.001$, 64% males from 3 sites).

Sellke (1936) observed that females are much less active than males and this was confirmed to be the case in the flightless *Molophilus ater* by a comparison of the number

of captures by detergent traps with the number of adults vacuum sampled from the study site (Hadley, 1966).

As detergent traps are only effective against active individuals this study was limited purely by the low density of *Tricyphona immaculata*. During both the autumn emergence of 1992 and the spring emergence of 1993, repeated searches were made for *Tricyphona immaculata* adults. Many days were used in the meticulous search for adults of *Tricyphona immaculata* to provide eggs for culture studies. The average daily success rate of finding adults was about five females. Males were slightly easier to find though both males and females were extremely difficult to find after about 11.00am. This perhaps due to a decrease in adult activity.

Due to the difficulty in obtaining adults the analysis here is based on adult numbers collected from 14 pit fall sites (described Chapter 2). The autumn and spring emergences are considered separately.

Results

Table 3.4.3c. The number of males and females of *Tricyphona immaculata* collected from 140 pit falls (14 sites) between mid-May 1992 and June 1993.

Date	No. Males	No. Females	% males	X^2, d.f.=1	P
29/5/92 to 12/6/92	535	362	59.6	32.9	<0.001
4/9/92 to 18/9/92	0	8	0.0	8	<0.001
12/5/93 to 9/6/93	86	65	56.9	2.64	>0.05

The X^2 value has been calculated using a null hypothesis that the sex ratio is equality.

3.5 Discussion

Studies so far carried out on craneflies have tended to concentrate on the larger, long-palped, destructive pest species of Tipulinae. The other two sub-families of the family Tipulidae, the Cylindrotominae and Limoniinae have received scant attention and very few in-depth studies have occurred. With the exception of *Molophilus ater*, very little is known about the short-palped craneflies other than the swarming behaviour in a few species (Cuthbertson, 1926) and the distribution and emergence ecology of some species in the New Forest Reserve (Freeman, 1968) and in the Moor House Reserve (Coulson, 1959)

Coulson (1959) has summarised the seasonal distribution of both long and short palped craneflies on the Moor House Nature Reserve. Of 20 long-palped craneflies listed, very few showed bivoltine emergence. *Tipula montium* Egger emergence took place between mid-May and June and then again in late September. *Tipula oleracea* Meigen emergence took place in June and then again in late September. However, many of the 45 seasonal distributions listed for short-palped craneflies show bimodal seasonal emergence patterns. *Tricyphona immaculata*, *Dicranota exclusa* Walker, and *Erioptera trivialis* Meigen all showed bimodal seasonal emergence in which the presence of more than 10 adults was recorded in a week. The seasonal distribution of *Tricyphona immaculata* is exceptional in that the spring distribution shows a far greater abundance of animals taken than the period of sampling during autumn. The emergence of *Tricyphona immaculata* at the Moor House Nature Reserve appears to be very similar to that at Chapel Fell. In graph 3.4.3aii it can be seen that only 8 females were taken during the autumn emergence of 1992. Eight months later during the spring emergence, starting and finishing in the first weeks of May and June respectively, a total of 65 females and 86 males were taken. Even with the large reduction in emergence numbers between the spring of 1992 and 1993 the autumn emergence of *Tricyphona immaculata* was barely noticeable and consideration is now given to this fact.

Many other species of both long and short-palped cranefly emerge in the autumn. The vulnerability of going through winter as an egg or first instar is not known. Butterfield

(1976a) reported that the physiological state of *Tipula subnodicornis* during December differed greatly from that of *Tipula pagana* (at the same temperature) in July. The summer diapause in *Tipula pagana* was found to be broken by a light:dark;16:8 photoperiod and long daylength also synchronised the rate of egg development.

Tipula melanoceros Schummel, emerges as an adult in September and although eggs are laid a month earlier than *Tipula pagana,* development in *Tipula melanoceros* is condensed between April and July and it seems likely that eggs remain in diapause throughout autumn and winter, (Butterfield 1976b)

The low level of activity during autumn and winter of *Tipula pagana* and *Tipula melanoceros* either represents a temperature constraint on development in eggs or an adaptation aimed towards overcoming harsh physiological conditions.

The study on the effect of photoperiod on eggs of *Tricyphona immaculata* revealed that eggs from spring emerging adults do not diapause under long or short day-length regimes. Although eggs from autumn emerging adults were not tested for photoperiod response it seems very unlikely that autumn eggs have a diapause as sampling of larvae from the field revealed that first instars of *Tricyphona immaculata* appear the following month after eggs are laid in September.

The situation regarding larval growth in the field is very interesting. Eggs laid in September soon give rise to first larval instars and from October until January development to the second instar stage is slow. This contrasts the work of Calvert (1929) on Odonata and work by Forbes (1934) and Beck (1950) on Lepidoptera who report the rate of progression from first to second instar to be relatively greater than any of the other instar growth rates. It is therefore suggested that development in *Tricyphona immaculata,* unlike that in *Molophilus ater* and *Tipula subnodicornis,* is dependent on temperature. After winter, progression to fourth instar is compressed between February and July. Pupation occurs in August.

In considering the autumn population, larvae move into the second instar during January and February so a short daylength induced diapause may perhaps be discounted. It seems more feasible that the development rate of these first instars is determined mainly by the low temperature of winter.

The over wintering development of the spring population is better understood than that of the autumn population. After examination of larvae from the spring emerging population it is apparent that larvae progress from first to second instar within only one month, between June and July. However, further development can be contrasted with the spring emerging *Tipula subnodicornis* giving further support to the above suggestion that growth in *Tricyphona immaculata* is dependent on temperature.

Unlike *Tipula subnodicornis*, which reaches peak weight during autumn and early winter and is restricted from progressing towards pupation by the short winter daylengths which induce diapause, *Tricyphona immaculata* larvae, from eggs laid in the spring, continue growing throughout winter. The fourth instar stage is reached in October at a very short larval length (and therefore small larval weight). Growth continues until March and April and the length of larvae in the fourth instar increases in total length by about a third before pupation in April and May. The situation for the *Tricyphona immaculata* spring population is also different to that of the spring emerging *Molophilus ater* in which there is little growth between November and March and only a slight increase in the spring (Hadley, 1966). After rapid growth between August and September *Molophilus ater* is inhibited from pupation by short daylength (with temperature threshold of between 5°C and 6°C). By late January larvae brought into the laboratory can reach pupation on both long and short photoperiod regimes at 10°C indicating that development has been stimulated in the field (Smith 1973). Unlike *Molophilus ater*, fourth instar larvae from spring laid *Tricyphona immaculata* do continue development throughout winter and it therefore seems unlikely that photoperiod inhibits this development at all.

Although *Tricyphona immaculata* larvae nearing spring pupation do not appear to increase their growth rate like *Molophilus ater*, the emergence synchronisation may be caused by a photoperiod threshold and not by a quantitative response to daylength. From larval growth measurements taken of *Tricyphona immaculata* it appears that all eggs laid in the spring time reach average fourth instar length by December. All fourth instars, originating from the previous spring, disappear after April and, as discussed in section 3.3.6, with the discrimination of small spring born larvae and rapidly growing autumn born larvae becoming unclear around April-May, laboratory procedures will be required

to maintain the two populations separately. Further investigation on the final instars of spring and autumn emerging *Tricyphona immaculata* is required to understand the following questions.

a) Does a window of pupation/emergence inhibition occur over the 3 months of summer.

b) If the second, separate population is not formed by a fraction of small individuals left over from spring, what is the reason for the marked contrast in emergence numbers in some years? Are there restricting factors on the development of the autumn population such as high winter mortality of first instars?

Hadley (1966) gave evidence that a small number of *Molophilus ater* individuals fail to pupate in May and remain in the fourth instar stage from July to September. As a second emergence period of *Molophilus ater* is not known to occur at Moor House the fate of such individuals remains unknown. The response of *Tricyphona immaculata* larvae, taken from the field in July, to short daylength photoperiod may reveal the controlling factor behind inducing pupation. It is suggested that *Molophilus ater* larvae fail to pupate in September because their development control differs from that of *Tricyphona immaculata*.

4 The lifecycles of other short-palped craneflies occurring at Chapel Fell.

Of the ten species of short-palped craneflies known to occur on Chapel Fell moorland, seven species were observed between September 1992 and August 1993 and the lifecycle findings are presented here for all but *T. immaculata*.

The 7 species which were found during this study are;

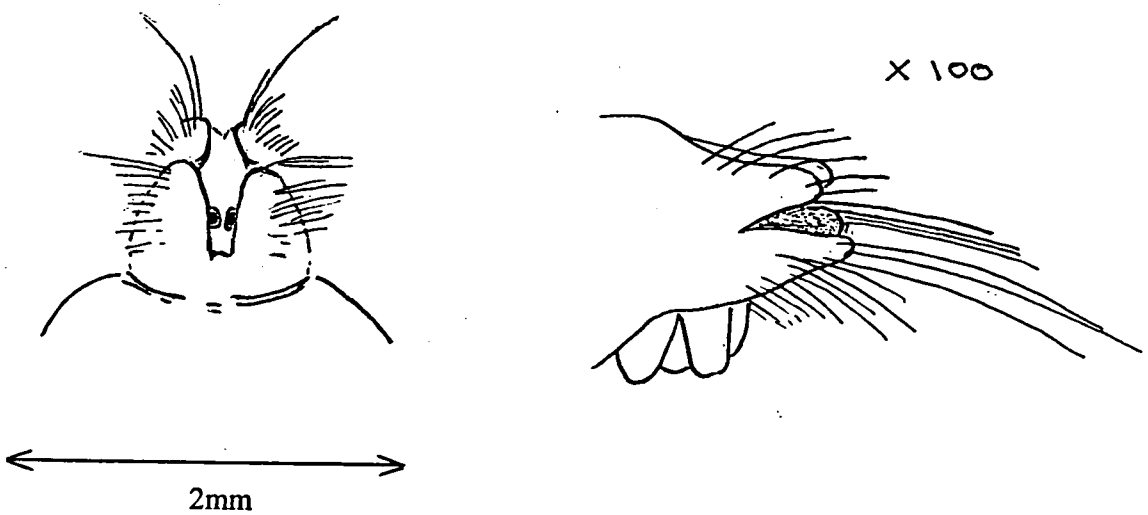
1) *T. immaculata* described in chapter 3.

2) *Limnophila meigeni* Verr. Found to be abundant previously at sites G, J, E, D, K, and B. Common at site C and scarce at sites L, F, H, A and M.

Limnophila meigeni is a peat inhabiting short-palped cranefly found prevalently on *Juncus squarrosus* moorland and in the semi-aquatic habitat of *Calluna-Sphagnum* vegetation, see section 8.4.

The larvae are characterised by the possession of very large anal palpillae and long hydrofuge (water-repelling) hairs.

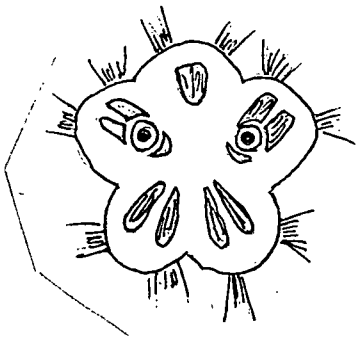
Figure 4a *Limnophila meigeni* posterior (*cf.* drawing in Nielsen, Ringdahl and Tuxen (1954).



3) *Erioptera trivialis* Mg. Found to be abundant previously at sites B and K. Scarce at sites L, G, J, H, F and M.

Erioptera trivialis is a common species occurring on *Juncus squarrosus* moorland and on the edge of small pools and streams. It is also associated with *Calluna-Sphagnum* moor and alluvial grassland (Coulson, 1959).

Figure 4b Posterior segment of *E. trivialis*. Spiracular disc size between 0.026mm for 1st instars and 0.09mm for fourth instars.



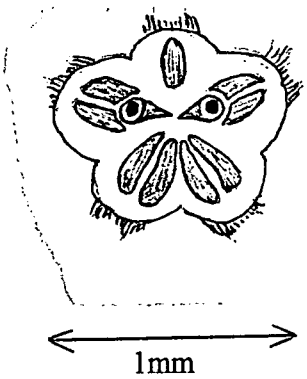
4) *Ormosia pseudosimilis* Lundstroem. Found to be abundant previously at sites D, A, M and K. Common at sites E, F, G, J, H and B and scarce at sites L.

Ormosia pseudosimilis is a common species inhabiting *Calluna* and *Juncus squarrosus* moor.

5) *Molophilus ater* Mg. Found to be abundant previously at site M and scarce at site L.

Although found commonly at Moor House Reserve *M. ater* is only abundant on one site at Chapel Fell. Both sexes are subapterous and habitat is similar to that of *Ormosia pseudosimilis.*

Figure 4c Posterior segment of *M. ater*.



6) *Limnophila pulchella* Mg. Found to be scarce previously at site B.

Limnophila pulchella is an uncommon species with adults being taken on the edge of *Sphagnum* bogs and *Eriophorum* moor. This species is recorded in the Cheetham collection as being common on the bog moors near Austwick, Yorkshire (Coulson, 1959).

7) *Limonia dilutior* Edwards. Found to be common previously at site A and scarce at sites C, J, G, F, L, K, D and M.

This is another rare species and larval habitat is not known. Coulson (1959) recorded less than ten individuals during the emergence in late July on Moor House Reserve. *L. dilutior* was collected from eight of the fourteen sites at Chapel Fell in 1992. Numbers were low on all sites though it is considered that data presented here are high for such a rare species. See also section 8 for *L. dilutior* site associations.

4.2 Collection of larvae and measurement of spiracular disc

Spiracular disc measurements were taken on all species collected from the field. The procedure for measuring the spiracular disc diameters in all species was similar to that described for *T. immaculata.* However, it was occasionally found that placing *L. meigeni* larvae vertically often led to obstruction of the discs by hair and closed lobes. Measurement was best obtained by placing these larvae horizontally on a petri dish in a small amount of alcohol and viewing the dorsal side of the anal segment.

Apart from the above modification for *L. meigeni* larvae, the procedure for measuring spiracular disc diameters was the same as that described in section 3.3.3.

4.3 Results

The frequency distributions of spiracular disc diameters for 4 of the above mentioned species are given as follows;

a) *L. meigeni* figure 4.2.2

b) *E. trivialis* figure 4.3.2

c) *O. pseudosimilis* figure 4.4.2

d) *M. ater* figure 4.5.2

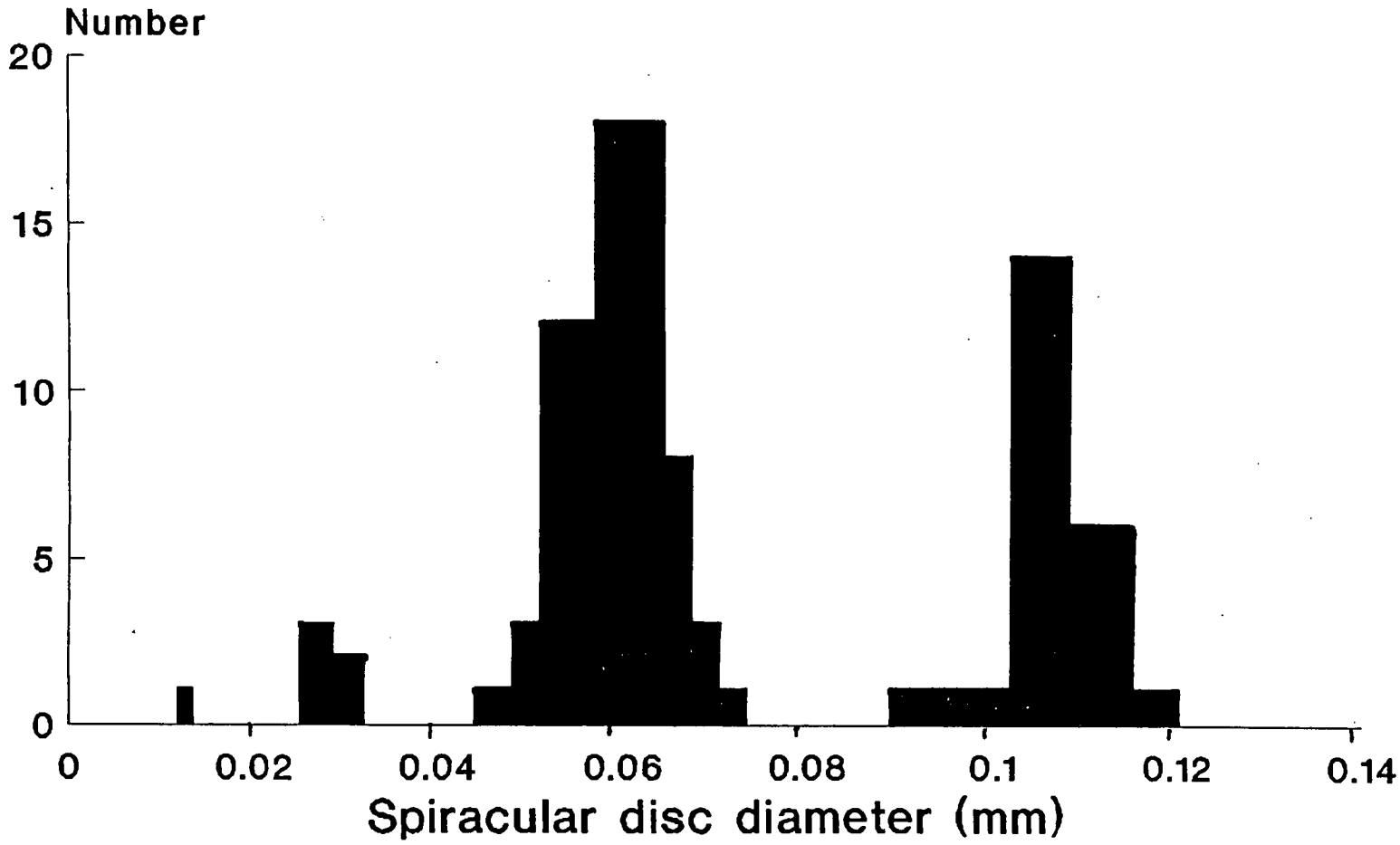


Figure 4.2.2 Maximum diameter of spiracle disc of *Limnophila meigeni* larvae. Frequency distribution histogram showing presence of 4 larval instars.

