STUDIES OF THE CHIRONOMIDAE (DIPTERA) OF SOME REEDBEDS

by

Timothy John Mountain B.Sc. (Exeter)

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IMAGING SERVICES NORTH
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ABSTRACT

The Chironomidae of a *Phragmites* reedbed in Cop Mere, Staffordshire, were investigated during 1979 and 1980; emergence from reedbeds was also followed at Linford, Buckinghamshire.

During the period from 1979 to 1980, a marked change occurred at the Cop Mere stations (S1 and S2) sampled within the reedbed benthos. In 1979, the larval population at S1 was relatively diverse as compared with 1980, with *Glyptotendipes* being common; few larvae were found at S2. By the summer of 1980, *Camptochironomus* larvae predominated at high densities at both stations and few other genera were found; the weather conditions during late spring 1980 have been implicated as a major cause of the abundance of *Camptochironomus* in the reedbeds. The spatial dispersion of *Camptochironomus* larvae was contagious.

Larvae, especially *Cricotopus*, *Glyptotendipes* and *Psectrocladius*, were particularly abundant on standing stems. The periphyton and stems served variously as food and habitat for different larvae.

Fallen, decaying stems provided a habitat and were colonised by chironomid larvae. Litter decay followed a diphasic pattern, and was enhanced by the presence of macroinvertebrates. Proportions of ash and nitrogen generally increased during the study, while those of α-cellulose and lignin fell.

Emergence of imagines from the reedbeds at Cop Mere in 1979 was generally greater than in 1980, and peak emergence occurred slightly earlier. The Orthocladiinae were particularly common, with *Cricotopus sylvestris* especially abundant. Total emergence from *Phragmites* reedbeds at Linford was similar to that at Cop Mere, although more species were recorded at Linford. There was no significant difference between the numbers of imagines emerging from six different reed

types at Linford, although emergence from *Scirpus maritimus* seemed to be greater in both years than from other species. Onset of emergence was thought to be governed primarily by the rate of larval development.

ACKNOWLEDGEMENTS

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CONTENTS

Chapter 1

INTRODUCTION

The initial impetus for the undertaking of this study was a suggestion, confirmed by a literature search, that very little work had been carried out concerning populations of Chironomidae in reedbeds. This contrasts with the large number of publications dealing with larval populations of the profundal and sub-littoral zones of lakes. (The term lake will be used here in the broad sense of a large body of water; strictly it should only be used where the body of water stratifies.) Investigations of these zones have produced data on, for example, population densities and life-histories (Mundie, 1957; Slack, 1967; Carter, 1976; Tait-Bowman, 1976; Titmus, 1979), production (Kajak & Dusoge, 1970; Charles *et al.*, 1974, 1976; Potter & Learner, 1974; Titmus & Badcock, 1980) and feeding behaviour (Kajak & Warda, 1968; McLachlan & Dickinson, 1977; Titmus & Badcock, 1981). Studies of adult emergence from profundal and sub-littoral zones have yielded additional information on species and their abundance (Mundie, 1957; Potter & Learner, 1974; Paasivirta, 1974; Titmus, 1979a).

Vegetation in these areas is limited mostly to floating algae, and only in the shallower, littoral zone, where light can penetrate to the benthos, does rooted vegetation appear.

Ponds and pools may be wholly littoral, since aquatic macrophytes are sometimes present as submerged or floating-leaved plants throughout the basin. Learner & Potter (1974) have examined adult emergence from two ponds in Hertfordshire, and Smith & Young (1973) have determined life-histories of some Chironomidae in two ponds in Merseyside.

In the Arctic tundra regions, the Canadians have examined the chironomid populations of shallow ponds, being especially interested in

the role of photoperiod in emergence (Danks & Oliver, 1972; Danks, 1978). Driver (1977) monitored adult emergence from emergent macrophytes in prairie ponds and showed a correlation between the diversity of the chironomid fauna and the successional age of the pond (which is reflected in the diversity of the plant species there).

Only two studies of chironomids within reedbeds of littoral zones of lakes have been found. In Poland, Opalinski (1971) undertook a limited investigation of the macroinvertebrates found in the benthos and on the erect reedstems of a *Phragmites* reedbed. He demonstrated the presence of an abundant macrofaunal community on the reeds, this being largely composed of larval chironomids. In Britain, the only outstanding study of a reedbed system is that of Mason & Bryant in the Norfolk Broads. In a comprehensive survey and series of papers, data have been obtained concerning macrophyte production (Mason & Bryant, 1975), periphyton production and macrofauna grazing (Mason & Bryant, 1975a), reed decomposition (Mason & Bryant, 1975; Mason, 1976) and the invertebrate community of the reedbed (Mason & Bryant, 1974). However, larval chironomids were not examined particularly by them, except in relation to the periphyton, the emphasis being more on overall macrophyte (*Phragmites* and *Typha*) production and community structure.

There do not seem to be any publications where the chironomid community of a reedbed has been reported in detail. This applies to benthic populations in the substratum, those found on erect or fallen reedstems, and the adult populations. There are probably at least two reasons for this:

1) Sampling in reedbeds is more difficult than in open-water zones because standard, recognised procedures (Ekman grabs, soft-deposit corers etc.) usually cannot be used, due to the nature of the substratum. Furthermore, access is often difficult either by boat or land. In

this study, a modified corer design was used to obtain benthic samples; access was fairly easy at the site chosen for study.

2) Taxonomic problems, until recently, have hindered chironomid research. This was especially true for the Orthocladiinae which are both abundant in reedbeds and often small organisms. Due to the extreme similarity between species at the larval stage, separation and identification is always difficult; imagines are easier to identify and rearing larvae from samples usually enables specific identification of the larvae. Older keys to chironomid adults and larvae are often incomplete and difficult to use, and the taxonomy and nomenclature were in a constant state of flux until recently, due to the different approaches to generic construction used by European and British taxonomists. The task of identifying chironomids in Britain has now been made easier due to the preparation of keys to genera of the larvae, especially the Orthocladiinae, by P. S. Cranston at the Natural History Museum, and to the adult males by L. C. V. Pinder of the Freshwater Biological Association. These keys are up to date, reliable and relatively easy to use. Rearing of larvae and emergence studies of the adults enabled most of the larval genera to be named specifically. The nomenclature used here is in accordance with Pinder (1978).

Before any predictive scientific theory or hypothesis can be made about a system, ecological, physiological or whatever, a general knowledge of that system is required. As already indicated, very little is known about populations of chironomids in reedbeds. Thus the essential aim of this study was to provide information about such populations through general survey techniques; the problems and questions raised during the course of the work, together with the background information should enable some hypotheses about particular aspects of chironomid ecology in reedbeds to be made and possibly

stimulate further research in the area.

The nearest and most suitable site to Keele with sufficient areas of reedbed is at Cop Mere, Eccleshall. The dominant species of reed is *Phragmites australis* (Cav.) Trin. ex Steud., the common reed, and a full description of the study site is given in the next chapter.

The investigation is essentially divided into four parts. Chapter 3 describes studies of the larval populations of the benthos in the reedbed zone, both in terms of the relative abundance of species found there and the spatial pattern of the predominant species *Camptochironomus tentans* (Fabricius). Chapter 4 reports on the larvae found on old and young standing stems of *Phragmites* and discusses the possible relationship of the larval populations with the periphyton on the stems. Larvae and other invertebrates associated with dead, fallen decomposing stems are discussed in chapter 5. Since very little work has been done as regards the loss of macromolecular fractions from stems, the breakdown was followed in some detail using litter bags; the role of invertebrates, including chironomids, in the decay of *Phragmites* litter is reviewed in light of the results.

The fourth part of the project concerned adult emergence from the reedbed zone and is described in chapter 6. A comparison of adult emergence from six different reed types was made using samples obtained from the Game Conservancy Wildfowl Reserve at Linford, Buckinghamshire. In addition, an analysis of the frequent samples taken there enabled an assessment of the influence of weather conditions on emergence to be made.

Finally, chapter 7 reviews the study and some general conclusions about chironomid populations in reedbeds are made.

Chapter 2

DESCRIPTIONS AND PHYSICAL CHARACTERISTICS OF THE STUDY SITES

Two sites were chosen for investigation. Cop Mere was studied intensively throughout 1979 and 1980, and Linford for the two summers of 1979 and 1980.

Cop Mere (Grid Reference SJ 80/30). Cop Mere is situated near Eccleshall, Staffordshire, some 24km south of Keele on land managed by the Sugnall Manor Estate (Fig. 2:1). It is of glacial origin overlying strata of alluvium, boulder-clay, sands and peat and is part of the R. Sow drainage system. Cop Mere is shallow compared with the majority of the meres in the Shropshire-Cheshire plain, since it has a recorded maximum depth of 2.7m, although with an area of 16.8ha it is among the largest of the group listed by Reynolds (1979).

Except for the south-east side, the surrounding land slopes quite steeply to the mere and supports growth of deciduous woodland which reaches and often overhangs the water. At the western side of the mere is a complex of small streams and abandoned fish ponds, with consequent damp Alder-Willow wood.

The land surrounding the south-eastern edge of the mere is, however, flatter and this has allowed the establishment of a substantial marginal vegetation, with for instance *Carex paniculata* L., *Sparganium erectum* L., *Cirsium palustre* L. Scop. and herbaceous marsh plants, which grades towards the water into quite extensive *Phragmites australis*-dominated reedbed with occasional *Typha angustifolia* L. stands.

Reynolds (1979) has classified Cop Mere as one of a group of isolated meres and there is argument as to whether it and some others in the Shropshire-Cheshire group are strictly meres. Nobody has

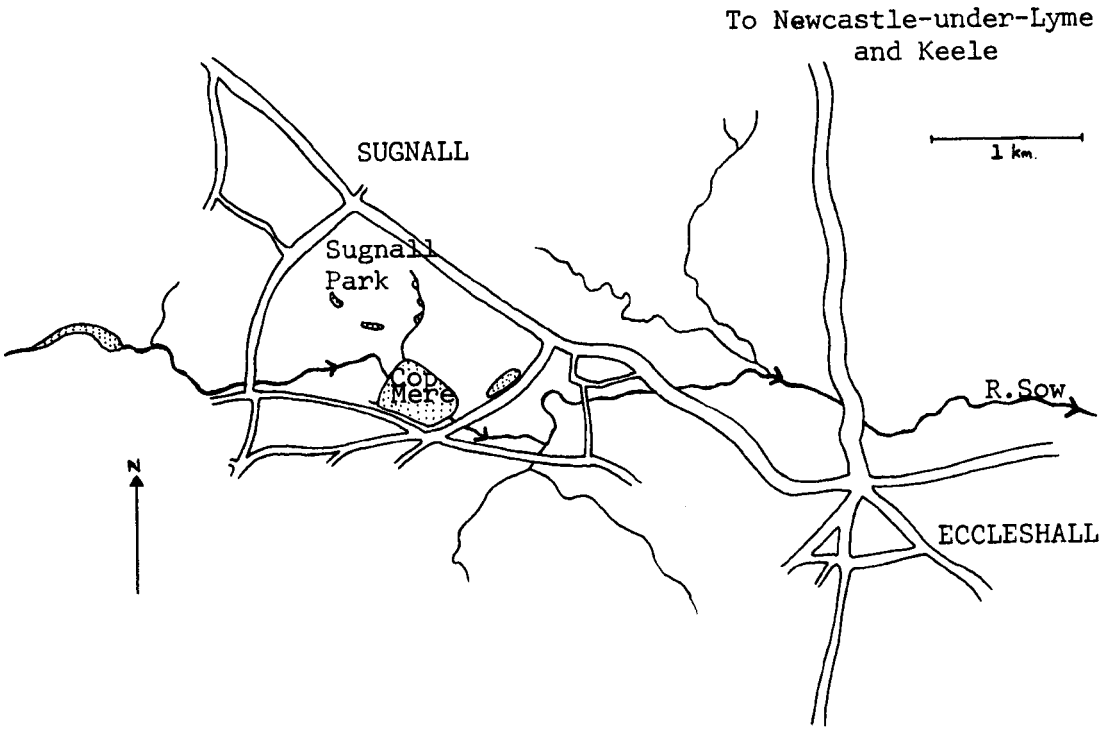
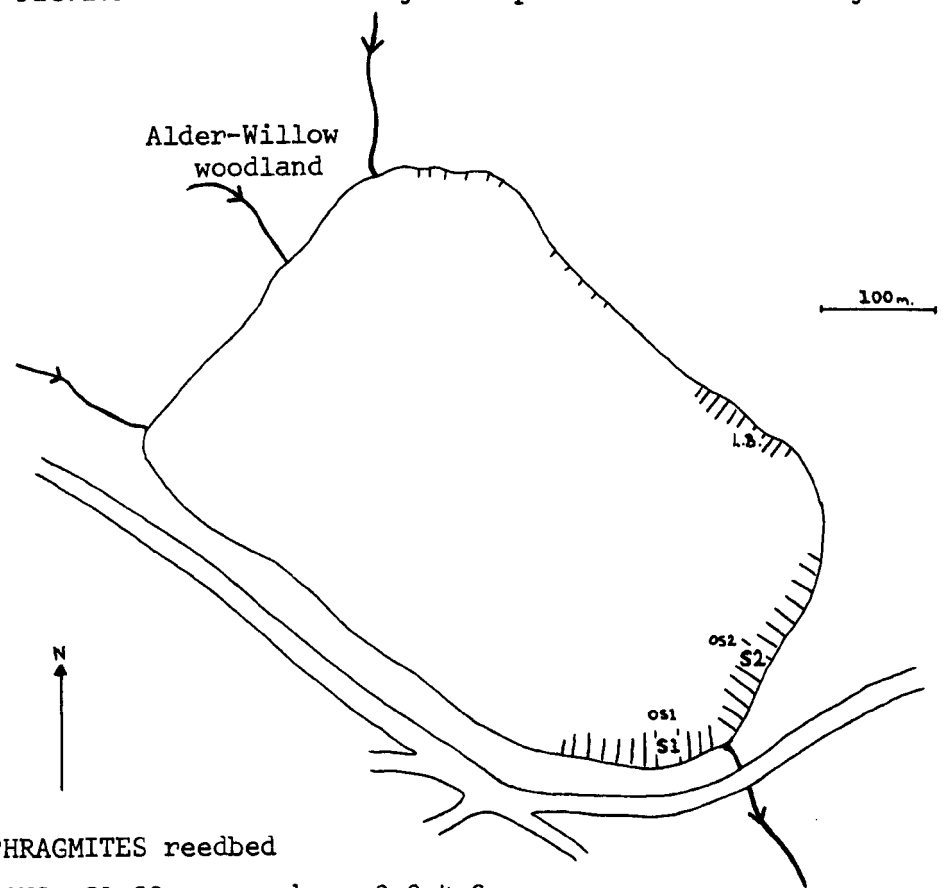


FIG.2:1 General locality of Cop Mere in River Sow system.



IIII PHRAGMITES reedbed

STATIONS: S1,S2 - see chaps.2,3,4,6.

OS1,OS2 - see chap.6.

L.B. - litter bags, chap.5.

FIG.2:2 Sampling stations within Cop Mere.

attempted a definition of a mere before Reynolds (1979) who proposes that it is "a small, potentially fertile lake occupying a hollow in glacial drift deposits and maintained principally by ground water flows." By this definition Cop Mere is not a mere since it has an inflow and outflow. But whatever the limnological wrangling over definitions and whether or not it is atypical, Cop Mere offers, more than any other body of water in the western midlands, sufficient areas of easily accessible reedbed and within a short distance of Keele. Furthermore it is a previously understudied mere, though possibly one of the earliest examined (Wardle, 1893).

Two stations within the reedbed zone were selected for regular sampling (Fig. 2:2). Station one (S1) was in the *Phragmites* bed to the west of the outflow and Station two (S2) was in the south-eastern reedbed; preliminary sampling had revealed that there might be a difference between the two parts of the reedbeds.

Much of the mere has a substratum of sand though on the northern side this is overlain by organic mud of allochthonous origin, largely from the overhanging trees. Particle fractionation analysis was carried out in summer 1979 on core samples from S1 and S2, following the method of Allen et al. (1974). The results confirmed that the substratum is predominantly sand with little silt or clay, and the two stations do not differ much as regards proportions of particles present (Table 2:1).

The organic content of the samples was estimated from loss in weight on ignition (Allen et al., 1974) and from Table 2:1 it can be seen that there is less than 1% present within the substratum. This must not be interpreted as meaning there is no organic matter on the floor of the littoral zone since litter and roots were separated from the sand by coarse sieves during the initial processing of the cores.

