A study of the swarming behaviour and the effects of the weather on the activity of trichocera (diptera:nematocera)

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A STUDY OF THE SWARMING BEHAVIOUR AND THE EFFECTS OF THE WEATHER ON THE ACTIVITY OF *TRICHOCERA* (DIPTERA:NEMATOCERA).

BY

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Being

A dissertation submitted as part of

the requirements for the degree of

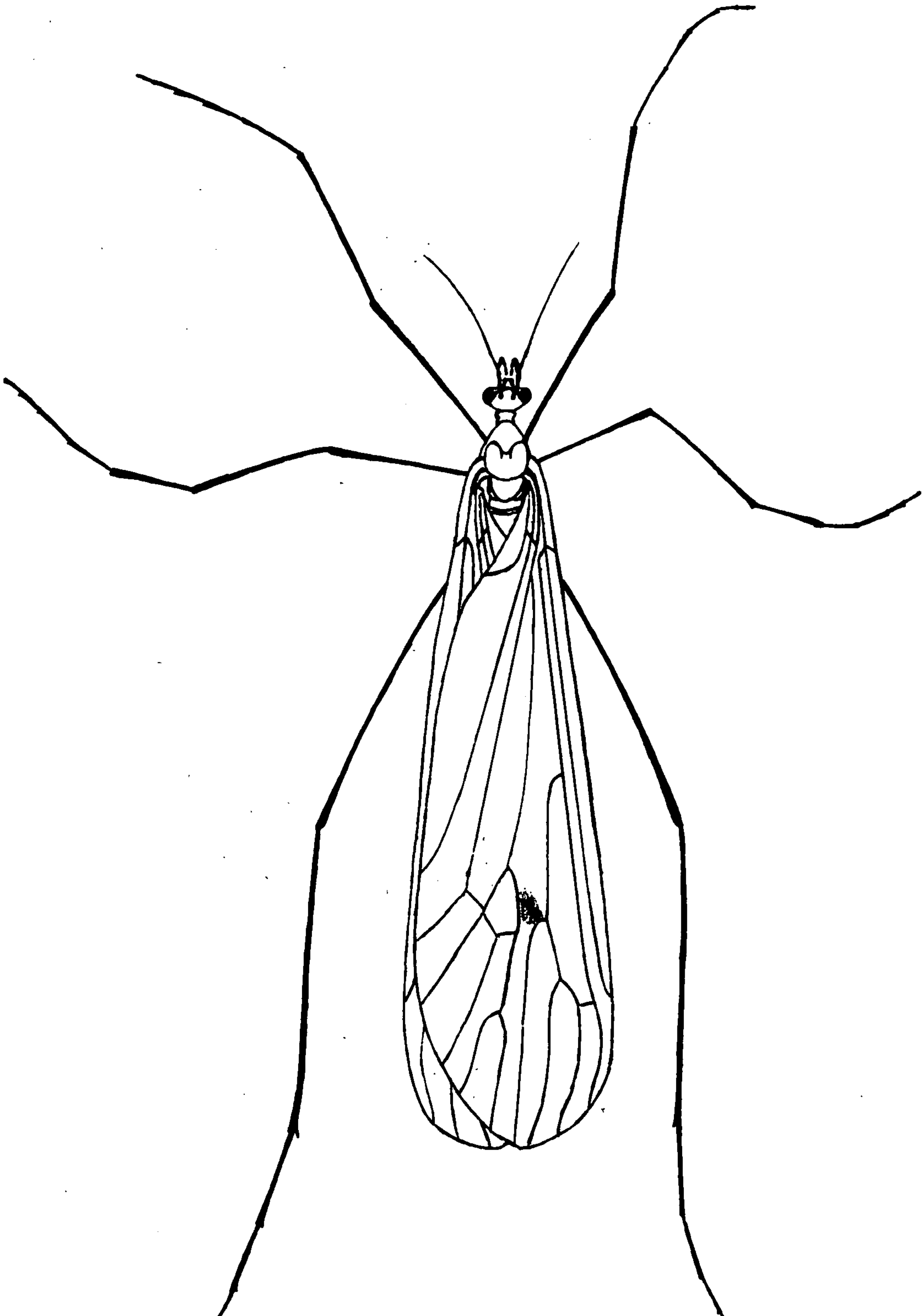
Master of Science

(Advanced Course in Ecology)

in the

University of Durham,

September, 1969.



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Since de Geer's observations on the swarming of winter gnats (Trichocera) in 1776, many studies have been made on them, but these have been mainly on their swarming behaviour and taxonomy, and relatively little is known about their ecology.

Among the studies on swarming Eaton (1881) gave approximate temperatures when swarming was observed; Ainslie (1907) described the flight pattern and mating behaviour; Alexander (1920) gave an account of the general biology including the swarming behaviour; and Cuthbertson (1926) gave the general conditions under which swarming occurs (calm, dry evenings after wet weather) and described how the swarms built up during the evening. Dahl (1965) made the first really detailed study of the weather conditions under which swarming occurs, and determined the limits for each species observed. Syrjamaki (1968) mentions (Trichocera swarming over grass tussocks in Spitsbergen, the only reference to swarm markers that I could find.

The genus Trichocera and its close relatives have been included in the families Tipulidae and Rhyphidae, as they show morphological resemblances to both, but are now put in a separate family, the Trichoceridae. Earlier keys used wing venation and colouration to separate the species (Edwards, 1921, 1938; Curran, 1934; Freeman, 1950), but modern workers consider these characteristics too variable and use wing vein setae (Laurence, 1957) and the detailed structure of the genitalia

(Dahl, 1957, 1966, 1967a, 1967b, 1968).

Brief mention is given to the Trichoceridae in most general entomological textbooks e.g. Imms (1957) p. 610. More detailed studies on single species have been carried out on the larva and pupa of T. regelationis Linn. by Rhynehart (1925); the early stages of T. maculipennis Meigen by Karandikar (1931); the larva and pupa of T. hiemalis de Geer by Keilin and Tate (1940); and the life history of T. saltator Harris by Laurence (1956).

In the present investigation I set out to study two things. The first was the swarming flight of Trichocera and the weather conditions governing it. This had to be started quickly while the adults were about, so I began the field work at the end of November, 1968, before I even had any equipment apart from a net, and without much foreknowledge of the animals or the work that had already been done on them. This may have led me into making mistakes, but it meant that the study was as unbiased as possible.

The second part of the investigation was on the Trichocera caught in the Rothamsted light trap at the Zoology Department Field Station. I decided to count and identify those caught each night during the 1968-69 Trichocera season, and to try to correlate the catch with the prevailing weather conditions, using similar methods to those used by Williams (1940). Study of the light trap catches also provided information on the seasonal occurrence of eight species of *Trichocera* at Durham during one year (12-13 July 1968 to 11-12 July 1969.) It is realised that this may not provide reliable data for certain species that may not be strongly attracted to a light trap.

PART I

THE SWARMING BEHAVIOUR OF *TRICHOCERA*

PART 1

The Swarming Behaviour of *Trichocera*

1. Equipment and Methods

(a) Equipment

The swarming behaviour of insects is markedly affected by the immediate weather conditions (Bates, 1949; Downes, 1955, 1958, 1969; Wolfe and Peterson, 1960; Dahl, 1965; Syrjamaki, 1968) and the factors recorded in this study were air temperature, wind speed and relative humidity.

Air temperature was measured by a Gallenkamp -5 to 50°C/0.1°C mercury thermometer. This was kept in an open sided wooden case for protection, and the case also acted as a screen.

Wind speed was measured using a Casella Air Meter (a vane anemometer) capable of measuring wind speeds from 30-100,000ft./min.

Percentage relative humidity was calculated using a Casella Whirling Hygrometer and a sliding conversion scale.

As Cloudsley-Thompson (1962) points out, these instruments are unsuitable for measuring micro-climates, but are suitable for measuring what Uvarov (1931) calls the ecoclimate - "the meteorological factors within a habitat."

I was not able to measure the effects of light intensity on the swarming activity of *Trichocera*, as the light meters available were not sufficiently sensitive to measure the low light intensities at dawn and dusk accurately. By the time I realised this and had a dual purpose meter made, that could measure both high and low light intensities, the swarming activities of *Trichocera* had ceased.

(b) Methods of Observing Swarming Behaviour

(i) Swarming Localities

Swarming was observed in three localities near the laboratory, three at the Field Station, half a mile away, and one six miles distant.

I Over a path beside a playing field, near a fence covered with ivy (*Hedera helix*).

II In a gulley where a stream enters the River Wear (see Pl. 1) The gulley contains rhododendron bushes (*Rhododendron ponticum*), holly bushes (*Ilex aquifolium*), and clumps of reed-grass (*Phalaris arundinacea*).

III Outside the rear entrance of the laboratory (see Pl. 2), where there are two white flagstones in the tarmac by the end wall of the workshop.

IV Over the stream at the Field Station (see Pl. 4). On the banks are various grasses, holly bushes, hawthorn bushes (*Crataegus monogyna*) and oak trees and seedlings (*Quercus petraea*.)

Plate 1 A gulley where a stream enters the River Wear, containing rhododendron and holly bushes, and clumps of reed-grass.

Plate 2 Outside the rear entrance of the laboratory, showing the white flag-stones in the tarmac.

Plate 3. Outside the Field Station hut, showing the white paving stones.

Plate 4. The stream at the Field Station, showing the various grasses on the bank, holly bushes and oak trees.

V Over the paving stones outside the Field Station hut (see Pl.3)

VI Over rotting logs at the Field Station.

VII Over gorse bushes (Ulex europaeus) near the River Wear at Willington, Co. Durham.

(ii) Procedure

When a swarm was found, records of the flight behaviour, swarm height and dimensions, swarm marker, and instrument readings, were made on a data sheet (see fig. 1). When the swarm was at its equilibrium size, i.e. the number of flies leaving the swarm was equal to the number joining it, it was captured in a sweep net with an extension on the handle. The swarm was taken back to the laboratory, the species and sex identified using Freeman's (1950) key, the number in the swarm counted, and the data sheet completed.

2. The Swarm

(a) Description

(i) Composition

All the swarms observed consisted mainly of males of *Trichocera regelationis*, Linn, but on two occasions there were females in the swarms, and on four occasions males of other species were present (see Table 1.) This was probably because the majority of the work was done in January and February, when most of the other species had disappeared, and *Trichocera regelationis* was by

Fig. I. Data sheet for recording information on <u>Trichocera</u> swarms.

TRICHOCERA SWARMING DATA

Date ...28.1.69... Time ...5:20 P.M.

Temperature ...7·90°C.. Humidity ..86%

Wind speed ...<30 FT./MIN.............

General weather conditions .Dull with.
..occasional light rain..........

Location .Gulley by river bank (II)
..Marker - my net.....................

Height ...2 FT.... Dimensions .3FT. x 1FT^2

Species ....T. regelationis...........

Sex .....♂......Number ....28.......

General remarks .Equilibrium swarm
..with individuals coming and
..going from surrounding.....
..vegetation (rhododendron, holly).

....

....

far the most common species (see fig. 4). According to Dahl (1965) the swarming behaviour of other species of Trichocera, and of females, is broadly the same as that of T. regelationis males.

(ii) Flight Pattern

During swarming flight the insects face into the wind and perform a distinctive rising and falling movement over the same spot. The individual moves upwards through a short distance by beating its wings, then it falls back through the same distance with its wings held out, horizontally, from the sides of the body. The distance involved is about 20-30cm. under calm conditions, but is much shorter when there is a breeze blowing.

When two individuals come within about 1cm. of each other they grasp each other with their legs, whirl briefly, and part again. I did not observe mating, but according to Ainslie (1907) and Dahl (1965) when a female enters a swarm of males she is grasped in this way, and the pair fall to the ground and copulate. However, on one occasion I did observe this sort of behaviour, but when I captured seven pairs falling from the swarm I found that each consisted of one T. regelationis male and one T. annulata Meigen male. I do not know whether the regelationis males had mistaken the annulata males for females, or whether this was a form of "territorial" behaviour, one species removing the other from its swarming area. From the method of removal used i.e. the "mating grasp", I would be inclined to favour the former explanation.

(iii) Swarm Markers

The swarm keeps its position visually by means of a swarm marker, as do many other species of Nematocera (Nielsen and Greve, 1950; Downes 1955 and 1956). The marker is an edge between two different coloured objects. The markers in the various localities were:

I The edge of the grey path and the grass.

II The edges of patches of dead leaves, and the dry leaves of Phalaris clumps.

III The banks of the stream, clumps of dead grass, and low bushes.

IV The edge of the white flagstones with the tarmac.

V The edge of the white paving stones and the grass.

VI The edge of the black hole in the rotting log.

VII The edge of the dark green bush against the dry grass.

Dahl (1965) says "no form of swarm marker could be found," but Syrjamaki (1968) reports Trichocera swarming over tufts of dry grass. I carried out several marker experiments showing that the swarm would form and dance over sheets of white paper laid on the ground, but perhaps the most convincing experiment was when I had a swarm over my white net. I moved the net slowly round in a 15ft. circle, and the swarm moved above it. I was able to repeat this several times on different occasions.