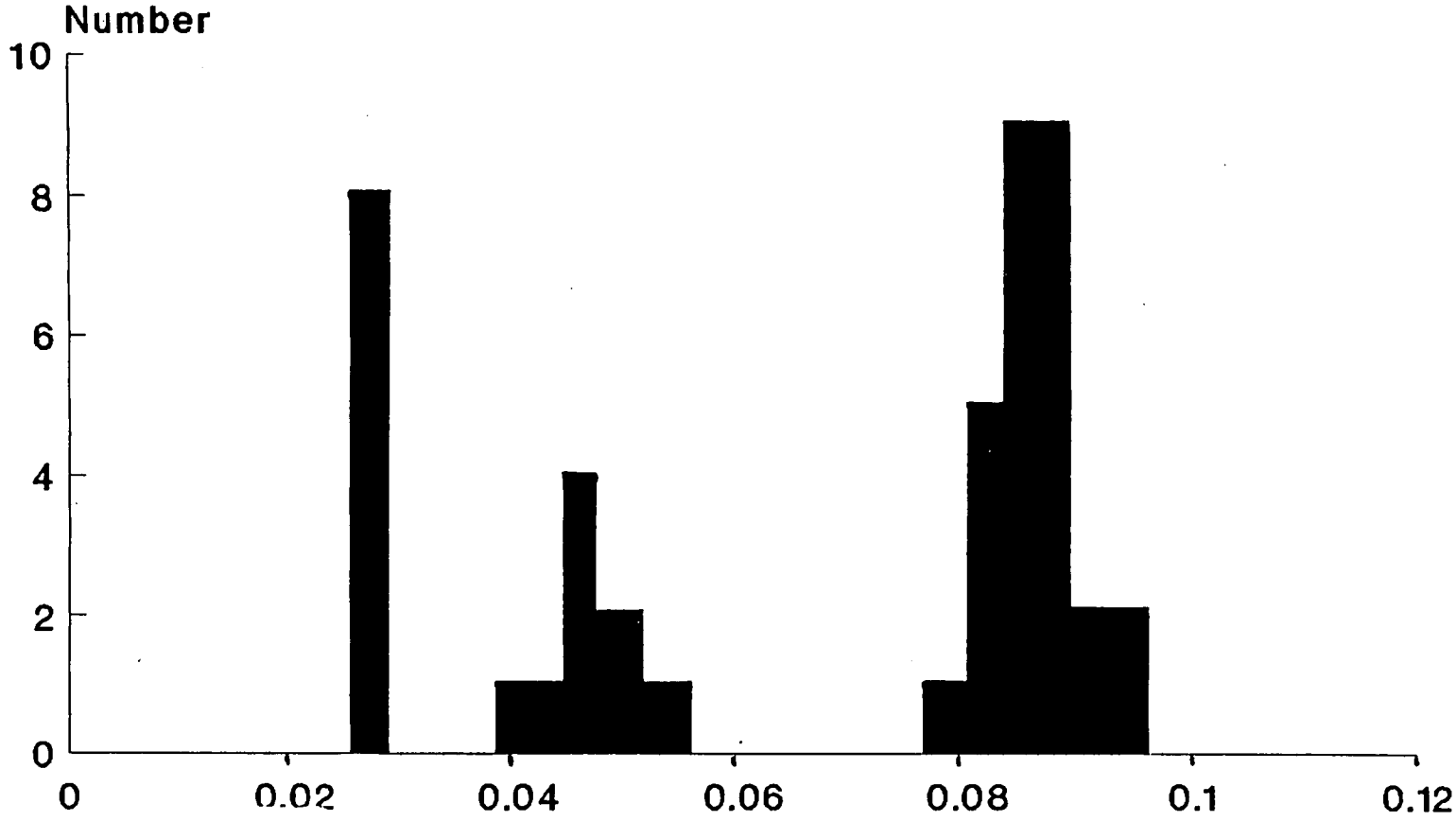


Figure 4.3.2 Maximum diameter of spiracle disc of *Erioptera trivialis* larvae. Frequency distribution histogram showing presence of 3 larval instars, the first of four instars believed missing.

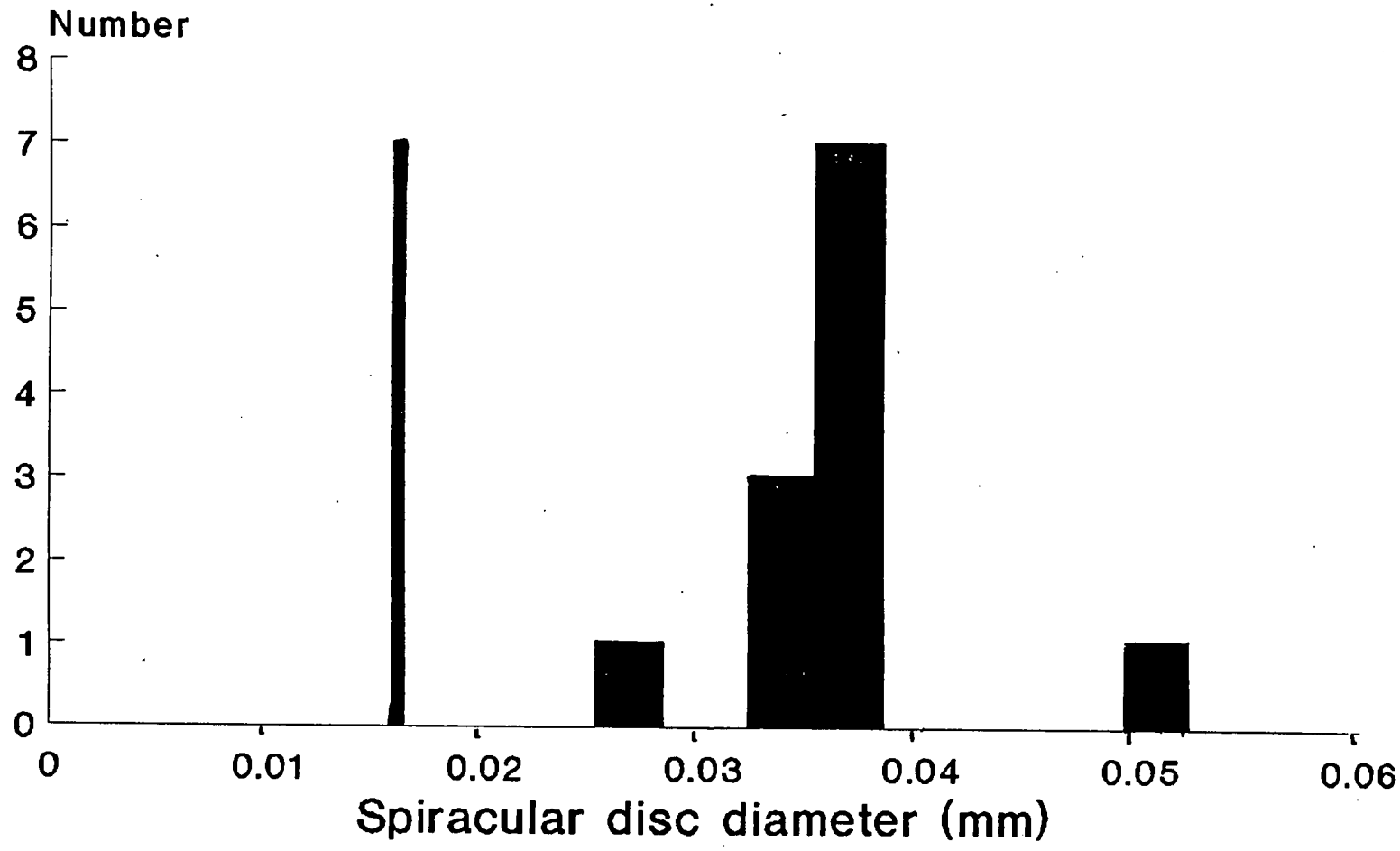


Figure 4.4.2 Maximum diameter of spiracle disc of *Ormosia pseudosimilis* larvae. Frequency distribution histogram showing presence of four larval instars.

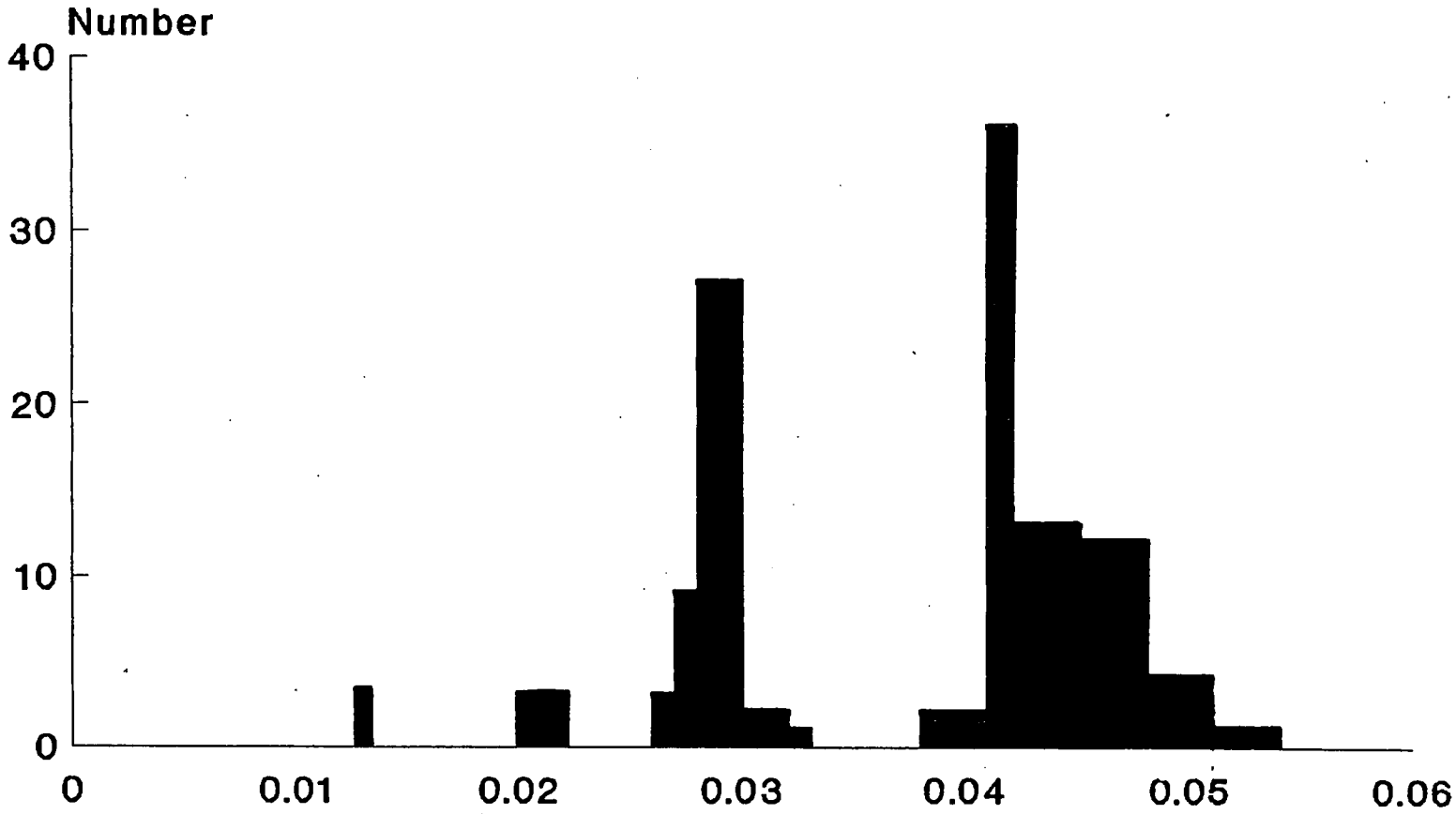


Figure 4.5.2 Maximum diameter of spiracle disc of *Molophilus ater* larvae. Frequency distribution histogram showing presence of four larval instars.

4.4 The adult stage

The sampling of adults took place throughout 1992 and 1993. For sampling procedure see section 3.4.

4.5 Results

Emergence information is presented for 1992 and 1993 in the following graphs;