Site and Station		Particle Diameter (mm) and Grade				Organic Matter
		0.2-2.0 Coarse sand	0.02-0.2 Fine Sand	0.002-0.02 Silt	<0.002 Clay	
Cop Mere	S1	39.6	57.9	0.3	0.3	0.44
	S2	44.5	51.3	0.3	0.3	0.74
Linford	L1	53.0	23.3	8.4	6.9	3.01
	L2	47.6	22.0	8.8	9.9	3.01
	L3	46.2	25.1	8.2	11.8	3.09
	L4	16.6	4.8	11.3	36.7	2.98
	L5	65.6	17.3	4.6	7.5	2.23
	L6	45.3	25.0	10.4	7.5	3.61
	L7	53.4	25.9	5.5	6.7	1.54
	L8	66.1	17.6	6.3	5.7	8.48
	L9	60.8	18.6	5.5	8.5	2.78
	L10	57.1	17.8	6.8	9.6	4.61
	L11	40.2	31.5	8.5	8.7	3.52
	L12	49.6	22.0	5.4	12.3	1.77

TABLE 2:1 Percentage composition of fractions and organic matter for substrata at Cop Mere and Linford. (Figures in body of table are percentages).

A rough estimate of the quantity of litter and roots present was obtained by combining two samples from a large 15 cm diameter corer (modified by R. Young (pers.comm.) from a Tvarinnine sampler (Finnish IBP-PM Group, 1969)) taken at each station, air drying them and separating the vegetation from the substrate by sieving, and weighing. No difference between S1 and S2 was found, there being approximately 10000 gm^{-2} material at each station (Table 2:2).

Temperature of the water in the littoral zone was followed monthly from May 1979 through to December 1980. No difference was evident between S1 and S2 so the temperature recordings have been combined and

Station	Wt. of Vegetation in sample (g)	Wt. of Sand in sample (g)	Amount of Vegetation (gm^{-2})
S1	185	300	10468
S2	182	250	10300

TABLE 2:2 A comparison of the vegetation (roots and litter) at the Cop Mere stations.

the changes are shown in Fig. 2:3. Water is warmest in July and August at about 20°C and coldest in winter at around 5°C. In January 1980 the water temperature was very low (1.5°C) because of thick ice cover in the reedbed zone. Due to the shallowness of the water (about 30-40 cms. in the summer and twice this depth in the winter), the reedbed and other littoral zones are likely to be more rapidly influenced by changes in air temperatures. This is in contrast to the mass of the water in the profundal of meres; furthermore, temperatures in the hypolimnion water of lakes tend never to rise as high as those in the littoral (Tait-Bowman, 1976). The higher temperatures and their relative instability in the littoral will have consequences for the biology of chironomid larvae and other organisms affecting their rate of development, respiration, activity and survival.

Oxygen in Cop Mere was measured in the field on an occasional basis using a portable Mackereth O_2 meter (manufactured by Lakes Instruments Ltd.) but on no occasions sampled did the meter record less than 90-100% saturation of the water. Wave action from breeze and wind, the shallowness of the water and the presence of algae in the summer all combine to keep the oxygen content of the water high, even though solubility will decrease in the summer because of the increasing temperatures. However, the substrate around root systems may suffer some oxygen deficit and respiration by algae at night during the summer may lower the O_2 levels in the water. The shallowness of the water and

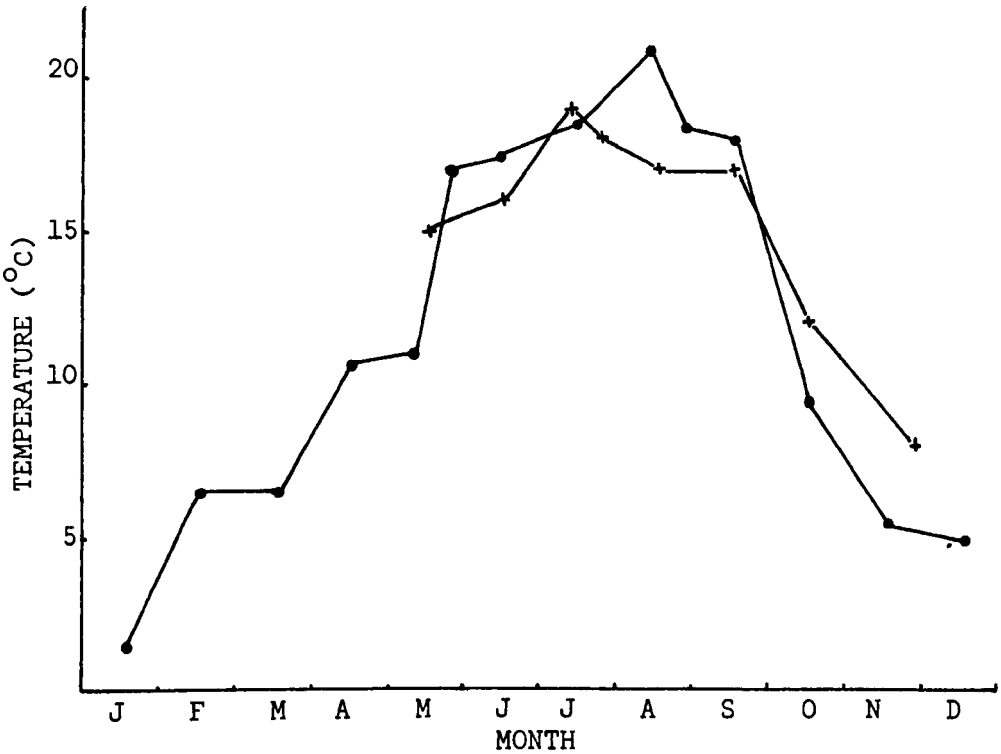


FIG.2:3 Changes in water temperature at Cop Mere during 1979 (+—+) and 1980 (•—•). Readings taken in reedbed.

its exposure to winds ensures that no stratification of the open water occurs during the hotter months; lack of stratification is in contrast to some other meres previously studied where the profundal zone suffers severe O_2 depletion in the summer (Reynolds, 1979; Tait-Bowman, 1976).

Conductivity and pH of the two stations in the reedbeds were measured in May 1980 and January 1981 by collecting water samples in 500 ml screw top plastic bottles and bringing them back to the laboratory for immediate measurement with electronic meters. No difference between S1 and S2 was recorded for pH (Table 2:3) though conductivity at S1 was slightly lower than at S2 on both occasions. Figures from Reynolds (1979), the NCC report (1980) and some unpublished data from the Biology Department, Keele University are included in Table 2:3 and it seems that pH and conductivity both change with the season. This

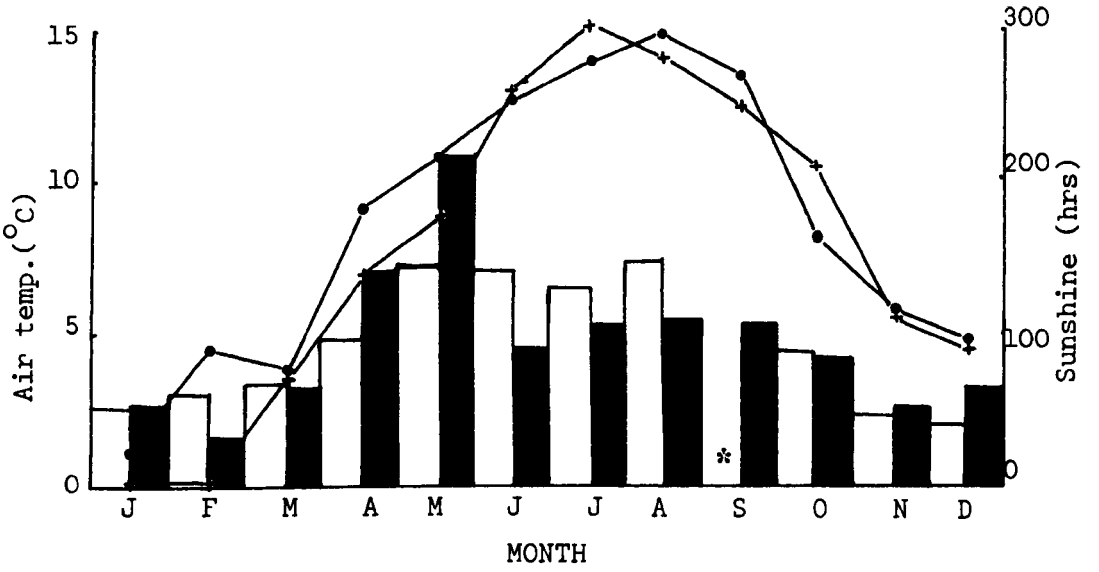


FIG.2:4 Mean monthly air temperatures during 1979 (⟷) and 1980 (●—●), and total monthly sunshine during 1979 (▭) and 1980 (▬) at Keele Meteorological Station.
* - no data available in 1979.

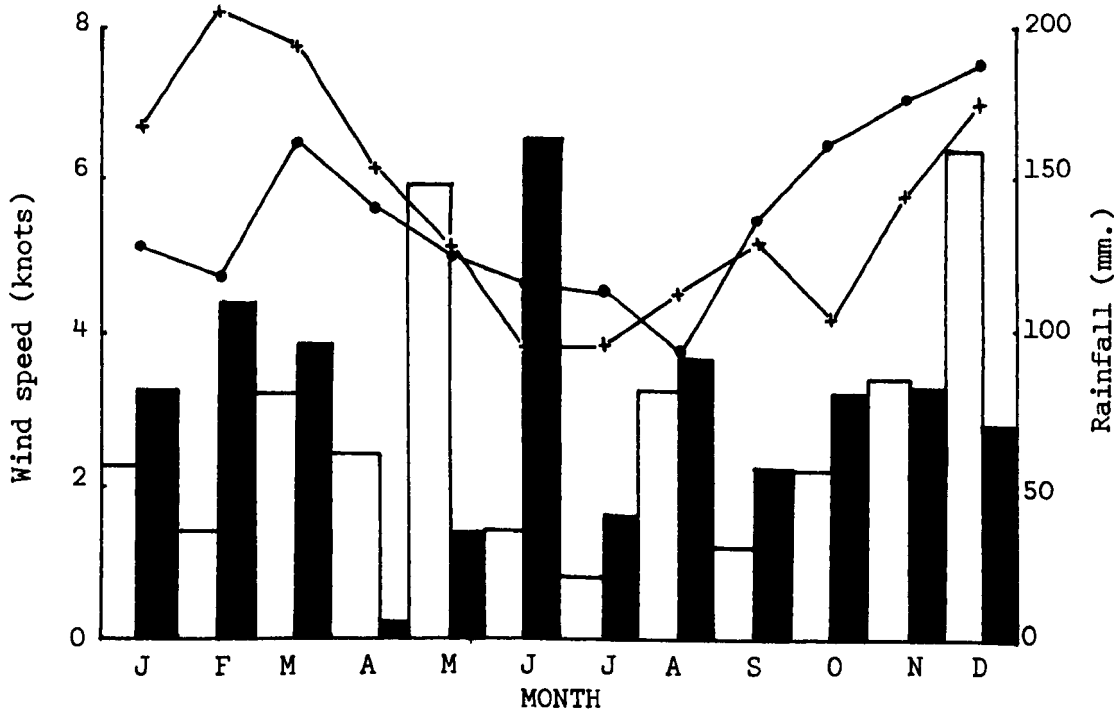


FIG.2:5 Mean monthly wind speed during 1979 (⟷) and 1980 (●—●), and total monthly rainfall during 1979 (▭) and 1980 (▬) at Keele Meteorological Station.

TABLE 2:3 pH and conductivity in Cop Mere

Study		pH	Conductivity $\mu Sm^{-1} \times 10^4$ at 25°C
Present			
May 1980	S1	8.5	3.70
	S2	8.5	3.80
Jan.1981	S1	7.8	4.65
	S2	7.8	5.74
Reynolds (1979)		7.6	4.55
NCC (1980) Sept.		9.0	4.00
Keele Univ. (1979) May		9.3	3.35

could be a reflection of the changes in water volume and algal populations (and hence photosynthesis) in the mere over the year.

Although no difference between S1 and S2 was found from the above measurements, it was noticeable that in summer the area of reedbed around S2 smelt strongly of rotting vegetation - this could have been largely from the surrounding marsh. Testing for the presence of H_2S in the water (using $CdCl_2$, Golterman *et al.*, 1978) gave a negative result for both S1 and S2.

From the above recordings, apart from minor differences it is clear that stations S1 and S2 are essentially similar in terms of the physical parameters measured. They differ, however, in their positions in the mere and it is possible that the proximity of the outflow to S1 has some effect (a very slight movement of water through the reeds?) and can account for some of the differences observed in the abundance of chironomids between the two stations.

In the following chapters larval distribution and adult emergence are discussed in relation to the weather conditions, and the climatological data is presented here. They were taken from records obtained at the Meteorological Station at Keele University, the nearest station to Cop Mere. Figs. 2:4 and 2:5 show changes in air temperature, hours of

sunshine, wind speed and rainfall during the months of 1979 and 1980. It can be seen that the weather conditions during the summer of 1980 (June to August) were generally worse than in 1979, with noticeably higher rainfall and less sunshine. Air temperatures were also lower, and the maximum temperature did not occur until August 1980, compared with July in 1979. In addition, there was a marked change during May and June 1980 when rainfall was very heavy. Average wind speeds did not fall as rapidly as in 1979, nor did the temperature rise as fast over this period. These poorer conditions were clearly reflected at Cop Mere, by a rise in the water level and a greater flow-through rate.

Large populations of the algae *Cladophora* and *Enteromorpha* which built up during early May were carried as masses of floating mats towards the reedbed during late May and early June at S1 and S2, aided by the increased water flow and prevailing winds. The presence of algae in such quantity during the early part of the summer of 1980, followed by its movement in the deteriorating weather conditions were thought to be partly responsible for the larval distribution patterns that year (see following chapters). In 1979 there was no marked algal bloom of this type.

Linford Pools. The pools and lakes at Linford in Buckinghamshire have arisen as a result of gravel extraction by the Amalgamated Roadstone Corporation over about the last 40 years along part of the River Ouse near Newport Pagnell (Grid. Ref. SP 83/43). A fuller description of the site and the formation of the pits can be found in Titmus (1979) and only the relevant points will be considered here.

The pools sampled in this study are in a lagoon complex on the

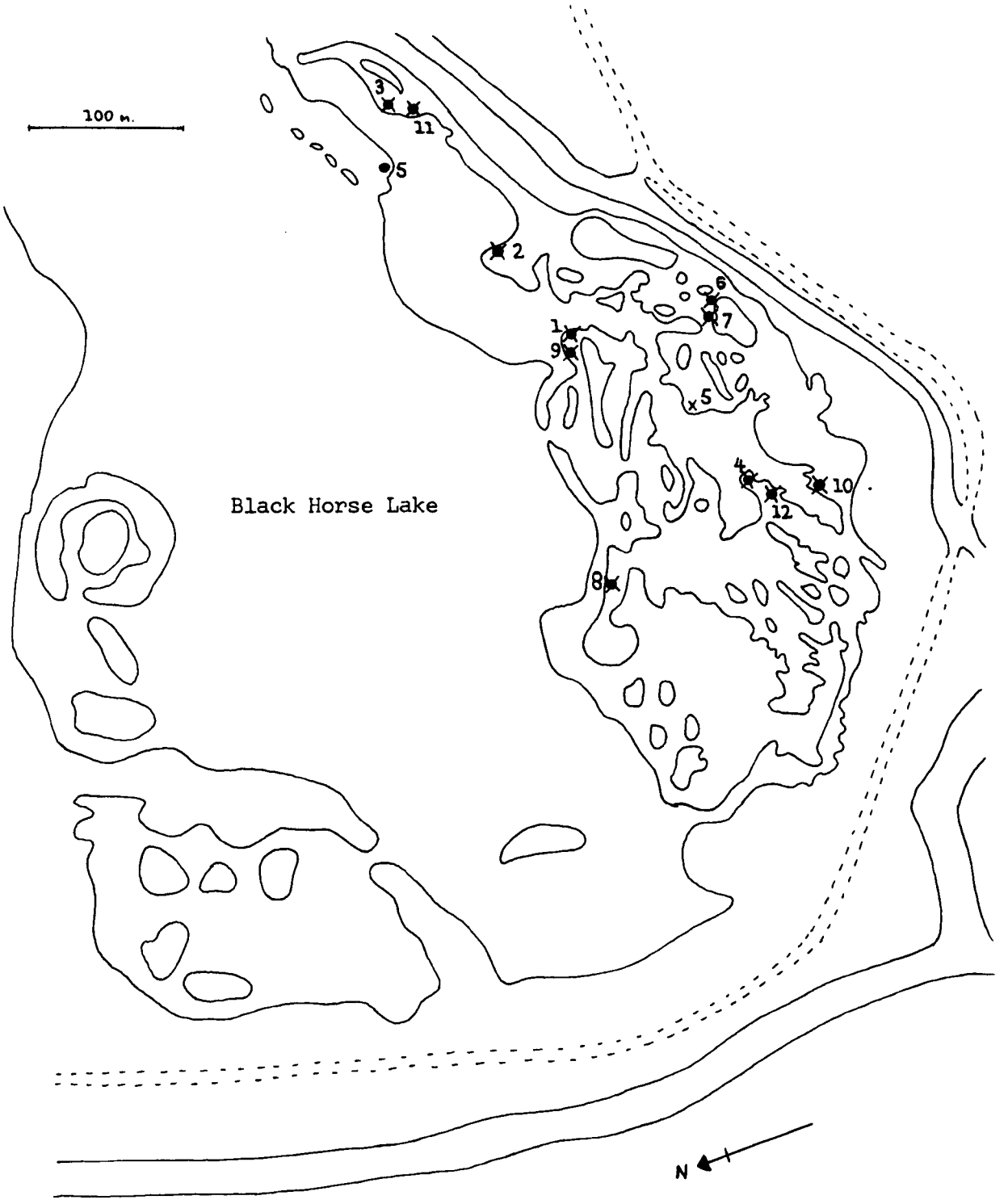


FIG.2:6 Trapping stations in the lagoon area of Black Horse Lake, Linford, marked: (●) L1-12, 1979 (×) L1-12, 1980.

southern edge of Black Horse Lake (Fig. 2:6), and are under the management of the Game Conservancy. The lagoon area is currently a conservation site for the study of the breeding ecology of the wildfowl that use the reclaimed gravel pits. Macrophytes have been planted in the pools and so provide both an ideal habitat for breeding waterfowl and a favourable sampling site for part of the investigations conducted in this study (see chapter 6).