(iv) Resting

Individuals can be seen joining and leaving the swarm, and they rest on nearby vegetation, hanging with their wings folded. When a swarm is captured it is replaced within a few minutes. When I captured each swarm as it reached equilibrium size, until I had captured all the *Trichocera* in the area, I calculated that about 10-12% of the flies were in the air at any one time.

(v) Dimensions

The best definition of a swarm is one or more individuals performing swarming flights in relation to a marker, as outlined above. The number of individuals in a swarm does not seem to be affected by climatic factors, and probably depends on the number of flies in the vicinity (see Table 1). Ainslie (1907) saw several swarms at once, and they were of different sizes and different heights above the ground. The height above the ground seems to be affected only by strong breezes, when the flies dance in a small, tight group about 30cm. above the ground. Under calm conditions the swarm is a column of insects about 30cm. in diameter, the length varying with the numbers present. The height of the swarm above the ground varies from about 1 to 4 metres.

(b) Weather Factors

The conditions of temperature, wind speed and relative humidity under which *Trichocera regelationis* was observed swarming are shown in Table 2 and figs. 2 and 3. Conditions recorded when no

TABLE 1

THE COMPOSITION OF THE *TRICHOCERA REGELATIONIS* SWARMS OBSERVED

Number of *T. regelationis*	Number of males	Number of females	Other species
8	8	-	-
55	55	-	-
10	10	-	-
7	6	1	-
96	97	-	*T. annulata*
48	47	1	-
16	16	-	-
8	8	-	-
15	16	-	*T. annulata*
28	28	-	-
3	4	-	*T. annulata*
10	10	-	-
8	8	-	-
19	19	-	-
26	26	-	-
14	14	-	-
1	1	-	-
14	15	-	*T. hiemalis*

TABLE 2

CONDITIONS RECORDED WHEN *TRICHOCERA REGELATIONIS* WAS SWARMING

Wind Speed (ft./min.)	Temperature (°C)	Relative Humidity (%)
< 30	9.40	85
< 30	8.50	85
< 30	10.00	90
50	12.50	90
75	9.80	80
75	8.50	80
80	12.00	-
< 30	11.50	-
< 30	9.70	-
< 30	7.90	86
< 30	6.75	86
< 30	8.00	72
< 30	6.10	72
< 30	8.50	75
50	10.40	45?

Fig. 2. Observed temperature range for swarming in *Trichocera regelationis*.

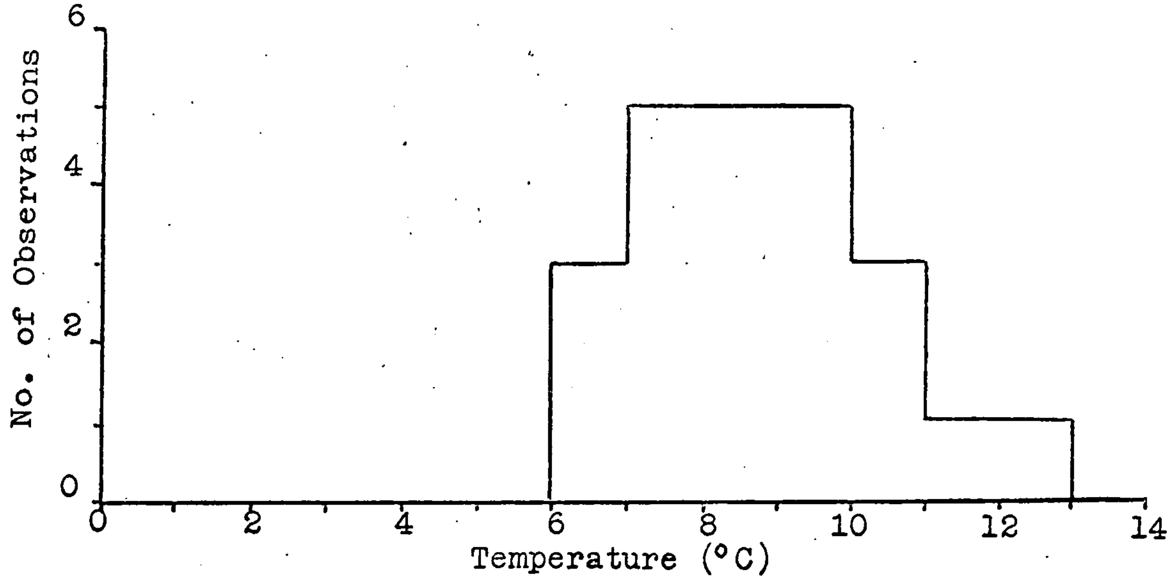


Fig. 3. Observed humidity range for swarming in *Trichocera regelationis*.

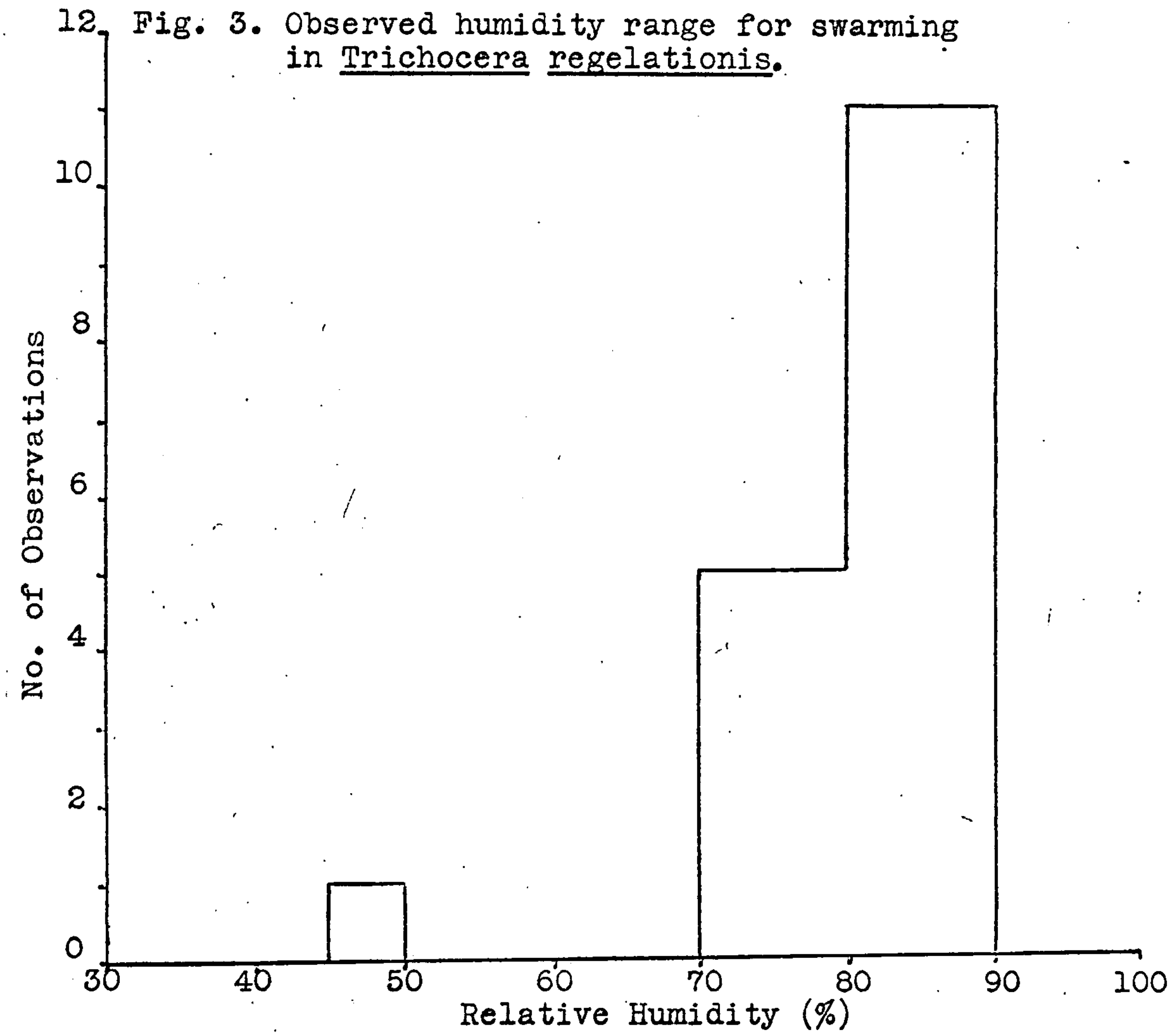


TABLE 3

CONDITIONS RECORDED WHEN NO *TRICHOCERA* SWARMING WAS OBSERVED

Wind Speed (ft./min.)	Temperature (°C)	Relative Humidity (%)
210	5.20	97
70	4.00	85
122	3.45	92
98	3.30	93
102	3.00	94
182	1.30	96
180	0.30	96
250	3.80	90
230	5.70	80
135	4.00	84
< 30	1.60	92
< 30	0.45	92
< 30	18.15	40
< 30	17.90	46
70	17.30	40
40	15.65	40
50	14.90	42
60	14.60	40

swarming was observed are shown in Table 3.

(i) Wind speed

The highest wind speed at which swarming was observed was 80ft./min. (0.41 m./sec.) The swarm was small and close to the ground, and the rising and falling flight was very short (about 10 cm.) As soon as the wind speed rose a small amount the swarm dispersed. The majority of observations were at speeds less than 30 ft./min. which was the lowest value to anemometer could record.

(ii) Air Temperature

The temperature range over which swarming was observed was 6.10 - 12.50°C. (see fig. 2.)

(iii) Relative humidity

Swarming was observed between 72 and 90% R.H. (see fig. 3.) The value of 45% recorded on one occasion is doubtful, as although the air was generally quite dry, the swarm was low over the surface of the stream, where the humidity was probably much higher.

(iv) The affect of weather factors

Comparison of Tables 2 and 3 shows that none of the sets of data recorded when swarming was observed overlaps with any when swarming was not observed.

On 13th February, 1969, there was a report in the Times of winter gnats swarming over snow in winter sunshine, after a very cold night. This shows that the animals are able to survive bad weather and swarm again as soon as conditions are suitable. It would be interesting to look into the physiology of this survival, but that is outside the scope of the present study.

Ordinary flight is possible under conditions when swarming is not, and the *Trichocera* fly in a straight line into the wind.

Dahl (1965) carried out a five year study on the swarming of *Trichocera*, using electronic recording instruments, so her figures are much more comprehensive than mine, but my records fall within the limits that she give for swarming in *Trichocera regelationis*. She also measured the effects of light intensity, which I was unable to do. I agree with her that swarms disperse at low light intensities at dusk, but I was unable to observe swarming at high light intensities around mid-day (see her fig. 13) although I could find the flies resting in the vegetation. Cuthbertson (1926) also observed trichocerids swarming only on calm evenings.

It is difficult to say which weather factor, if any, has the greatest effect on swarming. Swarming can only occur if all the factors are within the permitted limits, and different factors have a controlling influence at different times. Dahl is of the opinion, and I agree with her, that wind is of major importance, and it is certainly the most obvious factor affecting the swarming behaviour of *Trichocera*.

(c) The Reasons for Swarming

The factors affecting the swarming of trichocerids and other dipterans are fairly well known, but the actual reasons for swarming are not. Some authors have regarded swarming primarily as a mating activity, e.g. Gibson (1945), working on chironomids, but others have disagreed. Downes (1955) says that in ceratopogonids a swarm is a group of individuals reacting independently to a marker when weather conditions are right. Dahl (1965) agrees in part with this, although she found no response to swarm markers, and says the trichocerids are reacting individually to the controlling environmental factors.

More recently Downes (1969) comes to the conclusion that "the swarm itself is essentially a flight-station, an assembly point controlled by a land mark (swarm marker) at which the short range recognition and capture of the female can take place. The females are often captured almost immediately upon arrival and the pair leaves the swarm which, as a persisting entity, thus consists largely of males."

I agree with Downes. I have seen single trichocerids showing swarming behaviour, and also I have never observed mating, whereas in all cases the swarms were reacting to a marker. The primary stimulus for swarming to occur is not the urge to mate, but a reaction to a marker when conditions are suitable. Mating seems to be a secondary reaction when males and females of the same species are brought into contact by swarming.

PART II

TRICHOCERA FROM THE FIELD STATION LIGHT TRAP

PART II

Trichocera from the Field Station Light Trap.

1. Identification

(a) Key to Genera and Species.

The following key is due to Freeman (1950) and is based on that of Edwards (1938).