a) *L. meigeni* figure 4.2.3a & 4.2.3b

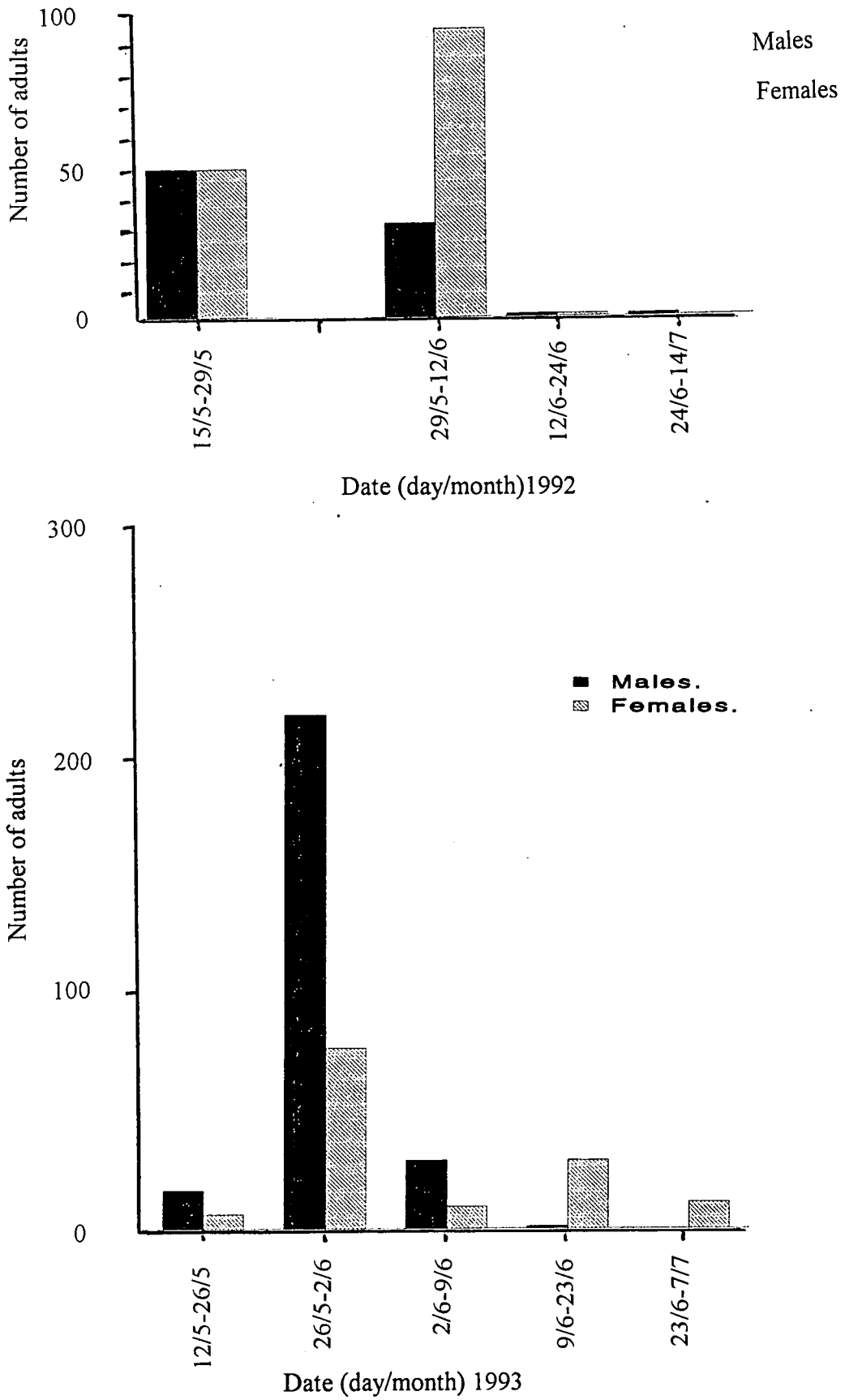
b) *E. trivialis* figure 4.3.3

c) *O. pseudosimilis* figure 4.4.3

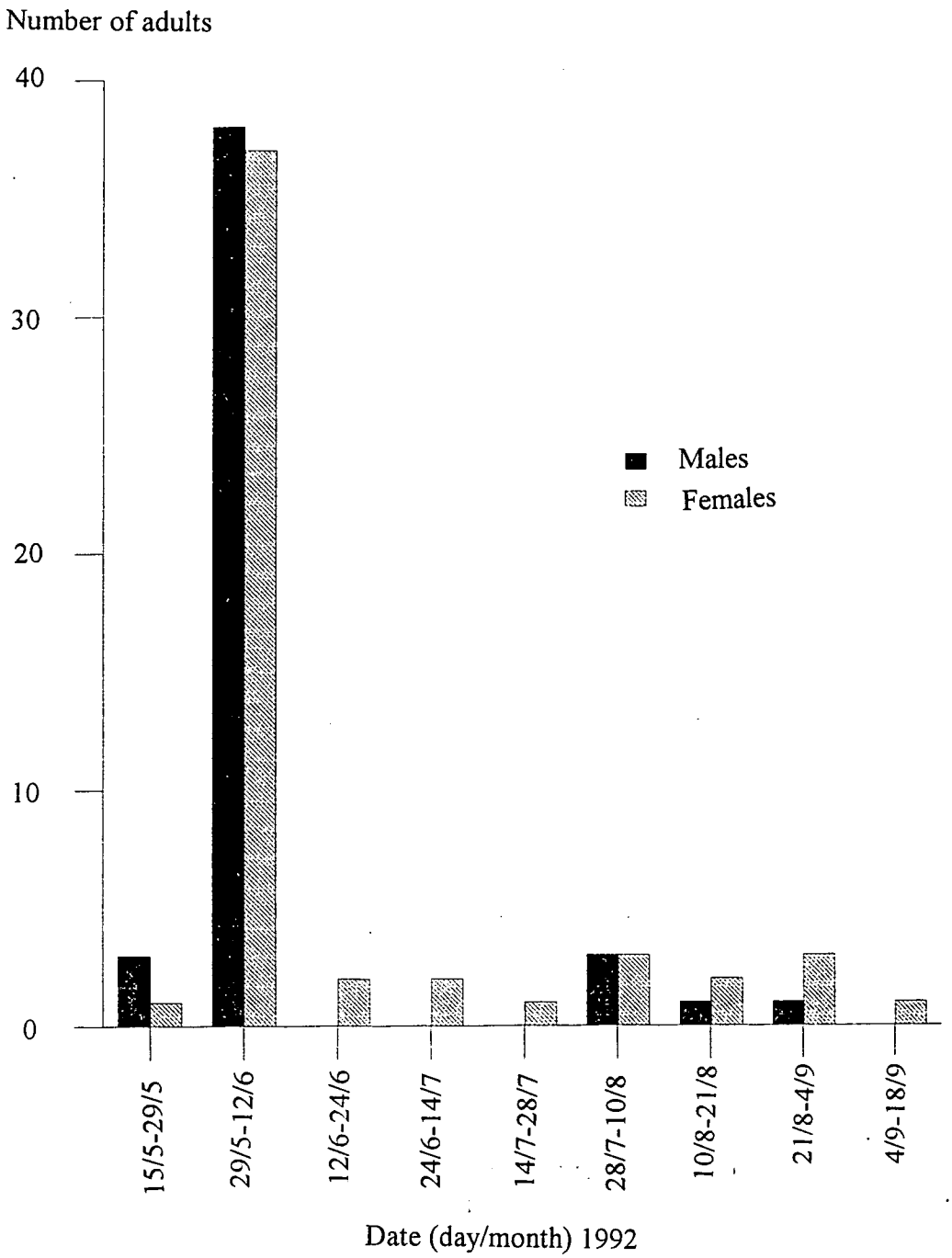
d) *M. ater* figure 4.5.3a & 4.5.3b

e) *L. pulchella* figure 4.6.2

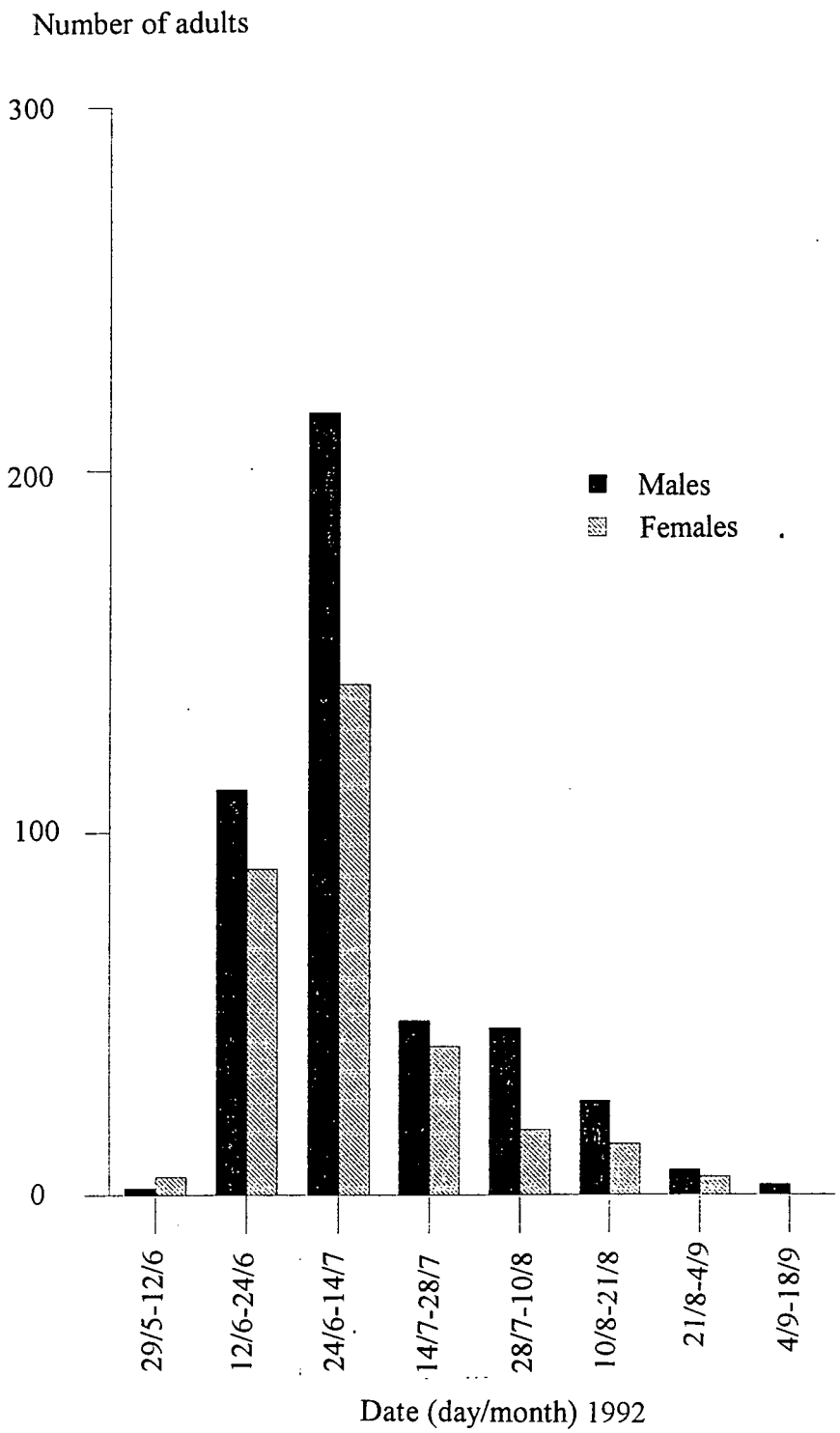
f) *L. dilutior* figure 4.7.2



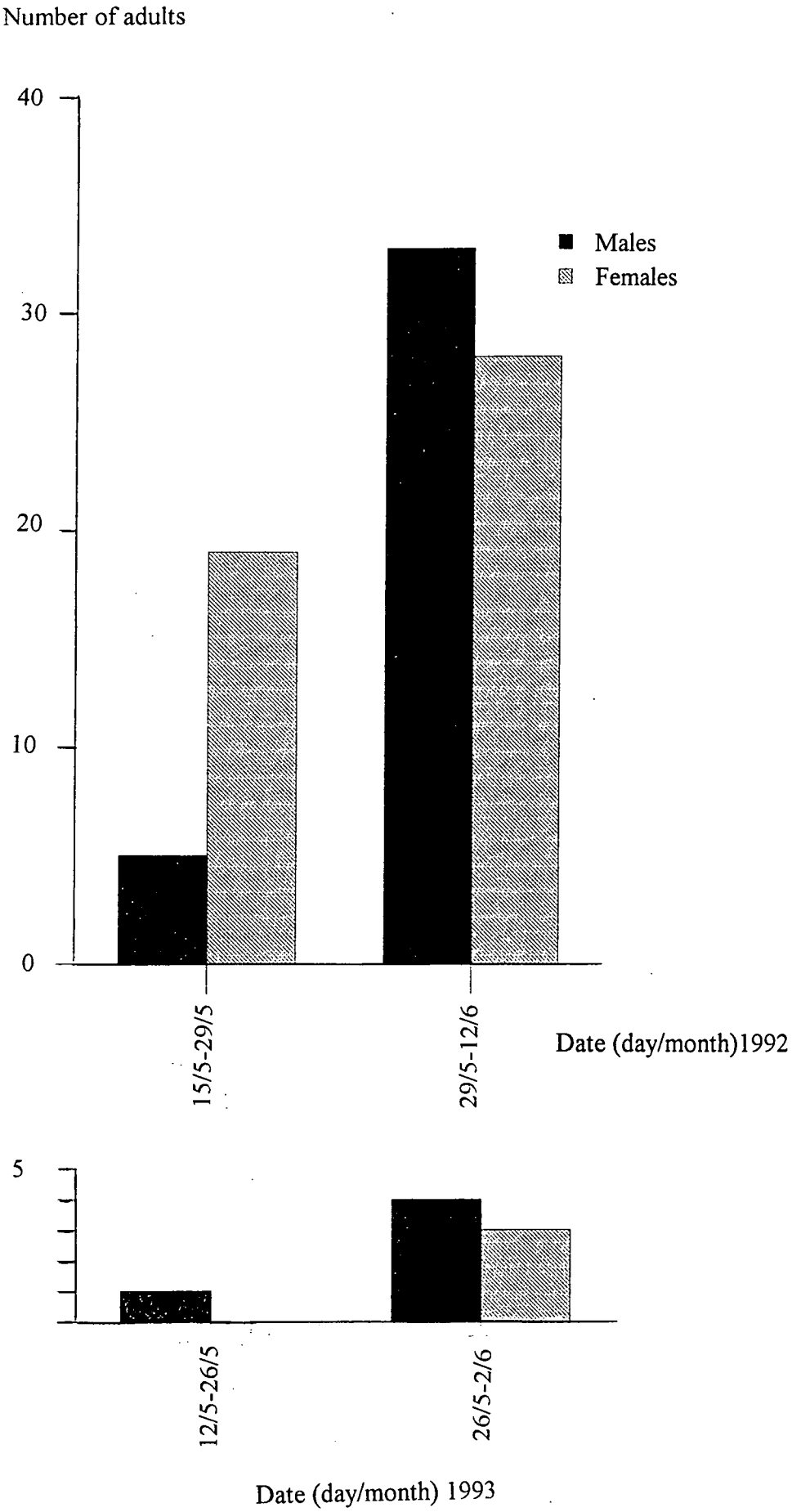
Graphs 4.2.3a & b *Limnophila meigeni* adult emergence numbers for 1992 and 1993.



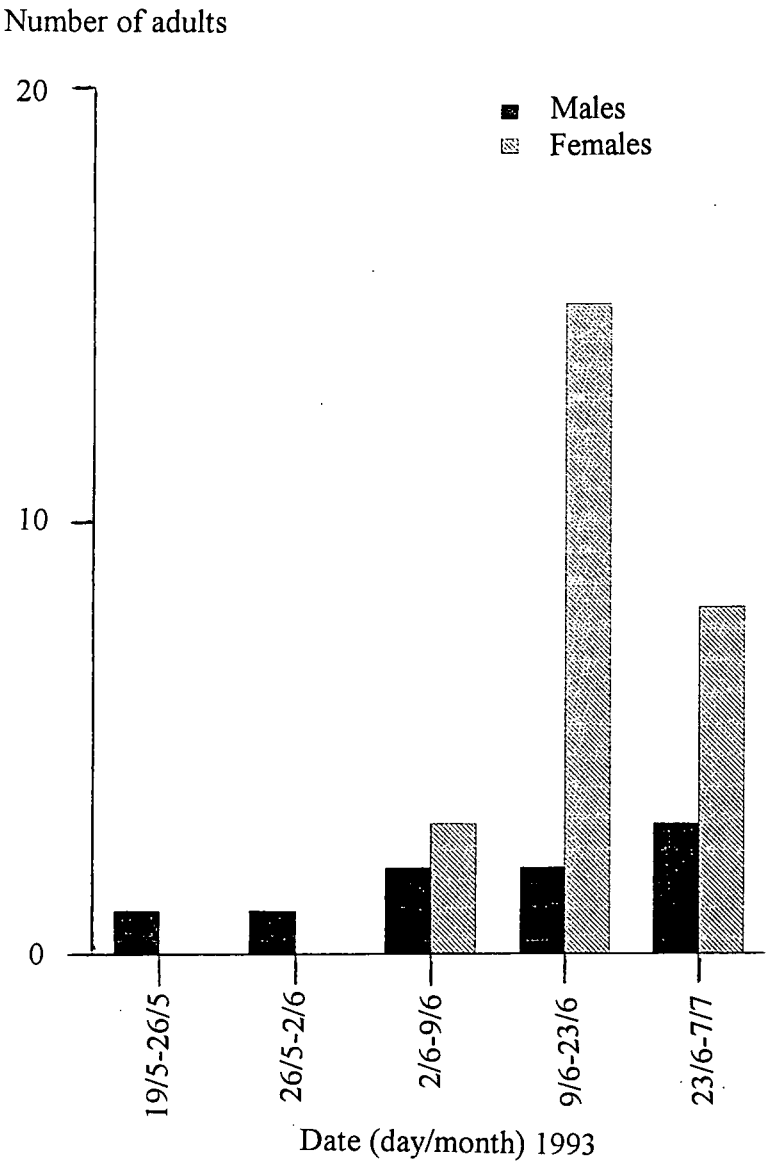
Graph 4.3.3 *Erioptera trivialis* adult emergence numbers for 1992.



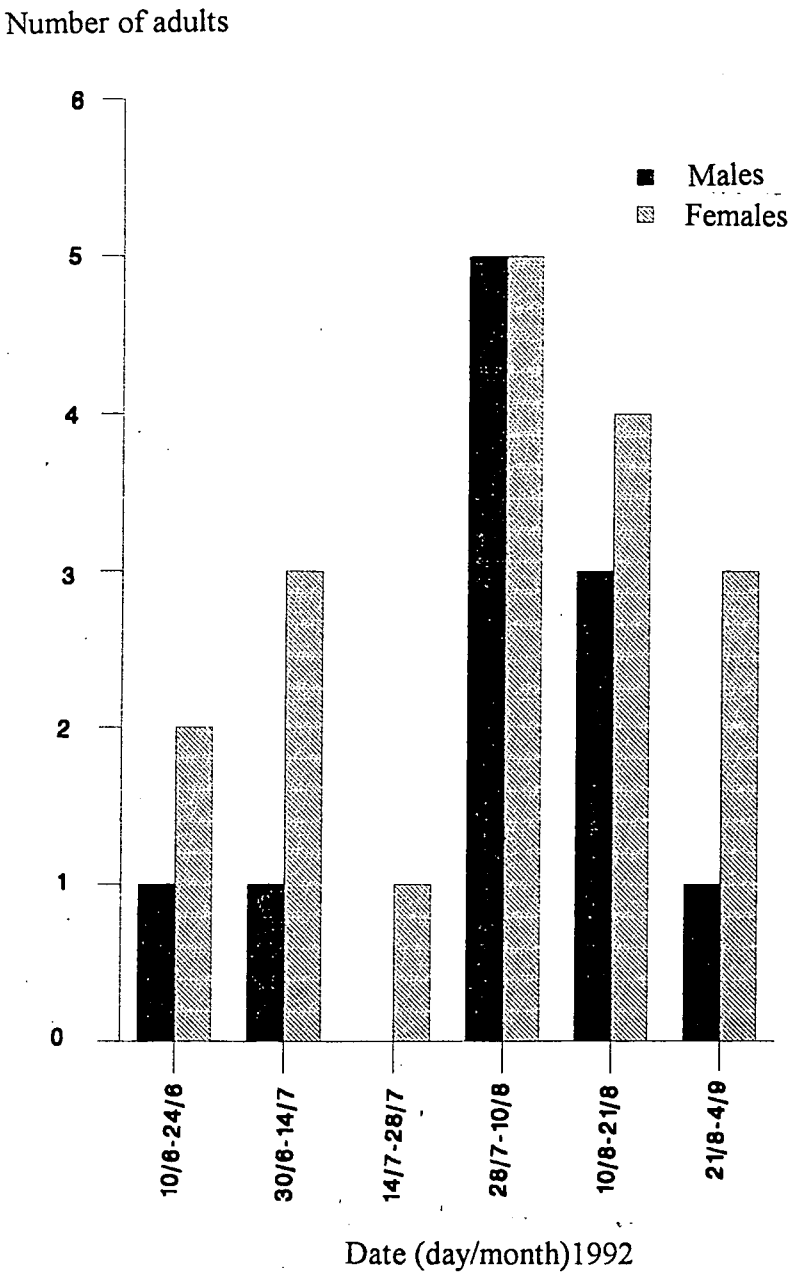
Graph 4.4.3 *Ormosia pseudosimilis* adult emergence numbers for 1992



Graphs 4.5.3a & b *Molophilus ater* adult emergence numbers for 1992 and 1993.



Graph 4.6.2 *Limnophila pulchella* adult emergence numbers for 1993.



Graph 4.7.2 *Limnophila dilutior* adult emergence numbers for 1992.

5 Emergence information on long-palped species found commonly at Chapel Fell

5.1 Introduction

Of the eight species of long-palped cranefly known to occur on Chapel Fell moorland, six of the species were observed and emergence information for (the most common of) these is given below.

The six species which were found during this study are;

1) *Tipula variipennis* Mg. Found to be scarce previously at sites J, H, F, L, A. and D.

Larvae of *Tipula variipennis* are confined to alluvial grassland areas were they are common. They have also been recorded from limestone grassland.

2) *Tipula subnodicornis* Zetterstedt. Found to be abundant previously at sites J, G, F, E, L, A, B, K, M, A and D. Common at site H.

T. subnodicornis is a very common tipulid found most abundantly on *Juncus squarrosus, Eriophorum* and *Calluna-Sphagnum* moor. Larvae have also been collected on *Sphagnum* bogland and *Calluna-Cladonia* moor.