Analysis of the particle sizes in the sediments at each trapping station (1-12) was carried out in summer 1979 as for Cop Mere above, and the results are listed in Table 2:1. Organic content was also estimated as for Cop Mere and these results are shown in Table 2:1. Proportions of particle sizes are similar in all stations, except that L4 has less sand and more clay than the others. Organic content is about 2-3%, but L8 had more at about 8%.

The physical and biological characteristics of each trapping station (such as reed types present) will be considered more fully in the discussion of imaginal emergence from reedbeds presented in chapter 6.

Chapter 3

LARVAL POPULATIONS OF THE LITTORAL BENTHOS

As noted in the first chapter, little work has been done on larval populations of the substratum within reedbeds. Opalinski (1971) examined the macroinvertebrate fauna of a *Phragmites* reedbed in a large Polish lake, determining larval chironomid densities in the benthos as well as on stems, but his study was only over a few months in the summer. Mason & Bryant (1974) include chironomid larvae in their results of the survey of reedbeds in the Norfolk Broads but did not separate individual genera, 'lumping' them all as Chironomidae. Other workers have sampled 'littoral' habitats (e.g. Slack, 1967; Tait-Bowman, 1976) but these are all at depths of greater than 1m. and not amongst emergent vegetation.

The aim of this chapter is to present data concerning the chironomid larvae found in the reedbed benthos, with the emphasis being on temporal changes in their abundance. The dispersion pattern of larvae is also discussed, with special reference to that of the predominant species, *Camptochironomus tentans* (Fabricius).

METHODS

In studies of production it is important that the number of organisms sampled is a known and true representation of the whole population, in order that the energy outputs from trophic levels can be accurately calculated. This entails use of an unbiased and quantitative sampling device. It is a truism that such a device does not, and probably never will, exist. Each habitat examined is different from the next. A profundal benthos, often comprising a mud 'ooze', obviously differs from that within a littoral reedbed zone. In the

latter case, root systems, decaying plant material and stems will be additional to the sediments. Reedbeds at different sites will also vary in terms of their type of substrata. At Cop Mere the substratum is sandy, while at Linford or in the Norfolk Broads, it is more organic and softer in nature.

The present study does not necessarily require a sampler that will yield an accurate estimate of population size since productivity is not under consideration. What the sampler should be able to do is supply information to detect relative changes in population densities over the year, taking reproducible samples even if these are not totally unbiased in their selection of only certain species or instars. Although no universal sampler exists, some types have become accepted as being suitable for given situations; the IBP handbook on secondary production (Edmonson & Winberg, 1971) and the FBA publication (Elliott & Tullet, 1978) describe some of the many samplers available.

The operation of grabs in reedbeds is impossible and a core sampler was thought to be the best solution. The substratum of Cop Mere is not soft mud but sand (see chapter 2) which excludes the use of standard mud corers. Accordingly, a manually-operated piston corer of brass was constructed.

The design and dimensions are shown in Fig. 3:1, and details of the construction are as follows. The piston rod is in two sections. A flat strip of brass is fastened to the top of the uppermost section to act as a handle for operating the piston; a collar, fixed by a small set-screw to the rod 9cms from the end, prevents the piston assembly from being pushed out of the casing at the lower end of the corer.

The piston assembly consists of a circular plate of diameter 4.5cms fastened to the bottom section of the rod, and a seal. The latter is made up of two plates between which are sandwiched two leather caps, each

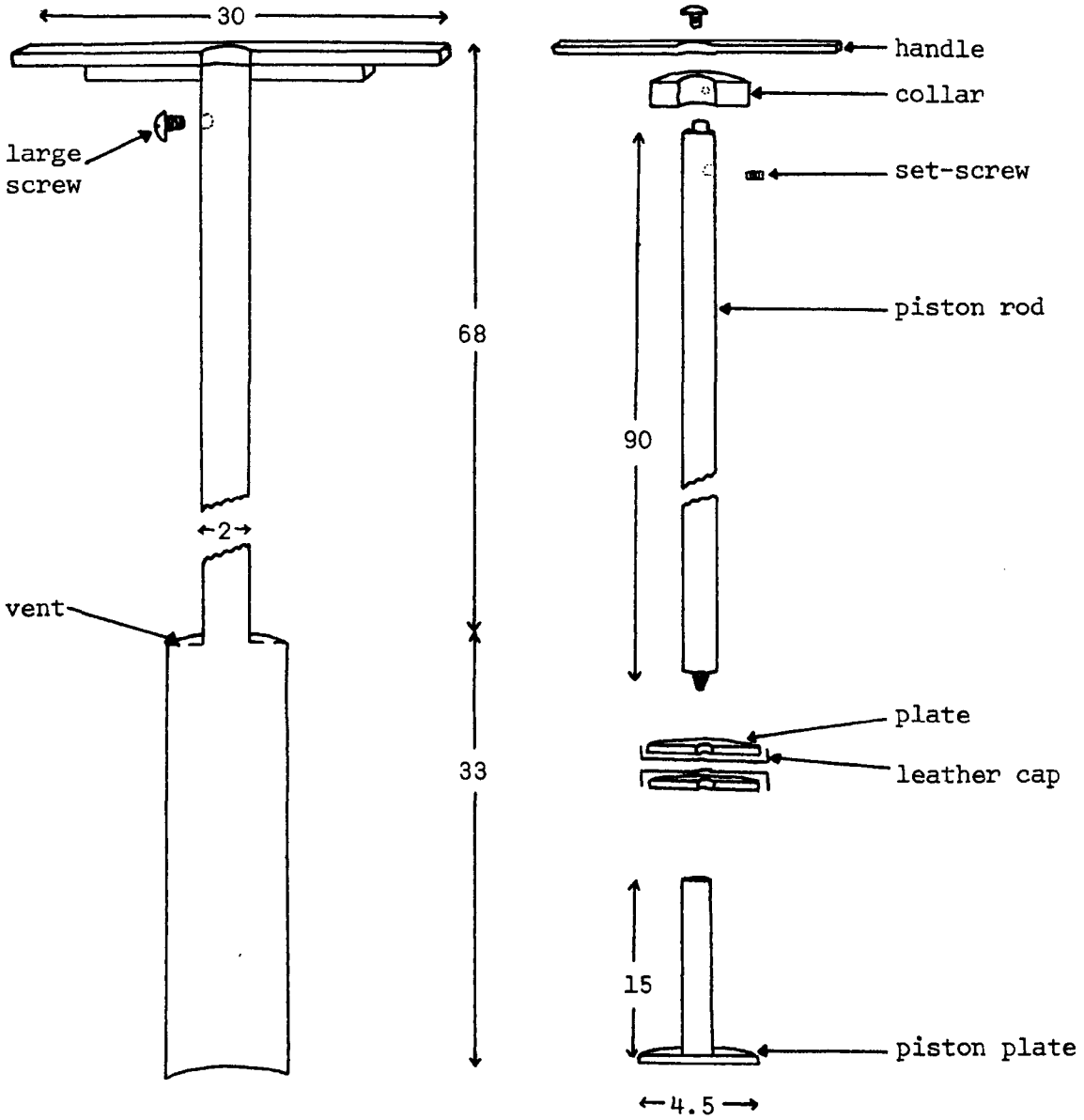


FIG.3:1 Piston-corer design. (Figures are cms; not to scale.)

one over-lapping one of the plates to form the seal between the plates and outer casing. The uppermost of these plates slips over the threaded end of the upper section of the piston rod, the bottom one of the pair screws on to the rod to mate with its counterpart, and finally the lower section of the piston rod, with plate, screws on to lock the piston-seal plates.

The whole of the piston rod assembly is enclosed by an outer casing, the total height being about 1m. The lower casing has a sharpened edge to help slice through any roots within the substratum, and four small holes through the top plate of the casing act as vents for air or water upon withdrawal of the piston rod during operation.

The corer is forced into the substratum and while still in position the rod is withdrawn slightly, to create a negative pressure between the plate and the core surface, (which was found to help retention of some sandy substrata), then fixed at this point by a large screw through the top of the casing. The corer is then removed and the core extruded into a plastic bag.

This corer was sturdy, portable, corrosion-resistant and could be operated by one person. The small area it sampled (0.0016 m^2) had advantages in that a small quadrat size (i.e. core surface area) is often necessary in detecting certain types of pattern in some populations (Elliott, 1977; Southwood, 1978) and samples could be sorted relatively quickly.

Samples of the substratum were taken in the reedbed at stations one and two (see Fig. 2:2, chapter 2), usually at monthly intervals, from June 1979 to January 1981. In addition, extra samples were taken during the summer of 1979 to try to follow short-term changes in populations of multivoltine species. However, this was not continued in 1980 because it was considered that this small amount of additional

information did not warrant disturbance of the reedbed so frequently.

Ten cores were taken at random at each station within the reedbed, each core being extruded into a plastic bag for transit to the laboratory. Depth of the cores was about 7-10 cms which was adequate to capture all larvae present (from preliminary trials; also Carter, 1976; Kajak & Dusoge, 1970). Individual cores were sorted in a white tray under strong light and a magnifier. In order to reduce errors due to loss of small larvae, samples were not sieved.

In June 1980 two samples per station were taken with a large-diameter corer (modified by R. Young, (pers. comm.), from a Tvarininne sampler (Finnish IB-PM Group, 1970), combined and then sorted to compare the larval catch with that of the corer.

In February 1981, forty randomly-taken cores from within an area of 1 m^2 at S2 were removed and examined for larvae. The information thus obtained was used to determine the spatial pattern of larvae within the reedbed; in addition it gave an indication of the accuracy of the sampling method.

Identification of the larvae was made to genus using a manuscript key supplied by P. S. Cranston. In addition a note was made of the proportions of each instar thought to be represented, based on head-capsule width.

RESULTS AND DISCUSSION

1) Total Larval Abundance

Total numbers of larvae found per core have been converted to mean number per metre squared per station for each sampling occasion.[1] These figures are given in Table 3:1; standard errors have been appended

1 The raw data from which graphs and tables have been constructed can be found in the Appendix.

DATE	DENSITY (Nos. larvae m^{-2})		NUMBER OF GENERA	
	Station 1	Station 2	Station 1	Station 2
28. 6.79	7063 ± 1767	313 ± 140	8	3
12. 7.79	13375 ± 1751	0	11	0
26. 7.79	3500 ± 957	0	7	0
9. 8.79	1375 ± 293	0	3	0
6. 9.79	438 ± 162	0	1	0
23. 9.79	625 ± 0	625 ± 0	1	1
11.10.79	1500 ± 283	625 ± 0	4	1
30.11.79	1125 ± 334	375 ± 138	2	4
29. 1.80	1063 ± 281	625 ± 294	4	3
20. 2.80	813 ± 188	375 ± 103	2	3
7. 3.80	475 ± 144	625 ± 140	3	2
18. 4.80	250 ± 138	0	1	0
21. 5.80	313 ± 140	375 ± 249	2	2
26. 6.80	5688 ± 1917	9188 ± 1775	2	3
30. 7.80	1250 ± 322	5375 ± 2374	2	1
3. 9.80	313 ± 105	4063 ± 899	2	4
15.10.80	1250 ± 279	3063 ± 650	2	2
11.11.80	2125 ± 376	4375 ± 1369	3	2
15.12.80	2125 ± 376	3125 ± 660	2	3
29. 1.80	938 ± 213	3875 ± 775	3	2

TABLE 3:1 Mean larval density (± 1 s.e.), and number of genera at Cop Mere, 1979-1981

to the means.

It should be emphasised that the means given in Table 3:1 must not be viewed as absolute population estimates, but that they indicate general changes in density over the season, assuming replicability of the sampling method.

The total number of larvae at S1 in June/July 1979 was estimated to be between 7000 and 13,000 m^{-2} (Fig. 3:2, Table 3:1). Subsequently a gradual fall occurred to a winter level of around 1000 m^{-2} and numbers continued falling to an April figure of 300 m^{-2}. Numbers then increased to a midsummer level similar to the previous year and fell to 1000 - 2000 m^{-2} over the winter months.

The pattern for S2 (Fig. 3:2) was dissimilar. Estimates of abundance up to September 1979 were significantly less than those at

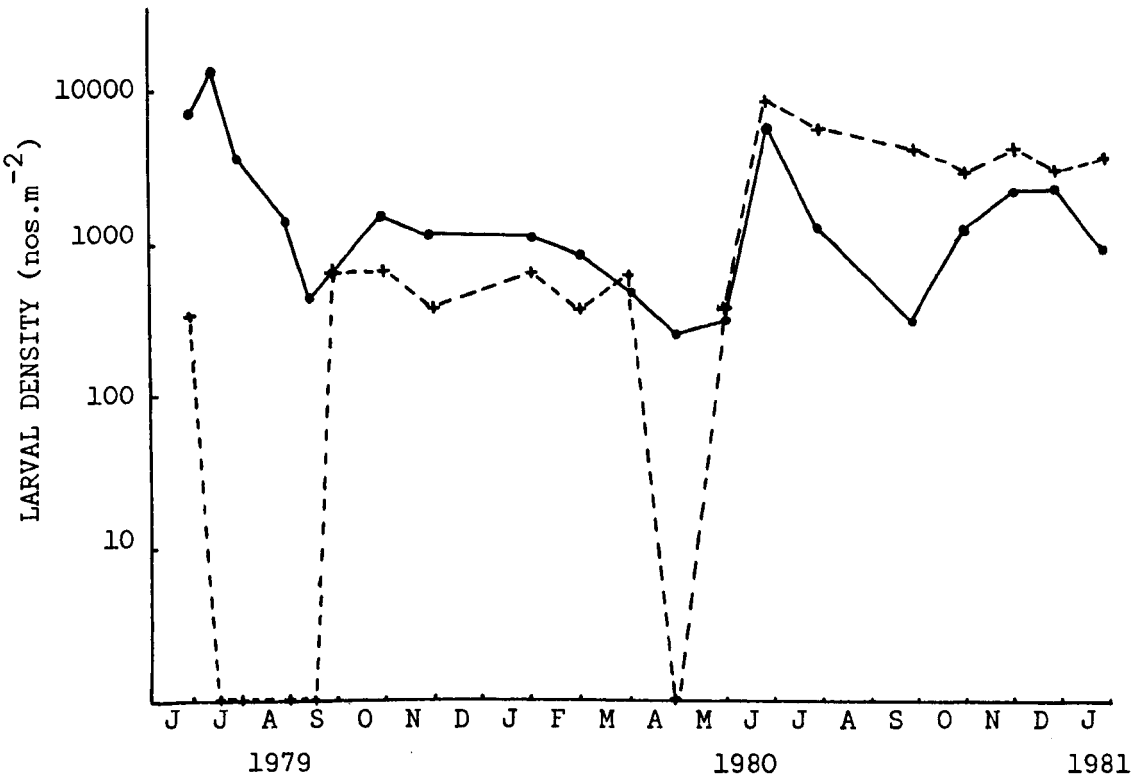


FIG.3:2 Mean larval density at S1 (•—•) and S2 (+--+) in Cop Mere.

S1 (Mann-Whitney U test, $p < 0.05$).[1] An initial June estimate of 300 m^{-2} dropped to about zero by the following month. Larval numbers recovered over the winter and were not significantly different from S1 estimates ($p > 0.05$) during this period; an unexplained drop then occurred in April, but numbers increased rapidly for the remainder of the study to an estimated 2000 - 5000 m^{-2}. Apart from the September 1980 and January 1981 values, where numbers at S2 were higher than at S1, there was no significant difference between the two stations ($p > 0.05$).

During the summer of 1979 the number of genera recorded at S1 was between 7 and 11, but by winter this had decreased to only 3 or

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1 In order to avoid the assumptions necessary for parametric tests to be carried out on data (e.g. see Siegel (1956), p. 19), testing for significant differences between two populations (two independent series of samples) has been performed using the Mann-Whitney U test, the most powerful non-parametric alternative to the t-test.

