This work is protected by copyright and other intellectual property rights and duplication or sale of all or part is not permitted, except that material may be duplicated by you for research, private study, criticism/review or educational purposes. Electronic or print copies are for your own personal, non-commercial use and shall not be passed to any other individual. No quotation may be published without proper acknowledgement. For any other use, or to quote extensively from the work, permission must be obtained from the copyright holder/s.

LIB. COPY.

THE ECOLOGY OF THE CHIRONOMIDAE IN A *PHRAGMITES* REEDBED AT COP MERE (STAFFORDSHIRE, ENGLAND).

by

Peter Geoffrey Bell B.Sc. Cert. Ed.

Thesis presented for the Degree of

Doctor of Philosophy

University of Keele, 1987

ABSTRACT

The Chironomidae occupying a *Phragmites* reedbed at Cop Mere, Staffordshire were studied during 1981 and 1982.

In 1981, reedstem-dwelling larvae were sampled at monthly intervals from three zones running parallel with the reedbed/open-water interface, lying at the front (lakeward edge) (Zone 1), middle (Zone 2) and back (landward edge) (Zone 3) of the aquatic part of the reedbed.

The highest monthly chironomid larval density and biomass usually existed in Zone 1 and the lowest in Zone 3. Significant interzonal density and biomass variation occurred at various times of the year; such variation was consistently manifest between Zones 1 and 3, except in density during April.

Seventeen chironomid taxa were identified on reedstems, *Glyptotendipes pallens* and *Camptochironomus tentans* being the most abundant of the nine Chironominae taxa found; eight Orthocladiinae taxa were represented, *Cricotopus sylvestris* accounting for over 95% of all reedstem-dwelling chironomid larvae.

For each taxon, ecologically significant interzonal abundance differences were often found. These were largely attributed to interzonal variation in epiphytic shelter. In some species (e.g. *Camptochironomus tentans*, *Cricotopus sylvestris* and *Parachironomus arcuatus*), higher densities towards open water may have reflected a positive phototactic response in early instars.

The benthic-dwelling larval community showed interzonal variation: the predominant species, *Camptochironomus tentans*, was most abundant towards the reedbed front, whereas *Glyptotendipes pallens* favoured the area around Zone 3. Interzonal substrate variation may have been the biggest influence on species distribution.

The semi-aquatic reedbed area supported a distinctive larval community; *Tanytarsus*, *Metriocnemus* sp. A and Pentaneurini sp. A predominated. Adult chironomid population data derived from emergence trap catches was used principally to supplement and corroborate information relating to larval populations.

Temporal chironomid density patterns appeared to be determined primarily by intrinsic species characteristics, especially those which govern seasonal patterns of egg-laying.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Miss R.M. Badcock, for her advice and constructive criticism during the course of this work. Thanks are also extended to Professors J.B. Lloyd and C. Arme for providing research facilities within the Department of Biological Sciences, and to the University of Keele for financial support.

Permission to work at Cop Mere was given by Mr. G.L. Jacques of the Sugnall Manor Estate.

Mr. M.J. Pilkington translated several papers from Russian to English and I am grateful for his help.

I am also grateful to Miss M. Cowen for her accurate and resolute typing of this thesis.

Dr. T.J. Mountain receives particular appreciation for his invaluable help, guidance and comments throughout the formative stages of this research project.

Finally, I wish to express my gratitude to the many friends and relatives who gave encouragement and support during my studies.

CONTENTS

Chapter 1:	INTRODUCTION	1
Chapter 2:	A DESCRIPTION OF COP MERE AND SOME ENVIRONMENTAL CHARACTERISTICS OF THE REEDBED STUDY SITE	10
Chapter 3:	THE CHIRONOMID LARVAL COMMUNITY OF PHRAGMITES REEDSTEMS AT COP MERE	39
Chapter 4:	THE POPULATION PATTERNS OF REEDSTEM-DWELLING CHIRONOMID LARVAE - AN INVESTIGATION OF EXTRINSIC DETERMINANTS	119
Chapter 5:	THE CHIRONOMID LARVAL COMMUNITY FROM THE FLOOR OF THE REEDBED AT COP MERE	172
Chapter 6:	EMERGENCE OF ADULT CHIRONOMIDS AT COP MERE	202
Chapter 7:	FINAL DISCUSSION	234
	SUMMARY	247
	REFERENCES	252
	APPENDICES	262

Chapter 1

INTRODUCTION

The Chironomidae is a family of insects to which a good deal of research has been devoted. More than eight thousand references are listed in "A Bibliography of the Chironomidae" by Fittkau *et al* (1976) and its supplement compiled by Hoffrichter and Reiss (1981). Much of this literature pertains to ecological studies in freshwater environments. The prominence of such work is a reflection of the opportunities for research afforded by the world-wide distribution of the family, the presence of chironomids in a great variety of aquatic habitats, and a recognition of the important role chironomids play in many freshwater ecosystems. Gaps in our knowledge of chironomid ecology are abundant however, the diversification and seeming ubiquity of the family presenting a vast potential for study which has been only partly realised.

Such a deficiency exists in relation to the ecology of the reedbed-inhabiting members of the Chironomidae, due to the paucity of investigations in this area, and the fact that those studies that have been made present an incomplete picture, leaving many important questions unanswered.

Reedbeds are characteristically found in lentic as opposed to lotic environments. Field studies in lentic waters can be arbitrarily categorised according to the habitat(s) from which samples are taken. Investigations relating to profundal-dwelling chironomids are abundant (e.g. Brundin, 1951; Jónasson, 1965; Slack, 1967; Lindegaard and Jónasson, 1975). Observations of benthic fauna at various water depths are equally plentiful (e.g. Potter and Learner, 1974; Carter 1976; Cantrell and McLachlan, 1977; Moore, 1979; Titmus and Badcock, 1981). Relationships between the larvae of certain chironomid species and submerged aquatic plants have been extensively documented (e.g. Berg, 1950; Czeczuga and Niedzwiecki, 1966; Soszka, 1974; Stimac and Leong, 1977). Studies of chironomids associated with emergent macrophytes are considerably fewer in number.

Several reasons can be put forward to account for the seemingly disproportionate attention paid to particular habitats. Firstly, the presence of a benthic zone is common to all bodies of freshwater, but the presence of emergent macrophytes is not. Thus, the opportunities for benthic work are potentially greater. Secondly, the physical and ecological characteristics of many benthic habitats are conducive to the statistical analysis of larval spatial patterning - interactions are often simple, involving only a small number of species, and where the floor is flat and of a homogeneous nature, as is frequently the case in sublittoral and profundal locations, accurate quantitative samples can be taken from sampling points set up with a high degree of spatial precision. In contrast, the collection of specimens in stands of emergent macrophytes can prove to be awkward - access is sometimes difficult or even hazardous, and the acquisition of quantitative samples constitutes something of a challenge. Thirdly, the identification of the comparatively high number of chironomid species found as larvae in association with littoral vegetation was, until recently, a daunting proposition because of the incomplete and confused state of the larval keys that were available. However, with the recent publication of a detailed key by Cranston (1982), and other advances in larval taxonomy, this problem has been alleviated to some extent.

Descriptions of the few emergent macrophyte studies that show any appreciable pertinence to the present work follow, the first three being based on information supplied by Dvořák and Lisková (1970).

Shcherbakov (1961) examined the fauna living on stems of *Phragmites* and *Equisetum* from May to October. Chironomids are identified at least to genus, as they are in Sokolova's (1963) investigation of the macrofauna found in stands of *Typha*, *Phragmites*, and *Scirpus* from June to October. Chironomids are treated as a family by Arenkova (1965) who collected samples of summer macrofauna from *Glyceria*, *Sparganium*, *Acorus* and

Phragmites. In each of these three studies, abundance and biomass values for total macrofauna are given and represent the seasonal averages. No other measurements were made, either in relation to macrofauna or environmental variables. Seasonal maxima for macrofaunal abundance and biomass were generally found in June or July.

Papers by Dvořák (1970; 1971) and Dvorák and Lisková (1970) concern the horizontal zonation of macrofauna and water properties in the emergent macrophyte stands of some South Bohemian ponds. Animals were collected from stands of *Carex*, *Glyceria*, and *Sparganium* on an occasional basis during the summer. Each sample contained both benthic and macrophytic material; therefore no distinction was made between benthic-dwelling and epiphyton-dwelling organisms. Epiphyton was not analysed but water properties were measured in these stands and also in areas of *Phragmites* and *Typha*. Chironomids are identified to genus at least. The greatest faunal density and biomass occurred at the front (lakeward edge) of each stand. Physico-chemical water properties, particularly oxygen content, were regarded as important influences on faunal dispersion patterns. A decline in oxygen content from the front (lakeward edge) to the back (landward edge) of the macrophyte stands was proposed as the main cause of a reduction in animal numbers towards land. On a seasonal basis, the chief abundance and biomass maxima for macrofauna were found in the early summer.

Opaliński (1971) examined the benthic and plant macrofauna of a *Phragmites* reedbed in a Polish lake. Quantitative samples were taken regularly from July to September and chironomid species determined. No zonation element or environmental monitoring was incorporated into the research programme. Opaliński found that chironomid larvae made up 50% of the total number of benthic macrofauna and 95% of the total number of reedstem-dwelling macrofauna. The highest faunal densities occurred in the littoral benthos.

Mason and Bryant (1974) looked at the macrofauna found in three zones of a *Phragmites* reedbed on the Norfolk Broads. Sampling was restricted to the month of July and only benthic material taken. Unfortunately, chironomids are identified no further than to family level. The faunal community was most numerous at the front (lakeward margin) of the reedbed. Environmental analysis was confined to the measurement of pH at each site. A fall in pH was noted from the front to the back of the reedbed. The relationship between epiphyton density and chironomid larval numbers on dead *Typha* stems and glass rods was examined by the same authors (Mason and Bryant, 1975a). They concluded that algal and larval density variations through time are interdependent with a 'predator-prey' type cycle operating.

Higler (1977) worked on the Dutch Broads and sought correlations between the occurrence of animal aggregations on *Stratiotes* plants and certain environmental characteristics. The main part of the collection programme was conducted in the summer but occasional observations were made at other times of the year. Samples were taken at predetermined points on transects running from open water to the shore, and the physical and chemical environment at each position was monitored in detail. The majority of chironomids found are listed at species level. Higler reported that the dispersion patterns of chironomid larvae vary on a taxonomic basis. Spatial variation in the water's oxygen content was considered to be a significant influence on faunal dispersion patterns.

The benthic and epiphytic macrofauna of emergent macrophyte (mainly *Phragmites*) stands in some Polish lakes are described by Pieczyński (1977), but chironomid identification is not taken beyond family level. No environmental monitoring was undertaken. Pieczyński found that the numbers and biomass of the benthic fauna were much higher than the numbers and biomass of the epiphytic fauna. The seasonal density dynamics of the two communities were fundamentally different.

The research which shows the greatest similarity to the present study is that by Mountain (1981) who investigated the chironomid communities of emergent macrophyte stands at Cop Mere, and Linford, Buckinghamshire. A twenty-month sampling programme in a *Phragmites* stand at Cop Mere involved the collection of larvae from the benthic and epiphytic habitats in the area of permanent standing water and the trapping of adults emerging from this part of the reedbed. Indeed, of all the studies reviewed, this is the only one to incorporate emergence trapping - a similarity shared by the present work.

The two studies differ fundamentally, however, in a number of aspects. Firstly, Mountain does not discriminate the chironomid communities found in different zones of the reedbed; his analyses are based on the premise that larval distribution and abundance is not spatially variable in this respect. The present study indicates that this is not the case. Secondly, his research does not cover the semi-aquatic landward part of the reedbed. Thirdly, Mountain did not carry out fieldwork investigations at any of the other meres that lie on the Shropshire-Cheshire Plain, although he does compare adult emergence from *Phragmites* stands at Cop Mere and Linford.

The extraction of supportive information from the works outlined above is frustrated by the fact that often chironomids are included in a wider faunal survey and consequently receive only a limited consideration. Also, the overall time constraints imposed on research projects may not permit payment of the unproportionately large amount of attention demanded by a family whose identification is difficult and taxonomy confused. Thus, in several surveys chironomid classification proceeds no further than to family level and few reports give comprehensive species lists - a situation discussed by Tait-Bowman (1976). A lack of detailed environmental analysis pervades a number of the reports and

reflects a tendency to offer description without explanation. The elucidation of causal factors is not aided by discontinuous sampling programmes which limit the study of temporal change.

For the present work, Cop Mere was chosen as the principal study location because of its convenient proximity to Keele, coupled with the fact that a fairly extensive and easily accessible *Phragmites* reedbed is present which offers favourable conditions for study. This reedbed lies on the south-eastern edge of the mere and shows a marked horizontal (i.e. from open water to dry land) variation in the types of habitats available for exploitation by chironomids. Some habitat variations are obvious; others are more subtle. One of the most noticeable is the division of the reedbed into a lakeward area of permanent standing water and a landward area where the water-table may be above, level with, or just below the ground surface.

In the area of permanent standing water, chironomid larvae can colonise the benthic substrate between *Phragmites* roots and also the epiphyton coating the submerged portions of reedstems. This epiphyton often shows characteristic horizontal differences and thus constitutes a variable habitat for colonising chironomids. Larvae of some species are sometimes found living in the exposed hollow interior of stems which have snapped below the water surface. Others are free-swimming and live an errant lifestyle amongst the reeds and benthic material.

Towards land, behind the area of permanent standing water, conditions in the reedbed are essentially semi-aquatic and chironomid larvae inhabit the decaying fragmented plant material of which the substrate here is almost exclusively composed.

An intensive sampling programme was conducted over a two-year period at Cop Mere, involving the collection of larvae and adults from all the habitats previously described. Samples were taken from predesignated zones lying parallel with the reedbed/open-water interface, each zone

covering a particular set of environmental conditions. By adopting this type of sampling pattern, the complete range of habitats found in the reedbed came under scrutiny.

The research which provided the data foundation for this thesis was initiated with the overall objective of producing an explanatory account of chironomid ecology in reedbeds. Detailed investigations at Cop Mere and a survey of seven other meres on the Shropshire-Cheshire Plain gave rise to the type of information on which certain generalisations can confidently be based. In order to construct a useful data foundation, which would permit valid extrapolation, answers were sought to three fundamental questions:

1) Which chironomid species frequent the reedbed at Cop Mere?

2) What are their collective and individual spatiotemporal patterns of distribution and abundance?

3) What factors determine the form of each to these patterns?

The chironomid sampling programme outlined in the previous paragraph was designed to answer questions 1 and 2. A concurrent programme of environmental monitoring and analyses included the investigation of physico-chemical water properties, weather influences, epiphyton characteristics, benthic substrate composition, and the nature of the faunal community as a whole. These were deemed to be the environmental factors which could influence patterns of diversity, distribution, and abundance, and would therefore have to come under careful consideration when seeking an answer to question 3.

An appraisal of the other works that pertain most closely to this study illustrates the overall uniqueness of the latter and the magnitude of the knowledge gap it is intended to fill. The research strategy of the present study was devised with an awareness in mind of the shortfalls of these past works. Field experiments and sampling programmes were designed to produce the most apposite data for the analytically derived revelation

of ecological principles relating to reedbed-inhabiting chironomids. An outline of the nature of work presentation in this thesis now follows.

Following this introduction, Chapter 2 contains a general description of Cop Mere and considers some of the environmental features of the reedbed study site where field work was undertaken. The features in question are vegetation and substratum characteristics, weather influences, and properties of the water pervading the reedbed.

Chapter 3 is concerned with the chironomid larval community living on the submerged portions of reedstems at Cop Mere. The first section deals with fieldwork planning, sampling methods, and the treatment of samples in the laboratory. The second section describes spatiotemporal patterns of abundance and diversity for the total population of epiphyton-dwelling chironomid larvae found on old reedstems during 1981; population patterns for individual taxa are revealed in Section 3. Annual variation in the diversity and abundance of the chironomid community found on old reedstems is discussed in Section 4, whilst a comparison of the larval populations living on old and new reedstems during 1981 is made in Section 5.

Chapter 3 is essentially descriptive, its considerable length reflecting, to a large extent, the importance of the epiphytic habitat in the reedbed in terms of larval taxonomic diversity and abundance. Where it is felt to be appropriate, explanation regarding particular population patterns is offered but the main body of explanation relating to the data presented in Chapter 3 is contained in the following chapter.

Chapter 4 is basically concerned with the environmental influences which may play a part in shaping the population patterns discussed in Chapter 3. An attempt is made to assess the relative effect of each of these influences in both time and space. Following a brief introduction to some relevant terms and concepts, consideration is given to the influence of spatiotemporal variation in epiphyton characteristics on

larval population patterns. Both quantitative and qualitive aspects of epiphyton variation are examined. The effects of spatiotemporal changes in physico-chemical water characteristics are investigated in Section 3, whilst Section 4 deals with several miscellaneous potential determinants of population patterns for reedstem-dwelling larvae.

The chironomid larval community from the floor of the reedbed is discussed in Chapter 5. The main emphasis is on comparison of the larval populations found at different distances from the front of the reedbed, rather than any precise determination of abundance or spatial patterning within a particular area. Differences in population density and taxonomic composition from the front to the back of the reedbed are revealed and the environmental factors which may account for these differences are considered.

Chapter 6 relates to adult emergence from the area of permanent standing water in the reedbed during 1981. The data presented here were principally collected to provide supportive information for the larval population investigations, both in terms of species identification and pattern interpretation. Spatial variation in emergence, from the front (lakeward edge) to the back (landward edge) of the area of permanent standing water, is examined.

The final discussion (Chapter 7) contains a review of the study at Cop Mere as a whole and includes an overall consideration of the conclusions drawn in previous chapters. A brief comparison is made between reedbed larval populations at Cop Mere and those found at the seven other meres mentioned earlier in this introduction, prompting some remarks on reedbed chironomid ecology in general.

PLATE 2:1:1 - A panoramic view of Cop Mere showing the densely wooded western and south-western banks in the distance, and the reedbed study site in the foreground.

Chapter 2

A DESCRIPTION OF COP MERE AND SOME ENVIRONMENTAL CHARACTERISTICS OF THE REEDBED STUDY SITE

2:1 Cop Mere - Site and Situation

Cop Mere (Grid Reference SJ 802298) lies in gently undulating country on the eastern side of the Shropshire-Cheshire Plain, about 3km west of Eccleshall and some 14km north-west of Stafford (Plate 2:1:1 and Figure 2:1:1). Together with the sixty or so other meres and pools exceeding one hectare which characterise the Plain, it owes its origins to the moulding of the landscape which took place during the deglaciation more than fourteen thousand years ago (Reynolds, 1979). Present day geology reflects the glacial influences of the past: Cop Mere is sited in a shallow valley in which Keuper Marl is partly covered by peat, glacial sands and gravels, boulder-clay, and alluvium (NCC Report, 1980).

The fact that Cop Mere is fed by a river, in addition to ground-water seepage, differentiates it from other meres. The headwaters of the River Sow rise just north-west of the village of Fairoak (Grid Reference SJ 766327) and from here the river runs south then east for about 9km before entering Cop Mere on its western edge (Figure 2:1:2). From an outflow point on the south-eastern side of the mere, the Sow flows towards Eccleshall and joins the River Trent just outside Stafford.

Two smaller streams enter the mere at its northern end after passing through a series of abandoned man-made fish ponds.

2:2 Cop Mere - Basin Morphology and Surrounding Vegetation

With an area of 16.8 hectares Cop Mere is the thirteenth largest of the forty-one meres listed by Reynolds (1979). It is the ninth shallowest (maximum depth 2.7m) of the thirty meres for which depths are given.

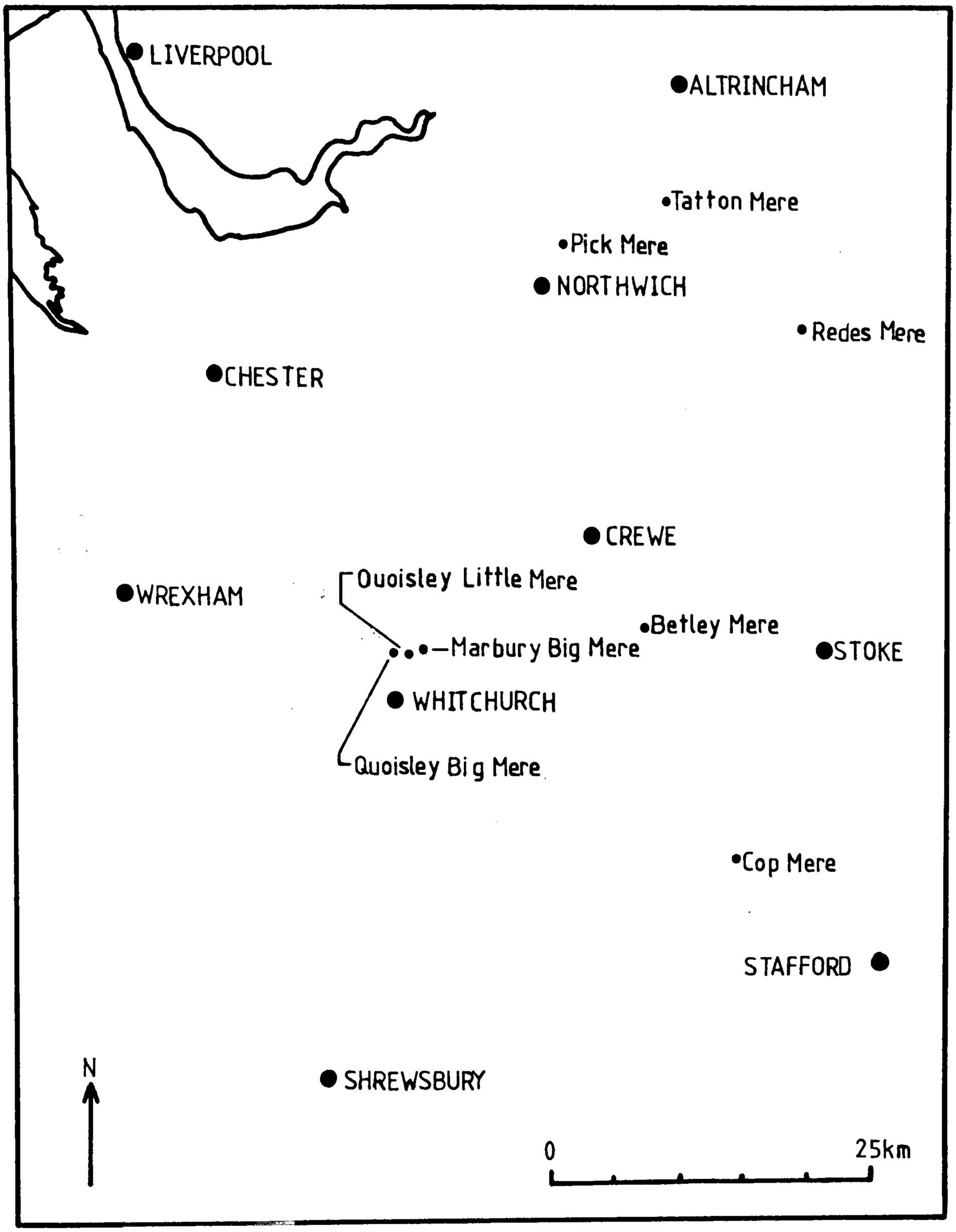


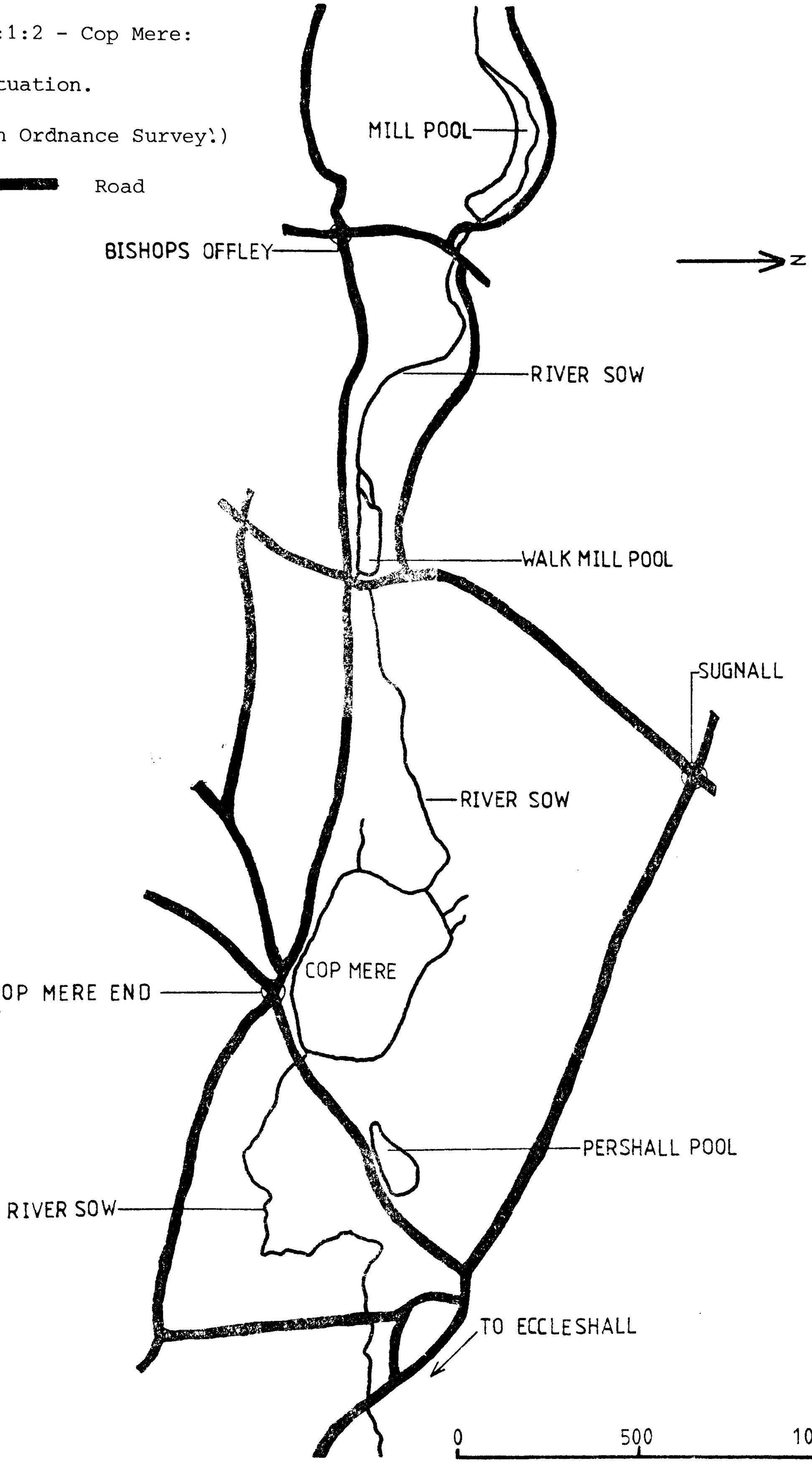
FIGURE 2:1:1 - The regional location of the eight meres for which information is presented in this thesis. (Based on Reynolds, 1979.)

FIGURE 2:1:2 - Cop Mere:

local situation.

(Based on Ordnance Survey.)

KEY Road



Mixed deciduous woodland surrounds much of the mere although it is represented by only a thin line of trees and bushes behind the reedbed on the south-eastern edge. Trees overhang the water where emergent macrophyte stands are absent. At its western end the mere is flanked by a damp Alder-Willow wood which grades westwards to dry Oak-Birch or mixed deciduous woodland.

The north-eastern and south-western banks slope steeply (upto 45^{o})[1] to the water's edge and continue to do so underwater in the littoral zone, allowing the presence of only a narrow disjunct fringe of *Typha angustifolia* (Linnaeus) with some *Phragmites australis* (Cavinilles) Trin. ex Steud. towards land.

On the south-eastern side the land slopes very gradually (about 3^{o}) and consequently the *Phragmites* reedbed in this location is comparatively broad (about 30m); it is here that a study site was selected for subsequent field-work (Figure 2:2:1).

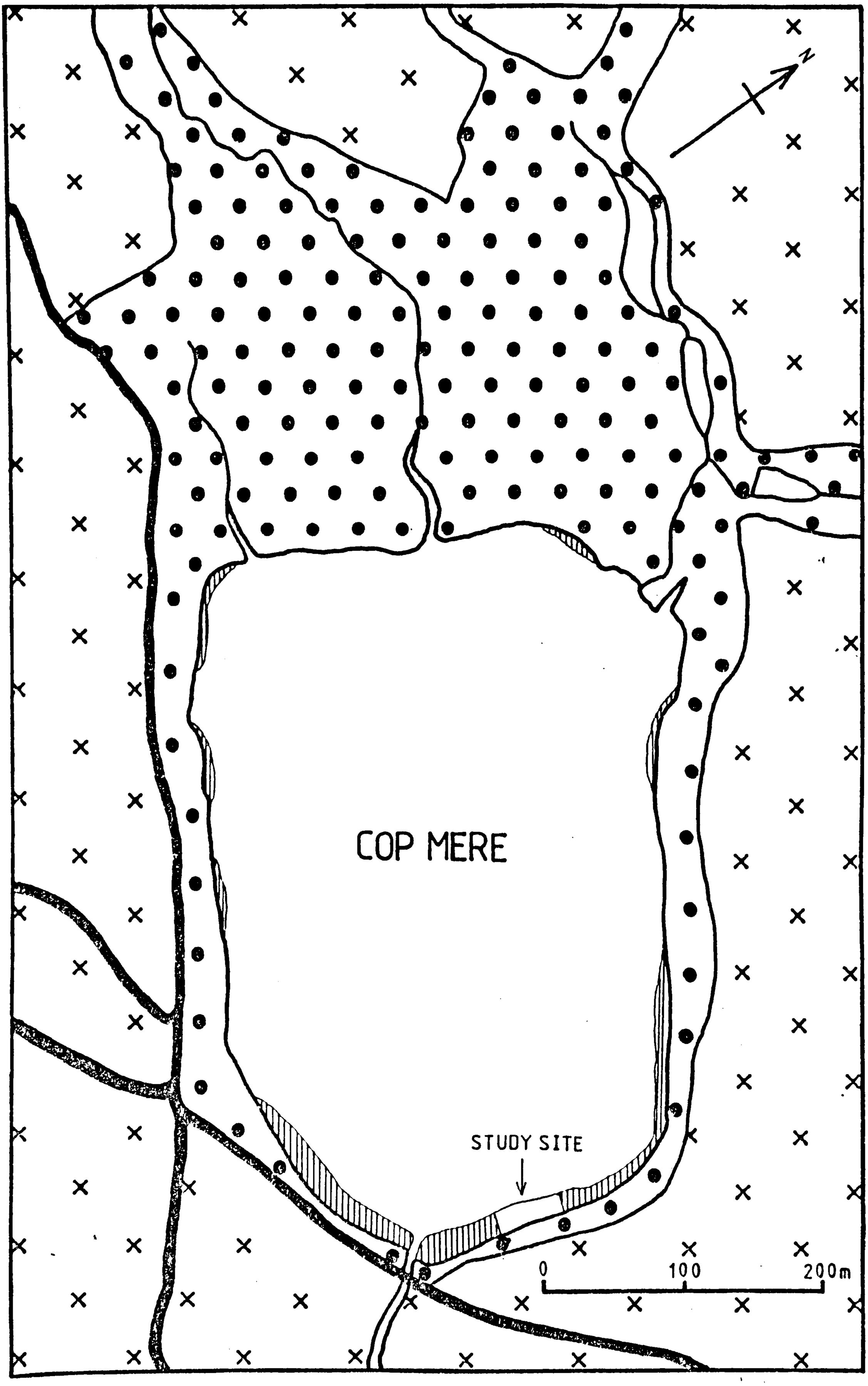
The substratum of the open mere consists of sand overlain by fine mud, except in the south-eastern sector where the sand is partly covered with pockets of plant debris from the reedbed and fringing trees. Detailed descriptions of substrate composition are given in chapter 5.

2:3 The Reedbed Study Site - Some Vegetation and Substratum Characteristics

A 50m long section of the reedbed/open-water interface was marked out with bamboo canes and the rectangular area of reedbed behind this line designated as the 'study site'. An environmental gradation exists from the front (lakeward edge) to the back (landward edge) of the reedbed. Three distinct areas can be recognised (Figure 2:3:1).

---

[1] Angles of slope were measured with an Abney Level and sighting poles.


N
COP MERE
STUDY SITE
0
100
200m

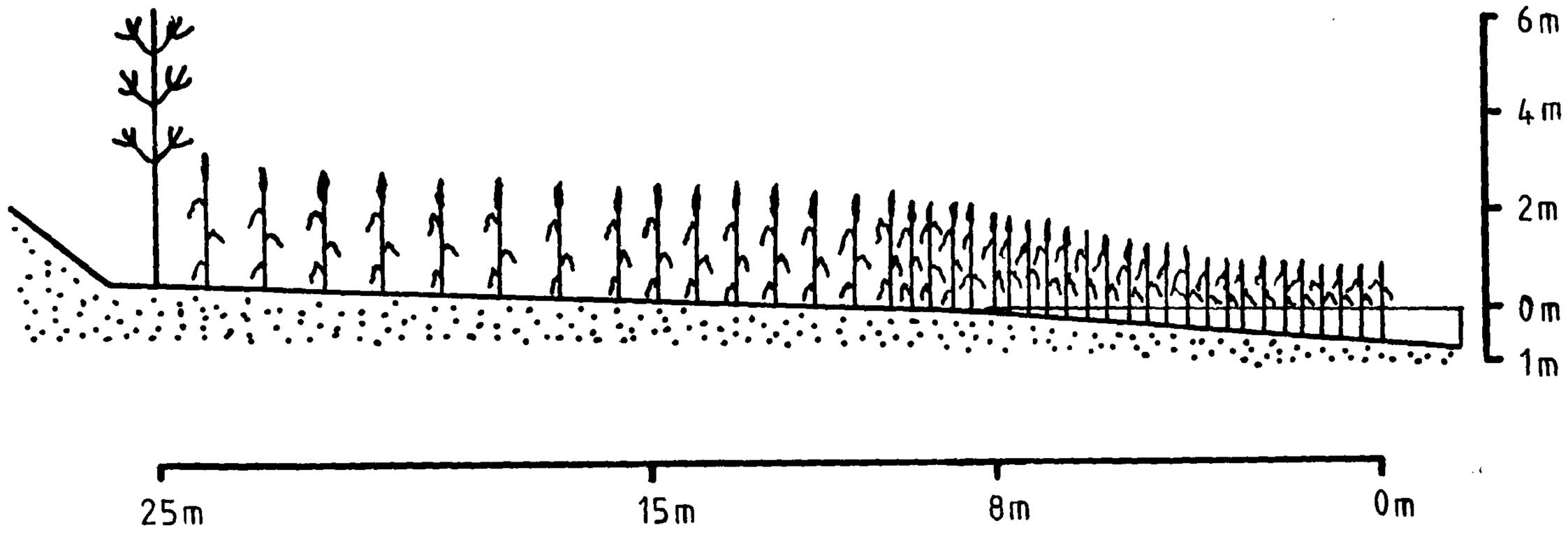


FIGURE 2:3:1 - A horizontal cross-sectional profile of the reedbed study site from open water to dry land, showing the distances from the *Phragmites*/open water interface at which distinct environmental changes occur (see text).

Deciduous trees and bushes

Phragmites australis

Permanent standing water extends roughly 8m into the reedbed. Here, *Phragmites australis* reaches its greatest densities and forms an unbroken monospecific fringe along the front of the study site (Plates 2:3:1 and 2:3:2). The submerged portions of reedstems acquire an epiphytic coating principally consisting of algal material and detritus. (See chapter 4 for a comprehensive analysis of the epiphyton make-up.) The nature of the epiphyton on a stem is dependent on the age and location of the latter. Old stems eventually snap and, together with allochthonous plant debris, form a carpet of decaying vegetation which covers much of the sandy reedbed floor in the area of permanent standing water.

During the summer months, algal mats and submerged plants build up over the mere as a whole and penetrate about 30cm into the *Phragmites* stand in the study site (Plate 2:3:2). Floating algal mats are composed principally of three genera: *Cladophora*; *Enteromorpha*; and *Hydrodictyon*. Submerged plants appear to be represented by one species: *Potamogeton berchtoldii* (Fieber).

At the edge of permanent standing water is a raised bank of accumulated plant debris formed by wave action. Immediately behind, and running parallel with this bank is an area about 1m wide where *Phragmites* cover is sparse and patches of open ground are visible throughout the year. This is possibly a relict footpath originally created by anglers. Occasionally the bank is breached when the water-level of the mere rises and standing water then extends further back into the reedbed, sometimes reaching the 15m mark.

Between 8 and 15m the density of *Phragmites* decreases and an assemblage of other plants if found, consisting of *Epilobium hirsutum* (Linnaeus) (Great Hairy Willow Herb), *Iris pseudacorus* (Linnaeus) (Yellow Flag), *Mentha aquatica* (Linnaeus) (Water Mint), *Scutellaria galericulata* (Linnaeus) (Skull-cap), *Solanum dulcamara* (Linnaeus)

PLATE 2:3:1 - A frontal view of the reedbed study site in February, showing the *Phragmites*/open water interface.

PLATE 2:3:2 - A frontal view of the reedbed study site in July, showing the *Phragmites*/open water interface and floating algal mats.

(Woody Nightshade), *Rumex hydrolapathum* (Hudson) (Great Water Dock), and *Urtica dioica* (Linnaeus) (Stinging Nettle). Several isolated specimens of *Typha angustifolia* occur towards the front of this area. The water-table rarely drops much below the ground surface in the 8-15m section of the reedbed and consequently the substratum here is nearly always wet with puddles of water present throughout most of the year. A thick poachy layer of decaying autochthonous and allochthonous plant material, with a high water retention capacity, forms the floor of the reedbed. Amongst the stems of well-established and closely grouped macrophytes the substratum can remain relatively undisturbed and here a low-level canopy of mosses is frequently found.

The most landward part of the study site (15-25m) supports a distinct fen-type community of plants. *Phragmites* is at its lowest density and is replaced by *Carex paniculata* (Linnaeus) (Greater Tussock Sedge), *Cirsium palustre* (Linnaeus) Scop. (Marsh Thistle), *Filipendula ulmaria* (Linnaeus) Maxim. (Meadow Sweet), *Phalaris arundinacea* (Linnaeus) (Reed-grass), and *Sparganium erectum* (Linnaeus) (Bur-reed). The substratum in which these plants grow is similar to that in the 8-15m area except it is not subject to inundation when the water-level of the mere rises. Although characteristically wet, it is the first part of the reedbed to experience drier conditions when the water-table retreats during a prolonged spell of fine weather. Puddles occur infrequently and analyses suggest they are derived from precipitation rather than a rise in the level of pre-existing ground-water.

Along the back of the reedbed a footpath runs through a line of deciduous trees and bushes. Here, a sharp transition in substratum type is apparent: the loose accumulation of partially decomposed plant debris found between 8 and 25m is replaced by a rich, black, humic soil containing an appreciable amount of mineral matter. Behind the trees a steep grassy bank rises to a pasture field.

The appearance of the reedbed changes dramatically through the seasons (cf. Plates 2:3:1 and 2:3:2). During the autumn, *Phragmites* stems begin to

show the first signs of senescence and by the end of November their colour has changed from bright green to light brown. Wind and wave action facilitates breakage of the brittle stems and tends to flatten down the aerial parts of those that remain intact. New shoots begin to appear in March and by mid-summer *Phragmites* stands have attained their maximum height and density. Other plants die back completely in the winter to reveal areas of bare exposed substratum which support a tall assemblage of vegetation during the summer.

2:4 The Reedbed Study Site - Weather Influences.

The nature of the reedbed environment is determined by a complex of interrelated factors which can be categorised as either biotic or abiotic. Abiotic factors can be subdivided into relatively stable physical characteristics, such as the profile of the reedbed floor, and the variable influences of weather and water chemistry.

Cop Mere is fortuitously located reasonably near to Keele University Meteorological Station (Grid Reference SJ 820447) which provides a variety of climatic data, including information relating to air temperature, wind velocity, precipitation, and sunshine. Lying at an altitude of 179m above sea-level, the station is about 90m higher than Cop Mere and is also some 24km further north. These slight differences in altitude and latitude may cause some variation in weather between the two locations but long-term climatic patterns should be similar.

A) AIR TEMPERATURE

On each visit to Cop Mere during 1981 and 1982 the air temperature at the centre of the study site was measured using the thermistor unit of a WPA environmental multiprobe kit[1]. Figures 2:4:1 and 2:4:2 show the

---

[1] The WPA environmental multiprobe kit is manufactured by Walden Precision Apparatus Ltd.

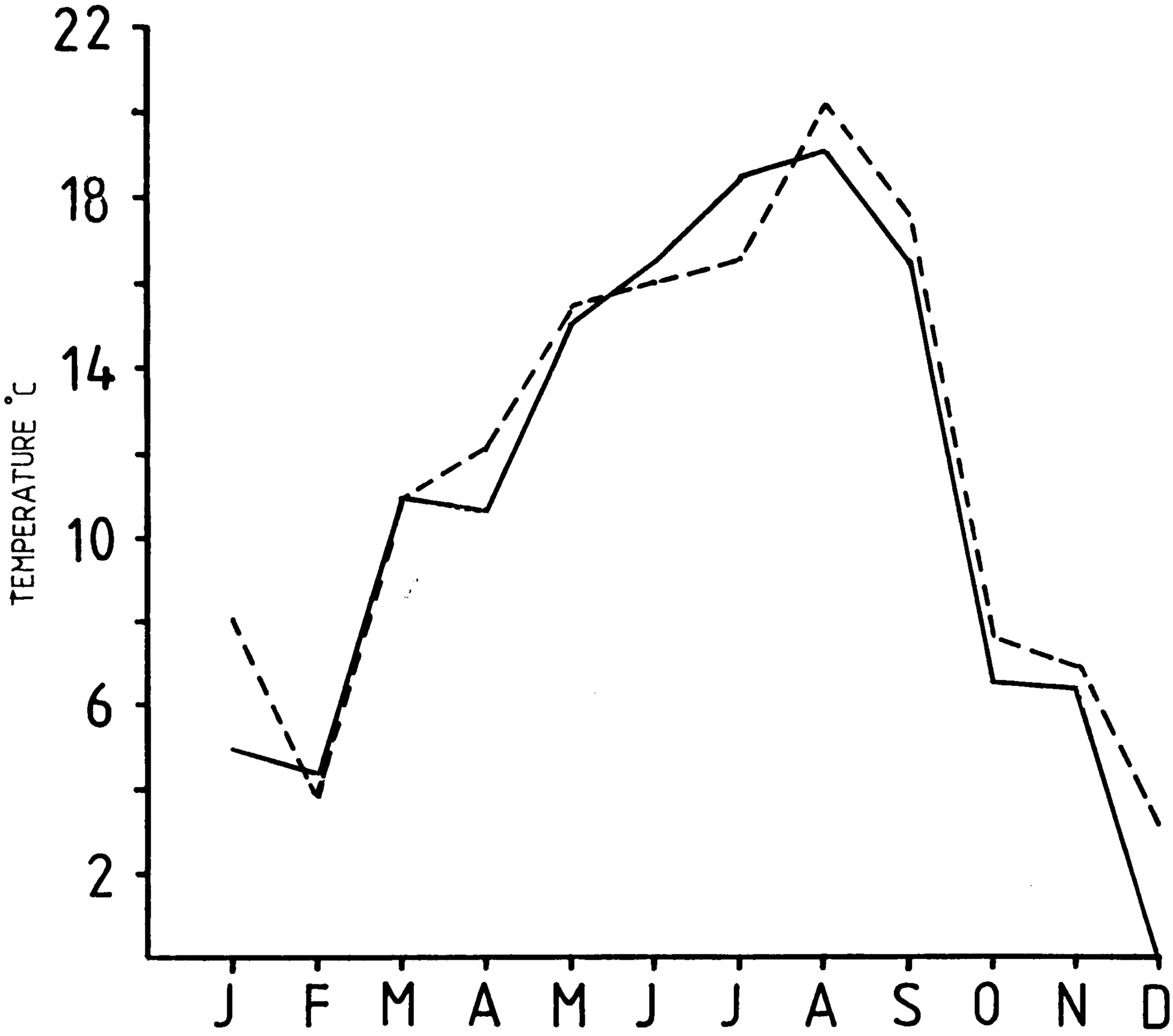


FIGURE 2:4:1 - Mean monthly air (- - -) and water (———) temperatures recorded in the reedbed study site at Cop Mere during 1981.

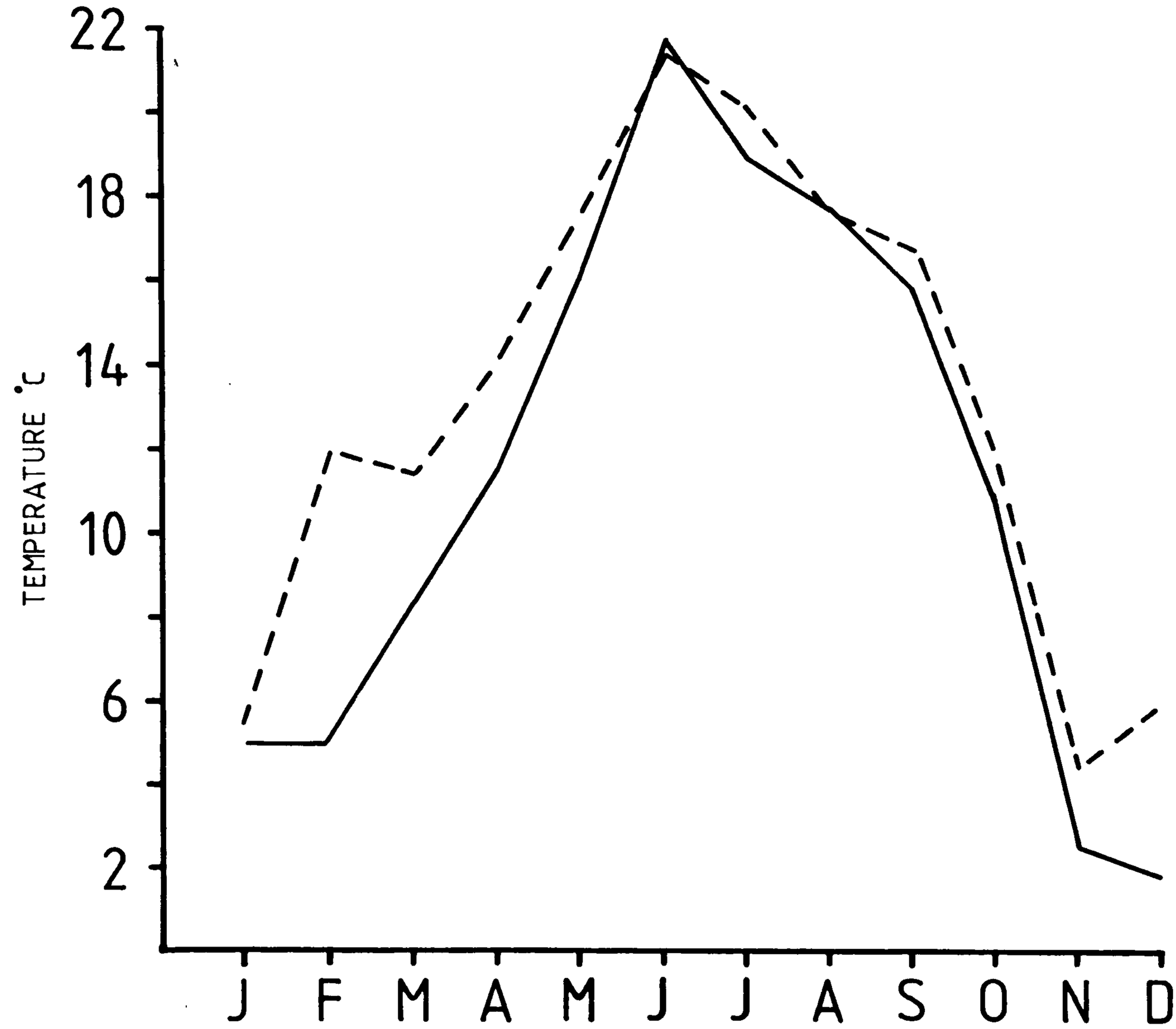


FIGURE 2:4:2 - Mean monthly air (- - -) and water (———) temperatures recorded in the reedbed study site at Cop Mere during 1982.

mean monthly values derived from these measurements. The maximum mean monthly temperature for each year is about the same (20.3°C in 1981 and 21.5°C in 1982) but occurs later in 1981 than 1982 (August as opposed to June). A comparison of these two graphs with their analogous counterparts showing mean monthly air temperatures at Keele (Figures 2:4:3 and 2:4:4) reveals both similarities and differences. Monthly values are, with one exception, higher for Cop Mere than for Keele, largely because readings at the study site were only taken during the day whilst values at the meteorological station are derived from both daytime readings and characteristically lower night-time recordings. The difference in altitude may also account for some of the temperature dissimilarities. The graphs relating to 1981 Cop Mere and Keele air temperatures are essentially congruous in form, with both peaking in August, whilst those for 1982 are less well-matched with a maximum mean in June at Cop Mere but July at Keele.

Mean temperatures recorded at the meteorological station must approximate more closely to the actual values for Cop Mere than those calculated from the readings taken on site, because station means are derived from continuous recordings as opposed to site means which are based on one to five daytime measurements per month.

A comparison of the Keele graphs affirms the fact that the maximum mean air temperatures are reached in different months (August 1981 and July in 1982). The mean daily range (the difference between the monthly mean maximum and minimum) is greater in the summer than the winter in both years.

B) WATER TEMPERATURE

Although water temperature is not a weather variable as such, it is inextricably linked to air temperature and is therefore discussed here.

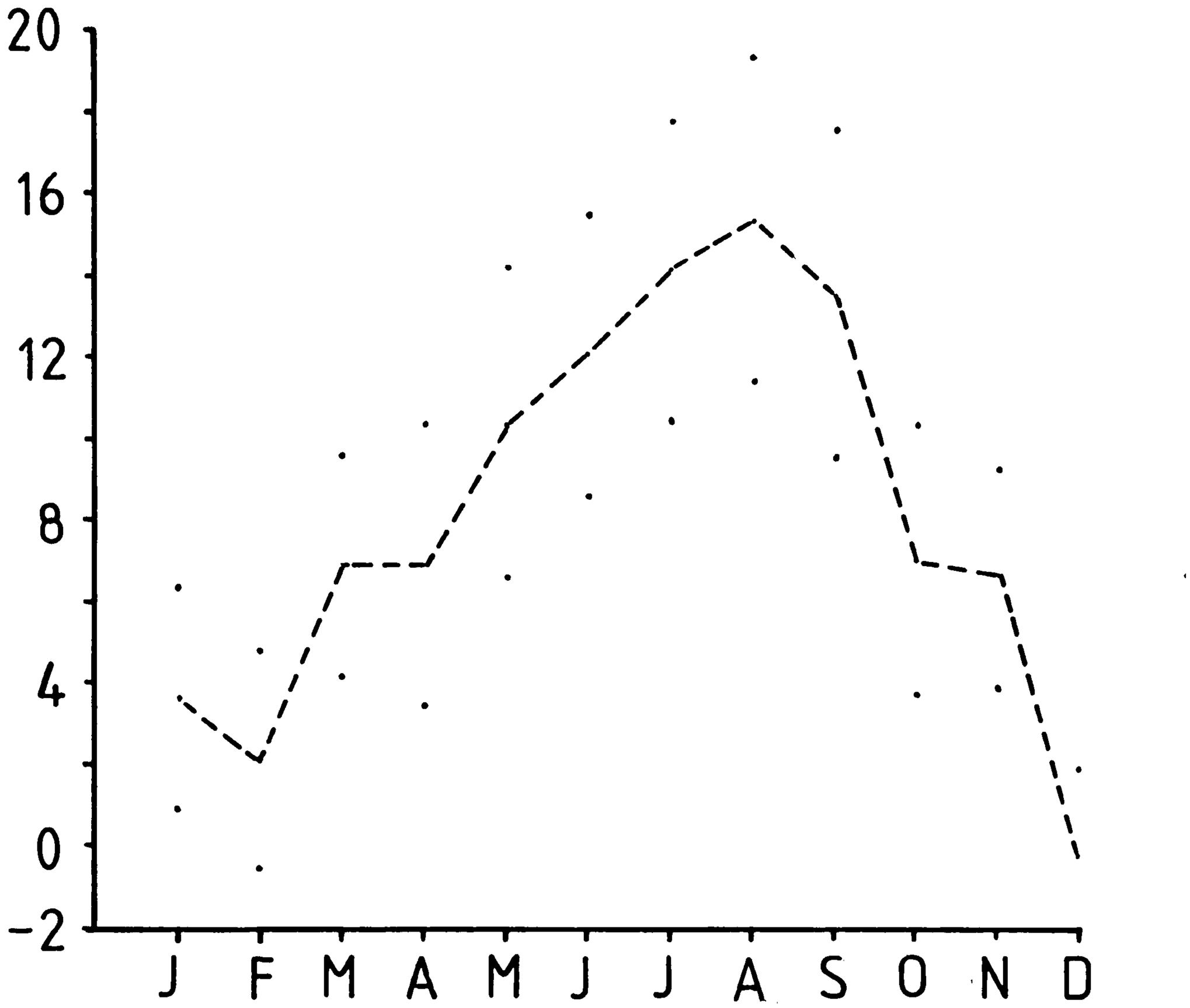


FIGURE 2:4:3 - Mean monthly air temperatures (- - -) with mean monthly maxima and minima (·) at Keele Meteorological Station during 1981.

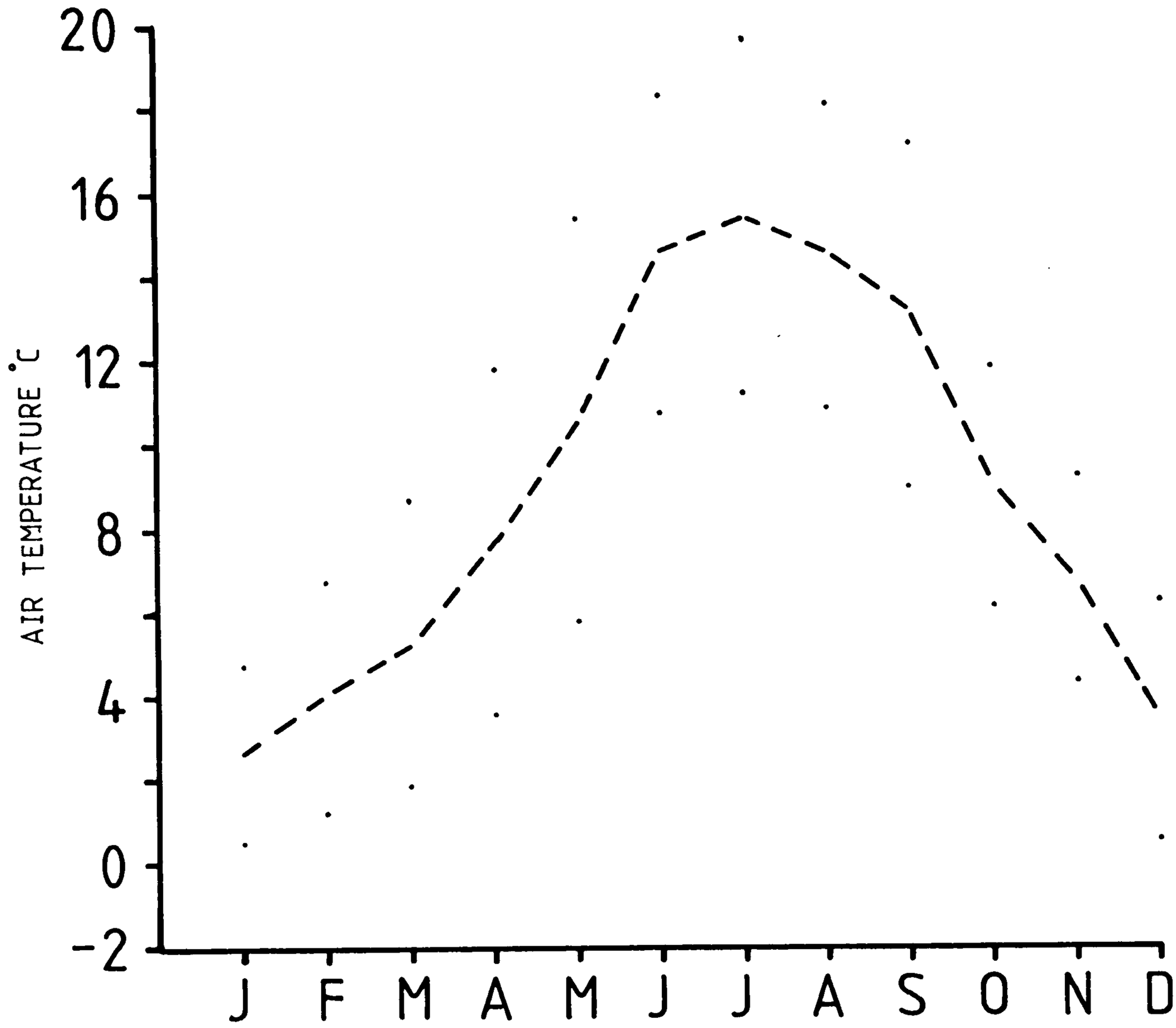


FIGURE 2:4:4 - Mean monthly air temperatures (- - -) with mean monthly maxima and minima (·) at Keele Meteorological Station during 1982.

Using the WPA thermistor probe, readings were taken at 20cm below the surface of the mere, in the centre of the permanent standing water area of the study site. The prevailing water temperature was noted on each visit to Cop Mere throughout 1981 and 1982. Figures 2:4:1 and 2:4:2 compare the monthly mean air and water temperatures recorded here over the two years. In most months the water temperature is slightly lower than the concomitant value for air but this trend is reversed in February and July, 1981 and June, 1982. The maximum mean water temperature is reached two months later in the first year than the second (August as opposed to June). Although the sampling regimes for air and water temperatures were identical in terms of the time and frequency of recording, the calculated means for water should be nearer to the true means than the calculated means for air are to their respective true means. This is because the high thermal capacity of water results in small diurnal temperature fluctuations and relatively slight deviations on a day-to-day basis.

C) PRECIPITATION

All data concerning precipitation are derived from Keele Meteorological Station where several features are noted, including the amount, duration, and number of raindays[1] per month. Figure 2:4:5 shows March and September to be wet months in both years in terms of total monthly precipitation, whilst June and August are much drier in 1981 - June being the wettest month in 1982. The amount of precipitation, its duration (Figure 2:4:6), and the number of raindays (Figure 2:4:7) generally increase and decrease in a consilient fashion. The most notable exception to this trend occurs between September and October in both years, where the duration of precipitation and the number of raindays increase but the amount of

---

1 A rainday is a day on which 0.2mm or more of rainfall is recorded.

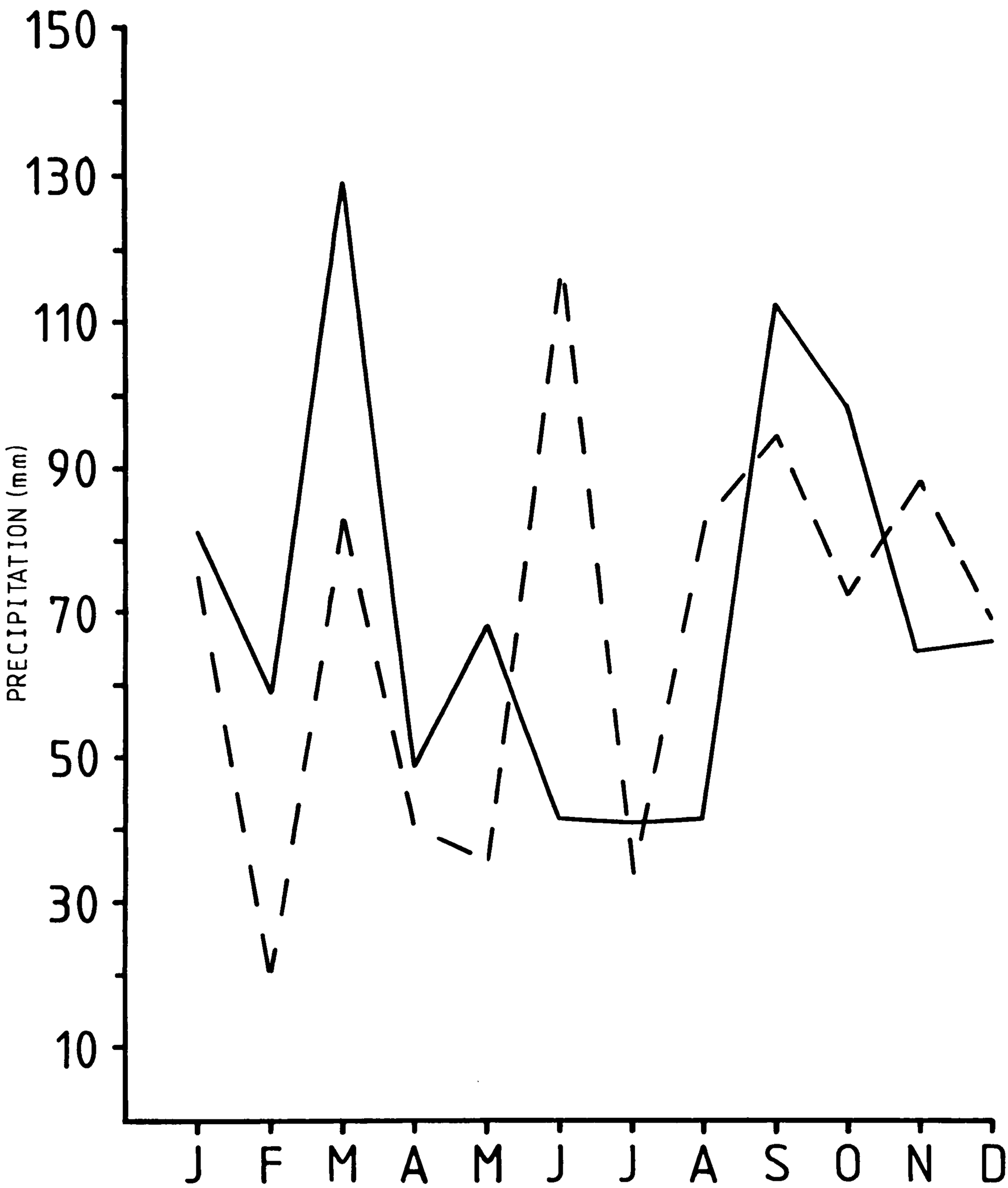


FIGURE 2:4:5 - Total monthly precipitation at Keele Meteorological Station during 1981 (———) and 1982 (- - -).

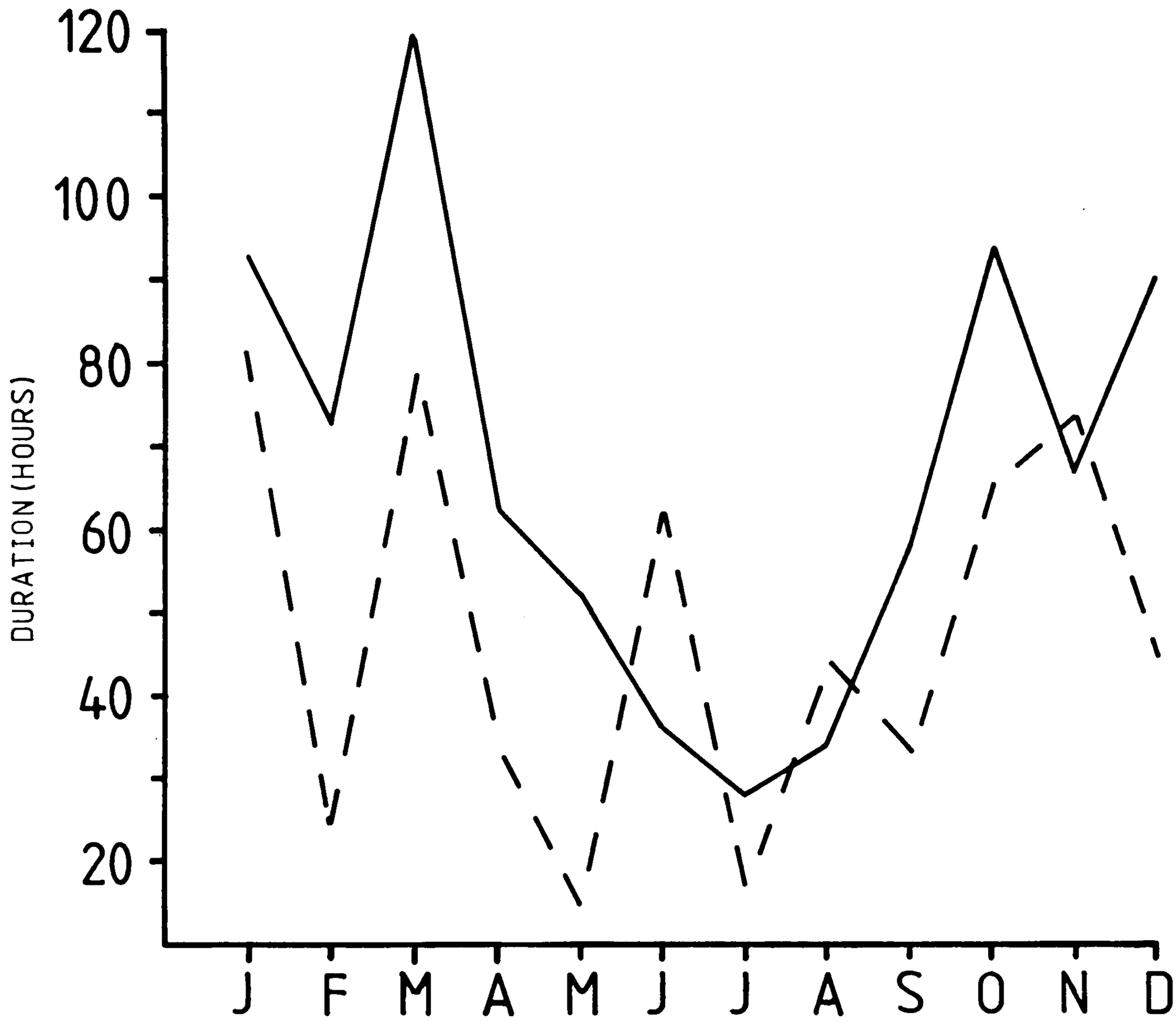


FIGURE 2:4:6 - Total monthly duration of precipitation at Keele Meteorological Station during 1981 (——) and 1982 (- - -).

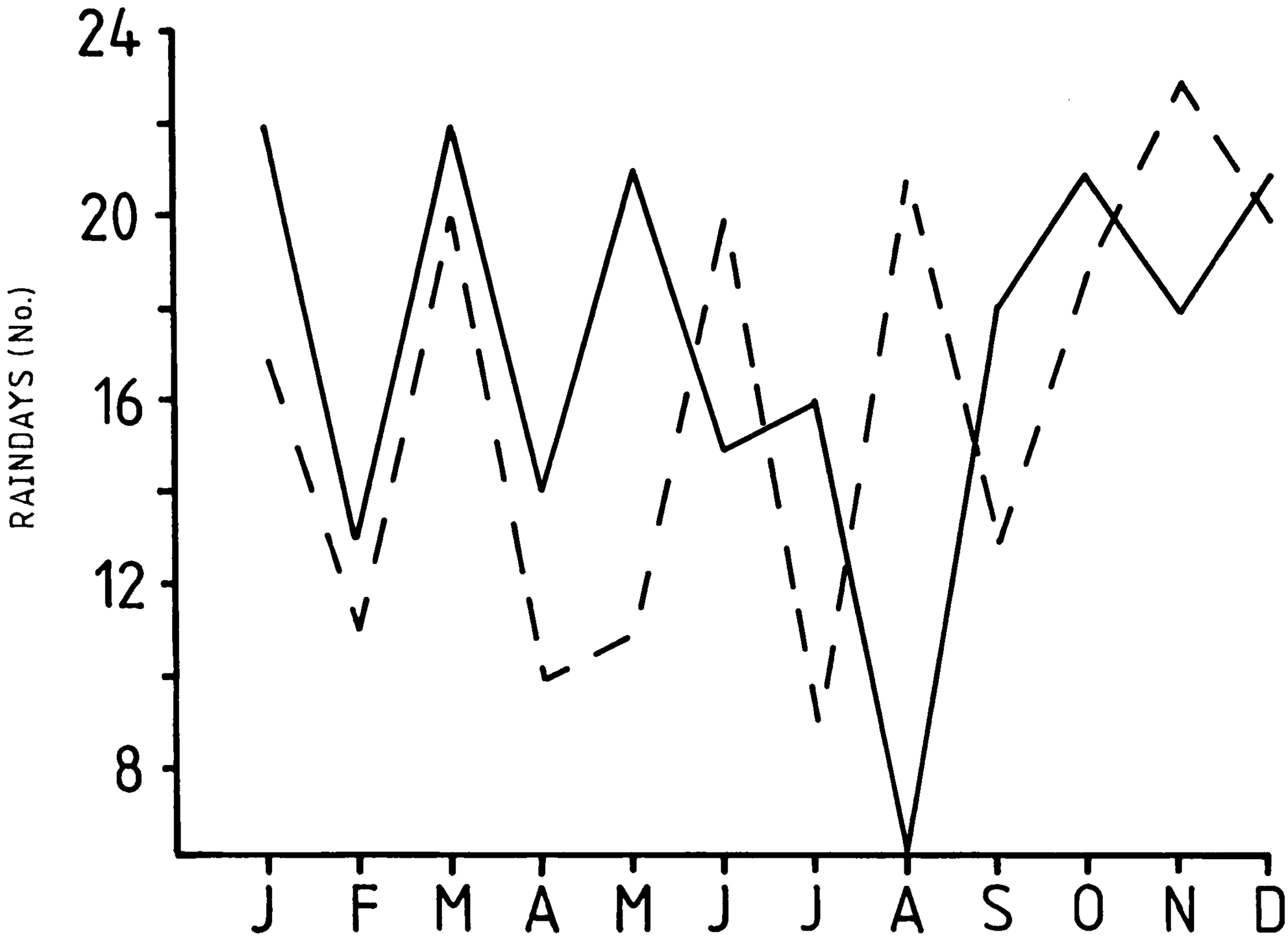


FIGURE 2:4:7 - Total monthly number of raindays (with 2mm or more rainfall) at Keele Meteorological Station during 1981 (———) and 1982 (- - -).

rainfall drops. This suggests a change from a period of intermittent, heavy showers to one of more prolonged, but lighter, rainfall.

D) SUNSHINE AND WIND VELOCITY

Total monthly sunshine hours and mean monthly wind velocity were recorded at the meteorological station. Figure 2:4:8 indicates that the sunniest month in 1981 is August and in 1982, May. The sunniest year is 1982 with 1262.4 hours, the 1981 sunshine total being 1101 hours.

Figure 2:4:9 shows that mean monthly wind velocities are, except for January, higher in 1982 than 1981. Some seasonal variation is found in 1981 where velocities are lower in the summer than at other times. Such variation is not evident in the following year.

2:5 The Reedbed Study Site - Mere-water Influences.

Certain features of the water pervading the reedbed constitute potential environmental influences with regards to the structure of the local biotic community. Temporal change in these characteristics may cause variation elsewhere in the ecosystem and must therefore be examined.

A) WATER DEPTH

Figure 2:5:1 gives the mean monthly water depth halfway along the reedbed/open-water interface in the study site and reveals a progressive drop over the two-year period. The year means for 1981 and 1982 are 71 and 63cm respectively. No apparent correlation exists between the amount of rain falling in a month (Figure 2:4:5) and subsequent water depths - the decreasing level of the mere is not due to any concomitant reduction in precipitation. A plausible explanation lies in the fact that, during 1981, drainage work was in progress on the River Sow just below Walk Mill Pool (Figure 2:1:2) and the flow capacity of the river above Cop Mere may have been cut. Assuming a significant percentage of Cop Mere's

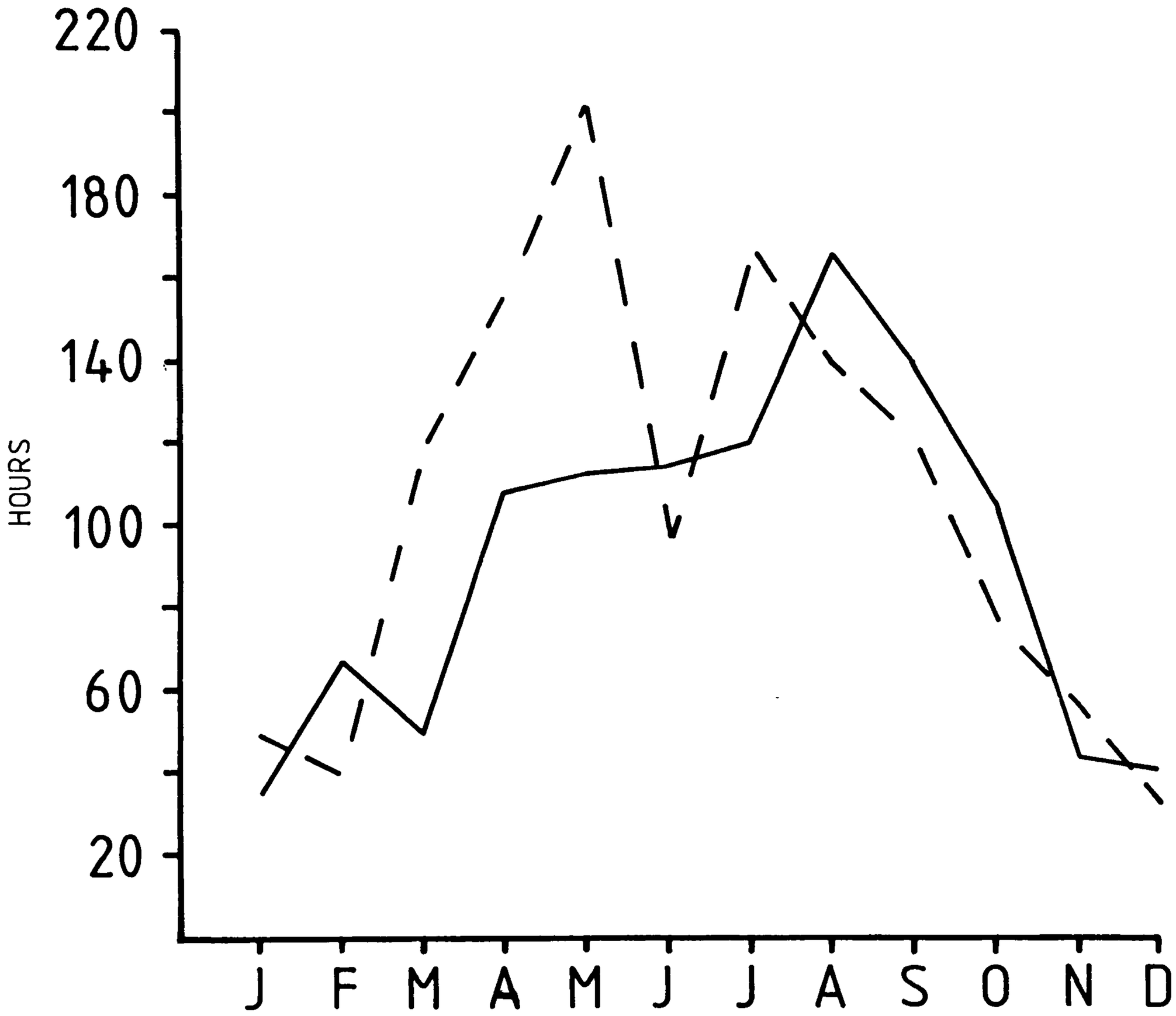


FIGURE 2:4:8 - Total monthly sunshine hours at Keele Meteorological Station during 1981 (———) and 1982 (- - -).

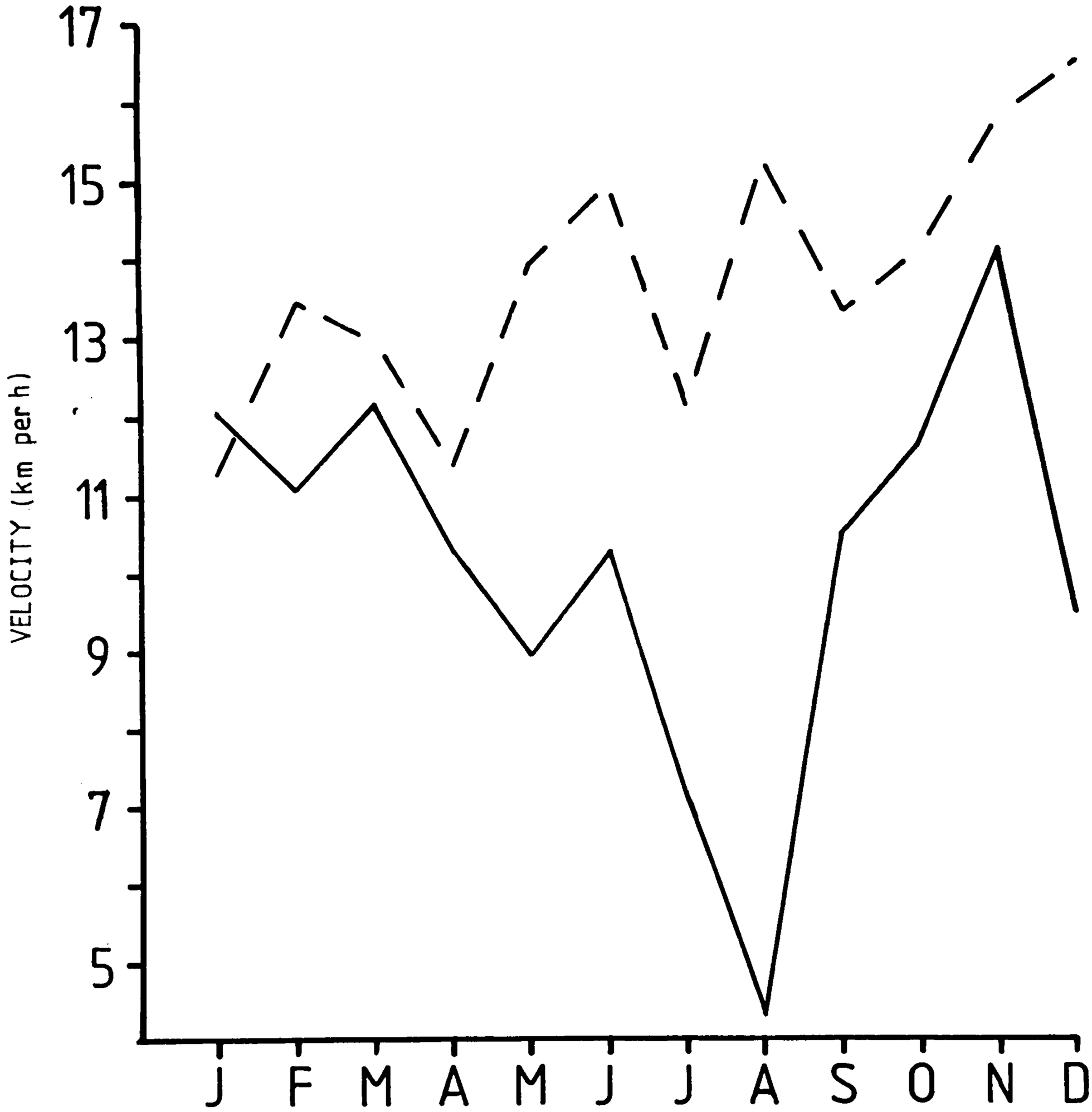


FIGURE 2:4:9 - Mean monthly wind velocity at Keele Meteorological Station during 1981 (——) and 1982 (- - -).