3) *Tipula paludosa* Meigen. Found to be abundant previously at site A. Common at site L and scarce at sites J, A, K and M.

Larvae of the common *T. paludosa* occur on alluvial and limestone grassland. Adults have been taken up to an altitude of 700m at Moor House (Coulson 1959) and Barnes (1925) has recorded this species at an altitude of 500m in north Wales.

4) *Tipula pagana* Mg. Found to be abundant previously at sites A and C. Scarce at sites H, F, E, L, K, M and D.

T. pagana is a common species on alluvial grassland at Moor House (Coulson 1959). Larvae have also been recorded on limestone grassland habitat and along the alluvial sides of streams.

5) *Tipula czizeki* de Jong. Found to be scarce previously at sites J and M.

Coulson (1959) reported taking only one adult of *T. czizeki* in 1955 at a altitude of 600m. *T. czizeki* has been recorded at over 300m on the Pentland Hills, near Edinburgh and at 2,100 metres in the Alps (Brown, 1947; Mannheims, 1946-51)

6) *Tipula marmorata*, Mg. Found to be scarce previously at sites G, F, L, A and D.

Coulson (1959) reported this species as uncommon at Moor House with adults existing in local populations. Larvae were recorded from stream bed mosses and from mosses on rocks.

Further information on long-palped craneflies occurring at Chapel Fell is given in chapters 1, 6, 7 and 8.

5.2 Collection of adults

The sampling of adults took place throughout 1992 and 1993. For sampling procedure see section 3.4.

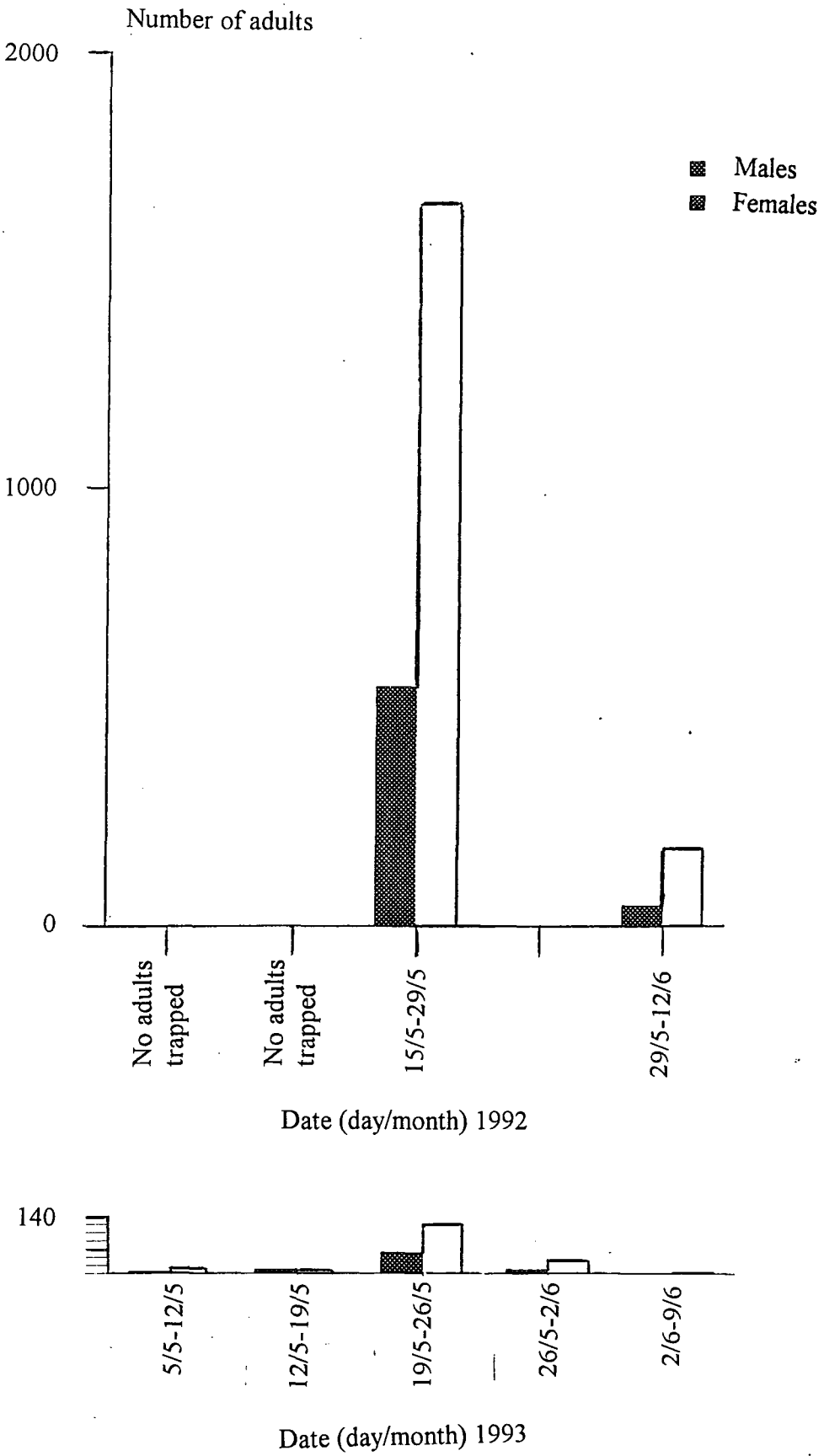
5.3 Results

Emergence information is presented for 1992 and 1993 in the following graphs;

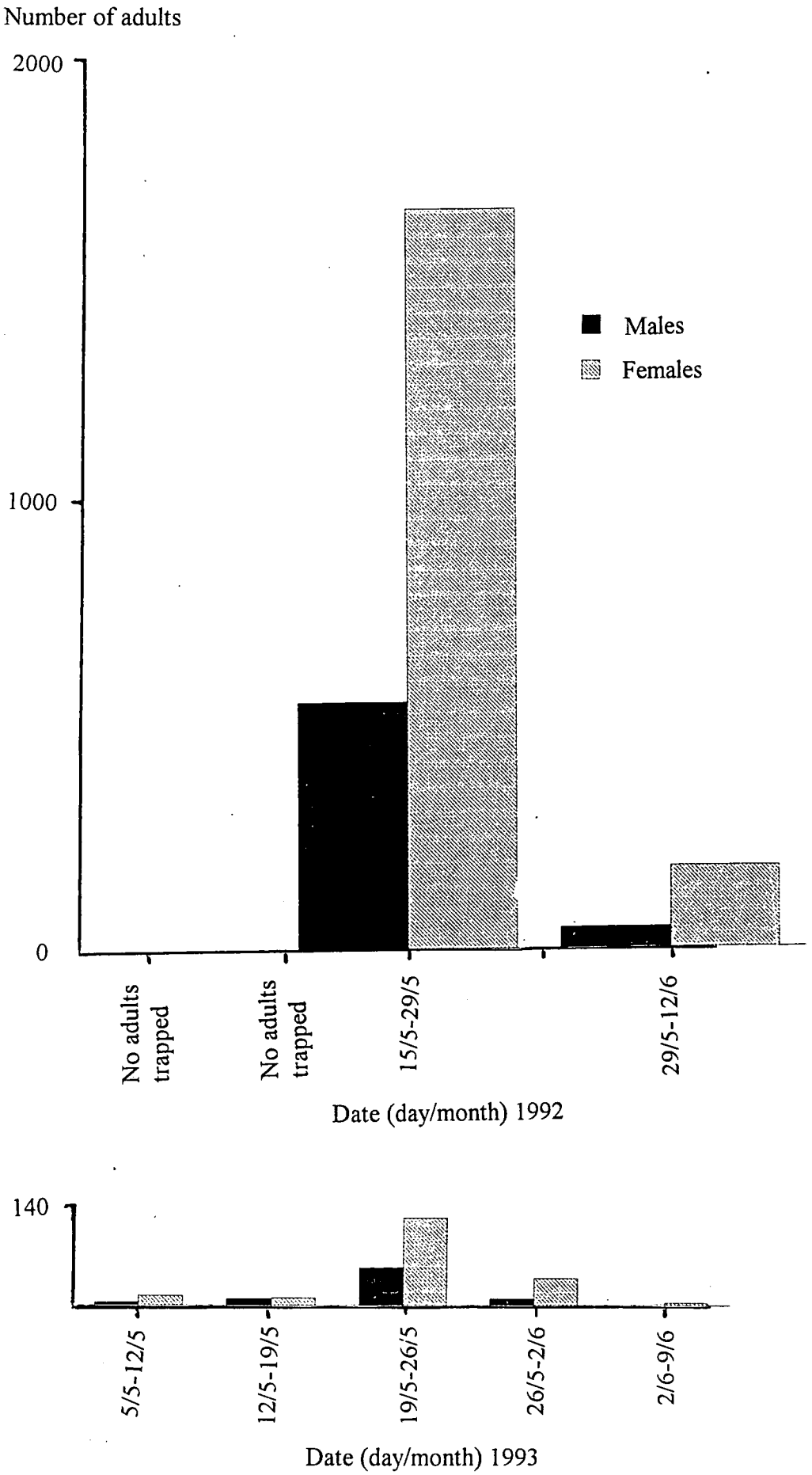
a) *T. variipennis* figure 5.2.2a & 5.2.2b

b) *T. subnodicornis* figure 2.3.2a & 5.3.2b

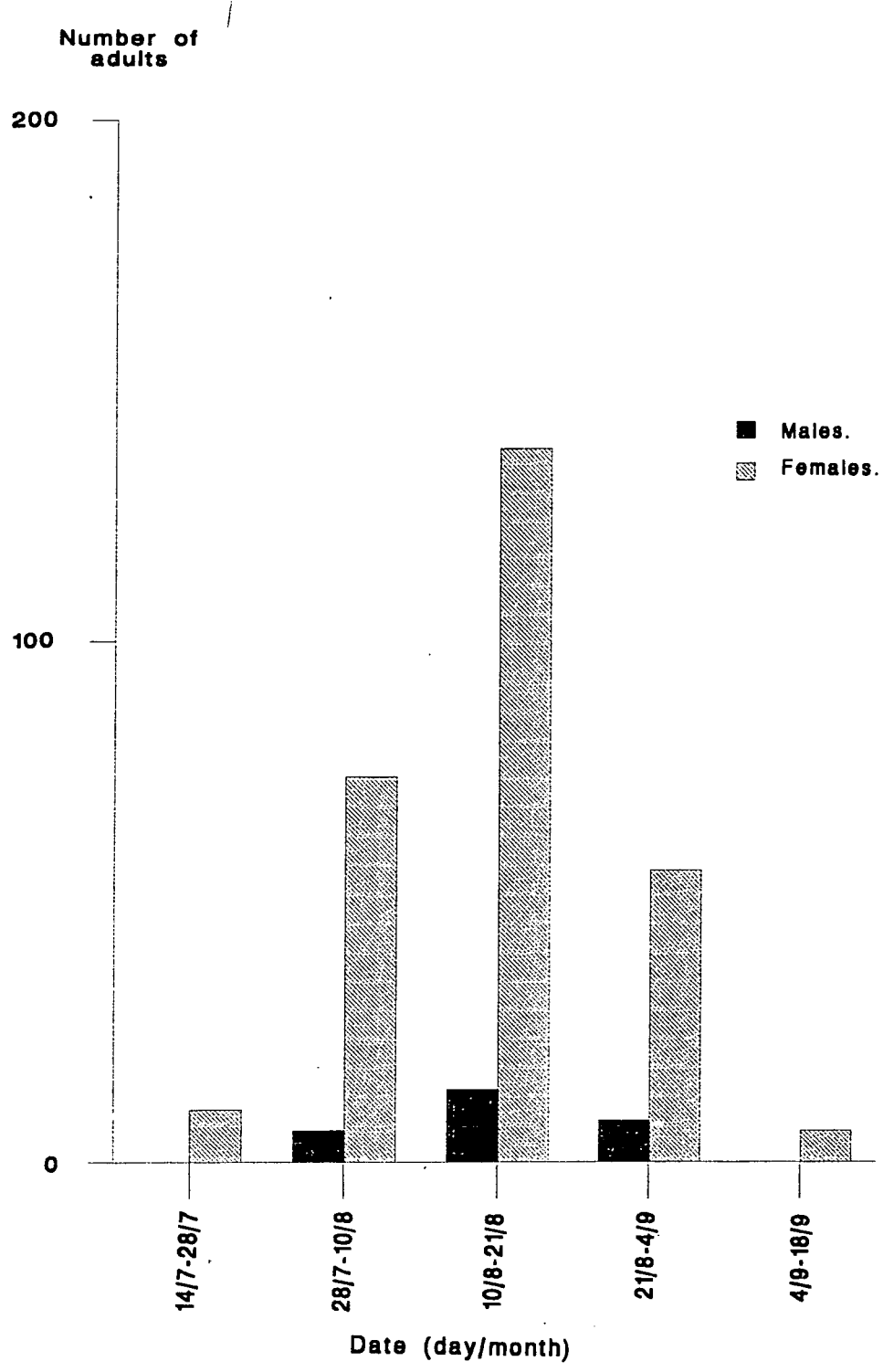
c) *T. paludosa* figure 5.4.2



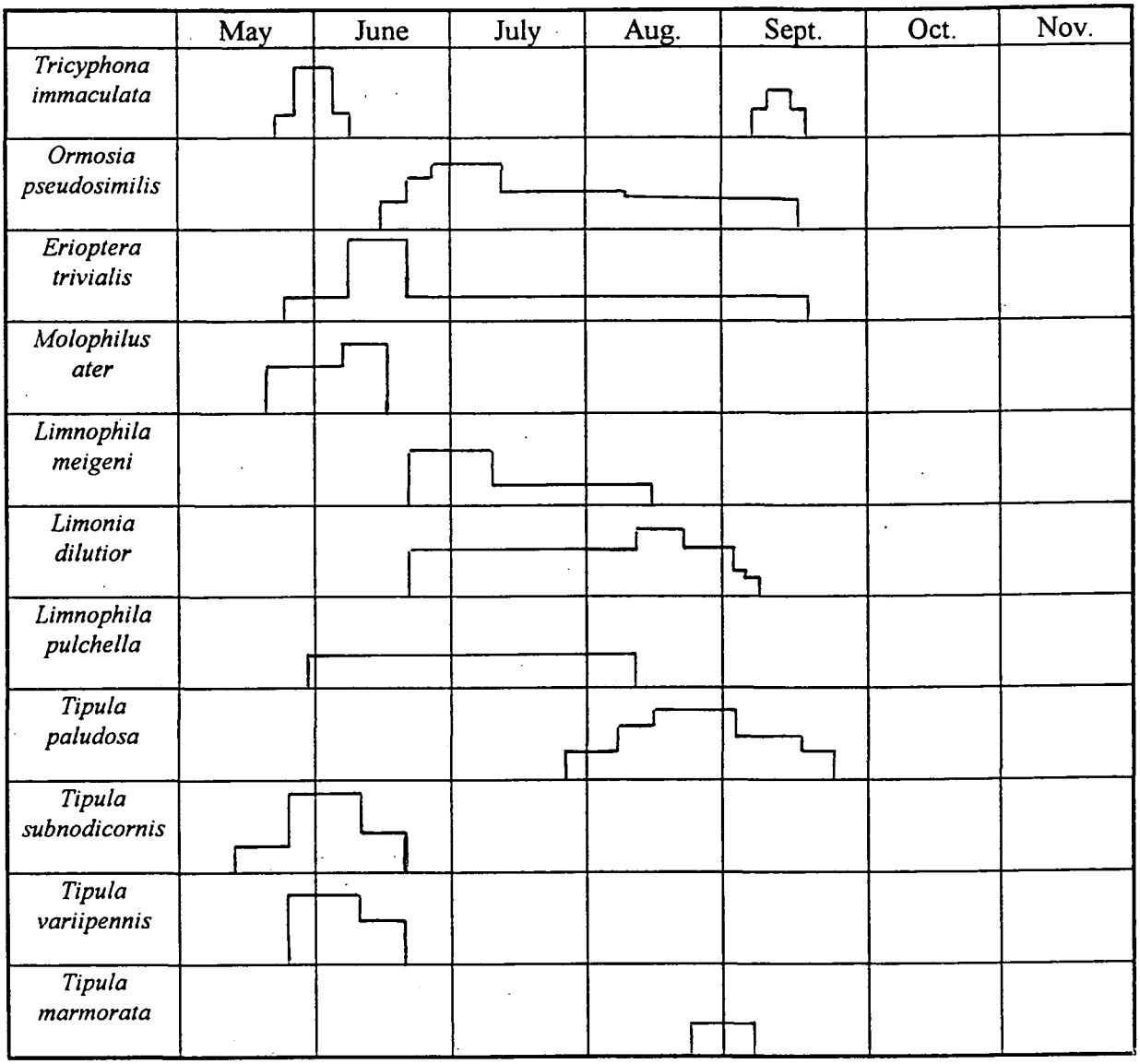
Graphs 5.2.2a & b *Tipula variipennis* adult emergence numbers for 1992 and 1993



Graphs 5.3.2a & b *Tipula subnodicornis* adult emergence numbers for 1992 and 1993.



Graph 5.4.2 *Tipula paludosa* adult emergence numbers for 1992.



5.b Seasonal distribution of common adult, short and long-palped craneflies at Chapel Fell.. (Relative scale only for each species)

6 The 1993 cranefly population crash at Chapel Fell

6.1 Introduction

Of the 14 sites used in this study between September 1992 and August 1993, 12 had been used since 1989 and sufficient pit fall data exist to assess insect population changes at Chapel Fell over the five year period 1989-1994. The 12 sites, representing the diversity of vegetation and soil type, showed dramatic fluctuations in taxa abundance between 1989 and 1991. Sensitivity of taxa groups to climatic changes varied considerably and even within specific groups, great variation was detected.