4 (Table 3:1). Numbers at S2 were always low throughout the study. During the summer and winter of 1980 very few genera were recorded at S1 and S2 in the benthos; *Camptochironomus* was the predominant one.

2) Individual Genera

Table 3:2a and b presents mean densities of larvae at each sampling occasion for individual chironomid genera; the head-capsule widths of the commoner genera are given in Table 3:3.

Glyptotendipes

This genus (probably *Glyptotendipes pallens* (Meigen) from emergence data) was common at S1 until the end of August 1979 at densities of between 100 and 6000 m^{-2}, but was then only occasionally recorded during the remainder of the study (Fig. 3:3, p.30). Numbers of larvae were low throughout the sampling period at S2. *Glyptotendipes* overwinters predominantly as fourth instars with some third instars also present, conclusions which are supported by litter-bag studies in chapter 5. The majority of total chironomid larvae present in the substratum at S1 during June to August 1979 were of this genus, comprising second, third and fourth instars with successive peaks in accordance with larval development and adult emergence studies (see chapter 6). Overwintering larvae were present at densities of between 100 and 500 m^{-2} but by April numbers of fourth instars had dropped to an estimated zero abundance. This is about the time that adults were being caught in emergence studies. A peak of larvae towards the end of 1980 is consistent with a late emergence of adults in September; the species is thus bivoltine. The low abundance of larvae during 1980 contrasts that of 1979 and possible reasons for this are discussed below.

		28.6.79	12.7.79	26.7.79	9.8.79	6.9.79	23.9.79	11.10.79	30.11.79
Procladius	3	188 (95)	250 (138)						
	4	188 (132)	250 (138)						
Cricotopus	2		375 (138)						
	3		188 (132)						
	4		188 (132)						
Psectrocladius	4		63 (63)						
Cladotanytarsus	3	63 (63)	688 (231)						
	4	688 (255)	2438 (725)	188 (132)					
Tanytarsus	4	188 (132)							
Camptochironomus	2	63 (63)		63 (63)		63 (63)	63 (63)		
	3					250 (103)		250 (138)	313 (140)
	4	63 (63)				125 (83)		375 (138)	375 (198)
Cryptochironomus	3	188 (95)							
	4		250 (138)	63 (63)					
Endochironomus	3		313 (213)	63 (63)					
	4		63 (63)						
Glyptotendipes	2	625 (322)	438 (132)						
	3	2875 (735)	6313 (881)	1125 (435)	125 (83)			63 (63)	63 (63)
	4	813 (229)	938 (283)	1938 (563)	1125 (293)			500 (243)	375 (211)
Limnochironomus	3	125 (83)	313 (168)		63 (63)				
	4	750 (403)	125 (83)					250 (103)	
Microtendipes	3							63 (63)	
	4		63 (63)						
Paratendipes	2		63 (63)		63 (63)				
Polypedilum	2	125 (83)							
	3	125 (83)	63 (63)	63 (63)					

TABLE 3:2a Mean larval densities (nos. per m^2) of genera at S1, 1979 - 1981. contd.....

		29.1.80	20.2.80	7.3.80	18.4.80	21.5.80	26.6.80	30.7.80	3.9.80
Procladius	3	63 (63)							
Cricotopus	4						63 (63)	63 (63)	63 (63)
Cladotanytarsus	4					125 (83)			
Camptochironomus	2					63 (63)	2250 (791)		
	3	313 (140)	438 (162)	188 (132)	188 (132)		3375 (1542)	375 (211)	
	4	313 (140)	250 (138)	250 (138)	63 (63)	125 (83)		813 (188)	250 (138)
Cryptochironomus	3	63 (63)							
Glyptotendipes	4	313 (140)	125 (83)	125 (83)					
Polypedilum	3			63 (63)					

		15.10.80	11.11.80	15.12.80	29.1.81
Cricotopus	2				63 (63)
Camptochironomus	2		63 (63)	63 (63)	
	3	563 (146)	563 (237)	1000 (257)	188 (95)
	4	625 (247)	1188 (316)	1000 (257)	625 (162)
Glyptotendipes	2		63 (63)		
	3	63 (63)	63 (63)		
	4		125 (83)		63 (63)
Microtendipes	3			63 (63)	
	4		63 (63)		

TABLE 3:2a Mean larval densities (nos.per m^2) of genera at S1, 1979 - 1981. Figures in parentheses represent ±1 standard error; figures to right of genera indicate larval instars.

		28.6.79	23.9.79	11.10.79	30.11.79	29.1.80	20.2.80	7.3.80	21.5.80
Cricotopus	2	63 (63)					63 (63)		
	3	63 (63)							125 (125)
	4	63 (63)							63 (63)
Camptochironomus	2		63 (63)						63 (63)
	3			63 (63)	125 (83)	188 (132)	63 (63)		
	4	63 (63)			63 (63)	313 (217)	125 (83)	250 (138)	125 (83)
Cryptochironomus	3					63 (63)			
Glyptotendipes	2	63 (63)							
	3						63 (63)		
	4				63 (63)	63 (63)	63 (63)		
Limnochironomus	3				63 (63)				
Microtendipes	2				63 (63)				
	4							63 (63)	

		26.6.80	30.7.80	3.9.80	15.10.80	11.11.80	15.12.80	29.1.81
Tanypus	3			63 (63)				
Cricotopus	4			187 (132)				
Camptochironomus	2	3813 (992)	313 (192)	125 (125)	63 (63)	500 (370)		63 (63)
	3	4438 (747)	3000 (1674)	1375 (243)	1375 (346)	2500 (907)	1688 (310)	2063 (536)
	4	563 (255)	2063 (567)	2063 (646)	1188 (300)	1063 (188)	1250 (427)	1563 (267)
Endochironomus	3						125 (125)	
Glyptotendipes	2	313 (140)		63 (63)		125 (125)		
	3				187 (95)		63 (63)	187 (95)
	4				250 (132)	187 (95)		
Limnochironomus	3	63 (63)						

TABLE 3:2b Mean larval densities (nos.per m^2) of genera at S2, 1979 - 1981. Figures in parentheses represent ±1 standard error; figures to right of genera indicate larval instars.

GENUS	INSTAR			
	1	2	3	4
Procladius			350	750
Tanypus			350	
Cricotopus		75	175	350
Psectrocladius				375
Cladotanytarsus			125	250
Tanytarsus			125	250
Camptochironomus	100	200	400	800
Cryptochironomus			250	500
Endochironomus			300	600
Glyptotendipes	100	200	400	800
Limnochironomus			250	450
Microtendipes			250	500
Paratendipes		150		
Polypedilum		150	300	

TABLE 3:3 Approximate head-capsule widths (in μm) for larval instars occurring in core samples at Cop Mere

Station	Genus	Instar	LARGE CORER Nos. of larvae per sample	PISTON CORER Nos. of larvae per sample
S1	*Procladius*	3	1.0	
		4	0.5	
	Cricotopus	4	6.5	1
	Camptochironomus	2	27.5	36
		3	106	54
		4	15	
	Glyptotendipes	3	1.5	
		4	0.5	
	Limnochironomus	3	0.5	
	TOTAL LARVAE		159	91
S2	*Camptochironomus*	2	16.5	61
		3	157.5	71
		4	34	9
	Glyptotendipes	2	0.5	5
	Limnochironomus	3		1
	TOTAL LARVAE		208.5	147

TABLE 3:4 Numbers of larvae sampled by large corer (mean of 2 samples) and piston corer (total of 10 samples) at S1 and S2 on 26.6.79

Camptochironomus

Apart from an isolated male *Chironomus plumosus* (L.) in 1980 from an open-water trap, the only *Chironomus*-type adults caught were large *Camptochironomus tentans* (Fabricius). It is likely that the majority of larvae identified as belonging to the *Chironomus "plumosus"* complex were therefore *Camptochironomus tentans*. In addition, many third and nearly all fourth instars of this genus possess a dorsal wedge-shaped mark on their head-capsules, making identification of the larvae relatively easy. Furthermore, some larvae were reared to adults in incubators to confirm identification. Second instars were assumed to belong to this species.

Numbers of larvae were uncommon at both S1 and S2 at the beginning of the sampling programme, with estimated densities of 100 - 400 m^{-2} (Fig. 3:4,p31) However, from May to June 1980, numbers increased rapidly at both stations to around 3000 - 4000 m^{-2} with the appearance of second and third instars in the cores. Larval abundance decreased during August and September but a second peak was observed around October and November; as was found for *Glyptotendipes*, larvae of *Camptochironomus* overwinter predominantly as fourth instars, and the species appears to be bivoltine. When adult emergence and larval development are compared for the 1980 season there is an apparent anomaly. The majority of adult *C. tentans* was caught during August 1980, which can explain the second peak of larvae later this year, and none was recorded during the 1979 trapping period. However, only one individual (in May 1980) had been caught prior to the sudden increase of early instar larvae in the littoral zone during June. It might have been expected that more adults would have been caught since the increase of larvae was quite large. A possible explanation is discussed below.

Other Genera

Procladius, *Tanypus* and *Cryptochironomus*.

Low numbers (about 200 m^{-2}) of third and fourth instar *Procladius* were recorded only at S1 in June and July 1979, with one individual being found in January 1980.

An individual *Tanypus* was found at S2 at the end of September 1980.

Cryptochironomus was recorded at densities of 200 m^{-2} at S1 in June and July 1979, with some individuals being taken in January 1980 at S1 and S2.

Procladius choreus (Meigen) was fairly common in emergence traps, and it is likely that larval populations were under-estimated. All three of these species are errant, *Tanypus* is a herbivore (Titmus, 1981), and *Procladius* and *Cryptochironomus* are predators. All will be inadequately sampled by small samplers because of their patchy dispersion (e.g. around a food source) and ability to avoid the sampler.

Cladotanytarsus and *Tanytarsus*

These small larvae (fourth instars have a head-capsule width of about 250 μm) were only recorded from S1, and with the exception of some individuals in May 1980, were found in the summer of 1979. High numbers (a maximum of approximately 2000 m^{-2}) of *Cladotanytarsus* larvae in June to August 1979 were correlated with adult emergence of *Cladotanytarsus nigrovittatus* Goetghebuer in the littoral zone.

Endochironomus, *Microtendipes*, *Limnochironomus*, *Polypedilum* and *Paratendipes*

These genera were recorded sporadically throughout the sampling period, though most were found during summer 1979. *Limnochironomus* was a common genus in litter bags (chapter 5); imagines of *Limnochironomus pulsus* (Walker) were commonly trapped in 1979.

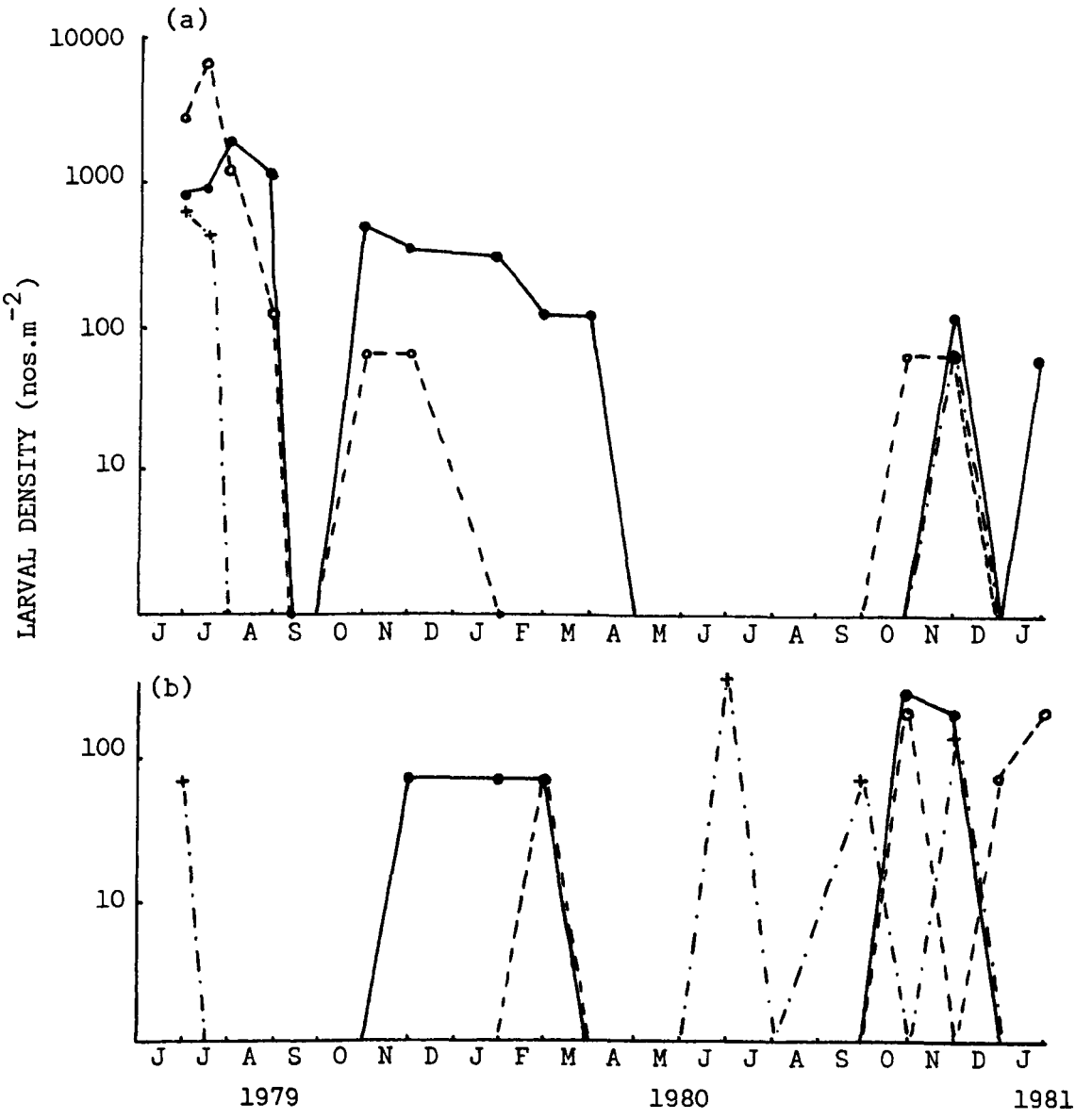

FIG.3:3 Mean larval density of *Glyptotendipes* at S1 (a) and S2 (b) in Cop Mere. Instars as follows: second(+--+), third(o--o), fourth(●—●).

Imagines of *Pentapedilum sordens* (van der Wulp) were commoner than those of the genus *Polypedilum* and it is possible that some of the larvae recorded as *Polypedilum* may have been *Pentapedilum* - the differential character is roundness of hypostomial teeth which are often worn down during larval development and it is thus not a particularly reliable character.