1. Eyes bare; ovipositor short and fleshy; tibial spurs minute, pale, only one to each tibia; wing veins conspicuously hairy; 2A longer (fig. 31), r-m straight and vertical; wings without markings........................ Diazosma Bergroth.
One species, rarely recorded, wing-length 5-8 mm. D. hirtipenne Siebke.
Eyes hairy; ovipositor horny, down-curved; tibial spurs small, distinct, two to each tibia; wing veins not conspicuously hairy; 2A very short, strongly curved (fig. 32) r-m usually oblique and curved......................... Trichocera Meigen....2

2. Abdomen more or less distincly banded..........................3
Abdomen unicolorous or at most with tip pale.....................4

3. Wings with spot or cloud over base of Rs, often extending across upper basal cell; cross veins more or less distinctly clouded; posterior margins of abdominal segments pale; male styles with small basal tubercle, parameres long and curved. Wing-length 7-8mm. T. maculipennis Meigen

Wings unspotted, though cross veins may be darkened or clouded; anterior margins of abdominal segments pale; male genitalia resemble maculipennis. *T. annulata* Meigen.

4. A more or less distinct cloud over r-m (fig. 32) other cross veins sometimes faintly darkened; male styles without basal tubercle, parameres long and recurved. Wing length 5-8 mm. Abundant everywhere in winter, also found on mountains in summer....*T. regelationis* Linnaeus

No trace of cloud over r-m..5

5. R_{2+3} (i.e. stalk of R_2 and R_3) shorter than first section of R_2 (it is advisable to use the genitalia as confirmatory characters)...................6

R_{2+3} longer than (rarely about equal to) first section of R_2...7

6. Largest British species (wing length 7-9.5mm); female brownish with long slender cerci (fig. 38) males styles long without basal tubercle parameres very short (fig.33). *T. major* Edwards.

Smaller species (wing length 5-7 mm.); female blackish with shorter thicker cerci (fig. 39); male genitalia unknown. *T. fuscata* Meigen.

7. Cell M_1 longer, more than twice as long as broad, nearly parallel-sided; male styles without basal tubercle......................................8

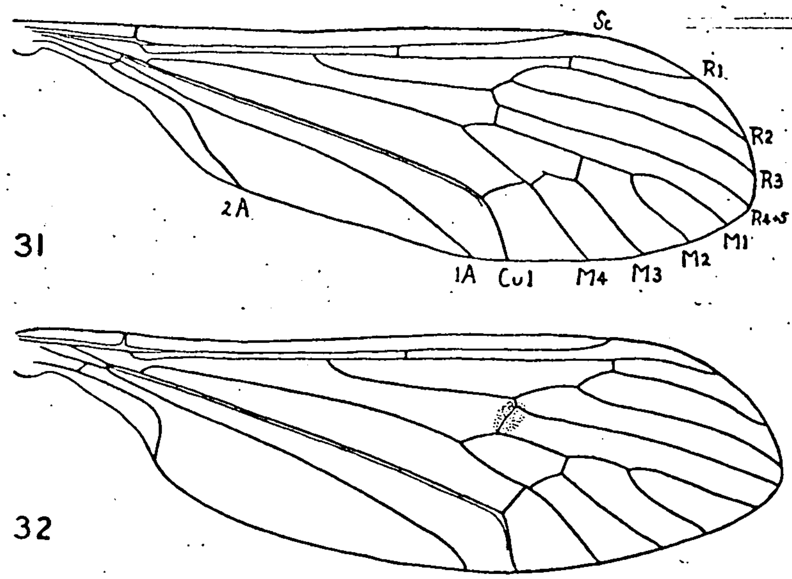
Cell M_1 shorter, usually not more than twice as long as broad, somewhat widened apically; male styles with small basal tubercle..............................9

8. Thorax largely reddish, only praescutum dark in the middle; scape yellowish; female cerci moderately long, as fuscata; male genitalia (fig. 34) as saltator, but paramers shorter. Wing length 5-6 mm. *T. rufescens* Edwards.

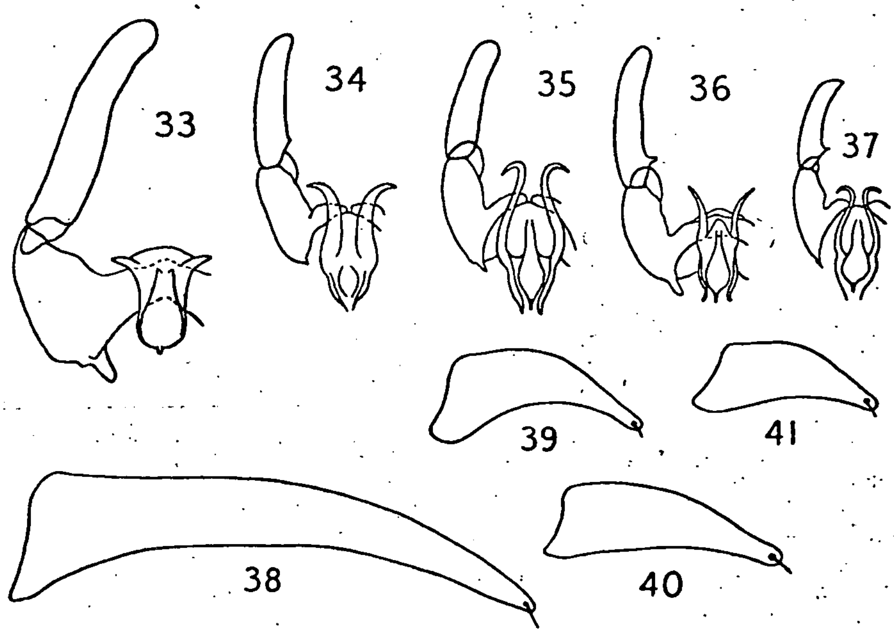
Thorax blackish; scape dark; female cerci moderately long (fig. 40); male parameres (fig. 35) long and recurved (var. ? rufulenta Edwards has much shorter cerci as in fig. 41 and reddish thorax.) Wing length 6-8 mm. Abundant everywhere in winter...<u>T.saltator</u> Harris

9. Smallish species; wings indistinctly pale basally; basal projections of male coxites forming a complete bridge (fig. 36) parameres long and recurved but not as long as in parva. Wing length 5-6.5mm. Abundant everywhere in winter......<u>T. hiemalis</u> Degeer

Very small species; wings whitish at the base; basal projections of male coxites not meeting in the middle (fig. 37) parameres longer. Wing length 4.5 - 5.5mm. <u>T. parva</u> Meigen.



FIGS. 31–32.—Wings of TRICHOCERIDAE. 31. *Diazosma hirtipenne*. 32. *Trichocera regelationis*.



FIGS. 33–41.—Hypopygia of males and ovipositors of females of *Trichocera*. 33. *T. major*. 34. *T. rufescens*. 35. *T. saltator*. 36. *T. hiemalis*. 37. *T. parva*. 38. *T. major*. 39. *T. fuscata*. 40. *T. saltator*. 41. *T. rufulenta*.

(from Freeman - Handbook for the Identification of British Insects IX (2).)

This key was used to identify all the material examined in this study.

I found that wing venation is usually a good initial guide, but can be ambiguous, and should be checked with the genitalia. The male genitalia are fairly easily identified (especially _hiemalis_ and _major_), but the female ovipositors are more difficult to distinguish between (except for _major_).

Colour can also be variable. If the abdomen of a female is full of eggs it appears paler than normal, and may appear "striped" if the plates are forced apart. Swelling of the abdomen can also make the ovipositor appear shorter.

Wing length can be useful in placing an individual (a useful tip is to know the distance between the points of your forceps, so that a rough estimate can be made quickly) but can be ambiguous e.g. a large _parva_ can have longer wings than a small _hiemalis_.

Laurence (1957) says that thekeys of Edwards and Freeman are unsatisfactory because _Trichocera_ often shows abnormalities of venation and variability in the lengths of veins and cells. He also says that the cloud over r-m on the wings of _regelationis_ is unsatisfactory. He recommends that identification should be based on the distribution of setae on the subcosta and radial veins of the wings.

Dahl (1966, 1967) says that because of the intraspecific, and sometimes interspecific variability of the above characters it was impossible to identify every specimen. She used dissection and careful examination of the parts of the genitalia to identify her trichocerids.

While I agree with the criticisms of Freeman's key, it is easy and quick to use, and this was of major importance with so many animals to identify in a limited period. The majority of Trichocera can be identified accurately from this key, and the small number that do not fit can be identified with reasonable certainty once one has handled a large number of "normal" types.

(b) Trichocera fuscata (Meigen)

Freeman's key says of T. fuscata, "R2+3 shorter than first section of R_2...... female blackish with shorter, thicker cerci; male genitalia unknown." The females that fit this description are quite easy to distinguish, and I also found males that fitted on colour and wing venation. The genitalia of the males appeared to be similar to those of rufescens, with shorter parameres than saltator. I later realised that the apparent length of the parameres on the whole animal depends on how much they are extended, and not their actual length, which can only be seen by dissection.

Edwards (1921) said of the male of fuscata, "claspers have no basal tubercle; parameres curved and pointed and longer than rufescens." Later (Edwards, 1938) he expressed doubt about the identity of fuscata and said it may be a variation of saltator.

Laurence (1957) kept saltator larvae taken from cow dung, and found that some of the resulting adults had R_{2+3} shorter than R_2 (fuscata), but they keyed out as saltator on wing setae, and the male genitalia were identical to those of saltator.

Dahl (1966) examined Meigen's original "type" specimen of a female of saltator (Harris). She says, "fuscata Meigen should be treated as a junior synonym for saltator, as suggested by Laurence."

The evidence seems to be conclusive that fuscata is saltator, but it is possible to distinguish two sorts of saltator female: those with R_{2+3} longer than R_2 and fairly long cerci; and those with R_{2+3} shorter than R_2 and short cerci. I have left my identification of the light trap material in its original form, with saltator and fuscata shown separately (see figs. 4. and 39 ., and the appendices), in accordance with the key I used.

2. The Light Trap Material

(a) The Trap.

The light trap, of the Rothamsted pattern (see Williams, 1948), was situated on the Field Station, about half a mile from the laboratory. It is half way up a grass slope, close to the hut, about 15 yards from a small wood consisting of pine (*Pinus sylvestris*) and beech (*Fagus sylvatica*), and about 20 yards from the stream already described (locality IV , Pl.4 .), which lies at the foot of the slope. There are also patches of brambles (Rubus fruticosus) close by, in which I have seen Trichocera resting.

The light trap consists essentially of a 200 W. filament bulb suspended above a 7lb. sweet jar, in which is a small jar containing cotton wool soaked in ethylene tetrachloride. The sweet jar is enclosed in a wooden box with a door in one side, and the bulb is in a perspex cone which leads down into the jar. The light is switched on and off automatically at preset times, which vary throughout the year according to sunset and sunrise.

Night flying phototropic insects are attracted to the light, overcome by the killing agent, and fall into the sweet jar.

(b) Material from the Light Trap

Since the 13th July, 1968, the insects caught in the light trap have been collected daily, so I decided to examine the catch for one year, from the night of 12-13th July, 1968, to the night of 11-12th July, 1969.

The nightly catch is sorted into the various insect orders, and Diptera are sorted into "tipulids," simuliids and miscellaneous flies. Trichocerids are included in the "tipulid" group, which is preserved in alcohol. I sorted out the trichocerids from each night's catch, using a low power (x 7) microscope (this can be

TABLE 4

The numbers of *Trichocera* caught in the Field Station Light Trap during the year July 1968-July 1969