The drought of 1989 produced a marked decline in number in all taxa (with the exception of a small rise in Hymenoptera) and the diversity of response in the Tipulidae was consistent with the general trend. The noticeable exception within the Tipulidae was *Molophilus ater* which showed a 188% rise in abundance between the drought of 1989 and the relatively warm, though wet, year of 1990 (Coulson *et al.* unpublished).

High mortality has been observed to occur in *M. ater* at the egg and (to a lesser extent) in the first instar stage (Smith, 1973). High mortality has also been observed in the adult stage with an average daily elimination rate of 80% for males and 88% for females (Hadley, 1966).

Smith (1973) reports that exceptionally low rainfall in May 1970 and July 1971 may have caused the high mortality observed in egg, first and second instar stages.

With egg mortality varying between 88% and 92%, even in favourable years (Hadley, 1966), reason for the rise in *M. ater* abundance between 1989 and 1990 is difficult to explain.

Further conflict is added to the situation by the large decrease observed in *M. ater* abundance (-82%) after the following year of 1990 when climatic conditions caused a rise in all other species. *Tipula subnodicornis*, a species which emerges at the same time as *M. ater*, mirrors strongly the response of *M. ater* to climatic conditions over 1989-1991.

The duration of field work for this study was only 12 months running from September 1992 until August 1993. In preparation for the spring emergences of 1993, all pit fall

samples from 1992 were processed to provide information on species-site associations, species emergence dates and species abundance for a seasonal comparison. This background work also gave identification familiarisation to most of the species encountered in 1993. During sampling of the spring emergence of 1993 it soon became apparent that abundance of all species had fallen since 1992. The striking decline observed is now presented to illustrate how cranefly populations fluctuate greatly from season to season.

6.2 Seasonal variation in adult numbers 1992-1993

The summer of 1992 was exceptionally dry and although recording of rainfall was not undertaken, sites became progressively dried out. Pupation, emergence and activity of spring populations was not detrimentally affected as counts from pit fall sampling indicated that craneflies were abundant.

The dates of pit fall collection from 1992 were closely matched in 1993 to keep the sampling of seasonal variation as synchronous as possible. Because data for 1993 only exists from May until July, species with an emergence period progressing or occurring after July are omitted from this comparison. The species compared are *Tricyphona immaculata, Molophilus ater, Limnophila meigeni, Tipula variipennis, and Tipula subnodicornis.*

Table 6.2a A comparison of the decline in Tipulidae between 1992 and 1993 on peat (n=10 sites) and mineral soils (n=4 sites) at Chapel Fell.

Taxa	Peat		Mineral		Percentage change 1992-1993	
	1992	1993	1992	1993	Peat	Mineral
Tipulidae	2855	811	1030	99	-72%	-90%

Table 6.2b The change in abundance of five species of spring emerging Tipulidae between 1992 and 1993.

Species	No. 1992	No. 1993	% Change
T. immaculata	902	160	-82%
M. ater	85	8	-91%
L. meigeni	227	427	+88%
T. variipennis	245	53	-78%
T. subnodicornis	2426	262	-89%

Table 6.2c The extent of reduction of Tipulidae on peat (10 sites) and mineral (4 sites) soil.

Species	No. 1992 (peat)	No. 1993 (peat)	Percentage change	No. 1992 (mineral)	No. 1993 (mineral)	Percentage change
T. immaculata	655	130	-80%	247	30	-88%
M. ater	85	7	-92%	0	1	+*
L. meigeni	202	417	+106%	25	10	-60%
T. variipennis	61	26	-57%	184	27	-85%
T. subnodicornis	1852	231	-87%	574	31	-94%

Mean percentage change in five species between 1992-1993 in peat soil = -42%, variance = 7022, n = 5.

Mean percentage change in four species between 1992-1993 in mineral soil = -82%, variance = 222, n = 4.

Percentage change between 1992-1993 was not significantly different between peat and mineral soil type ($t=0.83$, $P>0.1$, d.f. = 11)

* *M. ater* did not occur on mineral habitat in 1992. Only one specimen was taken on mineral habitat in 1993.

Table 6.2d The change in abundance of five species of spring emerging Tipulidae between 1989, 1990, 1991 (From Coulson, 1991 independent report) and 1993.

Species	No. 1989	No. 1990	No. 1991	No. 1993	% Change 1989-1993
T. immaculata	1583	510	1285	151	-90%
M. ater	164	473	83	8	-95%
L. meigeni	1293	161	60	434	-66%
T. variipennis	7	12	26	53	+657%
T. subnodicornis	10295	100	524	257	-98%

Due to the limiting time span of this study and the low density of *Tricyphona immaculata* larvae observed in the field, production of a survivorship curve, the simplest description of a life table, was not possible.

The observed fluctuation in cranefly numbers from table 6.2a-c between 1992 and 1993 can be analysed and compared to that observed after the drought of 1989.

The Tipulidae decline between 1992 and 1993 generally resembles that observed between 1989 and 1990. However, in comparing the two declines it is realised that the abundance changes of *Molophilus ater* and *Limnophila meigeni* do not fit the general pattern as both species show different responses to drought.

Each of these species shows an increase in number after the droughts of 1989 and 1992, *M. ater* and *L. meigeni* respectively.

From the data collected by John Coulson, it appears that after the increase in *M. ater* abundance in response to the drought of 1989 (tables 6.2d and 6.2c), abundance of *M. ater* was reduced over the next two years from 473 specimens taken (at 12 sites) to only 85 specimens in 1992 (table 6.2c) taken (at 14 sites sampled). This result is supported by the previous studies on *M. ater*, outlined in the introduction to this section. Vulnerability of eggs and first instars to desiccation and a low population abundance probably accounts for the observed decline in *M. ater* between 1992 and 1993. One possible reason why *M. ater* was not affected by the drought of 1989 may be site stability. It seems doubtful that *M. ater's* subapterous feature restricts the expansion and dispersal of the population and question must therefore be directed towards why *M. ater* occurs in such low densities at Chapel Fell and why only two sites are used by the species.

Site specificity seems very important to *M. ater* at Chapel Fell with adults only being observed at sites L & M and larvae only being found at sites J & M. Recognising the importance of the subtle differences in habitat at Chapel Fell obviously calls for long term species population studies. Species-site stability appears to be crucial to *M. ater* and much further understanding awaits.

L. meigeni was the exceptional species observed after the drought of 1992. With all other species showing a percentage decline change between 78% and 91%, *L. meigeni*

shows a large increase of 91% in abundance. When this change is broken down into peat and mineral soils an interesting contrast arises. *L. meigeni* shows a reduction in abundance of 41% on mineral habitat and a rise in abundance of 107% on peat habitat. Although larvae of *L. meigeni* do not occur on mineral habitat the observation of less *L. meigeni* on mineral between 1992 and 1993 is not in accordance with the extent of decline on mineral habitat observed in the adults of other species.

Density dependent factors may be regulating population numbers along with the non-density-dependant factor of climate. Horobin (1971) suggests that predation by species such as *T. immaculata* may regulate numbers of *M. ater*. However, as enchytraeid worms are taken by *T. immaculata* in preference to *M. ater*, worm abundance and distribution may be the primary correlation with such tipulid population changes. Standen and Latter (1977) have shown that seasonal distribution of the enchytraeid *Cognettia sphagnetorum* varied considerably in *Calluna* and *Eriophorum* habitat but not in *Sphagnum*. The moisture content of habitat was positively correlated with worm numbers and given that moisture is known to influence the distribution of enchytraeids and that worms are aggregated during the summer months, worm density and decomposition rate may affect tipulid numbers.

It is shown in section 8.4 that *L. meigeni* is more abundant in *Sphagnum* than in *Nardus* vegetation unlike the situation found in *M. ater*. The anatomical observation that *L. meigeni* possesses large anal palpillae and long water-repelling hairs compared to *M ater* is believed to be important in terms of osmoregularity capability. Environmental constraint due to physiological factors is beyond the scope of this thesis, however it is predicted that of all the short-palped craneflies encountered at Chapel Fell, both *T. immaculata* and *L. meigeni* are physiologically adapted to withstand high external water potentials. The ability of *Sphagnum* to retain water over long periods of drought, under subjection of a high wind evaporation factor, may be the primary reason for *L. meigeni's* observed abundance rise between 1992 and 1993. The warm temperatures of 1992 aiding the species development and reducing mortality.

Table 6.2d signifies the extent of fluctuation in cranefly populations between 1989 and 1993. In 1989 the number of *T. subnodicornis* collected was 10,295. Before the decline in number recorded in 1993, the 1992 collected total equalled a mere 2,426. It is

apparent that such a drought as that in 1989 may have long lasting affects. After two drought-free years (1990-1992) only a quarter of the original density of *T. subnodicornis* was regained. *T. variipennis* deserves attention here for unlike other species which have dwindled in number since 1989, *T. variipennis* has increased from a low 7 specimens trapped in 1989 to 245 specimens trapped in 1992. This was then reduced by 75% by the drought of 1992. However, even with this loss, *T. variipennis* still shows a 657% rise in abundance since 1989. When this is placed alongside the 98% decline (measured over the same span of time), observed in *T. subnodicornis* it may be said that the situation is of great interest and deserves further work.

7 Egg development in *Tipula czizeki*

7.1 Introduction

Tauber *et al.* (1986) speculated that variability observed over emergence dates may be a form of "bet hedging" against adverse and fluctuating environmental conditions.

Butterfield and Coulson (1988) showed that eggs of *Tipula pagana* develop more slowly and hatch less synchronously at 10°C than those of spring and summer emerging craneflies. Long day length (light-dark 18:6) increased both the rate of development and the degree of hatching synchrony.

Pritchard (1983) has reported egg diapause in three other species of Tipulidae with overwintering eggs; *Tipula czizeki, Tipula staegeri* and *Tipula luteipennis.* As the original sources of information (Laughlin, 1967; Freeman, 1967) offer no supporting evidence for diapause occurring in these species, investigations are required to establish the extent of egg adaptations to the adverse conditions during winter.

T. czizeki, a species of low abundance at Chapel Fell, emerging over September and October, was used in a study similar to that carried out by Butterfield and Coulson (1988) on *T. pagana* and also to the study detailed in section 3.2.4 on *Tricyphona immaculata.*

7.1a The effect of photoperiod on egg development in *T. czizeki*

Sampling of *T. czizeki* occurred in early September 1992 and adults were of very low density and proved difficult to find. (Only one adult was taken by pit fall for the month of September, two in October.) It had been hoped to test the rate of development in *T. czizek* eggs to temperature. However, only two adult females were found after much searching and it was thereafter decided to concentrate all eggs laid into two mixed batches for photoperiod response evaluation. These two batches contained 60 eggs each. Both were inspected daily and kept moist with cold water.

Photoperiod was controlled using two cabinets set to regimes of light-dark 18:6 and light-dark 6:18. Temperature of both cabinets was 10°C.

The results of the investigation are given in graphs 7.1 a and b.

Mean hatching date for eggs in light:dark; 18:6hr regime = 113 days, varience = 11. n = 54.

Mean hatching date for eggs on light:dark; 6:18hr regime = 110 days, varience = 6. n = 31.

Significant difference of means, $t = 3.22$, $P<0.01$, d.f.=40.

A small number of eggs from both photoperiod batches were moved from 10°C to 15°C (same light cycles) at 57 days into their development. Emergence dates are given below.

Table 7.1 Hatching distribution of *Tipula czizeki* eggs moved from 10°C to 15°C at 57 days into development

Light:dark; 18:6hrs Days to development	No. of larvae	Light:dark; 6:18hrs Days to development	No. of larvae
70	1	84	2
72	1	85	2
84	2	86	1
88	1	90	1
92	1	91	1
95	2	94	1
120	1		

As a means of comparing the eggs diapause situation in *T. czizeki* with that observed in the overwintering eggs of *T. pagana*, the hatching distribution of *T. pagana* eggs (subjected to the same conditions used on eggs of *T. czizeki*) is presented below (from Butterfield and Coulson, 1988.)

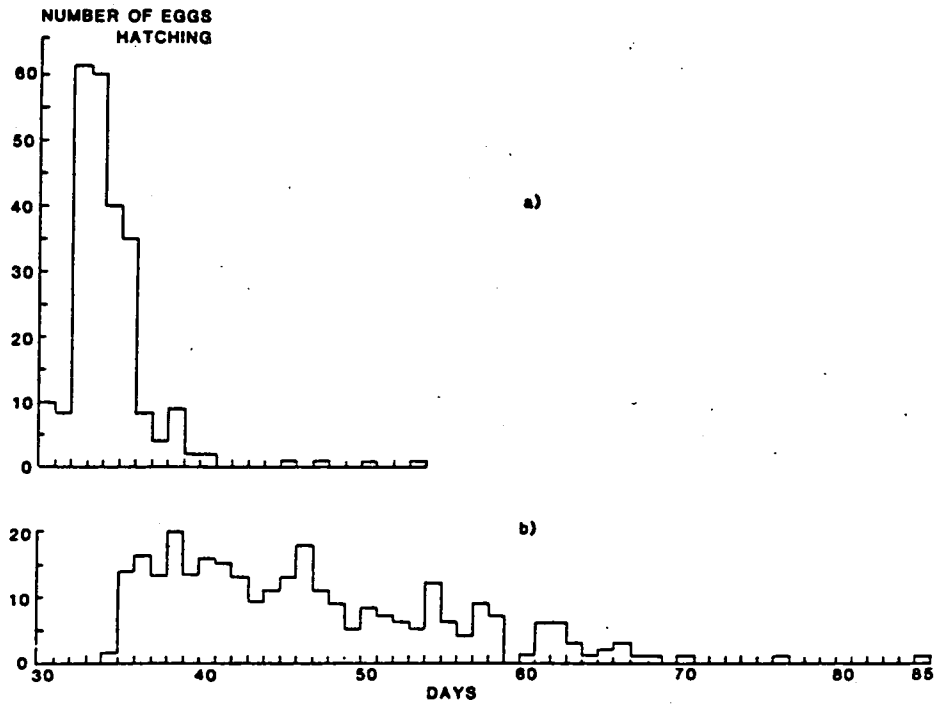


Fig. 1. The distribution of hatching of *T. pagana* eggs kept at 10°C under (a) light–dark 18:6 and (b) light–dark 6:18.

7.2 Discussion.

In comparing the hatching distributions of *T. czizeki* eggs with eggs of *T. pagana* a number of striking differences are noticed. Firstly, *T. czizeki* eggs do not respond to the same extent to long and short photoperiod regimes. Secondly, eggs of *T. czizeki* take far longer to develop at 10°C than eggs of *T. pagana* at the same temperature.

The last recorded hatching date for *T. pagana* eggs on the inhibiting short day length regime is at 85 days, approximately five days before the first hatching of a *T. czizeki* larvae.

The synchronising effect of long day length observed in *T. pagana* eggs is not important in the synchronisation of hatching in *T. czizeki* eggs. In *T. czizeki* both photoperiod regimes produced a spread of hatching over 40 days. Although this spread can be compared to that of *T. pagana* eggs on a long day length cycle, the emergence of *T. pagana* larvae on such a cycle is synchronous.

Rapid development at low temperatures has been reported in eggs of the grasshopper *Melanopus sanguinipes* (Hilbert *et al.* 1985) and further work is required on *T. czizeki* to evaluate the response of eggs to a temporary drop in temperature. If development is slowed further by a lower temperature than 10°C, larvae of *T. czizeki* are adapted to hatch well after the adverse conditions of winter are over. Development may be independent of temperature as is the case in larvae of *M. ater* (Coulson *et al.* 1976). Such metabolic independence to temperature has also been suggested to occur in poikilotherms (Newell, 1966). If egg development is independent of temperature this would be yet another adaptation for living over a wide range of altitudes and considerable mean annual temperature variation. Alternatively it may also be the case that development is faster at lower temperatures as shown in *Dasychira pudibunda* (Lepidoptera, Orgyidae) (Geyspitz and Zarankina, 1963). Both of the above situations seem unlikely as eggs of *T. czizeki* moved from 10°C to 15°C hatch earlier and therefore development appears dependant of temperature. Before further comment can be made regarding the development of *T. czizeki* eggs, information is obviously required on the response of eggs to temperatures encountered in the field.

8 Species-site habitat associations

8.1 Introduction

The purpose of this section is merely to give an indication of where, and in what numbers, species occur at Chapel Fell. The fourteen sites used in this study, chosen to represent the diversity of vegetation and habitat type, have been described in section 2 and reference to sites during this chapter will be by site name and not by vegetation common to the site (with the exception of table 8.2.1). Due to the technique used to extract animals from peat (see section 3.3.2) only short-palped larvae were obtained, identified and recorded between October 1992 and February 1993. Previous studies on tipulid species-habitat associations are given in section 1, 4 and 5.

Larval densities were recorded for all sites from October 1992 to January 1993. Adult-site association data is presented for 1992.

8.2 Habitats of short palped craneflies at Chapel Fell

8.2.1 Species-site larval densities

Preliminary studies on larval densities at Chapel Fell occurred during October 1992. All sites were sampled and species-site occurrence information is presented below.

Table 8.2.1 a Site occurrence of short palped larvae at Chapel Fell, October 1992.

Species	Occurrence sites in descending density ( )=same larval density	Water scale of sites 1-12	Site plant species in descending abundance	Organic content of sites %
T. immaculata	**J, K, (B, G)**	10, 11, 12, 8	*E. vaginatum, D. flexuosa, C. vulgaris.*	99, 99, 99, 96.
L. meigeni	**K, E,(B, D, J)**	11, 7, 12, 9, 10	*E. vaginatum, D. flexuosa.,*	99, 97, 99, 89, 99.
E. trivialis	**(K, B) G, E**	11, 12, 8, 7	*E. vaginatum, D. flexuosa, C. vulgaris.*	99, 99, 96, 97.
O. pseudosimilis	**G, E, K**	8, 7, 12	*E. vaginatum, C. vulgaris, Grasses, N. stricta, D. flexuosa.*	96, 97, 99.