Cricotopus and *Psectrocladius*

Considering the number of imagines of both these species caught in

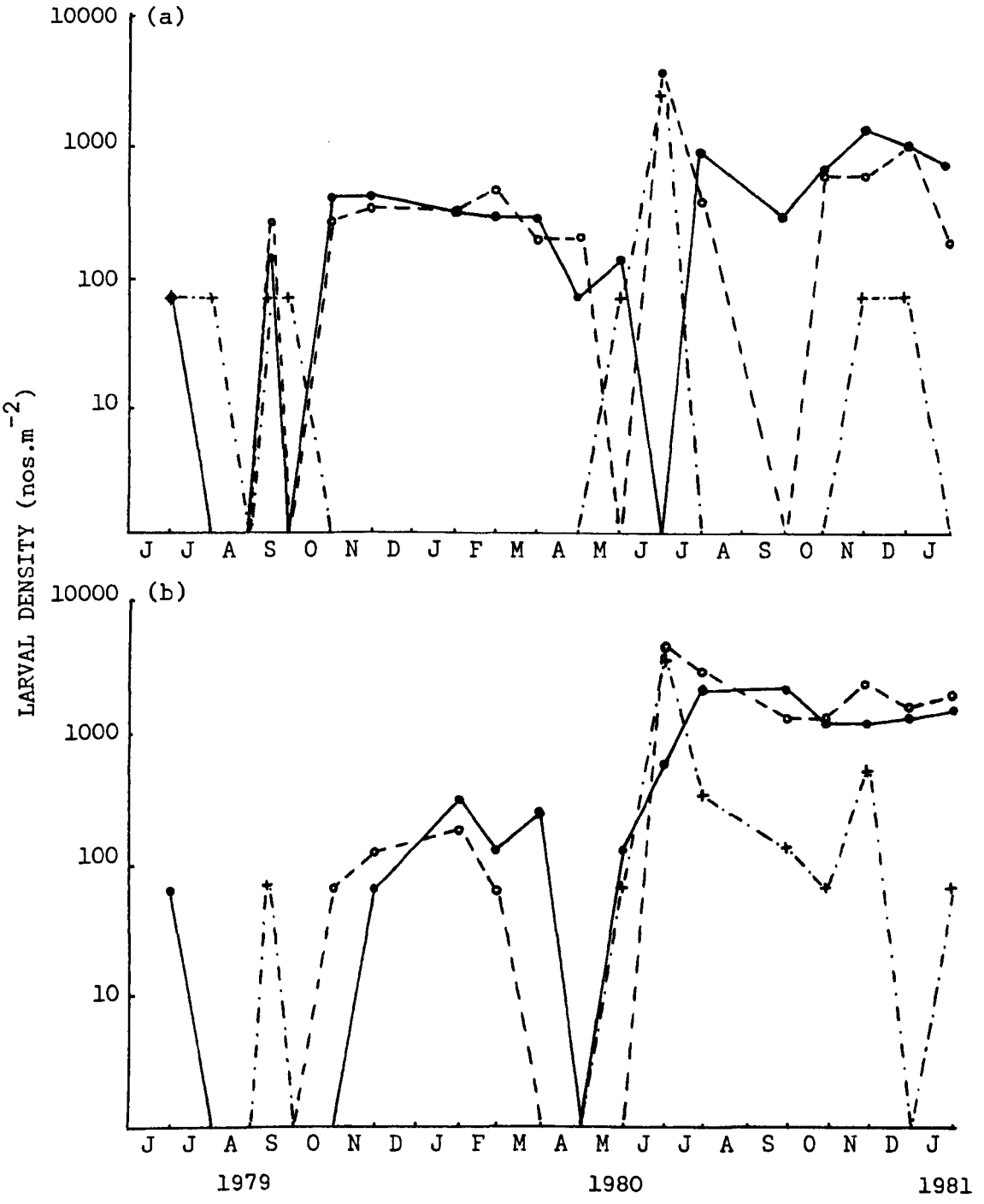

FIG.3:4 Mean larval density of *Camptochironomus* at S1 (a) and S2 (b) in Cop Mere. Instars as follows: second(+···+), third(o---o), fourth(●——●).

both years, the larvae were very sparse in cores. However, as will be seen in the next chapter, these larvae are commonly found on erect *Phragmites* stems and thus are not taken by bottom samplers in quantity.

Corynoneura

Though not recorded from cores, this genus was found in litter bags, but being an errant detritivore, it also will not be sampled efficiently by corers.

3) Comparison of the Piston Corer with a Large Corer

The large diameter corer used to sample the reedbed in June 1980 covered an area of 0.0175 m^2 which is approximately 10 times that sampled by the piston corer used throughout the study period. Thus on a purely mathematical basis, the numbers of larvae found in one sample from the large corer should be the same as the total from 10 of the smaller cores. This is not so (Table 3:4,p.27), large corer samples usually containing more larvae, about 1.4 - 1.7 times as many larvae found in one large core as in the sum of 10 smaller cores. These differences are not unexpected since 'edge-effects' will be greater for smaller sampling areas, but they do serve to indicate the problem of choosing a suitable sampler. Disadvantages of the large sampler are that it is heavy, disturbs a relatively large area of the reedbed and is time-consuming to use. It is interesting to note also, that on comparing the occurrence of instars from the two different samplers, cores taken with the smaller one captured greater numbers of early instar *Camptochironomus* and *Glyptotendipes* (about 200 μm head-capsule width). This could be due to errors during actual sampling when substratum has to be removed by hand and bilge-pump from inside the large corer, thus possibly leaving smaller larvae behind, a problem not encountered when using the small corer.

4) Larval Dispersion

Examination of the results (Appendix, Table A3:1) of larval numbers per core obtained during the sampling period indicated that the dispersion of larvae in the substratum of the reedbed was often not random but clumped (or contagious). If the probability of obtaining 0,1,2,3,...x individuals in a sampling unit can be described adequately by the terms of the Poisson series:

$$P_{(x)} = e^{-m} \frac{m^x}{x!}$$

where $P_{(x)}$ is the probability of x individuals in a sampling unit, m is the sample mean, then the dispersion pattern of the larvae in the substratum will be random (Elliott, 1977). In a Poisson distribution the mean ($\bar{x}$) equals the variance (s^2) and departure of the ratio $s^2/\bar{x}$ from unity is an indication of departure from randomness. A ratio of greater than 1 indicates contagion, of less than 1 regular dispersion of the sample. Significance of departure from unity is tested using chi-squared (χ^2), where $\chi^2 = s^2(n - 1)/\bar{x}$, (and n is the sample size, s^2 and $\bar{x}$ as defined above). Table 3:5, showing the mean numbers of larvae found per core, indicates with an asterisk those values where there was a significant departure from randomness (at $p < 0.05$), i.e. the samples were contagiously dispersed.

Various mathematical models have been suggested to describe the dispersion of populations of organisms (e.g. Southwood, 1978) and it was decided to test whether one of these, the negative binomial, could adequately describe the dispersion of the larval population in the substratum of the reedbed. A somewhat larger sample than 10 cores is needed for analysis and therefore, as reported above, 40 randomly-taken cores were used. The time of year (winter) was chosen when, hopefully, larval densities would be higher and pattern more stable

DATE	Mean nos. of larvae per core (± s.d.)	
	S1	S2
28. 6.79	11.3 ± 8.94*	0.50 ± 0.71
12. 7.79	21.4 ± 8.86*	0
26. 7.79	5.60 ± 4.84*	0
9. 8.79	2.20 ± 1.48	0
6. 9.79	0.70 ± 0.82	0
23. 9.79	1.00 ± 0	1.00 ± 0
11.10.79	2.40 ± 1.43	1.00 ± 0
30.11.79	1.80 ± 1.69	0.60 ± 0.70
29. 1.80	1.70 ± 1.42	1.00 ± 1.49*
20. 2.80	1.30 ± 0.95	0.60 ± 0.52
7. 3.80	0.76 ± 0.73	1.00 ± 0.71
18. 4.80	0.40 ± 0.70	0
21. 5.80	0.50 ± 0.71	0.60 ± 1.26*
26. 6.80	9.10 ± 9.70*	14.70 ± 8.98*
30. 7.80	2.00 ± 1.63	8.60 ± 11.36*
3. 9.80	0.50 ± 0.53	6.5 ± 4.30*
15.10.80	2.00 ± 1.41	4.90 ± 3.11*
11.11.80	3.40 ± 1.90	7.00 ± 6.55*
15.12.80	3.40 ± 1.90	5.00 ± 3.16*
29. 1.80	1.50 ± 1.08	6.20 ± 3.71*

TABLE 3:5 Mean number of larvae per core (± standard deviation) at S1 and S2, 1979-1981. (* denotes significant departure from randomness - see text)

Number per core (x)	Frequency (f)		
	Total Population (All instars)	Third Instars	Fourth Instars
0	3	8	11
1	5	7	8
2	6	11	16
3	5	3	2
4	6	3	1
5	4	4	2
6	3	2	
7	2	1	
8	3	1	
9	1		
10	1		
11	1		
Mean ($\bar{x}$)	4.05	2.43	1.50
Variance (S^2)	8.06	4.51	1.69
Number of samples (n)	40	40	40
Goodness of Fit with Poisson	$p < 0.05$	$p < 0.05$	$p > 0.05$
Goodness of Fit with Negative Binomial	$p > 0.90$	$p > 0.20$	$p < 0.01$
k	3.78	2.56	11.84

TABLE 3:6 Summary of data used to calculate dispersion of *Camptochironomus* larvae (see text)

than at other times during the season. Most larvae taken in fact were *Camptochironomus* - the only other genus was represented by four individuals of *Glyptotendipes* and for the purpose of analysis these have been omitted. Thus we are dealing essentially with a population of *Camptochironomus*. With the exception of one individual second instar larva, others sampled were third and fourth. For the analysis of dispersion, all instars have been treated as one population; in addition, third and fourth instars have been treated separately. Larval numbers for each of these three analyses have been arranged in frequency classes, and details are given in Table 3:6.

All three frequency distributions were tested, as described above, for randomness against a Poisson series, but using a χ^2 test for large samples (Elliott, 1977). No significant difference between the observed sampling distribution and a Poisson was found for fourth instars ($p > 0.05$, Table 3:6), but a significant departure from randomness was found for third instars and for the population grouped as a whole ($p < 0.05$).

All three distributions were then tested for agreement with a negative binomial model, though it would be expected that fourth instar dispersion would not fit such a model. The individual terms of the expansion are given by:

$$P_{(x)} = \left(1 + \frac{\bar{x}}{k}\right)^{-k} \frac{(k + x - 1)!}{x!(k - 1)!} \left(\frac{\bar{x}}{\bar{x} + k}\right)^{x}$$

where $P_{(x)}$ is the probability of x individuals in the sampling unit, $\bar{x}$ is the sample mean, and k is the negative binomial parameter. The value for k in the expansion was calculated by an iterative method (Elliott, 1977) and its values for the three distributions are given in Table 3:6. The expected binomial expansion was determined using

the values for $\bar{x}$ and k, and the observed data were tested for goodness of fit with it, using χ^2 to test significance (Elliott, 1977). No significant departure from a negative binomial distribution was found for the frequency distributions observed for third instar data or total population data, $p > 0.2$ and $p > 0.9$ respectively. As expected, fourth instar samples differed significantly from a negative binomial distribution ($p < 0.01$).

Knowing that the samples conform to a negative binomial distribution (i.e. the larval population of *Camptochironomus* as a whole is clumped), it is possible to estimate how many samples are required to give a reasonable estimate of the true population mean. Paterson & Fernando (1971) thought a reasonable estimate would be $\pm$ 30% of the true mean, Elliott (1977) one of $\pm$ 40%, and Shiozawa & Barnes (1977) allowed an estimate of $\pm$ 20% of the mean. Permitting an accuracy of $\pm$ 40% of the mean, and with 95% confidence limits attached to this estimate, the number of required samples (n) have been calculated for a range of means of x, assuming k is constant at all densities (for k = 3.78, see Table 3:6). The appropriate formula used to calculate n for a negative binomial distribution was that given in Elliott (1977, p. 130). The optimum sample sizes (n) for means ($\bar{x}$) are therefore:

$\bar{x}$	0.5	2	5	10	15	20
n	57	19	12	9	8	8

which covers the range of means calculated for samples taken at S1 and S2 over the sampling period (see Table 3:5). Of course, since the parameter k was estimated using data from a population of *Camptochironomus*, these optimum sample sizes are not strictly applicable to other species. Also, as has been shown, different instars will have different patterns of dispersion. Thus, for an estimate of $\pm$ 40% of the mean, 20 samples would be required for

contagiously dispersed third instars but 17 for randomly dispersed fourth instars (formulae again being given in Elliott, 1977, p. 130).

Nevertheless, it might be reasonable to assume that the contagious dispersions indicated in Table 3:5 may conform to a negative binomial distribution. Assuming a value of k = 3.78 as above for these (which is entirely reasonable at S2 during the last eight sampling occasions since larvae were mostly *Camptochironomus*) and referring to the optimum sample sizes presented above, the number of samples taken (10 cores) was usually sufficient to obtain an estimate of about $\pm$ 40% of the true mean. At certain times of the year, or when the dispersion was approaching randomness and $\bar{x}$ small, the number of samples should have been greater. However, this would have increased sampling and sorting time and would have been more detrimental to the reedbed; and for the purpose required here (to obtain an idea of relative changes in abundance) it does not justify the increase in precision of the estimate of a mean.

GENERAL DISCUSSION

As noted previously there appears to have been a marked change from a relatively species-rich to species-poor structure on the bottom of the reedbed between 1979 and 1980 at S1. Few larvae were found during 1979 at S2 and a high population of *Camptochironomus* was present during the later months of 1980 at both S1 and S2. Possible reasons for this are discussed below.

No detectable differences were found between the water at S1 and S2 in 1979 as regards the physical parameters that were measured, but it was also remarked in chapter 2 that the station at S2 had a noticeable odour of H_2S. Some of this would have come from the rotting vegetation in the marsh; however, if the sediments were experiencing

some anaerobic conditions, only tolerant larvae, e.g. *Camptochironomus*, could survive. However, towards the end of the year, turbulence of water would increase, and temperature decrease due to the autumn weather, so oxygen levels in the sediments would tend to recover. It was at this time that larvae became commoner in core samples at S2. Weather conditions during the summer months of 1980 were generally worse (chapter 2) and S2 possibly did not experience such anaerobic conditions as in 1979, thus allowing greater populations of larvae. S1 was nearer to the outflow and so there is possibly sufficient water movement through the reedbed (even though minimal) to prevent a serious oxygen deficit in the substratum there.

Additionally, not only were more larvae found at S2 during 1980, but these were almost all *Camptochironomus*. This chironomid also predominated at S1. Its occurrence at such high population densities at both S1 and S2 during the summer of 1980 is thought to be a result of the poorer weather conditions during this period. The pattern of adult emergence for *C. tentans* has already been described above. It is also worth noting that casual observation revealed large chironomid adults flying over the open water outside the reedbed in early May 1980. Some of these were *C. tentans* in the process of oviposition. As described in chapter 2, during the latter half of May 1980 the weather deteriorated with increased rainfall. The prevailing winds were towards the reedbeds at S1 and S2 and with the increased turbulence and water movement any egg masses and first instar larvae would have been carried into them. This would account for the massive increase of larvae at these stations during June 1980. (Although different factors may have been more important, the numbers of larvae of *Camptochironomus* were very low in litter bags in June 1980 in the leeward part of the mere). Also, as noted in chapter 2, there was a

large amount of floating algae in the mere which was blown into the reedbeds at this time - this would further increase the likelihood of the presence of early instar *Camptochironomus* larvae in the reedbeds, from egg masses deposited in the algae at the water surface. Davies (1976) has reported a similar occurrence in *Chironomus anthracinus* (Zett.) in Loch Leven, where the final distribution of larvae in the sediments depended upon wind distribution of egg masses rather than the oviposition site.

Occasional hand net samples taken just outside the reedbed zone at Cop Mere frequently captured larvae of *Camptochironomus* and it is possible the species is widespread in the lake. Slack (1967) reports the occurrence of *C. tentans* (named *Chironomus tentans* by him) in some lakes in Manitoba, Canada as being numerous and most frequent at water depths of up to 15m. He makes no mention of whether vegetation was present or how shallow his sampling stations were. Driver (1977) also records *C. tentans* in the reedbed benthos of prairie ponds in Canada. Tait-Bowman (1976) cites Sadler (1935) as saying that *Camptochironomus* was commonly found in "pools, ponds, shallow warm-water lakes and sluggish streams" and occurred especially where fertiliser had been added to the water. In a general survey of the meres around Keele by Tait-Bowman (1976), *Camptochironomus* was only found in Crose Mere, at a depth of 2m at low densities of 20 m^{-2}, and Cop Mere. This mere seems to be particularly attractive to the species, possibly because of a tolerance of warmer temperatures and/or ability to withstand lower oxygen concentrations than other Chironomini. In addition, larger larval size may enable it to use the coarser substratum. Edgar & Meadows (1969) found that larvae of *Chironomus riparius* Meigen could not build tubes using sand, but only when offered algae.

It is tempting to suggest that since *Camptochironomus* abundance at

both S1 and S2 increased with a concurrent decrease in other larvae, the change was the outcome of competition. Final instar *Camptochironomus* larvae are large and their presence may exclude smaller larvae of other species. Cantrell & McLachlan (1977) found that final instar *Chironomus plumosus* (L) larvae displaced larvae of *Tanytarsus gregarius* Kieffer. Similarly, relatively high densities of *Camptochironomus* at Cop Mere in 1980 could have 'crowded out' smaller, less numerous species.

However, competition may not be the only explanation. Titmus (1979) contends that there is a movement of larvae of *Glyptotendipes pallens* (*G. glaucus* in his thesis) to the newly emerging shoots of aquatic macrophytes and there is thus a decrease of larvae in the substratum samples taken in the summer. This may be part of the story but as has been seen *Glyptotendipes* was common in cores during the summer of 1979 at Cop Mere. As shown in the following chapters, *Glyptotendipes* larvae are commonly found in or on *Phragmites* stems. Under competition for space in the substratum they might lose out to larger larvae, but would still occur on *Phragmites*. *Glyptotendipes* larvae (*G. paripes* (Edw.) and *G. pallens* (Mg)) were commonly found by Carter (1976) in Lough Neagh in Ireland at depths of between 0.3 and 6m at similar densities to populations found in this study. Tait-Bowman (1976) similarly found *G. pallens* at depths of 2m and more in the Shropshire meres. In Loch Leven, Scotland, Maitland & Hudspith (1974) considered that *G. pallens* larvae preferred sandy substrata to mud in shallow water, since densities in the former were higher (4515 m^{-2}) than the latter (2310 m^{-2}). In Poland, Opalinski (1971) took *Glyptotendipes* in benthic samples from reedbeds. It appears that *G. pallens* is common in shallow waters, being often found and ubiquitously distributed, both in the substratum and in association with reedstems.