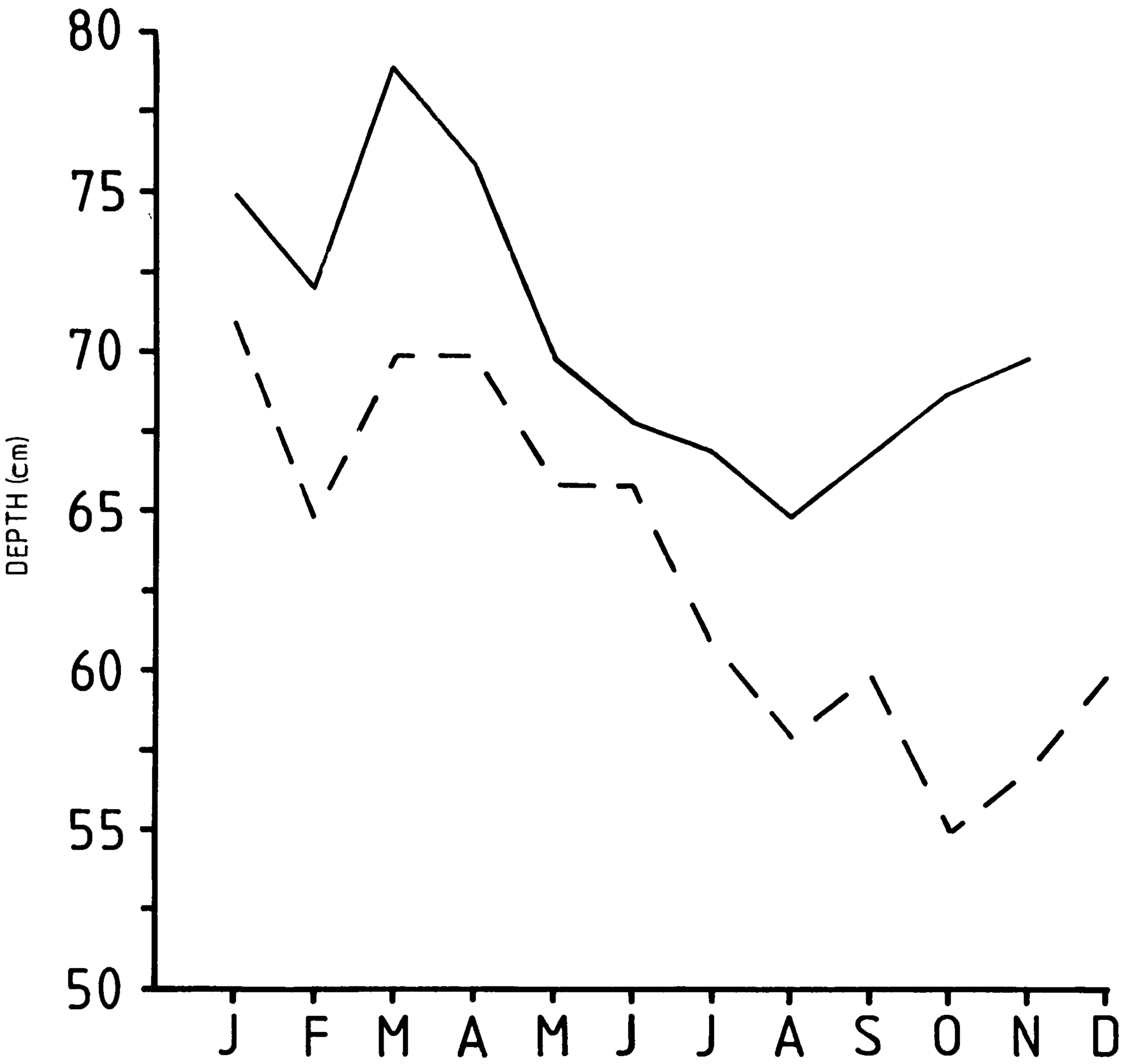


FIGURE 2:5:1 - Mean monthly water depths at the centre of the *Phragmites* open-water interface in the reedbed study site at Cop Mere during 1981 (———) and 1982 (- - -). (No information available for December, 1981.)

water is derived from the river, a sustained reduction of the latter's input volume might result in a long-term decrease in the level of the mere.

B) OXYGEN CONTENT

Oxygen readings are presented in Figure 2:5:2 and were made at a depth of 20cm in the centre of the permanent standing water area of the study site. Two devices were used: a Mackereth Oxygen Sampler (manufactured by Lakes Instruments Ltd.) and the oxygen recording unit from the WPA environmental monitoring kit. Discontinuities in the graphs are due to occasional instrument malfunction and unavailability. A unique and somewhat antiquated replacement battery for the Mackereth sampler proved difficult to obtain and the oxygen probe of the WPA kit had to be repaired several times. No measurements were taken before September, 1981. Any information deficiencies after this month are attributable to equipment failure.

Figure 2:5:2 shows the seasonal patterns of change in oxygen saturation and concentration are similar. Supersaturation is evident throughout most of the summer. For the remainder of the year the mean saturation level is about 70%, with actual values ranging from 38 to 100%+. The mean concentration of oxygen, taken from all measurements, is 13 mg/l. A maximum amount of 30 mg/l is reached in June, 1982 and the lowest content is the 3.8 mg/l noted in the following September.

C) pH AND CONDUCTIVITY

The pH and conductivity readings shown in Figures 2:5:3 and 2:5:4 respectively were taken with the WPA environmental monitoring kit at the same position in the study site as the readings for oxygen. Recording took place once a month.

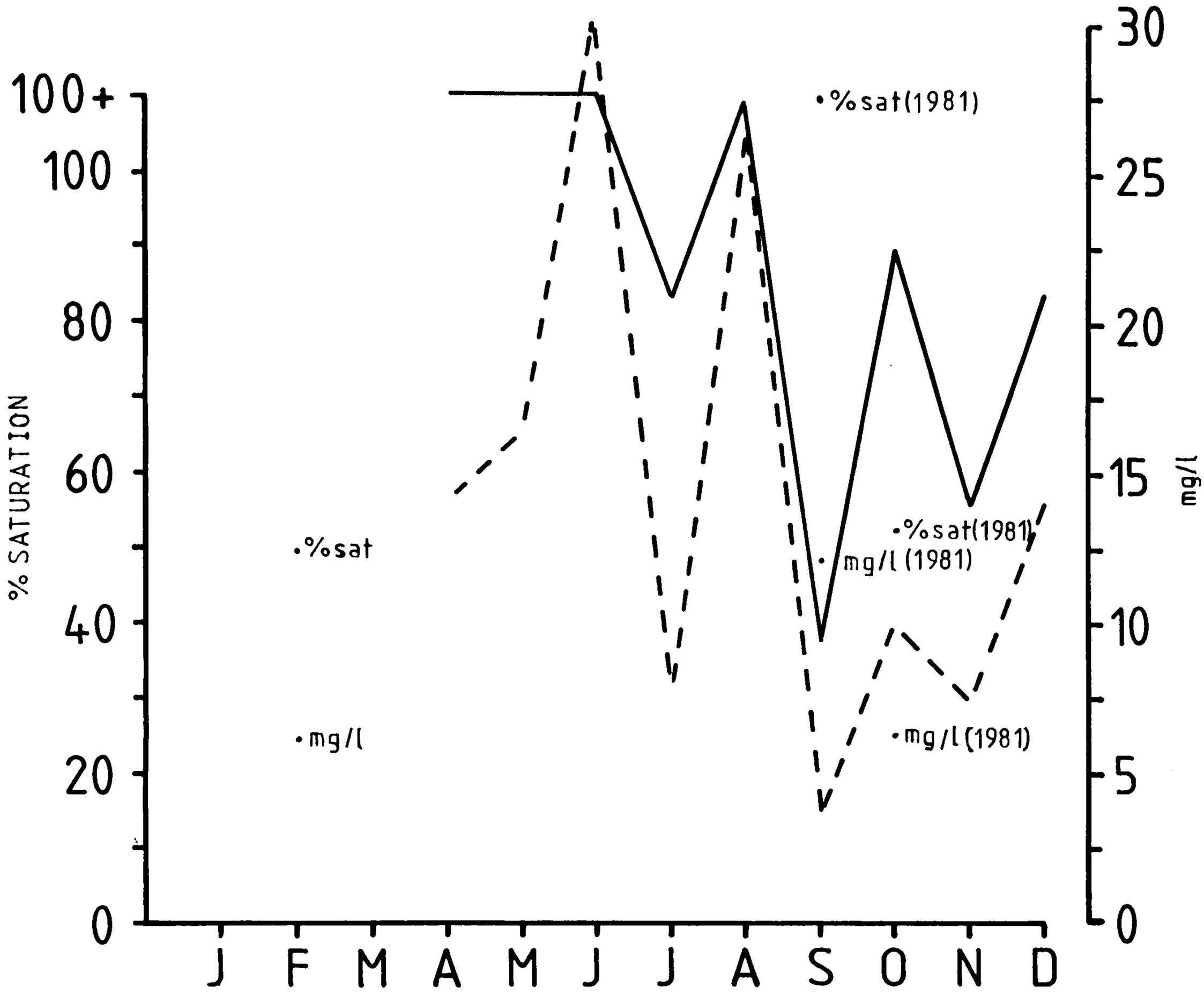


FIGURE 2:5:2 - Oxygen content readings taken in the centre of the permanent standing water area of the reedbed study site at Cop Mere during 1981 (where specifically indicated) and 1982. % saturation - (——) mg O_2/l - (- - -).

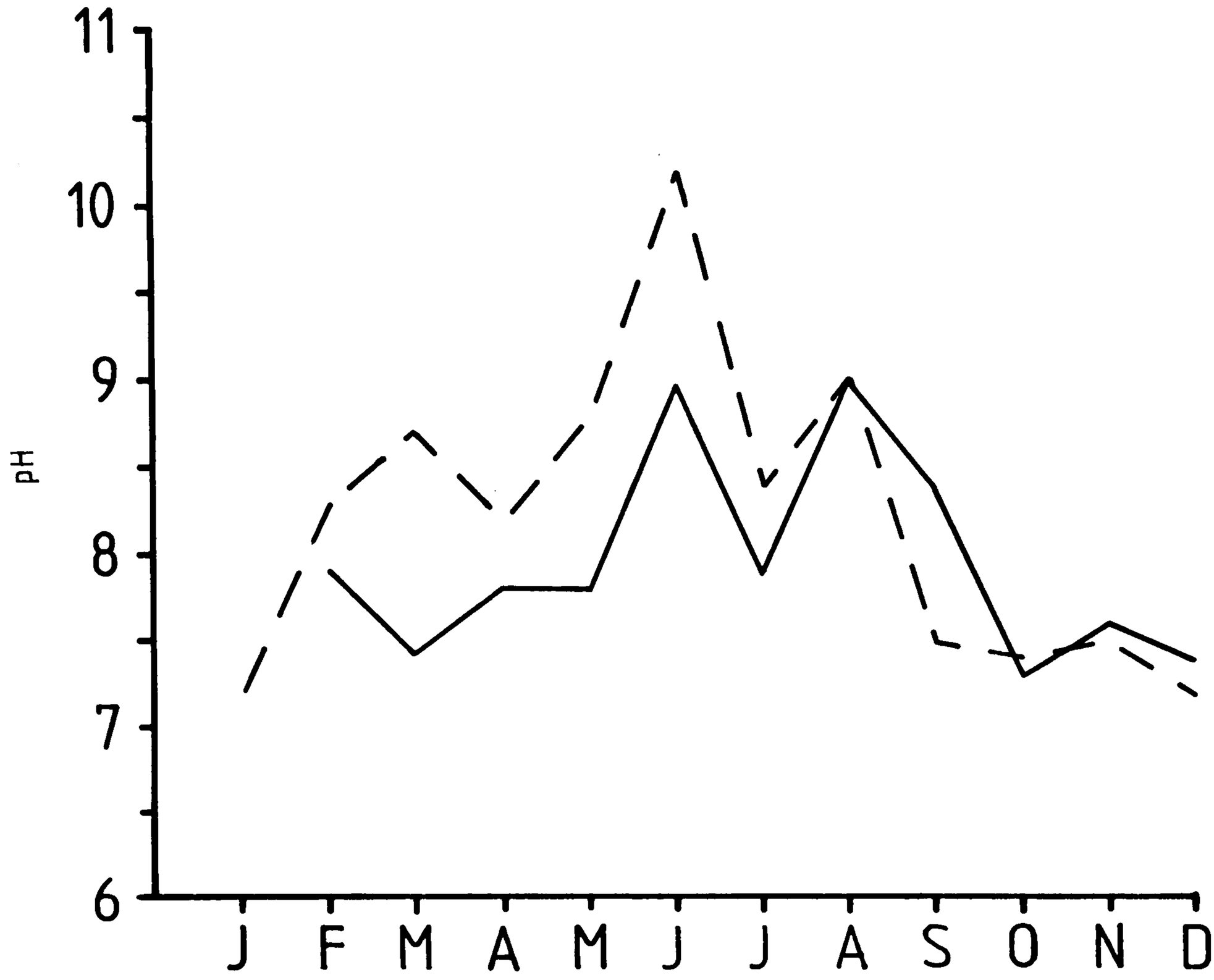


FIGURE 2:5:3 - pH values recorded at the centre of the permanent standing water area of the reedbed study site at Cop Mere during 1981 (——) and 1982 (- - -). (No information available for January, 1981.)

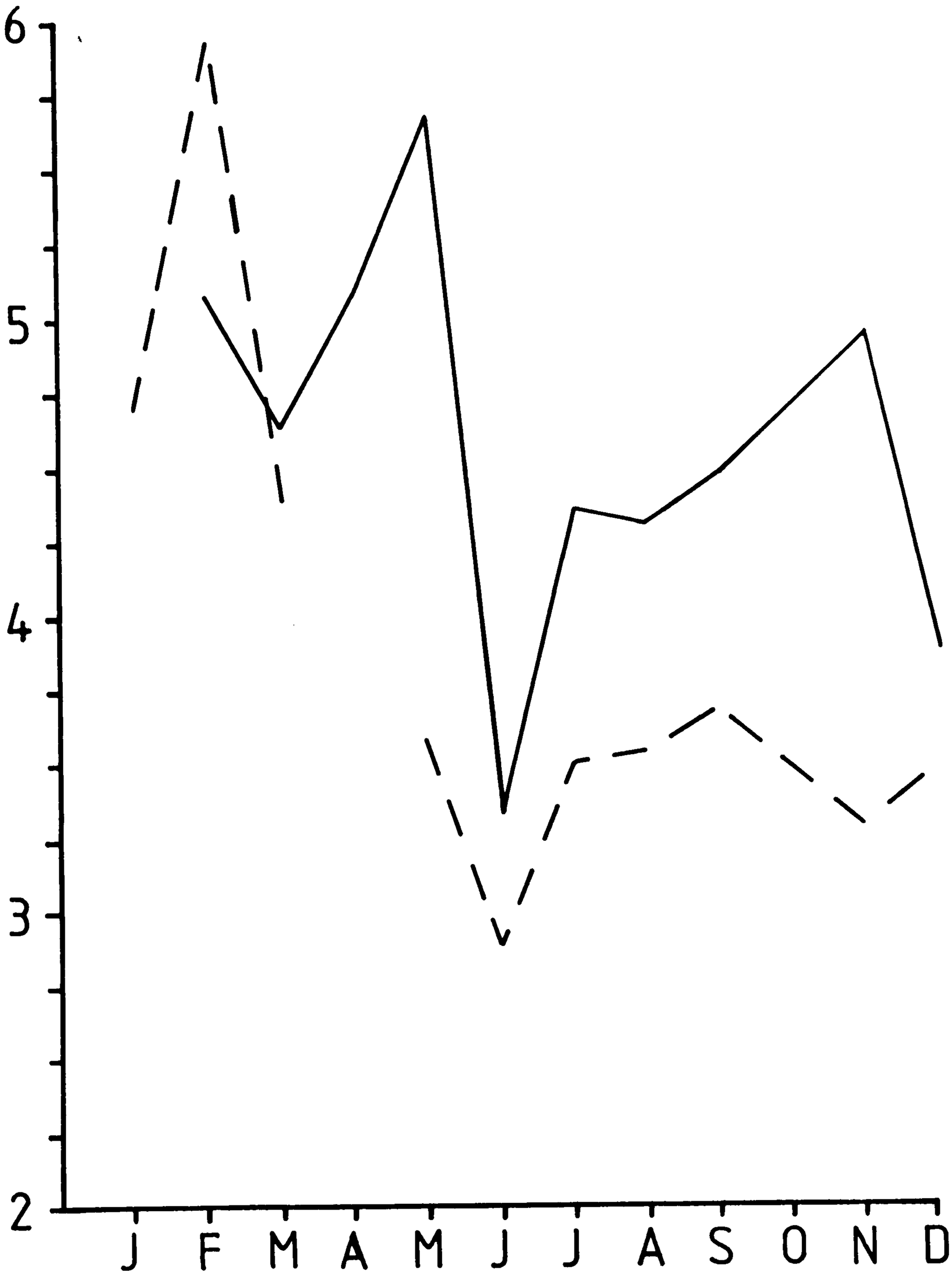


FIGURE 2:5:4 - Conductivity values recorded at the centre of the permanent standing water area of the reedbed study site at Cop Mere during 1981 (———) and 1982 (- - -). (No information available for April, 1982.)

The two graphs indicating pH fluctuations in 1981 and 1982 display a broad resemblance to each other, although values are generally lower in 1981 than in the following year. Both graphs show an overall rise in the summer and a subsequent fall in the autumn. A narrower range of values occurs in 1981 (7.3 to 9.0) than 1982 (7.2 to 10.2).

Summer conductivity levels are generally lower than in other seasons - conductivity and pH appear to be inversely correlated. The two year graph-lines in Figure 2:5:4 do not, however, show the same degree of mutual congruity as those for pH.

Chapter 3

THE CHIRONOMID LARVAL COMMUNITY OF PHRAGMITES REEDSTEMS AT COP MERE.

3:1 Field and Laboratory Work - Planning and Methods.

A) SAMPLING DESIGN

A preliminary observation of the *Phragmites* stands at Cop Mere suggested that the reedbed flanking the south-eastern margin would offer the best opportunities for useful study. Its width permits a spatial gradation of habitat types which is not found in the narrower, disjunct fringes of vegetation elsewhere. Access is relatively easy from either land or water and sampling conditions are favourable.

The extensive length of the broad *Phragmites* belt necessitated the selection of a representative study area of sufficient size to be reflective of the reedbed environment as a whole, yet small enough to allow the accurate demarcation of zones for which intrazonal variation in environmental conditions would be considerably less than that occurring on an interzonal basis. The criteria applied to the choice of study site location were that it should be in an area where the reedbed/open-water interface is comparatively straight, to facilitate the delineation of parallel zones at fixed distances from the frontal boundary of *Phragmites* and that habitat variation along the length of the reedbed (rather than from front to back) should appear to be minimal or absent. These prerequisites were fulfilled in that section of the reedbed chosen to be the study site.

Having designated a particular area for field-work, the next consideration was the formulation of a sampling programme which would reveal any spatial, as well as temporal, variation in the epiphyton-dwelling chironomid community of the reedbed. Of especial interest was the possible existence of characteristic significant differences between the larval populations found at varying distances from the front of the study site.

When a sampling scheme was being devised, two constraints had to be taken into consideration: the time available for larval sorting and the degree of compatibility between field methods and any statistical tests that might be used in the analytical treatment of field-derived data. A policy of 'blanket' sampling over the entire area of permanent standing water in the study site would have covered the widest habitat range but time restrictions impose an upper limit to the number of samples that can be dealt with under any scheme and this number would have been insufficient to provide more than a sparse coverage of the whole area. This, and the inherent demand for grouping in tests of variance, made it preferable to divide off arbitrarily three sampling zones[1] (Figure 3:1:1), running parallel with the front of the reedbed, which covered only a percentage of the permanent standing water area but which reflected a temporally variable horizontal gradation in the nature of the epiphytic habitat. The prerequisite for such a 'stratified' sampling technique is that variation within the strata (zones) is less than that within the population as a whole (Elliott,1977; Campbell, 1979). This prerequisite was met here, where intrazonal community and habitat variation was characteristically less than that existing on an interzonal basis.

Careful consideration was given to the problem of how to position the sampling points in each zone. Several pitfalls had to be avoided. If stem-samples were taken from the same points every month, appreciable habitat denudation would be risked. Also, there would be a remote possibility that the environmental conditions prevailing at these points might not be representative of the conditions found elsewhere in the zone - a programme of stem collection from identical positions on every sampling

---

[1]Bamboo canes were positioned at 10m intervals to mark out the three zones. Each zone was 1m wide and 50m long.

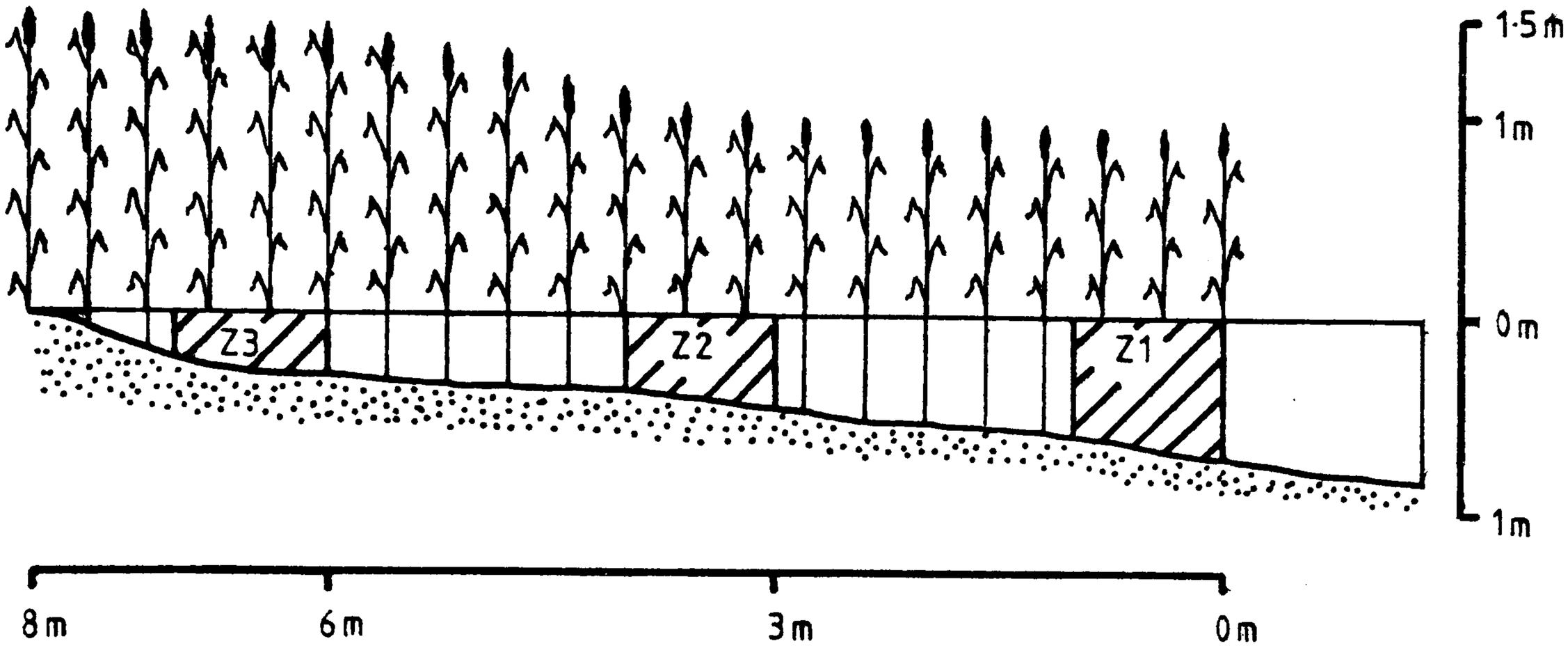


FIGURE 3:1:1 The position and horizontal extent of the three zones from which reedstem samples were taken.

occasion would not reveal this situation if it existed. The use of randomly spaced points might result in sample bunching and this could diminish the chances of detecting any lateral variation along each zone.

In order to avoid the problems referred to above, a 'systematic' scheme (Elliot, 1977; Hammond and McCullagh, 1974) was adopted, incorporating both random and non-random elements. This involved the random determination of one sampling position and the siting of others at regular intervals from this initial location.

In both January and February, 1981, fifteen stem-samples were removed from each of the three zones. From March to November[1] of the same year, ten stems were taken from each zone on a monthly basis. This reduction was needed to cope with a large increase in the number of larvae found.

Figure 3:1:2 shows the sampling point positions for March. The location of the first stem-sample in each zone was determined by randomly selecting a number between 1 and 5 inclusive; this number signified the distance in metres along the zone of the point from where the first stem was to be taken. The second stem was then taken at a point 5m further down the sampling line from the first, the third stem 5m from the second, and so on until ten stems had been collected. The process of random number selection was repeated every month, which ensured a good change of stems being taken from different positions each time, so helping to avoid the pitfalls of continually sampling in the same places. First stem positions are given in Appendix A. Fieldwork was carried out on one of the last three days of each month.

---

[1]The presence of a very thick ice cover prevented the collection of reedstem samples in December. Thus, no data relating to reedstem-dwelling chironomid larvae are available for this month.

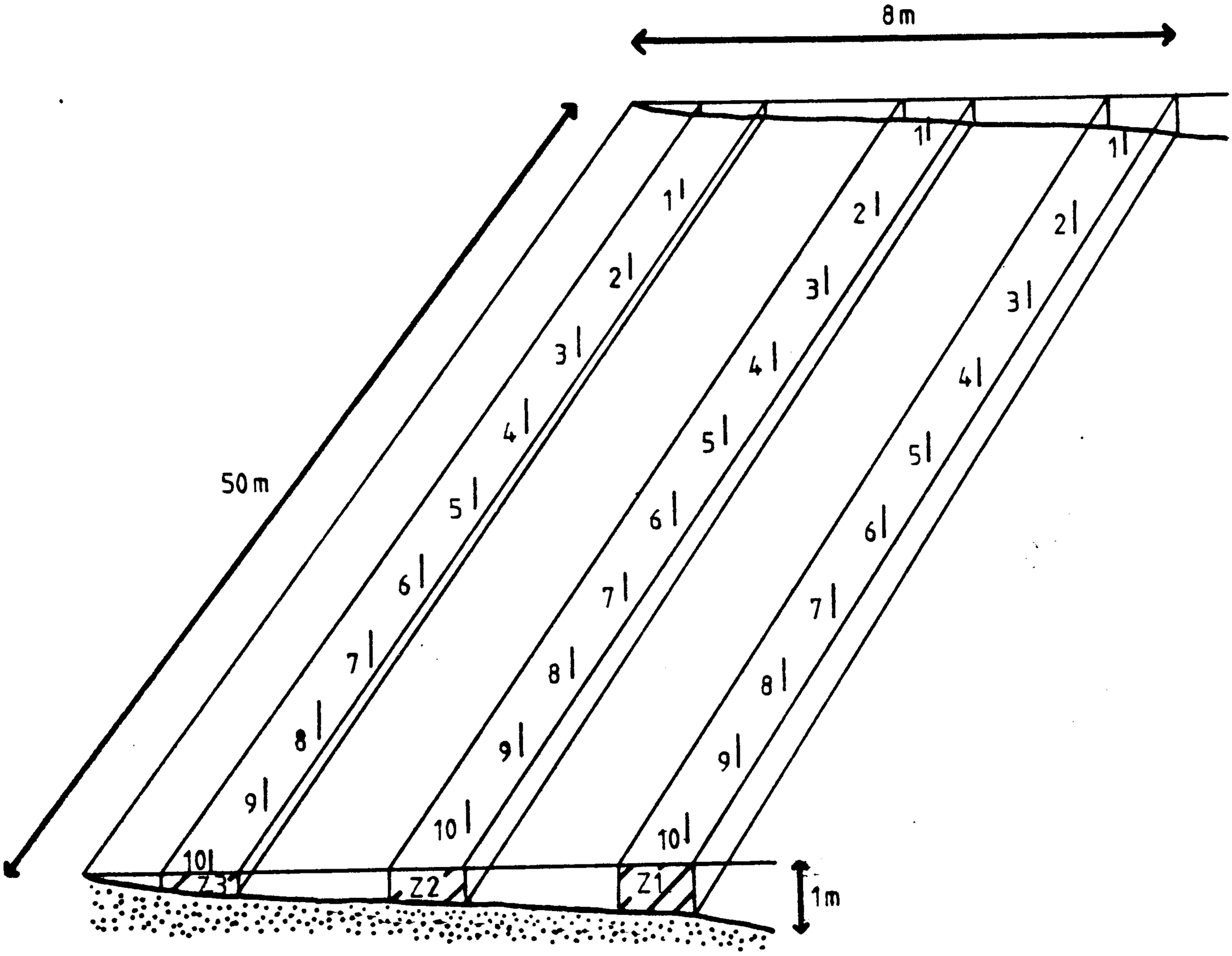


FIGURE 3:1:2 The basic zonal arrangement of stem-sample positions as exemplified by those for March, 1981.

In theory, exclusive use of whole numbers in determining a sample lay-out will mean that stems can only be taken at whole-metre distances along each zone. In practice, however, a stem was not always present at an exact predesignated location so the nearest one within a 0.5m radius was taken instead, with the result that contiguous sampling points existed at all distances along the zones. This deviation from a regular pattern will have done much to annul the inherent inexpediencies of statistical analyses that draw on data derived from a sampling scheme which, in theory anyway, incorporates a non-random component.

B) STEM REMOVAL AND SUBSEQUENT TREATMENT

Phragmites stems can be classed as either 'old' or 'new'. Old stems found between January and August are from the previous season's growth. By September these have become very rare and the vast majority of old stems standing at this time are those that grew at the beginning of the present season and have since died - these will then constitute the old stems existing between January and August in the following year. New shoots first appear in March and living stems are in evidence until October.

From June to October, 1981 both old and new stems were taken. All the stems taken in other months during this year were old.

Laboratory observations made before the initiation of the 1981 field-work programme revealed that when a *Phragmites* stem is disturbed, even gently, many chironomid larvae swim out and away from the epiphyton. It was realised that this could happen when a stem was cut in the field with true larval numbers consequently being underestimated. To counter the problem, a sampling method was devised involving the placing of a tube over the stem before cutting and removal. Plastic drain-piping proved to be ideal for this purpose. A length of tube, containing a foam rubber bung at its top end, is carefully lowered over the stem.

Air is expelled through the bung, allowing the tube to fill with water. The stem is then cut with a sharp blade and its air-filled interior causes it to rise. This upward movement is halted by the bung, and the stem's buoyancy effects its convenient retention in the tube which is quickly inverted and emptied into a polythene bag. The tube and foam rubber bung are rinsed after each sample has been dealt with. By enclosing the stem in a confining jacket, any larvae that are disturbed during removal will not be lost but will be emptied into the bag along with the stem.

Three pipes of different diameters were required, to accommodate the varying epiphyton growth through the seasons. Wider diameters were used when long filamentous algae were present, to minimise the possibility of removing epiphyton when the tube was lowered over a stem. It was deemed preferable to use tubes of three diameters rather than just the widest one, as this would reduce the risk of trapping any free-swimming larvae.

The cut stems were taken back to the laboratory in their polythene bags and immediately placed in a refrigerator set at $4^{o}C$ to arrest the development of larvae awaiting enumeration and identification. Each stem was placed in turn in a glass dish with a white base and its bag rinsed out into this receptacle. The epiphytic coat was classified at this stage on the basis of texture, hardness, and gross morphology. A strong jet of water washed many macroinvertebrates from their epiphytic refuge into the dish - these were picked out using a fine pair of forceps, the white base facilitating their detection. All animals were both killed and stored in 70% ethanol. Epiphyton was then scraped from the stem with a small scalpel and washed into the dish. At this point, a thorough search was made for any macroinvertebrates present in this material.

For smooth hard stems, scraping constituted a straightforward operation. With soft flakey stems, however, it sometimes resulted in small pieces of macrophytic material being removed with the epiphyton. Larger fragments were picked out individually with forceps. Smaller pieces could be separated from the heavier particles of epiphyton by rapid stirring which caused the lighter material to accumulate around the perimeter of the dish, from where it could be extracted with a pipette. The epiphyton that remained generally contained some mineral matter which had to be abstracted in order to obtain a pure algal sample, needed to evaluate biomass and relative growth rates. This separation was achieved when the water and algae were poured onto a pre-weighed glass fibre filter-paper in a Buchner funnel, leaving the heavier mineral particles behind in the dish. Water is drawn through the funnel by suction and the algae retained on the filter-paper. After filtration was completed, the algae and the paper were oven-dried to a constant weight at 105°C.

When all the epiphyton had been scraped off a stem, the latter's length was recorded. A micrometer was used to gauge the diameter at the top, middle, and bottom of the stem. From these measurements it was possible to arrive at a figure for surface area. Each stem was then cut open and any larvae dwelling inside were extracted.

C) FAUNAL ENUMERATION AND CLASSIFICATION

The majority of chironomid larvae can only be identified by detailed examination of slide-mounted head capsules. Over sixteen thousand individuals were collected from reedstems at Cop Mere during 1981 and 1982. Fortunately, 95% of these belonged to a single species (*Cricotopus sylvestris* (Fabricius)), which could be distinguished from the others by the presence of abdominal setal tufts, thereby precluding the need for decapitation and slide mounting. A number of *Cricotopus sylvestris* larvae were treated in this way, however, to corroborate identification.

Larvae bearing no abdominal setal tufts were slide-mounted in polyvinyl lacto-phenol. (Cranston (1982) gives a detailed account of slide preparation techniques.) Instar status was determined for all individuals, on the basis of head capsule width. Identification was undertaken with the aid of the following keys to immature chironomids: Pankratova, 1970, 1979; Bryce and Hobart, 1972; Mason, 1973; Roback, 1976; Tait-Bowman, 1976; Roback and Moss, 1978, Cranston, 1979, 1982. Reference was also made to Cranston's manuscript key to the genera of the larvae of British Chironomidae, dating from the late 1970's.

Where possible, juvenile chironomids were directly identified to species level. A lack of suitable species keys for larval Chironominae and Tanypodinae made this difficult for these subfamilies. Cranston's (1982) key to the larvae of the British Orthocladiinae proved very useful but not all the genera found at Cop Mere are described at species level in this work. In view of these inadequacies, an attempt was made to rear larvae to adults, for which comprehensive species keys are available. In addition, adult emergence data[1] were used to assist the specific identification of juveniles.

Non-chironomid invertebrates were classified with the aid of appropriate keys published by the Freshwater Biological Association. All the macroinvertebrates taken from reedstems during 1981 are listed in Appendix B; Appendix C gives a taxonomic and numerical breakdown of the macroinvertebrate community found on each stem.

---

[1] All references to adult emergence during 1981 in this thesis relate to information presented in Chapter 6, where emergence patterns are considered in detail.

3:2 Spatiotemporal Variation in the Chironomid Community found on Old Reedstems during 1981 - A Consideration of the Larval Population as a Whole.

A) PATTERNS OF VARIATION IN MEAN LARVAL DENSITY AND BIOMASS

Spatiotemporal variation in mean larval density[1] is illustrated in Figure 3:2:1. Interzonal differences are apparent throughout the year but in each zone densities are highest during the summer and are relatively low in the winter. The greatest larval density in each month is found in Zone 1, except for June when it occurs in Zone 2. The lowest is found in Zone 3, except in April when the abundance level for Zone 2 is fractionally lower.

A succession of peaks and troughs characterises the graph-lines for Zones 1 and 2. Numbers increase markedly during May and June[2] after which they fall and rise alternately, month by month, in a pattern largely determined by fluctuations in the *Cricotopus sylvestris* population with its massive numerical superiority (cf. Figures 3:2:1 and 3:3:4). Such a pattern does not exist in Zone 3 where one peak, with a June apex, punctuates an otherwise fairly level graph-line. Like the maximum density for Zone 3, the maximum density for Zone 2 is reached in June, whereas that for Zone 1 is not attained until August.

If the weights of larvae in a sample show sizeable variation (as they will do when different instars and genera are present), the biomass and density patterns of a population may exhibit notable incongruities. The biomass an area is sustaining may be of greater ecological significance than its larval density.

---

[1] Mean larval density is the mean of the individual stem values for total larvae per cm^2 in a zone.

[2] Because samples were taken at the end of each month figures have been drawn so that the graph-line between two consecutive months portrays the net rise or fall of a variable over the latter month.

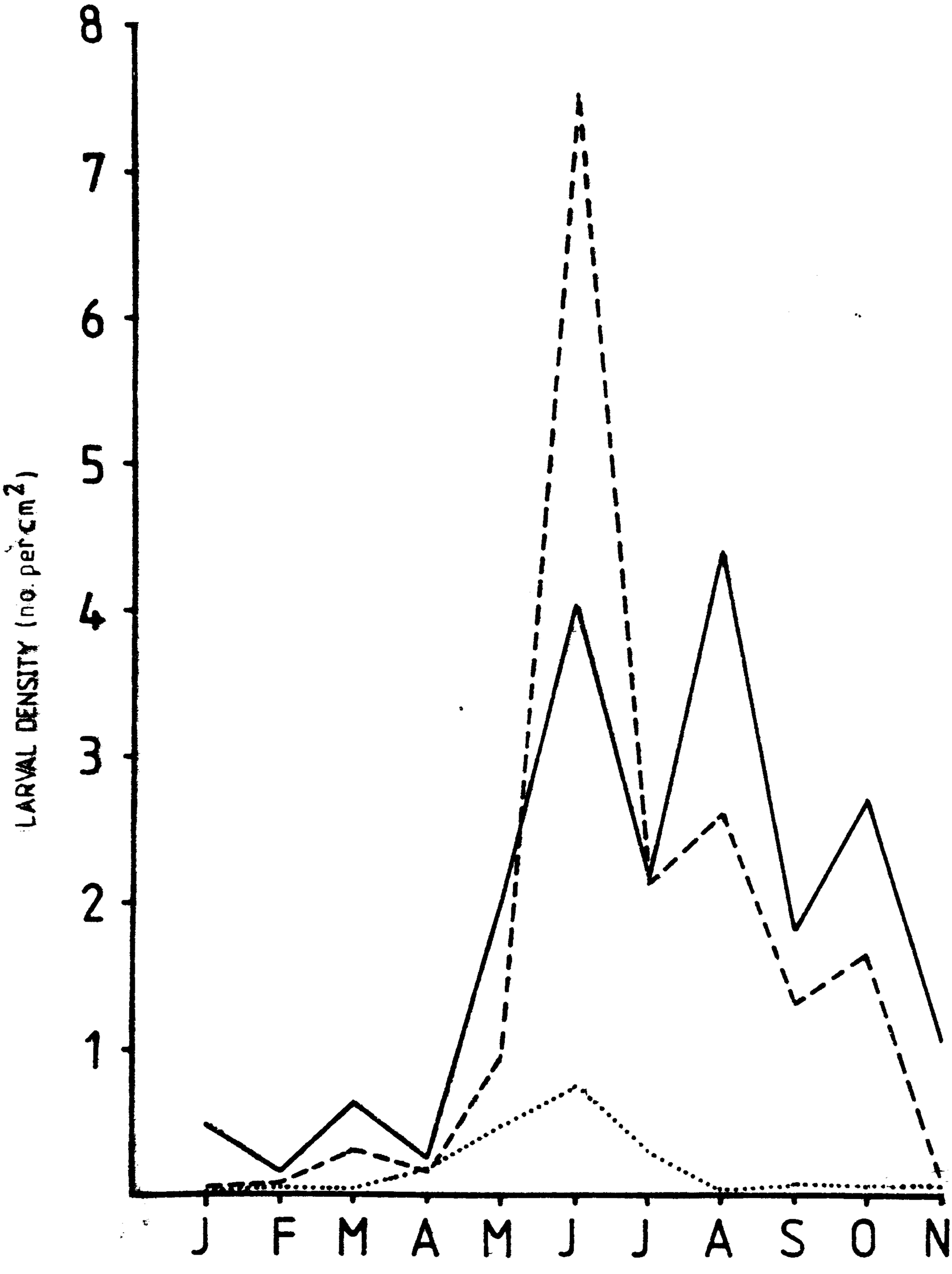


FIGURE 3:2:1 Mean chironomid larval density on old reedstems in Zone 1 (——), Zone 2 (---), and Zone 3 (·····) during 1981. (See Appendix D for standard errors.)

Representative biomass figures for particular instars and genera were obtained from several sources. (The figures and their sources are listed in Appendix E.) Figure 3:2:2 illustrates the spatiotemporal distribution of chironomid larval biomass[1]. As with the graph for chironomid larval density (Figure 3:2:1), the graph showing larval biomass variation mirrors its counterpart for *Cricotopus sylvestris* to a large extent (cf. Figures 3:2:2 and 3:3:5). Four peaks are evident for Zones 1 and 2; only one is manifest for Zone 3. As with density, the greatest biomass in each month is found in Zone 1, apart from June when it occurs in Zone 2. The lowest monthly weight is consistently found in Zone 3. The maximum biomass in Zones 1 and 3 is reached in May; that for Zone 2 is not attained until June.

The basic patterns of density and biomass have similarities and dissimilarities in form. It is felt that an explanation as to the nature of these patterns and why they should differ is more appropriate to the section dealing with *Cricotopus* (see page 71) because it is clear that the dynamics of the *Cricotopus sylvestris* population govern the fundamental structure of the density and biomass graphs for the chironomid community as a whole.

As regards the chironomid sample population, it is evident that interzonal differences in mean larval density and biomass do occur. Statistical tests can be applied to determine the likelihood of such variations being due to chance or signifying genuine population differences between the zones. Where three or more sample groups (here, the sample population of larvae in each zone constitutes a sample group) are under consideration, statistical convention requires the initial use of a test to detect any significant variation that exists between the groups,

---

[1]Mean larval biomass is the mean of the individual stem values for total larval biomass per cm^2 in each zone.

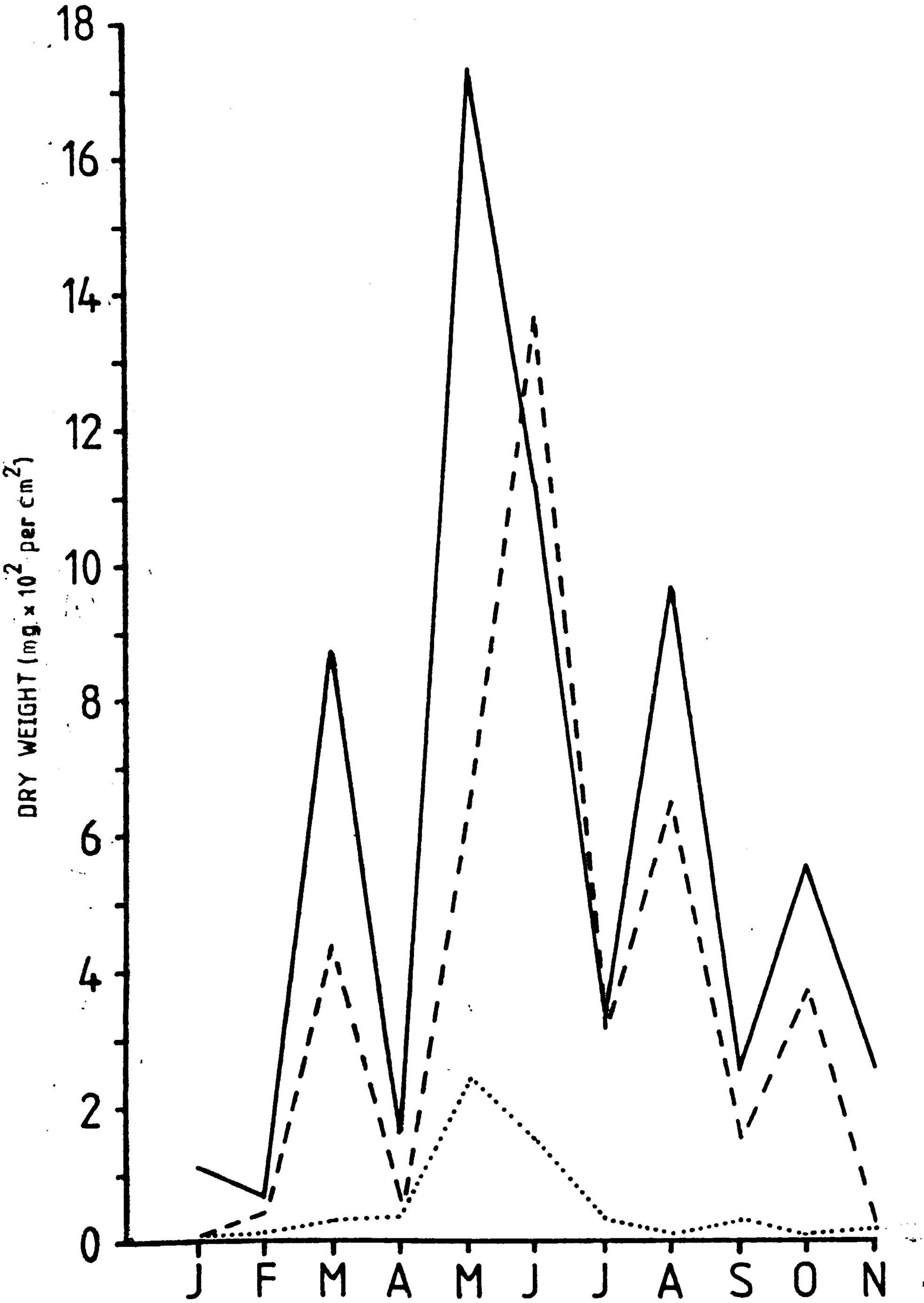


FIGURE 3:2:2 Mean chironomid larval biomass per cm^2 on old reedstems in Zone 1 (——), Zone 2 (---), and Zone 3 (···) during 1981. (See Appendix D for standard errors.)

although such a test will not actually reveal where this variation lies. Out of several potentially applicable techniques, the Kruskal-Wallis Analysis of Variance was chosen as this is regarded as the most efficient of the comparable non-parametric[1] tests, having a Power-efficiency of 95.5% (Siegel, 1956, p. 194). Significant variations, as exposed by this test, are shown in Figure 3:2:3[2]. Larval variation is evident throughout the year, apart from April where none was detected in density.

Having revealed the presence of significant differences, the next step is to find out where they lie. This was done by means of the Mann-Whitney *U* test - one of the most powerful of the non-parametric tests (Hammond and McCullagh, 1974, p. 173) - which is used to discover whether a difference in the means of two independent sample groups is statistically significant[3]. The information obtained from the Mann-Whitney analyses is presented in Figure 3:2:4. Appendices F and G give the actual *H* and *U* indices derived from the Kruskal-Wallis and Mann-Whitney tests respectively.

---

[1] Throughout this study non-parametric tests have been applied in preference to parametric tests, thus precluding the need for data to comply with the requirements for parametric analysis.

[2] Both Figures 3:2:3 and 3:2:4 give information relating to interzonal variation in epiphyton biomass. This information is presented here to facilitate the comparison of larval and epiphyton variation patterns made in Chapter 4 and is not relevant to the present discussion.

[3] In theory, the Mann-Whitney *U* test should only be used when the preceeding Kruskal-Wallis analysis has revealed significant variation, but the greater power of the Mann-Whitney *U* test enables the detection of significant differences that remain unexposed in the Kruskal-Wallis analysis. Both tests are, therefore, consistently applied together in this study.

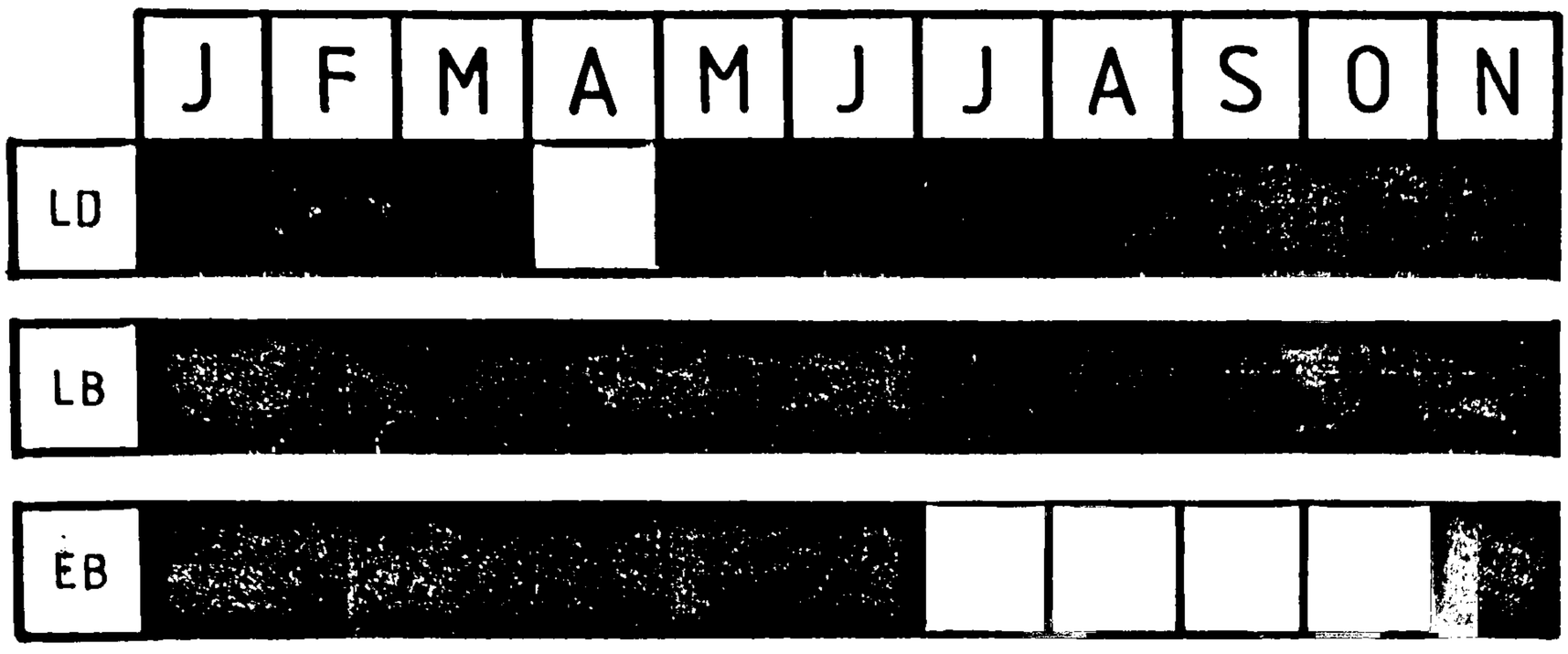


FIGURE 3:2:3 The presence ■ or absence □ of significant interzonal variation in larval density (LD), larval biomass per cm^2 (LB), and epiphyton biomass per cm^2 (EB) during 1981, as exposed by Kruskal-Wallis analyses of variance. (Significance level = 0.05 - for a two-tailed test.)

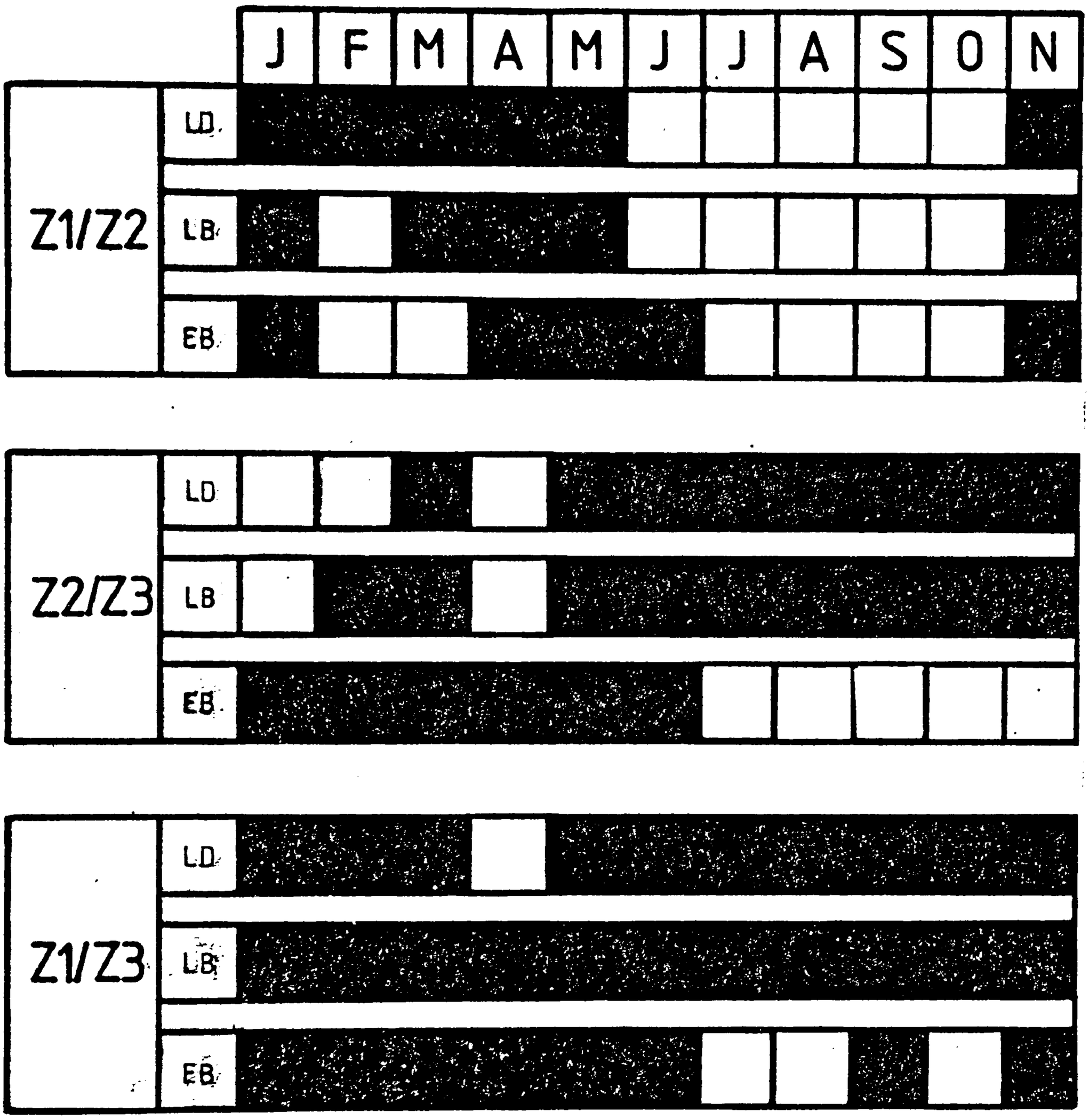


FIGURE 3:2:4 The presence ■ or absence □ of significant variation during 1981 between Zones 1 and 2 (Z1/Z2), Zones 2 and 3 (Z2/Z3), and Zones 1 and 3 (Z1/Z3) respectively, as exposed by Mann-Whitney analyses. (Significance level = 0.05 - for a two-tailed test.)

LD = larval density; LB = larval biomass per cm^2;

EB = epiphyton biomass per cm^2.

Figure 3:2:4 suggests a seasonal dichotomy in both larval density and weight relationships between Zones 1 and 2: through winter and spring (January to May) the zonal means differ significantly, except for larval biomass in February; in summer and autumn (June to October) no such variation is found. This situation is to some extent reversed with respect to Zones 2 and 3 where any differences that are insignificant occur from January to April. Significant larval variation between Zones 1 and 3 is manifest throughout the year, except in density during April.

From the patterns described above it can be inferred that, for the first four months of the year, Zone 2 shares a greater similarity with Zone 3 than it does with Zone 1; between June and October inclusive, Zone 2 shares a greater similarity with Zone 1 than it does with Zone 3.

B) PATTERNS OF INTRAZONAL VARIATION IN LARVAL DENSITY AND BIOMASS.

In the preceding discussion, consideration is given to the mean larval density in each zone along with the mean larval biomass. Here, attention is focused on the actual sample values from which these means are derived.

Intrazonal variation in the larval density and biomass on old reedstems was measured by calculating the coefficient of variation (V):

$$V = \frac{s}{\bar{x}} \times 100$$

where

s = standard deviation

$\bar{x}$ = arithmetic mean of the sample values.

Because variation is expressed as a percentage, that which occurs in one zone can readily be compared with that found in another.

Temporal change in the degree of larval density variation within each zone is illustrated in Figure 3:2:5. The least variation in each month is usually found in Zone 1 and the most in Zone 3. The narrowest range of variation values through the year occurs with respect to Zone 1; the broadest range occurs with respect to Zone 3, where month to month fluctuations in variation values are often comparatively large in relation to those for the other two zones. The convergence of the three graph-lines in March and April indicates a period of relative similarity in intrazonal variation levels.

The graph for intrazonal biomass variation (Figure 3:2:6) exhibits a fair degree of congruity in form with its counterpart for density, but often shows higher concomitant values.

During the 1981 sampling programme it was noted that occasionally there seemed to be a tendency for greater larval densities to occur at one end of the study site (that nearest to the river outflow) than the other. This apparent trend was statistically investigated by means of a runs test, which is used to discover whether a sequence of observations displays significant randomness (Hammond and McCullagh, 1974, p. 244). The sequence of observations in the present case consists of the larval density values for each zone; the order of the sequence reflects the spatial distribution of the stem-samples from which these values are derived. An application of the runs test was adopted which considers the position of each of the values in a sequence in relation to the median for the group (Bishop, 1980, p. 138). Each of the numbers in the sequence is assigned a plus or minus depending on whether it is above or below the median. The number of runs (r) of consecutive pluses and minuses is counted; a table of critical values is then consulted to decide whether this number is indicative of non-randomness in the sequence. Calculated and critical values of r are given in Appendix H.

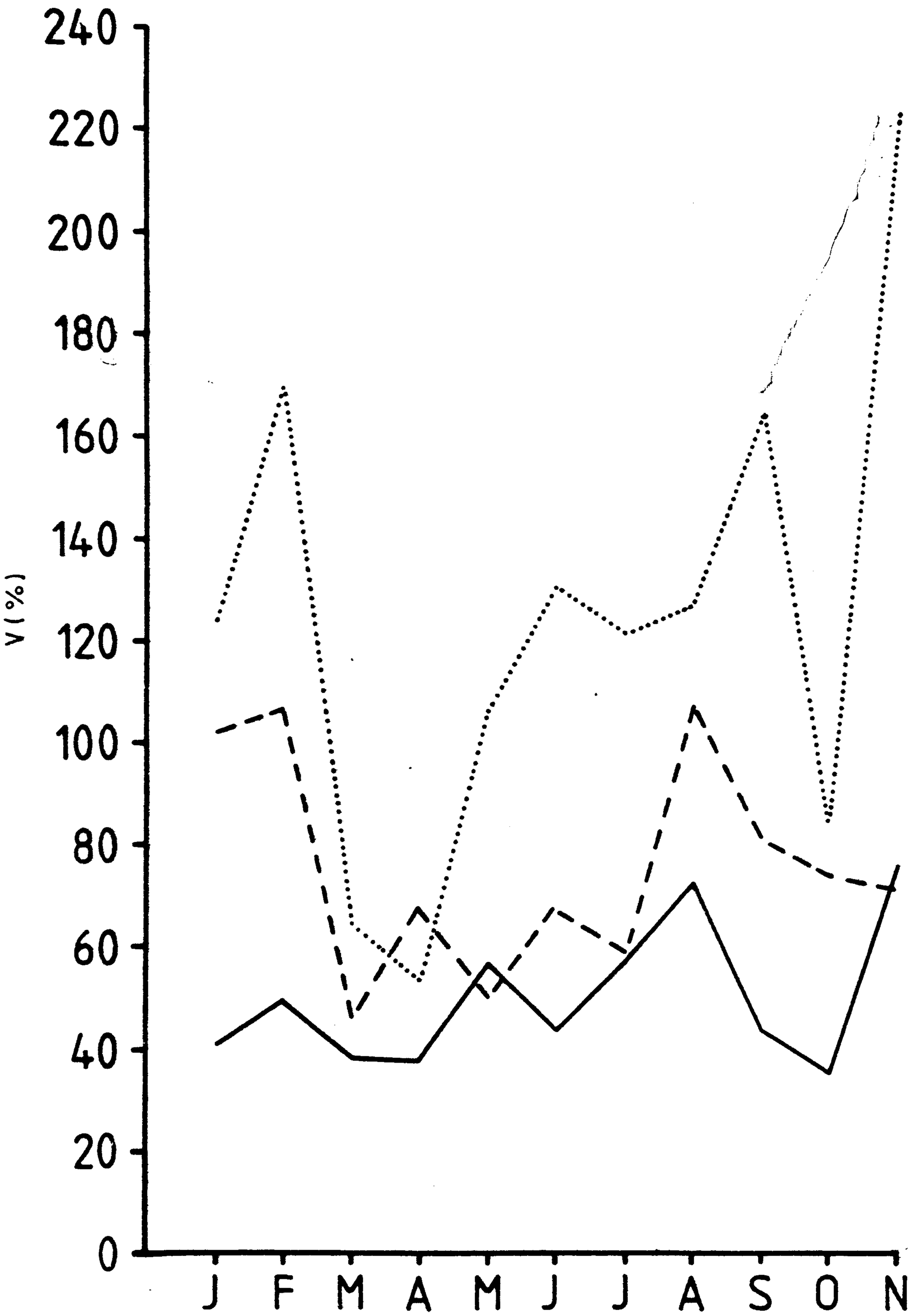


FIGURE 3:2:5 Chironomid larval density variation between old reedstems in each of Zones 1 (——), 2 (---), and 3 (···) during 1981, as expressed by the coefficient of variation (V).

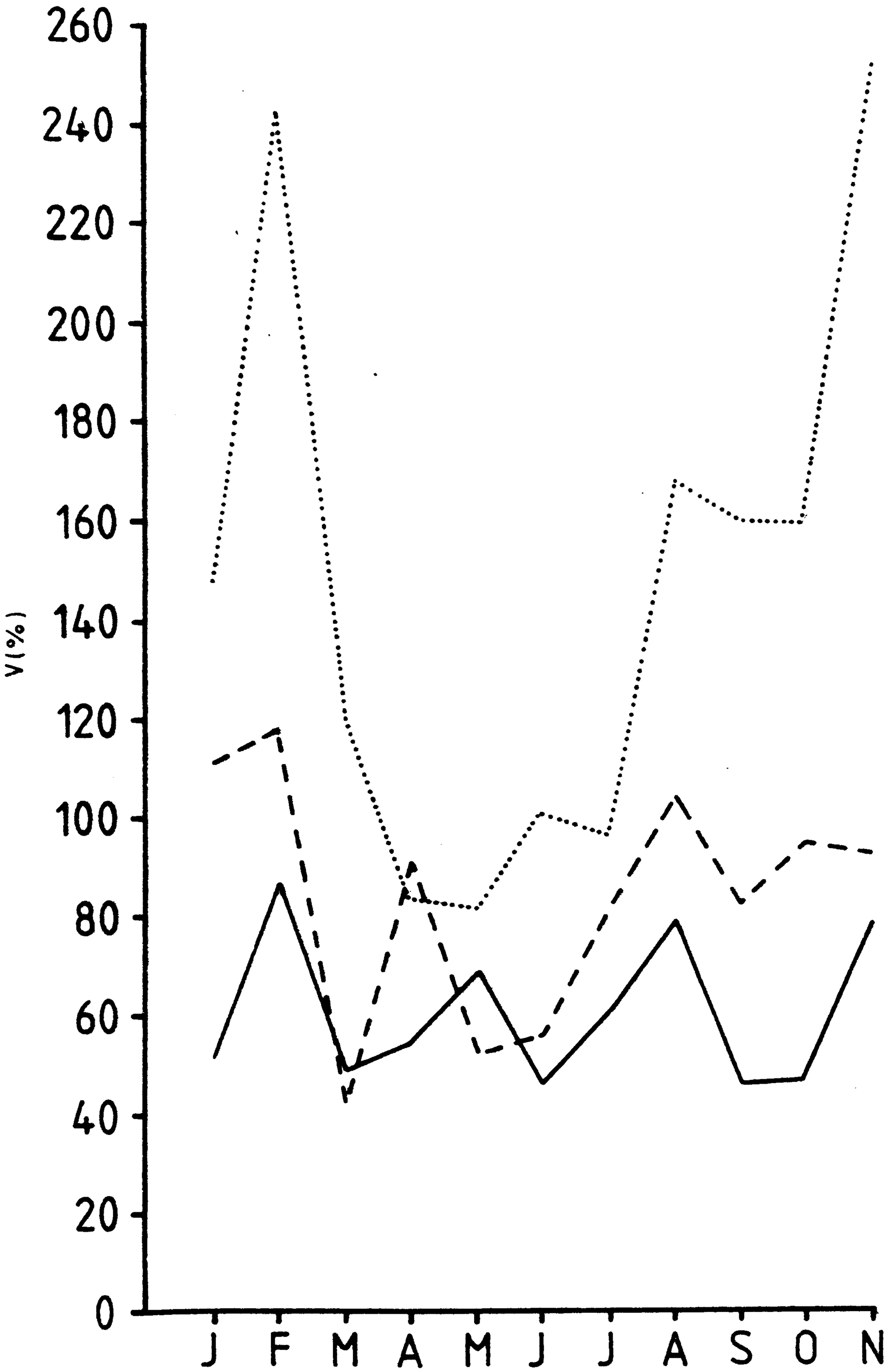


FIGURE 3:2:6 Variation in values for chironomid larval biomass per cm^2 between old reedstems in each of Zones 1 (——), 2(---), and 3 (···) during 1981, as expressed by the coefficient of variation (V).

No significant deviation from a random distribution was detected in any zone at any time of the year, although Figures 3:2:7a and 3:2:7c do suggest that from January to April, in Zones 1 and 3, higher than average densities tend to occur towards the river outflow. No such pattern appears to exist in Zone 2 (Figure 3:2:7b).

C) PATTERNS OF VARIATION IN POPULATION DIVERSITY LEVELS

Population diversity was measured on a generic basis, using the Shannon-Wiener function for species diversity (substituting genera for species):

$$H = -\sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

where

H = index of species diversity

s = number of species

p_i = proportion of total sample belonging to ith species.

This function incorporates two components of diversity: 1) number of species and 2) equitability or evenness of allotment of individuals amongst the species (Lloyd and Ghelardi, 1964). The index of diversity obtained from the Shannon-Wiener function is increased by a greater number of species and also by a more equitable distribution of the sample population amongst species. Equitability can be defined as the ratio

$$E = \frac{H}{H_{max}}$$

where

E = equitability range (0-1)

H = observed species diversity

H_{max} = maximum species diversity = $\log_2 s$

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
J	+	−	+	+	+	+	+	−	+	−	−	−	+	−	−
F	−	+	+	+	+	+	−	+	+	−	−	−	−	−	+
M	+	+	+	−	+	−	−	+	−	−
A	+	+	+	+	−	−	−	−	+	−
M	+	−	+	+	−	+	−	+	−	−
J		−	−	−	+	−	+		+	+
J	−		−	+	−	+
A	+		+	+	+		−	−		−
S	+	−	+		−		−		+	−
O		+		−	+	−		−		
N	+	+	−	−	+	−	−	+	−	+

FIGURE 3:2:7a Runs test sequences relating to larval densities on old reedstems in Zone 1 during 1981. (See text for explanation.) The numbers at the top of the figure refer to the individual stem-samples taken along the zone. (See Figure 3:1:2.) Stem-sample 1 is located at that end of the study site nearest to the river outflow; the highest numbered stem-sample in each month is located at the opposite end. Gaps in the sequence occur where new stems were taken.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
J	+	+	+	−	−	−	+	−	−	−	+	+	+	+	−
F	+	−	−	−	+	+	+	−	−	+	+	+	+	−	−
M	−	+	−	−	+	−	+	+	+	−					
A	+	−	+	+	−	−	+	+	−	−					
M	−	−	+	+	+	+	−	+	−	−					
J	−	−	+	+	+	+	+		−	−					
J	+	−	+	−	+	+		−		−					
A	+	−	−	+	+	−	+	+	−	−					
S	−	−	−		+			−	+	+					
O	+	+	−	−	+	+	−	+	−	−					
N	+	−	+	+	−	+	−	+	−	−					

FIGURE 3:2:7b Runs test sequences relating to larval densities on old reedstems in Zone 2 during 1981. (See text for explanation.) The numbers at the top of the figure refer to the individual stem-samples taken along the zone. (See Figure 3:1:2.) Stem-sample 1 is located at that end of the study site nearest to the river outflow; the highest numbered stem-sample in each month is located at the opposite end. Gaps in the sequences occur where new stems were taken.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
J	+	+	+	−	+	−	+	−	−	−	+	−	−	+	−
F	−	+	+	−	+	+	+	+	−	−	−	−	+	−	−
M	+	+	−	+	+	−	+	−	−	−					
A	+	+	+	+	−	+	−	−	−	−					
M	+	−	−	−	+	−	+	−	+	+					
J	+	−	+	−	+	+	−	−	−	+					
J	+	−	+	−	+	+	−	−	−	+					
A		+	+	−	+	−	−	+		−					
S	−	+				+	−	+	+	−					
O	+	+	+	−	−	+	−	−	−	+					
N	−	+	−	+	+	−	+	−	+	−					

FIGURE 3:2:7c Runs test sequences relating to larval densities on old reedstems in Zone 3 during 1981. (See text for explanation.) The numbers at the top of the figure refer to the individual stem-samples taken along the zone. (See Figure 3:1:2.) Stem-sample 1 is located at that end of the study site nearest to the river outflow; the highest numbered stem-sample in each month is located at the opposite end. Gaps in the sequences occur where new stems were taken.

Table 3:2:1 gives the diversity and equitability indices derived from Shannon-Wiener investigations of the larval communities found in each zone during 1981.

In Zones 1 and 2, maximum diversity occurs early in the year (in March and February respectively). During the summer, diversity levels in both zones tend to be low. The greatest diversity in Zone 3 is found in November; the levels in January and October are close to this maximum.

The hierarchical order of the zonal diversity indices often changes from month to month; maximum diversity is most frequently found in Zone 3.

In Zones 1 and 2, equitability rises and falls concomitantly in relation to diversity, with both maximum equitability and diversity occurring in March in Zone 1 and February in Zone 2. A similar concomitance is evident for Zone 3 but here the maximum levels for the two characteristics are not reached in synchrony: the greatest diversity occurs in November whereas the most equitable distribution exists in August.

As with diversity, the hierarchical order of the zonal equitability indices shows a number of permutations through the year. From June to November, the permutations relating to equitability are identical to their counterparts for diversity; from January to May they are not. The highest level of equitability in each month exists most frequently in Zone 3; the lowest is generally found in either Zone 1 or Zone 2.

3:3 Taxonomic Features of the Larval Chironomid Community found on Old Reedstems during 1981.

A) SUBFAMILY AND GENUS COMPOSITION OF THE TOTAL SAMPLE POPULATION FOR 1981.

Three subfamilies were represented in larval collections: the Chironominae, Orthocladiinae, and Tanypodinae. Larvae of the latter subfamily are free-swimming; therefore, the few individuals (eight Pentaneurini sp. C and one *Psilotanypus* sp.) captured in the sampling tube ar

	H			H_{max}			E		
	Z1	Z2	Z3	Z1	Z2	Z3	Z1	Z2	Z3
Jan	0.4872	0.3066	1.3542	3.0	1.5850	2.0	0.1624	0.1934	0.6771
Feb	0.7325	0.8420	0.4424	3.0	2.3219	1.5850	0.2442	0.2626	0.2791
Mar	1.1548	0.4560	0.9912	2.8074	2.0	1.5850	0.4113	0.2280	0.6254
Apr	0.8716	0.5075	0.3298	2.5850	1.5850	1.0	0.3372	0.3202	0.3298
May	0.5412	0.1881	0.5262	2.5850	2.3219	1.0	0.2094	0.0810	0.5262
Jun	0.3140	0.1140	0.3799	2.1699	2.5850	2.5850	0.0991	0.0441	0.1470
Jul	0.1844	0.1317	0.3976	2.5850	2.5850	1.5850	0.0713	0.0509	0.2509
Aug	0.2109	0.5071	0.9544	2.5850	2.3219	1.0	0.0815	0.2184	0.9544
Sep	0.2712	0.3072	0.0	2.5850	2.5850	0.0	0.1049	0.1188	0.0
Oct	0.3064	0.5860	1.2310	2.3219	2.5850	1.5850	0.1320	0.2276	0.7767
Nov	0.0737	0.1123	1.4138	1.5850	1.0	1.5850	0.0465	0.1123	0.8920

TABLE 3:2:1 Diversity and equitability indices relating to the generic composition of the chironomid larval population found on old reedstems in each zone during 1981. (See text for methods of calculation and explanation of symbols.)

not included in any consideration, statistical or otherwise, of epiphyton-dwelling larvae. The Orthocladiinae is by far the most numerous group: members of this subfamily constitute over 96% of the sample population, whilst larvae belonging to the Chironominae account for the remainder.

Seventeen genera were identified of which nine belong to the Chironominae and eight to the Orthocladiinae. For each genus, Table 3:3:1 shows the number of individuals caught and the percentage that this number comprises of the total number of larvae collected. The vastly superior position held by the Orthocladiinae, in terms of subfamily relative abundance, is directly attributable to the prominence of the genus *Cricotopus*, which accounts for over 95% of all larvae and over 98% of those belonging to the Orthocladiinae. Non-*Cricotopus* members of the Orthocladiinae constitute 1.42% of the total sample population; members of the Chironominae constitute 3.36%.

B) TEMPORAL OCCURRENCE PATTERNS FOR INDIVIDUAL TAXA - A COMPARATIVE DESCRIPTION.

Figures 3:3:1 and 3:3:2 illustrate the larval temporal occurrence patterns for Chironominae and Orthocladiinae taxa respectively. The genera belonging to the Chironominae show three basic types of temporal distribution in terms of presence or absence in each month: three genera (*Endochironomus*, *Glyptotendipes*, and *Limnochironomus*) are present thoughout all or most of the sampling period; four genera (*Cladotanytarsus*, *Microtendipes*, *Polypedilum*, and *Tanytarsus*) are so scarce and occur so infrequently that no genuine seasonal patterns can be identified; and two genera (*Camptochironomus* and *Parachironomus*) do not appear until late spring/early summer and are then found continuously through to October.

The set of distribution patterns for the Orthocladiinae differs characteristically from that for the Chironominae.

CHIRONOMINAE	No.	%
Camptochironomus	125	0.77
Cladotanytarsus	2	0.01
Endochironomus	30	0.18
Glyptotendipes	283	1.74
Limnochironomus	46	0.28
Microtendipes	1	0.01
Parachironomus	40	0.25
Polypedilum	4	0.02
Tanytarsus	2	0.01
ORTHOCLADIINAE		
Corynoneura	12	0.07
Cricotopus	15,494	95.32
Diplocladius	5	0.03
Metriocnemus	32	0.20
Orthocladius	2	0.01
Psectrocladius	89	0.55
Rheocricotopus	31	0.19
Thienemanniella	57	0.35

TABLE 3:3:1 The genera of chironomid larvae found on old reedstems during 1981, together with the number of individuals found in each genus, which is also expressed as a percentage of the total number of larvae found.

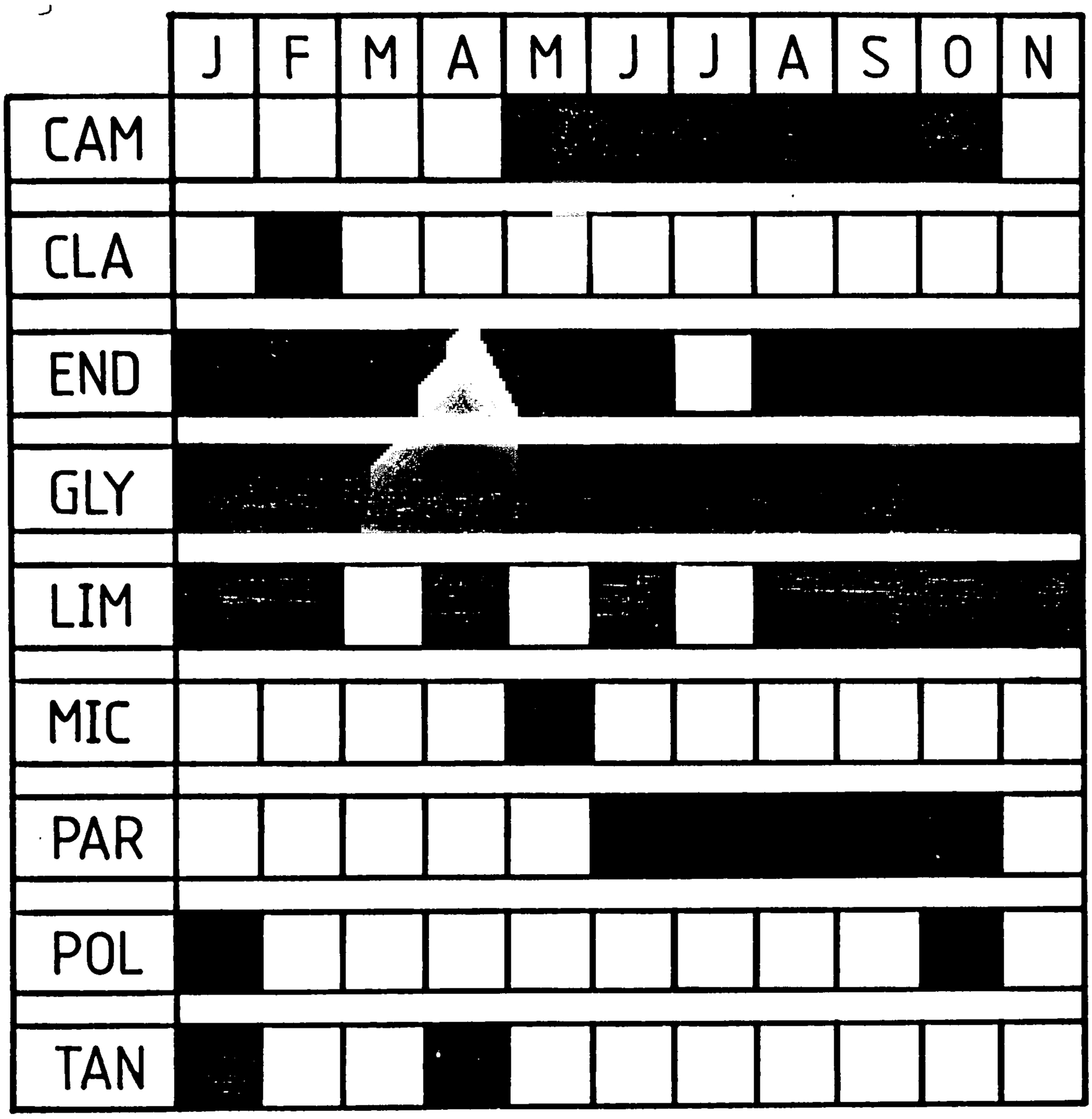


FIGURE 3:3:1 Larval temporal occurrence patterns for Chironominae genera found on old reedstems during 1981.

■ - present; □ - absent.