Water scale in ascending order of holding potential, calculated by averaging soil water contents taken during 89-91. Site order = **C,F,L,A,M,H,E,G,D,J,K,B.**

C,F,L and **A** are mineral sites.

Organic content % of soils in descending order; (**B,J,K** = 99), (**H,E** = 97), **G** = 96, **D** = 89, **L** = 61, **F** = 44, **C** = 33, **A** = 27.

M. ater was not found until December at site **J** and later at site **M.**

Following this investigation six sites were chosen which contained the highest densities of five species of short-palped cranefly. These sites were sampled fortnightly between November 1992 and February 1993. This information is presented in Graph 8.2.1 b.

Larvae of *T. immaculata* were observed to occur solely at sites B, G, K and J. Sampling effort for those three sites is presented in tables 8.2.1 c.

Graph 8.2.1b Density of five species of short-palped cranefly at six sites at Chapel Fell. Mean total with 95% confidence limits.

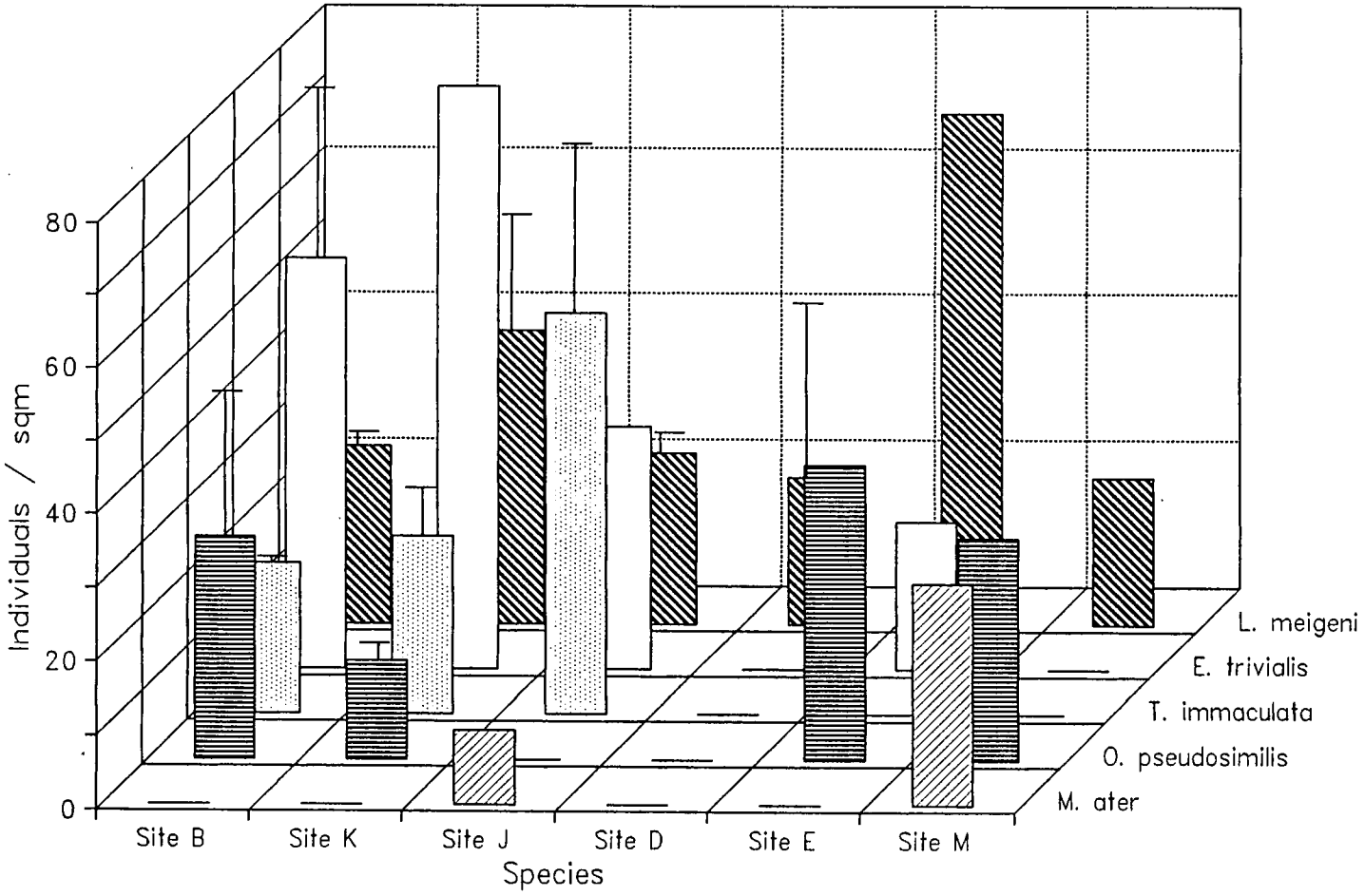


Table 8.2.1c Density of five species of cranefly at three sites on Chapel Fell moor, October-December 1992.

	Site B	Site K	Site J
Species	Average no./sqm	Average no./sqm	Average no./sqm
Erioptera trivialis	56.0	80.0	33.0
Limnophila meigeni	24.3	40.0	23.3
Molophilus ater	0.0	0.0	10.0
Ormosia pseudosimilis	30.0	13.3	0.0
Tricyphona immaculata	20.3	24.0	54.7

8.2.2. Species-site adult numbers

Sampling of adults took place between September 1992 and August 1993 using the methods described in section 3.4.2. Data, beginning May 1992, was obtained by processing specimens taken before commencement of my own field work in September. Emergence information for short-palped species in 1992 is presented in tables 8.2.2 a-f.

Table 8.2.2a & 8.2.2b

Emergence information for *Tricyphona immaculata* during 1992.

Site	Date							
	29/5		12/6		4/9		18/9	
	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females
A	60	32	1	1				1
B								1
C	28	13	27	6				
D	15	23	7	19				
E	5	9	3	19		1		
F	11	7	9	12				
G	6	2	1	9		2		
H			2	1				
J	41	25	1	14				
K	20	12	15	14		1		1
L	12	19	2	6				
M	195	42	70	74				
N	2	1						
P		2						
Total	395	187	138	175	0	4	0	1

Emergence information for *Molophilus ater* during 1992.

Site	Date			
	29/5		12/6	
	No. males	No. females	No. males	No. females
M	5	19	33	28
Total	5	19	33	28

Table 8.2.2c

Emergence information for *Limnophila meigeni* during 1992.

Site	Date							
	29/5		12/6		24/6		14/7	
	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females
A	2	3		5				
B	1		16	24				
C				6				
D				8				
E		1		8		1		
F				1				
G				11				
H				1				
J	42	36	9	15	1			
K	1	1	5	12				
L	2	6						
M	1	2	1	3				
N				1				
P							1	
Total	49	49	31	95	1	1	1	0

Table 8.2.2d

Emergence information for *Erioptera trivialis* during 1992.

Site	Date																	
	29/5		12/6		24/6		14/7		28/7		10/8		21/8		4/9		18/9	
	No. males	No. f.s	No. males	No. f.s	No. males	No. f.s	No. males	No. f.s	No. males	No. f.s	No. males	No. f.s	No. males	No. f.s	No. males	No. f.s	No. males	No. f.s
A			3															
B	2		25	24		1					1	2						
C																1		
D																		
E		1		2														
F																		
G				2							1	1						
H																		
J	1			1				1		1								
K			10	7		1		1			1		1	2	1	2		1
L																		
M				1														
N																		
P																		
Total	3	1	38	37	0	2	0	2	0	1	3	3	1	2	1	3	0	1

Table 8.2.2e

Emergence information for *Ormosia pseudosimilis* during 1992.

Site	Date															
	12/6		24/6		14/7		28/7		10/8		21/8		4/9		18/9	
	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No females	No. males	No. females
A	2	1	9	6	16	6	2		2	1	3	1	1			
B																
C			3	8	3	9			1	4	2	2				
D			2	3		3		2		2	2	1	3	2	2	
E			7	5	8	15	2	2			2					
F				2	1	2		6			2			1		
G					8	6	4	1	4	1	3	1				
H								1			1	3	3	2		
J			1	2	16	4		2								
K			1		7	4	4	5			1					
L					2	2	1									
M	1	2	89	64	155	90	31	21	35	10	1	2				
N							2		4		9	4			1	
P		1					2	1								
Total	3	3	112	90	216	141	48	41	46	18	26	14	7	5	3	0

Table 8.2.2f

Emergence information for *Limonia dilutior* during 1992.

Site	Date											
	24/6		14/7		28/7		10/8		21/8		4/9	
	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females
A							1	1		1		
B												
C								1				
D						1						
E												
F							1	1				
G												
H	1	1		1					1		1	1
J												
K												
L			1							1		
M												
N							2		1	1		2
P		1		2			1	2	1	1		
Total	1	2	1	3	0	1	5	5	3	4	1	3

8.3 Habitats of long palped craneflies at Chapel Fell

8.3.1 Species-site adult numbers

Sampling of adults took place between September 1992 and August 1993 using methods described in section 3.4.2. Data, beginning May 1992, was obtained by processing specimens taken before commencement of my own field work in September. Emergence information for 1992 is presented in tables 8.3.1 a-c.

Table 8.3.1a

Emergence information for *Tipula subnodicornis* during 1992.

Site	Date			
	29/5		12/6	
	No. males	No. females	No. males	No. females
A	6	11	1	1
B	7	31	4	18
C	10	97	8	21
D	31	166		19
E	26	45	1	6
F	9	74	1	6
G	14	46		
H	1	2		
J	90	348		10
K	19	176	7	33
L	68	236	6	19
M	268	417	18	47
N		1		
P	1			
Total	550	1650	46	180

Table 8.3.1b

Emergence information for *Tipula variipenis* during 1992.

Site	Date					
	29/5		12/6		24/6	
	No. males	No. females	No. males	No. females	No. males	No. females
A	5	30		2		
B						
C		2		2		1
D						
E						
F				2		
G						
H						
J	7	8		1		
K	3			2		
L	31	101	5	2		1
M	2	16	3	14		3
N				1		
P		1				
Total	48	158	8	26	0	5

Table 8.3.1c

Emergence information for *Tipula paludosa* during1992.

Site	Date									
	28/7		10/8		21/8		4/9		18/9	
	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No. females	No. males	No females
A		6	3	25	4	33	3	20		2
B						1				
C				10	1	25				1
D				2		3		2		
E										
F				2	1	18		4		
G				1				3		
H						1		1		
J								1		1
K								1		
L		3	3	23	8	38	4	21		2
M		1		11		16	1	2		
N						2		1		
P										
Total	0	10	6	74	14	137	8	56	0	6

8.4 *Tricyphona immaculata, Limnophila meigeni* and *Molophilus ater*

Habitat associations, Moorhouse National Nature Reserve.

Previous information given in Chapter 4 outlined habitat associations previously known to exist between the short-palped crane flies of Moor House Nature Reserve.

During this study two visits were made to the bog end site at MoorHouse to evaluate the density of *T. immmaculata* larvae. 25 sod samples produced the information presented in table 8.4.

Table 8.4 Densities of 3 species of short-palped cranefly recorded at Bog end, Moor House on 1.12.92. Sample size = 25 sods.

Species	Mean/sqm	S.E
Molophilus ater	420	0.24
Limnophila meigeni	100	0.08
Tricyphona immaculata	120	0.12

As bog end consisted of both *Sphagnum* and *Nardus* vegetation, a second trip to MoorHouse was arranged in an attempt to identify the type of habitat favoured by each species.

Abundances of *T. immaculata, L. meigeni* and *M. ater* in two different habitats are presented in table 8.4b.

Table 8.4b Distribution of 3 species of short-palped cranefly recorded in *Nardus* and *Sphagnum* habitat at bog end, Moor House, 8.12.92.

Species	*Sphagnum*		*Nardus*		Total
	Observed	Expected	Observed	Expected	
Tricyphona immaculata	14	6.84	3	10.16	17
Limnophila meigeni	35	20.53	16	30.47	51
Molophilus ater	15	36.63	76	54.37	91
Total	64		95		159

all expected frequencies exceed 5.0

$X^2 = 50.99$, degrees of freedom = 2

The two different habitats house highly significant different numbers of the 3 species of cranefly. There is therefore an association between the type of habitat and the proportion of certain species of crane flies.

In particular

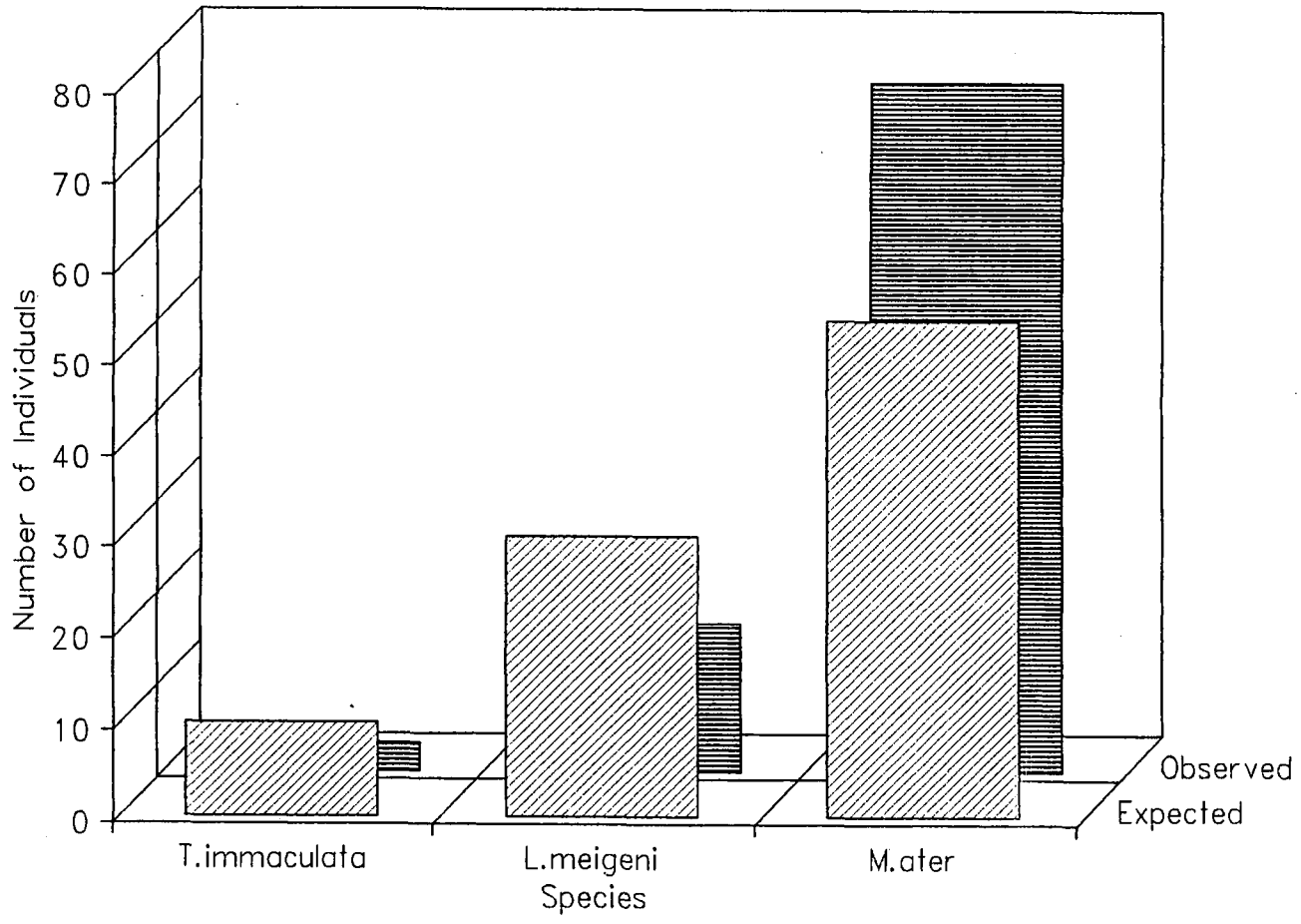
:- more *T. immaculata* in *Sphagnum* than expected but less in *Nardus* than expected,

:- more *L. meigeni* in *Sphagnum* than expected but less in *Nardus* than expected,

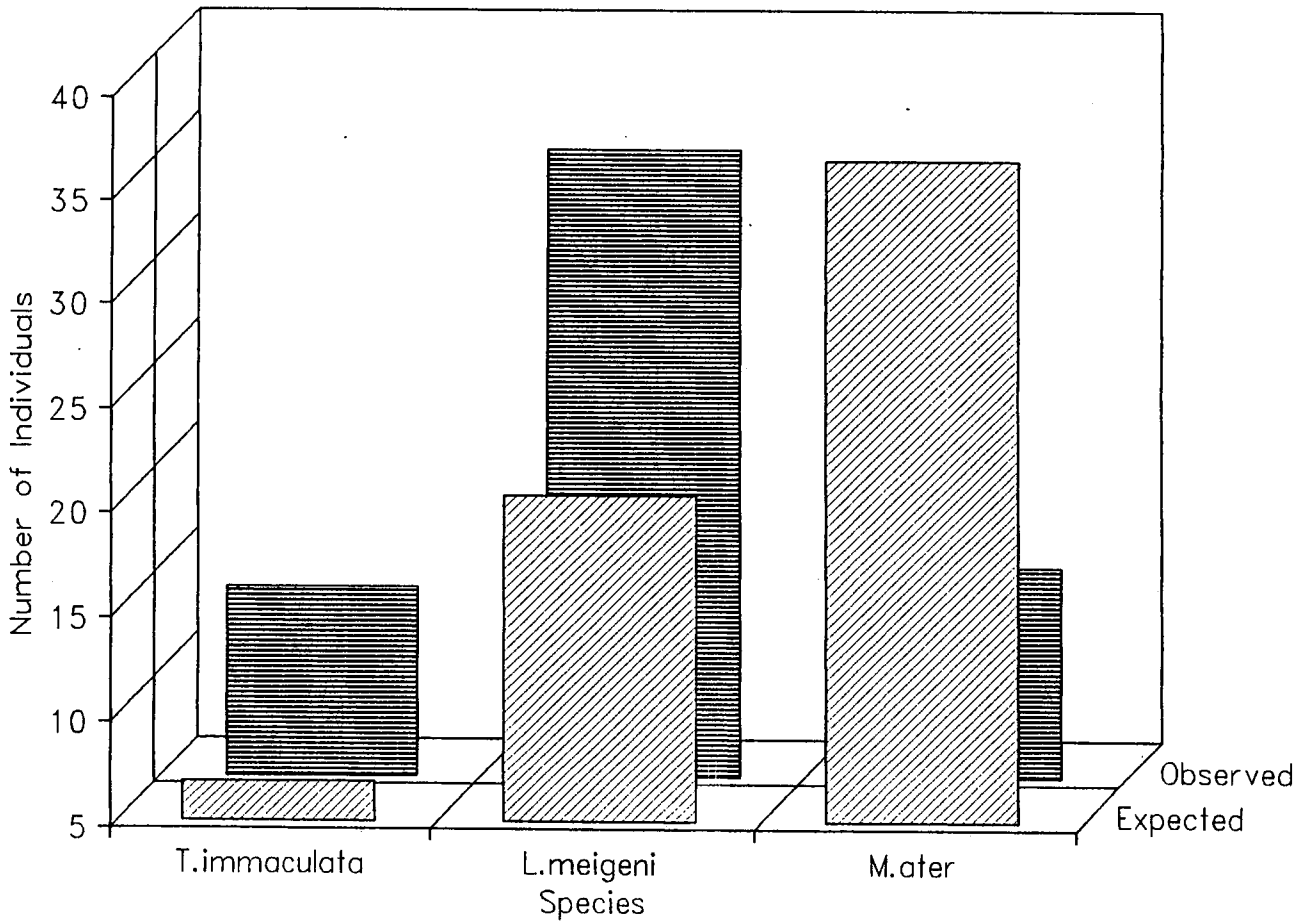
:- less *M. ater* in *Sphagnum* than expected but more in *Nardus* than expected.