Exactly why the number of larvae sampled in 1980 was lower in terms of species and abundance is not clear. It could be a combination of factors - competition for space or reduced survival of emerging adults during the early part of the 1980 summer because of the poorer weather, and hence lower numbers of larvae in the next generation of larvae later in the summer. As already discussed, *Camptochironomus* probably showed such a dramatic increase in larval density in 1980 due to the vagaries of the weather.

Usually dispersion has been examined for whole populations containing a number of taxa, but if considered at a species or instar level different patterns can often be detected. For example, it has been shown by Shiozawa & Barnes (1977) that the dispersion of *Chironomus frommeri* Atchley and Martin changes with instar. Clumping occurred in first and third instars but second and fourths were randomly dispersed. Various reasons can be suggested for contagion. Aggregation of newly-hatched larvae is probable around the egg mass and only later will larvae move out under competition pressures. The type of dispersion could also be related to the length of time a larva spends in a particular instar. Edgar & Meadows (1969) concluded that in *Chironomus riparius* Meigen older larvae are less likely to move whereas younger, third instars are more active, thus decreasing clumping by moving out from areas of high aggregation. Also mortality acting on a population will break it up and the dispersion will become less aggregated.

The dispersion observed here is probably the result of the winter behaviour of a population of *Camptachironomus* larvae. The contagion of third instars could be the result of aggregation around the rhizomes and roots of *Phragmites*; it is possible that because third instars of *Camptochironomus* are smaller than the fourth, they are able to utilise

the space among the roots and rhizomes more effectively than can fourth instars. Thus the contagious pattern may be a reflection of the dispersion of the *Phragmites* plant. Titmus & Badcock (1981) found *Chironomus* spp. larvae to be randomly dispersed and attributed this to the randomness of detritus upon which they feed. However, a reedbed is entirely different from the homogeneous substratum they were sampling. Furthermore, the size of the sampling unit is known to affect interpretation of the observed pattern (e.g. Elliott, 1977; Southwood, 1978). Titmus used an Ekman grab which can mask the occurrence of contagion since several clumps will be averaged together in one sample. Small samplers of the type used in this study are more likely to pick up contagion.

On comparing the occurrence of larvae found in the reedbed zone at Cop Mere with those of sub-littoral and profundal zones in other lakes (e.g. Carter, 1976; Tait-Bowman, 1976; Titmus, 1979) there are obvious differences. For instance, *Procladius* is very common in most of the samples from such lakes but in reedbeds is apparently scarce. This may be a reflection of the sampling method, but could also be due to lack of food. Small larvae of other species preyed upon by the Tanypodinae are uncommon in the substratum; they are more commonly found on the stems as will be seen in the next chapters. *Polypedilum* is also reported frequently in large numbers (Krzyzanck, 1970; McLachlan, 1971; Titmus, 1979), and Hamilton (1971) described it as characteristic of shallow, non-stratified lakes in association with *Procladius*. It was not common, however, in the reedbeds at Cop Mere.

The reedbed substratum differs from that of sub-littoral and profundal areas in that it has limited space because of stems, both living and fallen, and roots; also it may experience periods of anoxia because of a mass of decaying vegetation that is not necessarily

experienced by sub-littoral or profundal areas. Species may thus be restricted to opportunistic and ubiquitous ones such as *Camptochironomus* in the benthos, while *Glyptotendipes* and others utilise reedstems so escaping anaerobic conditions or competition for space. The next two chapters are concerned with the reedstem environment and an examination of some of the larvae which are found there more commonly than they are in the benthic substratum.

Chapter 4

THE MACROINVERTEBRATE COMMUNITY ON STANDING STEMS

INTRODUCTION

The surfaces of any aquatic macrophyte will support a community of algae, small-often microscopic-invertebrates (protozoans, rotifers, etc.) and larger, macroscopic invertebrates (annelids, molluscs and insects), together with detrital material. This community, the "aufwuchs", can be separated into two major components which will be referred to in the following pages. The periphyton is that part of the community most closely associated with the plant surface; it consists mainly of algae with small invertebrates not easily separable from it. The term epifauna is used for the macroinvertebrates present on the plant.

Associations between a wide range of invertebrates and submerged and floating-leaved aquatic macrophytes have been discussed by Berg (1950) on *Potamogeton*, McGaha (1952) on thirteen aquatic plant species and Krull (1970) on twelve species. The last two authors made a broad survey of invertebrate-plant interactions and their work was largely descriptive, but with some attempt at quantification of numbers of individuals and species associated with each plant. McGaha (1952) reviews some of the studies done earlier this century. Harrod (1964), working on four species of river macrophytes, concluded that differences in numbers of invertebrates found on the plants were due to factors such as "the morphological form of a plant, the periphyton on a plant surface, the chemical nature of a plant, and the habits of the various animals present." (Harrod, 1964, p. 341). Haslam (1978), in her extensive survey of river plants, mentions the importance of macrophytes in providing suitable surfaces on which invertebrates can live.

Investigations of chironomid populations and their relationships with reedstems seem to be limited to two, reported in papers by Opalinski (1971) and Mason & Bryant (1975a). The former author restricted his sampling to a period between July and September and concerned himself with determining and enumerating the macrofauna of the benthos, and also young and old reedstems of a *Phragmites* bed in a large Polish lake. Mason & Bryant (1975a) studied changes in periphyton and larval chironomid density on stems of *Typha* in a broad-land reedbed in Norfolk, over a period of a year, but only on old reedstems.

This chapter presents data on the periphyton and epifauna of *Phragmites* stems at Cop Mere during the year 1980 and is comparable in some respects to the study of Mason & Bryant.

METHODS

Stems of *Phragmites australis* were cut at monthly intervals from January to December 1980. From January until April old stems only (i.e. the previous season's growth) were available, but from May onwards both old and young (newly-emerged *Phragmites*) stems were present so both were taken. Usually twenty stems were removed; they were cut at their base and at water level and placed in plastic bags for return to the laboratory. Removal of the stems was carried out as quickly as possible to reduce loss of larvae through disturbance. On one occasion a few stems were cut after having passed a tube down over the stem, and a bung was then fitted to the bottom of the tube before removal from the water. However, the tube tended to scrape against the stem (so dislodging algae and larvae) and this method was also very laborious and time-consuming, so was not used subsequently.

Individual stems were washed and carefully scraped, the scrapings being collected in a shallow dish. Stems were also cut longitudinally

to collect any larvae living inside. Chironomids and other members of the epifauna were removed, killed and stored in 70% alcohol for identification and enumeration. Identification of the Chironomidae was made using a manuscript key by P. S. Cranston; other invertebrates with appropriate FBA keys.

The periphyton was filtered through previously weighed filter papers and dried to constant weight at 105°C in an oven. Surface area of the stems was determined simply by measuring their diameter and length and calculating, assuming a cylindrical stem shape. Samples of the periphyton collected each month were examined in simple preparations. Prescott (1970) was used to identify the algae.

The alimentary canals of fourth instar larvae were dissected out and simple preparations of the contents made in polyvinyl lactophenol for subjective analysis of the abundance of diatoms and other algae. Eleven guts of *Glyptotendipes* were examined, three from samples collected in July and eight in September, all from old stems. Eight *Psectrocladius* larvae were examined from July samples. Fourteen larvae of *Cricotopus* from old stems collected in July, and twenty from stems cut in September were examined. (The variability in numbers reflects the availability of larvae with full guts.) Abundance of algal types was categorised arbitrarily as 1) those taxa which predominated in the stem flora or gut contents, and 2) other taxa common or frequent but not predominating. This crude measure was intended only as a rough indication of the main species present and their abundance.

RESULTS AND DISCUSSION

1) Periphyton populations

The pattern of changes in periphyton density on old and young stems is shown in Fig. 4:1. Maximum standing crop on old stems occurred

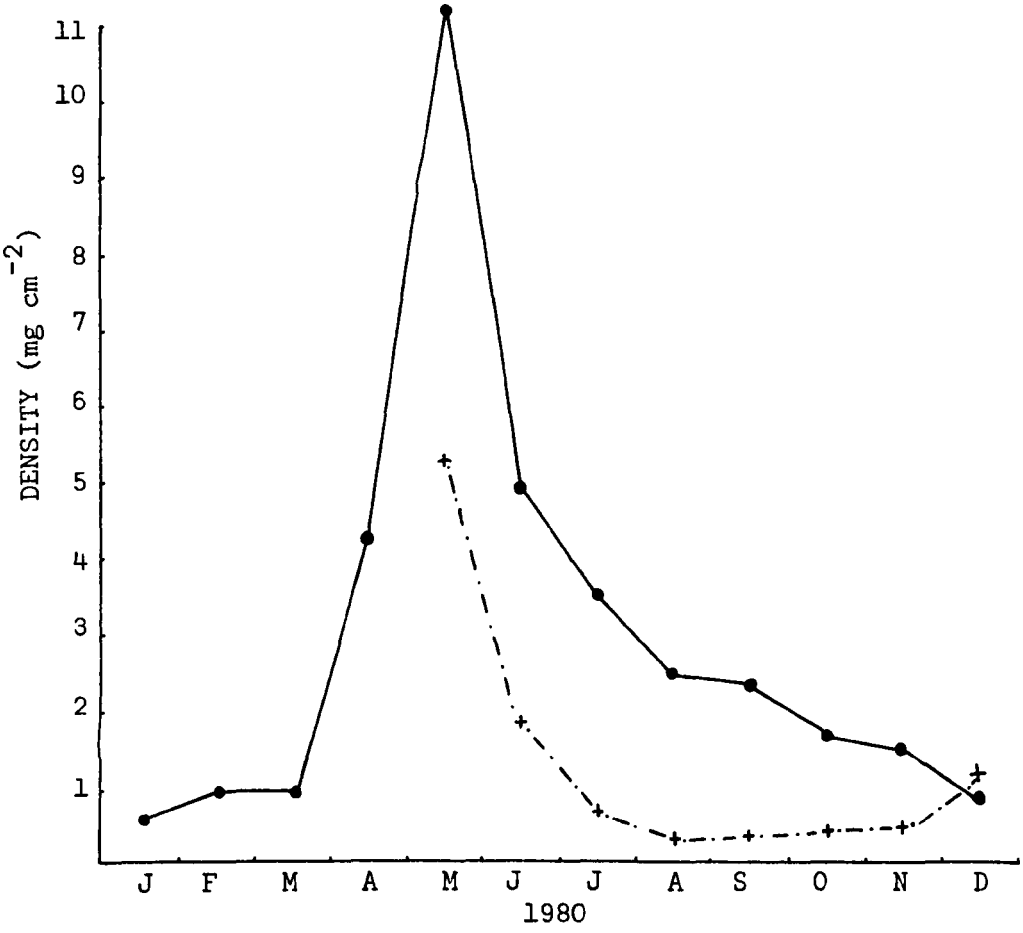

FIG.4:1 Changes in density of periphyton on old (●—●) and young (+···+) *Phragmites* stems.

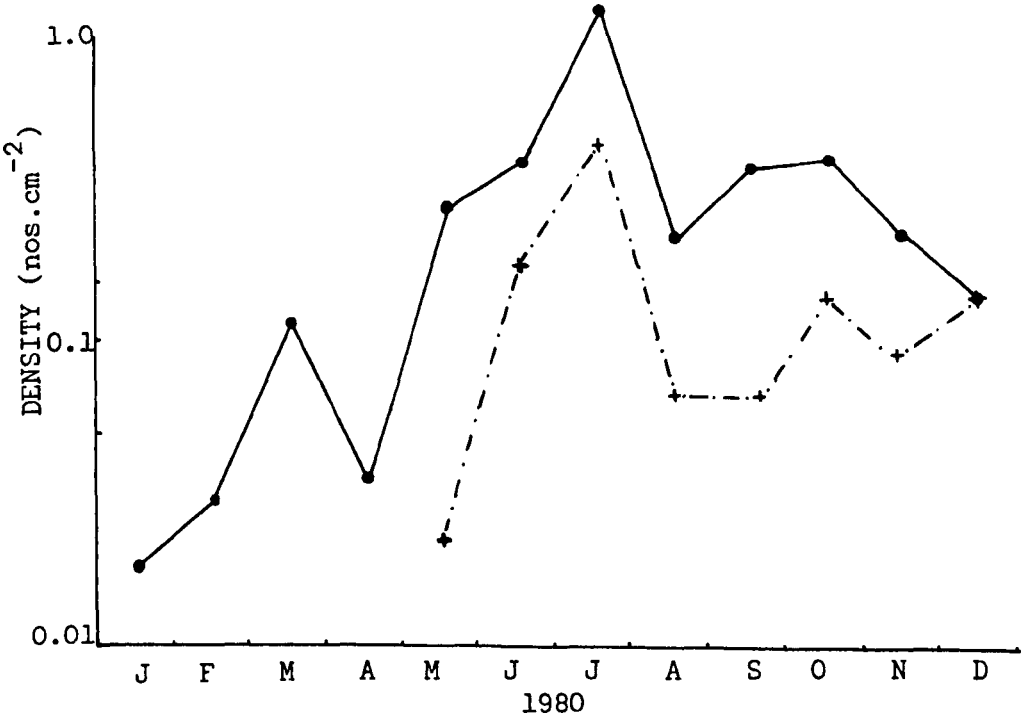

FIG.4:2 Changes in density of chironomid larvae on old (●—●) and young (+···+) stems.

in May at around 11 mg dry weight cm^{-2}, but had fallen to half this value (5 mg cm^{-2}) by June. By December, the density of periphyton had decreased to about 1 mg cm^{-2}, a figure somewhat similar to that found at the beginning of the year.

Young stems were not cut until May, and at this time the standing crop was at its maximum (5 mg cm^{-2}); as on old stems, algal density dropped over the summer and autumn. However, from September the standing crop on young stems began to increase and reached a similar level to that on old stems by December - and in fact there was significantly more periphyton on young stems in December (Mann-Whitney U test, $p < 0.05$). All other standing crop estimates on young stems were significantly less than those on old stems (at $p < 0.05$).

Table 4:1 gives details of the kinds of algae present on the two stem types during 1980. Most taxa of algae recorded were diatoms but only the more easily identifiable and commoner have been included in the table. The diatoms *Navicula*, *Achnanthes* and other related genera can only be distinguished by detailed examination, so here have all been grouped as "*Achnanthes*". Throughout the period, the commonest diatoms on both stem types were the genus *Rhoicosphenia* and the *Achnanthes* group.

The rapid increase in periphyton density from March to May (Fig. 4:1) was coincident with the rise in water temperature (Fig. 2:3, Chapter 2) and much of the weight of material on the stems in May was contributed by *Cladophora*, and to a lesser extent by *Ulothrix* and other filamentous algae. Old stems were densely covered with *Cladophora* which gradually died back during the next few months; young stems also had a covering of this alga, though not as much because of the less time available for colonisation. During May and June there was a large increase of filamentous algae (mostly *Cladophora* and *Enteromorpha*) in

Month	OLD STEMS		YOUNG STEMS	
	Predominant	Others	Predominant	Others
Jan	*Achnanthes* *Rhoicosphenia*	*Chlorella*		
Feb	*Achnanthes* *Rhoicosphenia*	*Chlorella* *Cymbella* *Gomphonema*		
Mar	*Achnanthes* *Rhoicosphenia*	*Cymbella* *Fragilaria* *Gomphonema*		
Apr	*Achnanthes* *Rhoicosphenia*	*Cladophora* *Enteromorpha*		
May	*Achnanthes* *Rhoicosphenia* *Cladophora*	*Enteromorpha* *Fragilaria* *Ulothrix* *Oscillatoria*	*Fragilaria* *Cladophora*	*Enteromorpha* *Ulothrix*
Jun	*Achnanthes* *Rhoicosphenia* *Cladophora* *Ulothrix*	*Enteromorpha* *Hydrodictyon* *Microspora*	*Achnanthes* *Cladophora* *Ulothrix*	*Enteromorpha* *Chaetophora* *Microspora*
Jul	*Achnanthes* *Rhoicosphenia*	*Cladophora* *Hydrodictyon* *Microspora* *Ulothrix*	*Achnanthes* *Rhoicosphenia*	*Microspora* *Ulothrix*
Aug	*Achnanthes* *Rhoicosphenia*	*Fragilaria* *Oscillatoria*	*Achnanthes* *Rhoicosphenia*	*Chlorella* *Ulothrix* *Oscillatoria*
Sep	*Achnanthes* *Rhoicosphenia* *Actinastrum*	*Oscillatoria* *Ulothrix*	*Achnanthes* *Rhoicosphenia* *Actinastrum*	*Oscillatoria* *Ulothrix*
Oct	*Achnanthes* *Rhoicosphenia*	*Oscillatoria*	*Achnanthes* *Rhoicosphenia*	*Oscillatoria*
Nov	*Rhoicosphenia*	*Achnanthes* *Cladophora*	*Rhoicosphenia*	*Fragilaria* *Achnanthes*
Dec	*Rhoicosphenia*	*Achnanthes*	*Rhoicosphenia*	*Achnanthes*

TABLE 4:1 Summary of the commoner types of algae found in the periphyton of old and young reedstems.