CAM - *Camptochironomus;* CLA - *Cladotanytarsus;*

END - *Endochironomus;* GLY - *Glyptotendipes;*

LIM - *Limnochironomus;* MIC - *Microtendipes;*

PAR - *Parachironomus;* POL - *Polypedilum;*

TAN - *Tanytarsus*

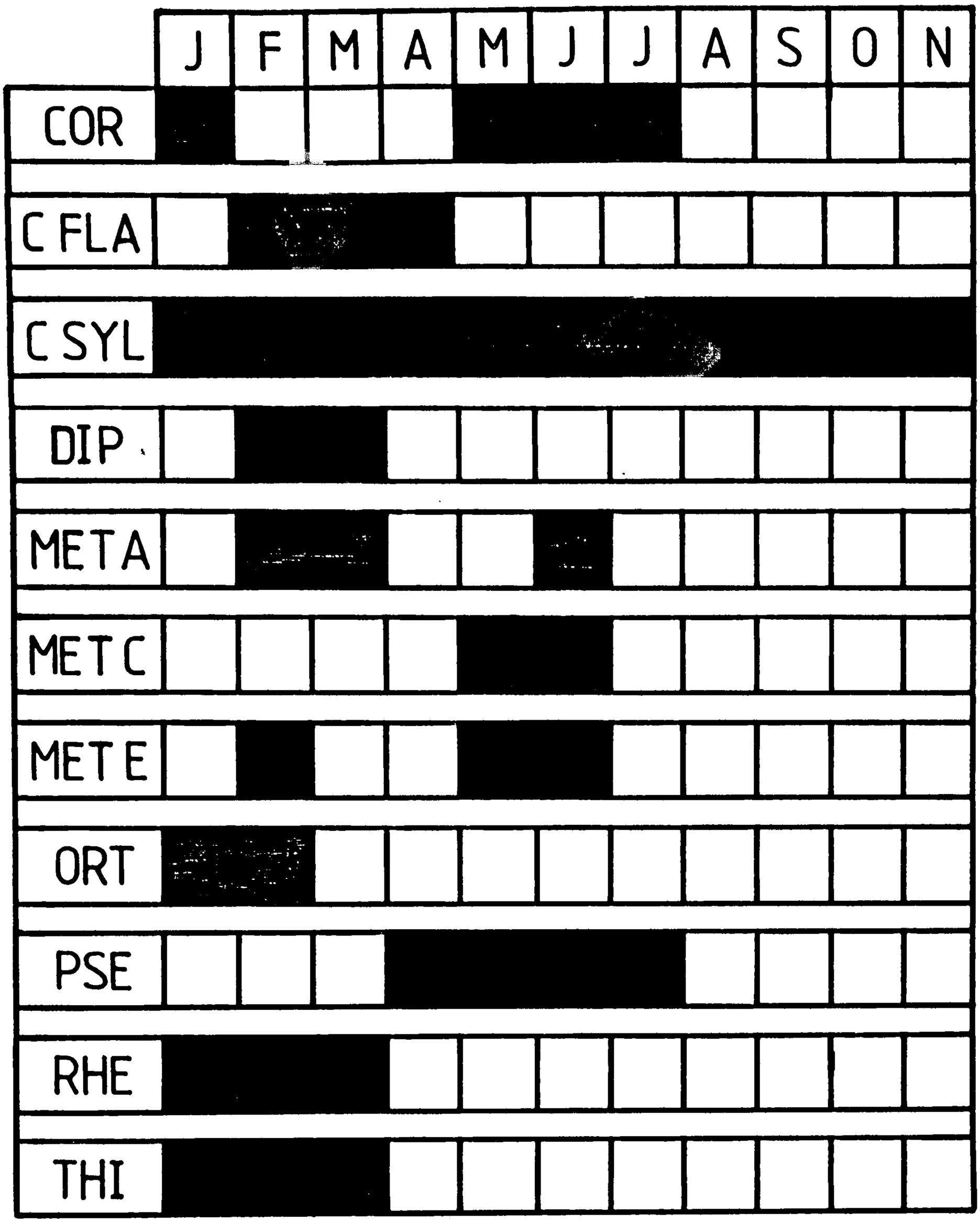


FIGURE 3:3:2 Larval temporal occurrence patterns for Orthocladiinae taxa found on old reedstems during 1981.

■ - present; □ - absent.

COR - *Corynoneura;* C FLA - *Cricotopus flavocinctus;*

C SYL - *Cricotopus sylvestris;* DIP - *Diplocladius;*

MET A - *Metriocnemus* sp. A; MET C - *Metriocnemus* sp. C;

MET E - *Metriocnemus* sp. E; ORT - *Orthocladius;*

PSE - *Psectrocladius;* RHE - *Rheocricotopus;*

THI - *Thienemanniella*

The only taxon represented in more than four months is *Cricotopus sylvestris*, which is present throughout the sampling period. The other Orthocladiinae appear at various times between January and July inclusive. Three taxa (*Corynoneura*, *Metriocnemus* sp. A, and *Metriocnemus* sp. E) occur intermittently whereas both *Metriocnemus* sp. C and *Psectrocladius* are confined to consecutive months during the spring and summer. The remaining taxa (*Diplocladius*, *Orthocladius*, *Rheocricotopus*, and *Thienemanniella*) are restricted to the winter months and have disappeared by April. Such winter-exclusive chironomids are not readily apparent in the Chironominae sample population.

The number of genera represented in monthly samples constitutes a simple measure of diversity. With respect to the Chironominae, this number remains fairly stable over the year; the Orthocladiinae, however, show a distinct seasonal variation with the highest genera counts occurring in the first three months of the year and the lowest existing between August and November inclusive. The total Chironominae genera counts for most months are similar, although a long-term decrease is evident from January and February, when diversity is maximal, to November when it falls relatively sharply to its lowest level.

It must be remembered that the measure of diversity discussed above does not take into account the relative abundance of each genus, unlike the Shannon-Wiener analysis where equitability is taken into consideration. Diversity values derived from genera counts and Shannon-Wiener analyses are not, therefore, directly comparable.

Table 3:3:2 gives the percental relative abundance values for the taxa making up each month's chironomid population. The monthly abundance patterns illustrated in this table are typical of those found in many communities in that the number of species that are relatively common is small in comparison with the number of species that are relatively rare (Krebs, 1972, p. 501).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
CAM	-	-	-	-	2.42	0.27	0.27	1.81	0.58	0.07	-
CLA	-	0.86	-	-	-	-	-	-	-	-	-
COR	0.21	-	-	-	0.12	0.14	0.13	-	-	-	-
C FLA	-	4.74	2.29	0.37	-	-	-	-	-	-	-
C SYL	92.36	84.48	80.25	88.06	93.22	97.78	98.14	94.98	96.45	92.94	96.71
DIP	-	1.29	0.42	-	-	-	-	-	-	-	-
END	0.41	0.43	1.87	1.12	0.12	0.10	-	0.03	0.25	0.21	0.17
GLY	1.65	2.16	2.49	8.58	0.83	0.54	0.73	2.50	1.90	4.56	2.09
LIM	0.83	0.86	-	0.37	-	0.15	-	0.31	0.33	0.76	1.04
MET A	-	0.43	0.21	-	-	0.02	-	-	-	-	-
MET C	-	-	-	-	1.30	0.08	-	-	-	-	-
MET E	-	0.43	-	-	0.06	0.02	-	-	-	-	-
MIC	-	-	-	-	0.06	-	-	-	-	-	-
ORT	0.21	0.43	-	-	-	-	-	-	-	-	-
PAR	-	-	-	-	-	0.02	0.20	0.37	0.50	1.24	-
POL	0.21	-	-	-	-	-	-	-	-	0.21	-
PSE	-	-	-	1.12	1.89	0.89	0.53	-	-	-	-
RHE	1.24	2.16	4.16	-	-	-	-	-	-	-	-
TAN	0.21	-	-	0.37	-	-	-	-	-	-	-
THI	2.69	1.72	8.32	-	-	-	-	-	-	-	-

TABLE 3:3:2 Monthly percentage relative abundance values for the chironomid taxa found on old reedstems during 1981. (See Figures 3:3:1 and 3:3:2 for key to taxonomic abbreviations.

C) INDIVIDUAL PATTERNS OF DISTRIBUTION AND ABUNDANCE - ORTHOCLADIINAE

i) *Cricotopus*

During 1981, two species were recorded from emergence traps: *Cricotopus sylvestris* and *Cricotopus flavocinctus* (Kieffer) - these occurring in a ratio of nine *sylvestris* to one *flavocinctus* in the total year count for *Cricotopus* adults. Identification of the two species in the larval stage proved to be a perplexing task. Laboratory rearing of *Cricotopus* larvae was not outstandingly successful and produced little of diagnostic value. Species determination was further hindered by the fact that the only key to take *Cricotopus* larval identification beyond the genus level (that of Cranston (1982)) was not published until after the completion of the 1981 sampling programme. Once this key had become available an attempt was made to distinguish between the larvae of *sylvestris* and *flavocinctus*. Head capsule examination of specimens identified beforehand as *Cricotopus*, due to the presence of distinctive abdominal setal tufts, revealed all of these to be *sylvestris* irrespective of the month or zone in which they were originally collected. A homogeneous group of larvae not previously classified as *Cricotopus*, because of a lack of abdominal setal tufts, was positively identified as *flavocinctus* on the basis of head capsule morphology - Cranston discloses the fact that not all *Cricotopus* species possess setal tufts.

The temporal abundance pattern of *flavocinctus* larvae presents something of an anomaly in that it bears little correlative resemblance to the pattern for *flavocinctus* adults recovered from emergence traps. Figure 3:3:3[1] shows larvae to be evident from February to April only, whereas the emergence period for adults extends without interruption

---

[1]The mean monthly density values shown in Figures 3:3:3, 3:3:7, and 3:3:9 -17 were obtained by dividing the total number of larvae taken from all stem-samples by the combined stem surface area. Standard errors of these means cannot, therefore, be calculated.

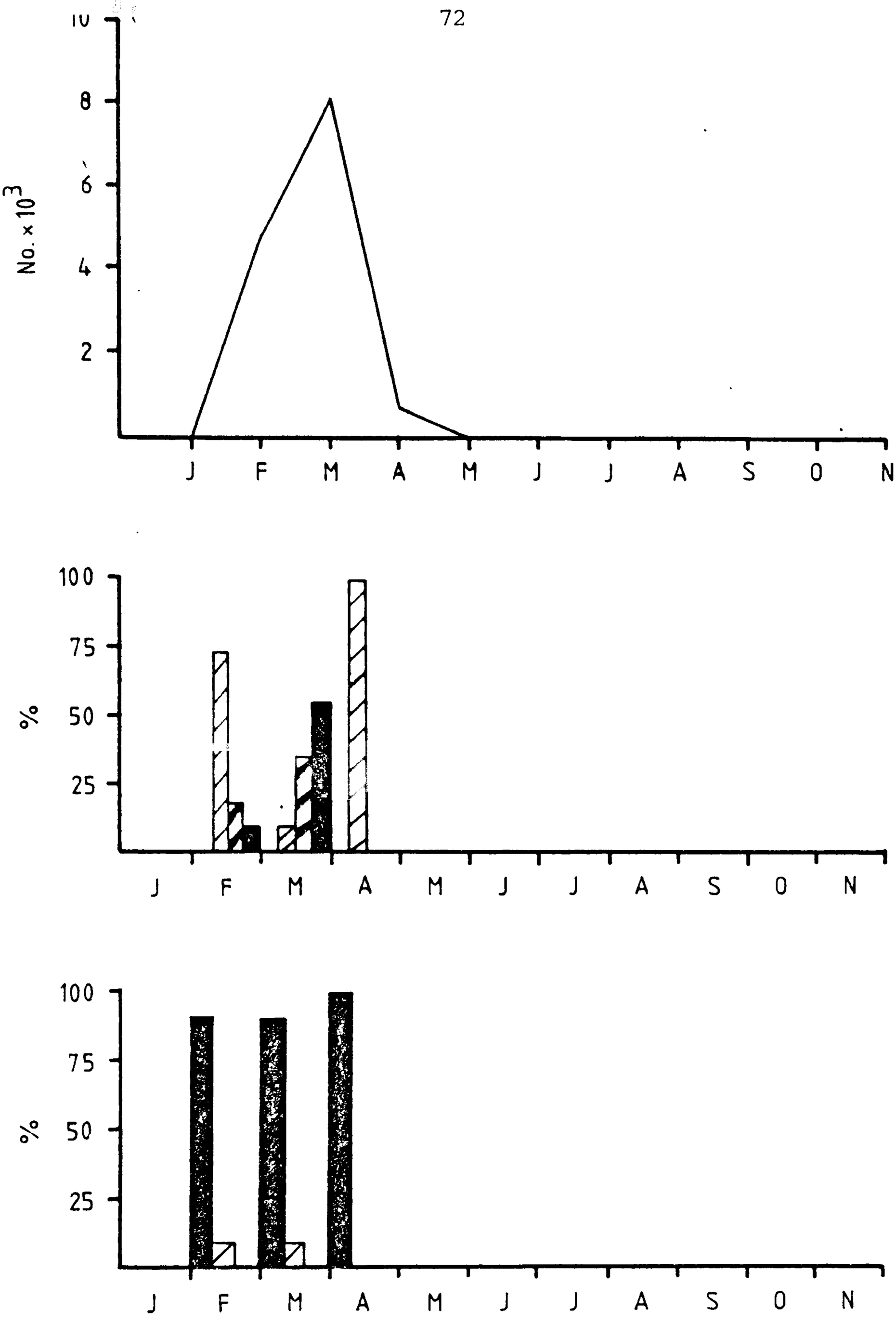


FIGURE 3:3:3 Population data for *Cricotopus flavocinctus* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd; ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *flavocinctus* population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

from April to October. *Cricotopus sylvestris* larvae outnumber *flavocinctus* larvae by an average[1] of 35:1 over the period when the latter are present and by 236:1 in the samples taken at the end of April. The decline in numbers of *flavocinctus* larvae during April is attributable to the onset of emergence in this species which commences at the beginning of the month. In comparison, April emergence of *sylvestris* occurs at an insignificant level, which accounts for the relatively large population of *sylvestris* larvae remaining at the end of the month.

Why *flavocinctus* should not be represented in larval samples from May onwards is unclear. The number of adults caught in emergence traps suggests larvae would have been present in sufficient quantities to be detected, considering that other species with far lower adult counts were found as larvae. There is no evidence to support the idea of a post-April colonisation of an alternative habitat within the reedbed and thus it seems reasonable to conclude that larvae and/or pupae must be entering the reedbed from elsewhere before emergence.

Figure 3:3:3 indicates that, in each month, all or the vast majority of *flavocinctus* larvae are found in Zone 1 and they are absent from Zone 3. Explanations as to the zonal distributions of all sampled species are given in the next chapter.

Although evidence is not entirely devoid of ambiguity, it can be affirmed that the graphs of *Cricotopus* density and biomass presented in Figures 3:3:4 and 3:3:5 are reliable representations of temporal and spatial variation in the *Cricotopus sylvestris* population. An allusive consideration of the graph patterns for this species has already been made, in respect of those for overall larval density and biomass

---

[1] This average is the mean of the monthly ratios existing over the period in question.

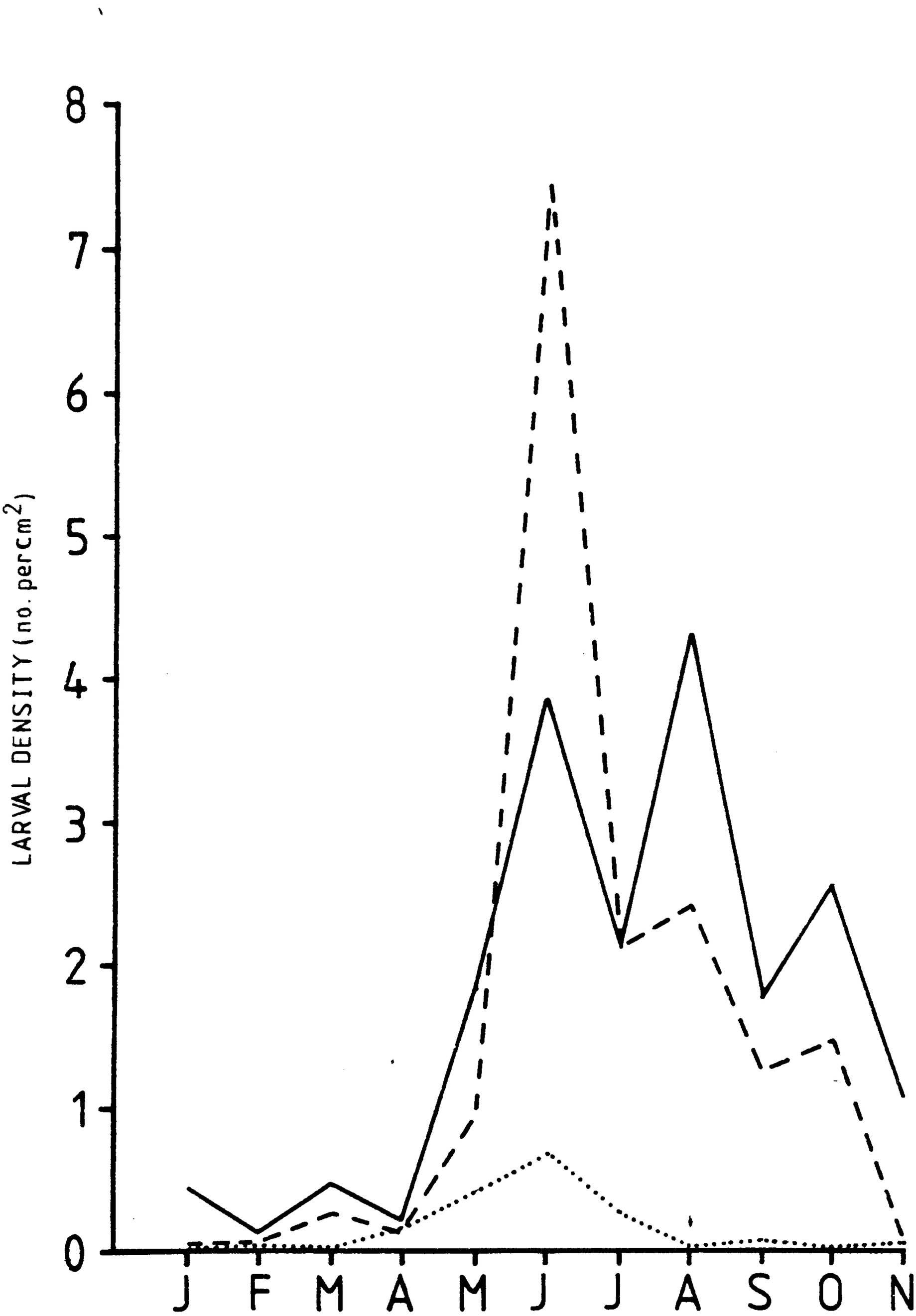


FIGURE 3:3:4 Mean *Cricotopus sylvestris* larval density on old reedstems in Zone 1 (——), Zone 2 (---), and Zone 3 (....) during 1981. (See Appendix I for standard errors.)

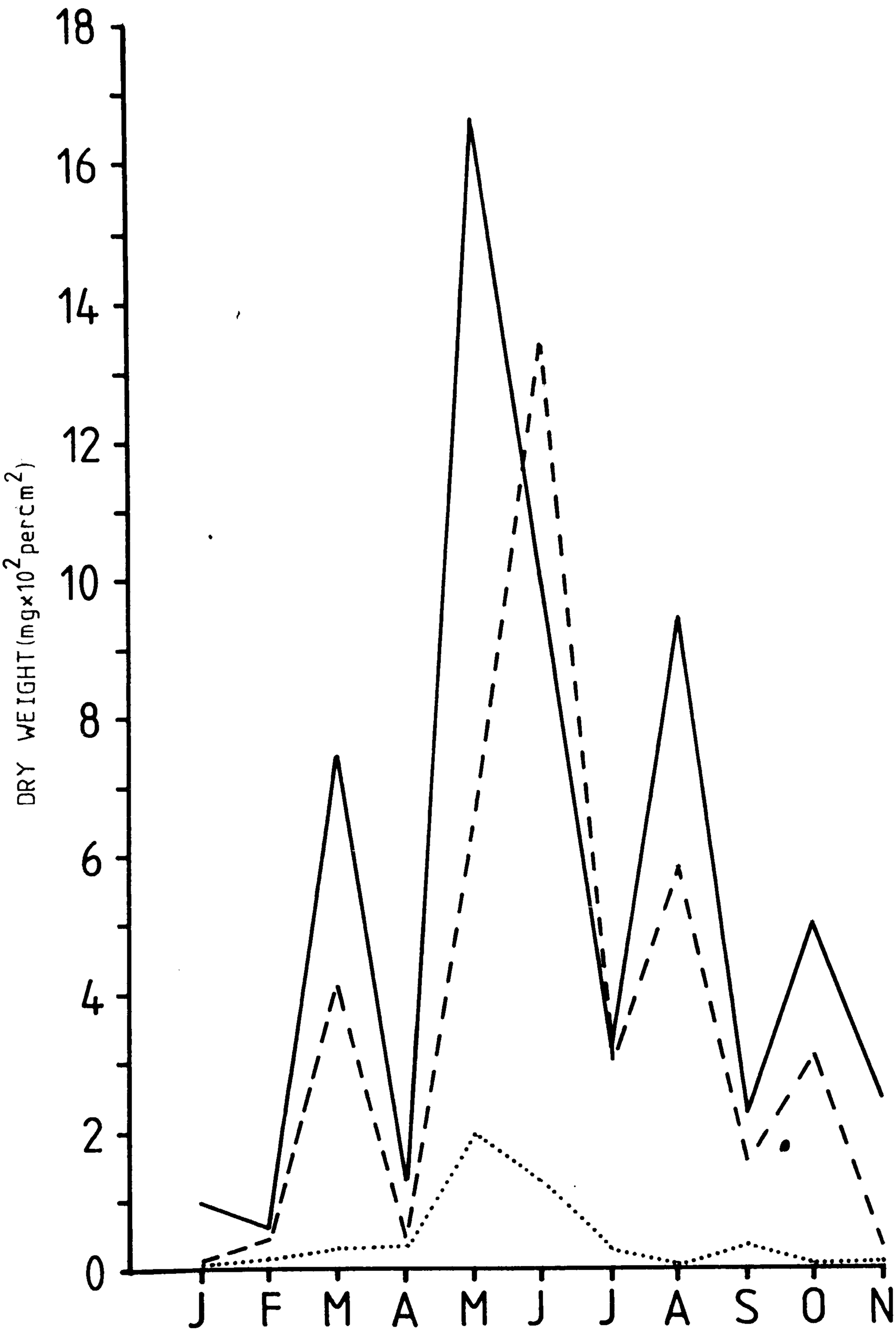


Figure 3:3:5 Mean *Cricotopus sylvestris* larval biomass per cm^2 on old reedstems in Zone 1 (——), Zone 2 (---), and Zone 3 (·····) during 1981. (See Appendix I for standard errors.)

	Zone 1		Zone 2		Zone 3	
	D	B	D	B	D	B
January	93.93	85.27	93.48	90.51	68.00	29.08
February	82.55	90.10	85.71	87.92	92.86	94.89
March	74.92	85.61	91.78	94.00	79.92	51.51
April	83.59	63.18	90.54	50.75	93.94	64.07
May	91.62	92.85	97.74	90.87	88.11	79.13
June	95.98	87.70	98.77	96.07	93.98	78.15
July	97.97	89.36	98.53	86.00	93.42	43.42
August	97.57	95.43	92.24	86.51	62.50	10.63
September	96.42	71.77	96.33	82.24	100	100
October	95.64	65.25	90.97	66.61	60.00	7.57
November	99.01	90.32	91.84	88.23	57.14	18.20

TABLE 3:3:3 The percentage contribution of *Cricotopus sylvestris* to the mean density (D) and biomass (B) of chironomid larvae collected from old reedstems during 1981.

(see Section 3:2). The important role that *Cricotopus sylvestris* plays in determining the basic patterns of the overall density and biomass graphs (Figures 3:2:1 and 3:2:2) can be deduced from Table 3:3:3. The most notable challenges to the predominance of this species occur in Zone 3, particularly in respect of biomass where several relatively low percentage contributions are manifest. In general, percentage contribution values for density are higher than their concomitant counterparts for biomass.

Temporal variation patterns for larval density in *Cricotopus sylvestris* (Figure 3:3:4) are best explicated by reference to Figures 3:3:6 and 3:3:7. Figure 3:3:6 indicates the instar composition of the total monthly *sylvestris* populations; Figure 3:3:7 shows the monthly mean densitities calculated for each instar.

From January to April density is comparatively low in all three zones. In January, almost 98% of the population is made up of second and third instars in a ratio of just over 2:1; a small number of fourth instars is also present. During February, third instars develop from the seconds with a consequent drop in the constituent percentage of the latter group. The percentage value for fourth instars rises but remains at a lower level than those for the other instar categories represented in this month. The rise or fall in the percentage contribution of each instar is accompanied by a similarly directed change in actual density.

By the end of March all second instars have evolved to a later developmental stage and many third instars have become fourths, the latter group comprising about 72% of the population at this time of the year. Although the percentage contribution of third instars drops, their mean density shows a noticeable increase.

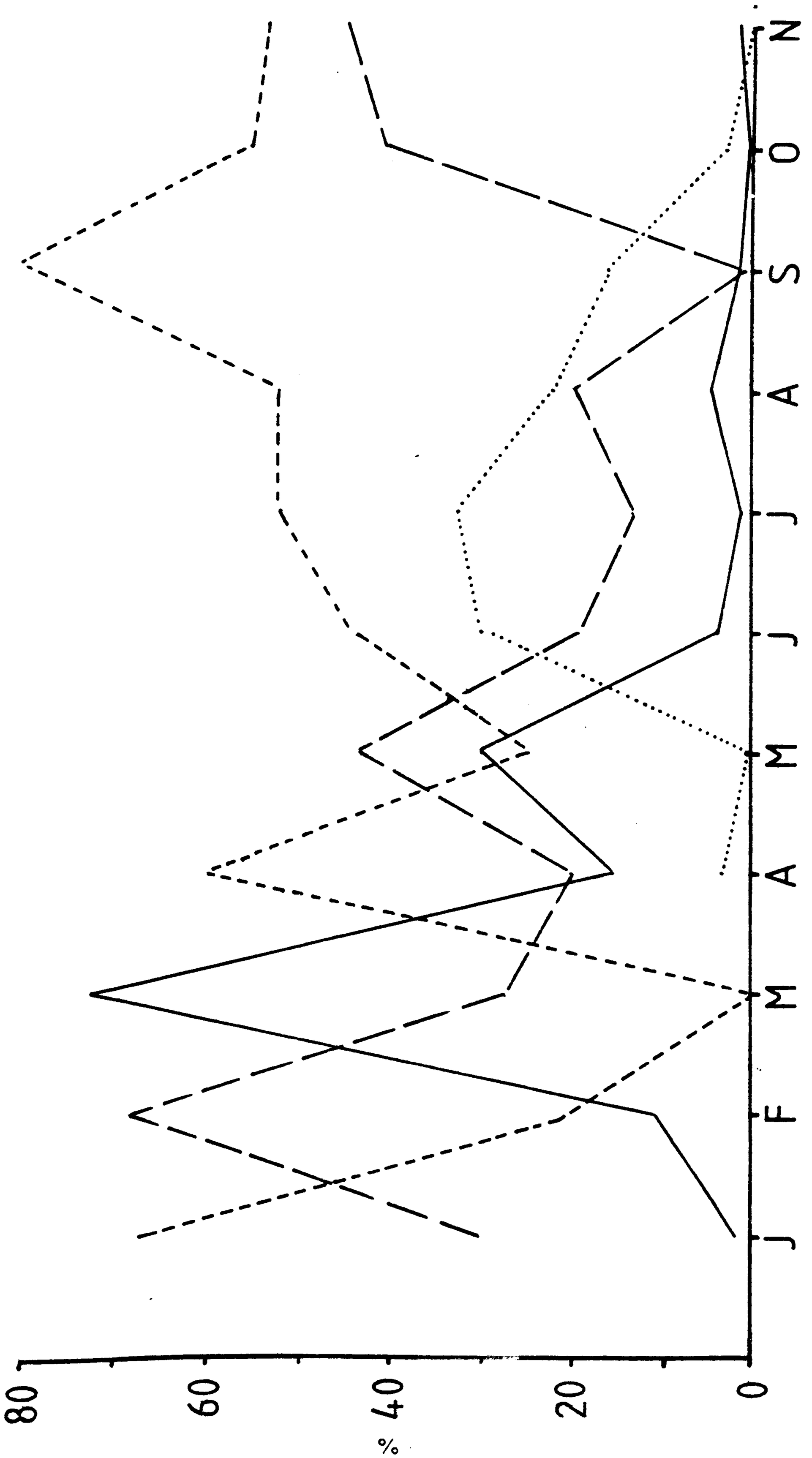


FIGURE 3:3:6 Monthly relative abundance values for 1st instar (——), 2nd instar (----), 3rd instar (— —), and 4th instar (——) *Cricotopus sylvestris* larvae found on old reedstems during 1981.

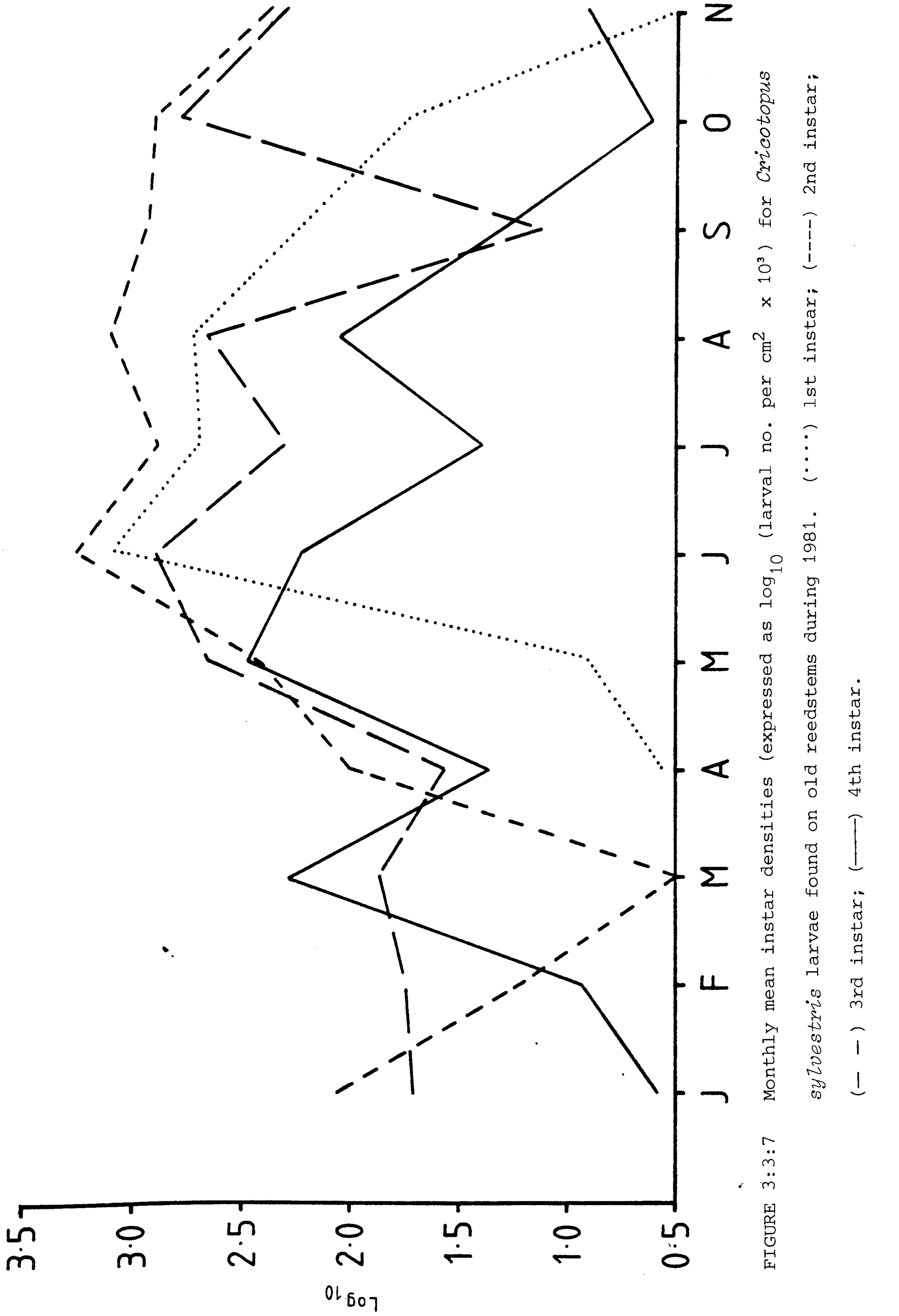


FIGURE 3:3:7 Monthly mean instar densities (expressed as $\log_{10}$ (larval no. per cm^2 x 10^3) for *Cricotopus sylvestris* larvae found on old reedstems during 1981. (····) 1st instar; (----) 2nd instar; (— —) 3rd instar; (——) 4th instar.

In April, the density and percentage contribution of fourth instars is diminished by the onset of emergence. Eggs laid by newly-emerged adults initially give rise to first instars, many of which subsequently progress to the second instar stage before the end of the month. The highest density and percentage contribution occurs with respect to the second instar larvae.

The overall mean density of *Cricotopus sylvestris* larvae increases markedly in May; each of the component instar densities exhibits a similar rise. Percentage values for first and second instars drop, however, as many of these larvae progressively develop to thirds and fourths, which command a proportionately larger share of May's total *sylvestris* population.

Emergence and consequent egg-laying occur at a greater level in June than at any previous time, resulting in a fall in the proportion of third and fourth instars and a sharp increase in the numbers and percentage values of firsts and seconds. The numerical increase in these latter instars accounts for most of the large rise in the overall mean density in this month.

Figure 3:3:4 indicates a drop in overall mean density during July. All four instars show a decrease in numbers, whilst their percentage contributions show comparatively little deviation from those recorded at the end of June. The fall in overall mean density suggests that the loss of larval numbers through emergence is of a greater magnitude than any gain emanating from the appearance of newly-hatched first instars.

The patterns of emergence and larval population variation in August do not appear to share the same degree of rational synchronisation as found previously: the density increase that occurs in all four instars is greatest in the third and fourths, even though it is these latter groups which might be expected to show a reduction in numbers due to the high level of emergence sustained for most of the month. The faster rate of

larval development that exists at this time of the year may be indirectly responsible for this apparent paradox: a rapid build-up of third and fourth instars could take place in the short time following the period of high emergence levels; if such a build-up were to be of sufficient size, it would effect the upward trend in density that occurs with respect to these instars in August.

Relatively stable percentage contributions over July and August, and uninterrupted high-level emergence throughout most of this period points to a larval population where a breakdown in the synchronistic development of individuals at one or more stages in the life-cycle has led to an overlap of generations, in so much as newly-hatched larvae join a pre-existing population of first instars. In this situation, instar relative abundance shows limited variation because the transition of larvae from any particular developmental stage to the next will always be compensated by recruitment from the preceding stage.

During September, overall mean density decreases as larval losses through emergence outnumber gains arising from egg-laying. This is reflected in a steeper fall in third and fourth instar densities than first and second instar densities. Although second instars diminish in numbers, their relative abundance increases due to the synergic effects of loss of higher instars through emergence and substantial recruitment from a first instar population whose replenishment through egg-laying has been considerably reduced.

By the end of October the vast majority of the larval population is made up of second and third instars; fourths are scarce whilst many firsts have progressed to a higher stage. No egg-laying occurs in October, as evidenced by a lack of emergence in this month, so the first instar individuals taken at the end of the month must have been present at the beginning, indicating a decline in the rate of larval development at this time of the year. The reason for the overall rise in larval numbers

during October is not readily apparent; chance variation may be an important factor here.

First instar larvae disappear during November; in this month the population contains a few fourth instars but is principally composed of seconds and thirds in subequal proportions. The evident drop in overall mean density must be attributable to a factor or factors other than emergence because this ceases at the beginning of October. The pattern of instar relative abundance in November resembles that found at the start of the year, which suggests the existence of characteristic seasonal trends in this respect.

Figures 3:3:8a, b, c, and d, indicate the percentage contribution each instar makes to the total mean density of the *sylvestris* population in each zone.

The first instar graph-lines for Zones 1, 2, and 3 exhibit a fair degree of mutual congruity with no one zone commanding the highest values for relative abundance throughout the year. A wide value range does occur in August, however, where first instars account for just over 20% of the larval numbers in each of Zones 1 and 2, but are not represented at all in Zone 3. The very small number (5) of larvae found in Zone 3 means the possibility of an instar being absent through chance is high.

The graph-lines for second and third instars display similar properties of congruity and intertwinement to those for first instars. From this it can be inferred that the relative abundance of each of these three instars shows essential spatial uniformity across the reedbed at any point in time and that, for each instar, the changes in its percentage contributions from month to month show a high degree of interzonal similarity.

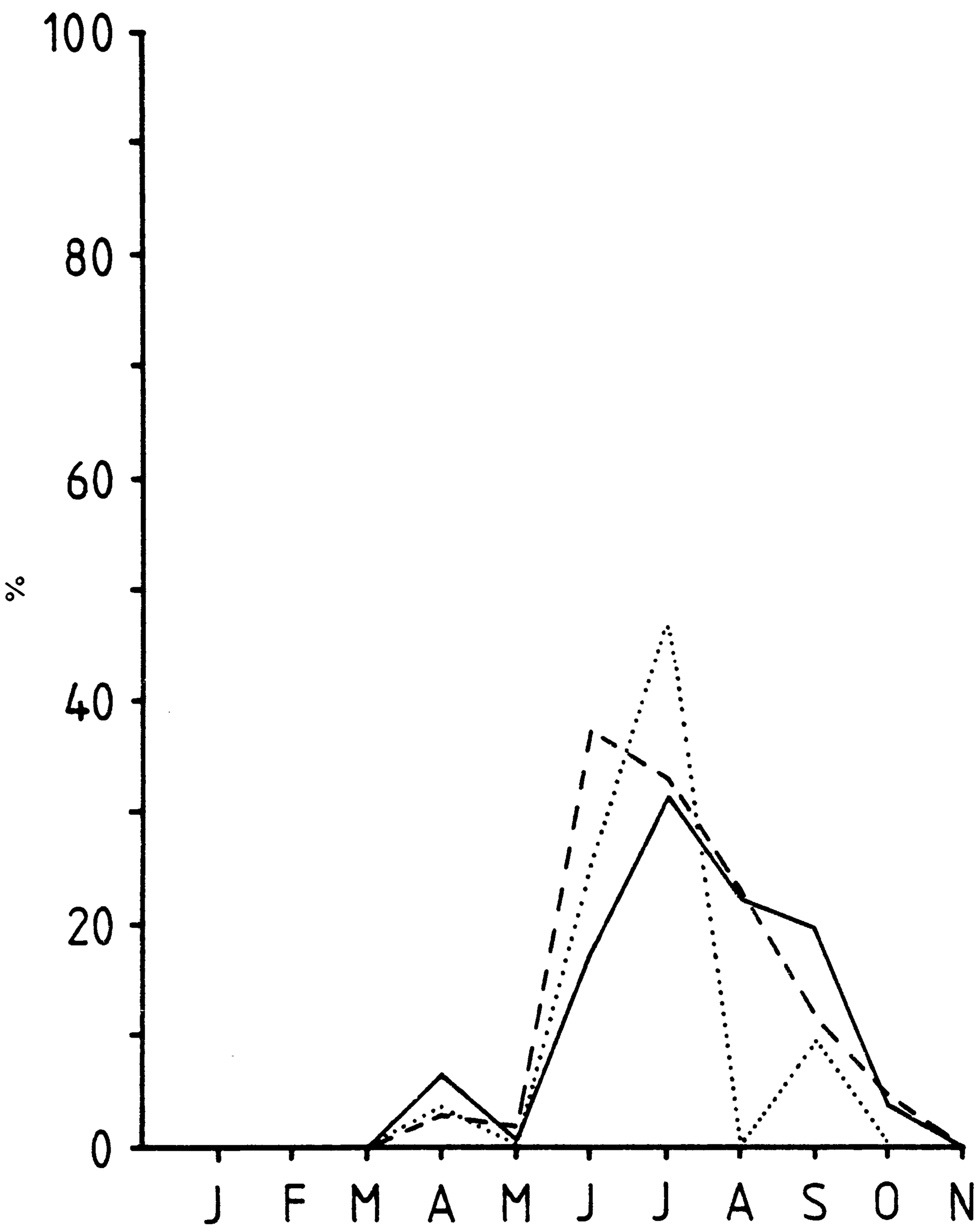


FIGURE 3:3:8a Percentage contribution of 1st instar larvae to the total monthly *Cricotopus sylvestris* population found on old reedstems in each of Zones 1 (——), 2 (---), and 3 (....) during 1981.

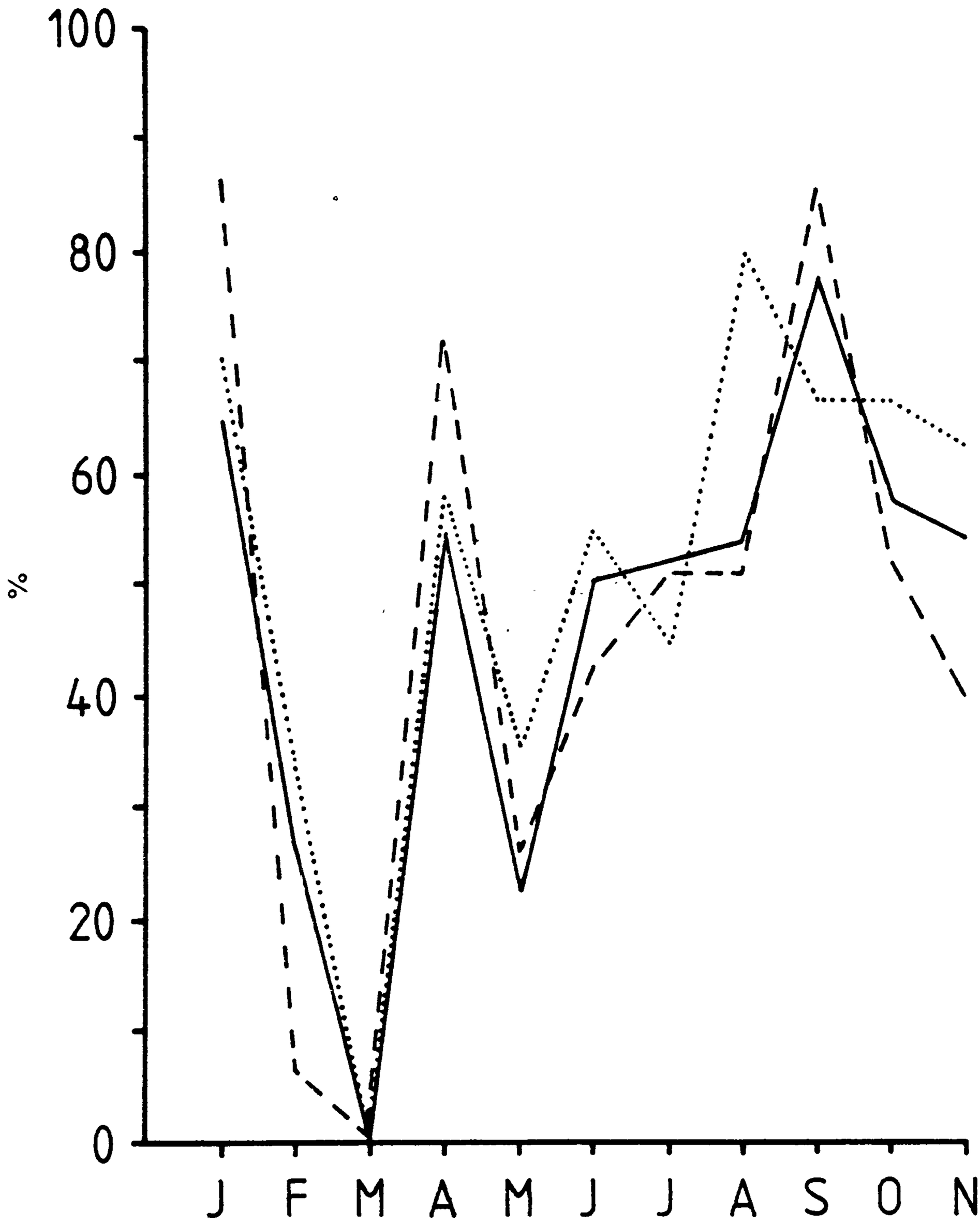


FIGURE 3:3:8b Percentage contribution of 2nd instar larvae to the total monthly *Cricotopus sylvestris* population found on old reedstems in each of Zones 1 (———), 2 (---), and 3 (····) during 1981.

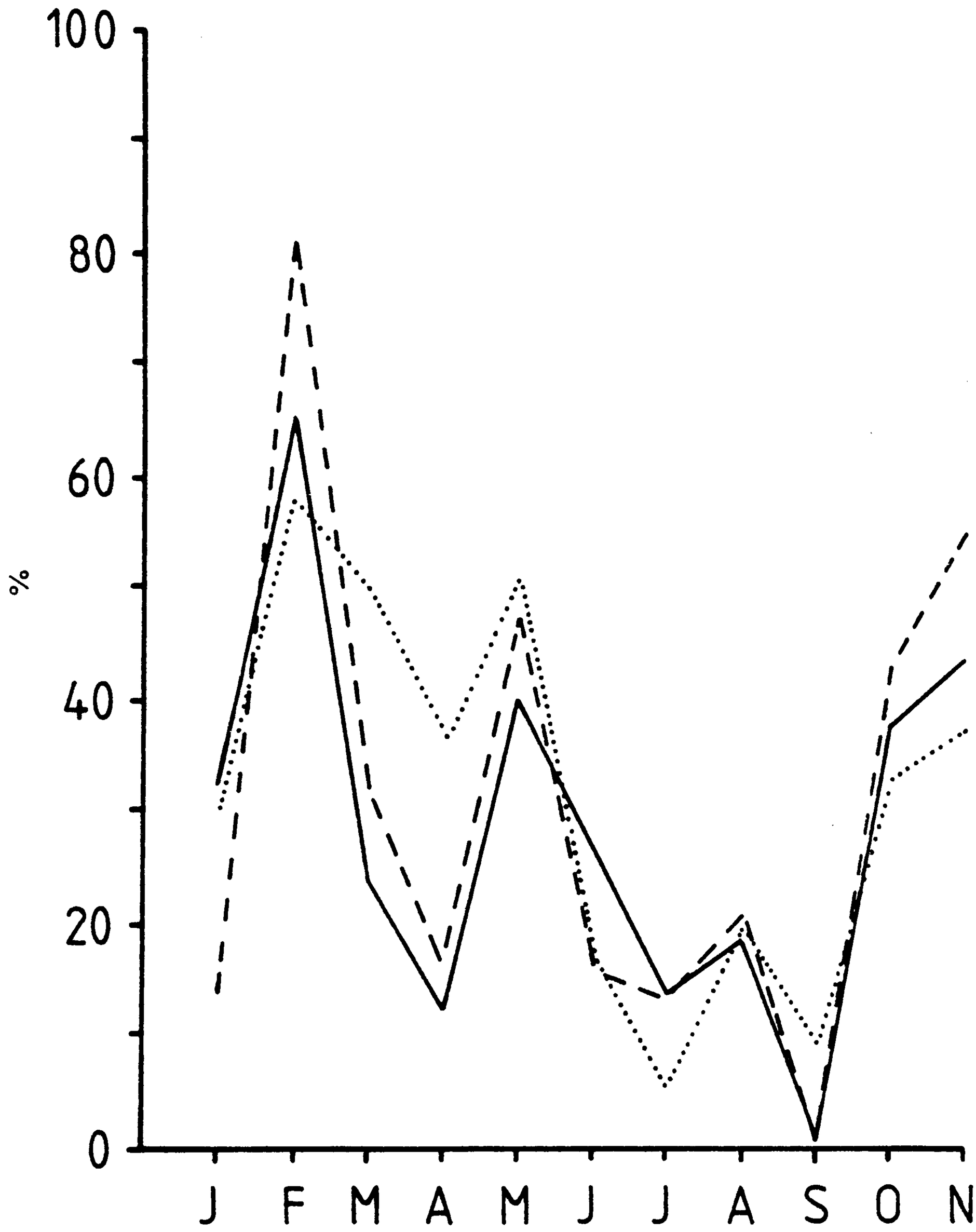


FIGURE 3:3:8c Percentage contribution of 3rd instar larvae to the total monthly *Cricotopus sylvestris* population found on old reedstems in each of Zones 1 (———), 2 (---), and 3 (····) during 1981.

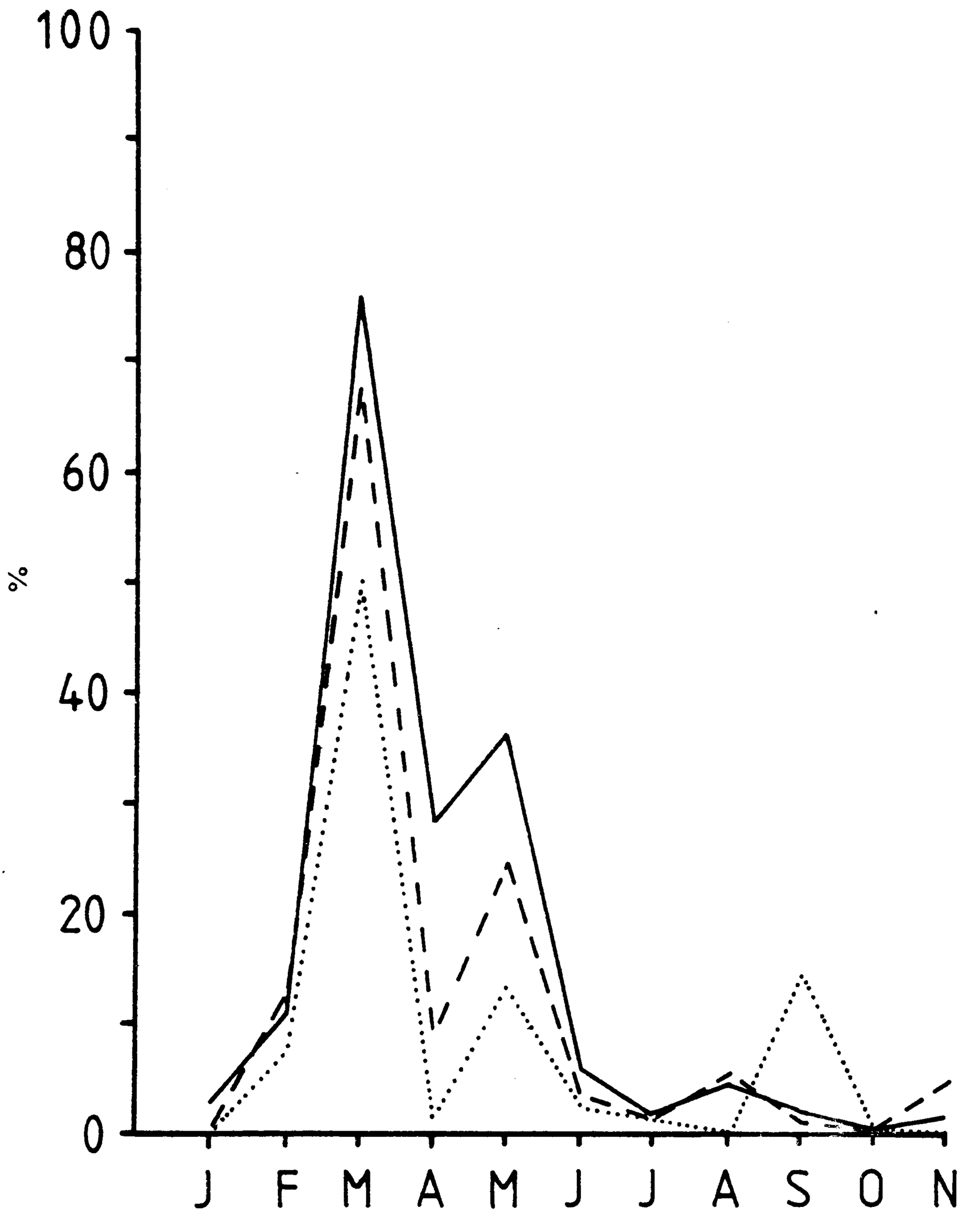


FIGURE 3:3:8d Percentage contribution of 4th instar larvae to the total monthly *Cricotopus sylvestris* population found on old reedstems in each of Zones 1 (———), 2 (---), and 3 (····) during 1981.

The patterns of fourth instar relative abundance differ in one basic aspect from those described above. Whilst temporal variation is essentially similar in all three zones, in ten out of eleven months (the exception being September) fourth instars account for a higher percentage of the *sylvestris* population in each of Zones 1 and 2 than in Zone 3. The consistent repetition of this situation suggests that it is not a product of chance.

In any interpretation of the biomass graph for *Cricotopus sylvestris* (Figure 3:3:5) the comparative mean weight of an individual in each instar category must be taken into consideration. Table 3:3:4 provides data relevant in this respect. (See Appendix E for sources.)

Instar	W	%	N
1	0.005		40
2	0.010	100.0	20
3	0.034	237.5	6
4	0.200	492.6	1

TABLE 3:3:4 - Mean dry weight (mg) (W) of one *Cricotopus sylvestris* larva in each instar category, the percentage increase in dry weight found in each instar in relation to the preceding stage, and, for each instar, the number (N) of larvae required to provide a weight equal to that of one fourth instar individual.

A comparison of Figures 3:3:4 and 3:3:5 reveals that biomass and density generally rise and fall in synchrony, although exceptions do occur. The comparative magnitude of concomitant peaks is dependent on the instar make-up of the population at the time.

During March, in Zones 1 and 2, both density and biomass rise but the increase in biomass is proportionately much larger. This is a reflection of the marked increase in fourth instar numbers at the expense of second instars as larval development proceeds - a pattern common to all three zones.

In Zone 1, biomass attains its maximum in May - a month in which the larval density for each instar rises, with the collective percentage density contribution of third and fourth instars jumping from 36 to 74%. These latter larvae account for 97% of the total *sylvestris* biomass in May.

During June, larval numbers continue to rise in Zone 1 but biomass falls substantially, a situation attributable to an upsurge in the quantity of first and second instars coupled with a concurrent decline in fourth instar density.

The next peaks of density and biomass in Zone 1 occur synchronously in August when all four instars show an increase in numbers and the relative abundance of third and fourths together goes up from 15 to 25% with a biomass contribution of 72%.

October rises in Zone 1 density and biomass are due to a proliferation of third instars which offsets both relative stability in the amount of seconds present over the month and a considerable drop in first and fourth instar numbers.

In November, the increase in fourth instar density in Zone 1 is not sufficient to compensate for biomass loss resulting from decreasing numbers in the other instar stages and an overall drop in biomass is therefore found.

The seasonal pattern of biomass distribution in Zone 2 is similar to that in Zone 1 with two exceptions: firstly, concomitant monthly values are generally lower in Zone 2 than Zone 1; secondly, the maximum biomass value for Zone 2 occurs in June whereas it is found in May in Zone 1.

All four instars show density increases in Zone 2 in June but first and second instars experience a disproportionately large rise in numbers which raises their collective biomass percentage contribution from 4 to 33%. This contrasts with the situation in Zone 1 where overall density rises but biomass falls, the latter being due to a sharp drop in the quantity of fourth instars.

The peak of biomass in Zone 3 in May punctuates an otherwise relatively even graph-line which portrays consistently low values. Temporal differences in population instar composition account for the lack of synchronisation between maximum biomass and maximum density.

ii) *Psectrocladius* (see Figure 3:3:9)

Adult emergence data affirmed the conclusion drawn from larval identification that the one species present was *Psectrocladius limbatellus* (Holmgren).

Juveniles appear from April to July, attaining a maximum density in June. This shows good agreement with information obtained from emergence trapping: adults were caught between May and August inclusive, with the peak of emergence in July. The temporal restriction of larvae to the April-July period raises the question of their whereabouts during the remainder of the year. Imagines do not appear until late May so it does not seem feasible that larvae found in April are derived from newly-laid eggs, especially as this larval population consists exclusively of third and fourth instars. Firsts and seconds occur only after emergence has proceeded. It would be expected that any presence of reedstem-dwelling larvae from January to April would be revealed through sampling: several genera with April densities similar to *Psectrocladius* were detected earlier in the year, in even lower numbers.

Although *Psectrocladius* larvae were not found in the samples taken at the end of August, emergence data indicate their presence during most of this month after which they disappear somewhat abruptly.

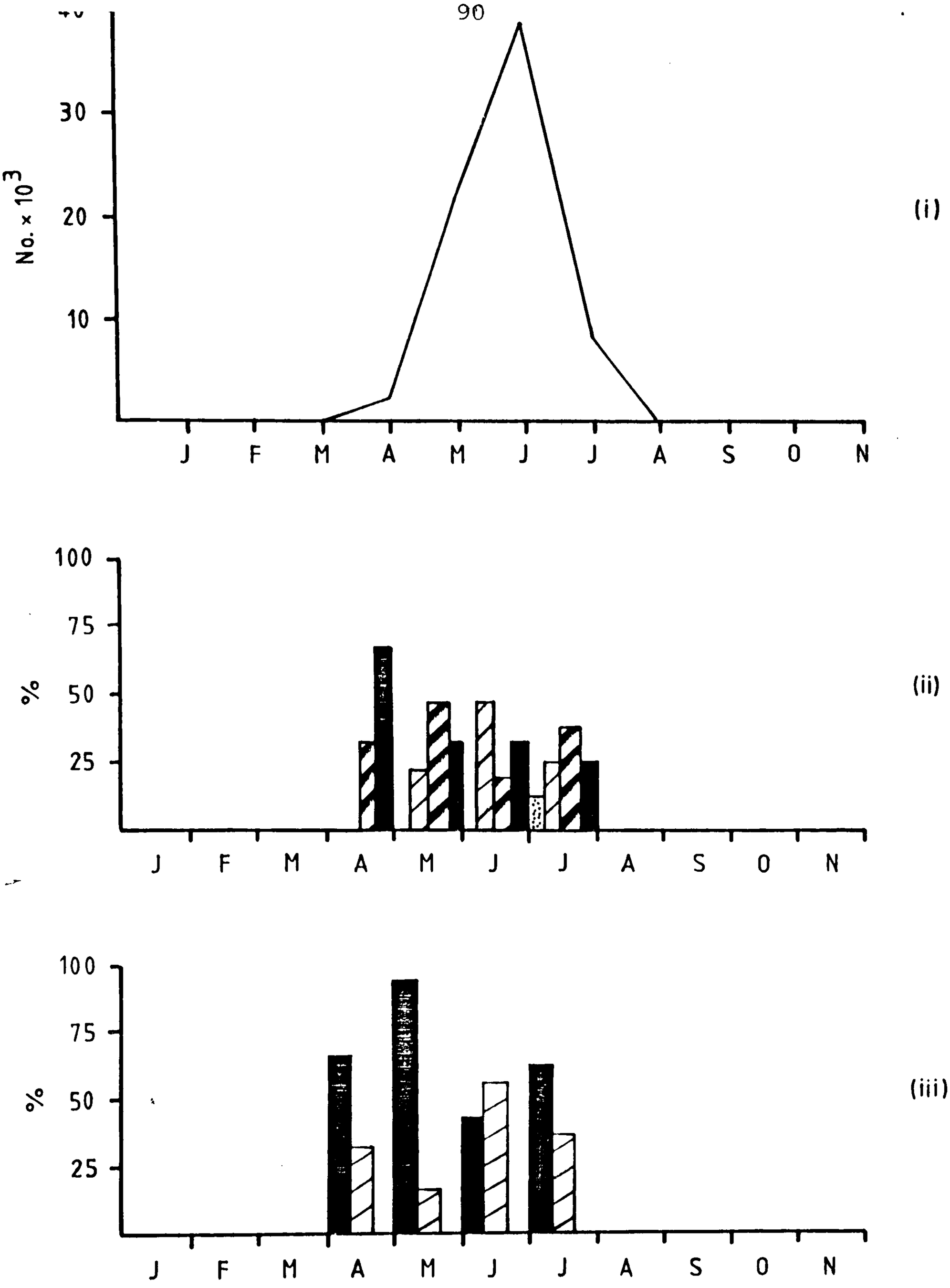


FIGURE 3:3:9 - Population data for *Psectrocladius limbatellus* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd; ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *limbatellus* population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

From the evidence put forward above it can be inferred that *Psectrocladius* spends the autumn and winter in a habitat other than that examined in the course of the reedstem sampling programme.

On a zonal basis *Psectrocladius* larvae are confined to Zones 1 and 2, the greatest densities tending to occur in the former area. Larvae are not restricted to the reedbed habitat, however: open-water vegetation samples taken in June and July contained a larval population of which *Psectrocladius* accounted for 26% and almost 43% of the *Psectrocladius* adults caught during 1981 were found in a trap set several metres out from the reedbed.

Langton (1981) reports that *limbatellus* is found in 'large, deep bodies of stagnant water'. If it were characteristically an open-water species, this would offer a credible explanation regarding its spatial and temporal distribution patterns in the reedbed. Such an explanation follows.

Larvae overwinter in an open-water habitat and move onto reedstems in April, when epiphyton constitutes a valuable food source. Algal mats and submerged macrophytes build up towards the end of May, at which time the first adults appear. Eggs are laid solely amongst this vegetation and many of the resulting larvae develop and emerge off-shore; some colonise reedstems in the two zones in closest proximity to open water (Zones 1 and 2). The penetration of algal mats into the frontal fringe of the reedbed facilitates this colonisation. During August, off-shore vegetation disappears; thus, the 'bridge' between open water and the reedbed is lost. Consequently, larvae hatching out at this time are likely to remain off-shore where they subsequently spend the winter.

iii) *Thienemanniella* (see Figure 3:3:10)

The keys available for the larvae of *Thienemanniella* species are incomplete and, in some respects, contradictory. Thus, a definitive identification of the one species present was not possible. Adults were

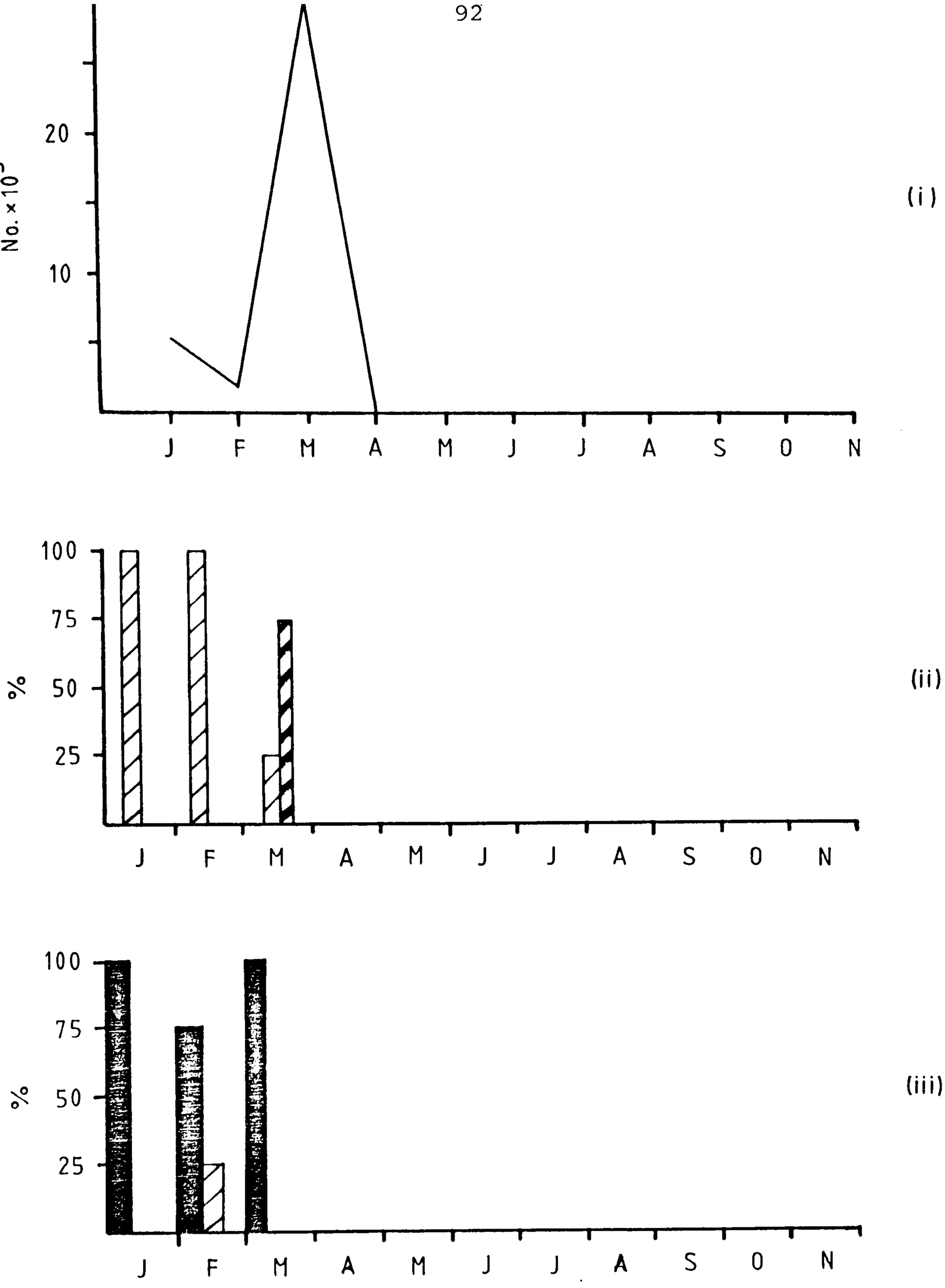


FIGURE 3:3:10 - Population data for *Thienemanniella* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd; ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *Thienemanniella* population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

represented by three individuals caught in emergence traps in May. These were identified as *Thienemanniella majuscula* (Edwards) but this offers no conclusive proof of the larval species.

Thienemanniella occurs exclusively from January to March, reaching its maximum density in the latter month. The majority of larvae are found in Zone 1, the remainder existing in Zone 2. During January and February, all larvae are at the second instar stage; in March the population is split between thirds and seconds in a ratio of 3:1.

Thienemanniella may seek to overwinter on reedstems if this habitat provides suitable environmental conditions. Alternatively, larvae may be involuntarily carried into the reedbed during the winter, when harsher weather leads to much water agitation which could displace them from their original abode. Environmental conditions change in spring and this may prompt *Thienemanniella's* disassociation from the reedbed habitat in April.

The exclusive occurrence of *Thienemanniella* in Zones 1 and 2 could be a reflection of the penetrative capacity of larvae entering the reedbed from open water: as these two zones are nearer open water than is Zone 3, they will be colonised first and may well accommodate all the larvae before Zone 3 is reached. This is supported by the fact that 90% of *Thienemanniella* larvae live in Zone 1, which runs along the front of the reedbed.

iv) *Rheocricotopus* (see Figure 3:3:11)

All larvae were positively identified as *Rheocricotopus fuscipes* (Kieffer) using Cranston's (1982) key. No emergence was recorded for this species, or any other in the same genus.

Like *Thienemanniella*, *Rheocricotopus fuscipes* is confined to the first three months of the year and attains its greatest density in March. Ninety per cent of all larvae were collected from Zone 1, the remaining 10% occupying Zones 2 and 3. Second, third, and fourth instars

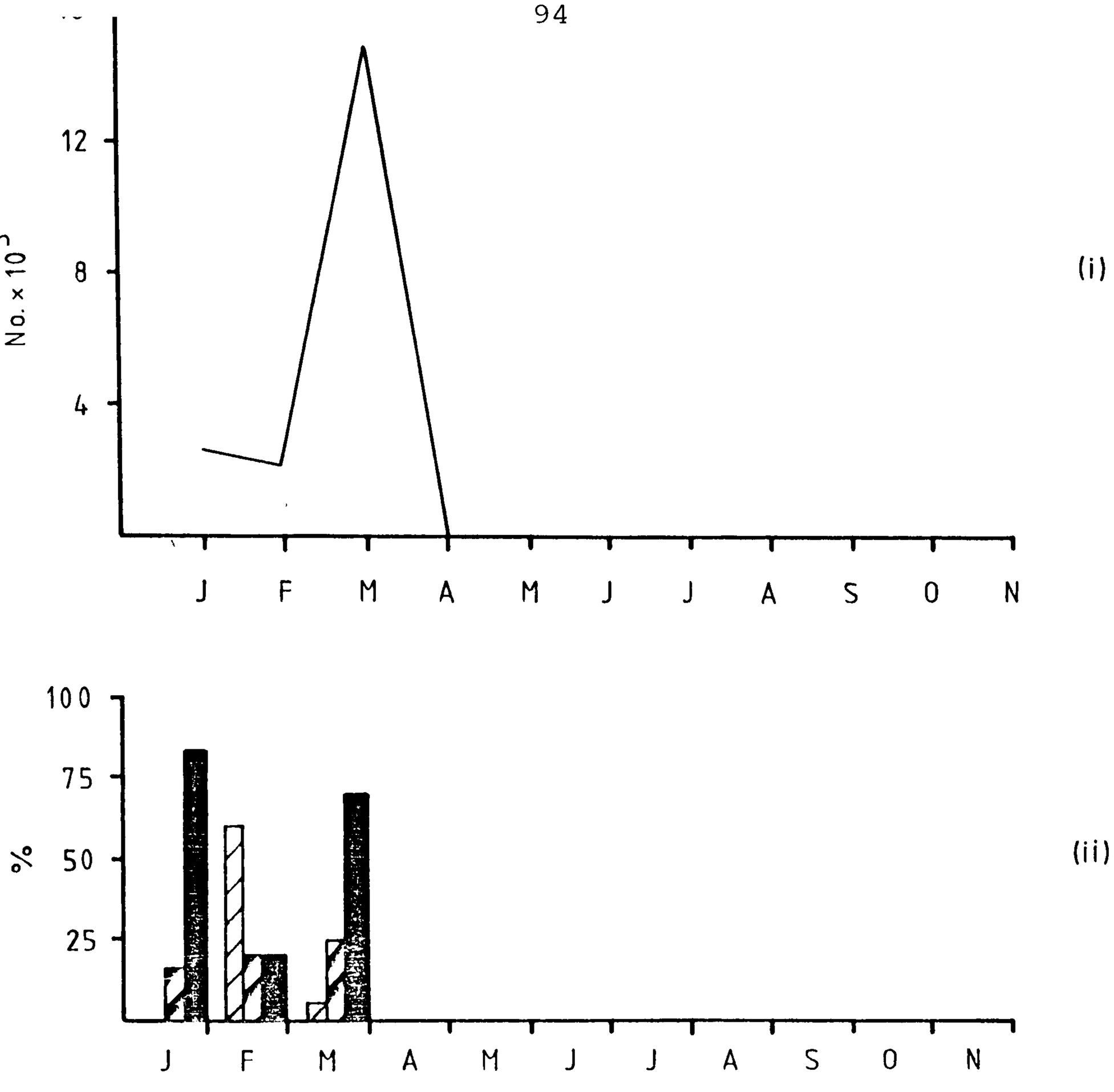


FIGURE 3:3:11 - Population data for *Rheocricotopus* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd; ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *Rheocricotopus* population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

make up 12, 23, and 64% of the overall population respectively.

The explanatory hypotheses propounded with respect to the temporal and spatial distribution patterns of *Thienemanniella* are equally applicable to *Rheocricotopus*.

v) *Metriocnemus* (see Figure 3:3:12)

The lack of a reliable species key for larval *Metriocnemus* frustrated attempts to identify the three species found, which are consequently described as species A, C, and E. (Species B and D were not found on reedstems; they occur elsewhere in the reedbed.)

Three species of *Metriocnemus* were caught in emergence traps: *atratulus* (Zetterstedt), *hirticollis* (Staeger), and *tristellus* (Edwards). A comparison of population patterns for adults and juveniles from the area of permanent standing water alone was of little deterministic value as far as larval species identification was concerned. Samples taken from the semi-terrestrial section of the reedbed yielded some valuable supplementary information, however. Four species of *Metriocnemus* inhabit this area; *Metriocnemus* sp. A accounts for 72% of the larvae found which belong to the genus. Records from adult trapping suggest sp. A and *hirticollis* are synonymous.

Bryce and Hobart (1972) provided a diagnostic key for the larvae of some *Metriocnemus* species. The validity of this key has since been questioned but it does give a strong indication that sp. C is synonymous with *atratulus*.

Metriocnemus sp. A and sp. E are uncommon on reedstems. The former species is represented by only three individuals, which were collected from Zone 1 in February, March, and June (one larva in each month). The latter is also represented by three individuals; these were taken from Zone 3 in February, May and June (again, one larva in each month).

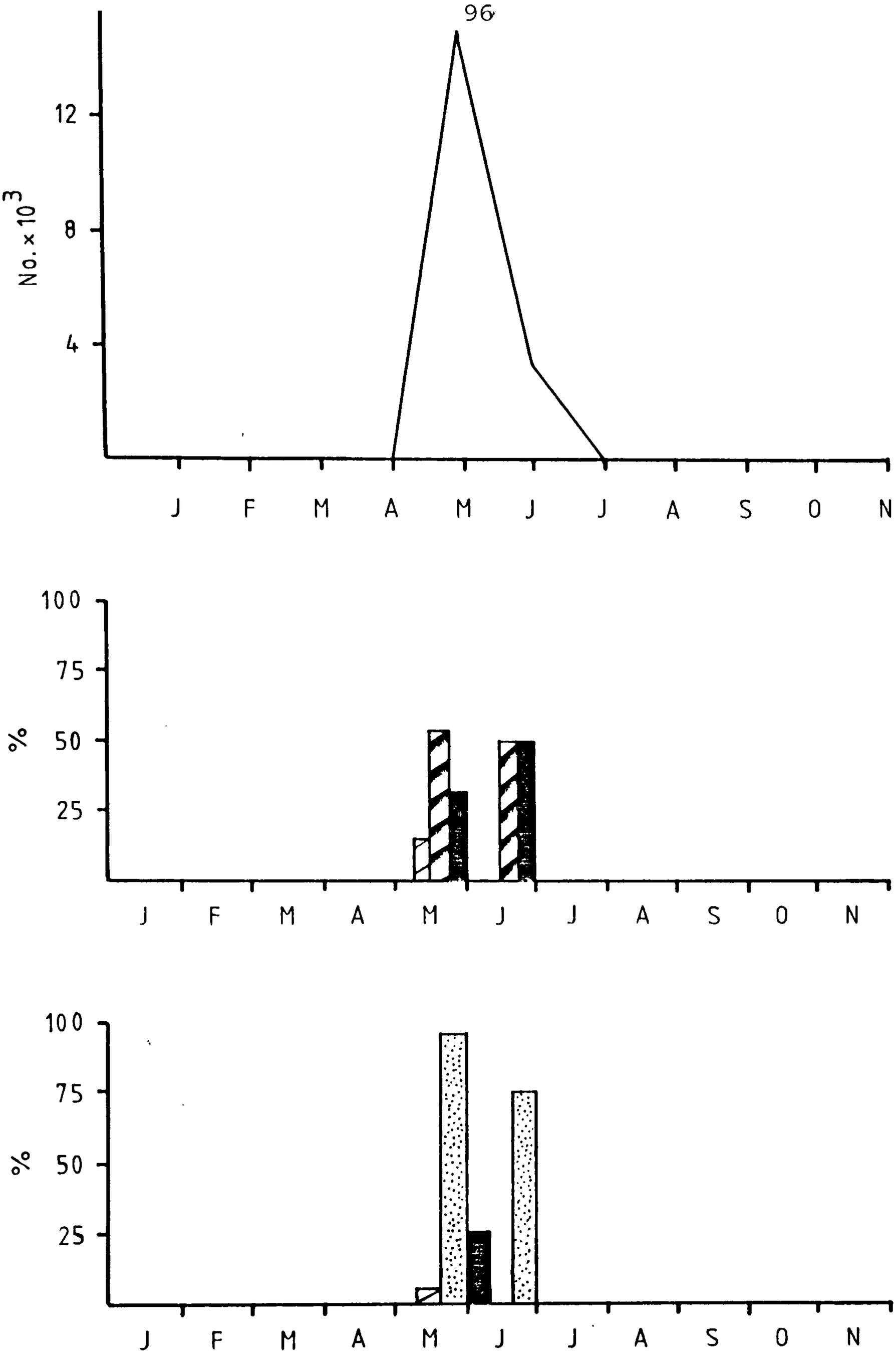


FIGURE 3:3:12 - Population data for *Metriocnemus* sp. C larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd; ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *Metriocnemus* sp. C population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

Metriocnemus sp. C is found during May and June, mainly in Zone 3 but also in Zones 1 and 2. The population is principally composed of third and fourth instars although some seconds do occur in the earlier month. The tendency to occupy Zone 3 could be a reflection of this zones adjacency to the semi-terrestrial part of the reedbed: if this latter area is the preferred habitat of the species, chance dispersion may result in some larvae entering the aquatic zone of closest proximity (Zone 3) and a smaller number reaching Zones 1 and 2. This constitutes a similar diffusion process to that suggested for *Psectrocladius* except that it operates in the reverse direction (from the back to the front of the reedbed rather than from the front to the back).

vi) *Corynoneura*

Two species were recovered from emergence traps: *carriana* (Edwards) and *edwardsi* (Brundin). Both are found in July and August.

Most of the twelve larvae collected in reedstem samples occur in May, June, and July, and almost certainly belong to one or both of the species mentioned above. (These two species are not included in Cranston's (1982) key to *Corynoneura* larvae.) The presence of an individual in January is indicative of *Corynoneura* being a resident genus in the reedbed. Intermittency in temporal occurrence may be a reflection of a failure to detect the existence of a very small larval population in some months, a problem exacerbated by the minuteness of many *Corynoneura* juveniles.

Of the twelve larvae collected, six were taken from Zone 1 and three from each of Zones 2 and 3. The small number of individuals involved means an assessment of the characteristic nature of zonal distribution in *Corynoneura* cannot be made with any great confidence.

vii) *Diplocladius*

This genus is represented by a single species (*Diplocladius cultriger* (Kieffer)) in Britain. Adults were not recorded at Cop Mere.

Of the five larvae collected, three were taken in February (two in Zone 1 and one in Zone 2) and two in March (both in Zone 2). It is possible that the appearance of *Diplocladius* at this time of year is governed by the same factors as that of *Thienemanniella* and *Rheocricotopus*. Instar status is indeterminable but the larvae fall into two size categories.

viii) *Orthocladius*

This is the rarest Orthocladiinae genus to be recovered from reedstem samples. Only two specimens were collected: one in January and one in February. Both were taken from Zone 1 as fourth instars and belong to a species that was not identified. The larvae of this chironomid can be classified as 'winter visitors' along with those of *Thienemanniella*, *Rheocricotopus*, and *Diplocladius*.

D) INDIVIDUAL PATTERNS OF ABUNDANCE AND DISPERSION - CHIRONOMINAE

i) *Glyptotendipes* (see Figure 3:3:13)

Laboratory rearing of larvae, and data from emergence trapping positively identified the one species present as *Glyptotendipes pallens* (Meigen).

Glyptotendipes pallens accounts for just over 53% of larvae belonging to the Chironominae and nearly 2% of the total population of larval chironomids. Occurring continuously throughout the year, it reaches its highest density levels in August and October; numbers are considerably lower in the other months.