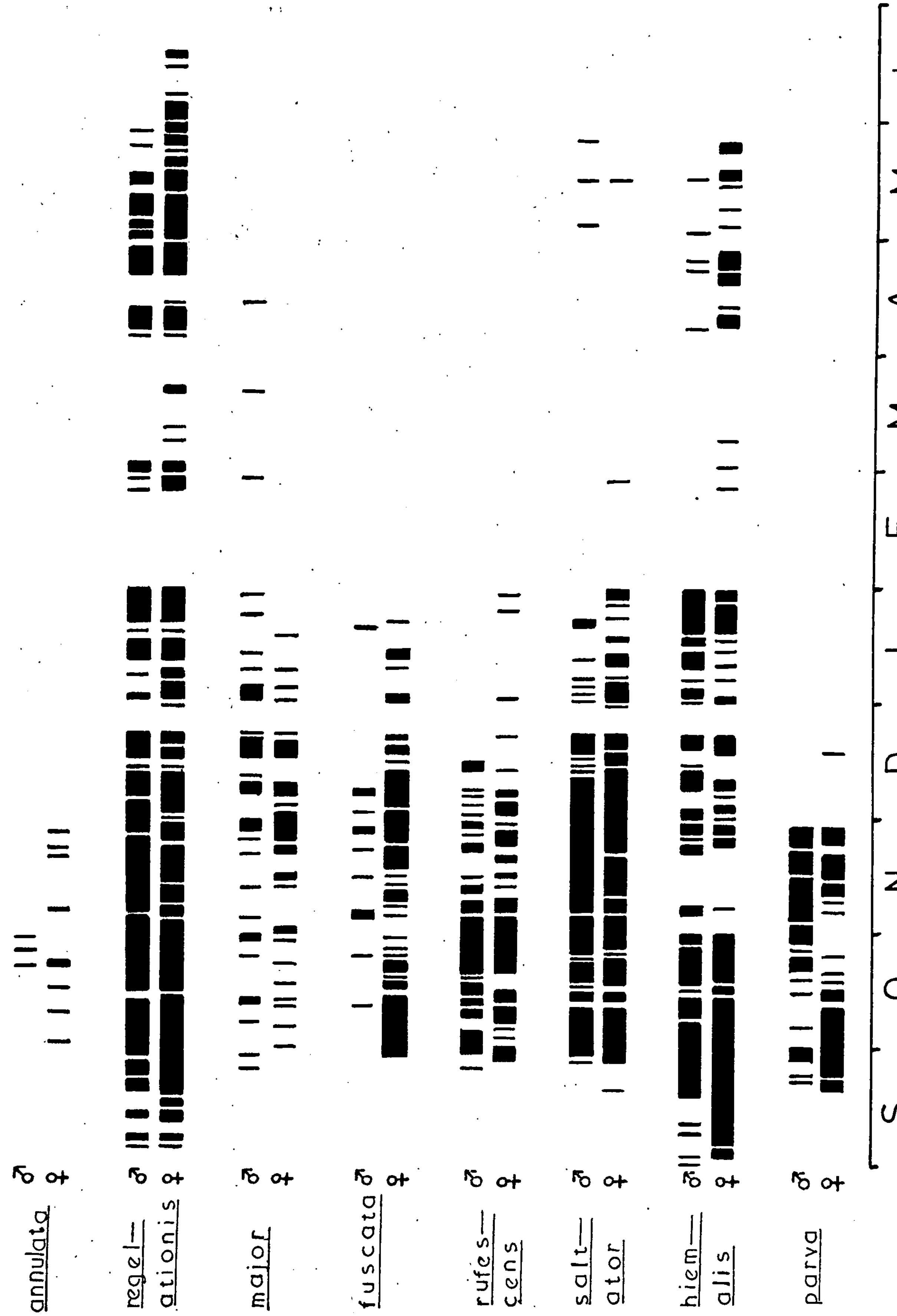
Species	Males	Females	Total
Annulata	31	54	85
regelationis	10,486	4,593	15,079
major	432	239	671
fuscata	208	1,160	1,368
rufescens	2,034	1,331	3,365
saltator	5,393	5,674	11,067
hiemalis	2,517	1,914	4,431
parva	650	329	979
Totals	21,751	15,294	37,045

done with the naked eye, but this increases the chances of missing them among other, similar sized, flies), and identified them, using a X 30 microscope. When there were more than about a hundred trichocerids in one night's catch I took a sample of around fifty individuals, identified them, and estimated the numbers of each species present in the total catch. The detailed results are shown in appendices 1 to 10.

The numbers of males and females and the total numbers of each species are shown in Table 4. T. annulata was caught in very low numbers, and T. major and T. parva in only moderate numbers. I do not know whether this is a true reflection of the numbers present in the area of the light trap, or whether some species are more attracted to light than others. Williams (1940) points out that nobody knows the area from which a light trap attracts and catches insects, but that this probably varies for different species, and even the same species on different nights.

Fig. 4 shows that the majority of the species were caught in the autumn and early winter period from September to January, and that after the severe weather in February only regelationis and hiemalis were caught regularly (Williams (1939) says that saltator, annulata and hiemalis are caught only during the winter (September to February) in light traps, but regelationis is also caught in March, April and May). In fact 35,859 trichocerids, 96.8% of all those caught in the light trap during the period studied, were

Fig. 4. Periods of capture of _Trichocera_ in the Field Station light trap for the year 1968-69.



taken in the September - January period. The numbers caught per month (fig. 5) shows this clearly, with a peak at 16,498 in November, and a trough at 83 individuals in February. There is also a small peak at 438 in April.

When the numbers of Trichocera are expressed as a percentage of the total insect catch (fig. 6) there is a peak in November due to the high numbers of trichocerids present, but the major peak is in February - March, indicating that Trichocera are more active in the severe weather than most other insects.

Fig. 5. Total Catch of <u>Trichocera</u> per Month from the Field Station Light Trap.

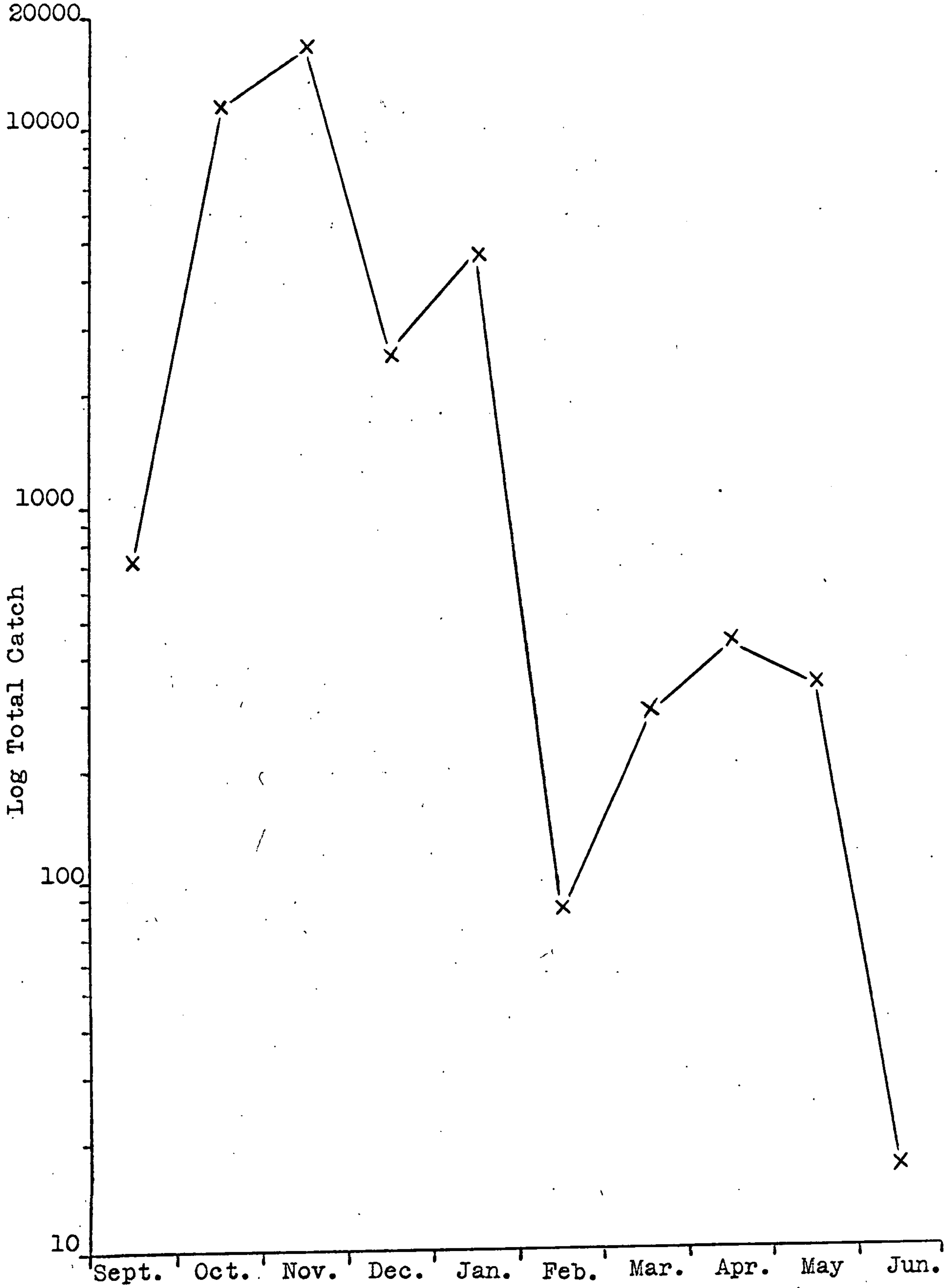
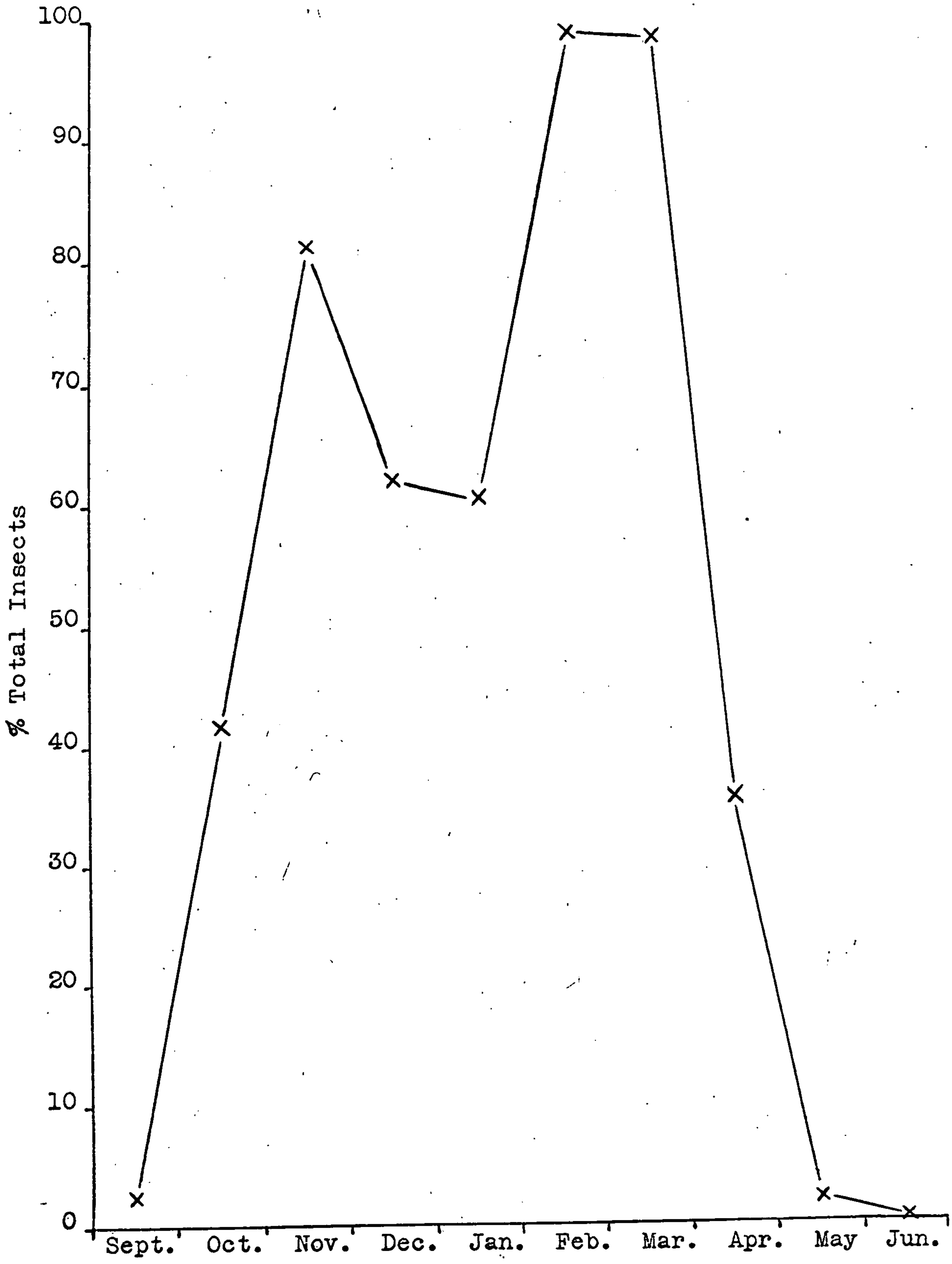


Fig. 6. Total Trichocera expressed as a percentage of all insects caught in the light trap per month.



PART III

THE EFFECT OF THE WEATHER ON THE *TRICHOCERA* CATCH

PART III

The Effect of the Weather on the *Trichocera* Catch.

According to Laurence (1956) the larvae of *Trichocera* (except *maculipennis*) remain in diapause until about September in cow dung or the surface layers of the soil. The adults emerge during the autumn and early winter, mate, and the females lay their eggs. This is the time during which they are caught in the light trap (Williams, 1939) (see fig. 4.).

During the 1968-69 *Trichocera* season the catch reached a peak in November (see fig. 5.), which can be assumed to be the peak of the emergence if the light trap samples the total population of the area in an unbiased manner. If, however, one looks at the nightly catches (see appendices 1 to 10), these are very variable, and I wanted to find the explanation for this variation. After consideration of the work of Eaton (1881), Uvarov (1931), Williams (1940, 1951, 1961, 1962) and my own field work, the obvious place to look was the prevailing weather conditions on the nights that the animals were caught.

1. The Meteorological Records Available

Daily meteorological observations are taken at Durham University Observatory, which is situated on a slight eminence about three quarters of a mile to the west of the Field Station.