Cop Mere; much of it was blown as dense mats into the reedbeds by wind action (see chapter 2). By the end of June and through July the algae had died down considerably. The blue-green alga, *Oscillatoria* 'bloomed' in both May and late August to September and some was found consequently on reedstems during these months. In September there was a population increase of a member of the Chlorococcales, tentatively identified as *Actinastrum*. This chiefly planktonic alga was found in some chironomid guts.

Until the last few months of the year the young stems lacked the 'ground layer' of diatoms and detrital material present on all old stems. During the last months of 1980 however, young stems began to resemble the old ones in terms of appearance, and types of algae present.

2) Chironomidae Populations

Results for total larval chironomid populations found on old and young stems have been expressed in terms of density (i.e. numbers of larvae per cm^2 surface area of stem), and changes over the season are shown in Fig. 4:2 (p.47). These are mean densities per stem and it should be noted that there was often considerable variability in numbers of larvae found on individual stems (Appendix, Table A4:4, A4:5). This will be a result of "clumping" of larvae similar to that described in the previous chapter, where, for instance, aggregation would occur around egg masses upon their hatching.

Larval density on old stems increased rapidly from April onwards to peak in July at about 1.22 cm^{-2} (equivalent to an average of 50 larvae per stem), after which they fell towards the end of the year. By December the density was 0.15 cm^{-2}, or roughly 6 per stem. A slight peak in October was due to late adult emergence in the autumn. On young stems densities rose from May to peak in July at 0.43 cm^{-2} (20 per stem), and again fell towards winter with another smaller peak in

October. In contrast to the population on old stems, densities increased on young reeds from September to December. Unlike the previous months, in November and December there was no significant difference between densities on the two types ($p > 0.05$).

The genera of Chironomidae found on the reedstems were *Procladius*, *Corynoneura*, *Cricotopus*, *Metriocnemus*, *Psectrocladius*, *(Campto?)chironomus*, *Endochironomus*, *Glyptotendipes*, *Limnochironomus*, *Microtendipes*, and *Pentapedilum*. Larvae of *Cricotopus*, *Psectrocladius* and *Glyptotendipes* all occurred frequently; the others were only occasionally found with a few individuals per stem - mostly during the summer months. Details are given in Appendix Tables A4:4 and A4:5. The temporal pattern of the three commoner genera will now be discussed.

Cricotopus

From the data resulting from emergence trapping of adults, the two commoner species were *Cricotopus sylvestris* (Fabricius) and *C. flavocinctus* (Kieffer); the former was the most abundant and the majority of larvae found were probably this species.

Cricotopus larvae were the most abundant chironomids recorded from reedstems, contributing about 80% of the total numbers found - their abundance here is in contrast to their paucity in core samples, discussed in the previous chapter. Three instars were recognised, and their pattern of development on stems is shown in Fig. 4:3, expressed as density (number per cm^2). On old stems, the results showed a rather complex series of peaks of the different instars; the pattern on young stems was simpler and here there seemed to be two peak periods - in July and around September and October. Interpretation of the successive peaks on the old stems is somewhat difficult, since other factors apart from normal instar development could have contributed to this pattern. For instance, two species of

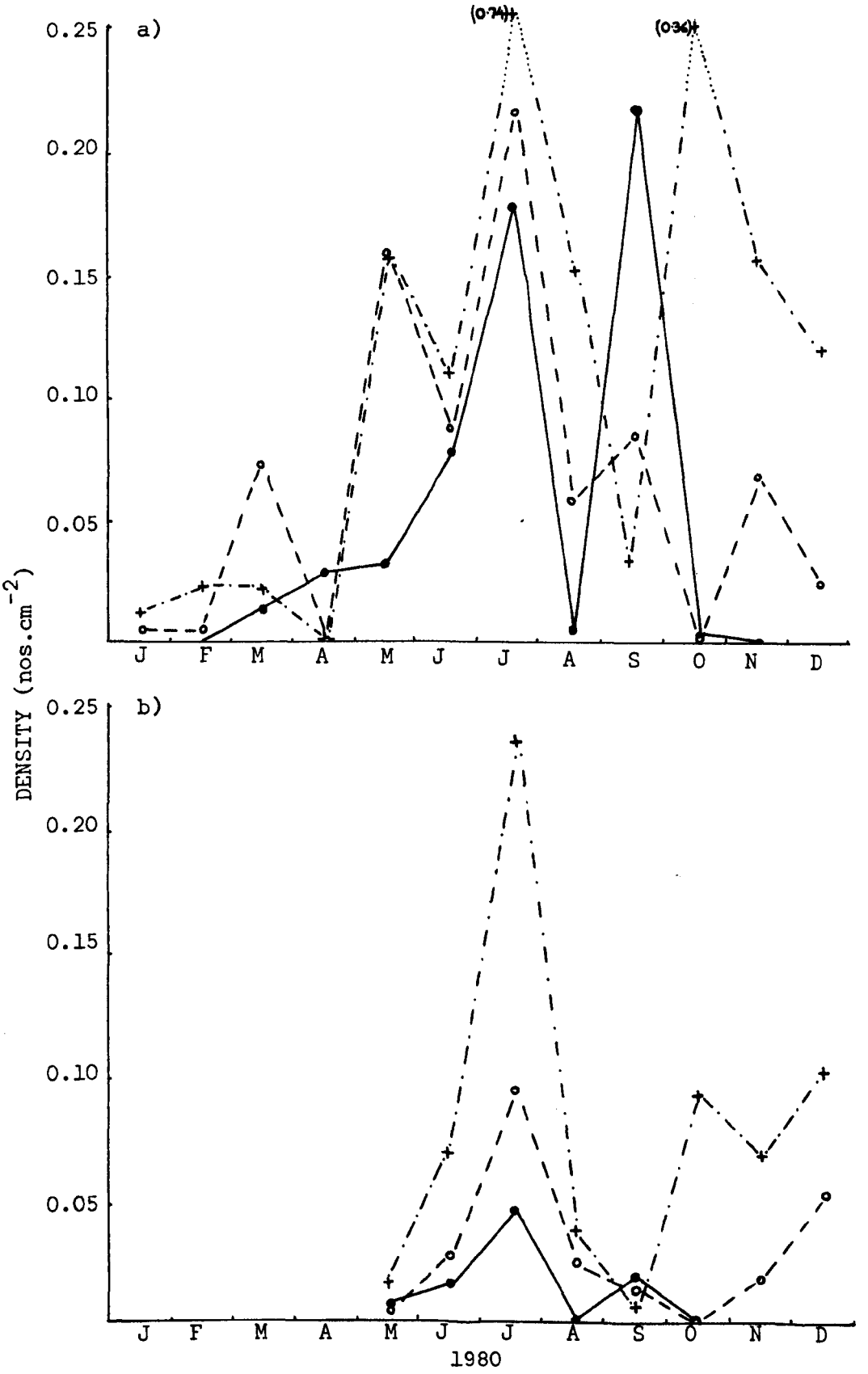

FIG.4:3 Changes in density of *Cricotopus* larvae on(a) old and (b) young stems. Instars as follows: second (+·—·+), third (o— —o), fourth (•———•).

Cricotopus are involved (although as already stated, *C. sylvestris* was the commonest), and an influx of larvae from eggs laid on floating algal mats could have occurred when the latter were blown into the reedbeds. However, using the emergence data from chapter 6, the following seems a reasonable explanation for the observed temporal pattern.

Overwintering second and third instars develop into fourths during March and imagines emerge in April. The resultant eggs hatch and quickly develop in the warmer water temperatures to give rise to more adults in late May and early June - consequently another peak of late instar larvae occurs in July. During the summer months emergence seems to be almost continuous, but the main peak of adult emergence is in July - this accounts for the large fall-off in numbers of larvae over the period to August. By September, fourth instars (resulting from development of eggs laid in July and August) are again predominant on stems and a final emergence of imagines occurred in this month. Developing larvae then overwinter as second (or some third) instars.

Berg (1950) quotes Kettisch (1936-1937) who describes how *Cricotopus* eggs can pass the winter attached to stems. No egg masses were noticed on any stems during the winter; however, some of the larvae occurring on the stems during March to May, when the water begins to warm up rapidly, could have arisen from the hatching of over-wintering eggs. These may be more capable of withstanding harsh winter conditions than larvae, which may suffer considerable mortality. However, in order to avoid such conditions, larvae probably migrate down the stems, as will be discussed in the last part of this chapter.

Larval development of small species like *Cricotopus* will be fast during the warmer water temperatures of summer - the peaks of instars observed, and their subsequent falls, correlating with adult emergence

indicate rapid generation times. Assuming numbers of other *Cricotopus* species to be contributing little to the overall pattern, *C. sylvestris* would thus seem to be quadrivoltine and this is in agreement with results of Learner & Potter (1974).

On young stems the two larval peaks would similarly have arisen from adults emerging in May/June and September. In contrast to the results obtained for *Glyptotendipes* and *Psectrocladius* larvae, there were usually significantly less larvae of *Cricotopus* on young stems than on old stems ($p < 0.05$). The exceptions were for second instars in June, November and December and third and fourth instars in August, where there was no difference between densities of larvae on the stems ($p > 0.05$); in December there were more third instars on young stems than on old. It is also interesting to note that densities of second and third instars fell from November to December on old stems, but rose on young stems. Significantly more third instar larvae were found on young stems in December compared with November ($p < 0.05$) but the rise in second instars on young stems and the decrease in densities of second and third instars on old stems were not significant ($p > 0.05$).

Psectrocladius

P. sordidellus (Zetterstedt) was sampled most frequently from emergence traps and it is probable that larvae on stems were of this species. *P. obvius* (Walker) was only sampled from open-water traps and was not as common (see chapter 6). Imagines of *P. sordidellus* were first captured in June but the main peak occurred in mid-July. During this month, on both stem types, larval densities decreased, for by August only a few individuals were found and only on old stems (Fig. 4:4). A number of interesting points arise from examining the

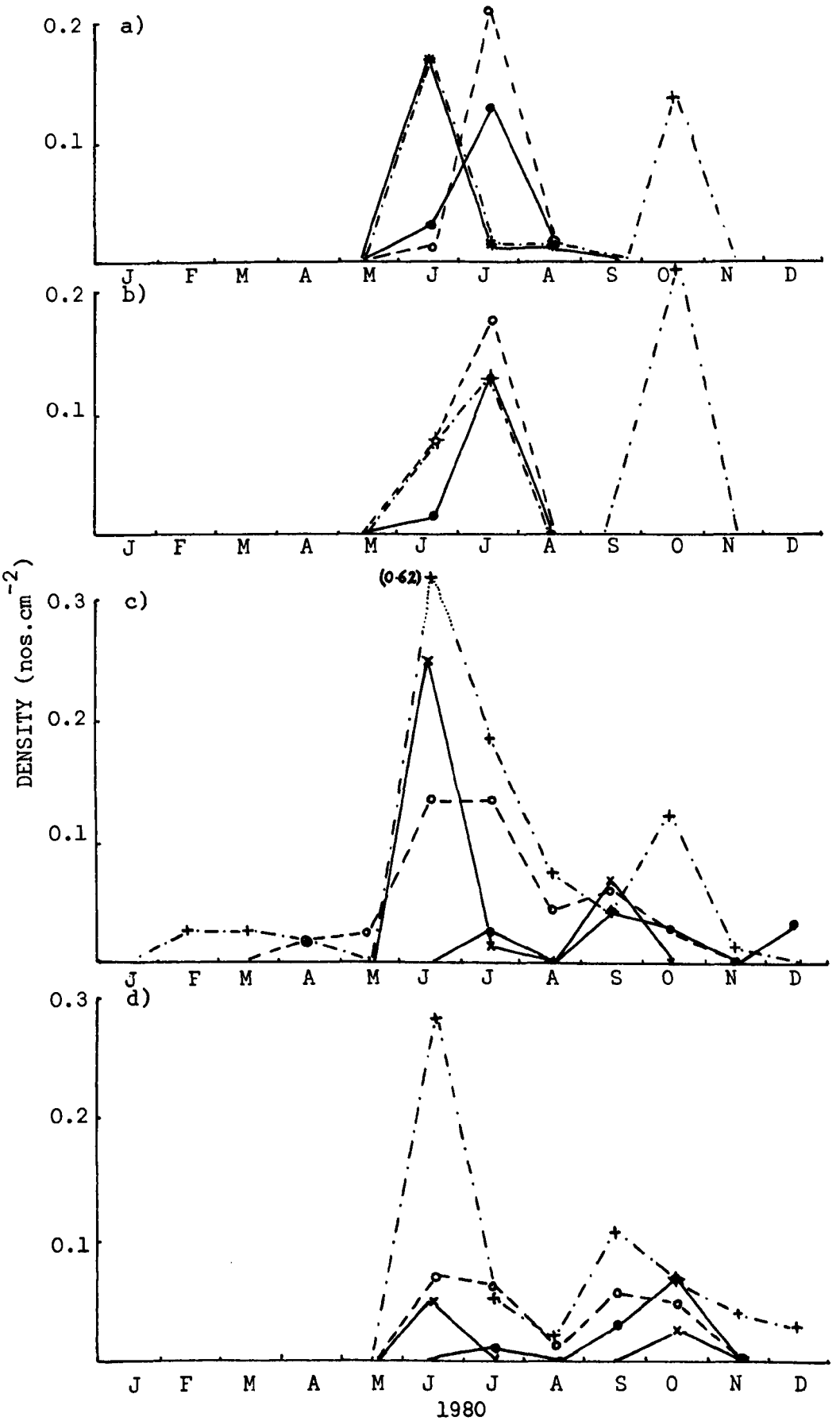

FIG.4:4 Changes in density of *Psectrocladius* larvae on(a) old and(b) young stems, and *Glyptotendipes* larvae on(c)old and(d) young stems. Instars as follows: first (×——×), second (+·—·+), third (o– –o), fourth (•——•).

data for larval occurrence on stems. Firstly, none appeared until June and those that did were mostly second instars. These could have arisen from a quick development of eggs laid by adults emerging in late May/early June, or from overwintering second instars. If the latter were true, why were no larvae found on old stems before June? A second point of interest is the gap of about two months between August and September when virtually no larvae were found at all - during this time it would have been expected that some be found after the adult emergence in June. Thirdly, a peak of second instars occurred in October (a consequence of a small emergence of imagines in September), but by the following month none was found on any stem sample. Finally, unlike *Cricotopus*, this chironomid showed no significant difference as regards densities between old or young *Phragmites* for any sampling occasion ($p > 0.05$).

This species appears to be bivoltine, as found also by Learner & Potter (1974), but this is not clearly reflected in larval samples from stems. Like *Cricotopus*, *P. sordidellus* was found in high numbers in open-water traps off the reedbed during June 1980, presumably emerging from the algae in the water beneath the traps, (chapter 6), and larvae on the stems could have originated from the populations on the algae drifting into the reedbed in late May and June. More data are needed; it is possible that larvae overwinter as second instars.

Glyptotendipes

As mentioned in the previous chapter, this species was probably *G. pallens*. Imagines were flying in April and August/September. Maximum numbers of larvae, largely composed of the two early instars, occurred in June, with a second peak of first and seconds in September

and October respectively (Fig. 4:4,p.55). The occurrence of the various instars on stems closely reflects larval development expected from adult emergence. As described in chapter 6, the species is probably bivoltine.

No significant differences were found ($p > 0.05$) between densities of *Glyptotendipes* larvae on old or young stems for any of the instars at each sampling occasion. Overwintering larvae, were at very low densities on stems. Apart from mortality as a factor affecting abundance, it is probable that some migration down to the benthos occurred. Some of the larvae found in benthic core samples over the winter (chapter 3) not only could have arisen from development of eggs from late-emerging adults in September, but also from migration of larvae from the stems.

It is interesting to note that fourth instars were often discovered inside the stems at the broken top end open to the water. Presumably, since *Glyptotendipes* larvae are large, some degree of protection is afforded through living inside the stems and this observation has also been reported by Opalinski (1971). Another feature peculiar to *Glyptotendipes* larvae is their use of empty caddis cases. Frequently *Athripsodes aterrimus* (Stephens) cases attached to the stems were inhabited by third or fourth instar larvae of *Glyptotendipes*.

3) Other Invertebrate Populations

A brief summary of the main taxa only will be made; the sampling data can be found in Appendix Tables A4:4 and A4:5.

ANNELIDA. Apart from an isolated individual, *Stylaria lacustris* L., the commonest oligochaete, did not occur on old stems until May. During the summer it averaged around 5-20 per stem on both types, but after September, only occasional individuals were found during the rest of the year.