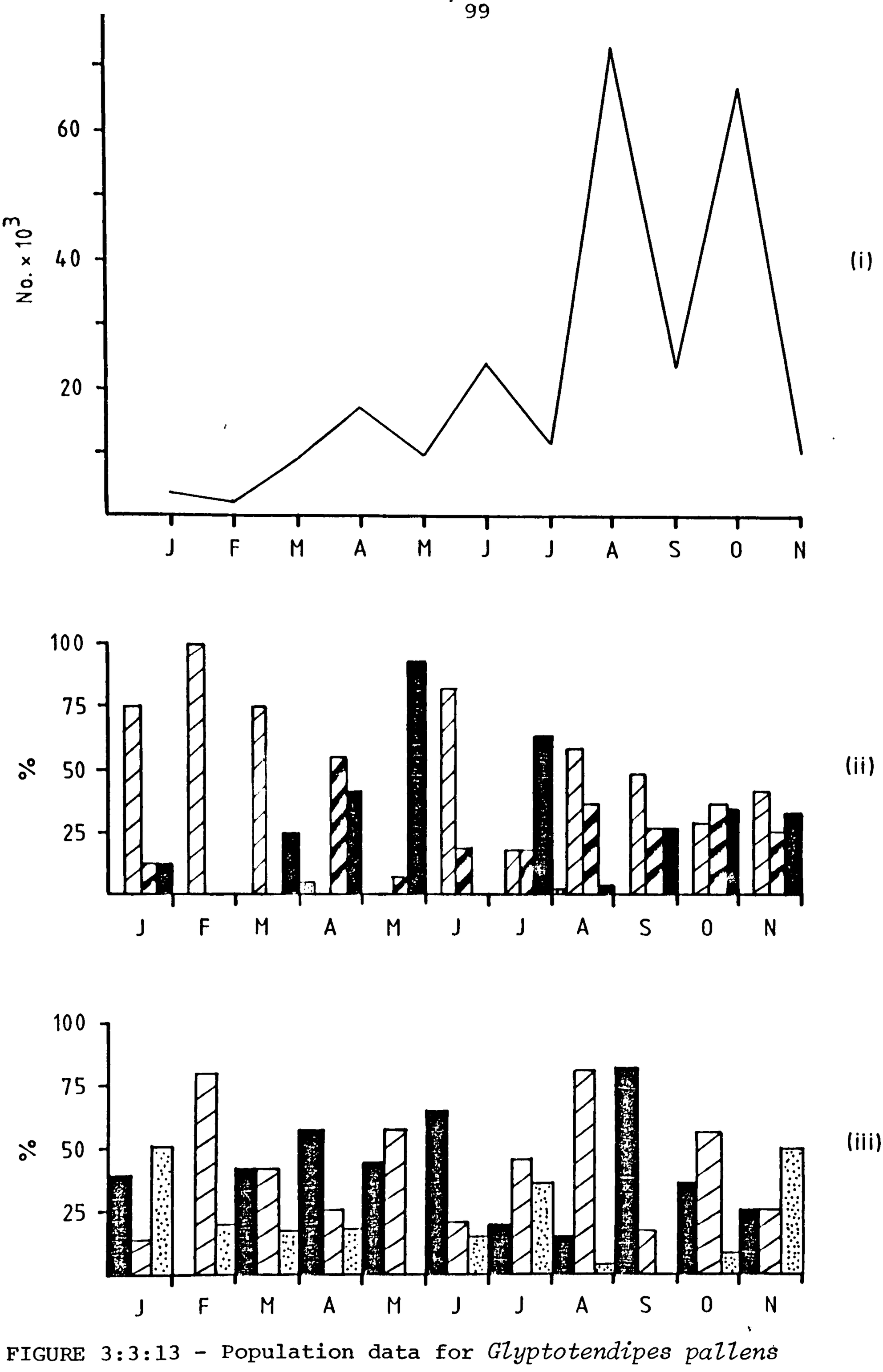


FIGURE 3:3:13 - Population data for *Glyptotendipes pallens* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (1st; 2nd; 3rd; 4th)

(iii) Percentage of each month's total *pallens* population found in Zone 1 ( ), Zone 2 ( ), and

Many third instar *Glyptotendipes* larvae, and the majority of fourths, dwell inside the cavity at the top of broken reedstems. This micro-habitat is not exploitable on all broken reedstems, however, which means that some temporal variation in the number of third, and particularly fourth, instars probably results from month to month differences in the number of sample-stems that offer a suitable dwelling-place for cavity-occupying larvae.

Second, third, and fourth instars are found during the winter with no category exhibiting a clear numerical dominance. The absence of third and fourth instars in February is very likely to be a manifestation of the situation described in the preceeding paragraph. Larval development in the spring increases the relative abundance of fourth instars, which subsequently emerge as adults from mid-May to mid-June. Flies may be airborne in April, however, as is the case in the following year when they appear on wing before any are caught in emergence traps. Egg-laying in April would account for the first instar presence at the end of this month.

Between mid-June and mid-July no emergence is apparent. Larvae hatched from eggs laid before this period develop through successive stages to give a relatively high fourth instar population towards the end of July, when emergence recommences. Egg-laying in August, as evidenced by first instar appearance, produces the greatest larval density for the year in this month with second and third instars exhibiting strong co-dominance in relation to firsts and fourths.

Emergence continues through most of September and appears to deplete larval numbers in this month. A late period of egg-laying activity at the end of September may account for the sharp rise in larval density during October.

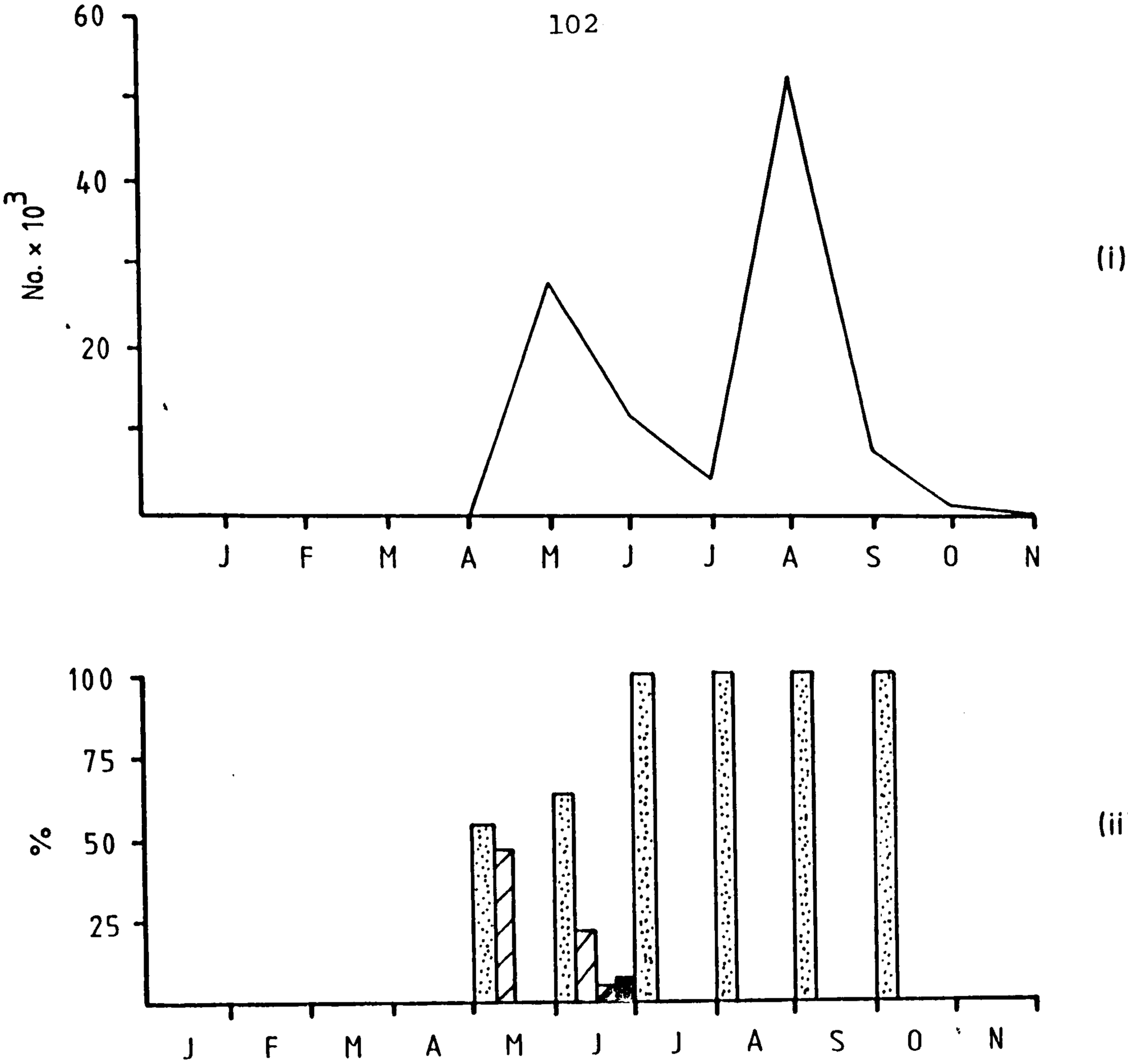
Interpretation of the population graphs for reedstem-inhabiting *Glyptotendipes* larvae is complicated by the fact that the reedstem habitat is not the only one that this genus readily frequents: *Glyptotendipes pallens* accounts for just over 3% of the benthic-dwelling chironomid larvae collected from the reedbed in 1981. Inter-habitat migration, if such a phenomenon exists, could constitute a determinant of temporal variation in larval density on reedstems. The sharp November drop in reedstem larval density, which occurs well after emergence has ceased, may be due to a movement of individuals away from stems to seek winter sanctuary in the benthic environment.

First instar *Glyptotendipes* are very rare on reedstems, from which it can be deduced that either they are found in greater numbers elsewhere or the transition to the second instar stage occurs after a relatively short period of time. Similarly sized first instar larvae of other species were successfully picked out from stem-samples so it seems unlikely that the scarcity of first instar *Glyptotendipes* larvae principally reflects detection problems.

For the greater part of the year, *Glyptotendipes* shows no evidence of restriction to a particular zone or zones: interzonal variations in population density and instar make-up do not occur in the same pattern from month to month. From August to October, however, when larval density reaches its greatest levels, a wide gap is maintained between the high density values for Zone 1 and/or Zone 2, and the low density values for Zone 3.

ii) *Camptochironomus* (see Figure 3:3:14)

Diagnostic features in the larval stage enabled species determination and all larvae were identified as *Camptochironomus tentans* (Fabricius). Emergence data provides corroborative evidence in this respect.



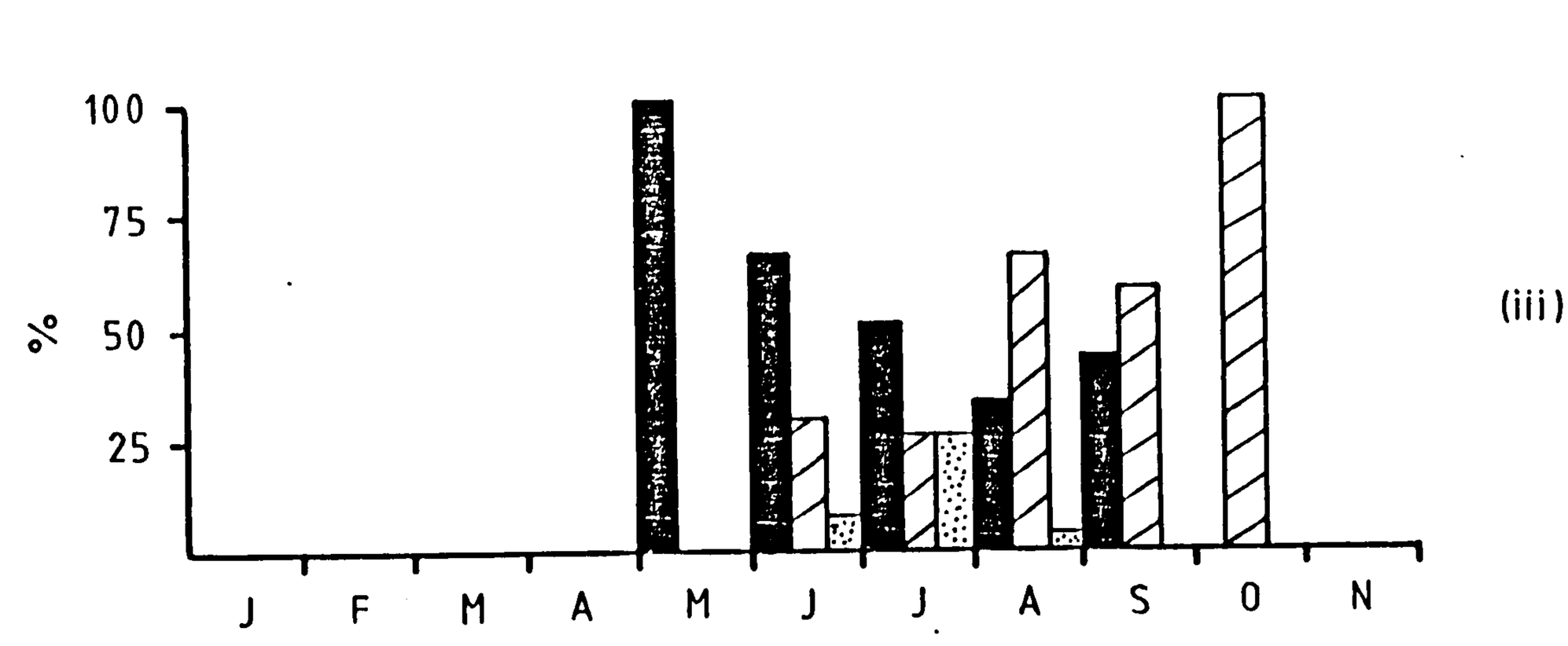


FIGURE 3:3:14 - Population data for *Camptochironomus tentans* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd; ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *tentans* population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

Camptochironomus is unique among the reedstem-dwelling chironomids found at Cop Mere in that it is recognised as essentially a benthic genus; it accounts for 93% of the larvae recovered from benthic core samples in 1981. The instar compositions of the reedstem and benthic populations differ significantly, however, as shown in Table 3:3:5. A high

	C		R	
Instar	No.	%	No.	%
1	1	00.12	101	80.80
2	111	13.59	22	17.60
3	371	45.41	1	00.80
4	334	40.88	1	00.80

TABLE 3:3:5 For each instar stage, the total number and relative abundance of *Camptochironomus tentans* larvae found in benthic cores (C) and on old reedstems (R) during 1981.

percentage of the larvae on stems are first instars; thirds and fourths are very poorly represented. This situation is reversed in core samples where third and fourth instars are co-dominant and first instars are extremely rare. It appears that *Camptochironomus* larvae initially develop on stems and then, as second instars, migrate down to the reedbed floor where they complete their larval development.

The two peaks of reedstem larval density in May and August correspond to periods of high level emergence; greater egg-laying capacity, which is a consequence of a rise in adult numbers, leads to an increased abundance of first instars.

Camptochironomus larvae overwinter as third and fourth instars, so the reedstem population, which is characteristically composed of first and seconds, is absent until emergence has commenced in late April. During

the autumn, larvae disappear from stems as emergence ceases and instar development proceeds.

The majority of stem larvae in each month inhabit either Zone 1 or Zone 2; the lowest numbers are generally found in Zone 3. This pattern is accentuated in the two months (May and August) with the highest larval densities.

iii) *Limnochironomus* (see Figure 3:3:15)

Emergence trap adults were identified as *Limnochironomus nervosus* (Staeger). It is probable that all larvae belong to this species - the population patterns for adults and juveniles display a mutual compatibility.

Limnochironomus is a resident chironomid, with larval representation in all seasons, although not in all months. Low densities in months when larvae are found suggest they may be present at other times but remain undetected because of their sparsity.

Larvae overwinter as third and fourth instars; emergence begins around the middle of May. There is no evidence to indicate that any egg-laying takes place before this time. Therefore, the appearance of a first instar individual in April constitutes a seemingly inexplicable anomaly.

High larval densities occur at the end of August, following the period of maximum emergence. The increase in larval numbers that occurs is attributable to renewed egg-laying activity with the consequent numerical rise in the first instar population.

Fluctuations in the population density after August are not easily interpreted on purely ecological grounds and the possibility that at least some of this variation occurs through chance cannot be discounted.

The zonal dispersion pattern of *Limnochironomus* shows considerable temporal variation but does not contain any recognisable element of non-randomness. Each of the three zones is inhabited for some of the year.

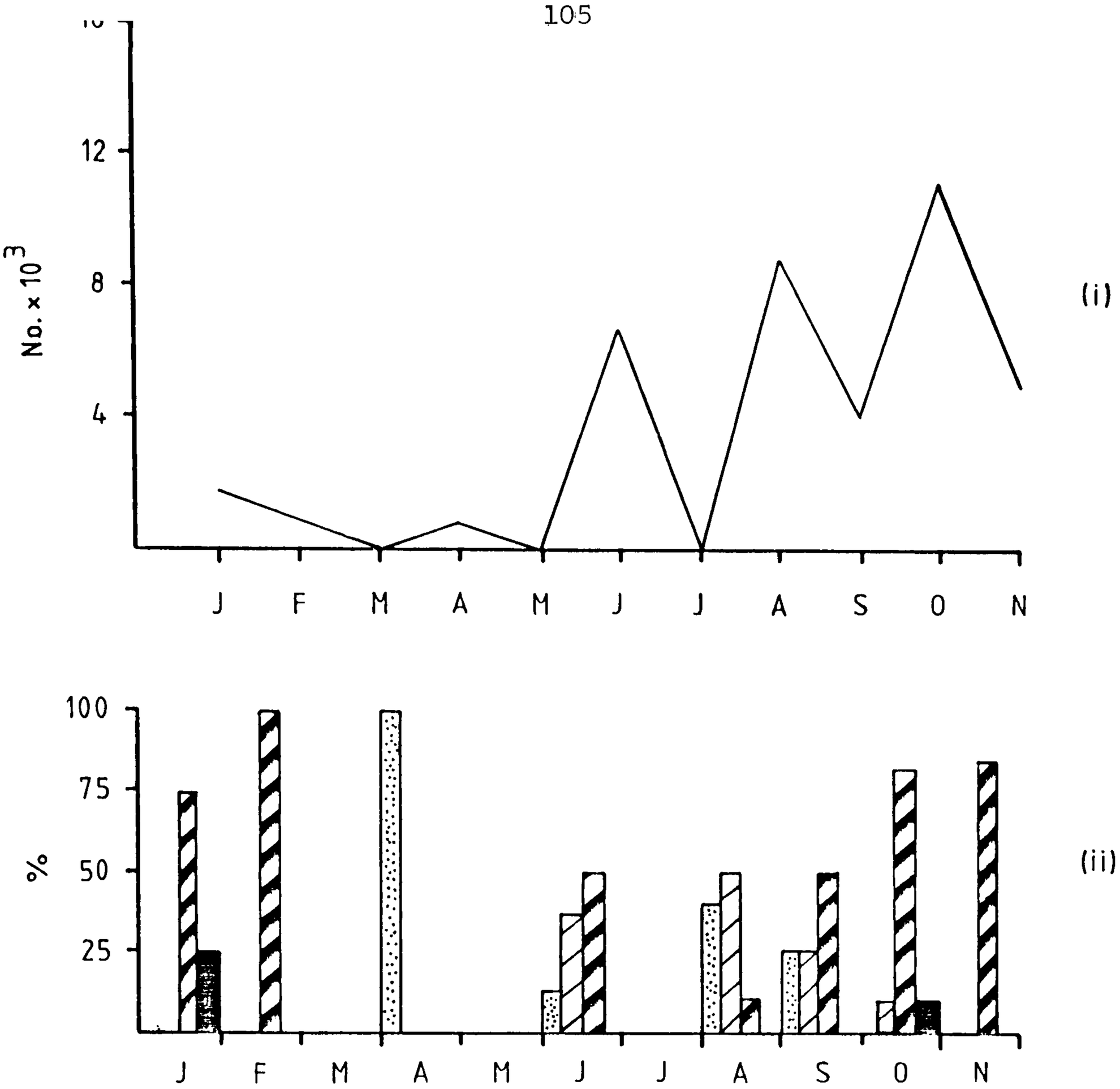


FIGURE 3:3:15 - Population data for *Limnochironomus* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd; ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *Limnochironomus* population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

iv) *Parachironomus* (see Figure 3:3:16)

The members of the monospecific larval population were identified as *Parachironomus arcuatus* Goetghebuer on the basis of a close concordance between larval and adult population patterns. (All *Parachironomus* flies caught in emergence traps belonged to this species.)

Parachironomus arcuatus is atypical of the other Chironominae species considered in this section in that the larvae are not resident all the year round but are restricted to the summer and early autumn (June to October).

Larval appearance on reedstems precedes emergence by several weeks, with first and second instars making up the initial juvenile population in June and July. The presence of these early instars at a comparatively late stage in the year indicates that they have not over-wintered but must be the product of recent egg-laying. The original location of such egg-laying and the larval source of the participating adults are not readily evident.

The first and second instars found in June and July develop into thirds and fourths during August. Emergence commences at the beginning of August and subsequent egg-laying gives rise to the first instars occurring at the end of this month and those that form the total larval populations in September and October. Emergence ceases in mid-September.

The larval density increase in August is attributable to the appearance of a fresh batch of first instars from recently laid eggs; that in October is harder to interpret ecologically and may be a product of chance.

By the end of November all larvae have disappeared and their fate is not known.

Parachironomus only inhabits Zones 1 and 2; in most months both zones are occupied with the highest density occurring in Zone 2.

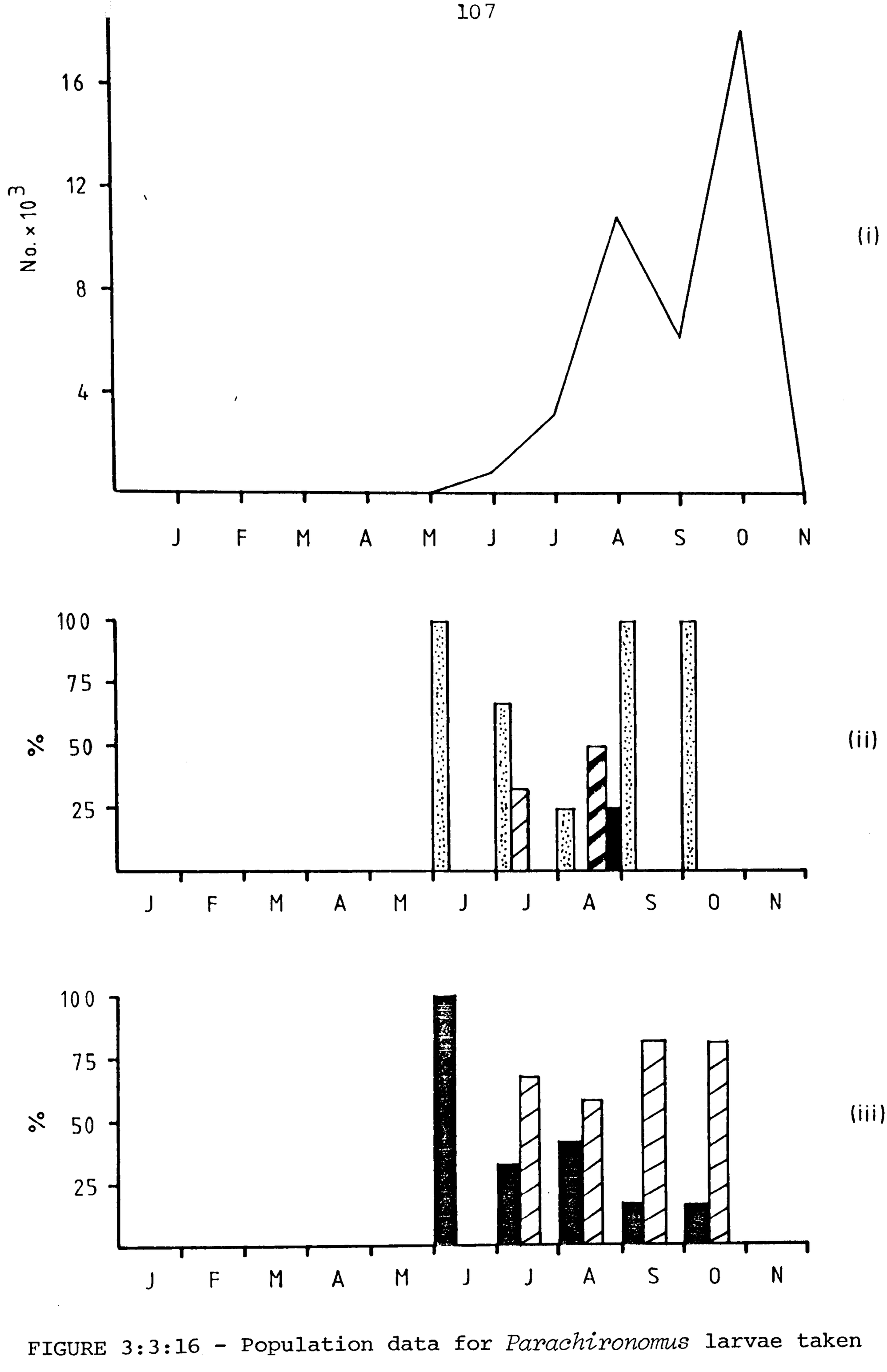


FIGURE 3:3:16 - Population data for *Parachironomus* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *Parachironomus* population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

v) *Endochironomus* (see Figure 3:3:17)

Adults of two species (*Endochironomus dispar* (Meigen) and *Endochironomus tendens* (Fabricius)) were recovered from emergence traps. Both species are poorly represented as adults, although *tendens* is much more numerous than *dispar*. This superiority very likely exists in the larval population as well.

Endochironomus larvae are found in every month except July. They occur at low densities and because of this there is a high probability that temporal variations in numbers are due to chance.

Most of the individuals collected over the year were fourth instars; the majority of over-wintering larvae belong to this category. First instar *Endochironomus*, like first instar *Glyptotendipes*, are very rare. Because the instar relative abundance graph is derived from low monthly number counts, the degree to which it is representative of the real situation is questionable.

Endochironomus larvae are exclusive to Zones 1 and 2, with the vast majority living in Zone 1. Possible reasons for this pattern of spatial dispersion are discussed in the next chapter.

vi) *Polypedilum*

No adults were caught in emergence traps and the one species present in the larval stage was not identified.

Only four individuals were taken in reedstem samples: one in January in Zone 3 and three in October in Zone 2. These few larvae are first and second instars.

vii) *Cladotanytarsus*

Two third instar larvae of the same undetermined species were recovered from Zone 1 in February. *Cladotanytarsus mancus* (Walker) adults were caught in emergence traps in 1982 so that larvae found in the previous year may belong to this species.

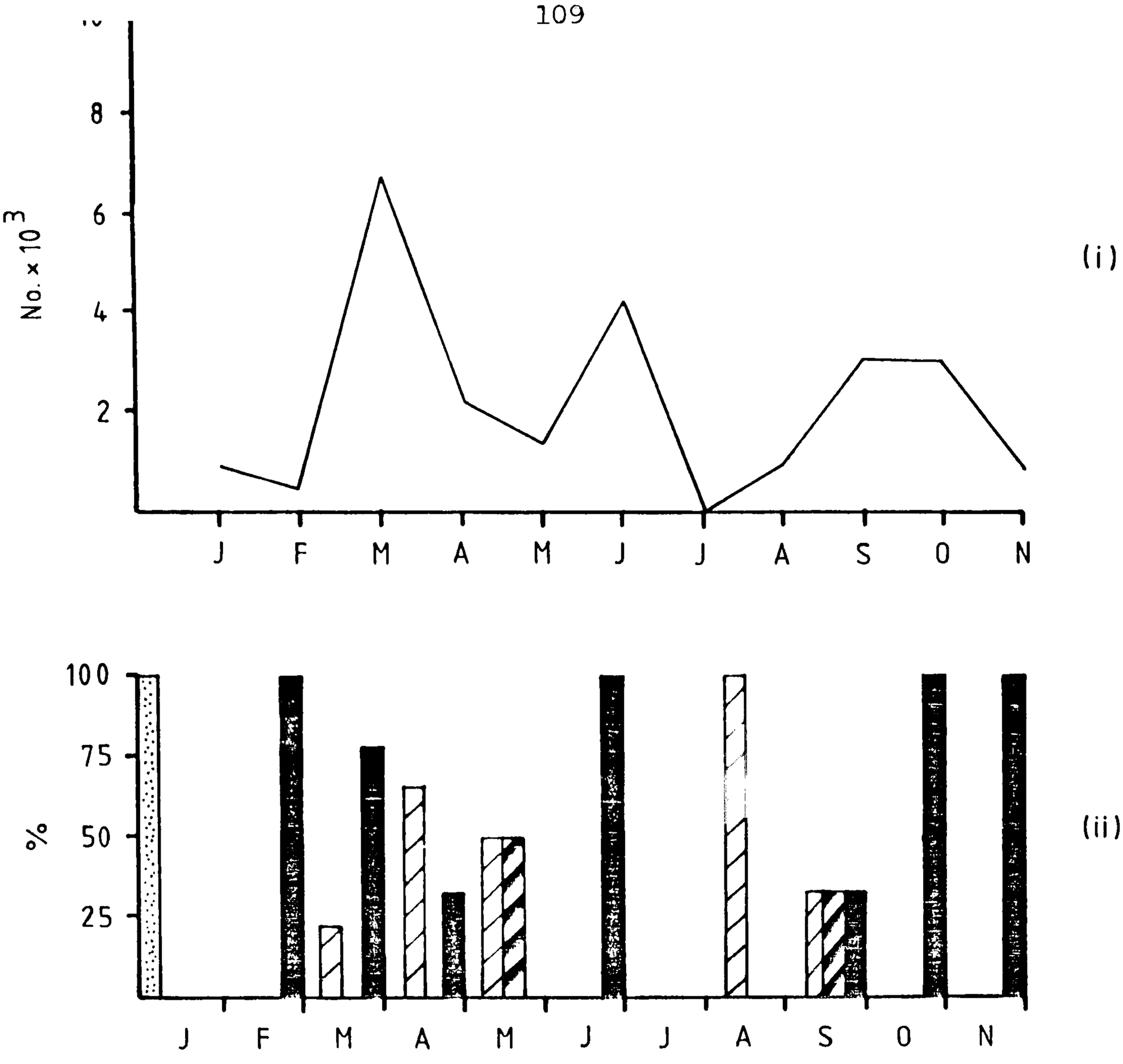


FIGURE 3:3:17 - Population data for *Endochironomus* larvae taken from old reedstems during 1981.

(i) Mean density (No. x 10^3 per cm^2)

(ii) Instar relative abundance (▩ 1st; ▨ 2nd; ◪ 3rd; ■ 4th)

(iii) Percentage of each month's total *Endochironomus* population found in Zone 1 (■), Zone 2 (▨), and Zone 3 (▩).

viii) *Tanytarsus*

Two individuals were taken from Zone 1: a second instar in January and a third instar in April. Both larvae belong to the same unidentified species.

ix) *Microtendipes*

One fourth instar individual was taken from Zone 2 in May. Benthic-dwelling larvae of the same genus were identified as *Microtendipes pedellus* (Degeer); it is probable that the larva found on a reedstem belongs to this species and had strayed from its original benthic habitat.

3:4 Annual Repetition in the Population Patterns of the Chironomid Community found on Old Reedstems.

A) A COMPARISON OF THE LARVAL POPULATIONS IN 1980 AND 1981.

Mountain (1981) took monthly samples of reedstem-dwelling chironomid larvae at Cop Mere during 1980 and his findings can be directly compared to those for 1981 discussed previously in this chapter.

Table 3:4:1 shows the genera of reedstem-dwelling chironomid larvae found at Cop Mere during 1980 and 1981 respectively. Of the eighteen genera listed, nine are common to both years. Only one (*Pentapedilum*) is present in 1980 but not in the following year. Eight genera are represented in 1981 but are absent in 1980; these larvae tend to occur towards the front (lakeward edge) of the reedbed and may have escaped detection in 1980, when all samples were taken well behind this zone.

Monthly total larval abundance figures are consistently greater for 1981 than 1980; the maximum density in 1981 is four times higher than that found in 1980. Density differences between the two years will partly reflect contrasts in sampling policy and technique: it has been shown

CHIRONOMINAE	1980	1981
Camptochironomus	+	+
Cladotanytarsus	-	+
Endochironomus	+	+
Glyptotendipes	+	+
Limnochironomus	+	+
Microtendipes	+	+
Parachironomus	-	+
Pentapedilum	+	-
Polypedilum	-	+
Tanytarsus	-	+
ORTHOCLADIINAE		
Corynoneura	+	+
Cricotopus	+	+
Diplocladius	-	+
Metriocnemus	+	+
Orthocladius	-	+
Psectrocladius	+	+
Rheocricotopus	-	+
Thienemanniella	-	+

TABLE 3:4:1 The genera of chironomid larvae found on old reedstems during 1980 and 1981. (+ = present; - = absent.)

Information for 1980 is derived from Mountain (1981).

in this study that larvae are usually most abundant towards the front of the reedbed, an area that was not investigated by Mountain in 1980; also, Mountain did not place a confining tube over his stems before removal and some larvae would have been lost because of this. These sampling dissimilarities between 1980 and 1981 will dissemble true differences in larval density. However, the magnitude of the gap between the mean larval density figures for 1980 (calculated from sample-stems taken from the middle of the reedbed) and their closest counterparts for 1981 (the mean larval density figures for Zone 2) suggests a real overall increase, of considerable proportions, occurs over the two years.

Synchronicity in population peaks is variable. In both years, numbers rise in March then fall in April. The highest density in 1980 is reached in July; that for 1981 is attained one month earlier. An August peak of abundance is evident in 1981 but not in 1980; synchronicity is found in October, however, where peaks are manifest in both years.

The relative abundance of those genera common to 1980 and 1981 remains essentially similar from one year to the next, with *Cricotopus* accounting for the vast majority of larvae and *Glyptotendipes* occupying the second position in the numerical hierarchy. *Psectrocladius* is also relatively common buts its position in 1980 as the third most abundant genus is occupied by *Canptochironomus* in 1981; *Camptochironomus* is comparatively rare in 1980.

B] A COMPARISON OF THE LARVAL POPULATIONS IN 1981 AND 1982

The comprehensive sampling programme adopted in 1981 was not continued in the following year. Instead, various sampling ploys were used which allowed a number of diverse investigations to be carried out but which also served to provide an intermittent record of diversity and abundance through the year.

Table 3:4:2 shows mean larval density where comparable figures are available for 1981 and 1982. The small size of the zonal populations in the first two months of 1981 and 1982 means there is a high probability that zonal density differences between the two years occur through chance. In later months, when larvae are much more numerous, substantially greater densities are found in 1981 than 1982 and the magnitude of the value differences suggests that they are non-random.

		Zone 1	Zone 2	Zone 3
January	A	0.48 (0.05)	0.05 (0.01)	0.03 (0.01
	B	0.80 (0.53)	0.14 (0.07)	0.01 (0.01)
February	A	0.16 (0.02)	0.09 (0.02)	0.05 (0.02)
	B	0.24 (0.07)	0.10 (0.05)	0.02 (0.01)
March	A	0.65 (0.08)	-	-
	B	0.21 (0.03)		
May	A	2.01 (0.38	-	-
	B	0.57 (0.23		
June	A	4.06 (0.67)	-	-
	B	0.75 (0.37)		
October	A	-	1.63 (0.40)	-
	B		0.76 (0.20)	

TABLE 3:4:2 Mean density (No. per cm^2) of reedstem-dwelling chironomid larvae during (A) 1981 and (B) 1982. (Figures in parentheses represent one standard error of the mean.)

Table 3:4:3 compares 1981 and 1982 patterns of temporal distribution for each chironomid genus represented by reedstem-dwelling larvae. As regards the Chironominae, a fundamental relationship between the distribution patterns for the two years is common to all genera: where larvae are absent in 1981, they are also absent in 1982; where larvae are

CHIRONOMINAE	Jan	Feb	Mar	May	Jun	Oct
Camptochironomus	–	–	–	+	+	+
	–	–	–	+	+	–
Cladotanytarsus	–	+	–	–	–	–
	–	–	–	–	–	–
Endochironomus	+	+	+	+	+	–
	–	+	–	–	–	–
Glyptotendipes	+	+	+	+	+	+
	+	+	–	+	+	+
Limnochironomus	+	+	–	–	+	+
	–	–	–	–	+	+
Parachironomus	–	–	–	–	+	+
	–	–	–	–	–	+
Polypedilum	+	–	–	–	–	+
	–	–	–	–	–	+
Tanytarsus	+	–	–	–	–	–
	–	–	–	–	–	–
ORTHOCLADIINAE						
Corynoneura	+	–	–	+	+	–
	–	–	–	–	–	+
Cricotopus	+	+	+	+	+	+
	+	+	+	+	+	+
Diplocladius	–	+	+	–	–	–
	–	–	–	–	–	–
Metriocnemus	–	+	+	–	+	–
	–	+	–	–	+	+
Orthocladius	+	+	–	–	–	–
	–	–	–	–	–	–
Psectrocladius	–	–	–	+	+	–
	–	–	+	–	–	–
Rheocricotopus	+	+	+	–	–	–
	–	+	–	–	–	–
Thienemanniella	+	+	+	–	–	–
	–	+	–	–	–	–

TABLE 3:4:3 - Temporal occurrence patterns of chironomid genera over the six months in 1981 and 1982 for which comparable information exists. (For each genus, the top line of symbols (+ = present; - = absent) refers to 1981 and the bottom line to 1982.

present in 1981, they may be present or absent in 1982. From this it can be deduced that an underlying compatibility exists between the patterns for each genus, and any dissimilarity is caused solely by a greater temporal restriction in larval occurrence during the latter year. The same conclusions can be drawn with regard to the Orthocladiinae, although three instances do occur where larvae are not found in 1981 but are present in the following year.

Changes in generic diversity over the two years are indicated in Tables 3:4:4 and 3:4:5. Table 3:4:4 shows that, in five out of six months, genera counts for both the Chironominae and Orthocladiinae are higher in 1981 than 1982. Table 3:4:5 provides information relating to the temporal occurrence of individual genera. Fourteen of the sixteen

	1981			1982		
	C	O	Σ	C	O	Σ
January	5	5	10	1	1	2
February	4	6	10	2	4	6
March	2	5	7	0	2	2
May	3	3	6	2	1	3
June	5	4	9	3	2	5
October	5	1	6	4	3	7

TABLE 3:4:4 - Genera totals for the reedstem-dwelling larvae found in the six months during 1981 and 1982 for which comparable information is available. (C = Chironominae; O = Orthocladiinae; Σ = total number of chironomid genera.)

genera are represented in fewer months in 1982 than in the preceding year. (The other two are found in an identical number of months in

both years.) The general drop in diversity from 1981 to 1982 is a reflection of this reduction in representation.

CHIRONOMINAE	1981	1982
Camptochironomus	3	2
Cladotanytarsus	1	0
Endochironomus	5	1
Glyptotendipes	6	5
Limnochironomus	4	2
Parachironomus	2	1
Polypedilum	2	1
Tanytarsus	1	0
ORTHOCLADIINAE		
Corynoneura	3	1
Cricotopus	6	6
Diplocladius	2	0
Metriocnemus	3	3
Orthocladius	2	0
Psectrocladius	2	1
Rheocricotopus	3	1
Thienemanniella	3	1

TABLE 3:4:5 - The number of months (out of the six shown in the previous three tables) in which each genus is represented during 1981 and 1982.

3:5 The Chironomid Larval Community found on New Reedstems during 1981.

New stems were taken in varying numbers between June and October inclusive. Table 3:5:1 compares monthly mean larval densities on old and new stems in Zone 1 during this period and shows that, in each month, larvae are much less numerous on new stems than old ones. This pattern is also evident in respect of Zone 2, but is not found in Zone 3 where spatial larval density variation between stems does not appear to be linked to the age status of the latter in any way.

A comparison of Tables 3:5:2 and 3:3:2 suggests that the larval communities on new and old reedstems share fundamental similarities as far as taxonomic composition and genus relative abundance are concerned, although the monthly genera counts for old stems tend to be higher, if only slightly, than their concomitant counterparts for new stems.

In relation to instar relative abundance, no characteristic differences between old and new stems are apparent for any genus.

	Old	New
June	4.06 (0.67)	0.29 (0.12)
July	2.18 (0.63)	0.40 (0.16)
August	4.43 (1.32)	0.52 (0.13)
September	1.82 (0.32)	0.31 (0.15)
October	2.71 (0.48)	1.14 (0.17)

TABLE 3:5:1 - Mean density (No. per cm^2) of chironomid larvae found on old and new reedstems in Zone 1 during 1981. (Figures in parentheses represent one standard error of the mean.)

	Jun	Jul	Aug	Sep	Oct
Camptochironomus	-	-	2.99	1.28	-
Corynoneura	-	1.03	-	-	-
Cricotopus sylvestris	85.71	85.57	92.54	91.03	94.52
Endochironomus	4.76	2.06	-	-	2.74
Glyptotendipes	-	1.03	2.99	6.41	1.37
Limnochironomus	-	-	-	-	0.46
Metriocnemus sp. C	-	-	-	1.28	-
Parachironomus	-	1.03	-	-	0.91
Polypedilum	-	1.03	-	-	-
Psectrocladius	9.52	8.25	1.49	-	-

TABLE 3:5:2 - Percentage relative abundance values for chironomid taxa found on new reedstems during 1981.

Chapter 4

The Population Patterns of Reedstem-Dwelling Chironomid Larvae at Cop Mere - An Investigation of Extrinsic Determinants.

4:1 An Introduction to Some Relevant Concepts in Population Regulation Theory

A) THE HISTORICAL BACKGROUND TO CURRENT IDEAS

Since the early 1900's, ecologists have sought a definitive theory, applicable to all biological populations, to explain how population density is regulated. Clark *et al.* (1967) review the most prominent works in this area, which include those of Andrewartha and Birch (1954), Bodenheimer (1930), Chitty, (1960), and Smith (1935). Many of the theories put forward concerning numerical fluctuations in animal populations are based on insect studies.

In each of the publications cited above, a different viewpoint is held as to what regulates density. Bodenheimer considers insect population density to be regulated primarily by the effects of weather and was one of the first ecologists to advocate a 'climatic' theory of population control. Smith coined the phrases 'density-dependent' and 'density-independent'. He suggests that the average density existing over a period of time is determined by density-dependent mortality factors, which are mainly biotic in nature and include parasitism, disease, and predation. Fluctuations in numbers around the mean level are attributable to density-independent mortality factors, which are mainly abiotic. The majority of these abiotic factors are climatic.

Andrewartha and Birch reject any clear-cut distinction between biotic and abiotic factors. They also reject the idea of density-dependent and density-independent influences, believing all population-regulating factors

to be, in effect, density-dependent. Instead, they divide the environment into four components - weather, food, other animals, and a place in which to live - and suggest that population size is dependent on these factors. The relative importance of each of these factors will vary from situation to situation, but usually one or two will preponderate.

Chitty emphasizes the idea of self-regulation in certain populations: sometimes a rise in numbers will eventually be curtailed by a deterioration in the quality of the population because this degeneration enables mortality factors to exert an effect on a greater proportion of individuals.

The theories outlined above are not necessarily mutually exclusive or contradictory; their inveteracy would appear to reflect some degree of intransigence on the part of the theorists rather than any fundamental contrariety in statement. Clark *et al.* (1967) believe there is a need for a 'generalised description of the ways in which insect abundance is determined' and that any such description should be based on a synthesis of some of the varying ideas put forward in the past. Solomon (1976) describes the present trend towards a more inductive approach to the question of population regulation, involving long-term field studies, statistical analysis of deterministic processes, and mathematical model-building.

This brief consideration of density determination theories has three purposes. Firstly, it introduces some of the key concepts in population study, which, even if their validity is not always accepted, are still relevant to any density investigation. Secondly, it puts the present study into perspective in relation to the contemporary climate of opinion regarding work on abundance patterns. Thirdly, it provides a necessary informatory background to the discussion on determinant classification and definition that constitutes the next part of this section.

B) CATEGORISING AND DEFINING ABUNDANCE DETERMINANTS

The level of population density existing at any time is determined by events which fall into two groups, succinctly described by Clark *et al.* (1967):

1) 'Primary events, such as births, deaths, and movements, which describe the basic demographic characteristics of the population, e.g. life cycle, annual generation sequence, etc., and express the inherited ability of individuals to survive and multiply'.

2) 'Secondary events which qualify the magnitude, extent, frequency, or duration of primary events....'

Morris (1957) describes the 'basic demographic characteristics' referred to in 1) above as 'intrinsic' factors and those responsible for secondary events as 'extrinsic' factors. This terminology is adopted in the present study.

Extrinsic processes can be divided into two groups, depending on their mode of action:

1) Those which affect the supply of life-maintaining resources to individuals.

2) Those which act directly upon individuals.

According to Clark *et al.* (1967), 'events affecting (resource) supply may involve abiotic agencies; other organisms that either favour the subject species or compete with it; and competition or co-operation between individuals within the population'.

Processes acting directly upon an individual can be either beneficial or detrimental and may involve abiotic agencies, predators, parasites, and the density of the population to which the individual belongs.

In Chapter 3, consideration is given to the contribution of intrinsic factors in the shaping of temporal larval density patterns. Analysis of monthly variation in instar relative abundance, and comparison of quantitative

changes in juvenile and adult populations, indicates that month to month fluctuations in larval density are largely determined by intrinsic species characteristics, especially those that govern seasonal patterns of egg-laying. In the present chapter, an examination is made of those extrinsic influences which conceivably could modify the basic temporal patterns of larval abundance set by intrinsic factors. Possible determinants of spatial distribution patterns are also investigated.

Two points should be borne in mind in relation to the discussion that follows in the remainder of this chapter. Firstly, emphasis is placed on those processes and events which affect larval numbers by acting directly upon individual larvae, rather than those which exert an indirect effect on juvenile abundance by influencing the adult population. Secondly, the studies of temporal variation in abundance are often inextricably linked to the studies of spatial variation in abundance and neither set of investigations can be viewed in total isolation from the other. Indeed, comparison between the spatial and temporal patterns of both environmental and larval density variation can help in the revelation and assessment of extrinsic density determinants operating in either or both dimensions.

4:2 Spatiotemporal Variation in Epiphyton Characteristics - The Effects on Larval Population Patterns

A) QUANTITATIVE ASPECTS OF EPIPHYTON VARIATION

The two fundamental resource requirements of a chironomid larva are food and shelter. For the majority of reedstem-dwelling chironomid species, epiphyton constitutes the source of supply for both these resources.

Epiphyton primarily consists of diatoms, unicellular algae, and filamentous algae. Quantities of detritus and mineral matter are frequently found amongst these plants. This complex of biotic and abiotic material harbours a variety of microscopic and macroscopic animals, including the chironomid larvae described in Chapter 3 (except for those *Glyptotendipes* individuals which inhabit the cavity at the top of broken stems). Almost all the food eaten by the epiphyton-dwelling larvae is either epiphytic algae or detritus.

Temporal and spatial differences in the quantity and/or quality of epiphyton could imply variation in its potential as a provider of food and shelter. If such variation existed, this might influence patterns of larval abundance.

Temporal and spatial differences in epiphyton quantity may imply variation in the amount of food and shelter available for larvae and, therefore, variation in the capacity for larval accommodation. Relationships between epiphyton quantity and larval density are considered in the following discussion.

Figure 4:2:1 illustrates the zonal patterns of epiphyton biomass[1] change for 1981. Although each of these patterns exhibits an obvious degree of individuality, common trends can be recognised, particularly with respect to Zones 1 and 2. Here, algal density rises quite steadily through the spring and reaches a maximum in June, after which it drops progressively to its low winter level.

The highest algal density in each month is generally found in Zone 1 and the lowest in Zone 3. It is clear that, as with larval density and biomass, sizeable interzonal differences can occur. The statistical

---

[1]Epiphyton biomass calculations are based on material consisting of both living algae and detritus. The terms 'epiphyton biomass', 'algal biomass', 'epiphyton density', and 'algal density' are used synonymously in the present discussion.

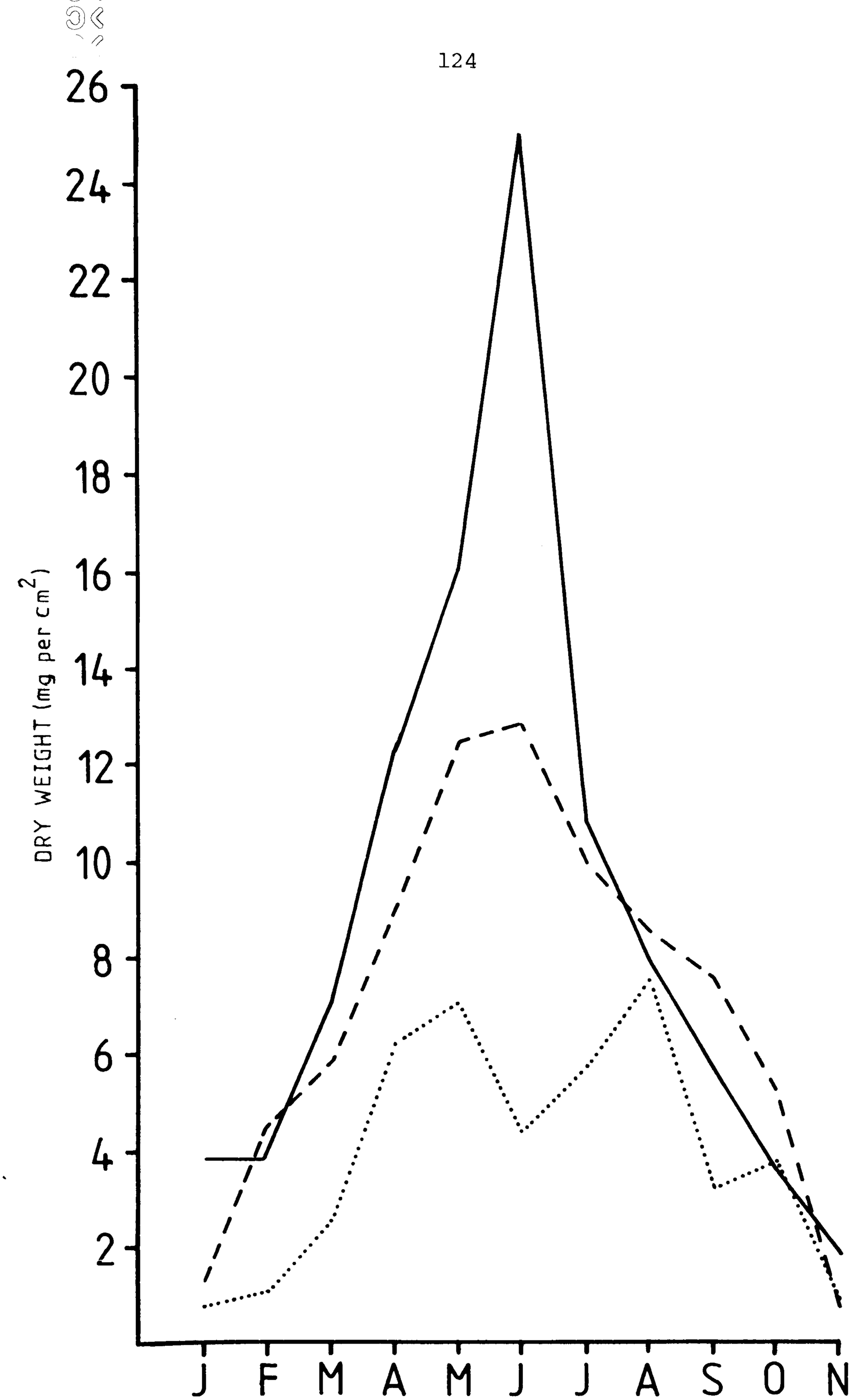


FIGURE 4:2:1 - Mean epiphyton density on old reedstems in Zone 1 (———), Zone 2 (- - -), and Zone 3(·····) during 1981. (See Appendix J for standard errors.)

significance of interzonal algal density differences was determined by the same tests as were used for larval density, and the results of these tests are indicated in Figures 3:2:3 and 3:2:4. (See Appendices F and G for actual index values.) The Kruskal-Wallis analysis of variance reveals a seasonal pattern of interzonal variation in epiphyton biomass: significant differences are found throughout the winter, spring, and early summer; no such significant differences are evident from July to October. Results from the Mann-Whitney investigations show where significant differences actually lie in the months for which significance is detected by the Kruskal-Wallis test. In each of these months, significant variation occurs between all zones, except for Zones 1 and 2 in February and March, and Zones 2 and 3 in November.

The relationship between epiphyton biomass and larval density can be viewed from several angles and analysed in a number of ways.

Mason and Bryant (1975a) investigated month to month differences in the quantities of epiphyton and chironomid larvae on dead *Typha* stems at Alderfen Broad, Norfolk, and concluded that algal and larval density variations through time are interdependent. A continuous fall in algal density from April to November is a result of grazing by larvae, whose own density drops as they deplete their food source. Larvae migrate down to the benthic habitat in autumn, returning to the stems in spring. Epiphyton builds up in late winter; its recovery is made possible by the absence of grazing pressure at this time. Mason and Bryant thus envisage the existence of a 'predator-prey' type cycle, perpetuated by the migratory habits of the larvae.

The present study offers no evidence to support Mason and Bryant's hypothesis: the density graphs for epiphyton and larvae (Figures 4:2:1 and 3:2:1 respectively) do not display the kind of synchronistic correlation that would be expected if algal and larval densities were mutually

dependent through time. Also, a mass autumnal exodus of larvae from the epiphytic to the benthic habitat is not readily apparent. Similar observations to these are made by Mountain (1981) who comes to the same conclusion that a larvae-epiphyton 'predator-prey' cycle does not operate at Cop Mere.

Mason and Bryant suggested that larval biomass rather than density would have given the best indication of grazing potential, owing to size-dependent differences in feeding capacities. As far as the present study is concerned, a comparison of the temporal variation patterns for algal and larval biomass (cf. Figures 4:2:1 and 3:2:2) gives no reason to reconsider or modify the conclusions drawn from the comparison of the algal biomass and larval density graphs.

The effects of grazing on epiphyton communities are reported by several workers, including Dickman (1968) and Eichenberger and Schlatter (1978). Dickman found that frog tadpoles were the likely cause of a large spring reduction in the standing crop of filamentous green algae in a Canadian lake. Eichenberger and Schlatter studied the effects of grazing by Orthocladiinae larvae on the benthic algal vegetation in artificial river channels in Switzerland. They discovered that the amount of vegetation lost as a result of chironomid feeding activity is dependent on larval density. Overgrazing became apparent at densities higher than 3 larvae/cm^2.

Any influence grazing pressure has on month to month changes in epiphyton density at Cop Mere appears to be subordinate to that of other determinants: it does not play a detectable part in the shaping of temporal patterns of variation in epiphyton density, as evidenced by comparison of Figure 4:2:1 with Figures 3:2:1 and 3:2:2.

So far, attention has been focused on purely temporal aspects of the quantitative relationship between larvae and epiphyton. It appears that larval density and biomass variation through time is largely determined

by intrinsic population characteristics and occurs independently of month to month changes in algal biomass. This does not rule out the possibility that spatial variation in epiphyton density influences spatial variation in larval quantity, however. This possibility is now examined.

Figure 3:2:4 allows convenient comparison of concomitant interzonal differences in larval density, larval weight, and epiphyton biomass. Regarding these three characteristics, the differences between Zones 1 and 2 are either all significant or all non-significant in eight of the eleven months. In those months where all variations between Zones 1 and 2 are significant, larvae and epiphyton values are consistently higher for Zone 1 than Zone 2. The situation in the eight months where concomitant interzonal differences are either all significant or all non-significant indicates the possible existence of a larvae/epiphyton causal relationship during this time.

From July to October, no significant differences are found between Zones 1 and 2 in either larvae or epiphyton. A different situation is evident at this time of the year for the other zonal pairings (Zones 2/3 and 1/3). Here, larval quantities differ significantly between zones. Algal densities show essential interzonal similarity, however, which means that the comparative paucity of the chironomid population in Zone 3 cannot be ascribed to any interzonal dissimilarity in epiphyton biomass.

Inherent inexpediency would be found in an examination of the quantitative relationship between larvae and epiphyton based solely on interzonal comparisons, because such an examination does not take into account the larvae/epiphyton relationship on individual stems - a relationship which may vary on an intrazonal basis. Analysis of individual stem-samples will give the best indication of any close positive correlation between larval and epiphyton quantities. If such

an association exists, it is probable that some sort of dependency is involved.

Correlation was measured using Kendall's rank correlation test, a non-parametric test with 91% of the power-efficiency of the parametric alternative (Hammond and McCullagh, 1974, p. 201). For each monthly set of zonal stem-samples, six correlations were sought: larval number with stem surface area, epiphyton weight[1], and epiphyton density; and larval weight with each of these latter three variables. Stem surface area acts as an ultimate control on larval numbers: competition for living-space will impose an upper limit on the number of larvae that can actually position themselves on a stem. Epiphyton weight is also limited by the amount of space available for colonisation.

Epiphyton weight may differ between two stems but epiphyton density (algal biomass per cm^2) may be similar. The reverse situation can also occur, where weights are similar but densities vary. For this reason, both epiphyton weight and epiphyton density were considered in the correlation investigations.

Figure 4:2:2 shows where significant positive correlations exist. (Actual correlation coefficient values and probability levels are given in Appendix K.) In Zone 1, the variable which appears to be most closely correlated with both larval numbers and biomass is epiphyton weight; no one variable possesses such conspicousness in either zones 2 or 3. More correlations are found in Zone 1 for each parameter pairing than anywhere else, suggesting some interzonal heterogeneity in the quantitative relationship between larvae and epiphyton.

---

[1] In this context, 'epiphyton weight' differs from 'epiphyton density' in that its calculation does not involve division by stem surface area - 'epiphyton weight' is the total weight of epiphyton per stem.

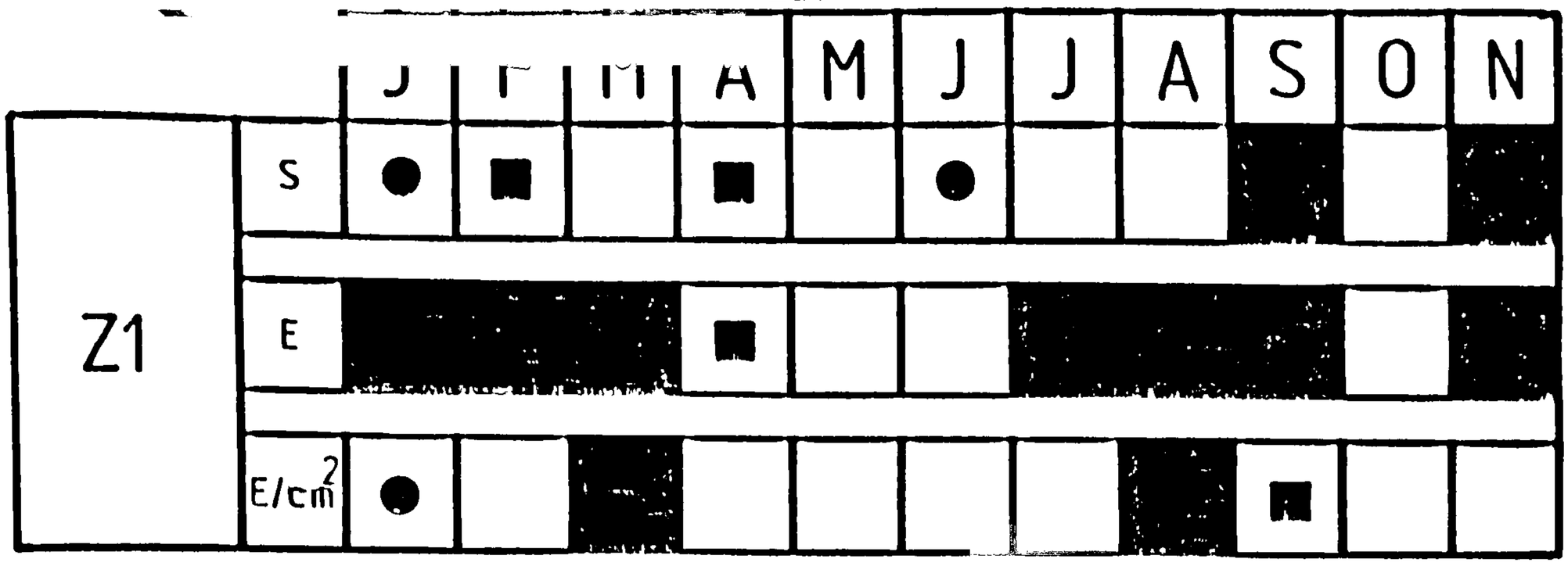


FIGURE 4:2:2 - Temporal occurrence patterns for significant positive correlations between variable pairs in Zones 1 (Z1), 2 (Z2), and 3 (Z3) during 1981.

Each variable shown is correlated with total larval number and also total larval biomass.

S = Stem surface area; E = Epiphyton weight (see text for definition); E/cm^2 = Epiphyton density.

■ = significant positive correlation with both total larval number and total larval weight

■ = significant positive correlation with total larval number only

● = significant positive correlation with total larval weight only

□ = absence of significant positive correlation

(Significance level = 0.05 - for a one-tailed test.)

A fundamental disadvantage with a correlation procedure involving ranking lies in the fact that it does not take into account the magnitude of sample to sample differences in a variable but only a quantitatively-based hierarchical sample order derived from these differences. This problem can be alleviated by complementing the correlation technique with an alternative approach that does not have the same deficiency.

In Chapter 3, interzonal differences in intrazonal larval quantity variation are given commensurability by calculating coefficients of variation for each zone (see p. 55). Figures 3:2:5 and 3:2:6 show the spatiotemporal patterns of variation in coefficient values for larval density and biomass respectively. A comparison with the concomitant pattern for epiphyton density (Figure 4:2:3) reveals that, in each month, the lowest intrazonal variation in each of the three variables (larval density, larval weight, and epiphyton density) is usually found in Zone 1 and the highest in Zone 3. This similarity in pattern form could be seen as providing circumstantial evidence that larval quantities and epiphyton density may be causally linked. Any such association would be strongest in Zones 1 and 2, where both larval and epiphyton variations are low; in Zone 3, larval variation is considerably higher than that found in epiphyton and here a close relationship cannot be envisaged.

The interpretations given in the preceding paragraph are not based on any consideration of the larvae/epiphyton relationship on individual stems. Such a consideration is desirable and can be made through a coefficient of variation analysis: for each stem the larvae/epiphyton relationship is quantified by dividing the number or weight of larvae by the algal biomass; for each zone, variance in the resultant values is determined and expressed as a coefficient of variation. It is inferable that the less the variation in the relationship, the more closely associated

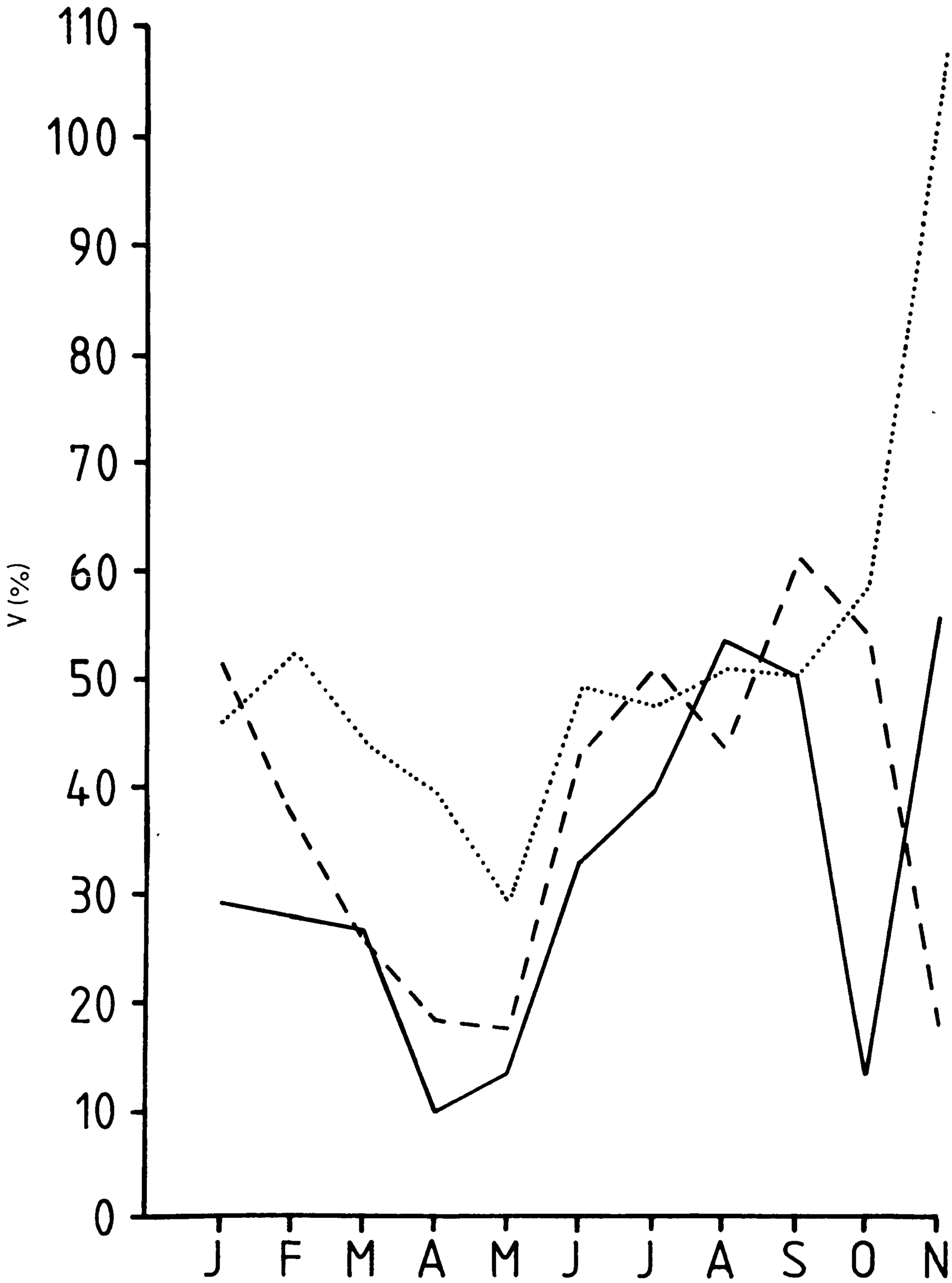


FIGURE 4:2:3 - Epiphyton density variation between old reedstems in each of Zones 1 (———), 2 (---), and 3 (·····) during 1981, as expressed by the coefficient of variation (V).

the larval and epiphyton quantities. Figures 4:2:4 and 4:2:5 show that the least variation in any month generally occurs in Zone 1 and the most in Zone 3, suggesting that a closer quantitative relationship between larvae and epiphyton exists in Zone 1 than Zone 3. This supports the conclusions drawn from the Mann-Whitney investigations, Kendall's rank correlation analyses, and the visual comparison of Figures 3:2:5 and 3:2:6 with Figure 4:2:3.

B) QUALITATIVE ASPECTS OF EPIPHYTON VARIATION

The resource potential of epiphyton as a source of food and shelter will be partly dependent on qualitative characteristics. Therefore, spatiotemporal variation in these characteristics may influence similar variation in larval abundance and population biomass.

Figure 4:2:6 illustrates monthly changes in the generic composition of the epiphyton found in each zone during 1981[1]. Information regarding the relative abundance of detrital material is also presented. Most of the algae listed are diatoms belonging to the order Pennales; the remainder are filamentous chlorophytes, except for *Chlorella* which is a unicellular chlorophyte.

A seasonal pattern of change in epiphyton make-up is evident. In the spring and early summer (March to June), generic diversity[2] is at its highest levels and zonal differences appear to be relatively insignificant. Throughout the rest of the year, fewer genera are found and diversity is generally greatest in Zone 1 and lowest in Zone 3. Much of the detrital material that accumulates over the summer is made up of the siliceous remains

---

[1]The relative abundance categorisations presented in this figure are based on subjective microscopical examination of quantitatively identical epiphyton samples taken from several stems in each zone. Algal genera were determined with the aid of Prescott (1970) and Belcher and Swale (1976).

[2]Here, the number of genera represented in each month constitutes the measure of generic diversity.

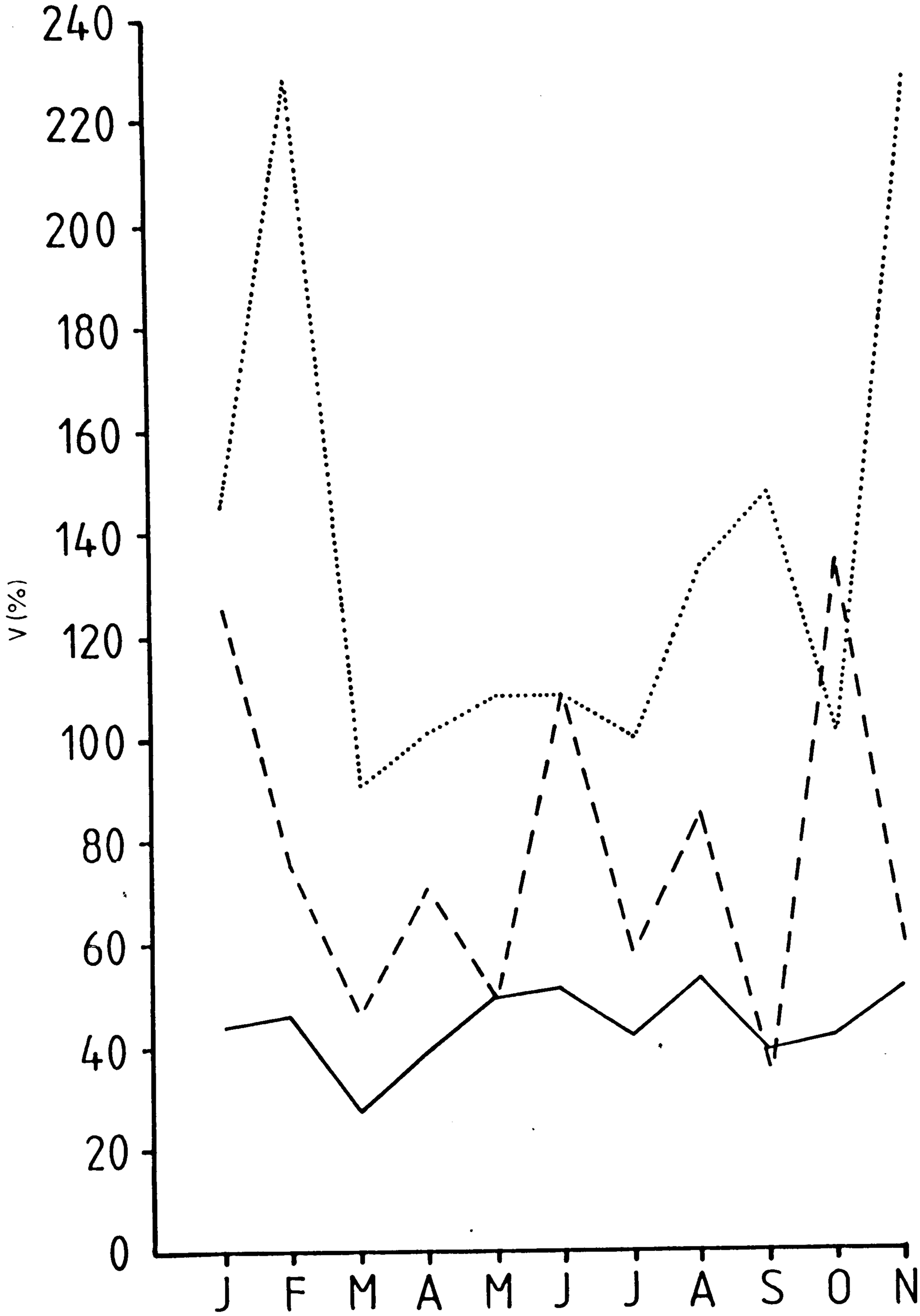


FIGURE 4:2:4 - Variation in old stem values for total larval number ÷ epiphyton weight in each of Zones 1 (———), 2 (---), and 3 (·····) during 1981, as expressed by the coefficient of variation (V).

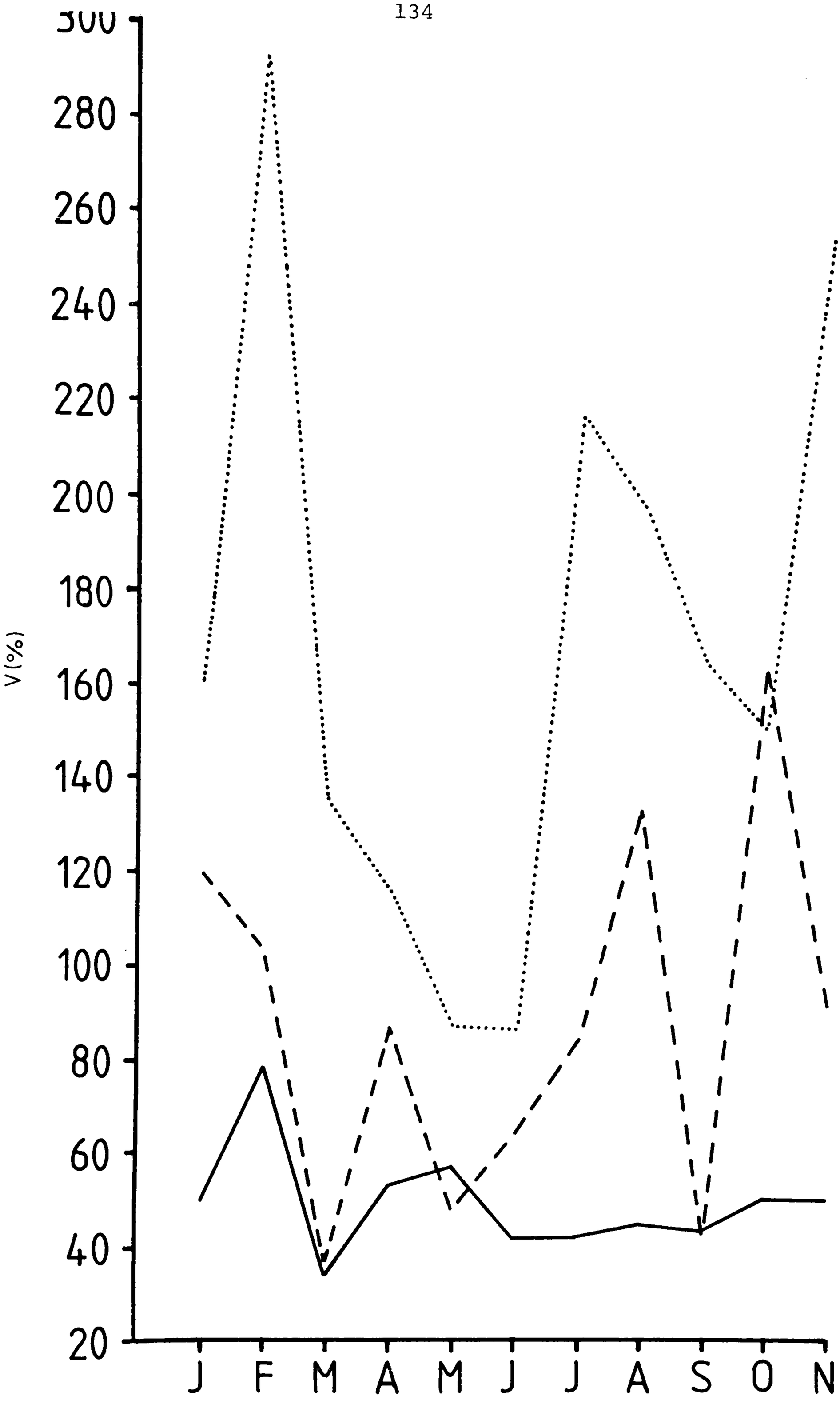


FIGURE 4:2:5 - Variation in old stem values for total larval weight ÷ epiphyton weight in each of Zones 1 (———), 2 (- - -), and 3 (·····) during 1981, as expressed by the coefficient of variation (V).

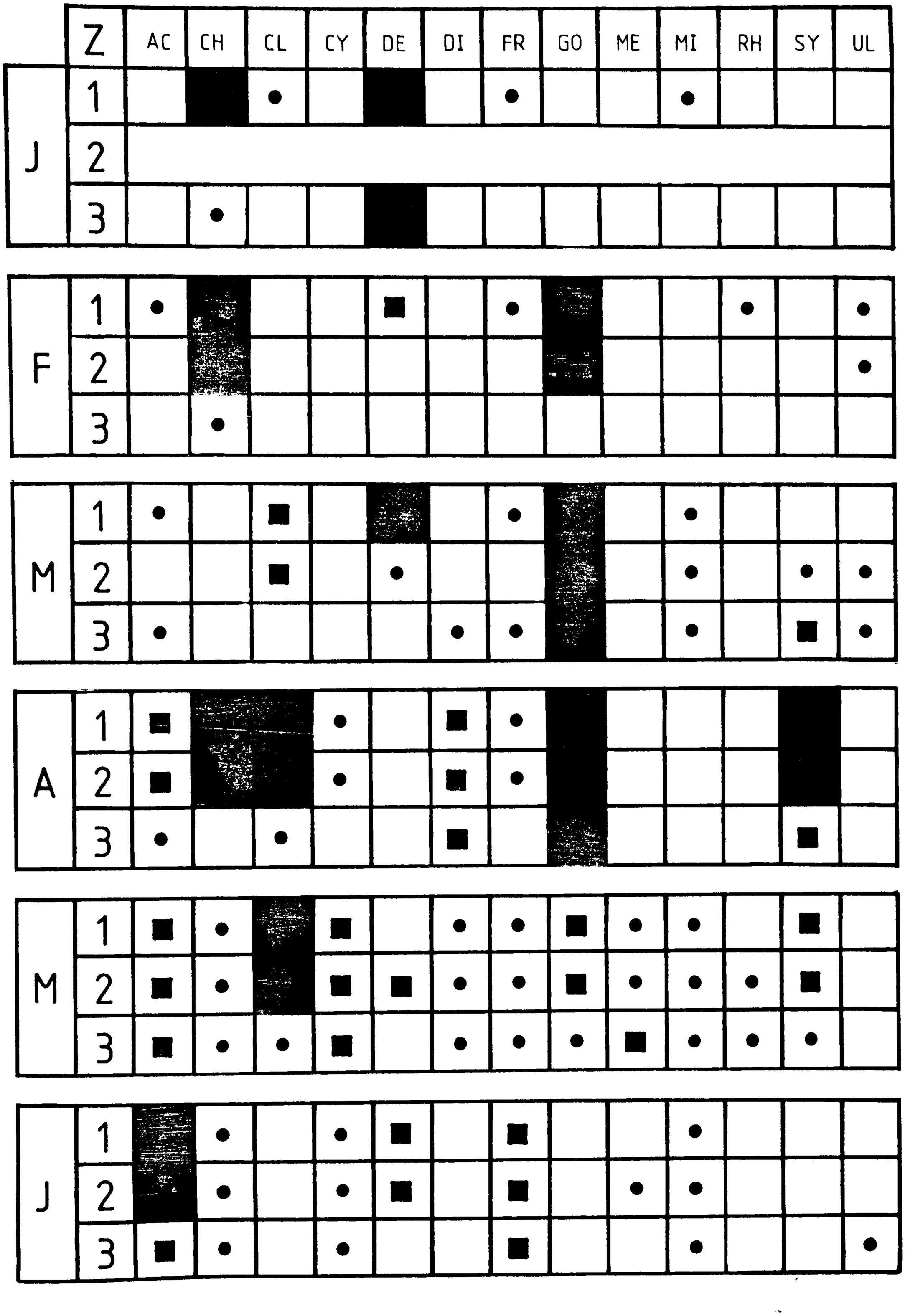


FIGURE 4:2:6 - (cont...) (See next page for legend.)