Records are available for maximum and minimum temperatures (Fahrenheit) from glass thermometers in a standard Stevenson screen; grass minimum temperature from a ground level thermometer; wet and dry bulb temperatures, from which I calculated the relative humidity; rainfall, measured in a standard 5 inch diameter rain guage; wind speed and direction measured by a Dines pressure tube anemograph, 53 feet above ground level; earth temperatures from buried thermometers; air pollution; cloud cover; and visibility. All readings are taken at 0900 hours G.M.T.

Average daily wind speed records are available until the end of 1968, but only the 9a.m. spot readings after that. Since these two readings usually correspond to within a few knots of each other, I hoped that any discrepancies would be overcome by using a set of wind categories. I used Williams (1940) values, for purposes of comparison.

Category	1	-	dead calm.
"	2	-	less than 2 m.p.h.
"	3	-	2-5 m.p.h.
"	4	-	5-10 m.p.h.
"	5	-	10-20 m.p.h.
"	6	-	greater than 20 m.p.h.

The lower categories cover a smaller range of wind speeds than the higher ones, as a small increase in wind speed at low speeds has a greater effect on insect flight than at high speeds.

2. Theory and Statistics of the Analysis.

(a) The Theory.

Williams has made extensive studies of the effects of weather conditions on both the activity and population numbers of insects, based on light trap catches. He has studied the total insect catch (1940) and several orders and families within the catches (1940, 1961, 1962). I decided to try to analyse the Trichocera figures for activity, using Williams's methods, so here is an outline of the theory on which it is based (see Williams, 1940).

The number of insects caught in the trap on any one night is mainly determined by two factors; (1) the activity of the insects, and (2) the total population available for sampling. The activity varies from night to night and is determined largely by the weather conditions of the moment. The population changes happen more slowly and are determined more by the weather conditions some time previous than by those at the moment. Thus, if one considers the difference in catch between two successive nights, the effect will be largely due to differences in activity.

(b) The Statistics

There are several sources of error in the method of collecting the data used.

(1) the trap is not perfect and some insects may not enter it. Inefficiencies of this kind are constant and should not affect the analysis. The failure of the lamp, or the escape of insects that

have entered the trap are more serious, and can only be overcome by replacing the bulb and killing agent regularly.

(ii) Several traps working simultaneously would help to eliminate the above trap errors, but since the material used all came from one trap any errors must be accepted. The bulb failed on one occasion during the Trichocera season (the night of 13-14 October, 1968) and this night was omitted from the calculations.

(iii) The unit of measurement of the catch is one insect. This has little significance in a large catch, but in a small catch the unit might be such a high proportion of the total as to mask small changes. This error can be avoided by using common insects or by dealing with periods of the year when insects are common. In this case the insects and the time of year are fixed, so the error must be accepted. It should be small as Trichocera are very common during their season.

(iv) There is an error due to the distance of the meteorological station from the trap. I think that they are close enough for their "macro climates", i.e. temperature and rainfall, to be similar, and that only with wind speed is there a possibility of any large errors, as the wind vane is in a much more exposed position, on the Observatory roof, than the insects near the gound. This error may be partly eliminated by using wind categories, which only give an indication of the general wind conditions of the area.

The nightly catches in a light trap throughout a year consist of a large number of small catches, and a small number of very large catches. This gives a markedly skewed frequency distribution which cannot be analysed by ordinary statistical methods, and also the effects of very large catches swamp those of small catches (e.g. by giving a high mean catch value) and they have much more importance than they really deserve. Williams (1937, 1940) has shown that by using the logarithm of the catch number (in practice log (catch + 1) to overcome the problem of zero catches, since the log of zero is minus infinity) a nearly normal distribution is obtained which can be analysed by normal statistical methods.

Williams analysed his results in various ways and found that, for the measurement of the effect of prevailing weather conditions on activity, the best results were obtained using deviations of both nightly catch numbers and weather factors from monthly and yearly mean values. This compensates for population changes changes during the period under consideration. He determined his mean values from four year periods of light trap catches and meteorological data. Since I had only one years results I could not use this method, so I resorted to Williams's second method, which gave him slightly less significant correlations. This uses the differences between pairs of successive days, comparing days 1 and 2, 3 and 4, 5 and 6, and so on. (see Williams, 1940). This also compensates for population changes.

I decided not to use pairs of days when both had zero catches, because once zero is reached there can be no fall in the insect catch (you cannot catch negative insects) but the weather factors can go on changing beyond the level that inhibits insect activity.

3. The Analysis

(a) Methods.

I wanted to see how far Williams's methods could be used for single species, and for single sexes of a species, but at the same time I decided to limit the analysis to the effects of single weather factors, to prevent it from becoming too complex to handle in the time available. I analysed the whole *Trichocera* season from September to May and also the monthly data separately, (it was necessary to put February, March and April together, and to miss out June, because of the low number of catches in these months). Because *regelationis* and *hiemalis* were caught throughout the season, I used the following catch figures in the analysis:

(i) total *Trichocera*
(ii) total males
(iii) total females
(iv) total *regelationis*
(v) *regelationis* males
(vi) *regelationis* females
(vii) total *hiemalis*
(viii) *hiemalis* males
(ix) *hiemalis* females.

From the meteorological records available I used the following data:

(x) wind speed category

(xi) maximum temperature of the previous day

(xii) minimum temperature of the night

(xiii) grass minimum temperature

(xiv) daily rainfall

(xv) relative humidity.

It was obvious that even for the simple, single factor analysis, this would involve calculating 56 correlation coefficients and regressions for each month and for the whole season, and that I could not do this by hand in the time available. So I took the problem to the University Computor Unit, where I was told that there was a standard multiple regression programme (DCL 14001) in the computor which would correlate any one factor with each of the others, and could also give a regression coefficient and its error for each pair of factors.

I turned the catch figures for each night into log. (catch + 1) values, and expressed them as changes between successive days on a plus-minus basis. The meteorological data was expressed as changes between successive days of the original figures. All the figures were punched onto cards and fed into the computor, which took about 15 seconds to work out each set of correlations and regressions, and

Fig. 7. Relation between log total catch and minimum temperature for the whole year from difference between successive days.

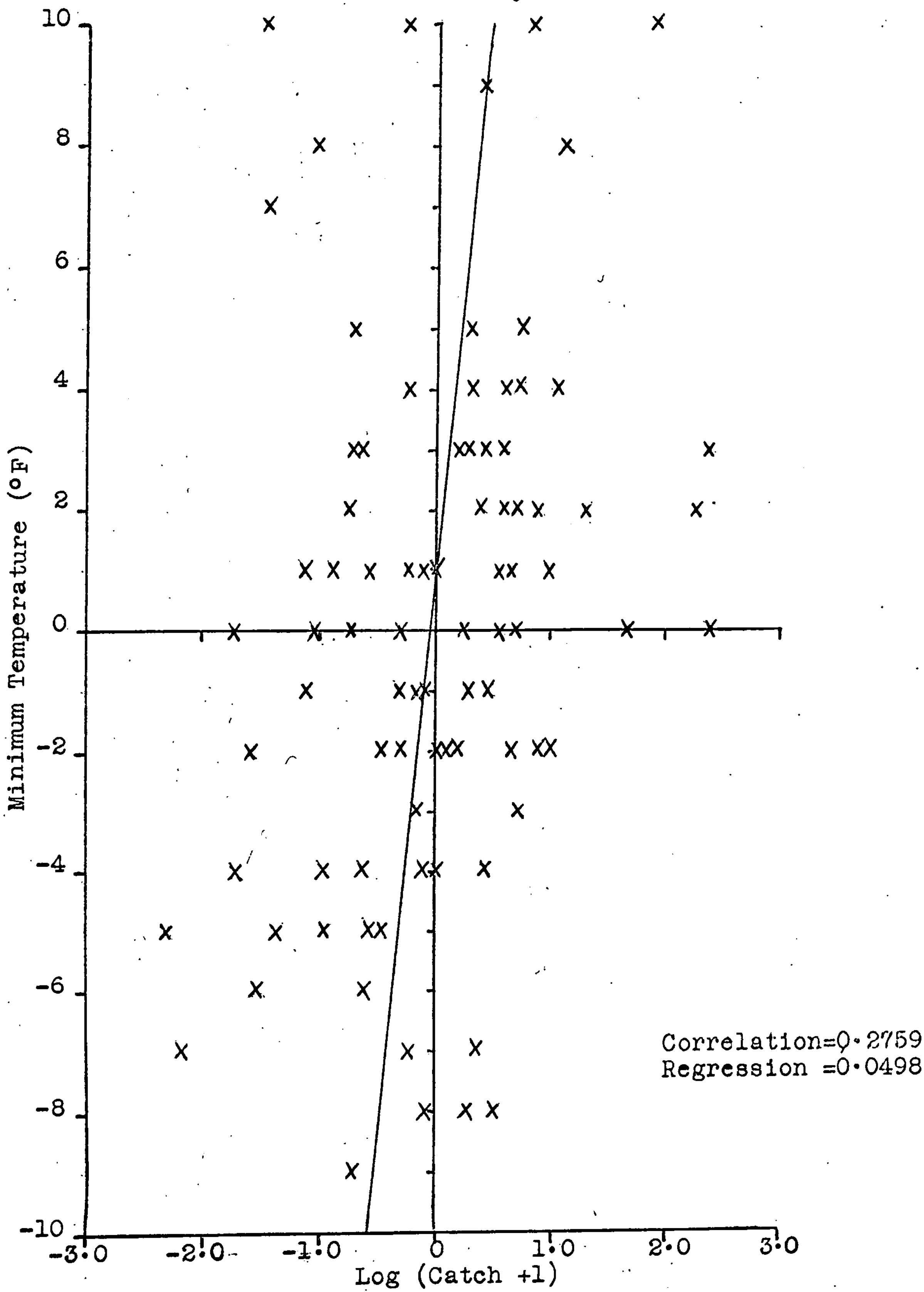
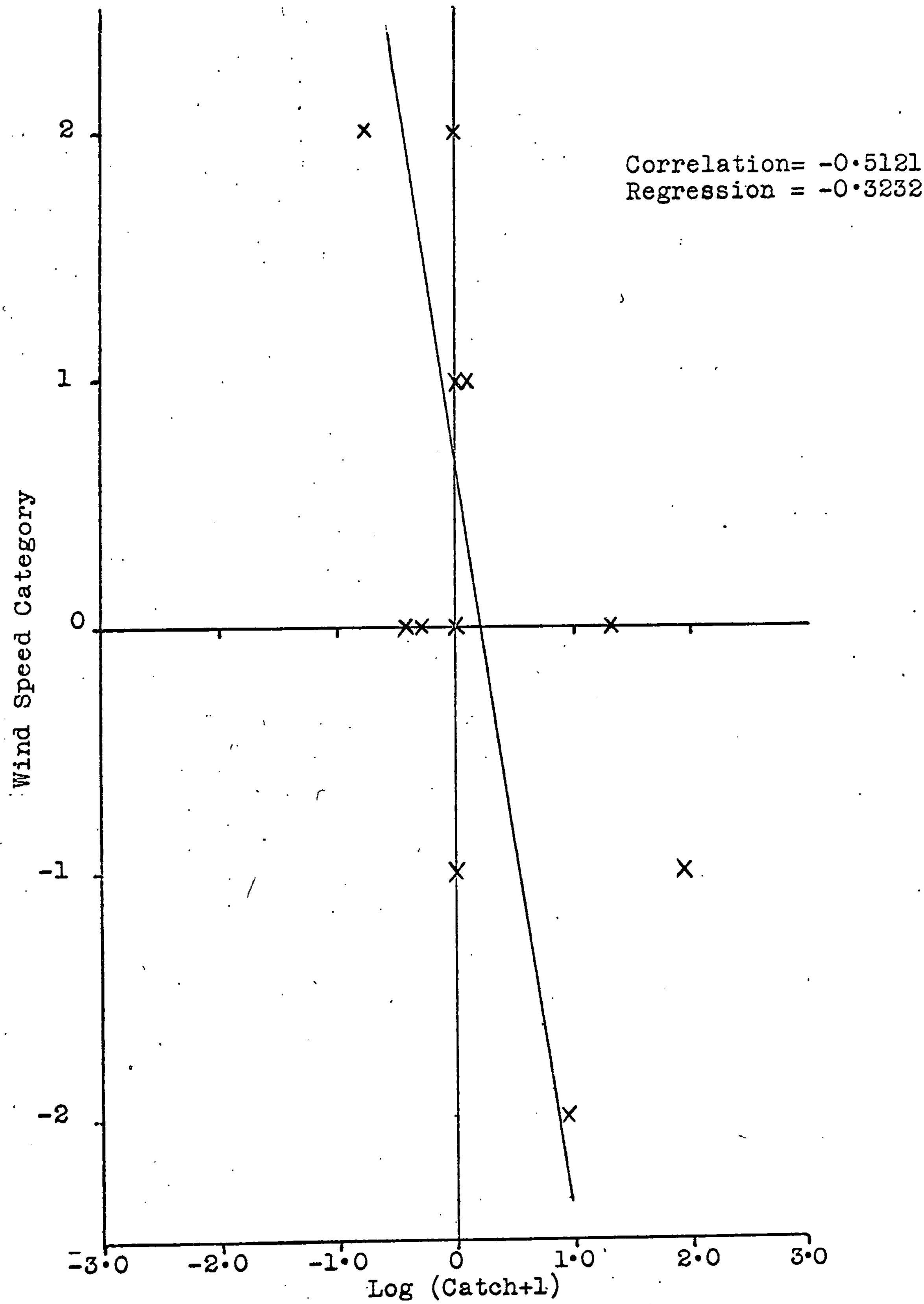


Fig. 8. Relation between log catch of _T.hiemalis_ males and wind speed for November 1968 from difference between successive days.



a further 20 seconds to print it out.