This information is presented in graphs 8.4 bi and bii.

Graphs 8.4bi Species distribution of 3 short-palped craneflies on *Nardus* vegetation, Bog end, Moorhouse, 8.12.92.



Graph 8.4.bii Species distribution of 3 short-palped craneflies on *Sphagnum* vegetation, Bog end, Moorhouse, 8.12.92.



Smith (1973) reported that *M.ater* was a very common cranefly on the Blanket bog of MoorHouse National Nature Reserve. The reason as to why MoorHouse is able to sustain much higher densities of *M. ater, T. immaculata* and *L. meigeni* and provide the correct ecological requirements for a greater number of species than that found at Chapel Fell, is beyond the scope of this thesis. However, concerning *M. ater's* absence from most sites at Chapel Fell, Smith (1973) reported that a limestone bed rock site, dominated by *J. squarrosus* did not support a *M. ater* population in the 1971- 1972 season. He suggests that *M. ater* may be adapted to a habitat that is nutritionally poor. However, Hadley`s (1966) observation that *M. ater* were not recorded on eroding peat areas appears to contradict Smith and much further understanding is required before a satisfactory explanation can be given on *M. ater*`s apparent site specificity at Chapel Fell.

Smith (1973) showed that 3 distinct micro habitats exist in *Calluna, Eriophorum* and *Sphagnum*. Using temperature probes at depths between 0.5cm for *Sphagnum* and 1.0 cm for *Calluna* and *Eriophorum* he found that *Sphagnum* warmed up quickest in the spring but become the coldest of the three from October to January. *Eriophorum* and *Calluna* were found to be about the same temperature during the winter though due to *Eriophorum* warming up quickly in the summer, *Calluna* habitat was found to be the coldest of the three for approximately 9 months of the year. The low nitrogen content of *Sphagnum* compared to that found in *Eriophorum* and *Calluna* (by the chemical section at the Marlewood research station, Nature Conservancy) is believed by Smith to be the reason why *M. ater* prefers a tussock habitat. This is further contradiction to his suggestion that *M. ater* is adapted to a low nutrition environment. Although very little is known about the exact diets of all cranefly larvae, *Tricyphona immaculata* has been observed to predate smaller species such as *M. ater* which is believed to be an algal feeder (Coulson, pers. comm.).

The present investigation on *M. ater`s* distribution, results of which can be seen in graphs 8.4.bi and 8.4.bii, certainly indicates that *M. ater* is observed to occur in *Sphagnum* at a far lower density, relative to that observed in *Nardus* habitat.

Conversely, *T. immaculata* and *L. meigeni* were observed to a far greater extent in *Sphagnum* habitat than *Nardus*. Reason for this may simply be that *T. immaculata* and *L. meigeni* are adapted to a more aquatic habitat than that existing in *Nardus*.

T. immaculata has been observed to predate enchytraeid worms (in preference to *M. ater* larvae), Horobin (1971). Although Standen (Moor House Annual report 13 and 1977) has shown that Enchytraeid worms grow better when feeding on *Eriophorum* and *Calluna* than on *Sphagnum* and that the enchytraeid worm *Cognettia sphagnetorum* is more prevalent in *Eriophorum* and *Calluna* than in *Sphagnum*, sufficient food must exist in *Sphagnum* to sustain high densities of *T. immaculata* and *L. meigeni*. The ability of *L. meigeni* and *T. immaculata* to survive in *Sphagnum* requires a physiological investigation to measure the environmental conditions of the different habitats. Factors such as pH, osmolarity and $[CO^2]pp$ must be measured along with the corresponding levels of tolerance different species are capable of surviving.

Information from Chapel Fell on larval-site densities and adult-site reportings show that *L. meigeni* has the greatest distribution over the 14 sites. *L. meigeni* was the only species to benefit from the drought of 1992 and reason for this may involve its possession of large anal papillae. These organs, thought to have an osmoregulatory function, may provide this species with a capability of remaining in or near water-holding *Sphagnum* in times of drought and desiccation. Much further work is obviously required.

9 Comparative assessment of species attributes

9.1 Larval characteristics

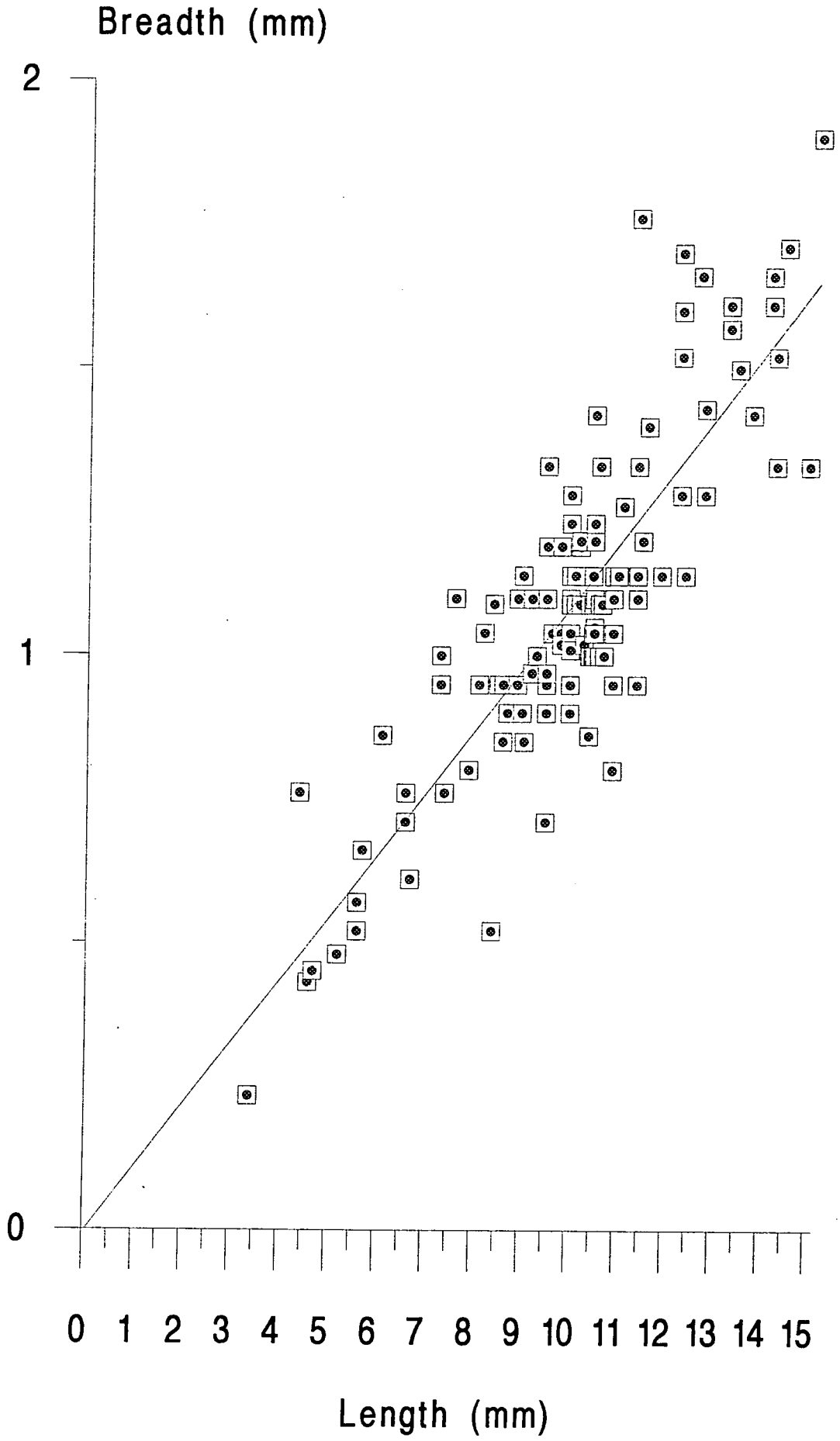
The purpose of this chapter is to present work started during my research year which was not completed due to shortage of time. Questions which aroused my interest throughout the course of my research will be given along with some of the inconclusive investigations started.

One of the first questions which occurred to me concerned the relationship between spiracular disc diameter and larval growth. As discussed earlier, spiracular disc size appears to double with every larval moult. Considering the huge increase in body volume that can occur between the third and fourth instar stage in tipulids, the increase in spiracular disc area for each moult appears very small, (if the diameter of the spiracular disc is doubled then the area of the disc increases by a factor of 4). I decided to investigate whether or not any difference could be observed in the growth dimensions of five species of short-palped cranefly. Using my collected specimens I made length and breadth measurements on all larvae collected and the growth of the five species in given in Graphs 9.1a-e

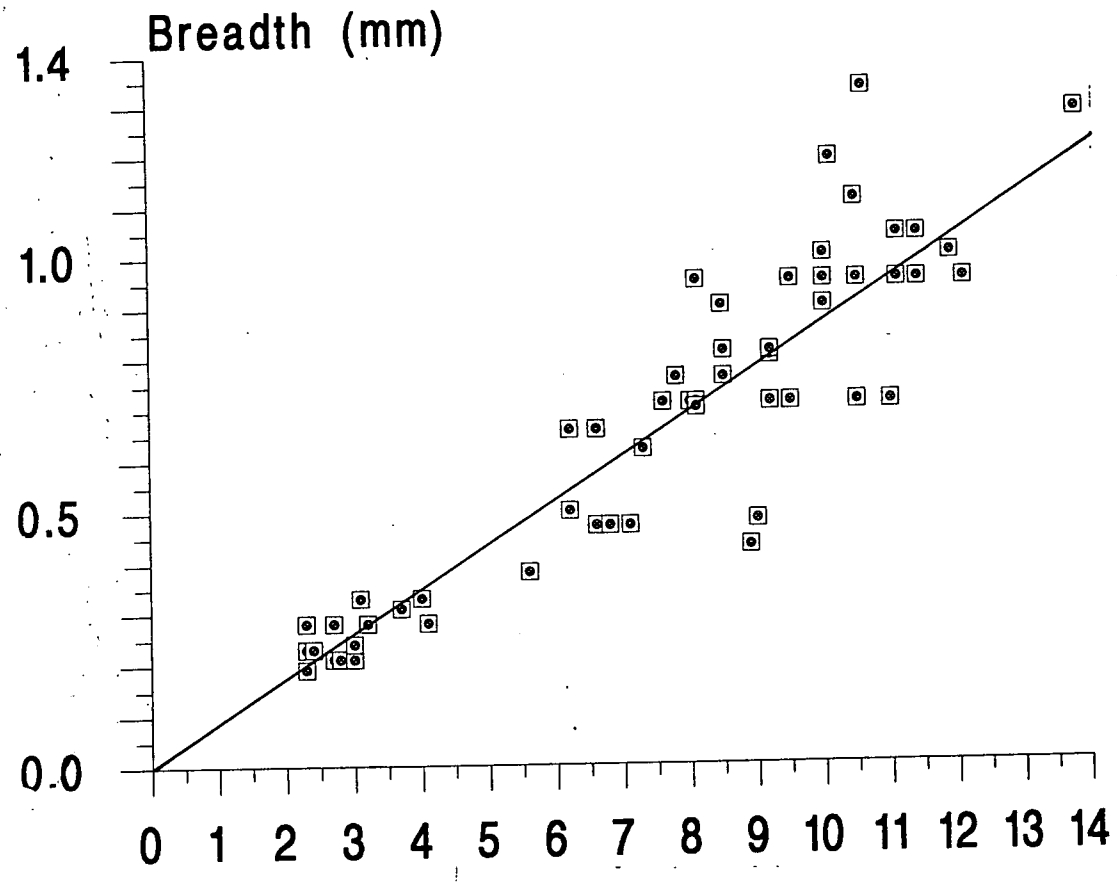
The slopes are compared in graph 9.1 f.

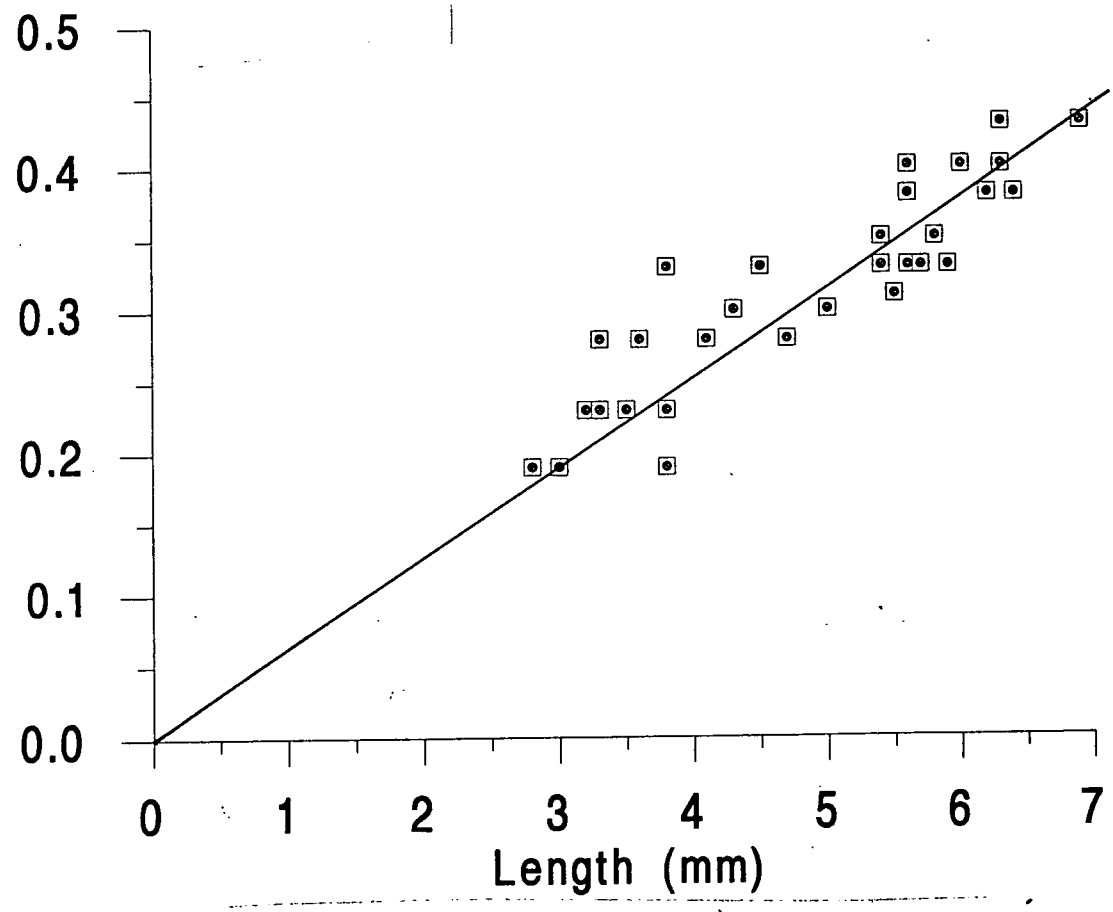
From the slopes and S.E. of slopes calculation was then made on regressional differences. P=0.05