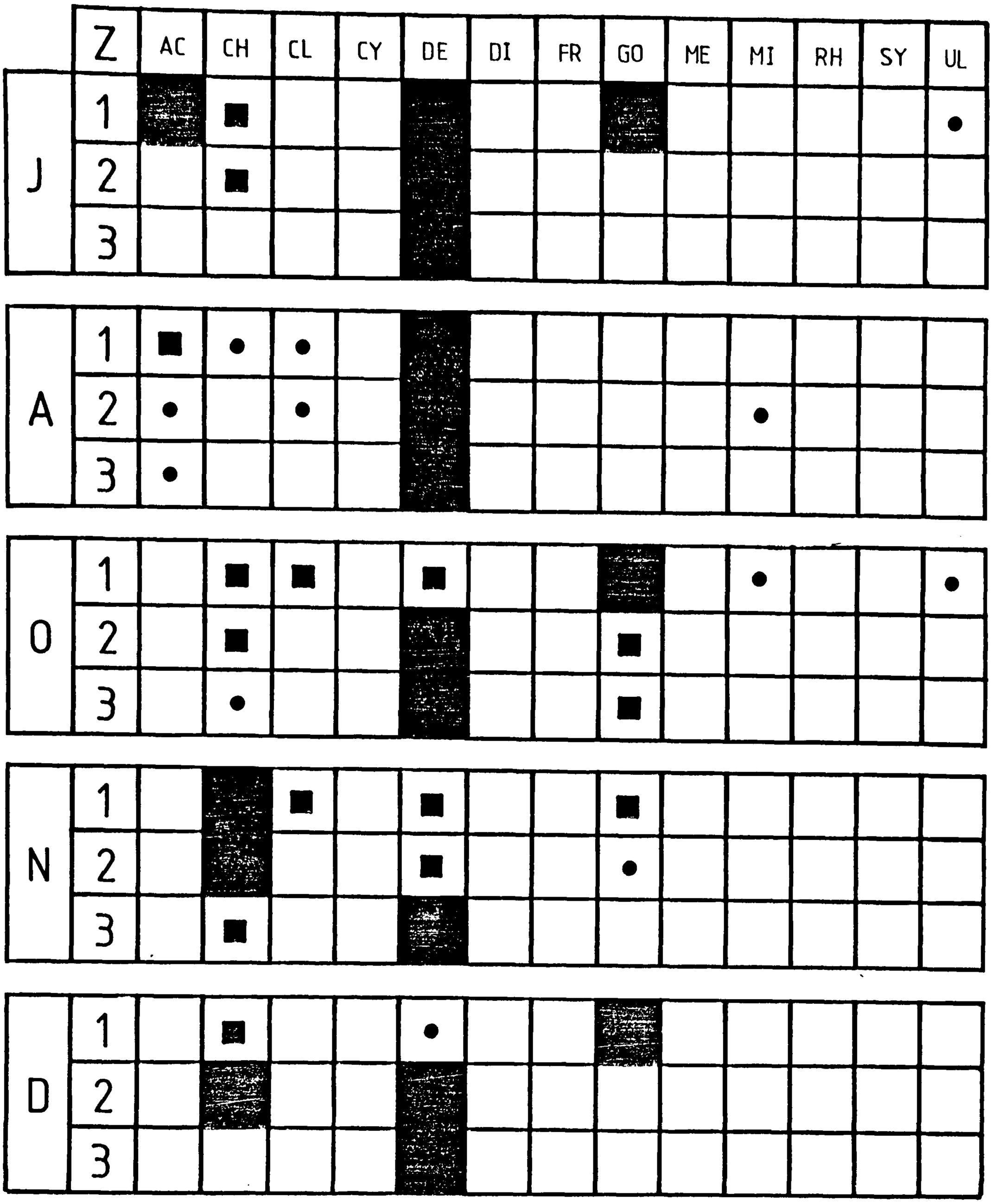


FIGURE 4:2:6 - (...cont.) - Epiphytic algal genera and detrital material found on old reedstems in Zone 1 (Z1), Zone 2 (Z2), and Zone 3 (Z3) during 1981. (No information available for Zone 2 in January nor any zone in September.)

AC - *Acnanthes*; CH - *Chlorella*; CL - *Cladophora*;

CY - *Cymbella*; DE - Detrital material; DI - Diatoma;

FR - *Fragilaria*; GO - *Gomphonema*; ME - *Meridion*; MI - *Microspora*

RH - *Rhoicosphenia*; SY - *Synedra*; UL - *Ulothrix*

● - Rare; ■ - Common; ■ - Very common

of the diatoms originally appearing in the spring. Detritus is often a very common component of reedstem coatings.

Any assessment of the role of food in influencing larval population patterns necessitates some knowledge of the food and feeding habits of the larvae in question. In the present study, the exceptionally high cost of certain requisite research materials unfortunately prohibited the type of investigations that would provide advantageous contributions to the knowledge gained from literature sources. Thus, the dietary information presented in the following discussion is derived exclusively from other works.

Certain generalisations regarding chironomid diets can be confidently reiterated: the majority of larvae are microphagous (Walshe, 1951; Oliver, 1971) and most of the Orthocladiinae and Chironominae can be classed as either algal or algal-detrital feeders, with diatoms constituting an important food source for many algae-consuming larvae (Oliver, 1971). Beyond these generalisations, little else can be stated where the same degree of widespread applicability is guaranteed. This is primarily due to knowledge gaps resulting from an insufficient number of investigations and the fact that those studies that have been undertaken are often lacking in quantitative content (Soszka, 1976) and, therefore, predictive value (Davies, 1975).

Spatiotemporal differences in detrital occurrence and the generic make-up of epiphyton are likely to have their greatest effect on larval population patterns where they connote variation in the favourableness of the food supply. The situation, in this respect, may vary characteristically from one chironomid species to another.

The feeding habits of *Cricotopus sylvestris* larvae are mentioned by several authors, whose findings suggest that this species will eat a wide variety of foodstuffs. Mountain (1981) examined the gut contents of thirty-four larvae collected from old reedstems at Cop Mere in July

and September, and found algal material (mainly diatoms and fragments of filamentous chlorophytes), fungal spores, and detritus. Gut content composition differed between the two months. Wasilewska (1978) also examined the gut contents of *Cricotopus sylvestris* larvae and found the material consisted of 57% detritus, 26% algae (mainly diatoms) and 18% mineral parts. LeSage and Harrison (1980) allude that *sylvestris* feeds on diatoms, filamentous algae, and detritus. In addition to these foodstuffs, Soszka (1976) found animal residues in the *sylvestris* larvae she examined. On the basis of evidence presented by Darby (1962), Beck (1977) categorises *sylvestris* as both a herbivore and predator. Popchenko (1971) reports that this species includes oligochaetes in its diet.

Dietary information concerning Orthocladiinae taxa other than *Cricotopus* is extremely scarce. Table 4:2:1 is a collation of the available information relating to non-Cricotopus Orthocladiinae genera represented by reedstem-dwelling larvae at Cop Mere. Apart from *Psectrocladius sordidellus*, the actual species listed are unknown at this location. Although intra-genera differences in feeding status are evident here and are reported elsewhere (e.g. Armitage, 1968; Izvekova, 1971; Kawecka *et al*, 1978), such variation is probably of less significance than that found on an inter-genera basis, giving some justification for the extrapolation of generic categorisations from species information.

Far greater attention has been devoted to the Chironominae than the Orthocladiinae in respect of feeding studies. Most of the reedstem-dwelling Chironominae found at Cop Mere are mentioned in the literature.

Sadler (1935) reveals that *Camptochironomus tentans* will eat a wide variety of materials, including diatoms, filamentous algae, and detritus of variable origin. Algae appear to be preferred to other foodstuffs.

Corynoneura scutellata (Winnertz)	Detritivore	Ramcharan and Paterson (1978)
Corynoneura taris (Roback)	Omnivore	Beck (1977)
Metriocnemus abdomino-flavatus (Picado)	Detritivore	Beck (1977)
Metriocnemus hamatus (Johannsen)	Herbivore	Beck (1977) source: Roback (1955)
Metriocnemus khabi (Coquillett)	Detritivore	Beck (1977)
Orthocladius annectens (Saether)	Herbivore	Beck (1977)
Orthocladius obumbratus (Johannsen)	Herbivore	Beck (1977) source: Roback (1955)
Psectrocladius sp.	Detritivore	Ramcharan and Paterson (1978)
Psectrocladius elatus (Roback)	Omnivore	Beck (1977)
Psectrocladius sordidellus (Zetterstedt)	Herbivore/Detritivore	Mountain (1981)
Rheocricotopus robacki (Beck)	Omnivore	Beck (1977)
Thienemanniella xena (Roback)	Herbivore	Beck (1977)

TABLE 4:2:1 - Literature-derived information relating to feeding behaviour in non-Cricotopus Orthocladiinae genera represented by reedstem-dwelling at Cop Mere during 1981.

Glyptotendipes pallens (formerly *glaucus* Meigen) often uses a filter-feeding mechanism, involving net-spinning, to trap planktonic food particles (Burtt, 1940; Walshe, 1951; Kalugina, 1958). Mountain (1981) found the gut contents of this species consisted mainly of diatoms, with very few filamentous algae. Kalugina (1958) states that *pallens* also feeds by substrate-scraping and Walshe (1951) discovered that larvae occasionally eat surrounding macrophytic tissue rather than net-caught phytoplankton.

Soska (1974) examined the gut contents of *Endochironomus tendens* larvae; most of this material was found to consist of periphytic algae (both diatom and non-diatom forms) and detritus of periphytic origin. Walshe (1951) suggests that feeding mechanisms and diet are similar in *Glyptotendipes pallens*, *Endochironomus dispar*, and *Endochironomus tendens*, but the *Endochironomus* larvae show a greater tendency to filter-feed. The dichotomous feeding behaviour exhibited by members of these two genera also occurs in *Polypedilum* (Berg, 1950). *Polypedilum* larvae examined by Titmus and Badcock (1981) contained a high percentage of detritus, together with a much smaller amount of algal material, mainly consisting of diatoms. Oligochaete predation has been detected in *Glyptotendipes*, *Endochironomus*, and *Polypedilum* (Loden, 1974). *Limnochironomus nervosus* is also known to eat both plants and animals: Beck (1977) classes this species as omnivorous. Many species of *Parachironomus* are similarly described. Higler (1977) classifies *Parachironomus* as a carnivore.

The remaining information extracted from the literature concerns essentially detritivorous larvae: *Cladotanytarsus mancus* and *Microtendipes pedellus* are described as such by Izvekova (1971); high percentages of detritus were found in *Tanytarsus* guts by Armitage (1968) and McLachlan *et al* (1978).

The categorisations presented in the preceding paragraphs are by no means definitive, nor is there any intention that they should be regarded as so. Attempts to provide rigid species classifications regarding diet and feeding behaviour may be confounded for several reasons. Firstly, age-specific differences in these characteristics are known to occur (Alekseev, 1978; McLachlan *et al.* 1978). Secondly, the dietary intake of insect larvae may change through the seasons, as illustrated by Chapman and Demory (1963), Armitage (1968), and Izvekova (1971). Thirdly, most aquatic insects appear to be polyphagous (Cummins, 1973) and their dietary composition at any time is likely to reflect the choice of food available in the immediate habitat, rather than an inherent requirement for a particular dietary make-up - a point Soska (1976) makes in reference to the Chironomidae, and exemplified in Sadler's (1935) study of *Camptochironomus tentans*.

Interzonal variation in the quality of food resources would only influence larval distribution if a) larvae showed a preference for certain areas because of the type of food they offered, or b) larvae were excluded or reduced in numbers in some places because the food quality there was less favourable than in others. In the first instance, the emphasis is on the ability of larvae actively to discriminate and choose between different sets of food conditions; in the second, larvae are envisaged as attempting to colonise different areas with equal conviction and in similar numbers (i.e. are non-discriminating), but are denied an even distribution by the conditions themselves. The situation referred to in alternative a) would necessarily involve some sort of selectivity[1] in feeding, which in aquatic insects is a seemingly rare phenomenon

---

[1]Cummins (1973) defines selective feeding as, 'the ingestion of only certain nutritive materials from a range of those that are equally available to the feeding insect'.

whose existence is occasionally evidenced (e.g. Davies, 1975) but extremely difficult to prove (Cummins, 1973). Certainly, the information gleaned from the literature offers no evidence to suggest that selective feeding would be an influencing factor in the determination of any larval patterns at Cop Mere. Alternative b) receives a similar lack of support, at least in one direction: the widespread occurrence of polyphagous adaptability tends to contra-indicate the idea of stem colonisation being inhibited in some areas by the epiphyton genus composition *per se*.

So far, epiphyton quality has only been considered in terms of generic composition. Certain qualitative characteristics exist, however, which can vary independently of algal make-up. One of these is energy content.

The energy content of zonal epiphyton samples was determined using a Gallenkamp CB-370 ballistic bomb calorimeter. (See Cummins and Wuycheck (1971) for a detailed account of bomb calorimetry methods.) This investigation produced data relating to three variables: ash content; energy value per gramme dry weight; and energy value per gramme ash-free dry weight.

Figure 4:2:7 illustrates interzonal differences in epiphyton ash content during 1981. From January to July, the greatest percentage of non-combustible material is usually found in Zone 1 and the lowest in Zone 3. From August to November, the position is, to some extent, reversed: values for Zones 1 and 2 fall whilst those for Zone 3 remain relatively stable, and by November the highest ash content is found in Zone 3 and the lowest in Zone 1.

Energy values per gramme dry weight are shown in Figure 4:2:8. Comparison with Figure 4:2:7 reveals close correlations. In each month, the zonal epiphyton which contains the highest percentage of non-combustible

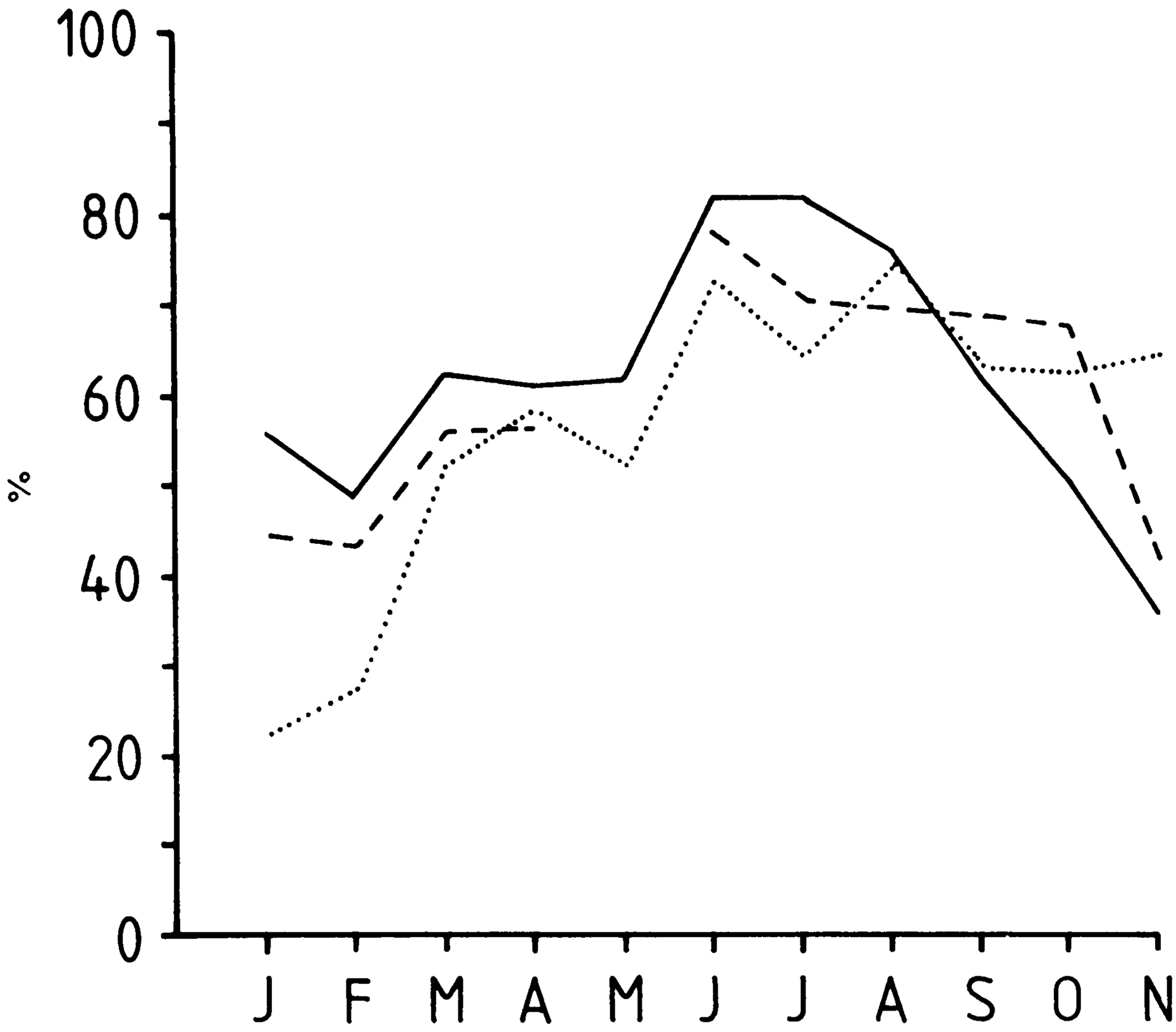


FIGURE 4:2:7 - Epiphyton ash content (expressed as a percentage of total dry weight) for old reedstems in Zone 1 (———), Zone 2 (- - -), and Zone 3 (·····) during 1981. (No information available for Zone 2 in May.)

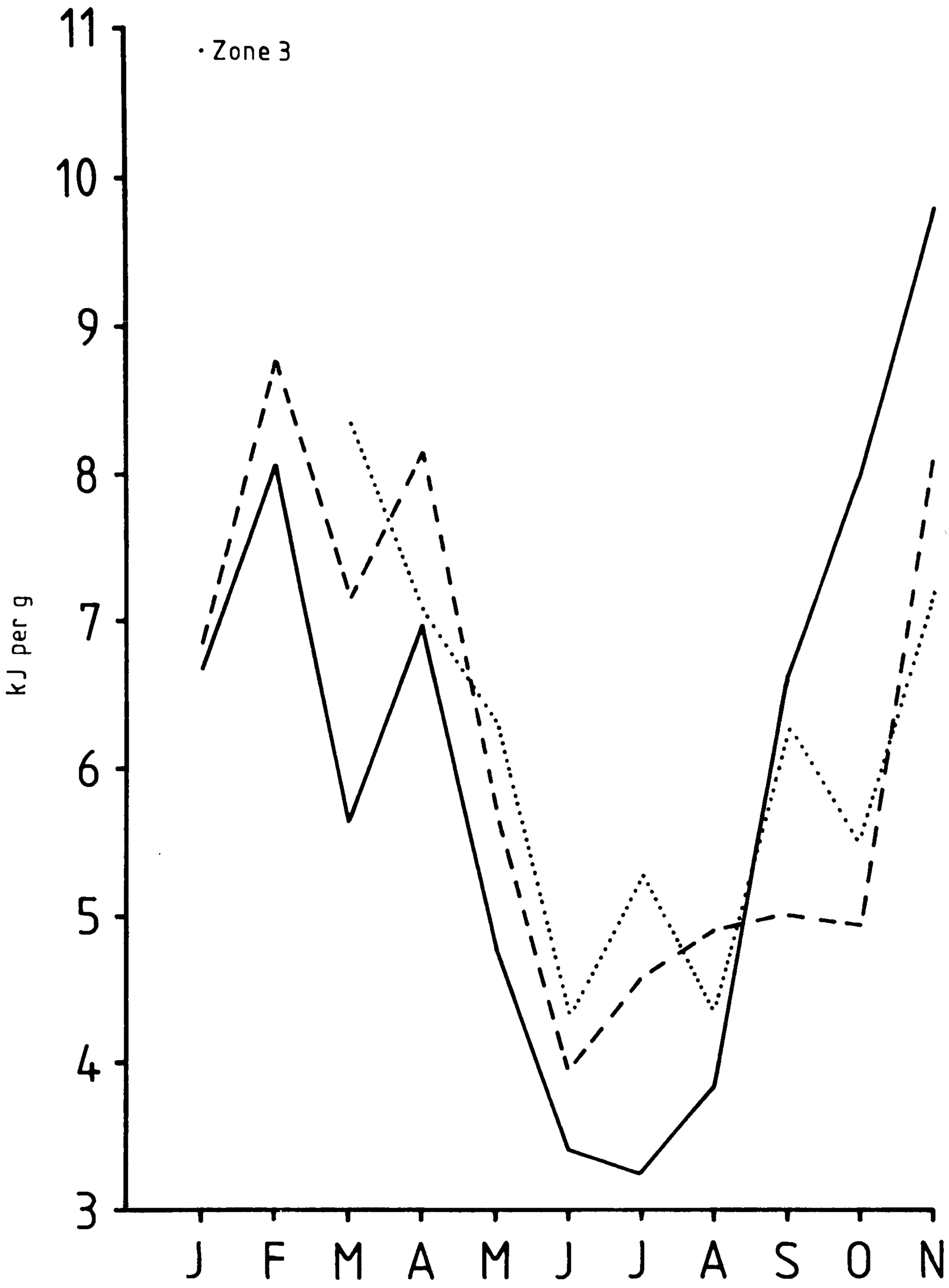


FIGURE 4:2:8 - Epiphyton energy content (kilojoules per gramme dry weight) for old reedstems in Zone 1 (———), Zone 2 (- - -), and Zone 3 (·····) during 1981. (No information available for Zone 3 in February.)

material also has the lowest energy content per gramme dry weight. Energy values throughout the reedbed are relatively low during the summer, when ash content is at its maximum levels due to an increase in the relative abundance of siliceous diatom remains.

Figure 4:2:9 portrays variation in the energy value of ignitable epiphytic material. One feature of prominence is the sharp drop in values during May. The reason for this fall is not readily apparent. A comparison of Figures 4:2:7, 4:2:8, and 4:2:9 suggests that variation in ash percentage, rather than variation in the energy content of ignitable material, is the underlying cause of month to month changes in the energy content of whole epiphyton. Neither Figure 4:2:8 nor 4:2:9 indicates any repeated similarity in zonal hierarchical order through the year.

Having established the spatiotemporal patterns of variation in epiphyton energy value, an attempt can be made to gauge their possible influence on patterns of larval density and biomass. Such an influence might exist if an increase in energy content meant more larvae could be sustained on the same amount of food. However, a comparison of the relevant graphs for larval density and biomass (Figures 3:2:1 and 3:2:2) with the graph showing epiphyton energy values per gramme dry weight (Figure 4:2:8) suggests larval variation occurs independently of energy content variation: during the summer, when larval quantities are at their highest levels, energy values are at a minimum; in addition, the zone which usually supports the greatest larval densities (Zone 1) also provides the lowest monthly energy values over most of the year.

An extensive literature search revealed an absence of information relating to the possible influence of variation in epiphyton energy content on populations of chironomid larvae. Some useful comparative data,

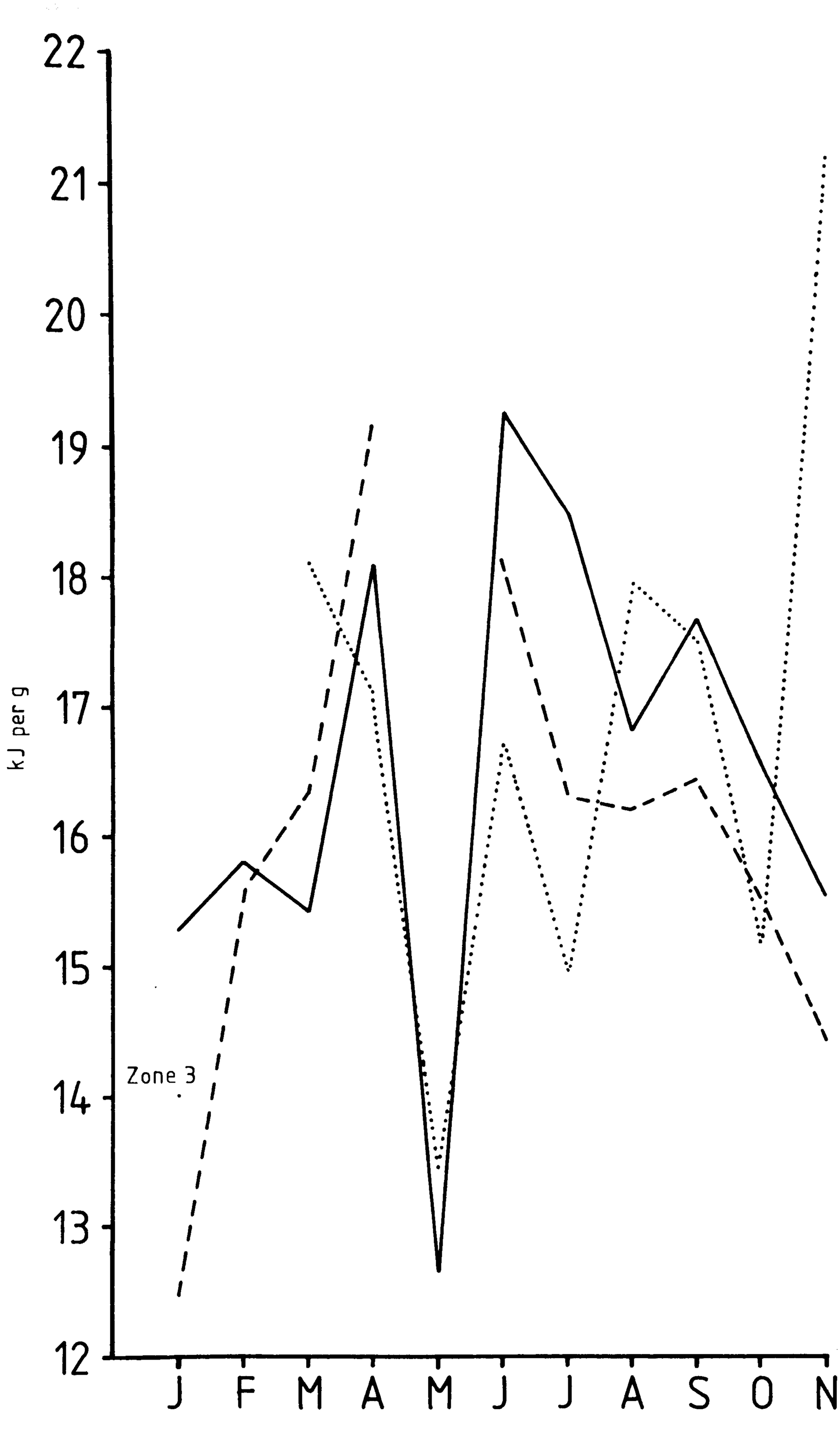


FIGURE 4:2:9 - Epiphyton energy content (kilojoules per gramme ash-free dry weight) for old reedstems in Zone 1 (———), Zone 2 (- - -), and Zone 3 (·····) during 1981.

(No information available for Zone 3 in February!)

	Z	SMOOTH	SOFT	ROUGH	HARD	F
J	1					
	2					
	3					

F	1					
	2					
	3					

M	1					
	2					
	3					

A	1					
	2					
	3					

M	1					
	2					
	3					

J	1					
	2					
	3					

FIGURE 4:2:10 (cont...) (See next page for legend.)

	Z	SMOOTH	SOFT	ROUGH	HARD	F
J	1					
	2					
	3					

A	1					
	2					
	3					

S	1					
	2					
	3					

O	1					
	2					
	3					

N	1					
	2					
	3					

D	1					
	2					
	3					

FIGURE 4:2:10 (...cont.) - Types of epiphytic reedstem coating found in Zone 1 (Z1), Zone 2 (Z2), and Zone 3 (Z3) during 1981.

F - Epiphytic filamentous algae

■ - present □ - absent

concerning the energy status of certain materials, is supplied by Cummins and Wuycheck (1971), however. They quote Kevern and Ball's (1965) figure of 4520 calories (18.93 kilojoules) per gramme ash-free dry weight for a laboratory culture of periphyton; in the present study, a mean value of 16.52 kilojoules per gramme was obtained for combustible epiphytic material. Cummins and Wuycheck also provide energy values for Bacillariophyceae and *Cladophora* (3814 calories (15.97 kilojoules) and 2120 calories (8.88 kilojoules) per gramme dry weight respectively); in the present study, the energy content of *Cladophora* was measured as 7.58 kilojoules per gramme dry weight. These figures indicate that *Cladophora* is a relatively low-energy food source; its summer increase at Cop Mere is, therefore, unlikely to have any positive food-related influence on the synchronous proliferation of larvae.

One aspect of epiphyton quality that has yet to be examined relates to the gross morphology and texture of the epiphytic reedstem coatings. These characteristics may affect the potential of epiphyton as a source of food and/or shelter.

Two basic types of reedstem coating can be recognised: a smooth, soft veneer of non-filamentous algal forms, which is generally found on newer stems, and a rough, often patchy, encrustation of mainly diatomaceous material, characteristic of long-standing old stems. Some filamentous alga may begin to build up on the newer stems, but it is most prevalent as a spatially intermittent overlay on stems in the latter category.

Figure 4:2:10 illustrates the spatiotemporal occurrence patterns for the two types of reedstem coating and filamentous algae during 1981. These patterns reflect, to a large extent, the ages of the stems taken in each month. From January to April, the only stems to be found are from the previous season's growth and acquire their thin but thickening layer of epiphyton through the winter and spring. By May, this layer has started to develop into the diatomaceous encrustation that

exists on all old stems over the summer (June to August). Stems from the previous season's growth become increasingly rare through the autumn and many of the 'old' stems cut from September onwards originally appeared at the beginning of the present season and had since died (see p. 19). The surface of these latter samples was covered with the same fresh algal veneer as found in the first part of the year.

Very little interzonal variation in coating type is evident. That which does occur is confined to October and November, and indicates that old, encrusted stems survive for a longer period of time in Zone 3 than elsewhere.

The resource potential of epiphyton as a food source could be partly dependent on its hardness: the solidification of diatomaceous epiphyton is likely to render some underlying material inaccessible to grazing larvae. The onset of the solidification process does not cause any reduction in larval density or biomass, however. Indeed, during the summer, when all old stems have a hard algal covering, larval quantities are at their maximum levels.

The two types of reedstem coating differ in the degree of shelter they offer: hard, coarse-textured epiphyton provides a surface in which larvae can firmly entrench themselves; soft, smooth epiphyton constitutes a less favourable surface for anchorage and concealment. The appearance of filamentous algal growths augments larval accommodation capacity. Thus, the optimum refuge conditions over the year are found in Zones 1 and 2 during May and June, when rough diatomaceous material is overlain by a prolific, filamentous growth of *Cladophora*. Larval quantities show a marked rise in these two months - this may be partly attributable to the concurrent arrival of the optimum conditions described above, which results in a greater capacity for larval accommodation. This increase in capacity is also dependent on higher epiphyton densities,

however, and the inextricable nature of many quantitative and qualitative algal changes prohibits a precise assessment of their respective impacts on the larval population. As such influences are unlikely to operate in mutual isolation anyway, no investigation deficiency is incurred.

Interzonal differences in the shelter afforded by epiphyton may be partly responsible for concomitant variation in larval quantities. Chironomids are most numerous in Zone 1, where the presence of refuge-providing filamentous algal growths is conducive to the existence of high larval densities; larvae are much less abundant in Zone 3, where these growths are absent.

A number of studies have shown spatial variation in substrate type to have a significant shelter-related influence on spatial patterns of larval density. Mason and Bryant (1975) examined the chironomid populations on *Typha* stems and glass rods. They found larvae were abundant on the stems but were absent from the rods and concluded that this latter absence was due to the lack of a suitable surface for anchorage or burrowing. Ali and Mulla (1976) investigated the spatial distribution of chironomids in relation to five substrate types in a Californian drainage system, and discovered that the species density of chironomid larvae varied from substrate to substrate. Filamentous algal carpets supported substantial numbers of *Chironomus* and *Cricotopus* (the two chironomid genera present in the drainage system), whereas bare concrete surfaces were sparsely populated. An analogy can be made with the interzonal differences in reedstem coatings and larval densities found at Cop Mere and described in the previous paragraph. Specific associations between particular larvae and algae were revealed by Neel (1968) in his study of a limestone stream; for example, *Spaniotoma* (O.) *nivoriunda tatrica* gr. was confined to areas of *Cladophora*. Species-dependent differential microhabitat exploitation is reported by LeSage and Harrison (1980)

with reference to fifteen species of *Cricotopus* in an algal-enriched stream. They found that a dense covering of diatoms and filamentous algae provided the best microhabitat for this genus. Four species, including *Cricotopus sylvestris*, reached their highest densities here and most of the others were also numerous.

Some interzonal patterns of chironomid species dispersion may reflect interzonal differences in the degree of shelter afforded by reedstem coatings. Size variation between instars could be important here: the characteristically large fourth instar larvae of certain species are likely to require a denser epiphytic growth in which to conceal themselves than smaller larvae of the same or different species. This provides a feasible explanation of the zonal distribution pattern of reedstem-dwelling *Endochironomus* larvae. These larvae are mainly fourth instars and are confined to Zones 1 and 2, where the epiphyton tends to give better protection than in Zone 3. The *Cricotopus sylvestris* larval population in Zones 1 and 2 contains a noticeably higher proportion of fourth instars than that in Zone 3 (see p. 87), another pattern which could be due to interzonal variation in the degree of shelter provided by epiphyton. The fact that the characteristically large fourth instars of another genus, *Glyptotendipes*, show no zonal restriction is no doubt a reflection of the fact that fourth instar *Glyptotendipes* live in the top of broken stems and do not rely on the epiphytic reedstem coating for protection.

4:3 Spatiotemporal Variation in Characteristics of the Ambient Water Environment - The Effects on Larval Population Patterns

A) TEMPORAL ASPECTS OF VARIATION IN THE WATER ENVIRONMENT

All larvae will have an optimum set of physico-chemical water conditions in which they can live most successfully. Preferences and tolerance ranges can differ according to species and instar status.

Potentially, spatiotemporal variation in water properties could influence similar variation in larval populations.

Four parameters were monitored during 1981 and 1982: temperature; oxygen content; pH; and conductivity. Temporal patterns of change in these characteristics are illustrated in Chapter 2. Month to month variations in water temperature (Figures 2:4:1 and 2:4:2) are likely to have the greatest influence on temporal differences in overall larval density (Figure 3:2:1). The rise in temperature that occurs through spring and into summer accelerates metabolic processes and hence the rate of larval development. This has important consequences in relation to emergence patterns and generation sequences, and temperature variation through time will, therefore, exert a fundamental control on temporal changes in larval density. Here, characteristic annual patterns of larval density change are inextricably linked to similarly characteristic temperature differences over the year - the expression of intrinsic population qualities is controlled, to a large extent, by an essentially predictable pattern of variation in an extrinsic factor.

Low winter temperatures may affect larval numbers in some species by triggering an inherent behavioural response. Danks (1971a) reports that vertical migration in benthic-dwelling *Einfeldia synchrona* (Oliver) larvae occurs synchronously with the onset of winter conditions. A number of chironomids are known to build cocoons for hibernation purposes; such behaviour has been observed in *Camptochironomus tentans*, *Endochironomus subtendens* (Townes), and *Limnochironomus nervosus* by Danks (1971b), Buscemi (1957), and Sokolova (1966) respectively. Migration and/or cocoon formation induced by low temperatures may partly account for a winter reduction in larval density in some reedstem-dwelling chironomid species at Cop Mere but substantial evidence is lacking in this respect. An increase in temperature during the spring could prompt the movement

of rheophilic Orthocladiinae (notably *Rheocricotopus* and *Thienemanniella)* away from the reedstem environment to seek preferably cooler conditions elsewhere.

Low temperatures may have an adverse effect on the survival of reedstem-dwelling larvae. Sturgess and Goulding (1968) studied three species of chironomid (*Glyptotendipes barbipes* (Staeger), *Anatopynia dyari* (Coquillet), and *Chironomus riparius* (Meigen)) and found cold tolerance in juveniles varied from species to species but all three suffered mortality when exposed to a temperature of 0°C.

An increase in water temperature can lead to mortality in larval populations by causing a reduction in oxygen availability. Figure 2:5:2 shows temporal changes in oxygen content at Cop Mere during 1981 and 1982; in both years, levels appear to be consistently high enough not to cause distress to larvae. During the summer, increased oxygen availability through greater photosynthetic activity more than compensated for any temperature-linked reduction in oxygen carrying capacity. The comparatively high saturation levels at this time were no doubt conducive to the well-being and accommodation of an expanding population of juvenile chironomids but increases in oxygen content and larval numbers are probably coincidental.

Figures 2:5:3 and 2:5:4 illustrate temporal variation in pH and conductivity respectively. Comparatively high pH values during the summer are a reflection of changes in water chemistry caused by an upsurge in photosynthetic activity. This also explains a simultaneous reduction in conductivity levels. There is no evidence to suggest that temporal differences in larval density and/or population species composition are in any way influenced by these changes in pH and conductivity.

B) INTERZONAL VARIATION IN THE WATER ENVIRONMENT

So far, relationships between physico-chemical water characteristics and larval population patterns have only been considered in a temporal

context. In certain cases, closer relationships might exist on a spatial basis because here larvae are often exposed to gradients in water characteristics through the reedbed and conditions in one area may be more favourable than those in another, a situation which could influence spatial patterns of larval abundance.

Table 4:3:1 shows interzonal differences in both water temperature and oxygen content during 1981 and 1982. The maximum interzonal difference in temperature at any time is only 0.3°C - the very small variations that occur through the area of permanent standing water in the reedbed cannot be envisaged as having any effect on population patterns. In his study of *Chironomus zealandicus* larvae, Barker (1966) recorded a maximum spatial temperature range of 2.1°C and concludes that variation of this magnitude or less is unlikely to be a dominant factor in determining distribution. Davies (1976a) states that there is little evidence to suggest temperature alone has a major influence on the distribution of juvenile Chironomidae within lakes.

Where an interzonal gradient in oxygen content exists, the highest content is found in Zone 1 and the lowest in Zone 3. Similarly directed oxygen gradients are reported by Dvorák (1970; 1971) and Dvorák and Lisková (1970) in studies relating to emergent macrophyte stands in some South Bohemian ponds. Dvorák suggests that spatial variation in the macrofauna communities of these stands is influenced by the marked spatial variation that is often found in oxygen availability. As with temperature, interzonal differences in oxygen content at Cop Mere are small and, because of this, their effect on chironomid larval distribution is probably non-existent or, at most, negligible.

Interzonal differences in pH and conductivity are shown in Table 4:3:2. The highest pH value in each month is generally found in Zone 1 and the lowest in Zone 3. Apart from September, 1981, where a difference of 2.3 exists between Zone 1 and Zone 3, monthly

	Temperature (°C)			Oxygen (% saturation)		
	Z1	Z2	Z3	Z1	Z2	Z3
Jan	-	5.0	-	-	-	-
	-	(5.0)	-	-	-	-
Feb	5.6	5.7	5.9	-	-	-
	-	(5.0)	-	(50.8)	(49.8)	(48.7)
Mar	-	11.0	-	-	-	-
	-	(8.3)	-	-	-	-
Apr	-	10.7	-	-	-	-
	(8.0)	(8.0)	(8.0)	(100+)	(100+)	(100+)
May	-	15.1	-	-	-	-
	(18.2)	(18.1)	(18.2)	(100+)	(100+)	(100+)
Jun	-	16.6	-	-	-	-
	-	(21.9)	-	(100+)	-	-
Jul	-	18.6	-	-	-	-
	-	(19.0)	-	(84.0)	-	-
Aug	-	19.2	-	-	-	-
	-	(17.8)	-	(100+)	-	-
Sep	18.5	18.4	18.4	100+	100+	99.0
	-	(15.9)	-	(37.9)	-	-
Oct	7.3	7.0	7.0	55.5	53.0	47.0
	-	(10.7)	-	(83.3)	(90.0)	(67.5)
Nov	-	6.5	-	-	-	-
	-	(2.5)	-	(56.3)	(56.3)	(56.3)
Dec	-	0.0	-	-	-	-
	(1.8)	(1.8)	(1.8)	(85.2)	(84.0)	(81.6)

TABLE 4:3:1 - Water temperature and oxygen content readings for Zones 1 (Z1), 2 (Z2), and 3 (Z3) taken during 1981 (top line) and 1982 (bottom line, in parentheses).

	pH			Conductivity (µS x 10^4)		
	Z1	Z2	Z3	Z1	Z2	Z3
Jan	-	-	-	-	-	-
	(7.3)	(7.2)	(7.1)	(4.85)	(4.70)	(4.90)
Feb	7.7	8.1	7.9	5.09	5.09	5.08
	(8.5)	(8.3)	(8.1)	(6.05)	(5.95)	(5.95)
Mar	-	7.4	-	-	4.65	-
	(8.8)	(8.7)	(8.4)	(4.35)	(4.40)	(4.20)
Apr	-	7.8	-	-	5.09	-
	(8.0)	(8.2)	(7.8)	-	-	-
May	-	7.8	-	-	5.72	-
	(8.8)	(8.8)	(8.9)	(3.17)	(3.29)	(3.21)
Jun	9.3	9.0	8.9	3.30	3.35	3.42
	(10.3)	(10.2)	-	(2.60)	-	-
Jul	8.3	7.9	-	4.31	4.37	-
	(8.5)	(8.4)	-	(3.20)	-	-
Aug	9.1	9.0	-	4.40	4.34	-
	(9.1)	(9.0)	-	(3.25)	-	-
Sep	9.0	8.4	6.7	4.13	4.50	5.54
	(7.5)	(7.5)	(7.5)	(3.40)	(3.40)	(3.40)
Oct	7.4	7.3	7.2	4.80	4.75	4.83
	(7.4)	(7.4)	(7.4)	(3.20)	(3.20)	(3.40)
Nov	7.6	76.	7.4	5.00	4.98	5.20
	(7.6)	(7.5)	(7.3)	(2.92)	(3.00)	(3.00)
Dec	-	7.4	-	-	3.90	-
	(7.3)	(7.2)	(7.1)	(3.20)	(3.20)	(3.30)

TABLE 4:3:2 - pH and conductivity readings for Zones 1 (Z1), 2 (Z2), and 3 (Z3) taken during 1981 (top line) and 1982 (bottom line, in parentheses).

interzonal variation in pH values is 0.4 or less. In his study of a littoral stand of *Glyceria aquatica* (L.) Wahlb., Dvorak (1970) found a similar directional trend in pH to that which exists in the reedbed at Cop Mere. He recorded a value of 8.25 at the lakeward edge of the stand and a value of 6.25 at the landward edge. No mention was made of this pH difference in relation to spatial variation in the macrofauna community of the area.

A literature examination reveals that investigations of the effects of different pH levels on chironomid larvae all seem to be concerned with greater variations than those occurring through Zones 1-3 at Cop Mere. Thornton and Wilhm (1974) studied the survival of *Chironomus attenuatus* (Walker) juveniles at three pH levels (6.2, 7.2, and 8.2) and found most larvae survived at pH 7.2. Significant differences in mortality were noted between the three treatments. Bell (1970) examined the effects of pH on the life cycle of *Tanytarsus dissimilis* (Joh.) and discovered that larvae survived in a range of pH levels from 5.0 to 7.8 with equal success.

Unless larvae actively seek particular pH conditions and are able to discriminate different levels over a very small range, the characteristic spatial pH gradient that exists through Zones 1-3 in the reedbed at Cop Mere is unlikely to influence larval population patterns. Literature evidence suggests differential mortality would not occur over such a narrow gradient.

Interzonal differences in conductivity are usually slight and a repeated hierarchical pattern of zonal values was not found. There is no evidence to suggest that small spatial variations in conductivity have any effect on the chironomid community of the reedbed.

4:4 Miscellaneous Factors - The Effects on Larval Population Patterns

A) INITIAL SPATIAL DISTRIBUTION OF EGG MASSES

The spatial pattern of egg-laying in a chironomid species with

epiphyton-dwelling larvae could be responsible, to some extent, for the spatial distribution of the larvae. This idea has been considered already, in relation to the zonal distribution pattern of *Psectrocladius limbatellus* juveniles (see p. 91). Assuming *limbatellus* eggs are laid in open water, unsettled larvae will arrive in Zone 1 before Zone 2 or 3 and most will remain at the lakeward edge of the reedbed. The egg masses themselves may collect along this frontal margin, carried here by water movements induced by northerly winds. Davies (1976b) investigated the wind distribution of *Chironomus anthracinus* (Zetterstedt) egg masses at Loch Leven and found oviposition site selection had little influence on the final distribution of larvae - wind-induced water currents led to floating egg mass accumulation along wind-exposed shorelines.

In May, 1982, a search was made at Cop Mere for egg masses attached to reedstems; nine were discovered in Zone 1, five in Zone 2, and four in Zone 3. This variation in numbers is not necessarily indicative of any zonal preference in ovipositing females and may reflect interzonal differences in reedstem density. (At the time of egg mass collection, the mean number of reedstems per m^2 in Zones 1, 2, and 3 was 127, 110, and 104 respectively.) Of eight masses identified for Zone 1, six were from *Camptochironomus tentans* and two were from *Endochironomus*. All those in Zones 2 and 3 belonged to *Camptochironomus tentans*.

Interzonal differences in egg mass numbers would only have the potential to cause interzonal larval density variation if larvae remained in the zone in which they hatched. Although large monospecific first instar aggregations on certain stems suggested these individuals had stayed close to their hatching location, a general lack of interzonal migration cannot be assumed as planktonic activity of several

hours duration has been recorded in the newly-hatched first instars of many chironomid taxa, including *Camptochironomus tentans* (Salder, 1935; Shilova, 1958); *Glyptotendipes pallens* (Mordukhai-Boltovskoi and Shilova, 1955); *Cricotopus sylvestris* and *Corynoneura* (Luferov, 1966b); *Endochironomus*, *Microtendipes*, *Parachironomus* and *Polypedilum* (Lellak, 1968); and *Cladotanytarsus* (Armitage, 1970). Such planktonic activity could take larvae well away from their hatching location.

B) PHOTOTACTIC LARVAL BEHAVIOUR

In many chironomid species, migratory behaviour in first instar larvae is closely linked to a positive phototactic response (Davies, 1976a). Such a response is not necessarily exclusive to first instars, however, although it appears to be strongest at this stage of development.

Interzonal variation in illumination could influence larval distribution through the reedbed. Table 4:4:1 gives zonal light penetration readings[1] taken during 1982. In general, light penetration progressively diminished from the front (lakeward edge) to the back (landward edge) of the area of permanent standing water, mainly because a taller canopy of aerial *Phragmites* stems exists towards land.

Luferov (1966b, 1971) investigated the phototactic behaviour of *Cricotopus sylvestris* larvae and found a noticeable positive phototactic response which is particularly strong in first and second instars; indeed, Luferov regards this species as one of the most light-requiring chironomids. Markosová (1974) also reports positive phototaxis in *Cricotopus sylvestris* larvae.

---

[1] Light recordings were made with the appropriate probe from the WPA environmental multiprobe kit referred to in Chapter 2. The readings are on an arbitrary scale but those taken in different zones at the same time will be related in a linear fashion.

Interzonal differences in light penetration are most pronounced during the summer, when a dense canopy of *Phragmites* in Zone 3 shuts out a great deal of illumination here. More light enters the water in Zones 1 and 2, where the *Phragmites* cover is sparser. This inequality in light penetration may explain the pattern of interzonal variation in chironomid larval density and biomass that exists from July to October, 1981 and is described in Figure 3:2:4; here, no significant differences are found in larval density or biomass between Zones 1 and 2 but larval quantities in both these zones are significantly larger than those in Zone 3. This cannot be explained by a similar pattern of variation in epiphyton biomass as interzonal differences in this variable from July to October are almost always insignificant.

	Zone 1	Zone 2	Zone 3
January	-	-	-
February	-	-	-
March	-	20	12
April	45	54	43
May	9	8	5
June	-	-	-
July	-	8	1
August	-	-	-
September	68	27	-
October	5	5	2
November	20	14	8
December	2	1	1

TABLE 4:4:1 - Light penetration recordings made at 20cm below the water surface in Zones 1, 2, and 3 during 1982. (See footnote 1 on previous page for explanation of values.)

Much bigger larval numbers may be found in Zones 1 and 2 than Zone 3 at this time because higher levels of illumination exist towards the front of the reedbed and, during the summer and early autumn, a large proportion of the reedstem-dwelling chironomid population is made up of strongly phototactic first and second instar *Cricotopus sylvestris* larvae.

The dispersion patterns of reedstem-dwelling larvae other than *Cricotopus sylvestris* may be influenced by light. Positive phototaxis has been recorded in the first instars of *Camptochironomus tentans* (Sadler, 1935); *Glyptotendipes pallens* (Mordukhai-Boltovskoi and Shilova, 1955); *Tanytarsus lewisi* (Lewis, 1957); *Endochironomus albipennis* and *Corynoneura* (Luferov, 1966b); *Cladotanytarsus* sp. (Armitage, 1970); *Psectrocladius psilopterus* type (Davies, 1976a); and *Polypedilum* gr. *nubecolosum* (Markosová, 1974).

The vast majority of the *Camptochironomus tentans* larvae living on reedstems at Cop Mere are first instars and most of these inhabit Zones 1 and 2. This tendency to exist in the better illuminated zones towards the front of the reedbed may reflect a positive phototactic response - the fact that *Camptochironomus* egg masses have been collected in sizeable numbers from all three zones suggests that some sort of migration takes place from Zone 3 into Zones 1 and 2.

The zonal distribution pattern of first instar *Parachironomus arcuatus* larvae is similar to that described above for *Camptochironomus tentans* and could also be a possible reflection of positive phototactic behaviour.

The first instar numbers of most of the chironomid species with reedstem-dwelling larvae are insufficient to draw conclusions regarding the role of differential illumination in determining their spatial distribution.

Sensitivity to changes in light intensity is most acute in early instars; older larvae are less able to discriminate differences in light intensity at the low illumination levels which they prefer (Luferov, 1966a) so their distribution in the reedbed, where illumination is poor compared with open water, is unlikely to be influenced by spatial variation in light penetration.

C) INTER-SPECIFIC RELATIONSHIPS WITHIN THE CHIRONOMID POPULATION

There is no evidence to suggest that the spatiotemporal patterns of larval abundance in any chironomid species are influenced by the patterns for another chironomid species. Larvae of several species are often found co-existing on the same stem with apparent success. The dietary investigations discussed in Section 2 of this chapter indicate that cannibalism is probably a very rare phenomenon, if it exists at all, and the resource potential of the epiphyton, in terms of food and shelter, appears sufficient to preclude the interspecific competition that might exist where these resources are in shorter supply.

D) PREDATION BY NON-CHIRONOMIDS

Apart from the chironomid larval population, the epiphyton on reedstems supports a non-chironomid faunal community that shows noticeable spatiotemporal variation in species composition (see Appendices B and C). Several members of this community are known to prey on chironomid larvae.

Four species of leech (Hirudinea) are found on reedstems at Cop Mere: *Erpobdella octoculata* (Linnaeus); *Glossiphonia complanata* (Linnaeus); *Helobdella stagnalis* (Linnaeus); and *Theromyzon tessulatum*

(Müller). *Erpobdella* is the most numerous, accounting for 80% of the total leech population collected from stems during 1981. Elliott (1973) found that this leech feeds principally on chironomid larvae from March to September; no feeding activity at all takes place between October and February. Dresscher and Engel (1960) also reveal that juvenile chironomids are eaten by *Erpobdella*.

Elliott and Mann (1979) state that *Helobdella stagnalis* consumes a variety of aquatic invertebrates including chironomid larvae. This species has been reported as preying on *Chironomus plumosus* (Linnaeus) larvae by Hilsenhoff (1963); Keim (1977) fed laboratory populations of *stagnalis* with juvenile *Camptochironomus tentans*, *Chironomus plumosus*, and *Chironomus thummi*. However, Davies and Everett's (1975) laboratory studies of feeding in *Helobdella stagnalis* suggest that, when this leech is presented with a range of food materials, chironomid larvae are generally ignored. Davies and Everett found similar feeding behaviour in *Helobdella stagnalis* and *Glossiphonia complanata*. Harding (1910) reports the consumption of chironomid larvae by the latter species.

Theromyzon tessulatum is a sanguivorous parasite of water birds (Elliott and Mann, 1979) and will not, therefore, have a predatory effect on juvenile chironomid populations.

Paterson (1970) investigated predation by water mites (Hydracarina) on the larvae of a number of chironomid species, including *Camptochironomus tentans* and *Glyptotendipes barbipes* (Staeger), and suggests that 'predation by water mites is of some importance in the ecology of lentic chironomid populations'.

Apart from leeches and water mites, other reedstem-dwellers are known to eat chironomid larvae, including *Polycelis tenuis* (Reynoldson and Young, 1965), *Planaria torva* (Reynoldson and Sefton 1976), larval Ceratopogonidae, larval Polycentropidae, and some species of Corixidae (Higler, 1977).

An analysis of Appendix C reveals that the only predators of chironomid larvae to occur in appreciable numbers are water mites and

Erpobdella octoculata. Table 4:4:2 shows the numbers of these animals found on reedstems in each zone during 1981. Throughout the sampling period, most individuals inhabit Zones 1 and 2, which also

	Erpobdella			Hydracarina		
	Z1	Z2	Z3	Z1	Z2	Z3
January	0	0	0	0	0	0
February	0	0	0	3	0	0
March	0	0	0	3	3	1
April	0	0	0	5	3	1
May	1	1	0	16	14	2
June	30	12	1	7	0	0
July	30	25	1	3	3	0
August	52	5	13	19	1	0
September	14	2	0	0	0	0
October	2	0	0	0	0	0
November	1	1	0	0	0	0

TABLE 4:4:2 - Numbers of *Erpobdella octoculata* and Hydracarina found on reedstems in Zones 1 (Z1), 2 (Z2), and 3 (Z3) during 1981.

tend to support the highest densities of chironomid larvae. There is no indication that spatiotemporal variation in larval density may be

influenced by the presence of predators. Certainly, no 'predator-prey' cycle appears to be in operation. Although *Erpobdella* and Hydracarina are the commonest predators, they are probably insufficiently numerous to have any recognisable impact on the chironomid population.

4:5 Interzonal Variation in Larval Populations - An Experimental Investigation of Determining Factors

A) EXPERIMENTAL PROCEDURE

During 1982, field experimentation was undertaken to test some of the propositions concerning larval dispersion made on the basis of the studies carried out in the previous year. This experimentation involved the use of bamboo canes, which provide an ideal substitute for reedstems.

In February, 1982, ten bamboo canes were 'planted' at five-metre intervals along each of Zones 1 and 3. These canes were left in position over the spring and summer, during which time they acquired a coating of epiphytic material.

On September 9th, 1982, five canes were removed from Zone 1 and five from Zone 3. The epiphyton-covered portions were wrapped in polythene bags to ensure moisture retention and the canes were then transported back to the laboratory. A strong jet of water was used to dislodge any epiphyton-dwelling chironomid larvae, which were subsequently counted and identified.

The following day, the five canes which originally came from Zone 1 were returned to the reedbed but were placed in Zone 3; the five canes which originally came from Zone 3 were placed in Zone 1. Six days later, these ten canes were again uprooted and taken back to the laboratory for larval identification and enumeration. This time,

epiphyton densities were calculated. On the same day (16th September, 1982), the five previously untouched canes in each of Zones 1 and 3 were removed and their larval populations examined.

All macroinvertebrates found on canes are listed in Appendix L.

B) EXPERIMENTAL RESULTS AND INTERPRETATION

Table 4:5:1 gives information relating to epiphyton density and the density and taxonomic composition of the larval chironomid populations examined during the course of the experiment. (The raw data from which this information is derived are presented in Appendix M.) Mann-Whitney *U* analyses were undertaken to reveal any significant difference between the two larval density means in each of Columns A, B, and C. The same test was used to compare the epiphyton density means in Column B. The presence or absence of significance is indicated in Table 4:5:1. (The actual *U* values obtained from the Mann-Whitney analyses are given in Appendix M.)

The principal question this experiment aimed to answer was whether the larval density of a stem is dependent on epiphyton characteristics or some other factor(s). In the latter case, non-epiphytic aspects of the ambient environment, or the actual location of the stem, may be important. By transferring canes from one zone to another, an attempt can be made to assess the relative importance of epiphytic and non-epiphytic factors.

The fact that, after six days, no significant difference in mean larval density is found between the canes from Zone 3 put in Zone 1 and the canes from Zone 1 put in Zone 3, yet at the same time the difference in mean larval density between the previously untouched canes from the two zones is significant, suggests that either a) insufficient time has been available for the attainment of a significant interzonal

	A		B		C	
	Z1	Z3	Z1(ex Z3)	Z3(ex Z1)	Z1	Z3
Larval Density	2.17	0.11*	1.17	0.41	5.67	0.07*
Epiphyton Density	-	-	3.00	9.30*	-	-
Camptochironomus	1.68	6.67	0.00	47.93	0.09	0.00
Cricotopus sylvestris	96.01	84.44	99.78	42.15	99.15	89.29
Endochironomus	0.50	0.00	0.00	1.65	0.12	0.00
Glyptotendipes	1.31	4.44	0.00	5.79	0.46	3.57
Limnochironomus	0.12	0.00	0.00	0.83	0.12	0.00
Parachironomus	0.37	0.00	0.00	0.00	0.03	0.00
Corynoneura	0.00	2.22	0.00	0.83	0.00	3.57
Metriocnemus sp. C	0.00	2.22	0.22	0.83	0.00	3.57
Metriocnemus sp. A	0.00	0.00	0.00	0.00	0.03	0.00

TABLE 4:5:1 - Results of cane experiment undertaken during September, 1982. The larval density (larval no. per cm^2) and epiphyton density (mg dry weight per cm^2) figures are means. (See Appendix M for standard errors.) Those figures referring to chironomid taxa are percentage relative abundance values relating to the total larval population of each set of canes. Column A refers to the larvae found in Zones 1 (Z1) and 3 (Z3) at the start of the experiment. Column B refers to the larvae and epiphyton found on repositioned canes after six days; Z1(ex Z3) canes are those originally from Zone 3 which were transferred to Zone 1; Z3(ex Z1) canes are those originally from Zone 1 which were transferred to Zone 3. Column C refers to previously untouched canes taken at the end of the six-day experimental period.

*indicates where a significant difference exists between two means, as exposed by Mann-Whitney *U* analysis (Significance level = 0.05 for a two-tailed test.)

density difference, or b) the ambient environment and epiphytic growth in Zone 1 are conducive to relatively high larval numbers, whereas the same characteristics in Zone 3 are not - by placing Zone 1 canes in Zone 3 and vice-versa, this disparity in environmental suitability is cancelled out and similar densities are reached in the two zones.

Over the six-day experimental period, mean larval density on original Zone 1 canes more than doubles (from 2.17 to 5.67), whilst the density for canes in Zone 1 that were originally in Zone 3 is lower than that found on Zone 1 canes at the beginning of the experiment (1.17 as opposed to 2.17). Larval density on original Zone 3 canes shows a slight fall over the six days (0.11 to 0.07) whereas a rise is evident between the density on Zone 3 canes at the start of the experiment and that on canes from Zone 1 that had been repositioned in Zone 3 (0.11 to 0.41).

The patterns described above suggest that the canes from Zone 1, when repositioned in Zone 3, may attract more larvae than original Zone 3 canes because of their higher epiphyton density - Zone 3 canes, when placed in Zone 1, may attract less larvae than original Zone 1 canes because of their lower epiphyton density. Certainly, interzonal variation in larval density appears to be influenced primarily by some aspect of interzonal variation in epiphyton characteristics.

Comparison of columns A and C (Table 4:5:1) shows that, over the six-day experimental period, the chironomid larval community in both Zones 1 and 3 remains essentially similar in terms of the taxa present and their relative abundance. Comparison of columns B and C, however, indicates noticeable community differences in each zone between native canes and those introduced from elsewhere. Apart from *Cricotopus sylvestris*,

the only taxon to colonise the ex Zone 3 canes in Zone 1 is *Metriocnemus* sp. C, whereas seven taxa are found on the previously untouched canes in Zone 1. More taxa colonise ex Zone 1 canes in Zone 3 than are present on canes native to Zone 3. Four are common to both sets of canes; the remaining three (*Camptochironomus*, *Endochironomus*, and *Limnochironomus)* occur exclusively on those canes transferred from Zone 1.

During 1981 and 1982, *Endochironomus* was never collected from any stems or canes native to Zone 3 but it does occur on ex Zone 1 canes in Zone 3 in the latter year, suggesting some aspect of interzonal epiphyton variation is the principal determinant of the interzonal dispersion pattern for this genus. This supports the conclusions drawn from the 1981 stem-sampling programme regarding the interzonal distribution of *Endochironomus*.

The high percentage of *Camptochironomus* larvae on ex Zone 1 canes in Zone 3 contrasts with their absence on native Zone 3 canes; from this it can be inferred that planktonic larvae colonise the former canes in preference to the latter. (The majority of the *Camptochironomus* larvae are first instars.) As with *Endochironomus*, the difference in epiphyton between the two sets of canes would appear to provide the most feasible explanation for such selective behaviour.

At the end of the six-day experimental period, *Cricotopus sylvestris* density is higher on ex Zone 1 canes in Zone 3 than on original Zone 3 canes (0.15 larvae per cm^2 as opposed to 0.06) so it seems that interzonal variation in *sylvestris* numbers is strongly linked to interzonal epiphyton variation because the only difference between the two sets of canes is in their epiphyton.

Obviously, the investigation considered in this section is limited in scope and the ecological picture built up will be an oversimplification of the real-life situation. However, it is felt that some useful results have been obtained, from which soundly-based conclusions can be drawn.

Chapter 5

THE CHIRONOMID LARVAL COMMUNITY FROM THE FLOOR OF THE REEDBED AT COP MERE

5:1 Field and Laboratory Work - Planning and Methods

A) SAMPLING DESIGN

The floor of the reedbed study site at Cop Mere shows a high degree of spatial variation in terms of habitat type. Distinct environmental changes occur from the front (lakeward edge) to the back (landward edge) of the reedbed. The most obvious difference in substrate environment is that which exists between the area of permanent standing water, which has a sandy floor, and the semi-aquatic area further inland, where the substrate almost entirely consists of decaying plant material.

The investigations considered in this chapter were undertaken with the intention of revealing any characteristic variation in chironomid larval populations that might exist from the front to the back of the reedbed. In order to expose any such variation, a zonal sampling scheme was devised which, in essence, is similar to that used for reedstem-dwelling larvae.

Figure 5:1:1 shows the position of the seven zones designated for substrate sampling. These zones, like their counterparts for reedstems, are one metre wide, fifty metres long, and lie parallel with the *Phragmites*/open-water interface. They are labelled A-G. Zone A fringes the front (lakeward edge) of the *Phragmites* stand in the area of permanent standing water; Zone G lies along the most landward margin of the reedbed.

Five benthic samples were taken from each of the four zones (A-D) which lie in the area of permanent standing water. The positions

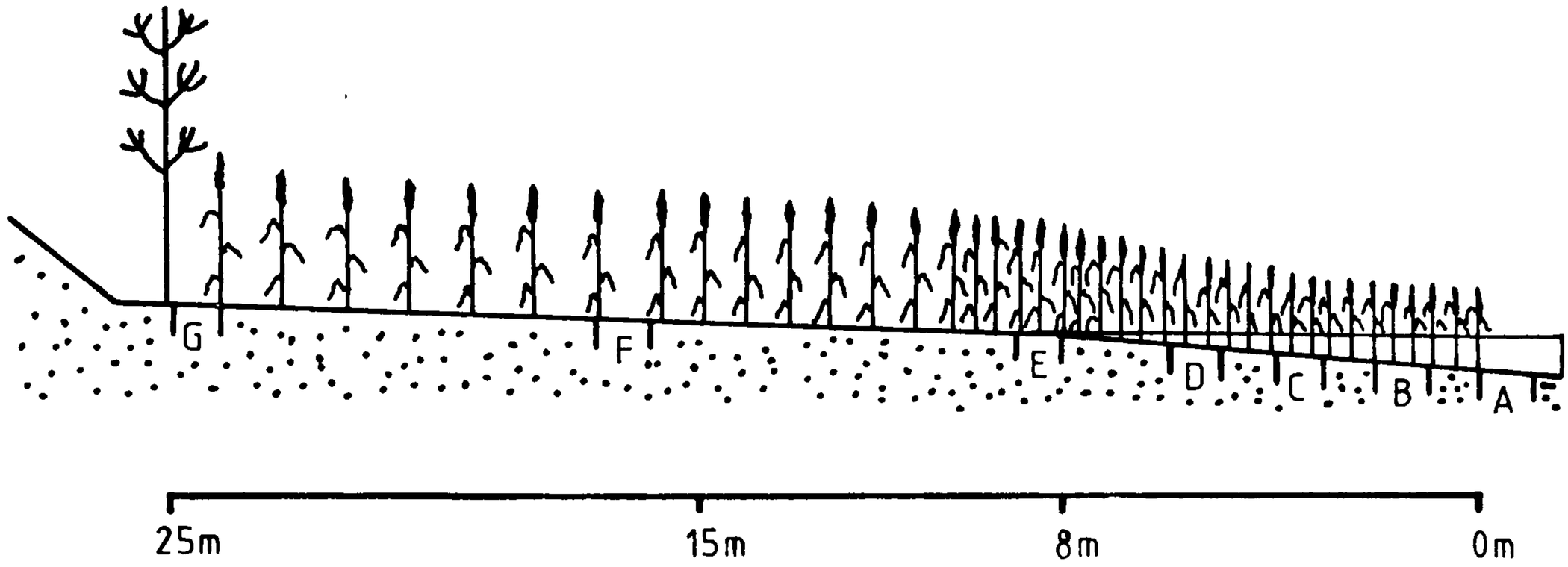


FIGURE 5:1:1 - The position of the seven zones in which substrate samples were taken from the floor of the reedbed.

of the sampling points in each zone were determined by following a 'systematic' procedure, similar to that adopted for reedstem samples, involving the random determination of one sample-point location in the first ten metres of each zone and the siting of the other four at regular intervals starting from this initial location. (See Appendix N for first sample positions.) Substrate samples from Zones A-D were taken at monthly intervals during 1981. (Substrate and reedstem collections were made at the same time.)

Zones E, F, and G mark the front, middle, and back of the semi-aquatic part of the reedbed respectively. Five samples were removed from Zone E, three from Zone F, and two from Zone G. This variation in numbers reflects a need to minimise sorting time. Sample-point positions in Zones E-G were determined in a similar way to those for Zones A-D. Collections were made on a monthly basis during 1981.

B) SAMPLING METHODS

Differences in sampling conditions and substrate composition between Zones A-D and E-G necessitated the adoption of two different sampling methods. The reedbed floor in Zones A-D is permanently covered by water and basically consists of a tight compaction of sand and *Phragmites* plant material. Here, a core sampler was considered to be the most practical device for substrate removal. A wide range of corers is available (Elliot and Tullet, 1978); the one used in the present study is a manually-operated piston corer of the type constructed by Mountain. (See Mountain, 1981 for a full working description of this apparatus.) Although only a small area (0.0016 m^2) of reedbed floor is covered with each core, replication of the sampling technique through Zones A-D means any investigation deficiencies incurred as a result of small cores will apply to all four zones; it is felt, therefore, that interzonal comparisons can be made legitimately.

In Zones E-G, the soft organic nature of the substrate makes the use of a corer impossible. Here, quasi-quantitative samples were taken by means of 'hand-grabs', involving the manual removal of handfuls of material, each handful constituting one sample.

Upon removal from the reedbed, all substrate samples were placed individually in polythene bags and transported back to the laboratory for subsequent examination.

C) SAMPLE SORTING

Individual cores and hand-grab samples were placed in a white tray and broken up with a jet of water. The cores from Zones A-D were divided into three principal components (excluding faunal populations): sand; large pieces of *Phragmites* roots; and small pieces of miscellaneous plant debris. Relative abundance values for these components were calculated for each core. Having separated out material in the tray, all macrofaunal inhabitants, including chironomid larvae, were picked out with the aid of an illuminated magnifying glass, to be killed and stored in 70% ethanol. As with reedstem-dwelling chironomids, enumeration and identification of core larvae were aided by a preponderance of one easily identifiable species (in this case, *Camptochironomus tentans*).

The macrofaunal inhabitants of core and hand-grab samples are listed in Appendices O and P; Appendices Q and R give a taxonomic and numerical breakdown of the chironomid community found in each sample.

5:2 Environmental Features of the Sampling Zones

A) SUBSTRATE CHARACTERISTICS

Substrate composition differedmarkedly between the two zonal groups A-D and E-G. Appreciable variation was also found within the first group: Table 5:2:1 gives percentage relative abundance values for the three principal components of core-samples (sand, large pieces of *Phragmites*

roots, and small pieces of plant debris) and indicates the existence of a characteristic pattern of interzonal variation in core composition. Figures for January and June are presented to highlight any marked differences in pattern between summer and winter. No such seasonal variation is apparent.

January	A	B	C	D
Sand	87.91	79.31	51.37	38.88
Roots	10.47	16.19	27.41	17.08
Debris	1.62	4.51	21.22	44.03

June	A	B	C	D
Sand	88.79	65.69	52.49	40.12
Roots	5.77	19.87	21.95	24.19
Debris	5.64	14.45	26.69	35.69

TABLE 5:2:1 - Mean percentage relative abundance values for core components, relating to samples taken in January and June, 1981 from Zones A-D. Figures refer to core volume.

In both months, the percentage contribution of sand shows a progressive decline from Zone A through to Zone D, whilst the percentage contribution of plant debris shows a progressive increase in the same direction. In Zone A, almost 90% of core volume is taken up by sand; in Zone D, the comparable figure is about 40% with debris accounting for a much higher percentage of volume. The lowest value for roots in each month relates to Zone A, reflecting the fact that this zone is located in

open water, at the frontal margin of the *Phragmites* stand.

Interzonal variation in substrate composition is not evident through Zones E-G: in each of the three zones, the substrate is almost 100% organic, principally consisting of decaying autochthonous and allochthonous fragmented plant material. As far as moisture content is concerned, however, some interzonal variation can occur: during prolonged spells of warm, dry weather, the reedbed floor tends to become drier in Zones F and G than in Zone E, although semi-aquatic conditions are nearly always maintained throughout the three zones.

B) PHYSICO-CHEMICAL WATER CHARACTERISTICS

Consideration was given to four features of the interstitial water within the floor substrate: oxygen content, temperature, pH, and conductivity.

In Zones A-D, where interstitial substrate water and the water above the floor constitute separate environments, practical limitations prohibited the measurement of oxygen content and temperature. Conductivity and pH readings were taken in February, 1981; these are presented in Table 5:2:2. Interzonal variations in each of these

	A	B	C	D
Conductivity	7.45	8.80	7.58	7.70
pH	7.20	7.20	7.10	7.10

TABLE 5:2:2 - Conductivity ($\mu S \times 10^4$) and pH readings for interstitial substrate water in Zones A-D, taken in February, 1981.

features are small. A directional pattern of variation in conductivity levels is not evident; pH values are slightly higher towards the front of the area of permanent standing water than the back.

Environmental conditions in Zones E-G allowed more extensive monitoring than that undertaken in Zones A-D: in addition to conductivity

	pH			Conductivity		
	E	F	G	E	F	G
Jan	--- (6.7)	--- (7.2)	--- (7.0)	---- (7.53)	---- (6.75)	---- (7.00)
Feb	7.9 (7.1)	7.5 (7.2)	7.0 (7.2)	5.70 (8.60)	9.65 (8.20)	9.62 (8.80)
Mar	7.2 (6.9)	--- (7.2)	--- (7.1)	9.20 (7.45)	---- (7.00)	---- (6.33)
Apr	--- (7.6)	--- ---	--- (7.4)	---- ----	---- ----	---- ----
May	--- (7.0)	--- (6.9)	--- (7.0)	---- (7.81)	---- (7.59)	---- (6.82)
Jun	7.2 (6.8)	6.9 ---	--- ---	8.17 (6.50)	7.45 ----	---- ----
Jul	--- (6.9)	--- ---	--- ---	---- (5.20)	---- ----	---- ----
Aug	--- (6.8)	--- ---	--- ---	---- (5.10)	---- ----	---- ----
Sep	6.7 (6.9)	--- ---	7.3 ---	7.30 (4.20)	---- ----	6.78 ----
Oct	6.8 (6.9)	6.8 (6.8)	7.0 ---	8.01 (4.60)	5.86 (4.60)	7.85 ----
Nov	6.9 (6.7)	7.0 (6.5)	6.9 ---	7.95 (4.40)	7.67 (3.89)	7.80 ----
Dec	6.8 (6.4)	6.8 (6.4)	6.9 (6.7)	5.62 (4.08)	3.99 (4.22)	6.80 (4.06)

TABLE 5:2:3 - Conductivity ($\mu S \times 10^4$) and pH readings for interstitial substrate water in Zones E-G, taken during 1981 and 1982. (Readings for 1982 are in parentheses.)

and pH, the oxygen content and temperature of the interstitial substrate water were measured.

Recorded values for conductivity and pH are given in Table 5:2:3. Ecologically significant spatial or temporal variation is not apparent in either variable.

Oxygen (% saturation)

	E	F	G
January	----	----	----
	----	----	----
February	----	----	----
	----	----	----
March	----	----	----
	----	----	----
April	----	----	----
	(72.1)	----	(55.0)
May	----	----	----
	----	----	----
June	----	----	----
	(13.3)	----	----
July	----	----	----
	(26.3)	----	----
August	----	----	----
	(30.8)	----	----
September	11.0	----	----
	(22.7)	----	----
October	3.0	3.0	3.0
	(45.0)	(38.3)	----
November	----	----	----
	(7.5)	----	----
December	----	----	----
	(36.0)	(18.0)	(63.6)

TABLE 5:2:4 - Oxygen content recordings for interstitial substrate water in Zones E-G, taken during 1981 and 1982. (Values for 1982 are in parentheses.)

Oxygen content values for Zones E-G are presented in Table 5:2:4. Readings are low in comparison with those for Zones 1-3 in the area of permanent standing water (cf. Tables 5:2:4 and 4:3:1). Distinct patterns of seasonal or interzonal variation are not evident.

Temperature measurements in Zones E-G were made in February and October, 1981; these measurements are shown in Table 5:2:5.

	E	F	G
February	6.7	7.0	---
October	6.6	7.0	6.3

TABLE 5:2:5 - Temperature (°C) readings for interstitial substrate water in Zones E-G, taken during 1981.

In February, the water in Zones E-G is about 1.0°C warmer than that in the area of permanent standing water where Zones A-D and 1-3 are situated; in October, the water in Zones E-G is about 0.5°C cooler than that in the permanent standing water area. These variations in temperature are no doubt due to volume-linked differences in the rates of heating and cooling between the two water bodies. Temperature variations between Zones E-G are probably caused by spatial differences in the degree of shading afforded by vegetation.

5:3 Features of the Larval Chironomid Community found in Zones A-D during 1981.

A) TAXONOMIC COMPOSITION OF THE TOTAL SAMPLE POPULATION FOR 1981

Table 5:3:1 lists the chironomid taxa found in core-samples during 1981, together with values relating to their actual and relative abundance. Three subfamilies are represented: the Chironominae, Orthocladiinae, and Tanypodinae. The Chironominae preponderate, in terms of both generic

CHIRONOMINAE	No.	%
Camptochironomus	817	93.37
Chironomus 'plumosus' type	3	0.34
Chironomus 'thummi' type	1	0.11
Cryptochironomus	1	0.11
Endochironomus	2	0.23
Glyptotendipes	30	3.43
Limnochironomus	4	0.46
Microtendipes	5	0.57
Paratendipes	1	0.11
ORTHOCLADIINAE		
Cricotopus	7	0.80
Psectrocladius	1	0.11
TANYPODINAE		
Procladius	2	0.23
Psilotanypus	1	0.11

TABLE 5:3:1 - Chironomid taxa found in benthic core-samples from Zones A-D during 1981, together with the number of individuals found in each taxon, which is also expressed as a percentage of the total number of larvae found.

---

diversity and larval abundance. Members of this subfamily account for almost 99% of all larvae collected. Of the eight Chironominae genera found, most are very poorly represented. One genus (*Camptochironomus*) heavily outnumbers the others and makes up 94% of the total Chironominae population.

B) SPATIOTEMPORAL VARIATION IN MEAN LARVAL DENSITY IN ZONES A-D - A CONSIDERATION OF THE LARVAL POPULATION AS A WHOLE

Figure 5:3:1 illustrates interzonal variation in mean larval density during 1981. Generally, the highest density in each month is found in Zone B which lies two metres in from the front (lakeward edge) of the reedbed. Larval numbers tend to fall progressively towards the back of the area of permanent standing water. One feature of note in Figure 5:3:1 is the absence of larvae between March and May in Zone D and in May in Zone A. The absence in Zone D may be due to chance as numbers in this zone are generally low; that in Zone A requires another explanation as numbers in this zone are usually much higher.

The disappearance of Zone A larvae in May, at a time when numbers remain relatively stable in Zones B and C, may be due to earlier emergence in Zone A, which lies at the front (lakeward edge) of the reedbed, or migration out of this zone for some reason. A comparison of Figure 5:3:1 with the zonal density graph for *Camptochironomus tentans* larvae (Figure 5:3:2) indicates that the pattern for this species largely accounts for the shape of the density graph relating to the total larval population. The May drop in larval density found in both the total chironomid and *Camptochironomus tentans* populations coincides with the period of maximum emergence in *Camptochironomus tentans* (cf. Figures 5:3:1, 5:3:2, and 6:2:5). The onset of chironomid emergence in spring appears to be controlled partly by photoperiod (Ryals and Ingram, 1973; LeSage and Harrison, 1980). If the actual intensity of the prevailing illumination is similarly important in this respect, the higher levels of light recorded towards the front (lakeward edge) than the back of the area of permanent standing water in the reedbed (see Table 4:4:1) may induce higher May emergence levels in Zone A than elsewhere and lead to the particular pattern of interzonal larval density variation found during this month.

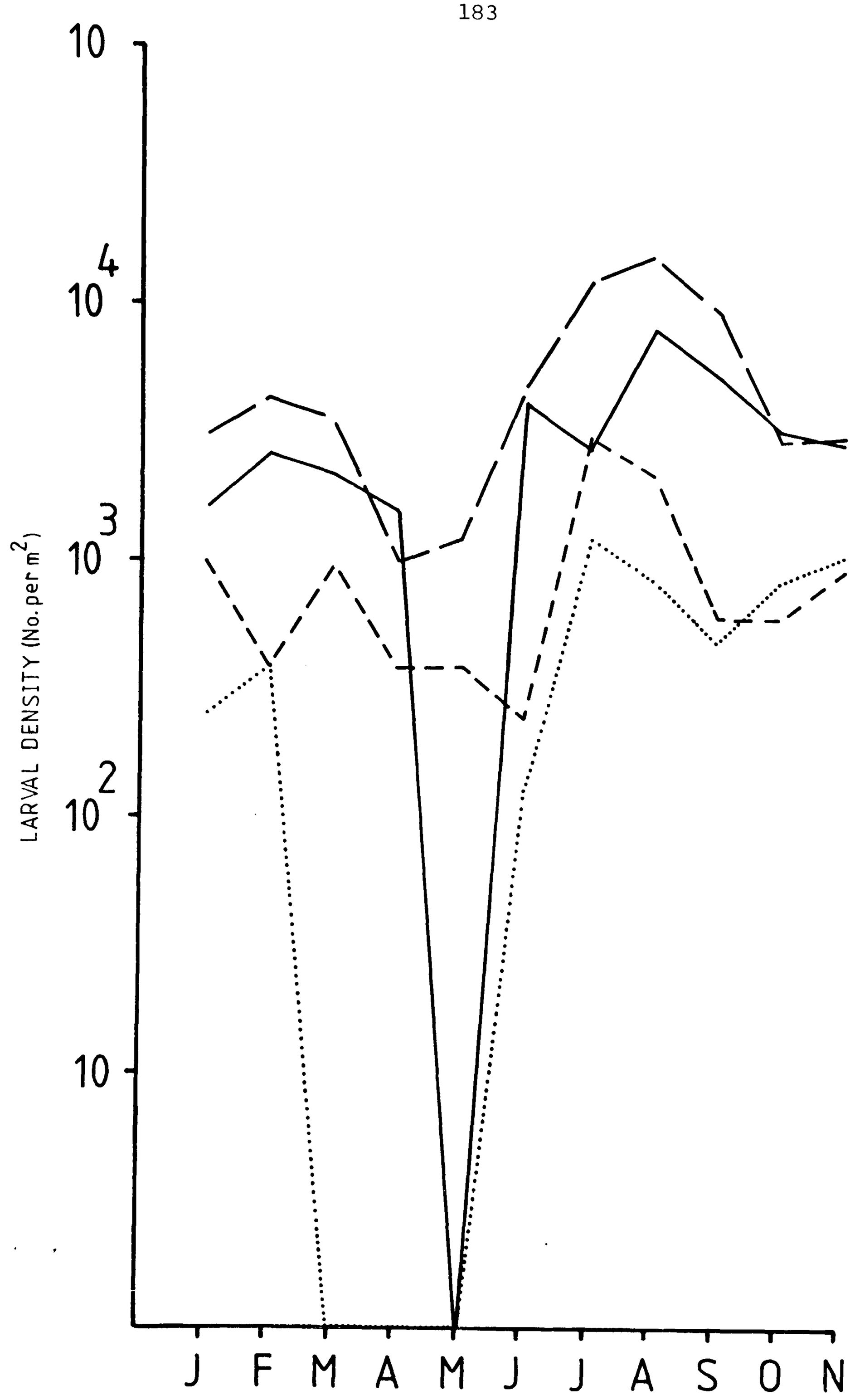


FIGURE 5:3:1 - Mean density of benthic-dwelling chironomid larvae in Zone A (———), Zone B(— —), Zone C (---), and Zone D (·····) during 1981. (See Appendix S for standard errors.)