(b) Results

The correlation coefficients, their significance levels, if any, and the significant regression coefficients (i.e. those in which the error is less than half the coefficient) are given in apprendices 11 to 18. Figs. 7 and 8 show two typical regression lines, one positive and one negative, which can be drawn through the original data points.

(c) Discussion of the Results

For the whole 9 month season (September-May) only minimum temperature and grass minimum temperature show significant correlations, for the total catch and for regelationis (hiemalis tends to give poorer correlations, and this may be due to the many zero values that were included). Minimum and grass minimum temperatures are also closely correlated with each other, with the very high correlation coefficient of 0.8000.

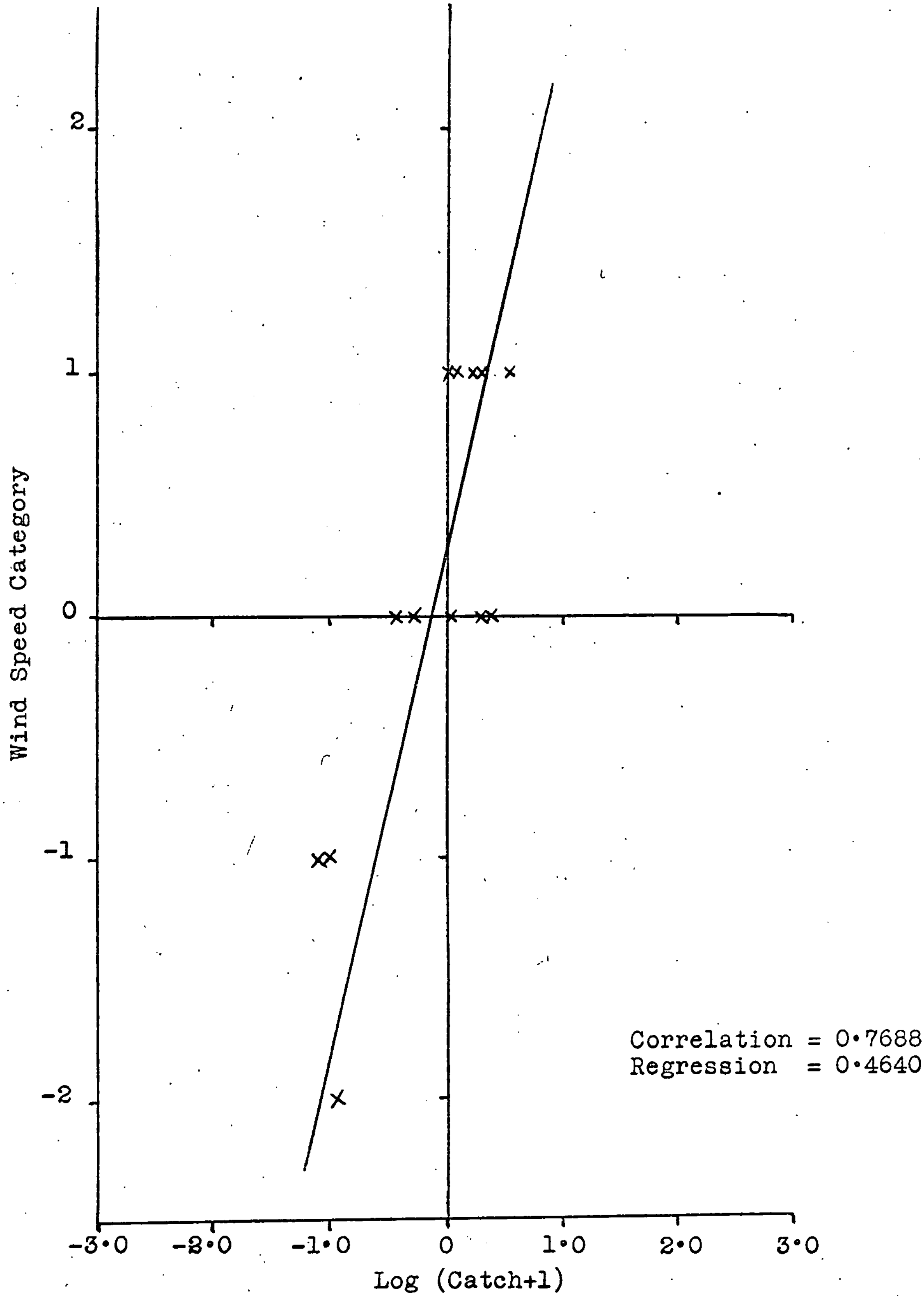
The figures agree fairly well with Williams's (1940) figures for the total insect catch of a year. My regression for minimum temperature on the total catch of Trichocera is 0.0498 compared to 0.060 given by Williams, and for grass minimum 0.0417 compared to 0.030.

Wind speed, maximum temperature, rainfall and humidity all have low correlations. Wind is positively correlated with the catch, which is unexpected, as high winds usually inhibit insect flight. Maximum temperature is positively correlated, and the correlation might be expected to be small, as most of the period considered is during the colder part of the year, when the night temperature drops quite considerably. Rainfall shows a negative correlation with the catch, which agrees with Williams's findings. Humidity also has a negative correlation, which is the opposite to what Williams found.

In the monthly results, minimum temperature is only correlated significantly with the catch in January, and grass minimum temperature only in May. Wind speed gives highly significant positive correlations in October and January (see fig. 9). There is a reasonable correlation between wind and minimum temperature in January (0.4920) so that the increase in temperature on windy nights could explain the increases in the catch, but there is no such good correlation in October, so the result is very difficult to explain. As Williams says, the presence of a high correlation between two factors is in no way proof that one factor is directly influencing the other, and it is frequently true that a relation between two correlated factors is not one of direct cause and effect, but both are correlatied with a third factor which has not appeared in the data provided.

The results of the analysis of the <u>Trichocera</u> catch in the light

Fig. 9. Relation between log total catch and wind speed for October 1968 from difference between successive days.



trap on the basis of meteorological data, using Williams's method are, on the whole, disappointing. The results for the whole year for the total catch and for <u>regelationis</u> are fairly reasonable and agree broadly with Williams's results, but the results for <u>hiemalis</u> and all the monthly results are very poor. This could be due to several reasons:

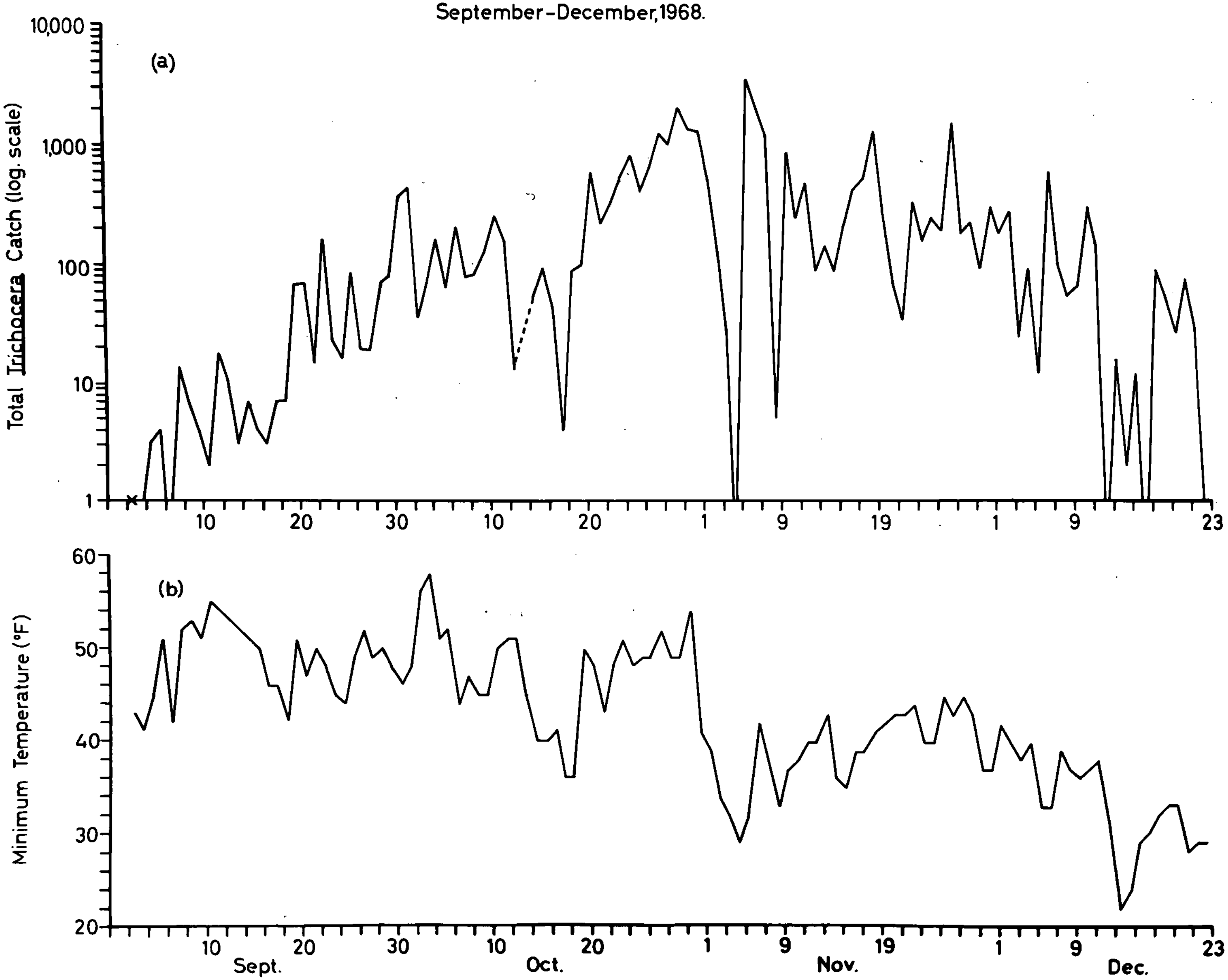
(i) the meteorological data are not sufficiently accurate. Many of the readings are spot values taken at 0900 hours, and may bear little relationship to weather conditions as much as 15 hours previously (the light trap goes on at 6 p.m. or earlier in the middle of winter);

(ii) the method used (differences between successive nights) is not the best method, but this needs previous data, as does refinement of the method used;

(iii) <u>Trichocera</u> are probably not the best insects to work with, as Williams points out that the rapid emergence of large numbers of insects changes the population quickly and upsets the basic argument. He also says that the emergence of <u>Trichocera</u> upset this autumn results by masking the fall in the total insect catch as the temperature falls. I think that this great rise in the numbers of Trichocera in the autumn could well be the reason for the lack of correlations during the September-December period, and may have caused spurious correlations elsewhere.

It may well be that <u>Trichocera</u>, and other groups of insects which show similar "explosive" emergences, will have to be analysed by some other method.

Fig.10. Graphs of (a) total _Trichocera_ catch, and (b) minimum temperature against the date, for the period September-December, 1968.



(d) Further Analysis

By plotting the total Trichocera catch against the data I obtained a curve for the September-December section which probably corresponds to the autumn emergence. I plotted minimum temperature against the date for the same period and obtained a line showing a downward trend. Comparison of these two graphs (fig. 10) shows that the major deviations of both from their general trends correspond with each other.

I thought I might be able to correlate the deviations from the trend lines, but these lines proved impossible to draw using normal methods, as the Trichocera catch graph is not a normal curve (this was shown by plotting the percentage cumulative frequency of the catch on arithmetic probability paper, when it did not given a straight line), and the temperature graph is neither a straight line nor a normal curve. The computor analysis already carried out had done a similar correlation to this anyway.

I then tried a simple comparison of the two graphs, giving a positive mark when they rose or fell together and a negative mark when one rose as the other fell, and then compared the numbers of positives and negatives obtained using a chi-squared test. Unfortunately the data would not stand up to such close scrutiny, and for the whole Trichocera season there were 111 positive marks and 92 negative marks, and

$$\chi^2 = 1.778 \quad p > 0.1$$

GENERAL DISCUSSION

General Discussion

The field studies of the swarming behaviour have confirmed that *Trichocera* swarm only under certain conditions, i.e. wind speeds less than 1 m.p.h., air temperatures between 6 and 13°C, and relative humidities over 70%, as shown by Dahl (1965). They have also shown that *Trichocera*, like many other dipterans, swarm in response to a marker, and that this is an edge between two distinct colours or shades. Except for a brief mention by Syrjamaki (1968) of trichocerids dancing over grass tussocks in Spitsbergen, this has not been shown before. It seems probable that the marker releases swarming behaviour in individuals, and that the swarm serves as a meeting place for the two sexes for the purposes of mating.