Graph 9.1a *Limnophila meigeni* body growth. n=104



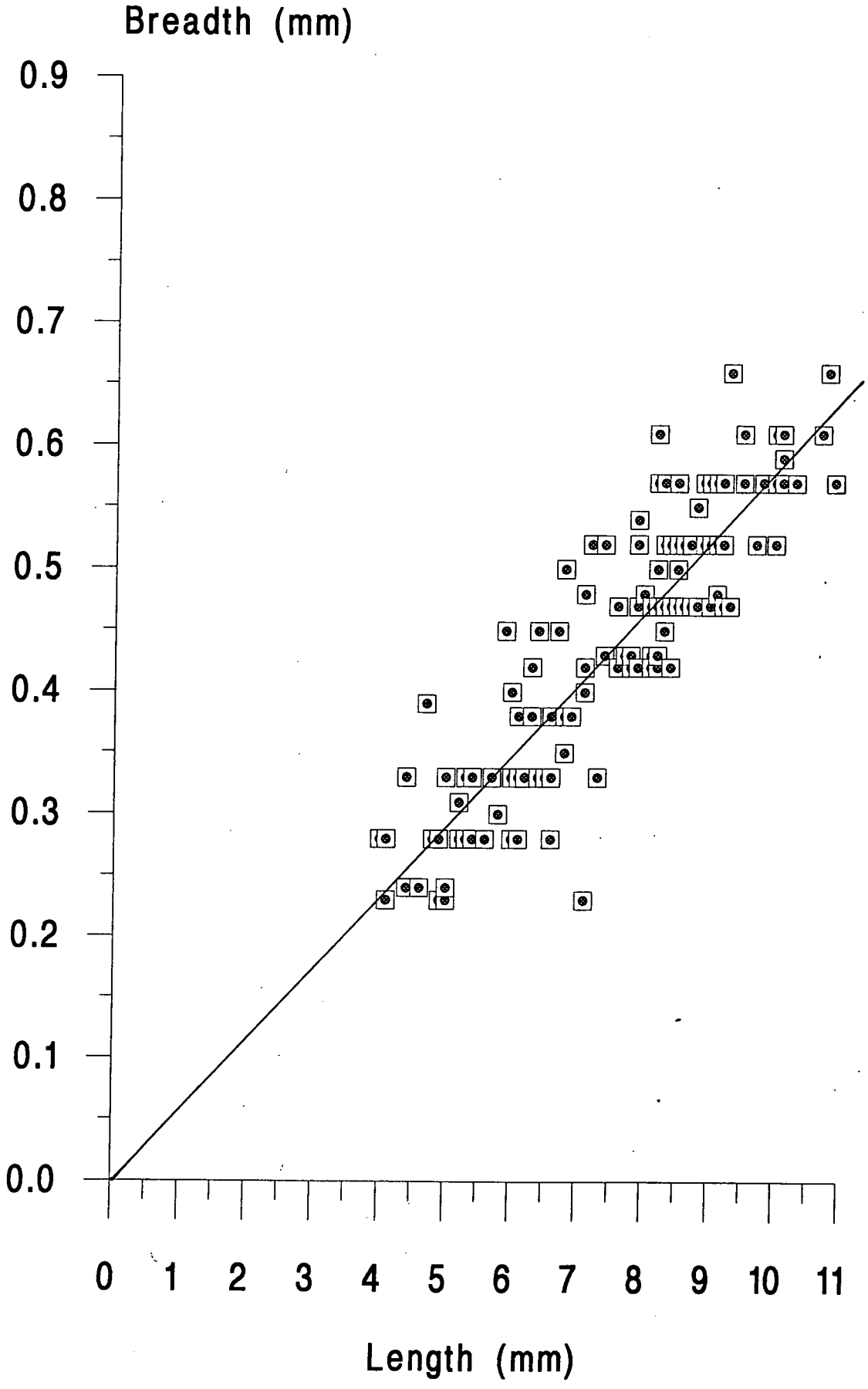
Graph 9.1c *Tricyphona immaculata* body growth. n=56



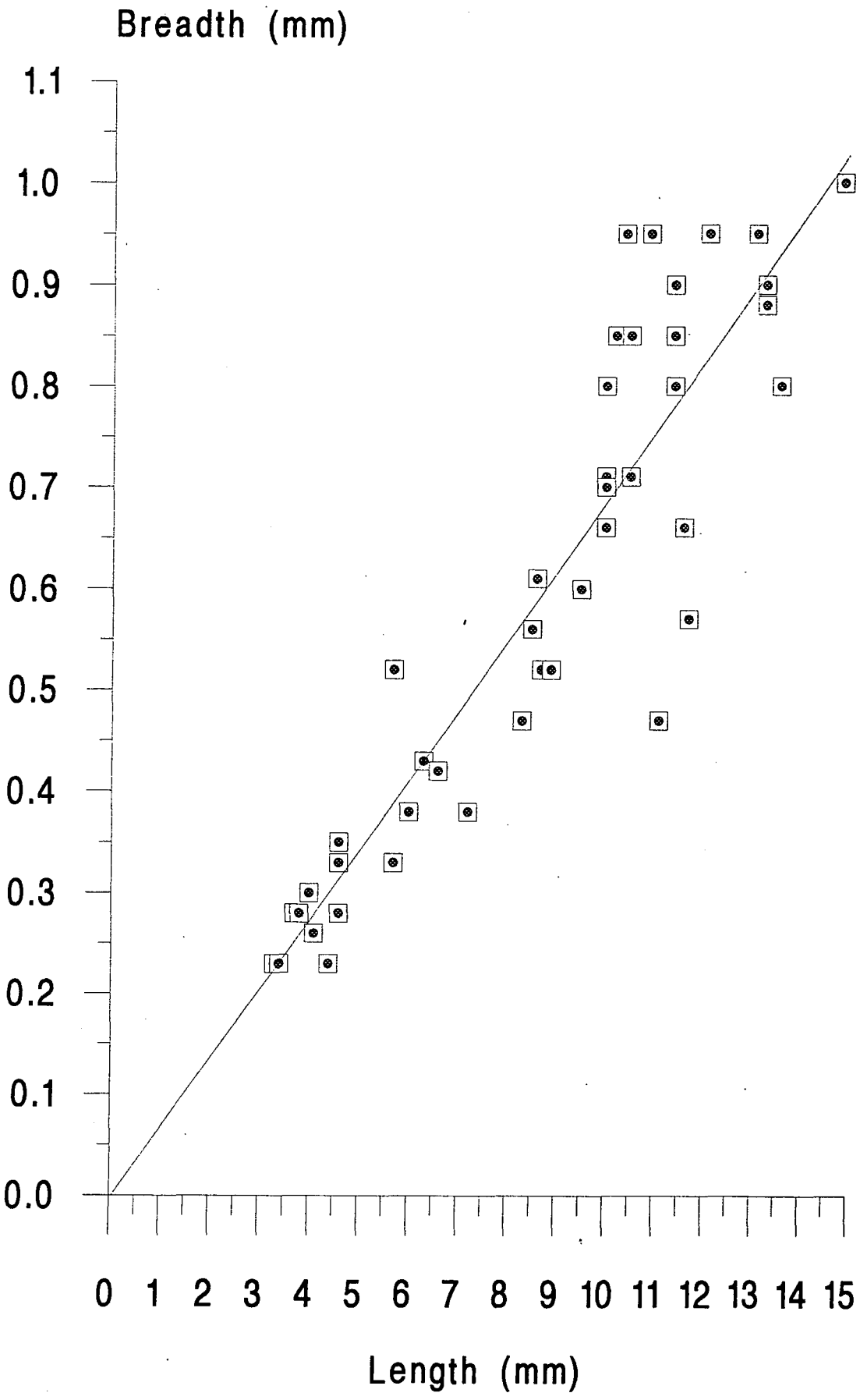


Graph 9.1b *Ormosia pseudosimilis* body growth. n=20

Graph 9.1d *Molophilus ater* body growth. n=141



Graph 9.1e *Erioptera trivialis* body growth. n=38



Graph 9.1f Breadth to length relationship in five species of short-palped cranefly with slope and S.E. of slope.

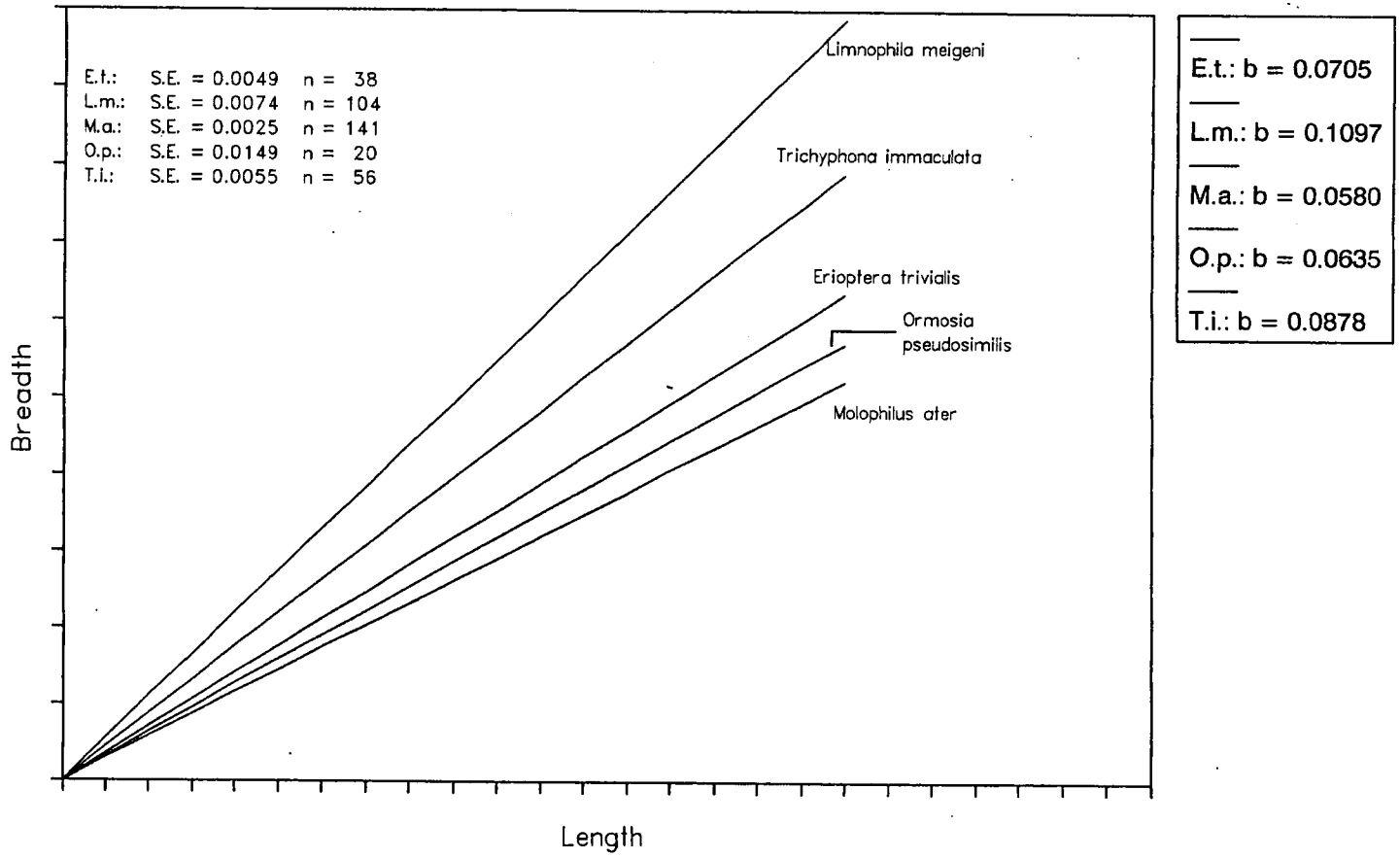


Table 9.1a Showing which species have a significantly different relationship between length/breadth based on a comparison of slopes. (See graph 9.1f)

	L. meigeni	*O. pseudosimilis*	*E. trivialis*	*T. immaculata*	*M. ater*
L. meigeni	---	sig. diff.	sig. diff.	sig. diff.	sig. diff.
O. pseudosimilis	sig. diff.	---	not sig. diff.	not sig. diff.	not sig. diff.
E. trivialis	sig. diff.	not sig. diff.	---	sig. diff.	sig. diff.
T. immaculata	sig. diff.	not sig. diff.	sig. diff.	---	sig. diff.
M. ater	sig. diff.	not sig. diff.	sig. diff.	sig. diff.	---

From this table it is apparent that the relationship between length and breadth in *L. meigeni* is significantly different to that found in the four other short-palped species studied. This is of great interest in that although larvae of *L. meigeni* do not possess relatively large spiracular discs, they are able to circulate enough oxygen through their respiratory system to sustain a large cross section of body. In terms of ultimate adult size and female fecundity this could well be hugely beneficial to the species.

9.2 Adult characteristics.

9.2.1 Relating the features of leg length, antennae length, head capsule width and body and abdomen length.

The variation in body size between adults of different species was observed after many months of familiarisation of the short-palped craneflies at Chapel Fell. The questions of interest centred around the subapterous nature of *M. ater*. Explanation for the reduction in wing length may be associated with the species small size and the windy, exposed nature of the species habitat. However, this theory is contradicted by the measurements taken from *O. pseudosimilis* and explanation is given below.

Table 9.2a *Molophilus ater* adult body measurements for 10 paired male:female specimens (mm).

Wing length		Abdomen length		Leg length		Body length		Antenna length		Head width	
M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.
1.53	1.57	2.14	1.90	5.50	4.33	3.38	3.04	0.76	0.71	0.41	0.41
1.60	1.58	1.85	1.82	5.80	4.44	2.25	3.00	0.86	0.74	0.44	0.41
1.85	1.75	2.27	2.02	6.19	4.98	3.57	3.33	0.91	0.71	0.46	0.44
1.5	1.53	2.07	2.02	5.43	4.22	3.19	3.33	0.74	0.76	0.42	0.41
1.9	1.72	2.34	1.97	5.90	4.56	3.52	3.09	0.79	0.79	0.44	0.44
1.72	1.58	2.04	1.72	5.77	4.66	2.84	3.00	0.74	0.81	0.44	0.44
1.75	1.85	2.02	3.00	5.80	4.32	2.98	4.19	0.74	0.81	0.43	0.41
1.60	1.85	2.12	3.04	5.35	4.93	2.25	4.33	0.81	0.86	0.41	0.41
1.65	1.65	2.09	1.73	5.90	4.46	3.33	2.96	0.74	0.86	0.44	0.41
1.77	2.09	2.16	2.57	5.77	4.96	3.76	3.8	0.74	0.86	0.44	0.43

Male body length; mean=3.10, S.D.=0.52, variance=0.27

Female body length; mean=3.40, S.D.=0.51, variance=0.26

Male wing length; mean=1.68, S.D.=0.13, variance=0.017

Female wing length; mean=1.71, S.D.=0.17, variance=0.029

Male antenna length; mean=0.78, S.D.=0.06, variance=0.003

Female antenna length; mean=0.79, S.D.= 0.06, variance=0.003

Male head width; mean=0.43, S.D.=0.01, variance=0.0001

Female head width; mean=0.43, S.D.=0.01, variance=0.0001

Table 9.2b *Ormosia pseudosimilis* adult body measurements for 10 paired male:female specimens (mm).

Wing length		Abdomen length		Leg length		Body length		Antenna length		Head cap. width	
M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.
3.33	2.95	1.60	2.30	6.95	5.08	2.83	3.47	1.5	1.13	0.41	0.39
3.52	3.71	2.28	2.61	7.52	6.90	3.52	3.80	1.80	1.11	0.44	0.42
2.85	3.09	2.33	2.34	7.14	5.66	3.33	3.45	1.60	1.11	0.44	0.44
3.47	3.19	1.76	2.34	7.80	5.43	3.09	3.45	1.92	0.98	0.44	0.39
3.09	3.14	1.66	2.22	6.42	5.80	2.76	3.33	1.58	1.06	0.41	0.41
3.14	3.09	2.02	2.28	7.66	5.71	3.25	3.33	1.87	1.07	0.46	0.39
2.71	3.09	1.75	2.56	6.43	5.52	2.86	3.67	1.65	1.03	0.41	0.39
3.14	3.14	1.83	1.85	6.33	6.00	3.35	2.95	1.72	0.91	0.43	0.39
2.80	3.01	2.12	1.87	5.71	6.12	2.99	3.03	1.65	0.99	0.43	0.39
3.19	3.05	2.09	2.17	6.47	5.35	3.33	2.28	1.65	1.01	0.41	0.39

Male body statistics; mean=3.13, S.D.=0.26, variance=0.06

Female body statistics; mean=3.33, S.D.=0.42, variance=0.17

Male wing length; mean=3.12, S.D.=0.27, variance=0.07

Female wing length; mean=3.14, S.D.=0.21, variance=0.04

Male antenna length; mean=1.69, S.D.=0.13, variance=0.017

Female antenna length; mean=1.04, S.D.=0.07, variance=0.005

Male head width; mean=0.43, S.D.=0.02, variance=0.0004

Female head width; mean=0.4, S.D.=0.02, variance=0.0004

From this information one can see that although there is no significant difference between the body lengths of *M. ater* and *O. pseudosimilis* (males; t=0.15, P>0.1, d.f.=18, females; t=0.32, P>0.1, d.f=18), the wing lengths of both male and female *M. ater* are

females; t=16.33, P<0.01, d.f.=18). The other interesting contrast is that although the head capsules of the two species are the same in dimension (males; t=0, P>0.1, d.f.=18, females; t=2.68, P>0.02, d.f.=18), the antennae of *M. ater* are far shorter than those of *O. pseudosimilis* (males; t=19.3, P<0.01, d.f.=18, females; t=8.38, P>0.01, d.f.=18). Function of the antennae in *O. pseudosimilis* appears sex linked for male antennae are significantly longer than female antennae (t=13.14, P<0.01, d.f.=18). Whether males of *O. pseudosimilis* are actively using their wings and antennae to search for females obviously requires much more work and such is the scope of this field that further comment is beyond the function of this thesis.

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