C) INDIVIDUAL PATTERNS OF DISTRIBUTION AND ABUNDANCE - CHIRONOMINAE

i) *Camptochironomus tentans* (see Figures 5:3:2 and 5:3:3)

Reference has been made already to the major part this species plays in determining the density patterns for the total benthic-dwelling larval population. A comparison of Figures 5:3:2 and 3:2:1 indicates that, except for the spring absences noted previously, chironomid larval numbers in cores do not show the same degree of temporal fluctuation as those on reedstems - in general, emergence of benthic-dwelling *Camptochironomus* larvae does not appear to have the same deterministic influence on density through the year as emergence of the predominant reedstem-dwelling species, *Cricotopus sylvestris*.

Figure 5:3:3 illustrates the instar composition of the total benthic-dwelling *Camptochironomus* population in each month. Larvae overwinter in the bottom sediment as third and fourth instars, the latter stage predominating in April as development proceeds and the first emergence commences. It has already been noted that first instar *Camptochironomus* are found principally on reedstems (see page 103), which explains their paucity in core samples. Benthic-dwelling second instars are most common during the summer, these having developed from first instar larvae which have migrated down to the reedbed floor from their original reedstem habitat.

ii) *Chironomus* 'plumosus' and *Chironomus* 'thummi' types (see Table 5:3:2).

These larvae could not be identified further than type groupings. Adult *Chironomus riparius* (Meigen) and *Chironomus venustus* (Staeger) were caught in emergence traps and benthic larvae may belong to these species.

The four juveniles recorded from core-samples are fourth instars. Their scarcity precludes any legitimate analysis of population density patterns relating to temporal distribution or interzonal variation.

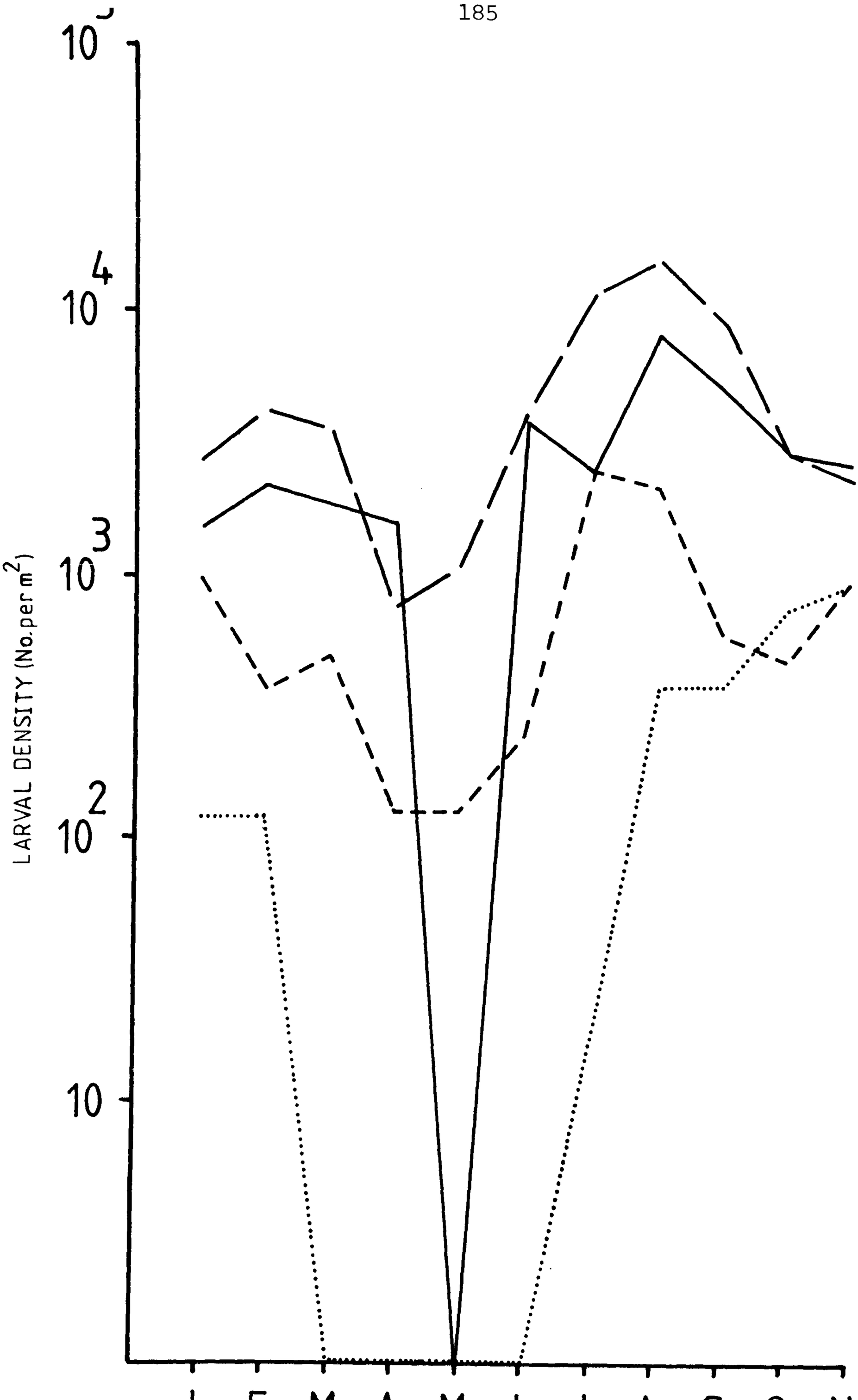


FIGURE 5:3:2 - Mean density of benthic-dwelling *Camptochironomus tentans* larvae in Zone A (———), Zone B(— —), Zone C(---), and Zone D'(·····) during 1981. (See Appendix S for standard errors.)

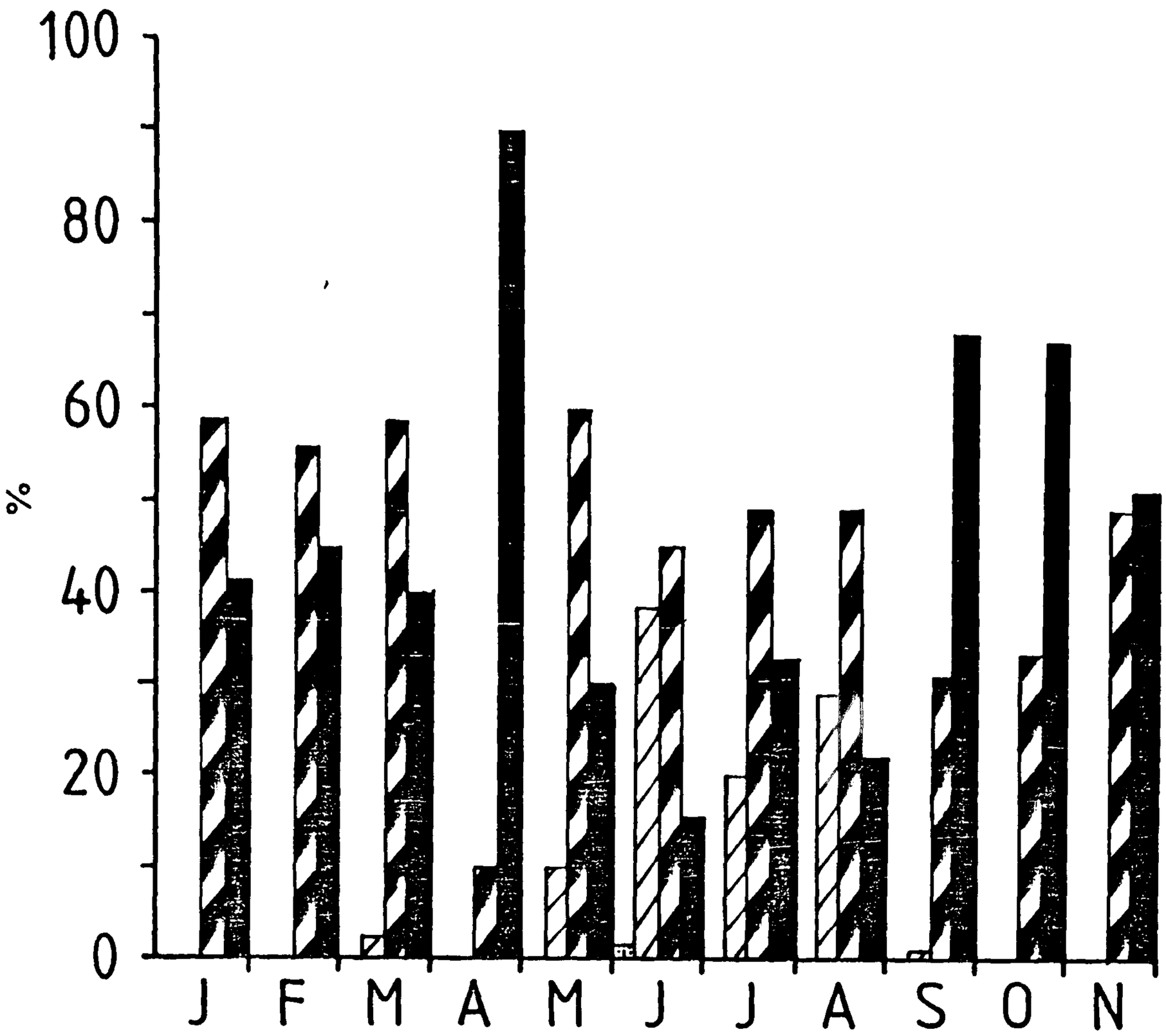


FIGURE 5:3:3 - Monthly relative abundance values for 1st instar (▩), 2nd instar (▨), 3rd instar (▨), and 4th instar (■) benthic-dwelling *Camptochironomus tentans* larvae found in Zones A-D during 1981.

CHIRONOMINAE		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
C. 'plumosus' type	A	1(*4*)	1(*4*)									
	B					1(*4*)						
	C											
	D											
C. 'thummi' type	A											
	B											
	C					1(*4*)						
	D											
Cryptochironomus	A											
	B	1(*3*)										
	C											
	D											
Endochironomus	A			1(*3*)								
	B											1(*4*)
	C											
	D											
Glyptotendipes	A			1(*3*)			1(*2*)				1(*4*)	1(*3*)
	B				1(*4*)							2(*3*)
												2(*4*)
	C			4(*4*)	1(*3*)	1(*4*)		1(*3*)			1(*3*)	
					1(*4*)			1(*4*)				
	D	1(*3*)	1(*3*)					2(*4*)	3(*3*)	1(*4*)	1(*4*)	1(*4*)
									1(*4*)			

TABLE 5:3:2 - The spatiotemporal distribution of benthic-dwelling chironomid taxa (excluding *Camptochironomus*) found in Zones A-D during 1981. Numbers out of parentheses are larval counts; italicised numbers in parentheses indicate instar status. (cont...)

CHIRONOMINAE (cont.)		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Limnochironomus	A						2(*4*)					
	B											
	C							1(*4*)				
	D						1(*4*)					
Microtendipes	A		2(*4*)	1(*4*)								
	B	1(*4*)										
	C							1(*3*)				
	D											
Paratendipes	A											
	B				1(*3*)							
	C											
	D											
ORTHOCLADIINAE												
Cricotopus	A						1(*4*)	1(*3*)				
	B						2(*3*) 2(*4*)					
	C											
	D		1(*3*)									
Psectrocladius	A						1(*4*)					
	B											
	C											
	D											

TABLE 5:3:2 (...cont...)

TANYPODINAE		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Procladius	A											
	B							1(*3*)				1(*3*)
	C											
	D											
Psilotanypus	A							1(*3*)				
	B											
	C											
	D											

TABLE 5:3:2 (...cont.)

iii) *Cryptochironomus* (see Table 5:3:2)

The individual found was identified as belonging to Bryce and Hobart's (1973) *Cryptochironomus* 'defectus' group but species status remains uncertain.

iv) *Endochironomus* (see Table 5:3:2)

Both *Endochironomus tendens* and *Endochironomus dispar* were found in emergence traps so the two larvae taken from Zones A and B are likely to belong to one or both of these species.

v) *Glyptotendipes* (see Table 5:3:2)

All larvae were positively identified as *Glyptotendipes pallens.* Most benthic-dwelling individuals are third and fourth instars and occur in every month of the sampling period. Seventy per cent of the population inhabits Zones C and D towards the back of the permanent standing water area in the reedbed.

The fact that second instars are much more abundant on reedstems (see Figure 3:3:13) than in benthic cores suggests that migration from stems to the reedbed floor may take place as larval development proceeds; a similar migration seems probable in the case of *Camptochironomus tentans* (see page 103).

vi) *Limnochironomus* (see Table 5:3:2)

Emergence data indicate that the juveniles taken from core-samples are *Limnochironomus nervosus*. The four individuals recorded are fourth instars.

vii) *Microtendipes* (see Table 5:3:2)

The one species found was determined as *Microtendipes pedellus* on the basis of emergence data. Most of the larvae are fourth instars and inhabit Zones A-C.

viii) *Paratendipes* (see Table 5:3:2)

Specific identification for the individual present, a third instar, was not possible. *Paratendipes* was absent from emergence trap catches.

D) INDIVIDUAL PATTERNS OF DISTRIBUTION AND ABUNDANCE - ORTHOCLADIINAE

i) *Cricotopus* (see Table 5:3:2)

All larvae were positively identified as *Cricotopus sylvestris*. This species is characteristically a reedstem-dweller in Cop Mere and the individuals recovered from benthic core-samples may well have strayed from their original epiphytic habitat.

ii) *Psectrocladius* (see Table 5:3:2)

The one larva found in the floor sediment was identified as *Psectrocladius limbatellus*, which is found in far greater numbers elsewhere. The situation outlined in relation to *Cricotopus* probably applies here too.

E) INDIVIDUAL PATTERNS OF DISTRIBUTION AND ABUNDANCE - TANYPODINAE

i) *Procladius* (see Table 5:3:2)

ii) *Psilotanypus* (see Table 5:3:2)

Emergence data suggest the species status of these two tanypods is *Procladius choreus* (Meigen) and *Psilotanypus rufovittatus* (van der Wulp). The fact that tanypods are free-swimming means these larvae probably inhabit the spatially intermittent layer of loose vegetative material on the surface of the reedbed floor, rather than the comparatively compact layer of material further down, where greater restrictions are imposed on errant behaviour.

5:4 Interzonal Variation in Larval Abundance through Zones A-D - A Consideration of Possible Influencing Factors

Although the small size and number of samples taken from each zone make statistical analysis of interzonal larval density variations

unfeasible, patterns of possible ecological significance are discernible for certain taxa.

Reference has been made already to the major role *Camptochironomus tentans* plays in shaping the pattern of variation in overall larval density through Zones A-D. Figure 5:3:2 shows that, in general, more *Camptochironomus* larvae are found towards the front (lakeward edge) of the reedbed's permanent standing water area than the back (landward edge), with a progressive drop in numbers from Zone B through to Zone D; after Zone B the next highest density is usually found in Zone A. This pattern may reflect noticeable differences in substrate characteristics through the four zones. Table 5:2:1 indicates that cores from Zones A and B are principally composed of sand with a relatively small amount of plant debris, whilst those from Zones C and D contain a much lower volume of sand and a much higher volume of plant debris. If *Camptochironomus tentans* larvae prefer a mainly sandy substrate to one containing a high degree of plant material, interzonal substrate variation could explain their relatively high densities in Zones A and B as opposed to Zones C and D.

Interzonal differences in pH and conductivity (see Table 5:2:2) would not appear to be of sufficient magnitude to have a significant effect on *Camptochironomus* larval numbers. Any interzonal oxygen variation that might exist could be more important in this respect, however. (It was not possible to measure the oxygen content of interstitial substrate water in Zones A-D.)

Of the other chironomid taxa besides *Camptochironomus tentans*, most seem to favour Zones A-C and are generally absent from Zone D. Only *Glyptotendipes pallens* is found in markedly greater numbers towards the back (landward edge) of the reedbed's permanent standing water area than the front, a distribution that may be due to this chironomid's habit of dwelling inside hollow *Phragmites* stems during its larval development,

as pieces of such material are most abundant in Zones C and D.

Studies of benthic-dwelling chironomid larvae are plentiful, a point made in the introduction to this thesis. Several of these investigations provide some pertinent and useful information relating to the ideas put forward in the preceding paragraphs of this section.

Acton and Scudder (1971) studied juvenile populations of *Camptochironomus tentans* in Europe and British Columbia and reported that larvae usually occur in shallow water containing a good deal of decaying vegetation and moderate amounts of organic pollution. They noted a preference for soft mud. Topping (1971) and Cannings and Scudder (1978) found patterns of dispersion in lake-dwelling *Camptochironomus tentans* larvae were partly influenced by the size composition of the mud substratum. Unlike Acton and Scudder, Cannings and Scudder discovered that the most favourable muds were those with a high percentage of particles in the 0.59-1.98 mm size category, indicating a preference for relatively coarse-grained material. This finding supports the suggestion that *Camptochironomus tentans* may favour the sandy substrate existing in Zones A and B at Cop Mere in preference to the mainly plant-derived benthic material occurring in Zones C and D. Edgar and Meadows (1969) investigated pupal case construction in a closely related species (*Chironomus riparius* (Meigen)) and found that sand grains are required to give structural support. Moore (1979) raised the point that sediments with a high organic level may not be conducive to larval tube-building.

Different chironomid taxa are known to show an inclination towards different substrate compositions (Tolkamp and Both, 1978). Whereas *Camptochironomus tentans* and closely allied species appear best suited to sandy conditions, *Glyptotendipes* is often associated with benthic material of organic origin. McLachlan and McLachlan (1975) studied two species of chironomid larvae in a bog lake in north-east England

and found that *Glyptotendipes paripes* (Edwards) only inhabits coarse sediments, which consist of peat particles. Webster and Simmons (1978) investigated the chironomids dwelling in litter bags in Claytor Lake, Virginia. The larval population of these bags was principally composed of *Glyptotendipes* spp. and Webster and Simmons concluded that these tube-building filter-feeders probably used the baskets of leaves primarily for attachment. The inhabitation of the hollow interior of *Phragmites* stems by *Glyptotendipes pallens* larvae was reported by Opaliński (1971). Note has been made of the fact that benthic-dwelling *Glyptotendipes* are most numerous in Zones C and D at Cop Mere, where plant-derived substrate material is found in greatest quantity.

Konstantinov (1971) examined the oxygen requirements of larvae belonging to several chironomid species and reveals that *Glyptotendipes pallens* requires more oxygen at 25°C than *Camptochironomus tentans*. At Cop Mere, the oxygen content of the interstitial substrate water in Zones C and D is likely to be less than that in Zones A and B, due to a higher level of vegetation decomposition in the former area. *Glyptotendipes pallens* attains its greatest densities in Zones C and D whilst *Camptochironomus tentans* is most numerous in Zones A and B. Bearing in mind Konstantinov's findings, these patterns of oxygen variation and larval distribution do not seem to be causally linked.

Competitive interactions between larvae of different chironomid species are considered in several reports (e.g. Kajak, 1963; Topping, 1971; Cantrell and McLachlan, 1977) and have been shown to influence larval dispersion patterns. Spatial distribution may be affected by food availability (Egglishaw, 1964; Kajak, 1977; Titmus and Badcock, 1981) and/or living-space requirements. However, the densities of benthic-dwelling chironomid larvae at Cop Mere would not appear high enough to be controlled to any great extent by competitive factors.

5:5 Features of the Larval Chironomid Community found in Zones E-G during 1981

A) TAXONOMIC COMPOSITION OF THE TOTAL SAMPLE POPULATION FOR 1981

Table 5:5:1 lists the chironomid taxa recorded during 1981 from Zones E-G which lie in the semi-aquatic area towards the back (landward edge) of the reedbed. Figures for actual and relative abundance are given.

Just over half of all the larvae collected belong to the Chironominae; members of the Orthocladiinae account for about 37% of the total population, whilst the Tanypodinae make up the remainder. One feature which distinguishes the population composition in Zones E-G from that in Zones A-D or on reedstems (Zones 1-3) is the lack of a predominant species. (*Camptochironomus tentans* predominates in benthic core-samples from Zones A-D; *Cricotopus sylvestris* does so on reedstems.) Three taxa are relatively abundant in Zones E-G: *Tanytarsus*, *Metriocnemus* sp. A, and Pentaneurini sp. A which together account for 85% of the total chironomid population.

The *Tanytarsus* population appears to be monospecific; investigations of chironomid swarms towards the back of the reedbed suggest the species represented at the larval stage is *Tanytarsus sylvaticus* (van der Wulp). Similar investigations suggest that *Metriocnemus* sp. A is *Metriocnemus hirticollis* and the one species of *Pseudorthocladius* present is *curtistylus* (Goetghebuer). The *Glyptotendipes* individual found was identified as *pallens*. Species status is indeterminable for the other taxa represented in substrate samples.

Metriocnemus larvae are known to frequent a wide range of habitats. Cranston (1982) found *Metriocnemus hygropetricus* (Kieffer) and *Metriocnemus hirticollis* living in springs in association with watercress beds. According to Cranston, these species also inhabit the thin water films of trickling filter sewage beds. Kitching (1971)

CHIRONOMINAE	No.	%
Chironomus 'thummi' type	2	0.66
Glyptotendipes	1	0.33
Paratendipes	3	1.00
Tanytarsus	148	49.17
ORTHOCLADIINAE		
Metriocnemus sp. A	73	24.25
Metriocnemus sp. B	17	5.65
Metriocnemus sp. C	10	3.32
Metriocnemus sp. D	1	0.33
Pseudorthocladius	9	2.99
TANYPODINAE		
Pentaneurini sp. A	35	11.63
Pentaneurini sp. B	1	0.33
Procladius	1	0.33

TABLE 5:5:1 - Chironomid taxa found in substrate samples from Zones E-G during 1981, together with the number of individuals found in each taxon, which is also expressed as a percentage of the total number of larvae found.

discovered *Metriocnemus cavicola* (Kieffer) in rot-holes in beech trees *(Fagus sylvatica)*.

B) SPATIOTEMPORAL PATTERNS OF DISTRIBUTION AND ABUNDANCE

Precise quantitative assessment of larval density is not possible owing to the 'quasi-quantitative' sampling technique adopted to cope with the substrate conditions existing in Zones E-G. Bearing this in mind, and the fact that more samples were taken from Zone E than from either Zone F or G, interzonal comparisons of larval populations must be made with caution. However, some basic patterns are evident from Table 5:5:2 that appear to be ecologically significant.

Tanytarsus occurs in all three zones; no zonal preference is obvious. Highest densities are found in the first half of the year and the maximum is attained in April.

Metriocnemus sp. A also occurs in all three zones but most larvae were collected from Zone G which may reflect a preference for the more terrestrial conditions that can exist in this area fringing the landward edge of the reedbed. As with *Tanytarsus*, the highest density is found in April.

Metriocnemus sp. B and C are spread through the three zones and do not exhibit an inclination to any particular area.

The greatest concentration of Pentaneurini sp. A larvae is found in Zone E although they do inhabit Zones F and G. The wetter conditions in Zone E are likely to be more favourable for this member of the Tanypodinae, a subfamily whose larvae are characteristically free-swimming. Other chironomids, including Tanytarsini, form an important part of the diet of many Pentaneurini larvae (Roback, 1969).

Two taxa normally associated with truly aquatic habitats (*Chironomus* 'thummi' type and *Glyptotendipes pallens*) have a distribution which may

CHIRONOMINAE		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
C. 'thummi' type	E				1(*3*)	1(*3*)							
	F												
	G												
Glyptotendipes	E				1(*3*)								
	F												
	G												
Paratendipes	E				1(*3*)						1(*2*)	1(*2*)	
	F												
	G												
Tanytarsus	E		1(*3*)	1(*3*)	3(*2*)	2(*3*)	1(*1*)	1(*3*)			1(*3*)		1(*3*)
			3(*4*)	6(*4*)	8(*3*)	1(*4*)	2(*3*)						
					7(*4*)		4(*4*)						
	F	2(*4*)			9(*3*)	1(*4*)	5(*3*)						2(*2*)
					6(*4*)		6(*4*)						3(*3*)
													1(*4*)
	G				3(*1*)		1(*4*)						1(*2*)
					21(*2*)								
					45(*4*)								

TABLE 5:5:2 - The spatiotemporal distribution of chironomid taxa found in Zones E-G during 1981. Numbers out of parenthese are larval counts; italicised numbers in parentheses indicate instar status. (cont...)

ORTHOCLADIINAE		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Metriocnemus sp. A	E			1(*4*)		1(*2*) 2(*4*)	1(*3*)				1(*3*)		
	F				2(*3*) 1(*4*)		1(*4*)						2(*2*)
	G			2(*3*) 12(*4*)	34(*4*)		1(*2*) 2(*3*) 1(*4*)		8(*4*)				1(*1*)
Metriocnemus sp. B	E								6(*3*)	2(*3*) 1(*4*)			
	F		1(*2*)							2(*3*)			
	G			4(*2*)						1(*3*)			
Metriocnemus sp. C	E						1(*1*) 2(*3*) 2(*4*)						
	F			1(*3*)			1(*4*)						
	G			1(*3*)			1(*3*) 1(*4*)						

TABLE 5:5:2 (...cont...)

ORTHOCLADIINAE (cont.)		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Metriocnemus sp. D	E			1(*4*)									
	F												
	G												
Pseudorthocladius	E												
	F									1(?)			
	G			6(?)							2(?)		
TANYPODINAE													
Pentaneurini sp. A	E		3(*2*)	10(*3*)	7(*3*)								
			2(*3*)	1(*4*)									
	F		2(*3*)	1(*3*)							1(*3*)		
	G								1(*3*)	3(*2*)		1(*4*)	2(*3*)
													1(*4*)
Pentaneurini sp. B	E												
	F		1(*3*)										
	G												
Procladius	E												
	F						1(*4*)						
	G												

TABLE 5:5:2 (...cont.)

reflect an inclination towards such conditions: they are confined to Zone E which is the closest zone to the area of permanent standing water. There is a high probability that this may be a chance distribution, however, as the numbers involved are small.

Chapter 6

EMERGENCE OF ADULT CHIRONOMIDS IN AND AROUND THE REEDBED AT COP MERE

6:1 Field and Laboratory Work - Planning and Methods

A) SAMPLING DESIGN

In Chapters 3, 4, and 5 attention is focused on spatiotemporal patterns of variation in the larval chironomid community of the reedbed. The present chapter is concerned with spatiotemporal patterns of variation in the emergence of adult chironomids, concentrating principally on the permanent standing water area of the reedbed study site.

Investigations of adult emergence were undertaken largely to supplement and corroborate information relating to the larval community of the reedbed - species identification of immature chironomids and explanation of larval population patterns is often aided by studies of adult populations. Environmental determinants of temporal distribution patterns do not come under close scrutiny; these are well-documented elsewhere (e.g. Palmén and Aho, 1966; Ryals and Ingram, 1973; Learner and Potter, 1974; Titmus, 1979b; LeSage and Harrison, 1980; Mountain, 1981).

Seven floating box-traps were used to catch emerging flies in and around the reedbed. (A full description of trap design is given under 'Sampling Methods'.) Figure 6:1:1 shows the positional lay-out for the traps. The arrangement chosen was considered to be the most suitable for the revelation of any ecologically significant spatial patterns of emergence. Obvious limitations exist in a scheme where only a small area (that under each trap) is taken to be representative of a much wider area; this problem would be alleviated to some extent if more traps were used but time constraints on sample sorting impose a restriction on the number of traps that can be put into service.

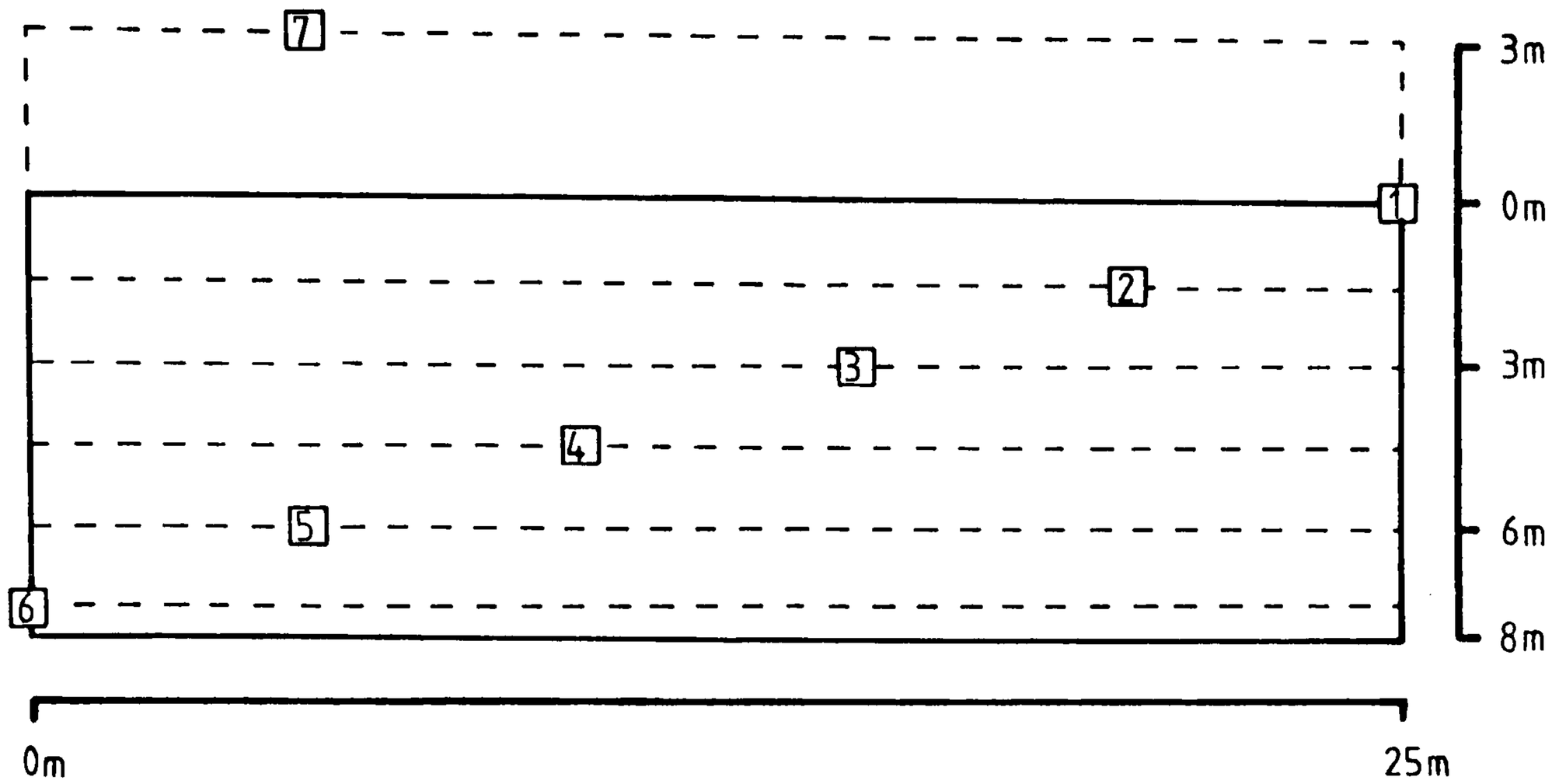


FIGURE 6:1:1 - Positional arrangement of the seven floating box-traps used to catch emerging chironomids at Cop Mere during 1981. Traps 1-6 are located in the permanent standing water area of the reedbed study site. Trap 1 is on the frontal (lakeward) margin of this area; trap 6 is situated close to the back edge fringing the semi-aquatic part of the reedbed. Trap 7 is located in open water.

B) SAMPLING METHODS

The emergence traps used in the present study are identical to those used by Mountain (1981), representing a modified version of the type described by Titmus (1979a), and based on a design conceived by Morgan *et al.* (1963) (see Plate 6:1:1). Titmus gives a full working description of his traps; the only difference between these and the ones used in the present study is that the latter have a single glass plate, rather than two half-plates, and this single plate covers a slightly smaller area (0.09m²).

The efficiency of floating emergence traps in comparison with that of other forms has been at the centre of several discussions in the literature (e.g. Morgan *et al.* 1963; Potter and Learner, 1974). Floating traps are generally regarded as being more efficient than submerged devices (Mountain, 1981). Certainly, in the reedbed habitat, operational considerations favour the use of floating apparatus.

Each trap was serviced on a weekly basis from the beginning of April to the beginning of October, 1981. Servicing involved the removal of the glass plate, which had been coated on its underside with Boltac[1], a gum resin, and the subsequent removal, with small forceps, of any chironomid flies adhering to this surface. This old plate was then replaced with a freshly coated one. Adult chironomids were taken back to the laboratory in small specimen tubes containing acetone.

Two problems were encountered with the traps during the sampling season: occasionally, strong winds and subsequent wave action caused the boxes to overturn or break free from their moorings; also, those traps

---

[1] Boltac greasebands (from which Boltac resin is obtained) are a product of Pan Britannica Industries Ltd.

PLATE 6:1:1 - A frontal view of the reedbed study site showing operational emergence traps in position.

sited towards the interior of the *Phragmites* stand were sometimes appropriated by nest-building coots (*Fulica atra*) to serve as base platforms - where this occurred a new trap would be placed alongside the existing one. Neither of these problems was seriously detrimental to the sampling programme as a whole.

C) ENUMERATION AND CLASSIFICATION OF ADULT CHIRONOMIDS

In the laboratory, flies were degreased in strong industrial detergent before enumeration and identification. Species determinations were made with the aid of keys by Pinder (1978) and Langton (1981). (See Pinder's key for a description of identification techniques.)

6:2 Features of the Emergent Adult Chironomid Population in 1981

A) TAXONOMIC COMPOSITION OF THE TOTAL SAMPLE POPULATION FOR 1981

The chironomid species recorded in emergence trap catches are listed in Table 6:2:1 together with values relating to their actual and relative abundance.[1] About 78% of the total population belongs to the Orthocladiinae, *Cricotopus sylvestris* accounting for over half of all flies collected. Most of the Chironominae and Orthocladiinae genera found in the adult list are also represented by larvae on reedstems and/or in benthic core samples. Five genera are not: *Micropsectra; Phaenopsectra; Limnophyes; Paraphaenocladius;* and *Smittia.* The Tanypodinae make up 8% of the total adult population; *Procladius* and *Psilotanypus* juveniles occasionally appear in reedbed samples but *Psectrotanypus* larvae are absent.

---

[1] The raw data from which the information presented in this chapter is derived are extensive and their bulk prohibits any appearance in an appendix; they are, however, available from the author on request. The positional arrangement adopted for the emergence traps prevents the calculation of standard errors relating to mean fly densitites.

CHIRONOMINAE	No.	%
Camptochironomus tentans (Fabricius)	105	4.41
Chironomus riparius (Meigen)	1	0.04
Chironomus venustus (Staeger)	2	0.08
Endochironomus dispar (Meigen)	1	0.04
Endochironomus tendens (Fabricius)	5	0.21
Glyptotendipes pallens (Meigen)	68	2.86
Limnochironomus nervosus (Staeger)	42	1.76
Micropsectra sp.	2	0.08
Microtendipes pedellus (Degeer)	17	0.71
Parachironomus arcuatus (Goetghebuer)	92	3.87
Phaenopsectra flavipes (Meigen)	1	0.04
ORTHOCLADIINAE		
Corynoneura carriana (Edwards)	2	0.08
Corynoneura edwardsi (Brundin)	18	0.76
Cricotopus flavocinctus (Kieffer)	161	6.76
Cricotopus sylvestris (Fabricius)	1336	56.13
Limnophyes truncorum (Goetghebuer)	3	0.13
Metriocnemus atratulus (Zetterstedt)	1	0.04
Metriocnemus hirticollis (Staeger)	65	2.73
Metriocnemus tristellus (Edwards)	1	0.04
Paraphaenocladius impensus (Walker)	5	0.21
Psectrocladius limbatellus (Holmgren)	238	10.00
Smittia leucopogon (Meigen)	19	0.80
Smittia pratorum (Goetghebuer)	1	0.04
Thienemanniella majuscula (Edwards)	3	0.13
TANYPODINAE		
Procladius choreus (Meigen)	149	6.26
Procladius signatus (Zetterstedt)	1	0.04
Psectrotanypus varius (Fabricius)	7	0.29
Psilotanypus rufovittatus (van der Wulp)	34	1.43

TABLE 6:2:1 - The species of chironomid flies caught in emergence traps during 1981, together with the number of trapped individuals belonging to each species, which is also expressed as a percentage of the total number of flies found.

B) TEMPORAL OCCURRENCE PATTERNS FOR INDIVIDUAL SPECIES - A COMPARATIVE DESCRIPTION

Figures 6:2:1, 6:2:2, and 6:2:3 illustrate the temporal occurrence patterns for adults belonging to the Chironominae, Orthocladiinae, and Tanypodinae respectively.

Regarding the Chironominae, considerable variation exists between the patterns for different species. The most extensive and uninterrupted emergence period is that of *Camptochironomus tentans* which extends with only two short breaks from the middle of April to the last week of September. *Glyptotendipes pallens* and *Limnochironomus nervosus* occur in traps from May to September but are often absent during June and July. Emergence in *Microtendipes pedellus* takes place intermittently from June to September, whilst *Parachironomus arcuatus* has a well-defined period extending continuously for seven weeks during August and September. As far as the remaining Chironominae species are concerned, emergence seems to be restricted to three weeks or less in the sampling period although these species are rare and it is possible that they appear at other times but are not detected.

Two members of the Orthocladiinae (*Cricotopus sylvestris* and *Cricotopus flavocinctus*) were taken in almost every week from the beginning of April to the beginning of October. *Metriocnemus hirticollis* and *Smittia leucopogon* also occur from April to October but on a more intermittent basis than the *Cricotopus* species. Emergence is confined to the summer months in *Corynoneura edwardsi* and *Psectrocladius limbatellus*. The other Orthocladiinae species were only caught on three or less occasions and are very scarce.

Of the Tanypodinae, *Procladius choreus* has the most extensive emergence season, being found in most weeks and in every month of the sampling period. *Psilotanypus rufovittatus* occurs in all but two weeks from April to June but is rare after this.

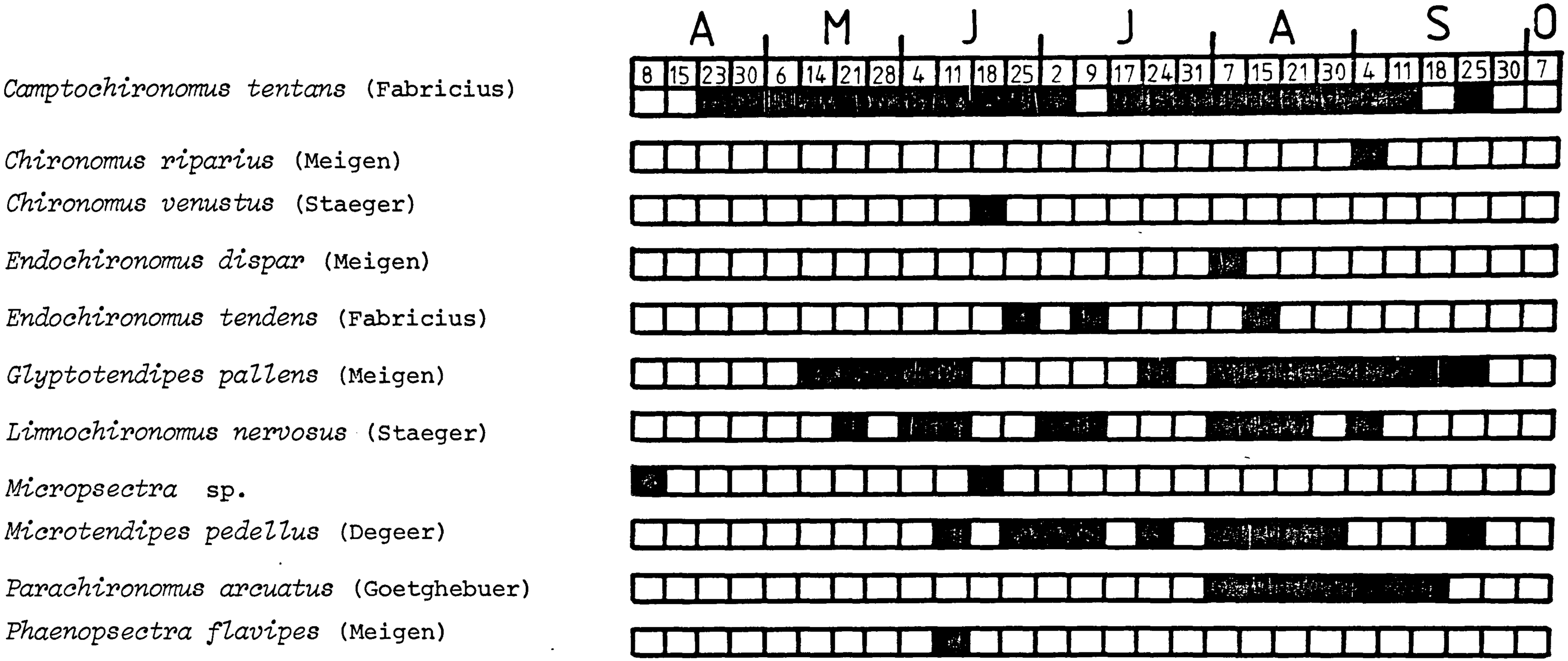


FIGURE 6:2:1 - Temporal occurrence patterns for adult Chironominae caught in emergence traps during 1981.

■ - present; □ - absent

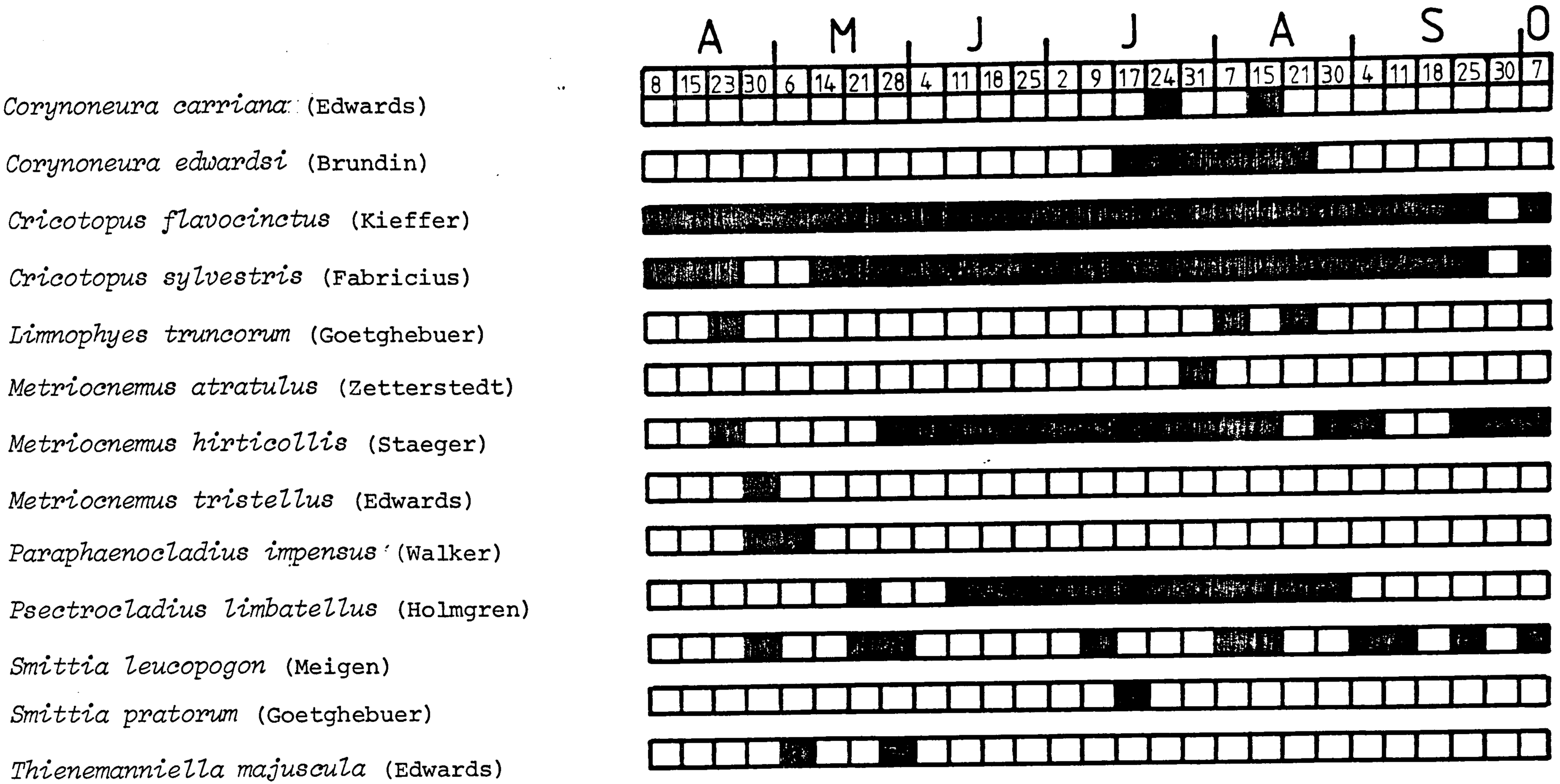


FIGURE 6:2:2 - Temporal occurrence patterns for adult Orthocladiinae cuaght in emergence traps during 1981.

■ - present; □ - absent

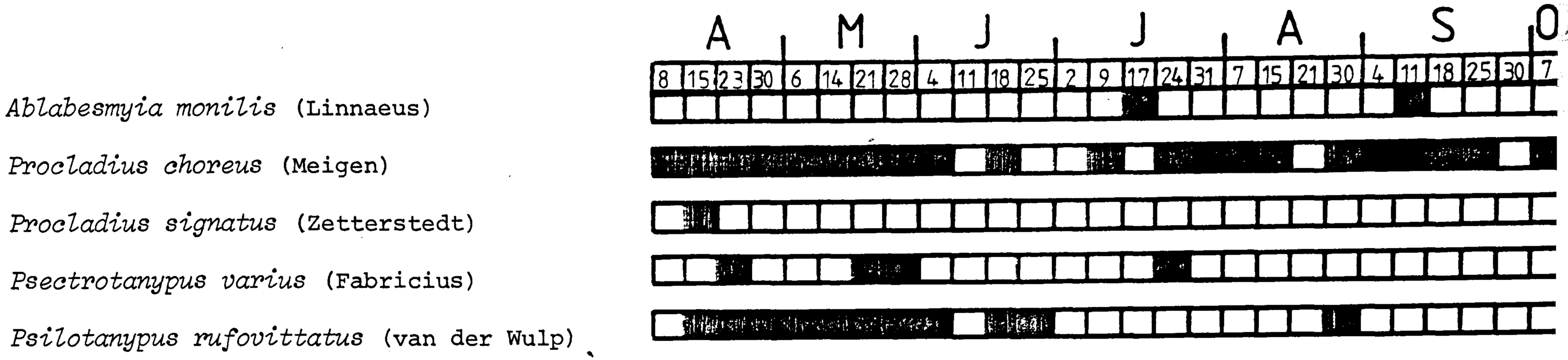


FIGURE 6:2:3 - Temporal occurrence patterns for adult Tanypodinae caught in emergence traps during 1981.

C) TEMPORAL DENSITY VARIATION IN THE TOTAL SAMPLE POPULATION DURING 1981

Figure 6:2:4 illustrates week to week density changes in the total sample population of adult chironomids during 1981. The sudden upsurge in numbers in the third week of July is largely attributable to a sharp increase in the emergence levels of *Cricotopus sylvestris* and *Psectrocladius limbatellus* at this time. On a monthly basis, the greatest intensity of emergence is found in August.

The graph form depicting temporal density variation in the total sample population is derived from the temporal patterns for individual species; these patterns, together with those relating to spatial variation in species emergence, are considered in the next part of this section.

D) INDIVIDUAL PATTERNS OF DISTRIBUTION AND ABUNDANCE - CHIRONOMINAE

i) *Camptochironomus tentans* (see Figure 6:2:5)

Two peaks of emergence are evident: the main one is centred on May and June, whilst a lesser peak occurs around the middle of August. The highest level of emergence is reached in the third week of May. This two-peaked pattern suggests *Camptochironomus tentans* is bivoltine, a status also proposed by Palmén and Aho (1966) and Mountain (1981) for this species.

Male flies often hold a position of numerical superiority over females and there is some evidence of protandry. Danks and Oliver (1972) believedprotandry in chironomids may assist in outbreeding or in mating success.

Table 6:2:2 indicates that most *Camptochironomus* flies emerge towards the front (lakeward edge) of the reedbed's permanent standing water area and are less numerous nearer the back, a distribution which mirrors that of *Camptochironomus* larvae taken from benthic core-samples. (Almost all *Camptochironomus* larvae about to pupate and subsequently emerge are found in core-samples.)

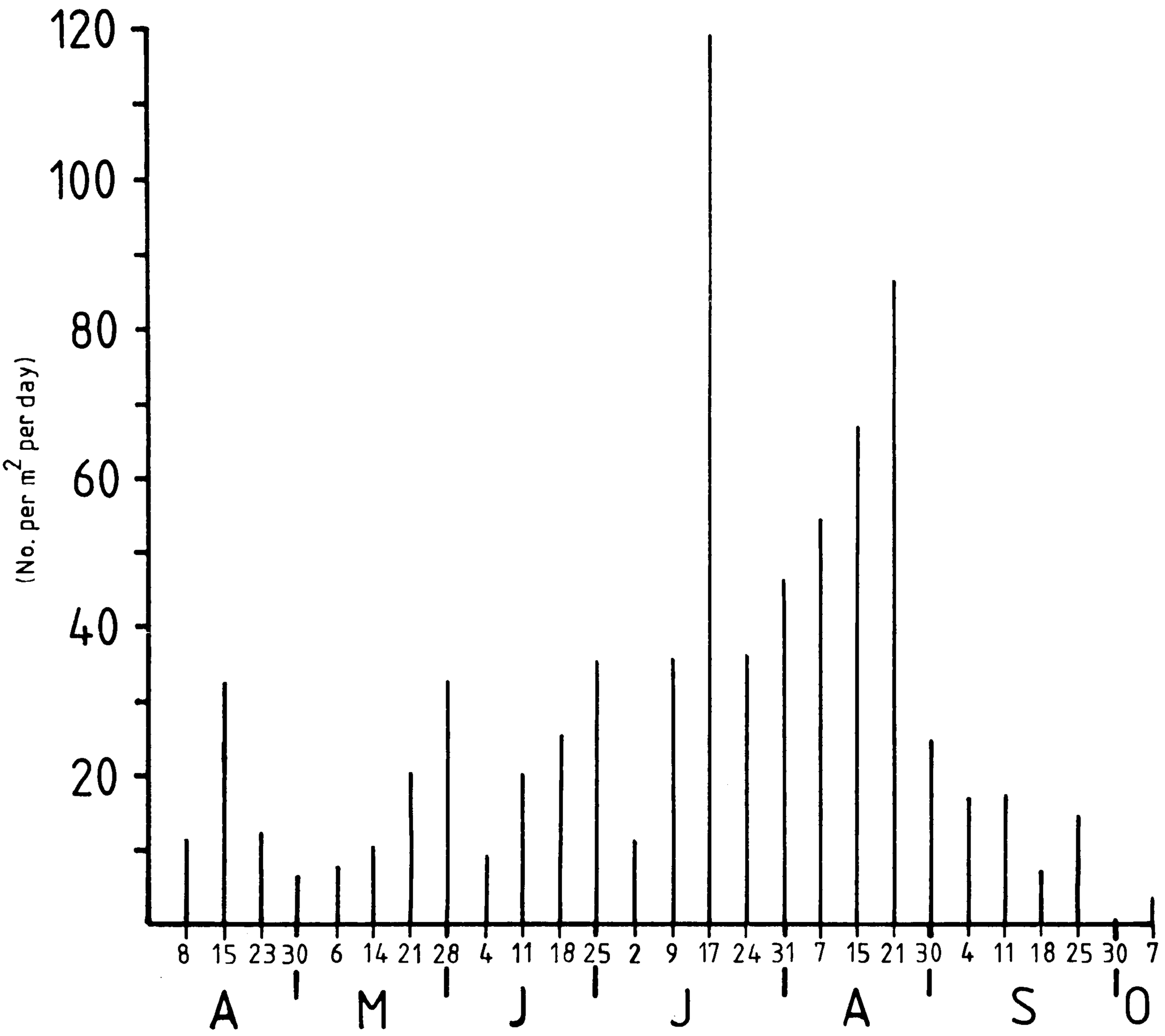


FIGURE 6:2:4 - Mean density of adult Chironomidae caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

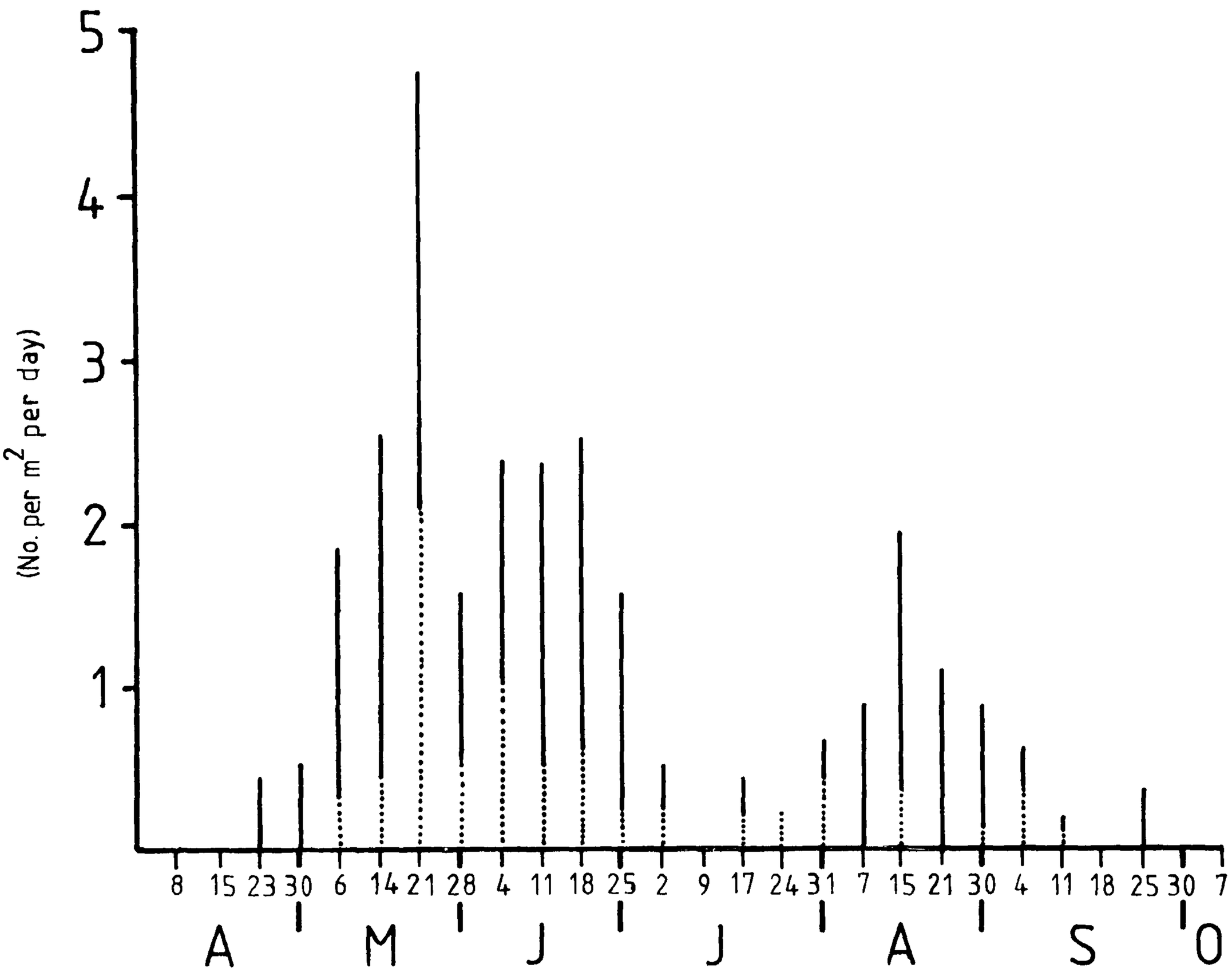


FIGURE 6:2:5 - Mean density of adult *Camptochironomus tentans* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

	1	2	3	4	5	6	7
Camptochironomus tentans	34	33	19	6	12	1	5
Chironomus riparius	0	0	0	1	0	0	0
Chironomus venustus	0	2	0	0	0	0	0
Endochironomus dispar	0	1	0	0	0	0	0
Endochironomus tendens	1	1	2	1	0	0	4
Glyptotendipes pallens	8	13	28	15	2	2	0
Limnochironomus nervosus	7	7	18	7	2	1	1
Micropsectra sp.	0	0	1	0	0	1	0
Microtendipes pedellus	0	0	7	9	1	0	0
Parachironomus arcuatus	18	19	36	13	3	3	1
Phaenopsectra flavipes	0	0	0	1	0	0	0

TABLE 6:2:2 - Chironominae taxa represented in emergence trap catches during 1981, together with the number of flies taken from each trap (1-7) over the sampling period.

(See Figure 6:1:1 for trap locations.)

ii) *Glyptotendipes pallens* (see Figure 6:2:6)

Figure 6:2:6 shows two distinct emergence periods, in May/June and August/September, indicating that this species is likely to be bivoltine. Maximum numbers occur in the third week of May. Mountain (1981) reported a similar temporal pattern of adult appearance. In their study based on two Hertfordshire ponds, Learner and Potter (1974) found *Glyptotendipes pallens* to be univoltine in 1961 and bivoltine in 1962.

A consistent numerical bias towards males or females is not apparent from Figure 6:2:6.

Most *Glyptotendipes* adults were recovered from Trap 3 (see Table 6:2:2), which is located three metres behind the lakeward edge of the reedbed. Few flies were recovered from the two traps (5 and 6) lying closest to land although reedstem- and benthic-dwelling larvae do frequent this area. Indeed, the latter group is particularly well-represented and is composed of third and fourth instars, suggesting interzonal migration of larvae or pupae may occur before emergence takes place.

iii) *Limnochironomus nervosus* (see Figure 6:2:7)

Three emergence periods are evident from Figure 6:2:7 although these are not so well-defined as those for *Camptochironomus tentans* and *Glyptotendipes pallens*. The first is around the end of May and the beginning of June, the second is in the first two weeks of July, and the third extends through August to the start of September. The greatest densities are reached in the latter period, when females are much more numerous than males. *Limnochironomus nervosus* appears to be trivoltine at Cop Mere although the possibility exists that the first two emergence periods constitute the start and finish of one longer period, which would give *nervosus* bivoltine status; Mundie (1955) found this species to be bivoltine in a storage reservoir habitat.

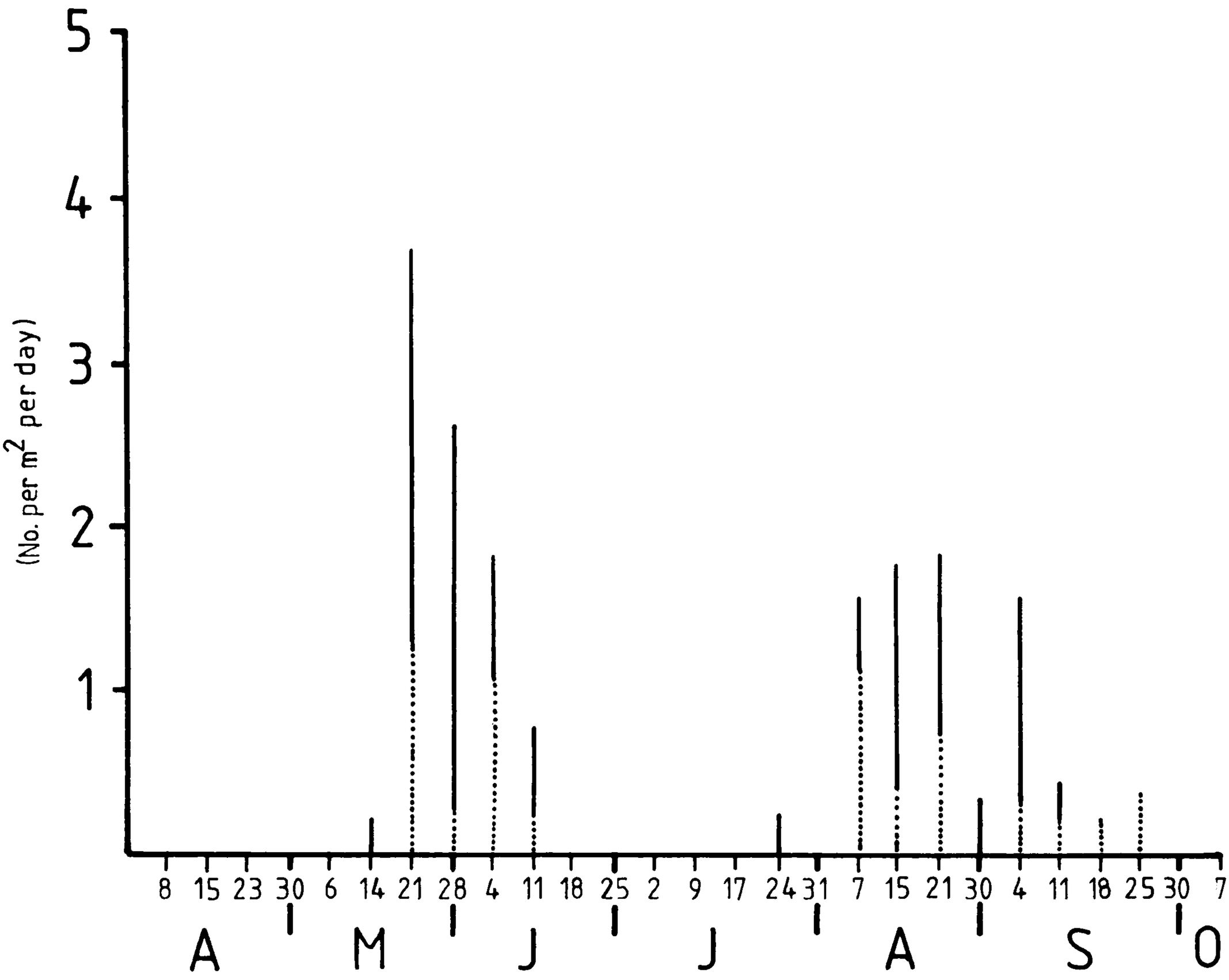


FIGURE 6:2:6 - Mean density of adult *Glyptotendipes pallens* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

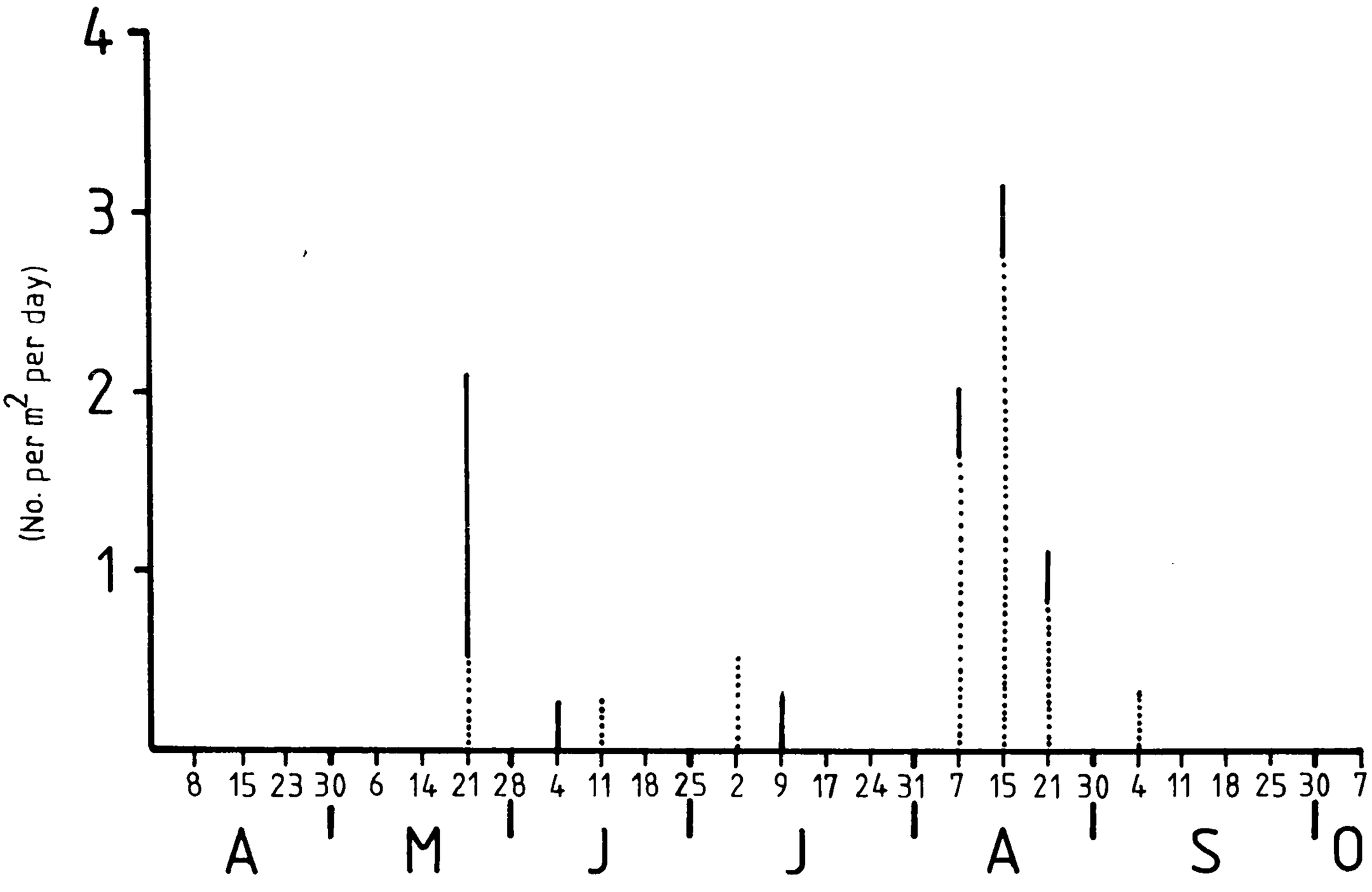


FIGURE 6:2:7 - Mean density of adult *Limnochironomus nervosus* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

Table 6:2:2 shows that *Limnochironomus* adults are more plentiful in trap catches towards the front (lakeward edge) of the reedbed than the back, a pattern which is replicated in the *Limnochironomus* juvenile population during the time of greatest larval densities (August to October).

iv) *Parachironomus arcuatus* (see Figure 6:2:8)

Parachironomus arcuatus adults appear continuously from the first week in August to the third week of September, suggesting that this chironomid is univoltine. However, the presence of reedstem-dwelling first instar *Parachironomus arcuatus* larvae as early as June implies an earlier spell of egg-laying, which would give this species bivoltine status. Working at a Midland wet gravel pit, Titmus (1979b) concluded that *Parachironomus arcuatus* was bivoltine, having one emergence peak in early May and another in mid-June. Mountain (1981) recorded a continuous flight period from June to September at Cop Mere in 1979.

Adults are scarce towards the back (landward margin) of the reedbed's permanent standing water area, a dispersion which is in concordance with that of the *Parachironomus* larval population, where individuals are restricted to zones lying further offshore.

The remaining Chironominae species occur so infrequently that genuine population patterns are not readily discernible. In the case of *Endochironomus tendens*, however, reedbed-dwelling adults are confined to the four traps lying in closest proximity to the frontal margin, complementing the distribution of the reedstem-inhabiting larval population, whose members only frequent the front and middle zones of the permanent standing water area.

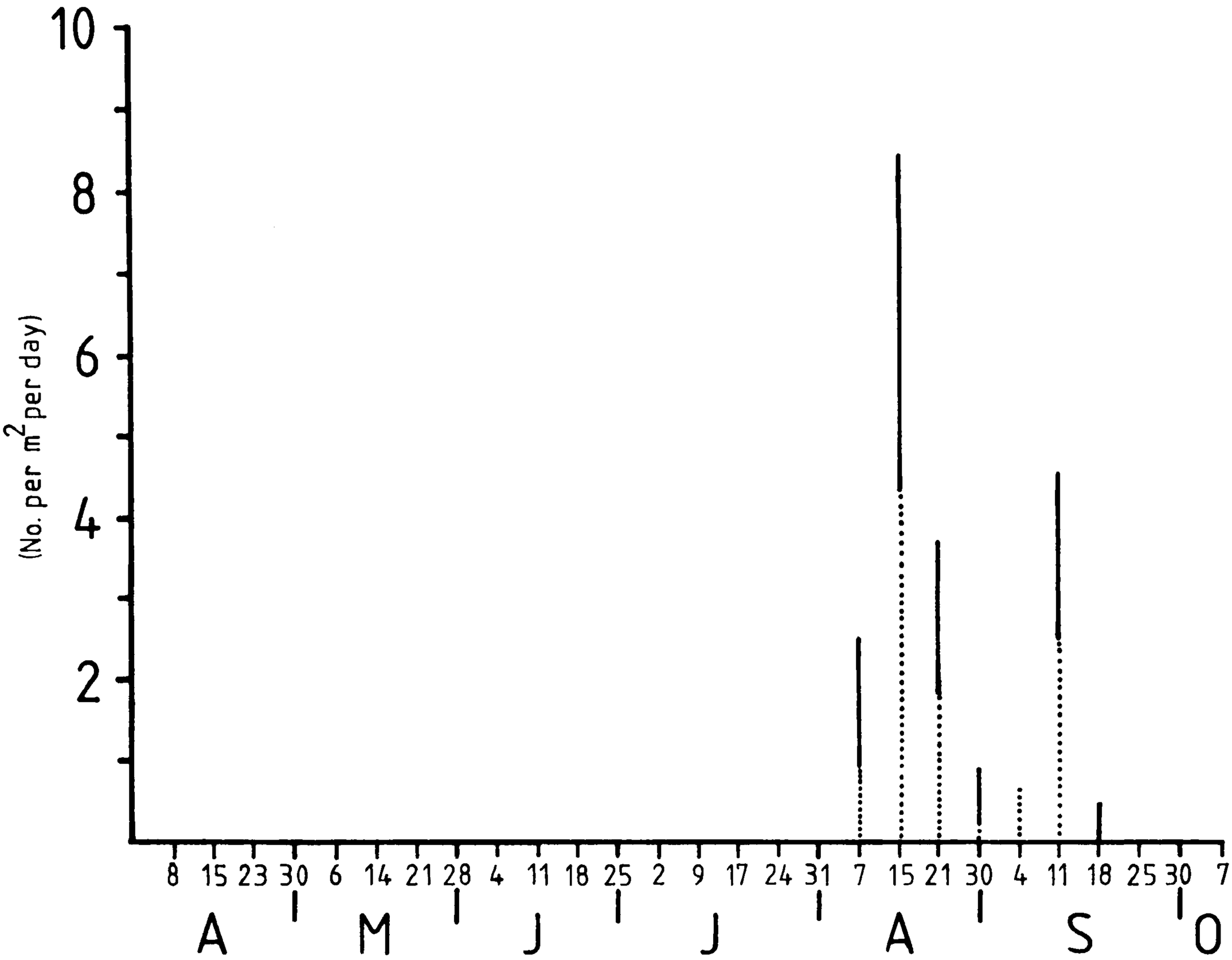


FIGURE 6:2:8 - Mean density of adult *Parachironomus arcuatus* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

In her study at Lough Neagh, Northern Ireland, Carter (1976) found *Microtendipes pedellus* emerging from May until August; in the present investigation, this species was caught over a similar length of time, from June to September.

Four species of Chironominae were taken from the open-water emergence trap: *Camptochironomus tentans; Endochironomus tendens; Limnochironomus nervosus;* and *Parachironomus arcuatus*. *Camptochironomus* is considerably less common in this trap than those sited towards the front (lakeward margin) of the *Phragmites* stand, which may be an indirect reflection of the better larval protection afforded in the reedbed than in open water. *Endochironomus* juveniles were present in samples of benthic vegetative material taken from open water in June and July, 1981; adult *Endochironomus* collected from the open-water emergence trap are probably derived from these larvae.

E) INDIVIDUAL PATTERNS OF DISTRIBUTION AND ABUNDANCE - ORTHOCLADIINAE

i) *Cricotopus flavocinctus* (see Figure 6:2:9)

Figure 6:2:9 shows flies to be relatively abundant early in the sampling period, attaining a maximum density at the end of May. A lack of temporal compatibility between the adult and larval populations has been discussed already (page 71). Adults are found in each month from April to October; it can be assumed, therefore, that this species has several generations per year. Hirvenoja (1975) recorded an emergence period extending from the start of June to mid-September for *Cricotopus flavocinctus* in Southern Finland. In their report based on two Hertfordshire ponds, Learner and Potter (1974) assigned bivoltine and trivoltine status to this species for 1961 and 1962 respectively.

Male flies are generally more common than females when any imbalance in the sex ratio exists.

The majority of adult *Cricotopus flavocinctus* are found around the front and middle of the reedbed's permanent standing water area (see Table 6:2:3).

[illegible]ive to these parts.

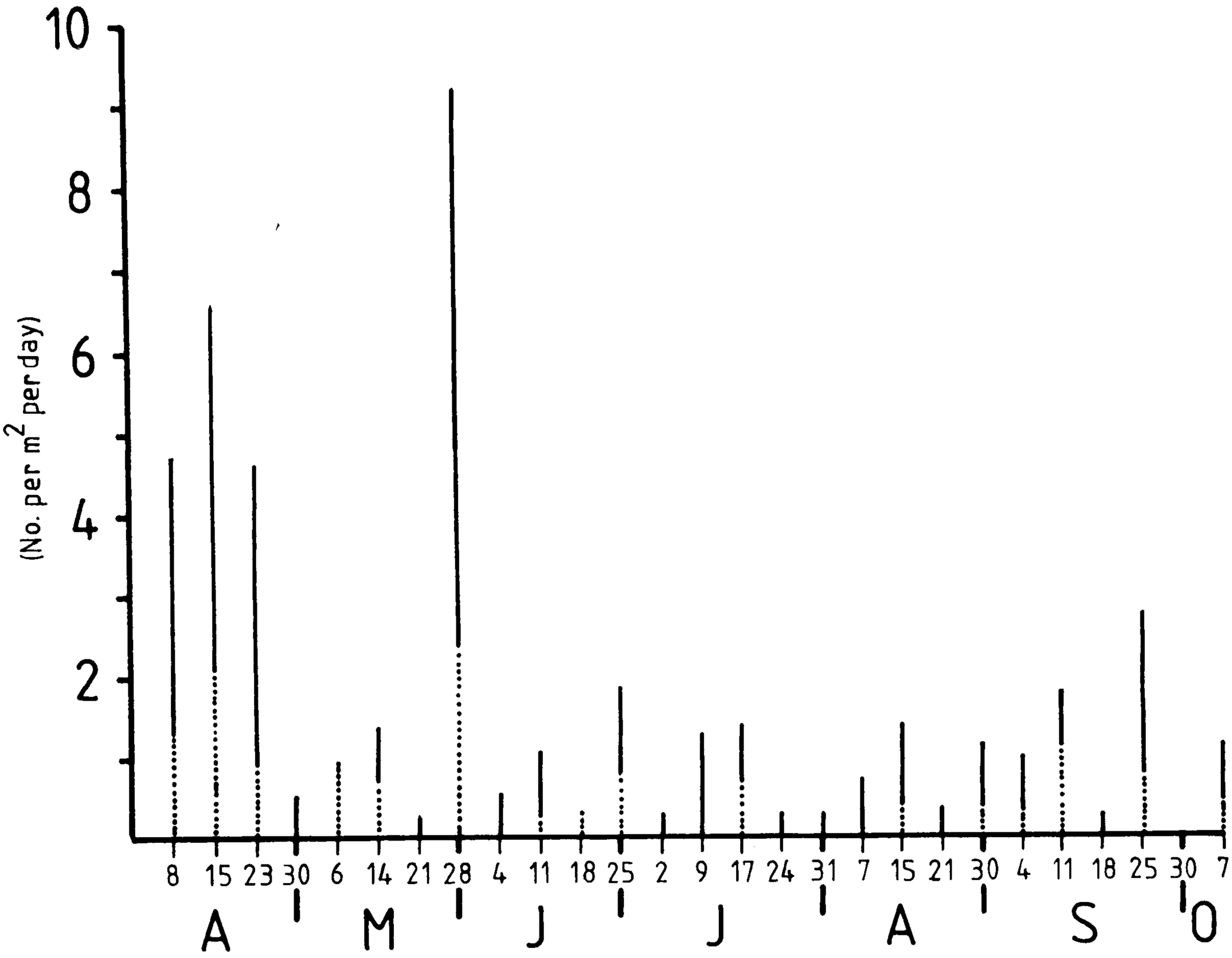


FIGURE 6:2:9 - Mean density of adult *Cricotopus flavocinctus* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

	1	2	3	4	5	6	7
Corynoneura carriana	1	0	1	0	0	0	0
Corynoneura edwardsi	3	1	5	5	0	4	1
Cricotopus flavocinctus	36	47	34	31	11	2	13
Cricotopus sylvestris	515	192	327	177	39	86	240
Limnophyes truncorum	1	0	0	1	0	1	0
Metriocnemus atratulus	0	0	0	0	0	1	0
Metriocnemus hirticollis	2	0	9	19	23	12	0
Metriocnemus tristellus	0	0	0	0	0	1	0
Paraphaenocladius impensus	0	0	0	0	0	5	0
Psectrocladius limbatellus	167	25	29	12	2	3	176
Smittia leucopogon	1	2	9	5	1	1	1
Smittia pratorum	0	0	0	1	0	0	0
Thienemanniella majuscula	1	0	0	0	2	0	0

TABLE 6:2:3 - Orthocladiinae taxa represented in emergence trap catches during 1981, together with the number of flies taken from each trap (1-7) over the sampling period.

(See Figure 6:1:1 for trap locations.)

ii) *Cricotopus sylvestris* (see Figure 6:2:10)

Flies are most numerous during July and August, with a maximum count in the third week of the latter month. Judging by the almost uninterrupted appearance of adults throughout the sampling period, *Cricotopus sylvestris* would seem to be multivoltine; studies of the juvenile population reveal generation overlap, a situation observed by Mountain (1981) at Cop Mere. This species can be univoltine, bivoltine, trivoltine, or quadrivoltine according to Learner and Potter (1974), whilst LeSage and Harrison (1980) recognisedmultivoltine activity at Salem Creek in Southern Ontario, Canada.

A well-balanced sex ratio is almost always maintained during the sampling period.