The analysis of the effect of the weather on activity shows that over the whole season the catch is mainly affected by the minimum air temperature and the ground temperature during the night, which is what Williams has shown forother insects. The more detailed monthly analysis does not show these results, and I think that this is because both activity and emergence are affected by the weather conditions, and the effect on one masks, or even conflicts with, the effect on the other. An indication of this can be seen by comparing the correlations of the September-December period with those of the January-April period (see appendices 11-17). Those of the former period, when the main emergence occured (see fig 10(a)) are usually low, whereas those of the January-April period, when the weather was worse and the emergence much less regular, are generally much higher.

The conditions favouring emergence are not known, but probably involve ground temperature (since the prepupae are in the surface layers of the soil) over a period of time, which may be several weeks. Conditions on a particular night may not be strongly correlated with those over a period of time previously, e.g. the minimum temperature of a night can alter markedly in a few hours if cloud cover is removed by upper air currents. This means that a night of favourable conditions for activity may follow a period with a high emergence, or a period with a low emergence, and therefore there is a poor short period correlation between activity and weather conditions.

The larvae of Trichocera are scavengers in rotting vegetation and dung (Rhynehart, 1924; Karandikar, 1931; Keilin and Tate, 1940; Laurence, 1956), but the adults, like all their relatives, have atrophied mouthparts and can only take liquid food. It is not known whether they feed in the natural state, but if they do it must presumably be on water, as there is no nectar available in the winter. The adults may, however, live for quite a long time (Laurence kept saltator adults alive on sugar water for up to 59 days in the laboratory) but several frosty nights may kill off a lot of ageing adults. If this is followed by a favourable night for activity the light trap catch may be relatively low due to the poor survival rate.

Although these insects must be adapted physiologically to carry out their life processes at low temperatures, they are doing so very near the limit for temperate climate insects, so that fairly small changes in weather conditions can have large quantitative effects on survival and activity.

When more is known about the biology of trichocerids, such as the conditions that affect emergence, how long the adults live and are available for catching, and how and when they react to the light trap, it may be possible to draw an "ideal" emergence curve, based only on the conditions that affect emergence, and then correlate any deviations from this with weather conditions that affect activity.

Such a project would involve laboratory studies to determine adult survival at different temperatures, the conditions controlling the so called larval diapause during the summer, which leads to pupation and emergence when it is broken, and the threshold temperature and thermal sum for the process, as well as field work on both adults and larvae, and counting and identifying the light trap catch. Catch figures and meteorological data for several previous years may also help in refining the methods used.

Although the results of may own analysis have not been as good as I had hoped, they have at least indicated the direction of further studies on <u>Trichocera</u>.

SUMMARY

Summary

Field studies were carried out on the swarming behaviour of *Trichocera* in the Durham area, and it was found that they swarmed over a marker at low wind speeds (less than 1 m.p.h.), temperatures between 6 and 13°C, and relative humidities over 70%. It was concluded that the marker releases the swarming behaviour, which brings the sexes together for mating.

The material from the Zoology Department Field Station light trap for the year July 1968-July 1969 was examined and the *Trichocera* present counted and identified. An attempt was made, using multiple regression analyses, to correlate the nightly catch with the prevailing weather conditions. For the whole *Trichocera* season (September 1968-June 1969) the catch numbers correlated significantly with the minimum air and ground temperatures during the night. A monthly analysis did not give good correlations, and it was thought that this was because the massive autumn emergence masked the effects of the weather on activity. The conclusion reached was that more information is needed on the conditions affecting the emergence of *Trichocera*.

APPENDICES

Appendices 1 - 10 show the nightly light trap catch for the ten months, September, 1968- June, 1969.

Appendices 11 - 18 show (a) the correlation coefficients, and (b) the regression coefficients of nine catch figures with six weather variables, for the whole season and for single months.

Appendix 1. September 1968.

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
31–1																	
1–2																	
2–3	1													1			
3–4																	
4–5	3													1	2		
5–6	4			1	2										1		
6–7																	
7–8	14			1	9										4		
8–9	7			1	4										2		
9–10	4													1	3		
10–11	2													1	1		
11–12	18				5										13		
12–13	10			2	1									2	5		
13–14	3													1	2		
14–15	7				1										6		
15–16	4				1										3		
16–17	3														3		
17–18	7				3										4		
18–19	7			1	2									1	3		
19–20	67			11	13								1	13	29		
20–21	68			1	25									10	32		
21–22	15				4									2	7		2
22–23	163			7	59									14	68	3	12
23–24	23			3	6									3	11		
24–25	16			2	6									2	3	1	2
25–26	86			3	25					1				4	45		7
26–27	19			2	3									1	11		2
27–28	19				6							2		1	5		5
28–29	69			1	22						3		1	4	23	1	13
29–30	79			1	9				6	11	3	1	4	32	7	2	3

Appendix 2 October 1968

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
30-1	368			44	24				20	16	36	4	52	140	16	4	12
1-2	432			50	50		2		25	10	30	5	40	180	30		10
2-3	36		2	6	2				4	2		2	6	1	8		3
3-4	70			6	1				7	4	1	2	14	12	18		5
4-5	164			9	9				6			6	57	12	52		12
5-6	64			3	2				8			1	14	8	23	1	4
6-7	208			4	4	4			4		4	96	20	12	44		16
7-8	79			1	10				11			2	8		36		11
8-9	83			4	6				10	6		3	4	12	31		7
9-10	130		2	2	10		1	1	6	6	2	6	12	26	48		8
10-11	255			45	80	5			5		5	25	15	5	70		5
11-12	152			12	15	1	1		6	6	3	12	6	75	15		
12-13	13				2					5	1			2	3		
13-14								bulb gone									
14-15	52			16	7					10	7				9	1	2
15-16	92		2	14	19				2	33	5	5	1	2	8		1
16-17	44			10	13		1		1	10	2	3	2		2		
17-18	4			3	1												
18-19	88			6	24				8	4		4	4	10	22	4	2
19-20	100			8	72								4	4	12		
20-21	572	1	1	240	110				20	110		10	10	10	50		10
21-22	218		1	40	50		1		5	65	5	5	5	15	25	1	
22-23	317			65	30				5	90	5	10	10	25	60	15	
23-24	506			90	20					180	10	40		100	30	40	
24-25	792			90	10	20		10	20	340	30	60	10	150	40		10
25-26	396	10		80	40					90	20	40		10	80	30	
26-27	641			180	130				10	180	20	20	20	70	10		
27-28	1245			640	340					40	20	60	60	20	60		
28-29	1034			460	200					40	180	80	40		20		
29-30	2050			1000	60	20	20		20	200	260	80	140	40	60	40	
30-31	1349	20		620	240	20				60	40	80	140	40	100	20	

Appendix 3 November 1968

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
31-1	1310			480	100		20			140	180	240	140			20	
1-2	501			220	20		20			30	30	140	30			10	
2-3	140			54	4					4	2	40	34			2	
3-4	28			5	1					1	3	10	8				
4-5													1480	40		20	
5-6	3518			720	80	40		40	80	180	180	680	260	20	20	60	
6-7	2024		20	1100	100			20		40	20	360	160			20	20
7-8	1197			640	20				20	40	20	260				1	
8-9	5			2							1	1	260			40	
9-10	869			20	40	20			40		20	400	96			20	10q
10-11	241			10	25				15			65	70			20	
11-12	475			220	10		10		30	20		110	24			2	4
12-13	88			8	2					2		46	42			12	3
13-14	146			33			3		9		6	39	44				2
14-15	88			14	8		2			2		16	95				
15-16	210			30	20			10	5			50					
16-17	430			170	10						10	220	80			20	
17-18	537			130	10				30			240	380	80		30	20
18-19	1311		20	80	20	60			20			480	80	5		120	60
19-20	294			30	10		5		35		5	75	17		3	25	5
20-21	70		1	15	9		5		3	4	4	3	9	2	3	5	1
21-22	34			8	1				2	3	1	2	180		20		2
22-23	336			70			10	1				40	65			20	
23-24	156			20		10	10		15			30	115		10	5	
24-25	247			5			5		65	5	15	10	55	10	25	5	10
25-26	188		5		10		5		45		15	5	360	100	40	5	
26-27	1558			220	20	60	20	80	100		40	480	45	20		20	20
27-28	181			20	10	10	5	5	15	5	5	40	45	25	10	5	5
28-29	226			45	15	10	20		10	10		35	33				
29-30	90			9			3		6			39					

Appendix 4 December 1968

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
30-1	313			70	20		10		50	10		60	70	20			
1-2	181			20			10		5		20	65	30	30			
2-3	282			80	20			20	10		10	50	50	20	20		
3-4	24			3	4		1			1	3	3	4		5		
4-5	93			27	9				6	3	3	24	21				
5-6	12				1				1			2	8				
6-7	597			80	60	20	22		180		20	80	120		20		
7-8	102			21	6	6	3	9	3	3	3	33	15				
8-9	55			13	4	2	1	2	6			10	14	1	2		
9-10	66			22	4				2			26	8	2	2		
10-11	305			90	60				30	10			80	20			
11-12	145			35	30	30			5			20	20	5			
12-13																	
13-14	16			4	2					1	2	1	1	5			
14-15	2									1			1				
15-16	12								1			2	9				
16-17																	
17-18	93			6	27	6	3		6			9	15		18	3	
18-19	54			15	12	5	1		2			3	15		1		
19-20	28			2		6	2					4	8	4	2		
20-21	78			3	18				3			3	24	6	21		
21-22	29			1	10	1	1		2		2	1	7	3	1		
22-23																	
23-24																	
24-25																	
25-26																	
26-27																	
27-28																	
28-29																	
29-30																	
30-31	3				1								2				

<u>Appendix 5 January 1969</u>

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
31-1																	
1-2	75			3	6	6	3		9		3	9	30	3	3		
2-3	130			35	25	20			15				25		10		
3-4	9				1	3						1	3	1			
4-5	12				5		1						4	2			
5-6																	
6-7	8				1							1	6				
7-8	48			7	18	1	2		2			3	8	1	6		
8-9																	
9-10																	
10-11																	
11-12	249			40	70				10				10	110	10		
12-13	556			280	80	20			20			40	40	80			
13-14	290			150	70								10	60			
14-15	98			45	45									6	3		
15-16	2			1	1												
16-17																	
17-18	236			60	100		10						30	30	10		
18-19	3													3			
19-20																	
20-21	399			30	10			10				10		290	40		
21-22	1027			520	160	20			40			20		220	60		
22-23	9			2	3								2	1	1		
23-24	197			100	50									25	20		
24-25	288			80	80									90	40		
25-26	312			40	180						10		10	10	60		
26-27	439			240	90									70	40		
27-28	120			45	50								10	5	10		
28-29	6			2	1	1							1	1			
29-30	79			12	18						6		3	9	30		
30-31	8			1	2									1	4		

Appendix 6 February 1969.

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
31-1																	
1-2																	
2-3																	
3-4																	
4-5																	
5-6																	
6-7																	
7-8																	
8-9																	
9-10																	
10-11																	
11-12																	
12-13																	
13-14																	
14-15																	
15-16																	
16-17																	
17-18																	
18-19																	
19-20																	
20-21																	
21-22																	
22-23	18			1	16										1		
23-24	15				15												
24-25	50			1	47	1						1					
25-26																	
26-27																	
27-28																	
28-29																	
29-30																	

Appendix 7 March 1969

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
28-1	187			5	182												
1-2	53			12	36										5		
2-3																	
3-4																	
4-5																	
5-6																	
6-7																	
7-8																	
8-9	22				21										1		
9-10																	
10-11																	
11-12	4				4												
12-13																	
13-14																	
14-15																	
15-16																	
16-17																	
17-18																	
18-19																	
19-20																	
20-21																	
21-22	10				9	1											
22-23	3				3												
23-24																	
24-25																	
25-26																	
26-27																	
27-28																	
28-29																	
29-30																	

<u>Appendix 8 April 1969.</u>

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
31-1																	
1-2																	
2-3																	
3-4																	
4-5	7			2	5												
5-6																	
6-7	2				2												
7-8	16			6	9									1			
8-9	19			2	15										2		
9-10	130			10	95										25		
10-11	37			3	33										1		
11-12																	
12-13	3				1	1									1		
13-14																	
14-15																	
15-16																	
16-17																	
17-18																	
18-19																	
19-20																	
20-21	17			2	14										1		
21-22	98			18	68										12		
22-23	43			21	20									2			
23-24	42			11	28										3		
24-25	15			3	10									1	1		
25-26	4			2	1										1		
26-27	3			2	1												
27-28	2				2												
28-29																	
29-30																	

Appendix 9 May 1969.