Table 6:2:3 illustrates the fact that over 50% of adult *Cricotopus sylvestris* taken from the reedbed were caught in the two traps lying nearest to the lakeward margin of the *Phragmites* stand (Traps 1 and 2); the highest densities of *sylvestris* larvae are usually found around this frontal edge.

iii) *Metriocnemus hirticollis* (see Figure 6:2:11)

Metriocnemus hirticollis was collected in every month from April to October. It reaches a maximum level of abundance in the fourth week of September, although it is most consistently found in relatively high numbers during June and July. Smith and Young (1973) investigated chironomid emergence from Little Crosby Pool on Merseyside, where *Metriocnemus hirticollis* was taken from late May to early August, appearing in greatest quantity from mid-June to the third week in July. At Cop Mere this species probably has several generations per year; Learner and Potter (1974) categorised it as bivoltine and quadrivoltine.

A consistent bias in the sex ratio is not evident although inequalities do occur.

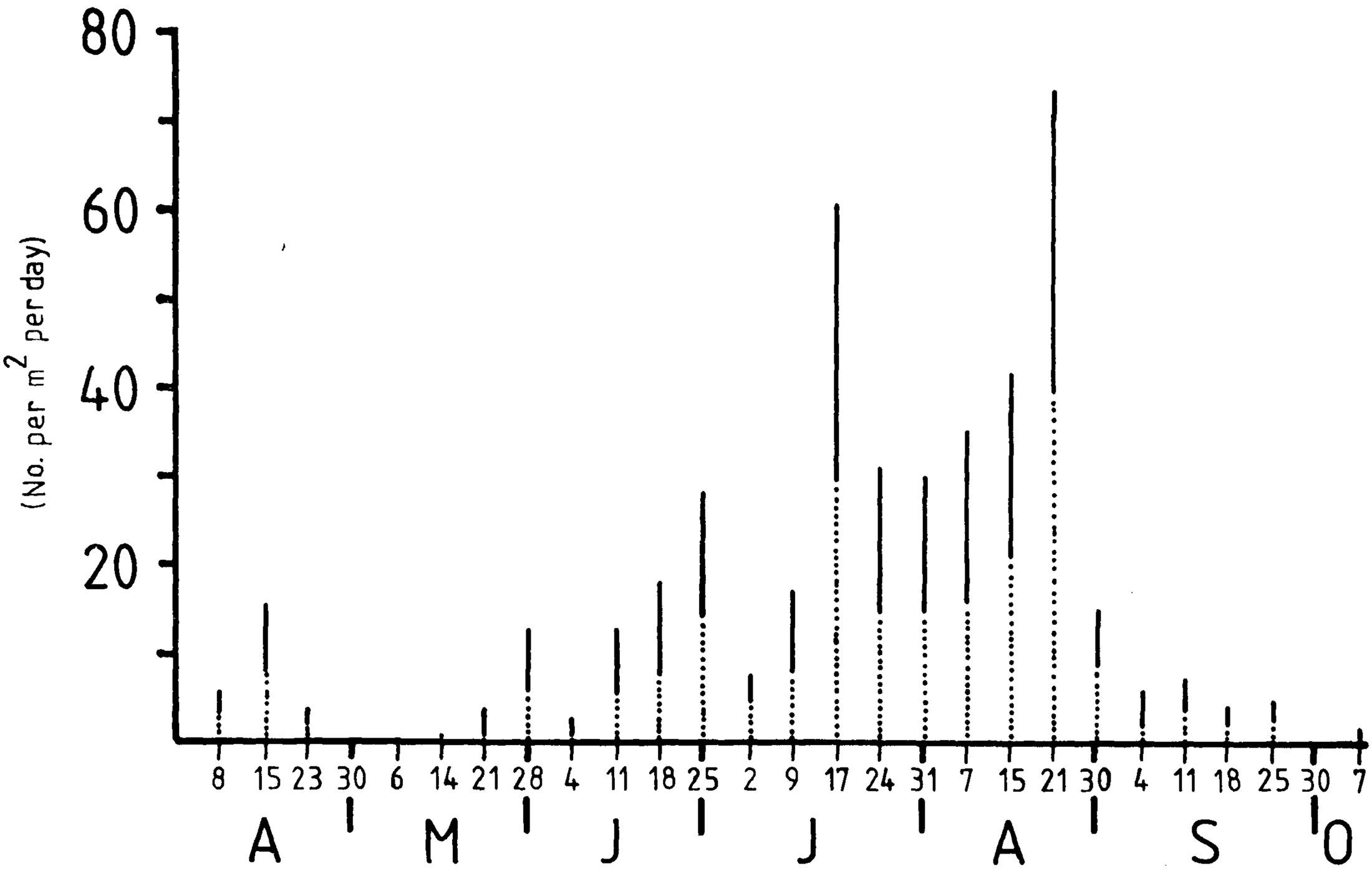


FIGURE 6:2:10 - Mean density of adult *Cricotopus sylvestris* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

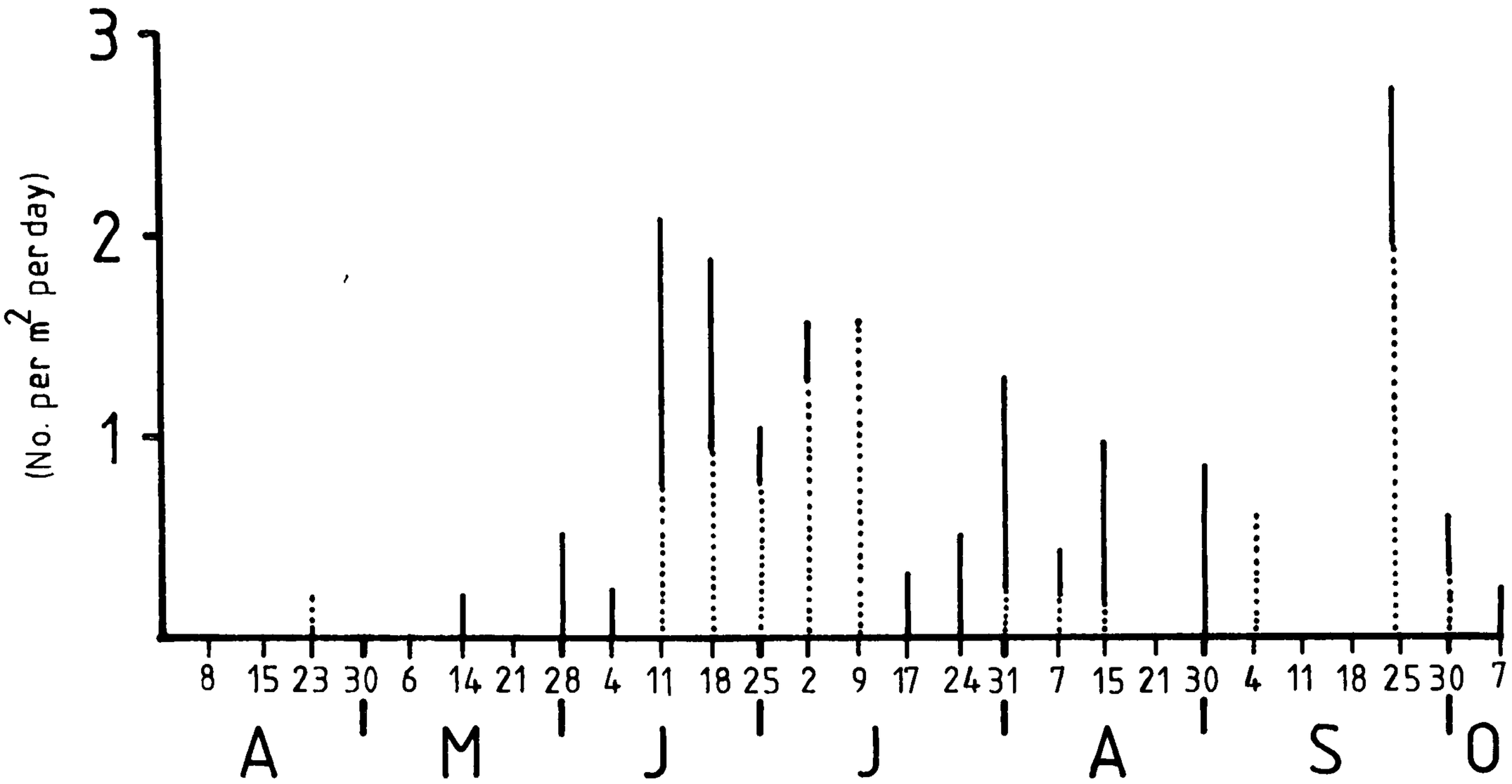


FIGURE 6:2:11 - Mean density of adult *Metriocnemus hirticollis* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

Metriocnemus hirticollis is atypical of the chironomids discussed so far in that many more adults are found in the traps nearer the back of the reedbed's permanent standing water area than the front. *Metriocnemus* larvae designated as sp. A, which seems to be synonymous with *hirticollis*, are very rare on reedstems but are common in the semi-terrestrial part of the reedbed lying immediately behind the area of permanent standing water. It is probable, therefore, that the adults caught in traps towards the back of this latter area are derived from larvae that have strayed from their original semi-terrestrial habitat.

iv) *Psectrocladius limbatellus* (see Figure 6:2:12)

The emergence period for *Psectrocladius limbatellus* is centred on the summer months of June, July, and August although a small number of flies were collected on one occasion in May. Maximum emergence takes place in the third week of July. The appearance of adults during May, followed by a break and then a reappearance in June, indicates that this species is likely to be bivoltine, the status assigned by Mountain (1981) to *Psectrocladius sordidellus* at Cop Mere. Mundie (1955) studied chironomid emergence from a storage reservoir and regarded *Psectrocladius limbatellus* as bivoltine.

A characteristically equal sex ratio is maintained over the greater part of the sampling season. Initially, however, only males are present but the numbers involved are small and the existence of protandry cannot be guaranteed.

Close agreement is found between the dispersion patterns for adults and larvae inhabiting the reedbed: Table 6:2:3 shows that the majority of flies were taken around the front (lakeward edge) and middle of the sampling area; larvae occur exclusively in these parts.

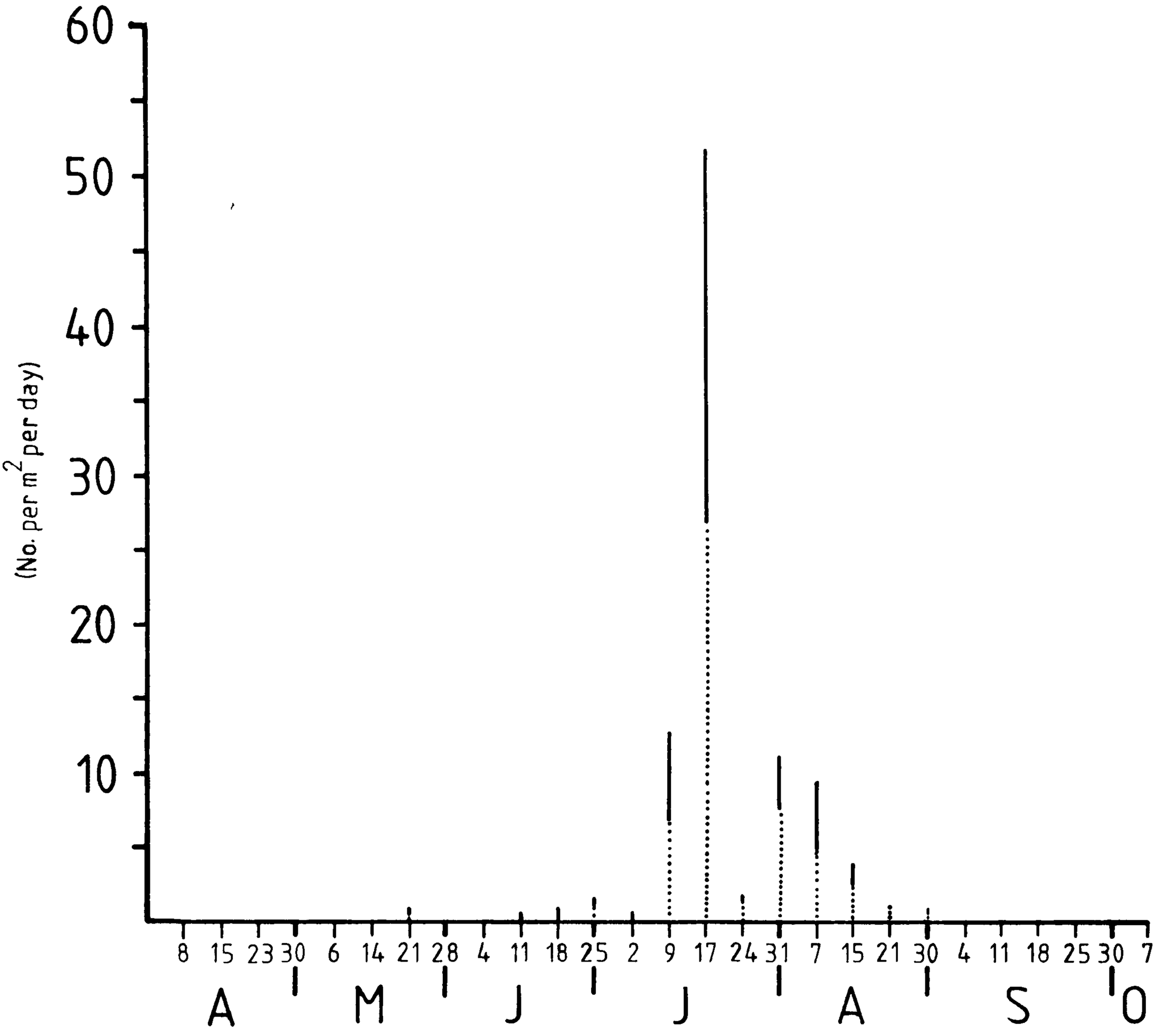


FIGURE 6:2:12 - Mean density of adult *Psectrocladius limbatellus* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

Other Orthocladiinae are much less numerous than the species discussed above, but some ecologically significant spatial distribution patterns can be discerned from Table 6:2:3.

Corynoneura edwardsi, the commoner of the two *Corynoneura* species in adult counts, is represented in July and August and flies were recovered from all parts of the trapping area; most *Corynoneura* larvae were collected from May to July and they frequent reedstems throughout the three reedstem-sampling zones. Thus, larval and adult dispersion patterns are compatible. Titmus (1979b) found emergence of *Corynoneura edwardsi* from a Midland wet gravel pit was restricted to the first week of June. The *Corynoneura* species inhabiting the reedbed at Cop Mere are probably univoltine.

Larvae of *Paraphaenocladius impensus* are associated with semi-terrestrial conditions. Furyk (1969) noted *impensus* larvae living at the water/land boundary of a Polish lake, whilst Lindegaard *et al.* (1975) discovered juveniles in the moss carpet of a Danish spring. This species has also been identified in forest foliage (Albu, 1971). At Cop Mere, the restriction of adults to the most landward emergence trap could reflect passive or active migration of larvae from the semi-terrestrial to the aquatic part of the reedbed, in a similar manner to that envisaged for *Metriocnemus hirticollis*. However, *Paraphaenocladius* larvae were absent from both aquatic and semi-terrestrial samples.

Two other species normally associated with semi-terrestrial environments *(Smittia leucopogon* and *Smittia pratorum)* are found in emergence traps nearer open water. *Smittia* larvae were not present in any samples from the reedbed and it may be that the adults taken from the glass plates on traps are not derived from aquatic pupae but alight on the greased surfaces when these are inadvertently exposed to open air during servicing.

Most of the Orthocladiinae removed from the open-water emergence trap are either *Cricotopus sylvestris* or *Psectrocladius limbatellus*. Just over 15% of the total *Cricotopus sylvestris* trap population were taken in open water; the respective figure for *Psectrocladius limbatellus* is 42%. These flies originate from the considerable larval populations of *sylvestris* and *limbatellus* that inhabit the floating algal mats covering a large part of the mere in summer.

F) INDIVIDUAL PATTERNS OF DISTRIBUTION AND ABUNDANCE - TANYPODINAE

i) *Procladius choreus* (see Figure 6:2:13)

This chironomid has two main spells of emergence, one starting early in April and continuing throughout May, and the other extending over September. A less numerically productive period occurs during July and August, which may represent the extended 'tails' of the two main periods. The highest emergence density exists in the second week of April.

Procladius choreus is probably bivoltine at Cop Mere, judging by the form of the graph in Figure 6:2:13. Learner and Potter (1974) reported mainly bivoltine, but also univoltine, activity; Potter and Learner (1974) found *Procladius choreus* to be bivoltine in a South Wales reservoir.

Any inequalities in the sex ratio are not consistently biased in favour of males or females.

Table 6:2:4 reveals that the majority of *Procladius choreus* flies tend to emerge nearer to open water than land, with almost 17% of the total adult population occurring in the open-water trap. As larval *Procladius choreus* are free-swimming, and are thus naturally scarce in reedstem and benthic samples, comparison of the dispersion patterns for juveniles and adults is unfeasible, although the close spatial compatibility generally found in other species suggests *Procladius choreus* larvae will be more plentiful towards the front (lakeward margin) of the reedbed's permanent standing water area than the back.

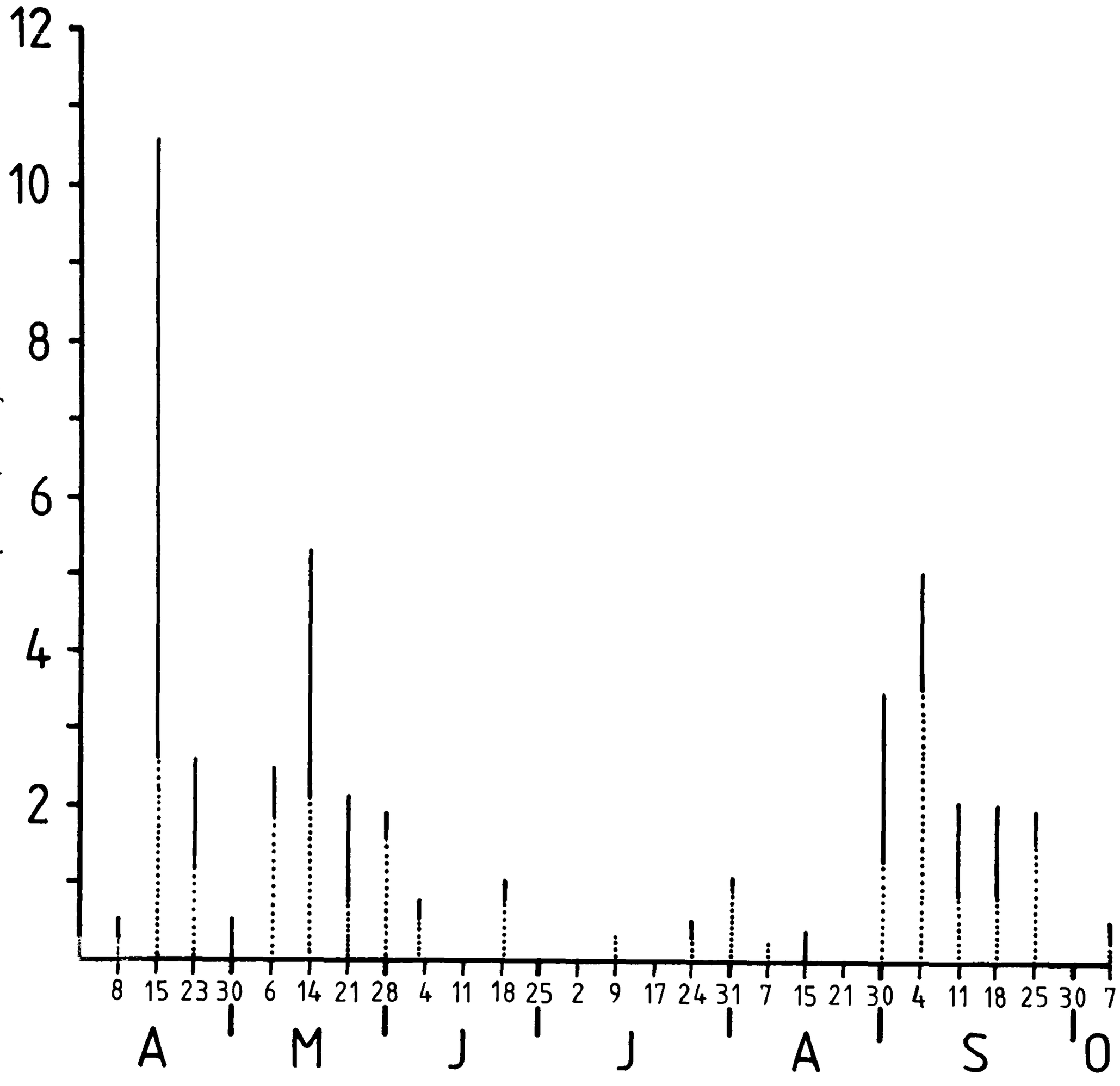


FIGURE 6:2:13 - Mean density of adult *Procladius choreus* caught in emergence traps during 1981, expressed as the number of individuals emerging per m^2 per day.

——— - males; ····· - females

	1	2	3	4	5	6	7
Ablabesmyia monilis	0	0	0	0	0	0	3
Procladius choreus	66	50	13	14	4	2	30
Procladius signatus	0	1	0	0	0	0	0
Psectotanypus varius	2	4	1	0	0	0	0
Psilotanypus rufovittatus	14	9	3	2	2	4	6

TABLE 6:2:4 - *Tanypodinae* taxa represented in emergence trap catches during 1981, together with the number of flies taken from each trap (1-7) over the sampling period. (See Figure 6:1:1 for trap locations.)

Of the remaining Tanypodinae, the most abundant is *Psilotanypus rufovittatus*, whose main emergence period extends from April to June. A small number of flies were collected at the end of August and it is probable that this species is bivoltine at Cop Mere. Mundie (1957) recorded an emergence period from May to August for *Psilotanypus rufovittatus* in storage reservoirs and considered it to be univoltine. In their study of a reservoir in South Wales, Potter and Learner (1974) also regarded *rufovittatus* as univoltine, with an emergence period extending from May to September. The spatial distribution pattern for this species at Cop Mere is similar to that of *Procladius choreus*.

Ablabesmyia monilis, *Procladius signatus*, and *Psectrotanypus varius* are not sufficiently numerous to allow valid comment regarding their temporal distribution patterns. *Ablabesmyia monilis* was only caught in the open-water emergence trap and may not be a reedbed-dwelling species; *Procladius signatus* and *Psectrotanypus varius* are found closer to the front (lakeward margin) of the reedbed's permanent standing water area than the back and were not present in the open-water trap.

In any consideration of temporal chironomid emergence patterns it must be remembered that both voltine category and flight periods can differ in the same species according to year and location (Sadler, 1935; Miroshnichenko, 1971; Learner and Potter, 1974; Hirvenoja, 1975; Carter, 1976; Beattie, 1978; Titmus, 1979b).

Chapter 7

FINAL DISCUSSION

In the introduction to this thesis, three questions are stated for which answers were sought through the research investigations considered in the following chapters. This is an appropriate point to reiterate these questions and discuss the answers that have been put forward. The questions are:

1) Which chironomid species frequent the reedbed at Cop Mere?

2) What are their collective and individual spatiotemporal patterns of distribution and abundance?

3) What factors determine the form of each of these patterns?

Information relating to Question 1 is presented in chapters 3, 5, and 6. In chapter 3, data from a comprehensive sampling programme involving the removal of reedstems indicate the types of chironomid larvae that live on the epiphytic coating of these stems. Identification to species level from larval characteristics alone is often not feasible; where possible, larvae were raised to adults, for which species identification is easier. Comparison of juvenile population patterns with those described in chapter 6 for emerging adults also provides soundly-based evidence regarding the species status of larvae.

Stem-samples were taken at monthly intervals through 1981 and on several occasions during 1982. These show the existence of a characteristic species composition for the epiphyton-dwelling chironomid population, although some inter-year variation is evident. This observation is supported by a comparison of the 1980 and 1981 populations. (Data concerning the 1980 epiphyton-dwelling larval population *are* derived from Mountain (1981).)

Seventeen chironomid genera were collected from reedstems during 1981, nine of these belonging to the Chironominae and eight to the Orthocladiinae. *Camptochironomus* and *Glyptotendipes* were the most

abundant representatives of the Chironominae of the eight Orthocladiinae, one species (*Cricotopus sylvestris*) accounts for over 95% of the total reedstem-dwelling larval chironomid population for the year.

In chapter 5, consideration is given to the juvenile chironomids inhabiting the floor of the reedbed. During 1981, samples of substrate material were taken from the reedbed's permanent standing water area and the semi-terrestrial part lying further inland. In terms of taxonomic composition, a sharp distinction exists between the larval communities living in the two areas. Most of the chironomid taxa frequent one or the other of these areas. The benthic community in permanent standing water is dominated by one species (*Camptochironomus tentans*) whilst three taxa (*Metriocnemus* sp. A, Pentaneurini sp. A, and *Tanytarsus*) are all relatively abundant in the semi-terrestrial part of the reedbed.

The reedstem-dwelling chironomid community contains a larger number of taxa than that inhabiting the floor between epiphyton-coated stems and larval densities are often considerably higher. These comparative observations are similar to those made by Pieczyński (1977) and Bailey *et al.* (1978). In his study of a Polish lake, Pieczyński found chironomids to be more important and dominant in the faunal community of emergent macrophytes than in the faunal community of the surrounding floor substrate. Working at a Tanzanian reservoir, Bailey *et al.* noted an increase in the variety of macroinvertebrates on stony and muddy shores when emergent macrophytes were present.

The sampling programme involving monthly collections of larvae from reedstem and floor substrate material is designed in such a way as to provide answers to Question 2, which relates to collective and individual spatiotemporal patterns of chironomid distribution and abundance. Emergence data, obtained from a concurrent fly sampling programme, reveals spatiotemporal patterns in the reedbed's adult chironomid community.

Spatial variations in the reedbed's larval communities were investigated by taking samples from a number of predesignated zones lying parallel with the *Phragmites*/open-water interface. These zones reflect the environmental gradation that exists from the front (lakeward edge) to the back (landward edge) of the reedbed in both the epiphytic and floor habitats. A considerable number of significant interzonal differences in species composition and abundance are evident during the year.

In the area of permanent standing water, the predominant benthic species (*Camptochironomus tentans*) favours the front of the *Phragmites* stand, whereas the second most common benthic chironomid (*Glyptotendipes pallens*) exists in its greatest numbers towards the back.

In the case of epiphyton-inhabiting juveniles, some species (e.g. *Cricotopus sylvestris* and *Camptochironomus tentans)* are common to all three reedstem zones whereas other taxa (e.g. *Cricotopus flavocinctus*, *Endochironomus*, and *Thienemanniella*) only occur in one or two zones. Dispersion patterns for emerging adults generally complement their counterparts for larvae which suggests that most species pupate and emerge in close proximity to their original larval habitat.

The reedstem-dwelling larval population is usually most numerous at the front (lakeward edge) of the reedbed and declines progressively towards land. Population biomass follows a similar trend. Maximum generic diversity is most frequently found on reedstems around the back (landward edge) of the permanent standing water area, due to a relatively high level of equitability in this location.

Sampling at regular intervals through the year enables the revelation of temporal distribution patterns. Where numbers are sufficient to discern genuine patterns of temporal occurrence, it is apparent that the stem-dwelling larval Chironominae fall into two categories: 'residents' (*Endochironomus*, *Glyptotendipes*, and *Limnochironomus)*,

which are found all the year round and 'seasonal visitors' (*Camptochironomus* and *Parachironomus*), which are exclusive to the summer and early autumn. Regarding the commoner larvae of the Orthocladiinae, *Cricotopus sylvestris* is present throughout the sampling period whilst *Psectrocladius* was collected from April to July. *Rheocricotopus* and *Thienemanniella* are evident from January to March and disappear by April.

Camptochironomus tentans and *Glyptotendipes pallens* are the only floor-inhabiting chironomid larvae to be found in every month of the sampling period; other species occur with variable intermittency.

In both *Camptochironomus* and *Glyptotendipes*, migration from epiphyton to the reedbed floor would seem to take place as larval development proceeds, although some fourth instar *Glyptotendipes* occupy the hollow tips of broken stems.

Question 3, concerning the factors determining the form of chironomid distribution and abundance patterns, proved the most difficult question to asnwer precisely. This is due largely to the inherent problems faced when attempting to isolate and evaluate different factors through a research programme that is basically orientated towards field-work.

The environmental factors that were regarded as potential influences on larval population patterns can be placed in three categories: substrate characteristics; physico-chemical water properties; and faunal interrelationships. These can be termed 'extrinsic' factors and are studied in detail. However, as far as temporal variation in larval abundance is concerned, month to month density fluctuations appear to be directly controlled to a large extent by 'intrinsic' population characteristics, particularly those which govern seasonal patterns of egg-laying. Extrinsic determinants will have a more immediately

recognisable influence on temporal density change in the adult chironomid population, where deterioration in the weather can cause rapid and pronounced mortality. Of course extrinsic factors controlling adult numbers may indirectly influence patterns of larval abundance if the timing and capacity of egg-laying is affected - this is an area of study that lies outside the scope of the present research.

Extrinsic factors have a direct effect on the spatial distribution of larvae. Several are involved in this respect and their influences are investigated in chapters 4 and 5.

Dispersion patterns in the predominant reedstem-dwelling species (*Cricotopus sylvestris*) appear to be controlled principally by spatial variation in epiphyton characteristics. Significant interzonal differences in epiphyton density are evident at certain times of the year and often a positive association exists between larval and algal quantities, both on an interzonal and intrazonal basis. Interzonal variation can also occur in qualitative epiphyton characteristics although this does not exert any recognisable control on larval dispersion. Epiphyton constitutes a source of food and shelter for colonising chironomids; its role as a shelter provider is the one which has the strongest impact in relation to spatial patterns of chironomid distribution.

The experiment described at the end of chapter 4, involving the inter-zonal transfer of epiphyton-coated bamboo canes, provides corroborative evidence that spatial variation in algal density can determine similar variation in larval numbers, especially with regard to *Camptochironomus tentans*, *Cricotopus sylvestris*, and *Endochironomus*.

The degree of algal shelter available to a reedstem-inhabiting chironomid larva will be partly dependent on the size of the larva. The characteristically large fourth instars of certain species require

a dense epiphytic growth for total concealment. This could explain the poor representation of fourth instar *Endochironomus* and *Cricotopus sylvestris* towards the back of the reedbed's permanent standing water area, where the algal growth is relatively sparse.

Relationships between fauna and epiphyton were examined by Rosine (1955) in Muskee Lake, Colorado. He suggested that differences in animal abundance on three plants (*Chara delicatula*, *Potamogeton gramineus*, and *Polygonum natans*) are caused, in part, by characteristic differences in the epiphytic coating of each plant species.

Apart from spatial variation in epiphyton characteristics, other potential determinants of larval dispersion patterns include spatial gradations in physico-chemical water properties (oxygen content, temperature, pH, conductivity, and light penetration), the initial distribution of egg-masses, inter-specific relationships within the chironomid community, and predation by non-chironomids.

Investigations of water property gradations suggest that the only one that might have any influence on larval dispersion is the gradation in light penetration. A positive phototactic response is found in the larvae of many chironomid species (e.g. *Camptochironomus tentans* and *Cricotopus sylvestris*), particularly in early instars. From July to October, 1981, most of the reedstem-dwelling larval population at Cop Mere is concentrated towards the front of the reedbed, where illumination levels are comparatively high. As the majority of the chironomids are first and second instar *Cricotopus sylvestris*, positive phototaxis offers a feasible explanation of this distribution, especially in view of the fact that interzonal differences in epiphyton density during this time are almost exclusively insignificant.

The initial distribution of egg masses within the reedbed does not appear to be a significant determinant of larval dispersion patterns. The first instar planktonic activity known to occur in a number of the resident chironomids could take larvae some distance from their hatching

location. Juvenile *Psectrocladius limbatellus*, *Rheocricotopus*, and *Thienemanniella* are characteristically found towards the front (lakeward edge) of the *Phragmites* stand, a distribution that may reflect an influx of larvae from an open-water hatching location. Similarly, reedstem-dwelling *Metriocnemus* sp. C, which are most abundant around the back (landward edge) of the permanent standing water area, may be derived from the adjacent semi-terrestrial habitat. (*Metriocnemus* sp. C larvae are known to frequent the latter environment.)

There is no evidence to suggest that the larval spatial distribution pattern for any reedstem-dwelling chironomid species is influenced in any way by that of another chironomid species. Predation by non-chironomids also seems unimportant as a determinant of larval dispersion; Drake (1983) reached the same conclusion in his study of the chironomid larvae living on bulrush leaves in a chalk stream. He found that the presence of predators (*Erpobdella octoculata*, *Helobdella stagnalis*, and flatworms (mainly *Polycelis* sp.)) had no recognisable effect on the density of any chironomid species.

As far as benthic-dwelling larvae are concerned, interzonal variation in density appears to be largely dependent on substrate characteristics. The predominant species (*Camptochironomus tentans*) may prefer the frontal part of the reedbed's permanent standing water area because of the relatively high percentage of sand in the floor substrate at this location - a sandy floor is conducive to larval tube-building and pupal case construction. The fact that *Glyptotendipes pallens* is found in its greatest numbers towards the back (landward edge) of the permanent standing water area may be due to an attraction for the large amount of plant material that accumulates here.

Where noticeable interzonal variation in species abundance occurs in the semi-terrestrial part of the reedbed, the principal determinant is likely to be the moisture content of the substrate. Some chironomid

types (*Chironomus* 'thummi' type, *Glyptotendipes pallens*, and Pentaneurini sp. A) are most numerous in the wetter environment towards the front (lakeward margin) of this area, whereas *Metriocnemus* sp. A attains its highest densities at the back, where more terrestrial conditions can prevail.

In the present study, the investigation of pattern-determining factors tends to be compartmentalised - the effect of each influence is considered in its own right. It must be remembered, however, that these influences might not operate in mutual isolation and some degree of synergic control is possible. Certainly, the real-life situation will be more complex than the picture built up from research, although it is felt that the present investigation has exposed the basic functional framework of chironomid ecology in the reedbed at Cop Mere.

When this research was initiated, it was realised that the chironomid ecology of one reedbed might differ in certain aspects from the chironomid ecology of another. The presence of reedbeds at a number of meres on the Shropshire-Cheshire Plain provides an opportunity for comparative study. In relation to the meres, faunal comparisons of any description are rare. Kennedy (1961) undertook a faunal survey of Crose Mere and Sweat Mere but only identified chironomids to subfamily level. Brinkhurst (1960) sampled the fauna of several meres (Blakemere, Colemere, Crosemere, Ellesmere, Newton Mere, and Whitemere) and found a high degree of uniformity, both in the number of individuals in each lake and in frequency of occurrence. Chironomids are not studied in detail.

During the third week of June, 1982, eight meres (Betley Mere, Big Quoisley Mere, Cop Mere, Little Quoisley Mere, Marbury Mere, Pick Mere, Redes Mere, and Tatton Mere) were visited and reedstem samples taken from each. (The regional locations of these meres are shown in Figure 2:1:1.) Information obtained from this sampling

programme is presented in Table 7:1[1]. Figures for total larval density vary widely and are not significantly correlated with those for epiphyton density. The reason for this variation in larval numbers remains undetected. In terms of diversity levels and the size range of percentage contributions, the taxonomic patterns for the eight meres are fundamentally similar. *Cricotopus* (identified as *sylvestris* at all locations) is universally predominant; its lowest relative abundance value (71.86) is at Pick Mere, where the percentage contribution of *Endochironomus* is unusually high (26.84). The eight taxonomic compositions share basic similarities with *Cricotopus*, *Glyptotendipes*, and *Limnochironomus* frequenting all or most of the reedbeds. The majority of the taxa listed are found at Cop Mere at some time of the year, if not during this particular sampling programme. It would seem that the reedstem-inhabiting chironomid communities of the meres have more similarities than dissimilarities, although there is a clear need for further invesigation.

The paucity of studies concerning reedbed-inhabiting chironomids is remarked upon in the introduction to this thesis. Indeed, faunal reedbed surveys of any description are scarce. This is reflected in the fact that literature-derived supportive information relating to the present research is necessarily drawn from a diverse selection of material.

Several of the papers mentioned in the introduction report on faunal variation through stands of emergent macrophytes but fail to consider all the habitats that exist in such areas, or do not make a distinction between the fauna found in different habitats. Dvorák (1970; 1971) and Dvorák and Lisková (1970) examined the horizontal zonation of macrofauna and

---

[1] A variable number of stems were removed from the front of the reedbed at each mere to provide the information presented in Table 7:1.

	B	BQ	C	LQ	M	P	R	T
Brillia	-	-	-	-	0.25	-	-	-
Camptochironomus tentans	-	0.31	0.25	-	-	-	-	-
Chironomus	-	-	-	-	-	0.26	0.11	1.11
Corynoneura	1.39	0.16	-	-	-	-	-	-
Cricotopus	94.44	97.66	97.52	79.73	96.88	71.86	99.12	88.02
Endochironomus	-	-	-	0.45	0.99	26.84	0.33	-
Glyptotendipes	0.69	1.25	1.49	7.66	1.49	0.35	0.22	8.08
Limnochironomus	2.78	-	0.25	11.71	0.50	0.17	-	1.11
Metriocnemus	-	0.16	-	-	-	-	-	-
Metriocnemus sp. C	-	0.31	0.25	-	-	-	-	-
Nanocladius	-	-	-	-	-	0.09	0.11	1.11
Parachironomus	-	-	-	-	-	-	0.11	0.56
Pentaneurini sp. C	-	-	0.25	-	-	-	-	-
Pentaneurini sp. F	-	-	-	-	-	0.17	-	-
Polypedilum	-	0.16	-	0.45	-	0.26	-	-
Psectrocladius	0.69	-	-	-	-	-	-	-
LARVAL DENSITY (no. per cm^2)	0.16	0.71	0.75	0.92	0.99	2.12	1.93	0.57
EPIPHYTON DENSITY (mg per cm^2)	7.50	12.00	8.80	3.80	3.90	6.80	3.10	2.00

TABLE 7:1 - Percentage relative abundance values for the chironomid taxa found on old reedstems at the eight meres visited during June, 1982, together with values for mean larval density and mean epiphyton density. B - Betley Mere; BQ - Big Quoisley Mere; C - Cop Mere; LQ - Little Quoisley Mere; M - Marbury Mere; P - Pick Mere; R - Redes Mere; T - Tatton Mere.

water properties in the emergent macrophyte stands of some South Bohemian ponds. The highest faunal density and biomass occurred at the front of each stand, a situation that usually exists at Cop Mere too. The only chironomid species known to frequent macrophyte stands at both Cop Mere and the South Bohemian ponds is *Cricotopus sylvestris*. As far as chironomid genera are concerned, *Chironomus*, *Cricotopus*, *Endochironomus*, *Microtendipes*, *Pentapedilum*, and *Polypedilum* have been identified from both locations. Differences in sampling techniques prohibit any further comparisons of the present study with those of the Czechoslovakian authors.

Mason and Bryant (1974) discussed horizontal zonation in the floor-dwelling macrofauna of a broadland reedswamp. As at Cop Mere, the greatest faunal density tended to be found at the front (lakeward margin) of the reedbed. Chironomid genera and species were not determined.

Higler (1977) studied horizontal macrofaunal zonation in *Stratiotes* stands on the Dutch Broads and found chironomid dispersion patterns vary on a taxonomic basis.

In all the investigations referred to above, physico-chemical water properties, particularly oxygen content, are regarded as important influences on faunal dispersion patterns. Measurement of oxygen content reveals a decline from the front (lakeward edge) to the back (landward edge) of emergent macrophyte stands. This decline has been proposed as the principal cause of a reduction in animal numbers towards land. Differences in sampling techniques prohibit close comparison of these findings with those of the present study; at Cop Mere, however, substrate characteristics are deemed to play a more significant part in determining zonal patterns of faunal distribution.

One of the few papers to deal in any detail with reedstem-dwelling chironomids is that of Opaliński (1971). Working at Mikołajskie Lake in Poland, he noted that *Glyptotendipes pallens* made up 40% of the total

epiphyton-inhabiting chironomid population; *Cricotopus sylvestris* was also numerous, whilst *Corynoneura* and *Endochironomus tendens* occurred in smaller quantities. All these chironomids are found on reedstems at Cop Mere, where *Cricotopus sylvestris* is the predominant species.

As with any ecological investigations, those embarked on in the present study have certain draw-backs and deficiencies. Constraints on time and manpower are important limiting factors in relation to the scope and quantity of field-work undertaken. Shorter time intervals between chironomid sampling might give a better indication of short-term changes in abundance. A sampling programme lasting a number of years would be valuable, as long-term population changes could then be monitored. The statistical tests used in the analysis of sample data are not infallible; at best, they give a good indication of ecological relationships but they cannot prove that a particular situation always exists.

Reedbeds are recognised as important ecological units in aquatic environments, playing a significant role in the functioning of many freshwater ecosystems. Westlake (1963) has shown that reedswamps are amongst the most productive habitats of temperate regions; the epiphyton on reedstems can make large contributions to aquatic primary productivity (Bowker and Denny, 1978). Many of the types of macroinvertebrates that are known to frequent reedbeds, such as chironomids, constitute an important source of food for fish (Dvorák, 1971; Bailey *et al.* 1978) and water-fowl (Krull, 1970; Danell and Sjöberg, 1978). In the Norfolk Broads, reedswamps have additional importance: they diversify and enhance the scenery, which is essential for the water-based tourist industry, and they support a local thatching industry (Mason and Bryant, 1975b). Clearly, distinct benefits will be gained from the acquisition of any information that may promote the preservation and understanding of reedbed ecosystems.

In the introduction to this thesis, mention is made of large gaps in our knowledge of chironomid ecology, not least in our understanding of reedbed-inhabiting communities. This study will have served a useful purpose if some of these gaps have been filled.

SUMMARY

1) The *Phragmites* reedbed at Cop Mere, Staffordshire, was studied during 1981 and 1982. Within the reedbed, an area of permanent standing water (adjacent to the open water of the mere) and a semi-terrestrial area (on the landward side), could be recognised.

2) Beneath the standing water the substratum consisted of sand and plant debris while in the semi-terrestrial part the surface layer was almost entirely plant debris.

The submerged portions of *Phragmites* stems were coated with epiphyton which was most abundant towards the front (lakeward edge) of the reedbed. The highest densities were found in summer (maximum in June, 1981 was 25.08mg dry weight cm^{-2}).

3) For the monthly sampling programme of chironomid larvae inhabiting the epiphyton of old reedstems, three zones were recognised: Zone 1 ran along the *Phragmites*/open-water interface; Zone 2 was parallel with this but in the middle of the standing water area and Zone 3 lay close to the landward edge of this area.

4) Throughout Zones 1 to 3, mean larval population density and biomass were maximal in late spring and summer; winter values were low. The maximal larval density and biomass in each month were generally found in Zone 1 and the lowest in Zone 3. Statistically significant differences in larval density and biomass occurred at various times throughout the sampling period.

5) Seventeen chironomid genera were collected from reedstems during 1981; nine of these belonged to the Chironominae and eight to the Orthocladiinae. *Camptochironomus* and *Glyptotendipes* were the most abundant Chironominae; one orthocladiinid species, *Cricotopus sylvestris*, accounted for over 95% of the total reedstem-dwelling larval chironomid population. The greatest generic diversity was most frequently found in Zone 3, due to the relatively high generic equitability that existed there.

6) Some reedstem-dwelling chironominid larvae (*Endochironomus*, *Glyptotendipes*, *Limnochironomus*) were resident throughout the year; others (*Camptochironomus* and *Parachironomus*) were seasonal visitors, exclusive to summer and early autumn. Of the commoner larval Orthocladiinae, *Cricotopus sylvestris* was present throughout the sampling period, whilst *Psectrocladius* was collected from April to July. *Rheocricotopus* and *Thienemanniella* were evident from January to March and disappeared by April.

7) Some reedstem-dwelling chironomids (e.g. *Cricotopus sylvestris* and *Limnochironomus*) occurred in all three sampling zones, whereas others (e.g. *Cricotopus flavocinctus*, *Endochironomus*, and *Thienemanniella*) were restricted to one or two zones.

8) Temporal patterns of change in larval density were largely determined by intrinsic species characteristics, especially those that govern seasonal patterns of egg-laying. However, through the effect of temperature on larval development, characteristic annual patterns of larval density change were inextricably linked to similarly characteristic water temperature differences over the year - the expression of intrinsic population qualities was controlled, to a large extent, by an essentially predictable pattern of variation in an extrinsic factor.

9) Chironomid density and biomass variation through time occurred independently of temporal change in epiphyton density.

10) In many of the reedstem-dwelling chironomid species, including *Cricotopus sylvestris*, interzonal variation in larval numbers was largely caused by interzonal variation in epiphyton density, which was often significant. The degree of shelter afforded by the epiphytic coating was a critical determinant of larval numbers on a reedstem; higher epiphyton densities supported greater quantities of larvae. Positive phototaxis in early instars of *Cricotopus sylvestris* explained their preference for Zone 1 from July to October, 1981, at a time when interzonal differences in epiphyton density were almost exclusively insignificant. The zonal dispersion patterns of some chironomid species may have reflected an influx of larvae from a hatching location away from the reedbed's permanent standing water area. Other potential determinants of dispersion patterns for reedstem-dwelling larvae included interzonal gradations in certain physico-chemical water properties (oxygen content, temperature, pH, and conductivity), the initial distribution of egg masses inside the permanent standing water area, inter-specific relationships within the chironomid community, and predation by non-chironomids. Investigations of these potential determinants showed their influence on dispersion to be insignificant.

11) For monthly benthic core-samples the reedbed's standing water area was divided into four zones, with Zone A at the lakeward edge and Zone D at the landward margin.

12) The highest mean density of benthic-dwelling larvae in each month was usually found in Zone B. The maximum mean density during 1981 was found in Zone B in August. Larval numbers tended to fall progressively towards the back of the reedbed's permanent standing water area.

13) Thirteen chironomid taxa were present in benthic core-samples during 1981. Nine of these belonged to the Chironominae, two to the Orthocladiinae, and two to the Tanypodinae. One species, *Camptochironomus tentans*, made up over 93% of the total benthic-dwelling chironomid population. *Camptochironomus tentans* and *Glyptotendipes pallens* were the only benthic chironomid larvae found in every month of the sampling period.

14) *Camptochironomus tentans* larvae were concentrated towards the front (lakeward edge) of the *Phragmites* stand, probably due to the relatively high percentage of sand there - a sandy floor is conducive to larval tube-building and pupal case construction. The greatest numbers of the second most common benthic chironomid, *Glyptotendipes pallens*, occurred towards the back of the permanent standing water area, probably attracted by the larger amount of plant material there.

15) In monthly samples from the semi-terrestrial part of the reedbed, twelve larval chironomid taxa were identified, the most abundant being *Tanytarsus*, *Metriocnemus* sp. A, and Pentaneurini sp. A, which together accounted for 85% of the total semi-terrestrial larval population.

16) Where noticeable interzonal variation in species abundance occurred in the semi-terrestrial part of the reedbed, the principal determinant appeared to be the moisture content of the substrate. Some chironomid types (*Chironomus* 'thummi' type, *Glyptotendipes pallens*, and Pentaneurini sp. A) were most numerous in the wetter environment towards the front (lakeward margin) of this area, whereas *Metriocnemus* sp. A attained its highest densities at the back, where more terrestrial conditions can prevail.

17) Twenty-eight species of adult chironomids emerging from the reedbed were collected in floating box-traps from April to October, 1981. Most of the genera found as imagines were also represented in populations of larvae in the reedbed. About 78% of the total adult population belonged to the Orthocladiinae, *Cricotopus sylvestris* accounting for over half of all the flies collected. Maximum chironomid emergence (120 flies per m^2 per day) occurred around the middle of July. Dispersion patterns for emerging adults generally complemented their counterparts for larvae, indicating that most species pupate and emerge in close proximity to their original larval habitat.

REFERENCES

ACTON, A.D. and SCUDDER, G.G.E. (1971) The zoogeography and races of *Chironomus* (= *Tendipes*) *tentans* Fab. *Limnologica*, 8 83-92.

ALBU, P. (1971) On the *chironomids* (*Dipt, Chironomidae*) captured in a light trap in Sinaia (Rumania). *Limnologica*, 8, 157-172.

ALEKSEEV, N.K. (1978) On the feeding of the larvae of *Chironomidae* during the planktonic period of life. *F.B.A. Transl (NS)*, 115, 3 pp.

ALI, A. and MULLA, M.S. (1976) Substrate type as a factor influencing spatial distribution of *chironomid* midges in an urban flood control channel system. *Envir. Ent.*, 5, 631-636.

ANDREWARTHA, H.G. and BIRCH, L.C. (1954) *The distribution and abundance of animals*. University of Chicago Press, Chicago. 782 pp.

ARENKOVA, R.L. (1965) Rastitel'nost' i fitofil' naya fauna prudov zapadnykh oblastei ukrainskoi SSR. *Sbornik Rybnoe Khozyaistvo*, 2, 75-82.

ARMITAGE, P.D. (1968) Some notes on the food of the *chironomid* larvae of a shallow woodland lake in South Finland. *Annls. Zool. Fenn.*, 5, 6-13.

ARMITAGE, P.D. (1970) The *Tanytarsini* (*Diptera, Chironomidae*) of a shallow woodland lake in South Finland, with special reference to the effect of winter conditions on the larvae. *Annls. Zool. Fenn.*, 7, 313-322.

BAILEY, R.G., CHURCHFIELD, S. and PIMM, R. (1978) Observations on the zooplankton and littoral macroinvertebrates of Nyumba ya Mangu reservoir, Tanzania. *Biol. J. Linn. Soc.*, 10, 93-107.

BARKER, M.A. (1966) The influence of physicochemical factors on the distribution of *Chironomus zealandicus* in Lake Pupuke. *Tane*, 12, 93-95.

BEATTIE, D.M. (1978) Life-cycle and changes in carbohydrates, proteins and lipids of *Pentapedilum uncinatum* Goet. (*Diptera; Chironomidae*). *Freshwat. Biol.*, 8, 109-113.

BECK W.M. (1977) *Environmental requirements and pollution tolerance of common freshwater Chironomidae.* Environmental Monitoring Series. US Environmental Protection Agency. Cincinnati, Ohio, 261 pp.

BELCHER, H. and SWALE, E. (1976) *A beginner's guide to freshwater algae.* Institute of Terrestrial Ecology/HMSO. 47 pp.

BELL, H.L. (1970) Effect of pH on the life cycle of the midge *Tanytarsus dissimilis*. *Can. Ent.*, 102, 636-639.

BERG, C.O. (1950) Biology of certain *Chironomidae* reared from *Potamogeton*. *Ecol. Monogr.*, 20, 83-101.

BISHOP, O.N. (1980) *Statistics for biology.* 3rd edn. Longman, Essex. viii + 215 pp.

BODENHEIMER, F.S. (1930) Über die Grundlagen einer allgemeinen Epidemiologie der Insektenkalamitaten. *Z. angew. Ent.*, 16, 433-450.

BOWKER, D.W. and DENNY, P. (1978) The periphyton communities of Nyumba ya Mungu reservoir, Tanzania. *Biol. J. Linn. Soc.*, 10, 49-65.

BRINKHURST, R.O. (1960) Survey of the fauna of the Shropshire meres. (unpublished manuscript)

BRUNDIN, L. (1951) The relation of O_2-microstratification at mud surface to the ecology of the profundal bottom fauna. *Rep. Inst. Freshwat. Res. Drottningholm*, 32, 32-42.

BRYCE, D. and HOBART, A. (1972) The biology and identification of the larvae of the *Chironomidae* (*Diptera*). *Entomologist's Gazette*, 23, 175-217.

BURTT, E.T. (1940) A filter-feeding mechanism in a larvae of the *Chironomidae* (*Diptera*: *Nematocera*). *Proc. R. ent. Soc. Lond.*, 15, 113-121.

BUSCEMI, P.A. (1957) First record of *Endochironomus subtendens* (Townes) larval overwintering cocoons from North America (*Diptera*: *Tendipedidae*). *Ent. News*, 68, 157-158

CAMPBELL, R.C. (1979) *Statistics for biologists* 2nd edn. Cambridge University Press, Cambridge. xii + 385 pp.

CANNINGS, R.A. and SCUDDER, G.G.E. (1978) The phenology of *Chironomus* spp. in saline lakes of central British Columbia. *Verh. int. Verein. Limnol.*, 20, 2641-2646.

CANTRELL, M.A. and McLACHLAN, A.J. (1977) Competition and *chironomid* distribution patterns in a newly flooded lake. *Oikos*, 29, 429-433.

CARTER, C.E. (1976) A population study of the *Chironomidae (Diptera)* of Lough Neagh. *Oikos*, 27, 346-354.

CHAPMAN, D.W. and DEMORY, R. (1963) Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. *Ecology*, 44, 140-146.

CHITTY, D. (1960) Population processes in the vole and their relevance to general theory. *Can. J. Zool.*, 38, 99-113.

CLARK, L.R., GEIER, P.W., HUGHES, R.D. and MORRIS, R.F. (1967) *The Ecology of Insect Populations in theory and practice.* Chapman and Hall, London. xiii + 232 pp.

CRANSTON, P.S. (1979) Provisional key to the holarctic *Orthocladiinae*. (unpublished manuscript)

CRANSTON, P.S. (1982) A key to the larvae of the British *Orthocladiinae* (*Chironomidae*). *Scient. Publs. Freshwat. biol. Ass.*, 45, 152 pp.

CUMMINS, K.W. (1973) Trophic relations of aquatic insects. *A. Rev. Ent.*, 18, 183-206.

CUMMINS, K.W. and WUYCHECK, J.C. (1971) Caloric equivalents for investigations in ecological energetics. *Mitt. int. Verein. Limnol.*, 18, 1-158.

CZECZUGA, A. and NIEDZWIECKI, E. (1966) Ecological-physiological aspects of the occurrence of the larvae of *Glyptotendipes* ex.gr. *gripekoveni* Kieff. (*Diptera*). *Bull. Acad. pol. Sci. Ser. Sci. biol.*, 14, 693-695.

DANELL, K. and SJOBERG, K. (1977) Seasonal emergence of *Chironomids* in relation to egg-laying and hatching of ducks in a restored lake (northern Sweden). *Wildfowl*, 28, 129-135.

DANKS, H.V. (1971a) Life history and biology of *Einfeldia synchrona* (*Diptera: Chironomidae*). *Can. Ent.*, 103, 1597-1606.

DANKS, H.V. (1971b) Overwintering of some north temperate and arctic *Chironomidae*. II. *Chironomid* biology. *Can. Ent.*, 103, 1875-1910.

DANKS, H.V. and OLIVER, D.R. (1972) Seasonal emergence of some high arctic *Chironomidae* (*Diptera*). *Can. Ent.*, 104, 661-686.

DARBY, R.E. (1962) Midges associated with California rice fields, with special reference to their ecology (*Diptera: Chironomidae*). *Hilgardia*, 32(1), 1-206.

DAVIES, B.R. (1976a) The dispersal of *Chironomidae* larvae: A review. *J. ent. Soc. sth. Afr.*, 39, 39-62.

DAVIES, B.R. (1976b) Wind distribution of the egg masses of *Chironomus anthracinus* (*Zetterstedt*) (*Diptera: Chironomidae*) in a shallow, wind-exposed lake (Loch Leven, Kinross). *Freshwat. Biol.*, 6, 421-424.

DAVIES, I.J. (1975) Selective feeding in some arctic *Chironomidae*. *Verh. int. Verein. Limnol.*, 19, 3149-3154.

DAVIES, R.W. and EVERETT, R.P. (1975) The feeding of four species of freshwater *Hirudinoidea* in Southern Alberta. *Verh. int. Verein. Limnol.*, 19, 2816-2827.

DERMOTT, R.M. and PATERSON, C.G. (1974) Determining dry weight and percentage dry matter of *chironomid* larvae. *Can. J. Zool.*, 52, 1243-1250.

DICKMAN, M.D. (1968) The effect of grazing by tadpoles on the structure of a periphyton community. *Ecology*, 49, 1188-1195.

DRESSCHER, T.G.N. and ENGEL, H. (1960) De Nederlandse bloedzuigers (Hirudinea). *Wet. Mededel. K.N.N.V.*, 39.

DVORAK, J. (1970) Horizontal zonation of macrovegetation, water properties and macrofauna in a littoral stand of *Glyceria aquatica* (L.) Wahlb. in a pond in South Bohemia. *Hydrobiologia*, 35, 17-30.

DVORAK, J. (1971) The zonation of environmental factors and the macrofauna of littoral emergent vegetation in ponds in South Bohemia. *Hydrobiologia*, 12, 325-329.

DVORAK, J. and LISKOVA, E. (1970) A quantitative study on the macrofauna of stands of emergent vegetation in a carp pond of South-West Bohemia. *Rozpr. Cesk. Akad. Ved. Rada Mat. Prir. Ved.*, 80, 63-114.

EDGAR, W.D. and MEADOWS, P.S. (1969) Case construction, movement, spatial distribution and substrate selection in the larvae of *Chironomus riparius* Meigen. *J. exp. Biol.*, 50, 247-253.

EGGLISHAW, H.J. (1964) The distributional relationship between the bottom fauna and plant detritus in streams. *J. Anim. Ecol.*, 33, 463-476.

EICHENBERGER, E. and SCHLATTER, A. (1978) Effect of herbivorous insects on the production of benthic algal vegetation in outdoor channels. *Verh. int. Verein. Limnol.*, 20, 1806-1810.

ELLIOTT, J.M. (1973) The diel activity pattern, drifting and food of the leech *Erpobdella octoculata* (L.) (*Hirudinea: Erpobdellidae*) in a Lake District stream. *J. Anim. Ecol.*, 42, 449-459.

ELLIOTT, J.M. (1977) Some methods for the statistical analysis of samples of benthic invertebrates. *Scient. Publs Freshwat. biol. Ass.*, 25, 2nd edn., 160 pp.

ELLIOTT, J.M. and MANN, K.H. (1979) A key to the British freshwater leeches. *Scient. Publs. Freshwat. biol. Ass.*, 40, 72 pp.

ELLIOTT, J.M. and TULLET, P.A. (1978) A bibliography of samplers for benthic invertebrates. *FBA Occ. Publ.*, 4, 61 pp.

FITTKAU, E.J., REISS, F. and HOFFRICHTER, O. (1976) A bibliography of the *Chironomidae*. *Gunneria*, 26, 177 pp.

FURYK, A. (1969) Initial investigations on the fauna of the shoreline ecotone-zone of the Jeziorak Lake. *Zesz. nauk. Uniw. Mikolaja Kopernika Torun-Pr. Sta. limnol.*, 25, 53-60.

HALL, D.J., COOPER, W.E. and WERNER, E.E. (1970) An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.*, 15, 839-928.

HARDING, W.A. (1910) A revision of the British leeches. *Parasitology*, 3, 130-201.

HAMMOND, R. and McCULLAGH, P.S. (1974) *Quantitative techniques in geography: an introduction*. Oxford University Press. xvi + 319 pp.

HIGLER, L.W.G. (1977) Macrofauna cenoses on *Stratiotes* plants in Dutch broads. *Verh. Rijksinst. Natuurbeh.*, 11, 1-86.

HILSENHOFF, W.L. (1963) Predation by the leech *Helobdella stagnalis* on *Tendipes plumosus* (*Diptera: Tendipedidae*) larvae. *Ann. ent. Soc. Am.*, 56, 252.

HIRVENOJA, M. (1975) Species of the genus *Cricotopus* v. d. Wulp (*Diptera, Chironomidae*) and its closest relatives in Eastern Fennoscandia, especially in Finland. *Annls ent. fenn.*, 41, 19-37.

HOFFRICHTER, O. and REISS, F. (1981) Supplement 1 to "A bibliography of the *Chironomidae*". *Gunneria*, 37, 1-68.

IZVEKOVA, E.I. (1971) On the feeding habits of *chironomid* larvae. *Limnologica*, 8, 201-202.

JONASSON, P.M. (1965) Factors determining population size of *Chironomus anthracinus* in Lake Esrom. *Mitt. int. Ver. Limnol.*, 13, 139-162.

KAJAK, Z. (1963) The effect of experimentally induced variations in the abundance of *Tendipes plumosus* L. larvae on intraspecific and interspecific relations. *Ekol. pol. Ser. A*, 11, 355-367.

KAJAK, Z. (1977) Factors influencing benthos biomass in shallow lake environments. *Ekol. pol.*, 25, 421-429.

KALUGINA, N.S. (1958) Mesta obitaniya i pitanie lichinok *Glyptotendipes glaucus* Mg. (*Diptera, Chironomidae*) iz Uchingskogo vodokhranilishcha. (On the habitats and feeding of larvae of *Glyptotendipes glaucus* Mg. (*Diptera, Chironomidae*) from Utcha water reservoir). *Zool. Zh.*, 37, 1045-1057.

KAWECKA, B., KOWNACKI, A. and KOWNACKA, M. (1978) Food relations between algae and bottom fauna communities in glacial streams. *Verh. int. Verein. Limnol.*, 20, 1527-1530.

KEIM, A. (1977) Electrophoretic analyses of the crop contents of *Helobdella stagnalis* (L.) (*Hirudinea*). *Z. Naturf.*, 32c, 739-742.

KENNEDY, C.R. (1961) Survey of the fauna of Sweat Mere and Crose Mere, Shropshire undertaken for the Nature Conservancy in July, 1961. (Unpublished manuscript).

KEVERN, N.R. and BALL, R.C. (1965) Primary productivity and energy relationships in artificial streams. *Limnol. Oceanogr.*, 10, 74-87.

KITCHING, R.L. (1971) An ecological study of water-filled tree-holes and their position in the woodland ecosystem. *J. Anim. Ecol.*, 40, 281-302.

KONSTANTINOV, A.S. (1971) Ecological factors affecting respiration in *chironomid* larvae. *Limnologica*, 8, 127-134.

KREBS, C.J. (1972) *Ecology: The experimental analysis of distribution and abundance*. Harper International Edition. x + 694 pp.

KRULL, J.N. (1970) Aquatic plant-macroinvertebrate associations and water-fowl. *J. Wildl. Mgmt.*, 34, 707-718.

LANGTON, P.H. (1981) The genus *Psectrocladius* Kieffer (*Diptera: Chironomidae*) in Britain. *Entomologist's Gazette*, 31, 75-88.

LEARNER, M.A. and POTTER, D.W.B. (1974) The seasonal periodicity of emergence of insects from two ponds in Hertfordshire, England, with special reference to the *Chironomidae (Diptera: Nematocera)*. *Hydrobiologia*, 44, 495-510.

LELLAK, J. (1968) Positive Phototaxis der *Chironomiden*-Larvulae als regulierender Faktor ihrer Ver-Teilung in stehenden Gewassern. *Ann. zool. fenn.*, 5, 84-87.

LeSAGE, L. and HARRISON, A.D. (1980) The biology of *Cricotopus* (*Chironomidae: Orthocladiinae*) in an algal-enriched stream: Part 1. Normal biology. *Arch. Hydrobiol./Suppl. 57*, 4, 375-418.

LEWIS, D.J. (1957) Observations on *Chironomidae* at Khartoum. *Bull. ent. Res.*, 48, 155-184.

LINDEGAARD, C. and JONASSON, P.M. (1975) Life cycles of *Chironomus hyperboreus* STAEGER and *Tanytarsus gracilentus* (HOLMGREN) (*Chironomidae, Diptera*) in Lake Myvatn, Northern Iceland. *Verh. int. Verein. Limnol.*, 19, 3155-3163.

LINDEGAARD, C., THORUP, J. and BAHN, M. (1975) The invertebrate fauna of the moss carpet in the Danish spring Ravnkilde and its seasonal, vertical, and horizontal distribution. *Arch. Hydrobiol.*, 75, 109-139.

LLOYD, M. and GHELARDI, R.J. (1964) A table for calculating the 'equitability' component of species diversity. *J. Anim. Ecol.*, 33, 217-225.

LODEN, M.S. (1974) Predation by *chironomid* (*Diptera*) larvae on *oligochaetes*. *Limnol. Oceanogr.*, 19, 156-159.

LUFEROV, V.P. (1966a) Role of light in distribution of *Chironomidae* in Karelian lakes. *Trudy Inst. Biol. vnutr., Vod 12*, 255-272.

LUKEROV, V.P. (1966b) Vliyanie osveshchennosti i temperatury na fotoreaktsiyu lichinok *Cricotopus* ex. gr. *silvestris*, *Corynoneura* sp. i *Endochironomus albipennis*. (Influence of light intensity and temperature on photoreaction of *Cricotopus* ex. gr. *silvestris*, *Corynoneura* sp. and *Endochironomus albipennis* larvae). *Trudy Inst. Biol. vnutr., Vod 12*, 273-285.

LUFEROV, V.P. (1971) The role of light in the populating of water bodies by epibiotic *chironomid* larvae. *Limnologica*, 8, 139-140.

MACKEY, A.P. (1977) Growth and development of larval *Chironomidae*. *Oikos*, 28, 270-275.

MARKOSOVA, R. (1974) Seasonal dynamics of the periphytic macrofauna in carp ponds in South-West Bohemia. *Bestn. csl. Spol. Zool.*, 38, 251-270.

MASON, C.F. and BRYANT, R.J. (1974) The structure and diversity of the animal communities in a broadland reedswamp. *J. Zool. Lond.* 172, 289-302.

MASON, C.F. and BRYANT, R.J. (1975a) Periphyton production and grazing by *chironomids* in Alderfen Broad, Norfolk. *Freshwat. Biol.*, 5, 271-278.

MASON, C.F. and BRYANT, R.J. (1975b) Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *J. Ecol.*, 63, 71-95.

MASON, W.T. (1973) *An introduction to the identification of chironomid larvae*. Analytical Quality Control Laboratory. National Environmental Research Center. US Environmental Protection Agency. Cincinnati, Ohio, 90 pp.

McLACHLAN, A.J., BRENNAN, A. and WOTTON, R.S. (1978) Particle size and *chironomid* (*Diptera*) food in an upland river. *Oikos*, 31, 247-252.

McLACHLAN, A.J. and McLACHLAN, S.M. (1975) The physical environment and bottom fauna of a bog lake. *Arch. Hydrobiol.*, 76, 198-217.

MIROSHNICHENKO, M.P. (1971) *Chironomid* larvae of the Tsimlyanskoya reservoir. *Limnologica*, 8, 107-109.

MOORE, J.W. (1979) Some factors influencing the distribution, seasonal abundance and feeding of subarctic *Chironomidae* (*Diptera*). *Arch. Hydrobiol.*, 85, 302-325.

MORDUKHAI-BOLTOVSKOI, F.D. and SHILOVA, A.I. (1955) O vremenno-planktonnom obraze zhizni lichinok *Glyptotendipes* (*Diptera, Tendipedidae*). (On the planktonic life of *Glyptotendipes* larvae (*Diptera, Tendipedidae*)). *Dokl. Akad. Nauk SSSR*, 105, 163-165.

MORGAN, N.C., WADDELL, A.B. and HALL, W.B. (1963) A comparison of the catches of emerging aquatic insects in floating box and submerged funnel traps. *J. Anim. Ecol.*, 32, 203-219.

MORRIS, R.F. (1957) The interpretation of mortality data in studies of population dynamics. *Can. Ent.*, 89, 49-69.

MOUNTAIN, T.J. (1981) Studies of the *Chironomidae* (*Diptera*) of some reedbeds. *PhD thesis*, University of Keele.

MUNDIE, J.H. (1955) On the distribution of *Chironomidae* in a storage reservoir. *Verh. int. Verein. Limnol.*, 12, 577-581.

MUNDIE, J.H. (1957) The ecology of *Chironomidae* in storage reservoirs. *Trans. R. ent. Soc. Lond.*, 109, 149-232.

N.C.C. (1980) England Field Unit Project No. 1: Survey of Shropshire, Cheshire and Staffordshire Meres. Nature Conservancy Council.

NEEL, J.K. (1968) Seasonal succession of benthic algae and their macroinvertebrate residents in a head-water limestone stream. *J. Water Poll. Contr. Fed.*, 40(2), 10-30.

OLIVER, D.R. (1971) Life History of the *Chironomidae*. *A. Rev. Ent.*, 16, 211-230.

OPALINSKI, K.W. (1971) Macrofauna communities of the littoral of Mikolajskie Lake. *Polskie Archwm Hydrobiol.*, 18, 275-285.

PALMEN, E. and AHO, L. (1966) Studies on the ecology and phenology of the *Chironomidae* (*Diptera*) of the Northern Baltic. 2. *Camptochironomus* Kieff. and *Chironomus* Meig. *Ann. zool. fenn.*, 3, 217-244.

PANKRATOVA, V.Ya. (1970) Key to the larvae of the genera of the subfamily *Orthocladiinae*. *F.B.A. Transl.* (*NS*), 54, 8 pp.

PANKRATOVA, V.Ya. (1979) The family of *chironomids* or midges-*Chironomidae* (keys to larvae and pupae). *F.B.A. Transl.*(*NS*), 116, 63 pp.

PATERSON, C.G. (1970) Water mites (*Hydracarina*) as predators of *chironomid* larvae (Insecta: *Diptera*). *Can. J. Zool.*, 48, 610-614.

PIECZYNSKI (1977) Numbers and biomass of the littoral fauna in Mikolajskie Lake and in other Masurian lakes. *Ekol. pol.*, 25, 45-57.

PINDER, L.C.V. (1978) A key to the adult males of British *Chironomidae*. Vol. 1, The key; Vol. 2, Illustrations of the hypopygia. *Scient. Publs. Freshwat. biol. Ass.*, 37, 169 pp. + 189 fig.

POPCHENKO, V.I. (1971) Consumption of *Oligochaeta* by fishes and invertebrates. *J. Ichthyol.*, 11, 75-80.

POTTER, D.W.B. and LEARNER, M.A. (1974) A study of the benthic macro-invertebrates of a shallow eutrophic reservoir in South Wales with emphasis on the *Chironomidae* (*Diptera*); their life-histories and production. *Arch. Hydrobiol.*, 74, 186-226.

PRESCOTT, G.W. (1970) *How to know the freshwater algae.* 2nd edn. Wm. C. Brown Co. Publishers. vii + 348 pp.

RAMCHARAN, V. and PATERSON, C.G. (1978) A partial analysis of ecological segregation in the *chironomid* community of a bog lake. *Hydrobiologia*, 58, 129-135.

REYNOLDS, C.S. (1979) The limnology of the eutrophic meres of the Shropshire-Cheshire Plain: a review. *Field Studies*, 5(1), 93-173.

REYNOLDSON, T.B. and YOUNG, J.O. (1965) Food supply as a factor regulating population size in freshwater triclads. *Mitt. int. Verein. Limnol.*, 13, 3-20.

REYNOLDSON, T.B. and SEFTON, A.D. (1976) The food of *Planaria torva* (Muller) (*Turbellaria - Tricladida*), a laboratory and field study. *Freshwat. Biol.*, 6, 383-393.

ROBACK, S.S. (1955) The *Tendipedid* fauna of a Massachusetts cold spring (*Diptera: Tendipedidae*). *Not. Nat. Acad. Nat. Sci. Phila.*, 270, 1-8.

ROBACK, S.S. (1969) Notes on the food of *Tanypodinae* larvae. *Ent. News*, 80, 13-18.

ROBACK, S.S. (1976) The immature *chironomids* of the eastern United States: 1. Introduction and *Tanypodinae - Coelotanypodini*. *Proc. Acad nat Sci. Philad.*, 127, 147-201.

ROBACK, S.S. and MOSS, W.W. (1978) Numerical taxonomic studies on the congruence of classifications for the genera and subgenera of *Macropelopini* and *Anatopyniini* (*Diptera: Chironomidae: Tanypodinae*). *Proc. Acad. nat. Sci. Philad.*, 129, 125-150.

ROSINE, W.N. (1955) The distribution of invertebrates on submerged aquatic plant surfaces in Muskee Lake, Colorado. *Ecology*, 36, 309-314.

RYALS, G.L. and INGRAM, B.R. (1973) Laboratory responses of midge larvae to daylength and temperature (*Diptera: Chironomidae*). *Am. Zool.*, 13, 1341.

SADLER, W.O. (1935) Biology of the midge *Chironomous tentans* Fabricius, and methods for its propagation. *Cornell Univ. agric. Exp. Stn. Mem.*, 173, 1-25.

SHCHERBAKOV, A.P. (1961) Productivity of the animal population of inshore vegetation in Lake Glubokoe. *Trudy Vsesoyuz. gidrobiol. obshchestva*, 11, 295-298.

SHILOVA, A.I. (1958) Material on the biology of mosquito larvae in the Rybinsk Reservoir. *Trudy Biologicheskoi Stantsii "Borok"*, 3.

SIEGEL, S. (1956) *Nonparametric statistics for the behavioural sciences*. McGraw-Hill Inc. xvii + 312 pp.

SLACK, H.D. (1967) A brief survey of the profundal benthic fauna of lakes in Manitoba. *J. Fish. Res. Bd Can.*, 24, 1017-1033.

SMITH, H.S. (1935) The role of biotic factors in the determination of population densities. *J. econ. Ent.*, 28, 873-898.

SMITH, V.G.F. and YOUNG, J.O. (1973) The life histories of some *Chironomidae* (*Diptera*) in two ponds on Merseyside, England. *Arch. Hydrobiol*, 72, 333-355.

SOKOLOVA, N. (1963) Fauna zaroski nekotorykh makrofitov Uchinskogo vodokhranilishcha. *Uchinskoe: Mozhaiskoe vodokhranilishcha (gidrobiol. i ikhtiol. issledovaniya): Izdatel'stvo Moskovskogo universiteta*, 108-153.

SOKOLOVA, G.A. (1966) O sposobe zimovki lichinok *Limnochironomus* ex. gr. *nervosus* Staeg. (*Diptera, Chironomidae*). (On the hibernation mode of larvae of *Limnochironomus* ex. gr. *nervosus* Staeg. (*Diptera, Chironomidae*)). *Zool. Zh.*, 45, 140.

SOLOMON, M.E. (1976) *Population Dynamics*. 2nd edn. Studies in Biology No. 18. Edward Arnold, London.

SOSZKA, H. (1974) *Chironomidae* associated with pond-weeds (*Potamogeton lucens* and *Potamogeton perfoliatus* L.) in the Mikolajskie Lake. *Bull. Acad. pol. Sci. Ser. Sci. biol.*, 22, 369-376.

SOSZKA, H. (1976) Uwagi o odzywianiu sig larw *Chironomidae* zwiazanych z roslinami. (Some remarks on the feeding habits of *Chironomidae* associated with plants. (*Diptera*)). *Wiad. ekol.* 22, 136-141.

STIMAC, J.L. and LEONG, K.L.H. (1977) Factors affecting *chironomid* larval abundance in three vertical aquatic weed habitats. *Envir. Ent.*, 6, 595-600.

STURGESS, B.T. and GOULDING, R.L. (1968) Tolerance of three species of larval *Chironomidae* to physicochemical stress factors occurring in stabilization lagoons. *Ann. ent. Soc. Am.*, 61, 903-906.

TAIT-BOWMAN, C.M. (1976) Factors affecting the distribution and abundance of *chironomids* in three Shropshire Meres, with special reference to the larval tracheal system. *PhD thesis*, University of Keele.

THORNTON, K. and WILHM, J. (1974) The effects of pH, phenol and sodium chloride on survival and caloric, lipid, and nitrogen content of a laboratory population of *Chironomus attenuatus* (Walk.). *Hydrobiologia*, 45, 261-280.

TITMUS, G. (1979a) Ecology of the *Chironomidae* (*Diptera*) in some gravel and sand pits. *PhD thesis*, University of Keele.

TITMUS, G. (1979b) The emergence of midges (*Diptera*: *Chironomidae*) from a wet gravel-pit. *Freshwat. Biol.*, 9, 165-179.

TITMUS, G. and BADCOCK, R.M. (1981) Distribution and feeding of larval *Chironomidae* in a gravel-pit lake. *Freshwat. Biol.*, 11, 263-271.

TOLKAMP, H.H. and BOTH, J.C. (1978) Organism-substrate relationship in a small Dutch lowland stream. Preliminary results. *Verh. int. Verein. Limnol.*, 20, 1509-1515.

TOPPING, M.S. (1971) Ecology of larvae of *Chironomus tentans* (*Diptera*: *Chironomidae*) in saline lakes in central British Columbia. *Can. Ent.*, 103, 328-338.

WALSHE, B.M. (1951) The feeding habits of certain *chironomid* larvae (subfamily *Tendipedinae*). *Proc. zool. Soc. Lond.*, 121, 63-79.

WASILEWSKA, B.E. (1978) Bottom fauna in ponds with intense fish rearing. *Ekol. pol.*, 26, 513-536.

WEBSTER, J.R. and SIMMONS, G.M. (1978) Leaf breakdwon and invertebrate colonisation on a reservoir bottom. *Verh. int. Verein. Limnol.*, 20, 1587-1596.

WESTLAKE, D.F. (1963) Comparisons of plant productivity. *Biol. Rev.*, 38, 385-425.

APPENDICES

	ZONE 1	ZONE 2	ZONE 3
JAN	2	3	1
FEB	4	3	1
MAR	2	1	5
APR	5	4	5
MAY	3	2	1
JUN	5	5	1
JUL	2	2	4
AUG	1	1	3
SEP	5	3	5
OCT	4	4	2
NOV	1	2	5

APPENDIX A - Distance (metres) along each zone of the points where first stem-samples were taken during 1981. Distances were measured from that end of the study site nearest to the outflow of the River Sow.

NON-CHIRONOMIDS	
Hydra sp.	Hyd
Planaria torva (Müller)	Pla
Polycelis tenuis (Ijima)	Poly
Gordioidea sp.	Gor
Lumbriculus variegatus (Müller)	Lum
Stylaria lacustris (Linnaeus)	Sty
Tubificidae sp.	Tub
Erpobdella octoculata (Linnaeus)	Erp
Glossiphonia complanata (Linnaeus)	Glo
Helobdella stagnalis (Linnaeus)	Hel
Theromyzon tessulatum (Müller)	The
Acroloxus lacustris (Linnaeus)	Acr
Bithynia tentaculata (Linnaeus)	Bit
Potamopyrgus jenkinsi (Smith)	Pot
Lymnaea peregra (Müller)	Lym
Physa fontinalis (Linnaeus)	Phy
Planorbis albus (Müller)	Plan
Valvata piscinalis (Müller)	Val
Pisidium sp.	Pis
Hydrachnellae (2 spp.)	Hydr
Asellus aquaticus (Linnaeus)	Ase
Gammarus pulex (Linnaeus)	Gam
Dytiscinae sp. (larva and adult)	Dyt (L) or (A)
Gyrinidae sp. (larva)	Gyr
Haliplidae sp. (larva and adult)	Hal (L) or (A)
Hydrophilidae sp. (larva)	Hydro
Ceratopogonidae sp. (larva)	Cer
Cyclorrhapha sp. (larva)	Cyc
Psychodidae sp. (larva)	Psy
Cloëon dipterum (Linnaeus) (larva)	Clo
Corixidae sp. (nymph and adult)	Cori (N) or (A)
Coenagrion sp. (larva)	Coe
Glossosoma intermedium (Klapálek) (larva)	Glos

APPENDIX B - List of macroinvertebrates found on *Phragmites* reedstems during 1981, with abbreviations used in Appendix C. (cont...)

Hydroptilidae sp. (larva)	Hydrop
Mystacides longicornis (Linnaeus) (larva)	Mys
Limnephilidae sp. (larva)	Limn
Phryganea varia (Fabricius) (larva)	Phr
Cyrnus flavidus (McLachlan) (larva)	Cyr
Holocentropus picicornis (Stephens) (larva)	Hol
Plectronemia sp. (larva)	Ple
CHIRONOMIDS	
Camptochironomus tentans (Fabricius)	Cam
Cladotanytarsus sp.	Cla
Endochironomus	End
Glyptotendipes pallens (Meigen)	Gly
Limnochironomus sp.	Lim
Microtendipes sp.	Mic
Parachironomus sp.	Par
Polypedilum sp.	Pol
Tanytarsus sp.	Tan
Corynoneura	Cor
Cricotopus flavocinctus (Kieffer)	C.fla
Cricotopus sylvestris (Fabricius)	C.syl
Diplocladius cultriger (Kieffer)	Dip
Metriocnemus sp. A	Met A
Metriocnemus sp. C	Met C
Metriocnemus sp. E	Met E
Orthocladius sp.	Ort
Psectrocladius limbatellus (Holmgren)	Pse
Rheocricotopus fuscipes (Kieffer)	Rhe
Thienemanniella sp.	Thi
Pentaneurini sp. C	Pen C
Psilotanypus sp.	Psi

APPENDIX B (...cont.)

APPENDIX C - (pp 265-281) A taxonomic and numerical breakdown of the macroinvertebrate community found on each reedstem taken during 1981.

See Appendix B for key to abbreviations. Arabic numerals in parentheses next to chironomid taxa refer to instar categories; Roman numerals refer to relative size where instar status is indeterminable.

* signifies a new reedstem. (All other stems are old.)

(cont...)

January

ZONE 1

STEM -	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sty	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Ase	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cori(A)	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
End(1)	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-
Gly(2)	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-
(3)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Tan(2)	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Cor(ii)	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
C.syl(2)	26	17	32	18	14	28	18	7	18	5	16	15	19	4	15
(3)	16	4	12	16	4	7	11	2	16	2	5	4	16	3	7
(4)	-	-	2	1	-	-	1	-	1	-	-	-	2	-	3
Ort(4))	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Rhe(3)	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
(4)	-	1	-	-	-	-	1	1	-	-	-	2	-	-	-
Thi(2)	-	1	2	2	1	-	-	-	-	-	-	1	2	2	2

January

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sty	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
The	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Acr	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Ase	3	-	-	-	-	1	1	1	1	-	-	-	-	-	1
Cori(A)	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Limn	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Hydrop	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Gly(2)	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-
Lim(3)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C.syl(2)	5	11	2	-	1	-	3	1	-	1	2	4	3	3	1
(3)	-	3	-	-	-	-	-	-	-	-	1	-	-	2	-

JANUARY

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sty	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Acr	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gam	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Gly(2)	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-
(4)	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Lim(3)	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-
(4)	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Pol(1)	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
C.syl(2)	2	-	4	-	-	-	3	-	-	-	3	-	-	-	-

APPENDIX C (...cont...)

February

ZONE 1

STEM -	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Hydr	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-
Ase	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-
Cla(3)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
End(4)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
C.fla(2)	-	-	-	-	-	-	-	1	-	1	1	3	-	2	-
(3)	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
C.syl(2)	1	1	5	4	4	4	1	3	1	1	1	1	2	-	1
(3)	1	5	16	4	16	5	3	5	7	5	1	2	3	-	8
(4)	-	3	1	-	5	-	-	-	1	-	1	-	-	1	1
Dip(i)	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-
Met A(2)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Ort(4)	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Rhe(2)	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-
(3)	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
(4)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Thi (2)	-	-	-	-	-	-	-	1	-	-	-	1	-	-	1

February

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sty	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
Gly(2)	-	-	-	-	-	-	-	-	-	2	-	2	-	-	-
Lim(3)	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
C.fla(4)	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
C.syl(2)	-	-	-	-	-	1	-	-	1	-	-	1	-	-	-
(3)	5	1	2	-	3	3	4	1	-	1	5	6	6	2	-
(4)	-	1	-	-	2	-	-	-	-	-	1	1	1	-	-
Dip(ii)	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Thi(2)	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-

February

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sty	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
Gly(2)	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Met E(2)	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
C.syl(2)	-	1	2	-	-	-	1	1	-	-	-	-	4	-	-
(3)	1	3	-	-	2	2	2	-	-	-	-	-	5	-	-
(4)	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-

APPENDIX C (...cont...)

March

ZONE 1

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	1	-	-	-	-	2	-	5	1	-
Glo	-	-	-	-	1	-	-	-	-	-
Plan	4	-	-	-	-	-	-	-	-	-
Val	2	1	-	-	1	2	-	2	-	-
Hydr	-	-	-	2	1	-	-	-	-	-
Ase	-	-	-	-	1	-	-	1	-	-
End(2)	-	-	-	1	-	-	-	-	1	-
(4)	1	-	-	-	2	1	1	-	-	1
Gly(2)	-	2	2	-	-	-	-	-	-	-
(4)	-	-	-	-	-	-	-	1	-	-
C.fla(2)	-	-	-	-	-	-	-	-	-	1
(3)	1	-	-	1	-	-	-	-	-	1
(4)	-	3	1	1	-	-	-	1	-	-
C.syl(3)	7	4	8	2	10	11	5	4	1	7
(4)	39	28	14	7	32	20	3	10	16	12
Dip(i)	-	-	-	-	-	-	-	-	1	1
Met A(1)	-	-	-	-	-	-	-	-	-	1
Rhe(2)	1	-	-	-	-	-	-	-	-	-
(3)	-	-	2	-	-	-	1	1	1	-
(4)	1	2	1	1	2	1	-	1	-	-
Thi(2)	2	-	-	1	3	-	1	2	-	1
(3)	1	1	2	8	4	1	3	9	-	1

March

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	-	-	-	-	-	-	1	1	-	2
Glo	-	-	-	-	-	-	-	-	1	-
Val	-	1	-	-	-	-	1	-	-	-
Hydr	1	1	-	-	-	-	-	-	-	1
End(4)	-	-	-	-	-	-	-	1	-	-
Gly(2)	-	2	-	-	2	-	-	-	-	1
C.fla(3)	-	-	-	-	-	-	-	-	-	1
C.syl(3)	6	6	2	2	2	-	2	7	12	4
(4)	6	16	2	7	10	3	11	13	13	10
Rhe(4)	1	-	-	-	1	1	-	1	-	-

March

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	-	-	-	-	-	-	7	1	1	-
Hydr	-	-	-	-	-	-	1	-	-	1
Gly(4)	-	-	-	-	-	-	1	-	-	1
C.syl(3)	1	1	-	1	-	1	1	-	-	-
(4)	-	1	-	2	1	-	-	1	-	-
Rhe(4)	-	-	-	-	1	-	-	-	-	-

APPENDIX C (...cont...)

April

ZONE 1

STEM -	1	2	3	4	5	6	7	8	9	10
Gor	-	-	-	-	-	-	-	-	1	-
Sty	18	9	12	50	51	37	30	18	21	45
Tub	-	-	1	-	-	-	-	-	-	-
The	1	-	-	2	-	-	-	-	-	-
Val	-	-	-	-	-	1	-	2	1	1
Hydr	-	-	3	1	-	1	-	-	-	-
Ase	-	1	1	-	1	1	-	1	-	-
Dyt(A)	-	1	-	-	-	-	-	-	-	-
Cori(N)	-	-	1	-	-	-	-	-	-	-
Cori(A)	-	-	-	-	1	-	-	-	-	-
Ple	-	-	1	-	-	-	-	-	-	-
End(2)	1	1	-	-	-	-	-	-	-	-
(4)	-	1	-	-	-	-	-	-	-	-
Gly(3)	-	-	1	-	1	1	1	1	3	-
(4)	-	1	1	2	-	-	-	-	-	1
Lim(1)	-	-	-	-	1	-	-	-	-	-
Tan(3)	-	-	1	-	-	-	-	-	-	-
C.fla(2)	-	1	-	-	-	-	-	-	-	-
C.syl(1)	-	1	1	1	-	-	2	-	2	-
(2)	16	8	8	5	3	1	5	5	5	1
(3)	1	-	1	1	3	-	3	1	1	2
(4)	5	4	4	3	-	4	-	3	6	1
Pse(3)	-	-	-	-	-	1	-	-	-	-
(4)	-	-	1	-	-	-	-	-	-	-

April

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	4	5	8	12	5	6	5	15	3	3
Val	-	1	-	-	-	1	-	-	-	-
Hydr	-	1	2	-	-	-	-	-	-	-
Ase	-	5	-	1	1	1	-	1	-	-
Gly(3)	-	-	1	-	-	-	-	2	-	-
(4)	-	-	-	1	-	-	-	1	1	-
C.syl(1)	-	-	-	2	-	-	-	-	-	-
(2)	8	2	5	11	4	4	4	9	-	1
(3)	-	1	1	1	1	1	-	5	-	1
(4)	-	-	1	-	1	-	2	1	-	1
Pse(4)	-	-	-	-	-	-	1	-	-	-

April

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	11	5	10	12	1	6	2	3	-	-
Tub	-	-	1	1	-	-	-	-	-	-
Hydr	-	-	-	1	-	-	-	-	-	-
Ase	-	-	-	-	-	3	-	1	-	1
Gam	-	-	-	-	-	2	-	-	-	-
Gly(3)	-	1	-	1	-	-	-	-	-	1
(4)	-	-	-	1	-	-	-	-	-	-
C.syl(1)	-	-	1	1	-	-	-	-	-	-
(2)	6	12	6	1	2	3	4	1	1	-
(3)	3	6	2	3	1	3	-	4	-	1
(4)	-	-	-	1	-	-	-	-	-	-

May

ZONE 1

STEM -	1	2	3	4	5	6	7	8	9	10
Gor	-	-	-	-	-	-	-	-	-	1
Sty	25	-	120	80	120	110	250	97	80	92
Erp	-	1	-	-	-	-	-	-	-	-
Hel	-	-	-	-	-	-	1	-	1	-
The	-	-	-	-	-	-	1	-	-	-
Bit	2	-	-	-	-	-	-	-	-	-
Pot	-	-	1	-	-	-	-	1	2	1
Phy	-	-	-	-	-	1	-	-	-	1
Plan	-	-	-	-	1	-	-	-	6	1
Val	1	-	2	3	2	3	19	4	24	4
Hydr	-	1	1	-	2	1	7	1	1	2
Ase	2	3	-	-	1	3	-	-	2	-
Gyr	-	-	-	-	-	-	1	-	-	-
Cer	-	2	-	-	-	-	2	2	-	-
Cyc	-	-	1	-	-	-	-	-	-	-
Hydrop	-	-	-	-	-	-	1	-	-	-
Cam(1)	1	-	-	-	1	-	1	-	18	1
(2)	-	-	-	-	-	-	-	-	18	1
End(2)	-	-	-	-	-	1	-	-	-	-
(3)	-	-	-	-	-	1	-	-	-	-
Gly(4)	-	1	-	-	-	2	-	-	2	1
Cor(i)	-	-	-	-	-	-	1	-	-	-
(iv)	-	-	-	-	-	-	1	-	-	-
C.syl(1)	-	-	-	1	2	-	1	-	-	-
(2)	21	16	35	34	39	34	15	8	5	5
(3)	25	13	58	44	50	80	27	26	19	21
(4)	21	8	43	31	24	90	24	32	14	41
Pse(2)	5	-	1	-	-	-	-	-	1	-
(3)	2	2	1	2	1	1	-	-	3	1
(4)	-	-	-	1	3	2	-	1	2	1

May

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10
Poly	-	-	-	-	-	-	-	-	-	1
Sty	14	37	2	1	31	2	3	-	-	-
Erp	-	-	-	-	-	-	-	-	-	1
Hel	-	-	-	-	-	-	-	-	-	1
Pot	-	1	-	1	-	-	-	-	-	2
Lym	-	-	-	1	-	-	-	-	2	1
Phy	-	-	-	-	-	1	-	-	1	2
Val	-	12	-	-	2	1	-	-	1	6
Hyd	-	1	-	-	-	-	5	1	3	4
Ase	1	1	-	1	1	-	-	-	1	5
Cer	-	-	-	-	-	-	-	-	-	1
Gly(3)	-	-	-	-	-	-	-	-	-	1
(4)	-	1	1	3	-	-	-	-	1	1
Mic(4)	-	-	-	-	-	-	-	-	-	1
C.syl(1)	-	1	-	1	3	-	1	2	-	-
(2)	18	15	11	18	40	14	10	9	2	-
(3)	41	12	9	24	33	54	16	50	4	4
(4)	13	14	8	8	26	23	9	22	4	1
Met C(3)	-	-	-	-	-	1	-	-	-	-
Pse(3)	-	1	-	1	-	-	-	-	-	-

May

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	4	2	3	1	2	-	9	-	3	-
Lym	-	-	-	-	1	-	-	-	-	-
Phy	-	-	-	-	1	-	1	-	-	-
Hydr	-	-	-	-	2	-	-	-	-	-
Ase	2	1	-	-	-	-	1	-	-	12
Gam	-	1	2	-	-	1	1	3	12	-
C.syl(1)	1	-	-	-	-	-	-	-	-	-
(2)	12	1	2	-	3	1	11	-	24	4
(3)	21	1	2	-	8	-	15	-	25	11
(4)	4	1	1	-	1	2	1	1	4	6
Met C(2)	-	-	2	-	-	-	-	-	1	-
(3)	-	2	2	-	-	-	-	4	1	2
(4)	-	-	4	-	-	-	1	-	-	2
Met E(4)	1	-	-	-	-	-	-	-	-	-

APPENDIX C (...cont...)

June

ZONE 1

STEM -	*1	2	3	4	5	6	7	*8	9	10
Hyd	1	6	6	11	1	1	4	3	1	11
Poly	-	-	-	-	-	-	3	-	-	-
Gor	-	-	-	1	-	-	-	-	-	-
Sty	10	50	132	17	42	6	37	9	155	60
Erp	-	1	-	12	8	4	1	1	-	3
Hel	-	1	-	-	-	-	-	-	-	-
Pot	-	4	1	-	-	5	-	-	1	1
Lym	-	-	-	-	-	-	1	-	-	1
Phy	-	-	-	-	-	5	-	-	-	-
Plan	-	-	2	1	-	3	-	-	-	2
Val	1	17	4	-	-	26	-	-	3	1
Hydr	-	-	-	2	1	1	1	1	-	1
Ase	5	26	7	5	34	100	5	-	5	28
Dyt(L)	-	-	-	-	-	1	-	-	-	-
Hal	-	1	-	-	-	21	3	1	5	2
Cori(N)	-	1	4	-	-	-	-	-	-	-
Glos	-	-	-	2	2	-	-	-	-	-
Cyr	-	-	-	-	-	-	-	-	1	-
Cam(1)	-	1	-	-	-	-	-	-	-	7
(2)	-	-	1	-	-	-	-	-	-	-
End(4)	-	2	1	-	-	1	-	1	-	-
Gly(2)	-	6	3	1	-	-	1	-	-	3
(3)	-	-	-	-	-	1	-	-	1	2
Lim(1)	-	-	-	-	-	-	-	-	-	1
(2)	-	-	-	-	-	1	-	-	-	1
(3)	-	-	-	-	-	-	-	-	-	3
Par(1)	-	-	-	-	-	-	1	-	-	-
Cor(i)	-	-	1	-	-	-	-	-	-	-
(iii)	-	-	1	-	-	-	-	-	-	-
C.syl(1)	-	2	24	15	56	1	26	5	83	77
(2)	2	57	103	84	166	10	104	2	148	150
(3)	2	21	107	71	33	12	39	3	81	81
(4)	4	6	36	10	4	5	5	-	18	12
Met A(3)	-	-	-	-	1	-	-	-	-	-
Met C(3)	-	-	1	-	-	-	-	-	-	-
Pse(2)	-	1	1	-	-	-	2	1	2	-
(3)	-	-	1	-	1	-	-	-	1	-
(4)	-	4	6	-	-	-	1	1	-	-
Pen C(1)	-	1	1	-	-	-	-	-	-	-
(3)	-	2	1	-	-	-	-	-	-	-
(4)	-	1	-	-	-	-	-	-	-	-
Psi(2)	-	-	1	-	-	-	-	-	-	-

APPENDIX C (...cont...)

June

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10
Hyd	-	-	-	-	-	5	-		-	
Pla	-	-	1	-	-	-	-		-	-
Poly	-	-	1	-	-	-	-		-	-
Sty	9	6	9	15	9	21	16		-	5
Erp	-	-	12	-	-	-	-		-	-
Pot	-	2	-	-	-	-	-		-	-
Phy	-	-	-	-	1	1	-		-	-
Plan	-	1	-	-	-	-	1		-	-
Val	-	-	30	1	-	-	-		-	-
Ase	-	9	2	5	21	-	-		2	5
Cer	-	-	-	-	-	1	-		-	-
Hal	-	-	-	-	1	-	-		-	-
Cam(1)	1	-	-	-	-	-	-		-	-
(2)	-	1	-	-	-	-	-		-	-
(3)	-	1	-	-	-	-	-		-	-
(4)	-	1	-	-	-	-	-		-	-
End(4)	-	-	-	-	1	-	-		-	-
Gly(2)	-	3	1	1	-	-	-		-	1
Cor(i)	-	-	-	-	-	-	-		1	-
Cor(iii)	-	-	1	-	-	-	-		-	-
C.syl(1)	53	6	262	119	49	412	182		69	33
(2)	64	27	145	236	175	331	258		72	33
(3)	32	11	42	120	65	121	76		12	18
(4)	7	15	6	22	7	17	27		-	9
Pse(1)	1	-	-	-	-	-	-		1	-
(2)	-	-	-	8	6	1	-		-	-
(3)	-	-	-	1	2	1	1		1	-
(4)	-	-	-	1	2	-	-		-	-

June

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	6	1	5	-	1	-	-	-	-	-
Erp	-	-	-	-	-	-	1	-	-	-
Ase	26	2	-	2	1	2	19	-	8	-
Gam	1	1	-	1	-	-	-	-	2	-
Cam(1)	-	-	-	-	-	1	-	-	-	-
Gly(2)	1	-	1	-	-	1	-	-	-	-
(3)	1	-	-	-	-	-	-	-	-	-
Lim(2)	-	-	-	-	-	1	-	-	-	-
(3)	-	-	-	-	-	1	-	-	-	-
Cor(i)	1	-	-	-	-	-	-	-	-	-
Cor(iv)	2	-	-	-	-	-	-	-	-	-
C.syl(1)	49	-	5	1	-	13	1	-	-	2
(2)	65	-	20	2	4	57	4	2	-	2
(3)	11	-	17	-	6	11	-	1	-	1
(4)	1	-	3	1	-	2	-	-	-	-
Met C(3)	-	-	-	-	-	-	-	-	-	1
(4)	-	-	-	-	-	-	-	1	-	1
Met E(3)	-	-	-	1	-	-	-	-	-	-

APPENDIX C (...cont...) (No data available for Zone 2 Stem 8.)

July

ZONE 1

STEM -	1	*2	3	4	5	6	*7	*8	*9	*10
Pla	-	-	-	-	-	-	-	-	-	1
Poly	2	-	-	-	-	-	-	-	-	-
Sty	1	-	1	-	4	1	-	6	-	7
Erp	1	17	1	-	-	-	-	-	6	5
Hel	1	3	-	-	-	-	-	-	-	1
The	-	3	2	1	-	1	-	-	-	4
Phy	-	-	1	-	-	-	-	-	-	1
Plan	-	4	-	6	2	1	-	3	4	7
Val	2	4	1	2	1	-	-	-	-	-
Hydr	-	1	-	-	1	-	-	1	-	-
Ase	1	1	3	3	1	-	-	-	-	4
Gam	-	-	1	-	1	-	-	-	-	-
Cer	1	1	-	-	-	-	1	-	-	-
Psy	-	-	-	1	-	-	-	-	-	-
Cori(N)	-	-	-	-	1	-	-	-	-	-
Glos	3	-	-	-	1	-	-	-	-	-
Hydrop	-	2	-	-	-	1	-	5	-	-
Mys	2	1	3	1	-	-	-	-	-	1
Cam(1)	-	-	-	2	-	-	-	-	-	-
End(2)	-	-	-	-	-	-	1	-	-	-
(3)	-	-	-	-	-	-	-	-	-	1
Gly(2)	-	-	-	-	1	-	-	-	-	-
(4)	1	1	-	-	-	-	-	-	-	-
Par(1)	1	-	-	-	-	-	-	-	-	-
(3)	-	1	-	-	-	-	-	-	-	-
Pol(2)	-	-	-	-	-	-	-	-	-	1
Cor(ii)	-	-	-	1	-	-	-	-	-	1
C.syl(1)	14	1	-	74	35	46	9	2	1	1
(2)	49	4	8	98	38	86	12	5	-	30
(3)	14	1	3	25	11	22	2	2	-	5
(4)	-	-	-	4	1	4	1	-	-	-
Pse(2)	-	-	-	1	-	1	-	-	-	-
(3)	-	-	-	-	1	-	-	1	-	-
(4)	-	-	-	1	1	-	-	3	-	4

APPENDIX C (...cont...)

July

ZONE 2

STEM -	1	2	3	4	5	6	*7	8	*9	10
Sty	-	-	4	-	4	2	-	1	-	4
Erp	1	2	2	-	2	-	-	2	15	1
Acr	-	-	-	-	-	-	-	-	2	-
Phy	-	-	-	-	1	-	-	-	-	-
Plan	1	-	-	-	-	-	1	-	1	-
Pis	-	-	1	-	-	-	-	-	-	-
Hydr	1	-	-	-	-	-	-	2	-	-
Ase	-	-	5	-	-	-	-	3	1	-
Gam	-	-	-	-	-	-	1	-	-	-
Cer	-	-	-	-	1	-	-	15	-	-
Glos	-	2	-	-	-	-	-	-	-	-
Hydrop	1	1	-	-	2	-	-	-	-	1
Cam(1)	-	-	-	-	1	-	-	-	-	-
Gly(3)	-	1	-	-	-	-	-	-	-	-
(4)	3	-	1	-	-	-	-	-	-	-
Par(1)	-	-	-	-	1	-	-	-	-	-
(2)	-	-	-	-	1	-	-	-	-	-
Cor(i)	-	-	1	-	-	-	-	-	-	-
C.syl(1)	42	25	31	63	87	31	4	6	-	5
(2)	70	19	42	17	113	121	1	48	-	17
(3)	14	4	8	5	18	60	2	6	-	4
(4)	1	2	-	-	1	10	-	1	-	-
Pse(1)	1	-	-	-	-	-	-	-	-	-
(3)	-	-	-	-	1	1	-	-	-	-
Pen C(2)	-	-	-	-	-	1	-	-	-	-

July

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	-	-	1	-	2	-	-	-	-	-
Erp	-	-	-	1	-	-	-	-	-	-
The	-	-	-	-	-	-	-	1	-	-
Phy	-	-	-	-	-	-	-	-	-	1
Plan	-	1	-	-	-	-	-	-	-	-
Ase	-	-	1	-	-	-	-	-	-	-
Gam	-	-	1	-	-	-	-	-	-	-
Cam(1)	-	-	-	-	1	-	-	-	-	-
Gly(2)	-	-	-	-	-	-	-	-	-	1
(3)	-	-	1	-	-	-	-	-	-	-
(4)	-	-	1	-	1	-	-	-	-	-
C.syl(1)	5	1	3	-	17	1	-	-	-	7
(2)	4	-	6	1	7	4	1	-	-	9
(3)	2	-	-	-	1	-	-	-	-	1
(4)	-	-	-	-	-	-	1	-	-	-

APPENDIX C (...cont...)

August

ZONE 1

STEM -	1	*2	3	4	5	*6	7	8	*9	10
Sty	-	2	-	2	-	2	-	-	-	-
Erp	3	10	-	-	1	17	-	8	12	1
Hel	-	1	-	-	-	-	-	-	-	-
The	-	-	-	-	-	-	-	2	2	-
Lym	1	-	-	-	1	21	-	-	-	-
Phy	-	-	-	-	-	-	-	3	-	-
Plan	1	2	-	-	5	2	2	2	2	2
Val	-	1	-	-	-	-	-	-	-	-
Hydr	1	3	1	-	4	2	-	2	-	6
Ase	2	-	-	-	18	-	1	3	1	-
Cer	-	-	-	-	1	-	-	-	-	-
Coe	-	-	-	-	-	-	1	-	-	-
Cam(1)	4	-	1	1	4	1	7	1	-	1
(4)	-	-	-	-	-	-	-	-	1	-
End(2)	-	-	-	-	1	-	-	-	-	-
Gly(2)	1	-	-	1	2	-	-	1	-	1
(3)	-	2	-	-	2	-	2	1	-	-
(4)	-	-	-	1	-	-	-	-	-	-
Lim(2)	1	-	-	1	2	-	-	-	-	-
Par(3)	-	-	-	-	3	-	-	-	-	-
(4)	-	-	-	-	2	-	-	-	-	-
C.syl(1)	151	6	73	47	60	2	33	1	1	5
(2)	256	16	271	127	176	6	48	5	2	11
(3)	36	9	108	45	94	5	14	6	6	6
(4)	9	4	15	9	37	1	-	3	2	1
Pse(4)	-	-	-	-	-	1	-	-	-	-

APPENDIX C (...cont...)

August

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10
Poly	-	-	-	-	1	-	-	-	-	-
Sty	3	-	5	2	-	-	-	1	-	-
Erp	1	-	-	-	1	2	-	-	-	1
Hel	-	1	-	-	-	-	-	-	-	-
Bit	-	-	-	-	1	-	-	-	-	-
Pot	-	-	-	-	-	-	-	-	1	-
Phy	-	-	-	-	-	-	-	-	1	-
Plan	-	2	-	-	1	-	-	-	-	1
Hydr	-	-	-	-	-	1	-	-	-	-
Ase	-	12	1	6	9	-	-	-	6	8
Gam	-	1	-	-	-	-	-	-	1	-
Hal	-	-	-	1	3	1	1	1	-	-
Cer	-	-	-	-	1	-	-	-	-	-
Cori(A)	-	1	-	-	-	-	-	-	-	-
Glos	1	-	-	-	-	-	-	-	-	-
Phr	-	-	-	-	-	1	1	-	-	-
Cam(1)	11	-	1	6	2	1	11	3	-	4
Gly(1)	-	-	-	-	-	1	-	-	-	-
(2)	36	-	-	-	1	1	1	-	-	1
(3)	22	-	-	-	-	-	-	-	-	1
(4)	1	-	-	-	-	-	-	-	-	-
Lim(1)	1	-	-	1	-	1	-	1	-	-
(2)	-	-	-	-	-	1	-	-	-	-
(3)	1	-	-	-	-	-	-	-	-	-
Par(1)	1	-	1	-	-	-	-	1	-	-
(3)	2	-	-	-	1	-	-	-	-	-
(4)	-	-	-	-	1	-	-	-	-	-
C.syl(1)	13	2	-	187	8	2	77	22	1	7
(2)	66	9	16	312	79	30	103	66	2	23
(3)	86	14	9	92	26	9	24	29	-	2
(4)	37	4	3	11	8	1	5	4	1	1

August

ZONE 3

STEM -	*1	2	3	4	5	6	7	8	*9	10
Erp	8	-	-	-	-	-	-	-	-	5
Glos	1	-	-	-	2	-	-	-	-	-
Phy	-	-	-	-	-	-	-	-	-	1
Plan	-	1	-	-	-	-	-	-	1	2
Ase	3	-	-	2	8	-	-	1	1	6
Gam	1	1	-	-	1	1	-	-	1	1
Hal	-	-	-	-	-	-	-	1	-	-
Phr	-	-	-	-	-	-	-	-	-	1
Cam(1)	1	-	-	-	-	-	-	-	-	-
Gly(2)	-	-	-	-	-	-	-	1	-	-
(3)	-	-	1	-	-	-	-	-	-	-
(4)	-	-	1	-	-	-	-	-	-	-
C.syl(2)	1	3	-	-	1	-	-	-	-	-
(3)	1	1	-	-	-	-	-	-	-	-

APPENDIX C (...cont...)

September

ZONE 1

STEM -	1	2	3	*4	5	*6	7	*8	9	10
Pla	2	-	-	-	-	-	-	-	-	-
Poly	-	-	1	-	-	-	-	-	-	-
Sty	9	2	5	-	-	-	-	-	-	-
Erp	6	1	1	-	-	1	-	-	3	2
Hel	1	-	-	-	-	3	-	-	-	1
The	-	-	-	-	-	1	-	-	-	-
Acr	-	-	-	-	-	-	-	-	-	1
Lym	-	1	-	-	-	2	-	-	-	-
Phy	-	-	-	3	-	1	-	-	-	-
Plan	-	-	1	-	-	-	2	-	-	-
Ase	61	5	9	2	5	11	12	1	17	7
Gam	3	-	-	-	-	-	-	-	-	-
Hal(A)	-	-	-	-	-	-	1	-	-	-
Clo	1	-	-	-	-	-	-	-	-	-
Glos	7	-	5	-	2	-	-	-	-	-
Cam(1)	1	-	-	-	1	1	-	-	1	-
End(3)	1	-	-	-	-	-	-	-	-	-
(4)	1	-	-	-	-	-	-	-	-	-
Gly(2)	5	1	1	1	-	2	-	-	1	1
(3)	1	-	-	1	3	1	-	-	-	2
(4)	-	1	-	-	-	-	-	-	3	-
Lim(3)	-	-	1	-	-	-	-	-	-	-
Par(1)	-	-	-	-	-	-	-	-	-	1
C.syl(1)	54	14	25	1	6	7	3	1	27	8
(2)	123	47	94	4	60	21	25	5	126	68
(3)	-	5	1	-	1	-	-	-	1	-
(4)	2	-	1	-	2	-	-	-	3	4

September

ZONE 2

STEM -	1	2	3	*4	5	*6	7	8	9	*10
Sty	-	-	-	2	-	-	-	-	-	-
Erp	-	1	-	-	1	-	-	-	-	-
The	-	-	-	-	-	-	-	-	-	1
Acr	-	1	-	-	-	-	-	-	-	-
Plan	-	1	-	-	-	-	-	-	-	-
Ase	-	3	-	1	-	-	-	2	-	2
Gam	-	-	1	-	-	-	-	-	-	-
Cam(1)	-	-	-	-	-	-	-	3	1	-
End(2)	-	-	-	-	-	-	-	1	-	-
Gly(2)	-	-	-	-	2	-	-	-	-	-
(4)	1	-	-	-	-	-	1	-	-	-
Lim(1)	-	-	-	-	-	-	-	1	-	-
(2)	-	-	-	-	-	-	-	1	-	-
(3)	-	-	-	-	1	-	-	-	-	-
Par(1)	-	-	-	-	1	-	-	4	-	-
C.syl(1)	2	12	-	2	5	-	1	18	14	1
(2)	5	39	15	16	160	-	25	103	37	6
(3)	-	-	-	1	3	-	-	1	-	-
(4)	-	1	-	1	1	-	-	2	2	-

APPENDIX C (...cont...)

September

ZONE 3

STEM -	1	2	*3	*4	*5	6	7	8	9	10
Acr	-	-	-	-	1	-	-	-	-	-
Gam	1	-	-	-	-	-	-	-	-	-
C.syl(1)	-	1	-	-	-	-	-	1	-	-
(2)	-	-	-	2	2	12	-	1	-	1
(3)	-	-	-	-	1	2	-	-	-	-
(4)	-	-	-	-	-	2	-	-	1	-
Met C(4)	-	-	-	-	1	-	-	-	-	-

October

ZONE 1

STEM -	*1	2	*3	4	5	6	*7	8	*9	*10
Poly	-	-	1	-	-	-	-	-	-	-
Erp	-	-	1	1	-	-	-	-	-	-
Glos	1	-	1	-	-	-	-	-	-	-
The	-	-	-	1	-	-	-	-	-	-
Plan	-	-	-	-	-	-	1	-	-	-
Val	2	-	-	-	-	-	-	-	-	-
Ase	-	3	16	8	3	1	-	-	-	-
Hal(A)	-	-	-	-	-	1	-	-	-	-
Cer	-	-	-	-	-	-	-	-	-	1
Glos	-	2	-	-	-	-	-	-	-	-
End(3)	-	-	-	-	-	-	1	-	-	-
(4)	1	1	-	-	-	-	4	2	-	-
Gly(2)	-	-	1	2	2	2	-	1	-	-
(3)	-	-	-	5	1	-	1	-	-	-
(4)	-	1	-	6	1	3	-	-	-	1
Lim(3)	-	-	-	1	-	-	-	-	-	1
Par(1)	-	1	-	-	2	-	2	-	-	-
C.syl(1)	-	6	1	4	7	5	1	2	-	1
(2)	23	103	23	49	133	50	29	58	21	20
(3)	25	59	13	12	121	25	21	44	14	12

APPENDIX C (...cont...)

October

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10
Gor	-	3	-	-	-	-	-	-	-	-
Lum	-	4	-	-	-	-	-	-	-	-
Sty	2	9	-	-	3	-	-	3	-	-
Acr	-	-	-	1	-	-	-	-	-	-
Ase	-	-	1	-	-	1	-	1	-	1
Cer	-	-	-	-	-	1	-	-	-	-
Glos	-	1	1	-	1	-	-	-	-	-
Cyr	-	1	-	-	-	-	-	-	-	-
Hol	-	1	1	-	-	-	-	-	-	-
Cam(1)	-	-	-	-	-	1	-	-	-	-
Gly(2)	1	6	-	-	-	1	-	2	-	2
(3)	-	9	-	-	5	1	-	1	1	-
(4)	-	3	2	-	-	1	-	-	2	-
Lim(2)	-	-	-	-	-	1	-	-	-	-
(3)	-	2	1	-	-	1	2	1	-	-
(4)	-	1	-	-	-	-	-	-	-	-
Par(1)	1	12	1	-	-	-	1	-	-	-
Pol(1)	-	1	1	-	-	-	-	-	-	-
(2)	-	1	-	-	-	-	-	-	-	-
C.syl(1)	7	8	2	1	2	1	-	6	-	1
(2)	49	65	24	13	38	30	23	70	18	11
(3)	19	112	16	10	18	20	14	55	17	3
(4)	-	1	-	-	-	-	1	-	-	-

October

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10
Ase	-	1	1	-	-	-	-	2	1	1
Hydro	-	-	-	1	-	-	-	-	-	-
Gly(3)	-	-	-	-	-	1	-	-	-	-
(4)	1	1	1	-	-	-	-	-	-	1
Lim(3)	-	-	-	-	1	-	-	-	-	-
C.syl(2)	1	2	-	-	-	1	1	-	-	1
(3)	-	1	-	1	-	1	-	-	-	-

APPENDIX C (...cont...)

November

ZONE 1

STEM -	1	2	3	4	5	6	7	8	9	10
Sty	1	-	-	-	-	-	-	-	-	-
Erp	-	1	-	-	-	-	-	-	-	-
The	-	-	-	-	-	-	-	1	-	-
Ase	1	-	1	-	-	-	-	-	-	-
Glos	1	-	-	-	1	-	-	-	-	-
End(4)	-	-	-	-	-	-	-	1	-	-
Gly(2)	1	-	-	-	-	-	-	-	-	-
(4)	-	-	-	1	-	1	-	-	-	-
C.syl(2)	76	19	2	5	46	14	9	58	12	30
(3)	55	13	4	5	47	12	6	47	7	23
(4)	2	1	-	1	-	-	-	2	-	2
Pen C(2)	-	-	-	-	-	-	-	1	-	-

November

ZONE 2

STEM -	1	2	3	4	5	6	7	8	9	10
Acr	-	-	-	1	1	-	-	1	-	-
Plan	-	-	-	-	-	1	-	-	-	-
Erp	-	-	-	-	-	-	-	-	-	1
Ase	1	-	-	-	-	-	-	-	-	-
Cer	-	-	-	-	-	-	1	-	-	-
Phr	-	-	-	-	1	-	-	-	-	-
Gly(2)	-	-	1	-	-	-	-	1	-	-
(3)	-	-	1	-	-	-	-	-	-	-
C.syl(2)	4	-	8	1	-	-	1	1	3	-
(3)	6	1	2	3	1	8	1	2	-	1
(4)	-	-	-	-	-	2	-	-	-	-

November

ZONE 3

STEM -	1	2	3	4	5	6	7	8	9	10
Ase	-	1	-	-	-	-	-	1	-	-
Hol	-	1	-	-	-	-	-	-	-	-
Gly(2)	-	2	-	-	-	-	-	-	-	-
(3)	-	2	-	-	-	-	-	-	-	-
(4)	-	2	-	-	-	-	-	-	-	-
Lim(3)	-	6	-	-	-	-	-	-	-	-
C.syl(2)	-	5	-	4	-	-	-	-	1	-
(3)	-	4	-	1	-	-	-	-	1	-

(i) Mean chironomid larval density (no. per cm^2)

	ZONE 1		ZONE 2		ZONE 3	
JAN	04.8	(0.05)	0.05	(0.01)	0.03	(0.01)
FEB	0.16	(0.02)	0.09	(0.02)	0.05	(0.02)
MAR	0.65	(0.08)	0.31	(0.05)	0.04	(0.01)
APR	0.26	(0.03)	0.16	(0.04)	0.18	(0.03)
MAY	2.01	(0.38)	0.96	(0.16)	0.49	(0.18)
JUN	4.06	(0.67)	7.54	(1.83)	0.74	(0.32)
JUL	2.18	(0.63)	2.14	(0.48)	0.31	(0.12)
AUG	4.43	(1.32)	2.62	(0.51)	0.04	(0.02)
SEP	1.82	(0.32)	1.31	(0.44)	0.09	(0.06)
OCT	2.71	(0.48)	1.63	(0.40)	0.05	(0.01)
NOV	1.06	(0.60)	0.10	(0.02)	0.08	(0.06)

(ii) Mean chironomid larval biomass (mg x 10^2 dry weight per cm^2)

	ZONE 1		ZONE 2		ZONE 3	
JAN	1.17	(0.16)	0.07	(0.02)	0.07	(0.03)
FEB	0.73	(0.17)	0.46	(0.15)	0.19	(0.13)
MAR	8.84	(1.45)	4.42	(0.62)	0.36	(0.14)
APR	1.68	(0.31)	0.57	(0.17)	0.41	(0.12)
MAY	17.44	(4.02)	6.47	(1.13)	2.45	(0.67)
JUN	11.30	(1.96)	13.85	(2.77)	1.58	(0.53)
JUL	3.39	(1.03)	3.16	(0.98)	0.39	(0.13)
AUG	9.74	(3.13)	6.55	(2.30)	0.12	(0.07)
SEP	2.56	(0.48)	1.58	(0.53)	0.35	(0.23)
OCT	5.52	(1.29)	3.73	(1.18)	0.09	(0.05)
NOV	2.57	(0.68)	0.30	(0.09)	0.22	(0.19)

APPENDIX D - (i) Mean chironomid larval density (no. per cm^2) and (ii) biomass (mg x 10^2 dry weight per cm^2) on old reedstems during 1981. (Figures in parentheses represent one standard error of the mean.)

CHIRONOMINAE	(1)	(2)	(3)	(4)
Camptochironomus	0.005	0.040	0.450	1.300
Cladotanytarsus	-	-	0.020	-
Endochironomus	0.005	0.020	0.150	0.300
Glyptotendipes	0.005	0.020	0.150	0.450
Limnochironomus	0.005	0.010	0.020	0.100
Microtendipes	-	-	-	0.100
Parachironomus	0.005	0.010	0.020	0.100
Polypedilum	0.005	0.020	-	-
Tanytarsus	-	0.010	0.020	-
ORTHOCLADIINAE				
Corynoneura	0.005	0.007	0.010	0.038
Cricotopus	0.005	0.010	0.034	0.200
Diplocladius	-	0.010	0.034	-
Metriocnemus	0.005	0.010	0.034	0.200
Orthocladius	-	-	-	0.150
Psectrocladius	0.005	0.010	0.034	0.200
Rheocricotopus	-	0.010	0.034	0.200
Thienemanniella	-	0.007	0.015	-

APPENDIX E - Mean larval instar dry weights (mg) for each chironomid genus found on old reedstems during 1981.

Sources - values for the following larvae were recorded by the author: third instar *Endochironomus* and *Glyptotendipes*; fourth instar *Cricotopus*, *Endochironomus* and *Psectrocladius*.
Values for other larvae are derived from Hall *et al* (1970) and Mackey (1977).

Dry weights were obtained by oven-drying larvae at 60°C for 24 hours, as recommended by Dermott and Paterson (1974).

	A		B		C	
JAN	29.57	(5.99)	29.06	(5.99)	31.33	(5.99)
FEB	17.39	(5.99)	16.90	(5.99)	29.46	(5.99)
MAR	23.10	(5.99)	21.78	(5.99)	17.92	(5.99)
APR	4.88	(5.99)	12.50	(5.99)	17.55	(5.99)
MAY	15.11	(5.99)	17.78	(5.99)	21.86	(5.99)
JUN	15.51	(5.99)	17.45	(5.99)	20.92	(5.99)
JUL	12.94	(5.99)	12.07	(5.99)	5.42	(5.99)
AUG	15.63	(5.99)	15.91	(5.99)	0.26	(5.99)
SEP	12.18	(5.99)	10.03	(5.99)	3.78	(5.99)
OCT	18.73	(5.99)	18.11	(5.99)	2.01	(5.99)
NOV	19.64	(5.99)	18.20	(5.99)	15.88	(5.99)

APPENDIX F - *H* values derived from Kruskal-Wallis analyses of variance undertaken to expose significant interzonal variation in (A) larvael density (no. per cm^2), (B) larval biomass (dry weight per cm^2), and (C) epiphyton biomass (dry weight per cm^2) on old reedstems during 1981. (Such significant variation occurs where the calculated *H* value is greater than the critical *H* value (in parentheses).)

(i) Larval density (no. per cm^2)

	Z1/Z2		Z2/Z3		Z1/Z3	
JAN	2.5	(64)	75.0	(64)	1.0	(64)
FEB	48.0	(64)	68.0	(64)	18.0	(64)
MAR	10.5	(23)	11.0	(23)	0.0	(23)
APR	23.0	(23)	43.0	(23)	28.0	(23)
MAY	15.5	(23)	21.5	(23)	7.0	(23)
JUN	20.0	(15)	4.0	(20)	4.0	(17)
JUL	18.0	(8)	3.0	(17)	4.0	(8)
AUG	26.0	(14)	1.0	(17)	0.0	(13)
SEP	16.0	(11)	2.0	(11)	0.0	(11)
OCT	9.0	(8)	0.0	(23)	0.0	(8)
NOV	2.0	(23)	20.5	(23)	4.0	(23)

(ii) Larval biomass (dry weight per cm^2)

	Z1/Z2		Z2/Z3		Z1/Z3	
JAN	1.0	(64)	80.5	(64)	3.0	(64)
FEB	65.5	(64)	59.0	(64)	15.0	(64)
MAR	17.5	(23)	1.0	(23)	0.0	(23)
APR	14.0	(23)	43.5	(23)	6.5	(23)
MAY	15.0	(23)	15.0	(23)	2.0	(23)
JUN	31.5	(15)	1.0	(20)	1.0	(17)
JUL	17.5	(8)	0.0	(17)	5.0	(8)
AUG	28.0	(14)	0.0	(17)	0.0	(13)
SEP	12.0	(11)	7.0	(11)	3.0	(11)
OCT	13.0	(8)	0.0	(23)	0.0	(8)
NOV	3.0	(23)	19.5	(23)	6.0	(23)

APPENDIX G - *U* values derived from Mann-Whitney *U* analyses of variance undertaken to expose significant interzonal differences in (i) larval density (no. per cm^2), (ii) larval biomass (dry weight per cm^2), and (iii) epiphyton biomass (dry weight per cm^2) on old reedstems during 1981. (Such significant differences occur where the calculated *U* value is lower than the critical *U* value (in parentheses).)

(cont...)

(iii) Epiphyton biomass (dry weight per cm^2)

	Z1/Z2		Z2/Z3		Z1/Z3	
JAN	4.5	(64)	51.0	(64)	0.0	(64)
FEB	98.0	(64)	3.0	(64)	7.0	(64)
MAR	37.0	(23)	5.5	(23)	0.0	(23)
APR	10.0	(23)	22.5	(23)	2.0	(23)
MAY	12.0	(23)	4.0	(23)	0.0	(23)
JUN	4.0	(17)	7.0	(23)	0.0	(17)
JUL	18.5	(8)	17.5	(17)	8.5	(8)
AUG	30.5	(14)	35.5	(17)	26.0	(13)
SEP	21.5	(11)	13.0	(11)	10.0	(11)
OCT	14.0	(8)	35.5	(23)	21.0	(8)
NOV	0.0	(23)	42.0	(23)	9.5	(23)

APPENDIX G (...cont.)

	ZONE 1		ZONE 2		ZONE 3	
JAN	8	(4)	6	(4)	10	(4)
FEB	6	(4)	6	(4)	7	(4)
MAR	6	(2)	7	(2)	6	(2)
APR	4	(2)	6	(2)	4	(2)
MAY	8	(2)	5	(2)	7	(2)
JUN	-		3	(2)	7	(2)
JUL	-		-		7	(2)
AUG	-		6	(2)	-	
SEP	-		-		-	
OCT	-		6	(2)	5	(2)
NOV	7	(2)	8	(2)	-	

APPENDIX H - *r* values derived from runs test investigations of intrazonal variation in larval density (no. per cm^2) on old reedstems during 1981.

Significant departure from randomness occurs where the calculated *r* value is less than or equal to the critical *r* value (in parentheses).

(Significance level = 0.05)

(i) Mean *Cricotopus sylvestris* larval density (no. per cm^2)

	ZONE 1		ZONE 2		ZONE 3	
JAN	0.45	(0.05)	0.05	(0.01)	0.03	(0.01)
FEB	0.13	(0.02)	0.07	(0.02)	0.05	(0.02)
MAR	0.48	(0.08)	0.28	(0.05)	0.03	(0.01)
APR	0.22	(0.03)	0.14	(0.03)	0.16)	(0.03)
MAY	1.85	(0.39)	0.94	(0.16)	0.44	(0.18)
JUN	3.90	(0.66)	7.46	(1.84)	0.69	(0.31)
JUL	2.13	(0.62)	2.11	(0.47)	0.29	(0.12)
AUG	4.32	(1.31)	2.43	(0.93)	0.02	(0.02)
SEP	1.76	(0.31)	1.26	(0.41)	0.09	(0.06)
OCT	2.58	(0.50)	1.49	(0.35)	0.03	(0.01)
NOV	1.05	(0.26)	0.09	(0.02)	0.05	(0.03)

(ii) Mean *Cricotopus sylvestris* larval biomass (mg x 10^2 dry weight per cm^2)

	ZONE 1		ZONE 2		ZONE 3	
JAN	0.99	(0.16)	0.07	(0.02)	0.04	(0.03)
FEB	0.60	(0.15)	0.41	(0.13)	0.18	(0.13)
MAR	7.50	(1.31)	4.16	(0.63)	0.32	(0.13)
APR	1.31	(0.23)	0.43	(0.11)	0.35	(0.08)
MAY	16.71	(3.97)	6.41	(1.15)	1.97	(0.63)
JUN	10.13	(1.84)	13.41	(2.78)	1.31	(0.53)
JUL	3.18	(0.99)	3.08	(0.98)	0.31	(0.10)
AUG	9.41	(3.06)	5.80	(1.85)	0.03	(0.03)
SEP	2.24	(0.41)	1.54	(0.51)	0.35	(0.23)
OCT	5.01	(1.21)	3.07	(0.87)	0.05	(0.02)
NOV	2.49	(0.62)	0.27	(0.09)	0.09	(0.06)

APPENDIX I - (i) Mean *Cricotopus sylvestris* larval density (no. per cm^2) and (ii) biomass (mg x 10^2 dry weight per cm^2) on old reedstems during 1981. (Figures in parentheses represent one standard error of the mean.

	ZONE 1		ZONE 2		ZONE 3	
JAN	3.93	(0.31)	1.33	(0.18)	0.75	(0.09)
FEB	3.93	(0.30)	4.53	(0.46)	1.13	(0.16)
MAR	7.09	(0.63)	5.89	(0.52)	2.62	(0.39)
APR	12.01	(0.40)	9.04	(0.55)	6.27	(0.83)
MAY	16.11	(0.73)	12.45	(0.73)	7.10	(0.70)
JUN	25.08	(3.11)	12.86	(1.85)	4.44	(0.73)
JUL	10.90	(2.14)	10.04	(1.94)	5.77	(0.91)
AUG	8.04	(1.76)	8.60	(1.25)	7.59	(1.12)
SEP	5.70	(1.18)	7.56	(1.90)	3.23	(0.66)
OCT	3.64	(0.25)	5.25	(0.95)	3.76	(0.74)
NOV	1.79	(0.34)	0.67	(0.04)	0.93	(0.34)

APPENDIX J - Mean epiphyton density (mg dry weight per cm^2) on old reedstems during 1981. (Figures in parentheses represent one standard error of the mean.)

(i) Larval numbers (Zone 1)

	S		E		E/cm^2	
JAN	+0.254	(0.097)	+0.429	(0.014)	+0.314	(0.055)
FEB	+0.365	(0.036)	+0.520	(0.004)	+0.051	(0.421)
MAR	+0.111	(0.345)	+0.467	(0.036)	+0.432	(0.045)
APR	+0.539	(0.018)	+0.494	(0.025)	-0.230	(0.184)
MAY	+0.022	(0.500)	+0.200	(0.212)	-0.067	(0.421)
JUN	+0.357	(0.138)	+0.071	(0.452)	+0.143	(0.360)
JUL	-0.200	(0.408)	+1.000	(0.008)	+0.633	(0.117)
AUG	+0.429	(0.119)	+0.714	(0.015)	+0.714	(0.015)
SEP	+0.714	(0.015)	+0.714	(0.015)	+0.619	(0.035)
OCT	+0.400	(0.242)	+0.400	(0.242)	+0.477	(0.242)
NOV	+0.644	(0.005)	+0.733	(0.002)	+0.207	(0.212)

(ii) Larval weight (Zone 1)

	S		E		E/cm^2	
JAN	+0.333	(0.045)	+0.371	(0.029)	+0.335	(0.045)
FEB	+0.220	(0.136)	+0.410	(0.018)	+0.030	(0.460)
MAR	+0.333	(0.097)	+0.689	(0.004)	+0.477	(0.029)
APR	+0.244	(0.184)	+0.378	(0.067)	-0.114	(0.345)
MAY	-0.111	(0.345)	+0.067	(0.421)	-0.022	(0.500)
JUN	+0.643	(0.016)	+0.357	(0.138)	+0.143	(0.360)
JUL	-0.200	(0.408)	+1.000	(0.008)	+0.600	(0.117)
AUG	+0.524	(0.068)	+0.810	(0.005)	+0.810	(0.005)
SEP	+0.619	(0.035)	+0.619	(0.035)	+0.524	(0.068)
OCT	+0.400	(0.242)	+0.400	(0.242)	+0.477	(0.242)
NOV	+0.556	(0.014	+0.733	(0.002)	+0.299	(0.115)

APPENDIX K - Kendall's correlation coefficient (τ) values relating to (i) larval numbers and (ii) larval weight on old reedstems in Zone 1 during 1981. Each of these two variables is correlated with stem surface area(s) epiphyton weight (E), and epiphyton density (E/cm^2). Figures in parentheses show the probabilities of correlations occurring through chance. (cont...)

(iii) Larval numbers (Zone 2)

	S		E		E/cm^2	
JAN	+0.309	(0.055)	+0.041	(0.421)	-0.084	(0.345)
FEB	+0.118	(0.274)	+0.375	(0.029)	+0.478	(0.008)
MAR	+0.250	(0.159)	+0.296	(0.136)	+0.116	(0.345)
APR	-0.159	(0.274)	+0.159	(0.274)	+0.023	(0.500)
MAY	+0.467	(0.036)	+0.333	(0.097)	-0.023	(0.500)
JUN	-0.056	(0.460)	+0.500	(0.038)	+0.394	(0.090)
JUL	+0.214	(0.274)	+0.357	(0.138)	+0.143	(0.360)
AUG	+0.360	(0.081)	+0.405	(0.055)	+0.405	(0.055)
SEP	+0.238	(0.281)	+0.905	(0.001)	+0.732	(0.015)
OCT	+0.556	(0.014)	₱0.156	(0.274)	+0.156	(0.274)
NOV	+0.424	(0.045)	+0.660	(0.005)	+0.325	(0.097)

(iv) Larval weight (Zone 2)

	S		E		E/cm^2	
JAN	+0.339	(0.045)	+0.080	(0.345)	-0.081	(0.345)
FEB	+0.202	(0.159)	+0.414	(0.018)	+0.398	(0.023)
MAR	+0.111	(0.345)	+0.289	(0.136)	+0.250	(0.159)
APR	-0.111	(0.345)	+0.289	(0.136)	+0.382	(0.067)
MAY	+0.511	(0.023)	+0.378	(0.067)	+0.023	(0.500)
JUN	+0.278	(0.179)	+0.500	(0.038)	+0.282	(0.179)
JUL	+0.071	(0.452)	+0.214	(0.274)	+0.143	(0.360)
AUG	+0.378	(0.067)	+0.333	(0.097)	+0.333	(0.097)
SEP	+0.238	(0.281)	+0.905	(0.001)	+0.732	(0.015)
OCT	+0.422	(0.045)	+0.200	(0.212)	+0.200	(0.212)
NOV	+0.368	(0.081)	+0.644	(0.005)	+0.159	(0.274)

APPENDIX K (...cont.) - Kendall's correlation coefficient (τ) values relating to (iii) larval numbers and (iv) larval weight on old reedstems in Zone 2 during 1981. Each of these two variables is correlated with stem surface area(s), epiphyton weight (E), and epiphyton density (E/cm^2). Figures in parentheses show the probabilities of correlations occurring through chance. (cont...)

(v) Larval numbers (Zone 3)

	S		E		E/cm^2	
JAN	+0.237	(0.115)	+0.106	(0.309)	+0.259	(0.097)
FEB	-0.053	(0.421)	+0.095	(0.345)	+0.055	(0.421)
MAR	+0.025	(0.460)	+0.076	(0.382)	-0.025	(0.460)
APR	+0.511	(0.023)	+0.378	(0.067)	+0.112	(0.345)
MAY	-0.090	(0.382)	+0.315	(0.115)	+0.494	(0.025)
JUN	+0.360	(0.081)	+0.494	(0.025)	+0.360	(0.081)
JUL	-0.506	(0.023)	+0.184	(0.242)	+0.276	(0.136)
AUG	+0.206	(0.360)	+0.041	(0.548)	+0.041	(0.548)
SEP	-0.159	(0.386)	+0.582	(0.035)	+0.476	(0.119)
OCT	+0.466	(0.036)	+0.123	(0.309)	+0.074	(0.382)
OCT	+0.466	(0.036)	+0.123	(0.309)	+0.074	(0.382)
NOV	+0.183	(0.242)	+0.243	(0.184)	+0.065	(0.421)

(vi) Larval weight (Zone 3)

	S		E		E/cm^2	
JAN	+0.129	(0.274)	+0.294	(0.067)	+0.208	(0.159)
FEB	+0.010	(0.500)	+0.176	(0.184)	+0.139	(0.242)
MAR	+0.215	(0.212)	+0.169	(0.274)	+0.072	(0.421)
APR	+0.778	(0.001)	+0.289	(0.136)	-0.067	(0.421)
MAY	-0.067	(0.421)	+0.111	(0.345)	+0.289	(0.136)
JUN	+0.511	(0.023)	+0.467	(0.036)	+0.333	(0.097)
JUL	-0.450	(0.036)	0.000	(0.500)	+0.180	(0.242)
AUG	+0.081	(0.452)	-0.081	(0.452)	0.000	(0.548)
SEP	-0.293	(0.281)	+0.781	(0.015)	+0.683	(0.035)
OCT	+0.549	(0.014)	+0.358	(0.081)	+0.362	(0.081)
NOV	+0.183	(0.242)	+0.243	(0.184)	+0.065	(0.421)

APPENDIX K (...cont.) - Kendall's correlation coefficient (τ) values relating to (v) larval numbers and (vi) larval weight on old reedstems in Zone 3 during 1981. Each of these two variables is correlated with stem surface area (S), epiphyton weight (E), and epiphyton density (E/cm^2). Figures in parentheses show the probabilities of correlations occurring through chance.

NON-CHIRONOMIDS

Stylaria lacustris (Linnaeus)
Erpobdella octoculata (Linnaeus)
Helobdella stagnalis (Linnaeus)
Acroloxus lacustris (Linnaeus)
Physa fontinalis (Linnaeus)
Planorbis albus (Müller)
Hydrachnellae sp.
Ostracoda sp.
Asellus aquaticus (Linneaus)
Gammarus pulex (Linnaeus)
Haliplidae sp. (larva)
Ceratopogonidae sp. (larva)
Cyclorrhapha sp. (larva)
Limnobiidae sp. (larva)
Ephemeroptera sp. (larva)
Corixidae sp. (nymph)
Glossosoma intermedium (Klapálek) (larva)
Hydroptilidae sp. (larva)

CHIRONOMIDS

Camptochironomus tentans (Fabricius)
Endochironomus
Glyptotendipes pallens (Meigen)
Limnochironomus sp.
Parachironomus sp.
Corynoneura
Cricotopus sylvestris (Fabricius)
Metriocnemus sp. A
Metriocnemus sp. C

APPENDIX L - List of macroinvertebrates found on bamboo canes in September, 1982.

(i)

ZONE 1

CANE -	1	2	3	4	5
Cam(1)	2	5	7	1	12
C.syl(1)	114	82	142	129	102
(2)	100	75	102	65	182
(3)	48	35	46	20	85
(4)	77	41	36	43	16
End(2)	1	-	1	-	-
(3)	1	1	-	3	-
(4)	-	1	-	-	-
Gly(2)	7	1	5	-	1
(3)	3	-	-	1	-
(4)	1	1	-	1	-
Lim(2)	-	-	-	-	1
(3)	-	-	1	-	-
Par(1)	-	-	4	1	1

ZONE 3

CANE -	1	2	3	4	5
Cam(1)	-	1	2	-	-
C.syl(1)	3	-	1	-	1
(2)	16	-	2	1	-
(3)	5	1	-	-	-
(4)	6	1	1	-	-
Gly(2)	-	1	1	-	-
Cor(iii)	1	-	-	-	-
Met C(1)	-	-	-	1	-

ZONE 1

Mean chironomid larval density (no. per cm^2) = 2.17
One standard error of the mean = 0.27

ZONE 3

Mean chironomid larval density (no. per cm^2) = 0.11
One standard error of the mean = 0.07

Calculated and critical *U* values derived from a Mann-Whitney comparison of the zonal means for chironomid larval density:

Calculated = 0.0 Critical = 4.0

APPENDIX M - (i) Taxonomic and numerical information relating to the chironomid larval community found on bamboo canes at the start of the cane experiment undertaken in September, 1982.

(See Appendix B for key to abbreviations. Arabic numbers next to taxa refer to instar categories; Roman numerals refer to relative size where instar status is indeterminable.)

(cont...)

(ii)

ZONE 1 (EX ZONE 3)

CANE -	1	2	3	4	5
C.syl(1)	200	-	44	7	17
(2)	85	2	18	15	12
(3)	34	2	6	4	2
(4)	6	1	4	1	-
Met C(3)	-	-	-	1	-

ZONE 3 (EX ZONE 1)

CANE -	1	2	3	4	5
Cam(1)	14	1	25	6	7
(2)	-	1	1	-	-
(3)	-	1	1	-	-
(4)	-	1	-	-	-
C.syl(1)	1	-	1	2	-
(2)	5	2	2	5	1
(3)	1	8	4	4	-
(4)	4	5	2	2	2
End(3)	1	-	-	-	-
(4)	-	-	-	1	-
Gly(1)	-	-	-	-	2
(2)	-	-	2	1	2
Lim(3)	-	-	1	-	-
Cor(iii)	1	-	-	-	-
Met C(3)	-	-	-	-	1

ZONE 1 (EX ZONE 3)

Mean chironomid larval density (no. per cm^2) = 1.17
One standard error of the mean = 0.74

Mean epiphyton density (mg dry weight per cm^2) = 3.00
One standard error of the mean = 1.36

ZONE 3 (EX ZONE 1)

Mean chironomid larval density (no. per cm^2) = 0.41
One standard error of the mean = 0.12

Mean epiphyton density (mg dry weight per cm^2) = 9.30
One standard error of the mean = 3.48

Calculated and critical U values derived from a Mann-Whitney comparison of the zonal means for chironomid larval density:

Calculated = 9.5 Critical = 4.0

Calculated and critical U values derived from a Mann-Whitney comparison of the zonal means for epiphyton density:

Calculated = 4.0 Critical = 4.0

APPENDIX M (...cont.) - (ii) Taxonomic and numerical information relating to the chironomid larval community and epiphyton found on repositioned canes at the end of the cane experiment undertaken in September, 1982. (cont...)

(iii)

ZONE 1

CANE -	1	2	3	4	5
Cam(1)	-	-	1	1	1
C.syl(1)	1396	744	378	78	29
(2)	143	104	123	50	33
(3)	24	14	28	16	11
(4)	17	7	21	8	27
End(4)	-	-	3	-	1
Gly(2)	-	-	-	-	2
(3)	-	1	-	1	2
(4)	1	-	-	2	6
Lim(2)	-	-	-	-	2
(3)	-	-	-	-	2
Par(1)	1	-	-	-	-
Met A(3)	1	-	-	-	-

ZONE 3

CANE -	1	2	3	4	5
C.syl(1)	-	-	1	-	-
(2)	18	-	-	2	-
(3)	2	-	-	-	-
(4)	2	-	-	-	-
Gly(4)	1	-	-	-	-
Cor(i)	1	-	-	-	-
Met C(1)	-	-	1	-	-

ZONE 1

Mean chironomid larval density (no. per cm^2) = 5.67
One standard error of the mean = 2.43

ZONE 3

Mean chironomid larval density (no. per cm^2) = 0.07
One standard error of the mean = 0.06

Calculated and critical *U* values derived from a Mann-Whitney comparison of the zonal means for chironomid larval density:

Calculated = 0.0 Critical = 4.0

APPENDIX M - (...cont.) = (iii) Taxonomic and numerical information relating to the chironomid larval community found on previously untouched canes at the end of the cane experiment undertaken in September, 1982.

	ZONE A	ZONE B	ZONE C	ZONE D
JAN	7	6	5	2
FEB	5	4	2	10
MAR	2	7	1	6
APR	4	5	10	8
MAY	6	8	2	1
JUN	4	8	3	2
JUL	3	9	1	7
AUG	4	9	4	5
SEP	3	9	6	2
OCT	2	8	5	3
NOV	4	7	7	9

APPENDIX N - Distance (metres) along each zone where first core-samples were taken during 1981. Distances were measured from that end of the study site nearest to the outflow of the River Sow.

NON-CHIRONOMIDS

Planaria torva (Müller)
Gordioidea sp.
Lumbriculus variegatus (Müller)
Stylaria lacustris (Linnaeus)
Tubificidae sp.
Erpobdella octoculata (Linnaeus)
Glossiphonia complanata (Linnaeus)
Helobdella stagnalis (Linnaeus)
Theromyzon tessulatum (Müller)
Bithynia tentaculata (Linnaeus)
Potamopyrgus jenkinsi (Smith)
Physa fontinalis (Linnaeus)
Planorbis albus (Müller)
Valvata piscinalis (Müller)
Hydrachnellae sp.
Ostracoda (2 spp.)
Daphnia sp.
Asellus aquaticus (Linnaeus)
Gammarus pulex (Linnaeus)
Donaciinae sp. (larva)
Haliplidae sp. (larva and adult)
Platambus sp. (adult)
Cyclorrhapha sp. (larva)
Corixidae sp. (nymph and adult)
Agrypnia pagetana (Curtis) (larva)
Phryganea varia (Fabricius) (larva)

APPENDIX O - List of macroinvertebrates found in core-samples taken from Zones A-D during 1981, with chironmid abbreviations used in Appendix Q. (cont...)

Holocentropus picicornis (Stephens) (larva)
Plectronemia sp. (larva)

CHIRONOMIDS

Camptochironomus tentans (Fabricius)	Cam
Chironomus 'plumosus' type	C.plu
Chironomus 'thummi' type	C.thu
Cryptochironomus sp.	Cry
Endochironomus	End
Glyptotendipes pallens (Meigen)	Gly
Limnochironomus sp.	Lim
Microtendipes pedellus (Degeer)	Mic
Paratendipes sp.	Para
Cricotopus sylvestris (Fabricius)	C.syl
Psectrocladius limbatellus (Holmgren)	Pse
Procladius sp.	Pro
Psilotanypus sp.	Psi

APPENDIX O - (...cont.)

NON-CHIRONOMIDS

Polycelis nigra (Müller)

Gordioidea sp.

Enchytraeidae sp.

Lumbricidae

Glossiphonia complanata (Linnaeus)

Pisidium sp.

Stylommatophora sp. (land slug)

Labidognatha sp. (terrestrial spider)

Acarina sp. (terrestrial mite)

Hydrachnellae (2 spp.)

Chilopoda sp.

Diplopoda sp.

Asellus aquaticus (Linnaeus)

Gammarus pulex (Linnaeus)

Dytiscinae sp. (larva)

Helodidae sp. (larva)

Hydrobius fuscipes (Linnaeus) (adult)

Ptiliidae sp. (adult)

Staphylinidae sp. (adult)

Collembola (2 spp.)

Ceratopogonidae sp. (larva)

Culicini sp. (larva)

Cyclorrhapha sp. (larva)

Dicranota sp. (larva)

Limnobiidae sp. (larva)

Pericoma sp. (larva)

Ptychopteridae sp. (larva)

Stratiomyidae sp. (larva)

Syrphidae sp. (larva)

Tipulinae sp. (larva)

Tubifera sp. (larva)

Adicella filicornis (Pictet) (larva)

Limnephilidae sp. (larva)

APPENDIX P - List of macroinvertebrates found in hand-grab samples taken from ZONES E-G during 1981, with chironomid abbreviations used in Appendix R. (cont...)

CHIRONOMIDS

Chironomus 'thummi' type	C.thu
Glyptotendipes pallens (Meigen)	Gly
Paratendipes sp.	Para
Tanytarsus sp.	Tan
Metriocnemus sp. A	Met A
Metriocnemus sp. B	Met B
Metriocnemus sp. C	Met C
Metriocnemus sp. D	Met D
Pseudorthocladius sp.	Pseu
Pentaneurini sp. A	Pen A
Pentaneurini sp. B	Pen B
Procladius sp.	Pro

APPENDIX P (...cont.)

APPENDIX Q - (pp 302-306) A taxonomic and numerical breakdown of the chironomid community found in each core-sample taken from Zones A-D during 1981.

See Appendix O for key to abbreviations. Numbers in parentheses next to chironomid taxa refer to instar categories.

(cont...)

January

ZONE A

CORE -	1	2	3	4	5
Cam(3)	1	-	1	6	-
(4)	1	2	-	1	-
C.plu(4)	1	-	-	-	-

ZONE B

CORE -	1	2	3	4	5
Cam(3)	3	2	2	3	6
(4)	3	2	-	-	1
Cry(3)	1	-	-	-	-
Mic(4)	1	-	-	-	-

ZONE C

CORE -	1	2	3	4	5
Cam(3)	-	-	-	-	1
(4)	-	4	1	1	1

ZONE D

CORE -	1	2	3	4	5
Cam(4)	1	-	-	-	-
Gly(3)	-	1	-	-	-

February

ZONE A

CORE -	1	2	3	4	5
Cam(3)	7	-	-	3	3
(4)	3	-	-	-	2
C.plu(4)	-	1	-	-	-
Mic(4)	1	-	1	-	-

ZONE B

CORE -	1	2	3	4	5
Cam(3)	2	2	3	3	7
(4)	3	3	1	9	1

ZONE C

CORE -	1	2	3	4	5
Cam(3)	-	-	-	1	-
(4)	-	1	-	-	1

ZONE D

CORE -	1	2	3	4	5
Cam(4)	-	1	-	-	-
Gly(3)	-	1	-	-	-

March

ZONE A

CORE -	1	2	3	4	5
Cam(3)	-	-	1	3	4
(4)	2	1	-	3	1
End(3)	-	-	-	1	-
Gly(3)	-	-	-	1	-
Mic(4)	-	1	-	-	-

ZONE B

CORE -	1	2	3	4	5
Cam(2)	-	-	1	-	-
(3)	1	5	4	4	5
(4)	-	4	2	3	-

ZONE C

CORE -	1	2	3	4	5
Cam(3)	1	-	-	-	-
(4)	-	-	2	1	
Gly(4)	2	-	-	2	-

ZONE D - no larvae found

APPENDIX Q (...cont...)

April

ZONE A

CORE -	1	2	3	4	5
Cam(3)	-	-	-	1	-
(4)	2	-	3	5	2

ZONE B

CORE -	1	2	3	4	5
Cam(3)	-	-	1	-	-
(4)	-	-	3	1	2
Gly(4)	-	-	1	-	-
Para(3)	-	1	-	-	-

ZONE C

CORE -	1	2	3	4	5
Cam(4)	-	-	1	-	-
Gly(3)	-	-	-	1	-
(4)	-	-	-	-	1

ZONE D - no larvae found

May

ZONE A - no larvae found

ZONE B

CORE -	1	2	3	4	5
Cam(2)	1	-	-	-	-
(3)	6	-	-	-	-
(4)	-	-	1	1	-
C.plu(4)	1	-	-	-	-

ZONE C

CORE -	1	2	3	4	5
Cam(4)	-	-	-	-	1
C.thu(4)	-	1	-	-	-
Gly(4)	-	-	-	1	-

ZONE D - no larvae found

June

ZONE A

CORE -	1	2	3	4	5
Cam(1)	1	-	-	-	-
(2)	8	-	-	-	-
(3)	14	1	-	-	-
(4)	5	1	-	-	-
C.syl(4)	-	-	-	1	-
Gly(2)	-	-	1	-	-
Lim(4)	-	-	2	-	-
Pse(4)	1	-	-	-	-

ZONE B

CORE -	1	2	3	4	5
Cam(2)	1	2	1	13	-
(3)	4	1	1	6	-
(4)	2	-	2	-	-
C.syl(3)	-	-	-	2	-
(4)	-	-	1	1	-

ZONE C

CORE -	1	2	3	4	5
Cam(3)	2	-	-	-	-

ZONE D

CORE -	1	2	3	4	5
Lim(4)	-	-	1	-	-

APPENDIX Q (...cont...)

July

ZONE A

CORE -	1	2	3	4	5
Cam(2)	-	1	1	-	-
(3)	1	3	1	-	1
(4)	-	7	3	-	3
C.syl(3)	1	-	-	-	-
Psi(3)	1	-	-	-	-

ZONE B

CORE -	1	2	3	4	5
Cam(2)	11	1	2	-	1
(3)	51	3	6	1	6
(4)	14	-	1	1	-
Pro(3)	1	-	-	-	-

ZONE C

CORE -	1	2	3	4	5
Cam(2)	-	1	1	-	-
(3)	-	8	9	-	-
(4)	-	1	1	-	-
Gly(3)	1	-	-	-	-
(4)	1	-	-	-	-
Lim(4)	-	-	1	-	-
Mic(3)	1	-	-	-	-

ZONE D

CORE -	1	2	3	4	5
Cam(3)	2	3	-	1	-
(4)	2	-	-	-	-
Gly(4)	-	2	-	-	-

August

ZONE A

CORE -	1	2	3	4	5
Cam(2)	-	2	1	9	4
(3)	3	4	1	16	18
(4)	2	3	1	2	2

ZONE B

CORE -	1	2	3	4	5
Cam(2)	5	6	-	7	30
(3)	33	14	2	4	6
(4)	4	5	4	5	5

ZONE C

CORE -	1	2	3	4	5
Cam(3)	4	-	-	2	-
(4)	3	3	-	5	1

ZONE D

CORE -	1	2	3	4	5
Cam(4)	-	-	-	-	3
Gly(3)	-	-	3	-	-
(4)	-	-	1	-	-

September

ZONE A

CORE -	1	2	3	4	5
Cam(3)	1	-	-	2	5
(4)	10	4	6	9	7

ZONE B

Cam(2)	-	1	-	-	-
(3)	1	5	23	1	1
(4)	7	4	27	-	7

ZONE C

CORE -	1	2	3	4	5
Cam(4)	1	-	2	1	1

ZONE D

Cam(3)	1	-	-	-	-
(4)	1	1	-	-	-
Gly(4)	-	-	1	-	-

APPENDIX Q (...cont...)

October

ZONE A

CORE -	1	2	3	4	5
Cam(3)	-	-	1	6	1
(4)	2	1	5	5	5
Gly(4)	-	-	-	-	1

ZONE B

CORE -	1	2	3	4	5
Cam(3)	-	-	3	4	5
(4)	1	-	6	3	5

ZONE C

Core -	1	2	3	4	5
Cam(4)	-	1	-	3	-
Gly(3)	-	-	-	-	1

ZONE D

CORE -	1	2	3	4	5
Cam(3)	-	-	-	2	-
(4)	-	1	-	3	-
Gly(4)	-	-	1	-	-

November

ZONE A

CORE -	1	2	3	4	5
Cam(3)	2	-	4	2	4
(4)	3	1	5	1	1
Gly(3)	1	-	-	-	-

ZONE B

CORE -	1	2	3	4	5
Cam(3)	-	8	1	3	1
(4)	-	2	2	2	1
End(4)	-	-	-	1	-
Gly(3)	2	-	-	-	-
(4)	1	-	1	-	-
Pro(3)	1	-	-	-	-

ZONE C

CORE -	1	2	3	4	5
Cam(3)	-	-	2	-	-
(4)	2	-	4	-	-

ZONE D

CORE -	1	2	3	4	5
Cam(3)	-	-	2	-	-
(4)	-	-	6	-	-
Gly(4)	-	-	1	-	-

APPENDIX Q (...cont.)

APPENDIX R - (pp 307- 311) A taxonomic and numerical breakdown of the chironomid community found in each hand-grab sample taken from Zones E-G during 1981.

See Appendix P for key to abbreviations. Arabic numerals in parentheses next to chironomid taxa refer to instar categories; Roman numerals refer to relative size where instar status is indeterminable.

(cont...)

January

ZONE E - no larvae found

ZONE G - no samples taken

ZONE F - no samples taken

February

ZONE E

ZONE G - no samples taken

GRAB -	1	2	3	4	5
Pen A(2)	-	-	-	2	1
(3)	-	-	2	-	-
Tan(3)	-	-	1	-	-
(4)	-	2	1	-	-

ZONE F

GRAB -	1	2	3
Met B(2)	-	-	1
Pen A(3)	-	-	2
Pen B(3)	-	1	-
Tan(4)	-	2	-

March

ZONE E

GRAB -	1	2	3	4	5
Met A(4)	1	-	-	-	-
Met D(4)	1	-	-	-	-
Pen A(3)	4	-	-	2	4
(4)	-	-	-	1	-
Tan(3)	-	-	-	1	-
(4)	5	1	-	-	-

ZONE G

GRAB -	1	2
Met A(3)	1	1
(4)	11	1
Met B(2)	2	2
Met C(3)	1	-
Pseu(i)	5	1

ZONE F

GRAB -	1	2	3
Met C(3)	-	-	1
Pen A(3)	-	-	1

APPENDIX R (...cont...)

April

ZONE E

GRAB -	1	2	3	4	5
C.thu(3)	-	1	-	-	-
Gly(3)	-	-	1	-	-
Met C(1)	-	-	-	1	-
(3)	-	-	-	-	2
(4)	-	-	-	1	1
Para(3)	-	-	-	-	1
Pen A(3)	-	-	4	2	1
Tan(2)	-	-	-	3	-
(3)	-	-	-	8	-
(4)	-	1	1	5	-

ZONE F

GRAB -	1	2	3
Met A(3)	-	1	1
(4)	1	-	-
Met C(4)	-	1	-
Tan(3)	9	-	-
(4)	6	-	-

ZONE G

GRAB -	1	2
Met A(4)	34	-
Met C(3)	1	-
(4)	1	-
Tan(1)	3	-
(2)	21	-
(4)	44	-

May

ZONE E

GRAB -	1	2	3	4	5
C.thu(3)	1	-	-	-	-
Met A(2)	-	-	-	-	1
(4)	-	-	-	-	2
Ten(3)	-	-	-	2	-
(4)	-	-	1	-	-

ZONE F

GRAB -	1	2	3
Tan(4)	1	-	-

ZONE G - no larvae found

June

ZONE E

GRAB -	1	2	3	4	5
Met A(3)	1	-	-	-	-
Tan(1)	-	-	-	-	1
(3)	1	1	-	-	-
(4)	-	-	3	-	1

ZONE F

GRAB -	1	2	3
Met A(4)	1	-	-
Pro(4)	-	1	-
Tan(3)	-	4	1
(4)	-	6	-

ZONE G

GRAB -	1	2
Met A(2)	-	1
(3)	2	-
(4)	1	-
Tan(4)	1	-

July

ZONE E

GRAB -	1	2	3	4	5
Tan(3)	-	-	-	-	1

ZONE F - no larvae found

ZONE G - no larvae found

August

ZONE E

GRAB -	1	2	3	4	5
Met B(3)	5	-	1	-	-

ZONE F - no larvae found

ZONE G

GRAB -	1	2
Met A(4)	-	8
Pen A(3)	-	1

September

ZONE E

GRAB -	1	2	3	4	5
Met B(3)	-	1	-	-	1
(4)	-	-	-	-	1

ZONE F

GRAB -	1	2	3
Met B(3)	-	-	2
Pseu(i)	-	-	1

ZONE G

GRAB -	1	2
Met B(3)	-	1
Pen A(2)	1	2

October

ZONE E

GRAB -	1	2	3	4	5
Met A(3)	-	-	-	1	-
Para(2)	-	-	-	1	-
Tan(3)	-	-	-	1	-

ZONE F - no larvae found

ZONE G - no larvae found

APPENDIX R (...cont...)

November

ZONE E

GRAB -	1	2	3	4	5
Para(2)	-	-	-	-	1

ZONE G

GRAB -	1	2
Pen A(4)	-	1

ZONE F - no larvae found

December

ZONE E

GRAB -	1	2	3	4	5
Tan(3)	-	1	-	-	-

ZONE G

GRAB -	1	2
Pen A(3)	2	-
(4)	1	-
Tan(2)	-	1

ZONE F

GRAB -	1	2	3
Met A(2)	-	-	2
Pen A(3)	-	1	-
Tan(2)	-	-	2
(3)	-	3	-
(4)	-	1	-

(i) Mean chironomid larval density (no. per m^2)

	ZONE A		ZONE B		ZONE C		ZONE D	
JAN	1635	(760)	3145	(820)	1006	(427)	252	(154)
FEB	2642	(1167)	4277	9920)	377	(154)	377	(252)
MAR	2264	(810)	3648	(853)	1006	(427)	0	(0)
APR	1635	(616)	1006	(427)	377	(154)	0	(0)
MAY	0	(0)	1258	(954)	377	(154)	0	(0)
JUN	4403	(3474	4655	(2408)	252	(252)	126	(126)
JUL	2893	(1136)	12454	(9027	3145	(1591)	1258	(660)
AUG	8554	(3130)	16354	(4407)	2264	(924)	881	(548)
SEP	5535	(1002)	9687	(5525)	629	(199)	503	(235)
OCT	3397	(1136)	3145	(1177)	629	(345)	881	(583)
NOV	3019	(853)	3271	(853)	1006	(734)	1132	(1132)

(ii) Mean *Camptochironomus tentans* larval density (no. per m^2)

	ZONE A		ZONE B		ZONE C		ZONE D	
JAN	1510	(760)	2678	(583)	1006	(427)	126	(126)
FEB	2264	(1170)	4277	(920)	377	(154)	126	(126)
MAR	1887	(660)	3648	(853)	503	(235)	0	(0)
APR	1635	(616)	755	(367)	126	(126)	0	(0)
MAY	0	(0)	1132	(830)	126	(126)	0	(0)
JUN	3774	(3468)	4151	(2073)	252	(252)	0	(0)
JUL	2642	(1261)	12328	(8901)	2642	(1621)	1006	(511)
AUG	8554	(3130)	16345	(4407)	2264	(924)	377	(377)
SEP	5535	(1102)	9687	(5525)	629	(199)	377	(252)
OCT	3271	(1115)	3145	(1177)	503	(367)	755	(610)
NOV	2893	(834)	2516	(1071)	1006	(734)	1006	(1006)

APPENDIX S - (i) Mean chironomid larval density (no. per m^2) and (ii) mean *Camptochironomus tentans* larval density (no. per m^2) found in benthic core-samples during 1981. (Figures in parentheses represent one standard error of the mean.)