Date	Total Catch	annulata		regelationis		major		fuscata		rufescens		saltator		hiemalis		parva	
		M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.
30-1	3			1	2												
1-2	20				19									1			
2-3	29			3	26												
3-4	23			7	14							1			1		
4-5	5				5												
5-6	17			1	16												
6-7	21			1	20												
7-8	57			10	38										9		
8-9	38			8	30												
9-10	7			3	4												
10-11	4				4												
11-12																	
12-13	3				3												
13-14	10				9										1		
14-15	36			1	35												
15-16	26			1	20							1	1	1	2		
16-17	3				2										1		
17-18																	
18-19	3				3												
19-20	1				1												
20-21																	
21-22	1				1												
22-23																	
23-24	7				6										1		
24-25	7			1	5										1		
25-26	3				2							1					
26-27																	
27-28	12			2	10												
28-29	1				1												
29-30	1				1												

Appendix 10 June 1969

Date	Total Catch	annulata M.	annulata F.	regelationis M.	regelationis F.	major M.	major F.	fuscata M.	fuscata F.	rufescens M.	rufescens F.	saltator M.	saltator F.	hiemalis M.	hiemalis F.	parva M.	parva F.
31-1	2				2												
1-2	1				1												
2-3	9				9												
3-4																	
4-5																	
5-6																	
6-7	1				1												
7-8																	
8-9																	
9-10																	
10-11																	
11-12																	
12-13																	
13-14																	
14-15	1				1												
15-16																	
16-17	2				2												
17-18	1				1												
18-19																	
19-20																	
20-21																	
21-22																	
22-23																	
23-24																	
24-25																	
25-26																	
26-27																	
27-28																	
28-29																	
29-30																	

Appendix 11. Whole Season 1968-69

(a) Correlation coefficients (103 degrees of freedom).

	Wind speed		Max. Temp.		Min. Temp		Grass Min.		Rainfall		Humidity	
	r	p	r	p	r	p	r	p	r	p	r	p
Total catch	0.0656		0.1503		0.2759	0.01	0.2711	0.01	-0.0640		-0.1375	
" males	0.0728		0.1466		0.2007	0.05	0.2214	0.05	-0.0964		-0.1277	
" females	0.0707		0.1497		0.2729	0.01	0.2392	0.02	-0.0539		-0.1456	
<u>regelationis</u>	0.0469		0.1664		0.3220	0.001	0.3089	0.01	-0.0424		-0.1338	
" males	0.0283		0.1918		0.2722	0.01	0.2623	0.01	-0.0583		-0.0707	
" females	0.0768		0.1578		0.2760	0.01	0.2647	0.01	-0.0245		-0.1439	
<u>hiemalis</u>	0.1556		0.1873		0.2379	0.02	0.1764	0	0.0412		-0.0100	
" males	0.1356		0.1005		0.0574	0	0.0566		-0.0713		-0.0100	
" females	0.1939		0.1844		0.2811	0.01	0.2037	0.05	0.0663		0.0000	

(b) Regression coefficients

Total catch			0.0498	0.0417		
" males			0.0302	0.0284		
" females			0.0464	0.0346		
<u>regelationis</u>			0.0563	0.0460		
" males			0.0405	0.0332		
" females			0.0443	0.0362		
<u>hiemalis</u>			0.0316			
" males						
" females			0.0320	0.0197		

Appendix 12. September 1968.

(a) Correlation coefficients (14 degrees of freedom).

	Wind speed		Max. Temp.		Min. Temp.		Grass Min.		Rainfall		Humidity	
	r	p	r	p	r	p	r	p	r	p	r	p
Total catch	0.1507		0.3689		0.010		0.1072		-0·0959		0.2834	
" males	0.1466		0.2689		-0.0762		-0.0480		0.0100		0.1453	
" females	0.1421		-0.3696		0.0866		0.0436		-0.3812		0.1778	
regelationis	0.1327		0.3848		0.0721		0.0943		-0.0100		0.0529	
" males	0.0781		0.1766		0.1020		0.0424		0.0283		0.3633	
" females	0.1187		0.4031		0.0000		0.0700		-0·0854		0.0906	
hiemalis	0.0800		0.2834		-0.0100		-0.0200		0·0245		0.2520	
" males	0.0000		0.2049		-0.1196		-0.0906		-0·2083		0.2565	
" females	0.1682		0.3100		0.0361		0.0000		0·0265		0.1594	

(b) Regression coefficients. - none significant.

Total catch						
" males						
" females						
regelationis						
" males						
" females						
hiemalis						
" males						
" females						

Appendix 13 October 1968

(a) Correlation coefficients (14 degrees of freedom).

	Wind speed		Max. Temp.		Min. Temp.		Grass Min.		Rainfall		Humidity	
	r	p	r	p	r	p	r	p	r	p	r	p
Total catch	0.7688	0.001	-0.1311		-0.1077		0.0000		0.0224		0.2133	
" males	0.7930	0.001	-0.1900		-0.2646		-0.1428		0.3010		0.0000	
" females	0.7413	0.01	0.1908		0.0640		0.1386		0.0566		0.2794	
<u>regelationis</u>	0.5130	0.05	0.1311		0.1631		0.1897		0.0663		0.0265	
" males	0.4666		0.1926		0.1257		0.0735		0.2592		0.1990	
" females	0.4635		0.0787		0.1109		0.2317		0.0283		0.1597	
<u>hiemalis</u>	0.2360		0.2510		0.1543		0.1082		0.4142		0.2243	
" males	0.3614		0.0346		-0.1292		-0.0224		0.5063	0.05	0.2076	
" females	0.0200		0.5214	0.05	0.2927		0.1622		0.3010	0.05	0.1334	

(b) Regression coefficients.

Total catch	0.4640					
" males	0.5895					
" females	0.4341					
<u>regelationis</u>	0.3305					
" males						
" females						
<u>hiemalis</u>						
" males					5.3787	
" females		0.0732				

Appendix 14. November 1968.

(a) Correlation coefficients

	Wind speed		Max. Temp.		Min. Temp.		Grass Min.		Rainfall		Humidity	
	r	p	r	p	r	p	r	p	r	p	r	p
Total catch	-0.2354		0.0995		0.0748		0.3140		-0.1706		-0.2551	
" males	-0.3084		-0.0700		0.1432		0.4483		-0.2326		-0.1631	
" females	-0.2898		0.2358		-0.0714		0.0000		-0.1775		-0.3010	
regelationis	-0.1131		-0.0693		0.1982		0.4021		-0.1404		-0.2263	
" males	-0.1158		-0.1360		0.1688		0.4352		-0.2236		-0.1221	
" females	-0.1769		0.2012		0.0000		0.0300		0.0300		-0.2435	
hiemalis	-0.3804		0.4378		0.0173		0.1204		-0.1288		-0.0490	
" males	-0.5121	0.05	0.1020		-0.0781		0.1476		-0.3339		-0.0975	
" females	0.2052		0.0529		0.3486		0.3022		0.3130		0.2795	

(b) Regression coefficients.

Total catch						
" males						
" females						
regelationis						
" males						
" females						
hiemalis						
" males	-0.3232					
" females						

Appendix 15 December 1968

(a) Correlation coefficients (11 degrees of freedom).

	Wind speed		Max. Temp.		Min. Temp.		Grass Min.		Rainfall		Humidity	
	r	p	r	p	r	p	r	p	r	p	r	p
Total catch	-0.3629		0.5485		0.0000		-0.0574		-0.1507		-0.5098	
" males	-0.3763		0.4459		0.1597		0.1288		-0.1091		-0.4119	
" females	-0.3058		0.5297		-0.0748		-0.1145		-0.1237		-0.4386	
regelationis	-0.3709		0.5227		-0.0348		-0.0510		0.0283		-0.3607	
" males	-0.3663		0.3738		0.1836		0.1664		-0.0812		-0.2995	
" females	-0.1549		0.4530		-0.1606		-0.0959		0.0933		-0.2663	
hiemalis	-0.2514		0.2583		-0.2506		-0.2126		0.3085		0.0000	
" males	-0.3217		0.4375		-0.0800		-0.1311		-0.0100		0.0000	
" females	0.0781		-0.0265		-0.3980		-0.2700		0.3323		-0.1315	

(b) Regression coefficients. - none significant.

Total catch						
" males						
" females						
regelationis						
" males						
" females						
hiemalis						
" males						
" females						

Appendix 16 January 1969

(a) Correlation coefficients

	Wind speed		Max. Temp.		Min. Temp.		Grass Min.		Rainfall		Humidity	
	r	p	r	p	r	p	r	p	r	p	r	p
Total catch	0.7330	0.01	0.2718		0.6021	0.02	0.04450		-0.1682		-0.4378	
" males	0.7125	0.01	0.2970		0.5630	0.05	0.3825		-0.1127		-0.4432	
" females	0.7147	0.01	0.3184		0.6300	0.01	0.4605		-0.1513		-0.4244	
regelationis	0.6440	0.01	0.3365		0.6322	0.01	0.4577		-0.1634		-0.4244	
" males	0.5426	0.05	0.3688		0.5436	0.05	0.3528		-0.0911		-0.3775	
" females	0.6557	0.01	0.2832		0.6344	0.01	0.4573		-0.1860		-0.4214	
hiemalis	0.7956	0.001	0.2256		0.5363	0.05	0.3960		-0.1265		-0.3987	
" males	0.8383	0.001	0.1990		0.4442		0.2867		-0.0173		-0.4394	
" females	0.6552	0.01	0.3089		0.5275	0.05	0.4194		-0.1442		-0.3069	

(b) Regression coefficients.

Total catch	0.5981		0.1152			
" males	0.5041		0.0934			
" females	0.5225		0.1080			
regelationis	0.4783		0.1101			
" males	0.3544		0.0833			
" females	0.4244		0.0963			
hiemalis	0.5067		0.0801			
" males	0.4825					
" females	0.3103		0.0586			

Appendix 17 February, March and April 1969.

(a) Correlation coefficients

	Wind speed		Max. Temp.		Min. Temp.		Grass Min.		Rainfall		Humidity	
	r	p	r	p	r	p	r	p	r	p	r	p
Total catch	-0.3719		0.2427		0.4662		04695		-0.0889		-0.2276	
" males	-0.4246		0.4200		0.4442		0.6032	0.02	-0.2293		-0.0447	
" females	-0.3444		0.2035		0.4541		0.4344		-0.1039		-0.2191	
regelationis	-0.3759		0.2460		0.4481		0.4532		-0.0837		-0.2241	
" males	-0.4220		0.4063		0.4110		0.5872	0.02	-0.1900		-0.0640	
" females	-0.3423		0.2145		0.4397		0.4205		-0.1086		-0.2184	
hiemalis	-0.1077		0.2943		0.6454	0.01	0.7671	0.001	-0.2604		-0.0877	
" males	-0.1954		0.4721		0.1114		0.1418		-0.1761		0.0100	
" females	-0.0100		0.1237		0.6679	0.01	0.6851	0.01	-0.2138		-0.0954	

(b) Regression coefficients.

	Wind speed	Max. Temp.	Min. Temp.	Grass Min.	Rainfall	Humidity
Total catch						
" males				0.0674		
" females						
regelationis						
" males				0.0629		
" females						
hiemalis			0.0630	0.0614		
" males						
" females			0.0679	0.0571		

Appendix 18 May 1969

(a) Correlation coefficients

	Wind speed		Max. Temp.		Min. Temp.		Grass Min.		Rainfall		Humidity	
	r	p	r	p	r	p	r	p	r	p	r	p
Total catch	0.4735		-0.1459		0.3608		0.6979	0.01	0.0173		0.3010	
" males	0.4285		0.0922		0.18 03		0.5139	0.05	0.0671		-0.0707	
" females	0.4927	0.05	-0.1603		0.3444		0.6893	0.01	0.0346		0.3336	
<u>regelationis</u>	0.4738		-0.1338		0.3661		0.6909	0.01	0.0000		0.3324	
" males	0.3387		0.3357		0.2131		0.3946		-0.0872		-0.0854	
" females	0.4859	0.05	-0.1849		0.3302		0.6942	0.01	0.0374		0.3401	
<u>hiemalis</u>	0.4971	0.05	0.0557		0.1261		0.2236		0.1288		0.1005	
" males	0.3635		-0.3707		-0.0400		0.2565		0.2837		0.4699	
" females	0.4147		0.1565		0.1039		0.1513		0.0141		0.0173	

(b) Regression coefficients.

Total catch				0.0788		
" males				0.0258		
" females	0.1414			0.0802		
<u>regelationis</u>				0.0755		
" males						
" females	0.1355			0.0784		
<u>hiemalis</u>	0.0780					
" males						
" females						

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ACKNOWLEDGEMENT

Acknowledgements.

I wish to thank Dr. L. Davies for his guidance during this study, and also

Miss C.A. Cockbain for typing the dissertation,

Mr. J. Richardson for his help with the light trap material,

Mrs. J. Hines and the computor unit for their help with the regression analysis,

Mr. E. Hendeinson for the photographic work.

The study was carried out while the writer held a N.E.R.C. Advanced Course Studentship.