Genus	Month	Number of larvae	Predominant	Others
Glyptotendipes	July	3	Ac,Fr,Os	Rh,Pe,In,Fu,Ul
	Sept	8	At	Ac,Rh,Go,Cy,In,Fu,Pe
Cricotopus	July	9	Ac,Rh,Di,Cl,Ul	Fr,Bo
		4	Cl,Di	Ac,Rh,Bo,Ul
		1	Cl	Ac,Rh,Di
	Sept	15	At,Ac,Rh	Di,Cl,Bo,Fu
		3	At,Cl	Ac,Rh,Di
		2	Rh	At,Ac,Di
Psectrocladius	July	5	Cl	Ac,Rh,Di
		3	Rh	Ac,Cl,Di

KEY: Ac - *Achnanthes*, At - *Actinastrum*, Bo - *Botryococcus*, Cl - *Cladophora*, Cy - *Cymbella*, Di - detrital material, Fr - *Fragilaria*, Fu - fungal spores, Go - *Gomphonema*, In - insect parts, Os - *Oscillatoria*, Pe - *Pediastrum*, Rh - *Rhoicosphenia*, Ul - *Ulothrix*.

TABLE 4:2 Summary of the subjective analysis of the gut contents of the commonest chironomid genera.

The commonest leech was *Erpobdella octoculata* (L.), maximum numbers being in July. Leeches were commoner on young stems (a maximum of about 2-3 per stem) and this could be owing to easier prey detection and capture in the absence of the thicker covering of periphyton found on old stems.

MOLLUSCA. *Acroloxus lacustris* (L.) was found on old stems from January to March in densities of 2-4 per stem (similar to those reported by Mason & Bryant (1975a)). After April, none was sampled during the summer and they only reappeared in October. The limpet was present on young stems in May, but disappeared over the summer and was not found again until September. Adults of *Ancylus fluviatilis* Müller died soon after spawning in late April in a brook (Russell-Hunter, 1961) and it is probable that the disappearance of *Acroloxus* (which is closely related) on stems at Cop Mere was similarly due to death of

adults. It is perhaps also possible that the mollusc moves away from stems during the summer in response to environmental factors such as oxygen depletion. However, this last is unlikely since measurements showed that oxygen concentration was high in the reedbed. Other molluscs were sampled sporadically, but most species were caught during the summer.

TRICHOPTERA. These were variable in occurrence. *Athripsodes aterrimus* was the commonest, but in July, hydroptilids were found on a quarter of the stems. Mention has already been made of the use of empty cases of *Athripsodes* by *Glyptotendipes* larvae.

4) Periphyton and chironomid feeding

A summary of the results of the gut analyses is given in Table 4:2. For each set of larvae examined individuals with similar gut contents (subjectively assessed) have been grouped. Though the assessment is not quantitative, some trends can be seen. Firstly it was apparent that no two larvae of a given species appeared to be ingesting the same algae in the same amounts - though as already stated, for ease of comparison an attempt has been made at grouping larvae. Secondly, larvae examined in July had different algae in their guts from those dissected in September. This is probably a reflection of the variability of algae in the environment (in the water and on the stems). Thirdly, the data indicate that *Glyptotendipes* is probably a filter-feeder (as discussed below) whereas *Psectrocladius* and *Cricotopus* are principally grazers. Larvae of the last two commonly contained filamentous algae (*Cladophora* and *Ulothrix*) and diatoms closely associated with stems (*Rhoicosphenia* and *Achnanthes*). Their guts also contained a substantial amount of ill-defined detrital and diatomaceous material, expected if grazing from a stem surface. There appeared to be more variability of gut contents between larvae of

Cricotopus and *Psectrocladius*, unlike *Glyptotendipes*, where in July or September the larvae tended to have similar gut contents. *Glyptotendipes* contained very little filamentous algae, but mostly diatoms, e.g. *Achnanthes* types as well as additional, more planktonic, forms such as *Fragilaria* and *Pediastrum*. The guts had very little noticeable detrital material. The guts of *Glyptotendipes* and *Cricotopus* in September contained the alga *Actinastrum*. It predominated in *Glyptotendipes*, as might be expected if larvae were filter-feeding since *Actinastrum* is usually planktonic; however, it was not as frequent in *Cricotopus*. The alga was also recorded from the standing crop on stems (Table 4:1) in September as noted previously, but its occurrence there was probably due to its settling out.

GENERAL DISCUSSION

Clearly, changes in densities of periphyton and epifauna occur over the year within a reedbed. These are not unexpected, and are in agreement with the limited survey reported by Opalinski (1971) on *Phragmites* stems and the more extensive study on *Typha* done by Mason & Bryant (1975a). Changes in densities of either periphyton or epifauna would occur irrespective of changes in the other through the influence of environmental changes in temperature, light and nutrients. The question to be asked is whether there is any causal relationship between, say, a rise in chironomid density and the fall in periphyton on the stems, or whether the observed changes are to a large extent independent of each other. The results presented above can go some way to answering this question.

The majority of macroinvertebrates of the epifauna were larval Chironomidae, comprising mostly *Cricotopus*, *Glyptotendipes* and to a lesser extent *Psectrocladius*. *Glyptotendipes* is primarily filter-feeding

(as also found by Walshe (1951) and Opalinski (1971)). Thus its presence will not have much effect on periphyton density, except perhaps (remotely) when large numbers occur, building tubes and so competing for space with the algae. It would be expected that larvae of *Glyptotendipes* select stems not according to the amount of periphyton present but merely on the basis of their being suitable substrata on which to construct tubes. Thus, as shown above, no differences between densities of larvae on old and young stems were found.

Although probably a grazer, *Psectrocladius* did not show any stem type preference. However, numbers were always low and as discussed above, these larvae exhibited a peculiar temporal pattern of colonisation. More data are needed before any firm conclusions regarding the habits of this species are made. *Cricotopus sylvestris* has been reported by Berg (1950) as channelling in and feeding on the superficial tissues of plants. However, the gut contents of larvae in this study, and of Mason & Bryant (1975a) indicate that the species feeds primarily on epiphytic algal material, though some of the unidentifiable detrital material in the guts could have been of macrophyte origin. Because of its large numbers and food source, *Cricotopus* is the only chironomid likely to have any pronounced effect on periphyton density. Mason & Bryant (1975a) compared larvae and periphyton on old *Typha* stems with those on glass rods. The overall pattern was similar to that reported here, though densities were lower in their study. They found a maximum density of periphyton in April of 1.8 mg cm^{-2} compared with a maximum at Cop Mere of 11.2 mg cm^{-2} in May. Peak chironomid density in their study occurred in late May at about 0.6 cm^{-2}, compared with a peak of 1.2 cm^{-2} in July in this investigation. Periphyton on their glass rods rose to peak at 1.93 mg cm^{-2} at the end of May and fell to about 1.6 mg cm^{-2} by August, at which level it remained until the end

of the year. Since the density on glass rods in December was higher compared with *Typha* stems (1.6 mg cm^{-2} and about zero respectively) and virtually no larvae were found on the glass rods, they attributed the fall of periphyton on stems to the presence of herbivorous larvae. Although they state that *Glyptotendipes* and *Cricotopus* larvae were present on the stems, they give no indication about the proportions of either, and as already mentioned, the former will not have any effect on periphyton populations.

In the present study periphyton on old stems rose to peak in May and then fell; concurrently larval numbers increased rapidly from April to July and then started to decrease. At first glance this could be a manifestation in part of a 'classic' predator-prey cycle. However, such oscillations in prey or predator numbers can occur in the absence of the other. For example, snowshoe hares and lynx were known to have this cycle, and it was assumed that the abundance of the one limited the population of the other. Then it was discovered that in the absence of the predator, the hares still exhibited their cyclical pattern in population density (cited in Krebs, 1972, p. 265). One should therefore be careful in interpreting apparently causally related cyclical patterns. Other factors could be responsible for the fall-off in periphyton density on the stems. Larval chironomids may not be as important as Mason & Bryant suggest.

During spring, algal abundance will increase as temperature and light increase. Filamentous algae (e.g. *Cladophora*) rapidly increased in early spring and contributed to much of the biomass of stems in May. Mason & Bryant (1975a) reported that *Cladophora* was abundant on *Typha* stems, whereas only diatoms were found on glass rods. Apart from the possibly unsuitable nature of this substratum for growth, *Cladophora* may not have grown on glass rods because they were situated

under polystyrene floats and thus could be limited by light. It is possible that *Cladophora* in Mason & Bryants' and in this study could have begun to die back from May onwards owing to the decrease in light as new shoots of the reed began to emerge, or as nutrients became limiting. Weight on the stems would thus fall rather sharply since much of it was due to filamentous algae rather than diatoms. Other herbivores apart from chironomids can affect periphyton density, for example, tadpoles were thought to be the agents responsible for die-back of filamentous algae in the study of Dickman (1968). Other herbivores such as molluscs and caddis were also frequently found on the stems at Cop Mere.

Another observation from this study, lending support to the idea that larval chironomids do not particularly affect standing crop, is the fact that die-back began before there were many larvae on the stems. Half the weight was lost on old and young stems over the period May to June at a time when only an average increase of 3 - 6 larvae occurred per stem.

Mason & Bryant (1975a) considered that the fall-off in chironomid numbers which they observed over the autumn was due to the movement of larvae down into the benthos as a response to depletion of food and drop in temperature, the mud being a source of food for the larvae during the winter. In this study, although a decrease in larval density occurred, a residual population of *Cricotopus*, the commonest larvae found on the stems in the previous months, remained on them during the winter; core samples (chapter 3) did not reveal an increase of this genus in the benthos during the autumn. Larvae of *Cricotopus* in fact became commoner on young stems during the period from November to December; perhaps migration to them occurs in response to a difference in periphyton quality/quantity between the two types at this

time of year. Mason & Bryant did not sample young stems so would have missed any larvae on them during the winter. However, it is also possible that *Cricotopus* (and other larvae) not only migrate to younger stems, but also move down the stems towards their base and roots to avoid harsher winter conditions nearer the surface of the water, caused by wind and wave action or ice. Fourth instars of *Glyptotendipes* probably were protected somewhat from adverse conditions during the winter by living inside broken tops of old stems.

Larval migration at the onset of winter seems to occur, as Mason & Bryant suggest; this, however, is not necessarily to the benthos itself but could be to the base of stems and, in the case of *Cricotopus* or other grazers, also to other stems which offer a greater quantity/ quality of periphyton on their surface.

Standing stems are a major component of habitat diversity in the littoral at Cop Mere and support large populations of midge larvae. *Cricotopus*, not commonly found in core samples, would seem to be utilising the periphyton on stems for food and possibly shelter, and is the commonest macroinvertebrate of the epifauna. The data do not necessarily warrant an inference that chironomid grazing is primarily responsible for the fall of periphyton on stems - much of rise and fall in biomass is contributed by filamentous algae and their growth can be affected by factors other than grazing. *Glyptotendipes*, in addition to having a benthic population, is also found on stems, both inside and on the surface. *Psectrocladius* is found during the summer but little is known about its movements in the winter. Other chironomid genera occur sporadically, and these are not always found in benthic samples - much of the adult population, especially the Orthocladiinae, will originate from the epifauna. The imagines are considered further in chapter 6.

Chapter 5

THE DECOMPOSITION OF PHRAGMITES STEMS AND THE ASSOCIATED FAUNA

INTRODUCTION

In previous chapters larval chironomid populations within the littoral zone of Cop Mere have been discussed. An important factor not yet considered is the relationship between decaying, fallen, emergent macrophytes and the littoral fauna. This chapter describes investigations into rates of decomposition of *Phragmites australis* in Cop Mere, faunal associations with such litter and the contribution of dead *Phragmites* stems to the littoral ecology.

The physical breakdown and chemical decomposition of plant matter has received much attention over recent years. Studies undertaken to investigate litter decomposition in aquatic habitats have been principally concerned with allochthonous material in lotic waters (e.g. Kaushik & Hynes, 1968, 1971; Mathews & Kowalczewski, 1969; Petersen & Cummins, 1974; Suberkropp *et al.*, 1976). However, studies in lentic habitats are not as common. Decomposition has been followed in *Typha latifolia* L. (Boyd, 1970), *Myriophyllum spicatum* L. (Kistritz, 1978) and *Phragmites australis* (Mason & Bryant, 1975; Úhlelová, 1978; Polunin, 1979). In addition, Howard-Williams & Davies (1979) looked at decay of *Potamogeton pectinatus* L. in a brackish lake, while Harrison & Mann (1975) investigated decomposition of *Zostera marina* in shallow waters off the Atlantic coast. Research into litter breakdown has usually centred on following changes in mineral ion content (Boyd, 1970; Mason & Bryant, 1975; Kistritz, 1978; Howard-Williams & Davies, 1979) and not always *in situ* - Planter (1970) followed elution of ions from *Phragmites* stems in the laboratory. Studies of losses of organic macromolecules from litter are infrequent; Suberkropp *et al.*

(1976) followed changes in the commoner macromolecules during breakdown of the leaves of two species of tree in a stream, while Kormondy (1968) and Egglishaw (1972) studied cellulose decay from natural and artificial substrates. The recent work of Polunin (1979) reports on the breakdown of cellulose, under various conditions, in the form of filter paper. There seemed to be a need therefore for data concerning breakdown of *Phragmites* stem litter, and losses of the commoner macromolecules from it, in the reedbed; this chapter aims to provide some of this information.

The role of bacteria and fungi in decay of litter has been studied by several workers including Kaushik & Hynes (1971), Suberkropp & Klug (1976), Wetzel & Manny (1972), Mason (1976), Kistritz (1978), Polunin (1979), and weight losses have been attributed to the presence of microbial populations on the litter. Other work on *Gammarus* (Bärlocher & Kendrick, 1973), *Asellus* (Rossi & Fano, 1979), *Chironomus lugubris* Zetterstedt (McLachlan & Dickinson, 1977) and *Chironomus thummi* (Kieffer) (Baker & Bradnam, 1976) has implied utilisation of the microflora itself rather than the detritus as the food source, although Marcus & Willoughby (1978) have questioned these claims in light of their work on *Asellus*. It is beyond the scope of this study to investigate microbial populations; rather the emphasis is on observations of interactions between macroinvertebrates and litter, especially as regards chironomids, and the possible effects of the fauna on weight loss and macromolecule loss during stem decay.

METHODS

Following other workers such as Mathews & Kowalczewski (1969) and Mason & Bryant (1975), mesh bags were used to enclose samples of *Phragmites* litter.

In March 1979, standing stems of *Phragmites* from the previous year's growth were harvested from Cop Mere, those standing near the water but not actually in it being taken. Flower heads and roots were removed from the main stem, the stems cut into lengths of about 10 cms and air-dried at room temperature to constant weight. To minimise surface-area differences between bags, 12 stem lengths (totalling about 4-5 g) were weighed into tared bags, a numbered plastic tag added and the bags heat-sealed.

The bag size was 15 x 15 cms and two mesh pore sizes were used. The coarser mesh was a plastic netting sold in garden centres as 'Rokolene' with apertures of about 5 x 3 mm and the finer mesh was a polypropylene material supplied by G. H. Heath & Son (UK) Ltd. with apertures of 500 x 300 μm. It had been hoped to use an even finer mesh of 45 μm but the material had not arrived at the start of the experiment. (This mesh size would have allowed access to microbes, but excluded most invertebrates and vertebrates.)

A total of 120 bags, in groups of 5, were tied with nylon monofilament, fastened to canes, had weights attached and were then placed into the reedbed zone of Cop Mere at the end of May 1979. To avoid interference from fishermen, the bags were positioned in the north-eastern reedbed of the mere (Fig. 2:2, chapter 2). At intervals of 1, 2, 3, 4, 8, 12 and 26 weeks, 5 bags of each mesh size were removed and each immediately placed into individual plastic bags to be taken to the laboratory. At 40 weeks, 10 bags of each size were removed and at 54 weeks 15 bags. The bags were opened in a white tray of water, and sediments were rinsed from the stems; these were cut open to ensure capture of stem-inhabiting animals, and put into aluminium trays to dry at room temperature to constant weight. All animals were killed and stored in 70% alcohol for identification and enumeration.

After air-drying and weighing, each sample was ground in a laboratory mill. An initial sample of stems used to fill the bags had also been dried, ground and then treated as for other samples. Samples from the 5 coarse (and similarly for the fine) mesh bags were pooled for weeks 1-26 to give sufficient material for analysis; two sets of 5 pooled samples were available for week 40 from both coarse and fine mesh, and one set (all 15 bags due to lack of material) and three sets of pooled samples resulted from coarse and fine mesh bags respectively for 54 weeks. Because of a malfunction of the mill, all samples for the fine mesh set at week 12 were lost. Samples were stored in glass jars until analysis.

For corrections to an oven-dry weight basis, sub-samples were dried at 105°C.

Ash content was determined by ignition in a muffle furnace at 550°C as described in Allen *et al.* (1974).

Total nitrogen was determined by micro-Kjeldhal analysis using mercury catalyst tablets (Allen *et al.*, 1974). A boric acid mixed indicator solution was used in place of that suggested to collect the distillate (see Appendix).

Total carbon was analysed using a modified Walkley-Black rapid titration method (Hesse, 1971). The barium diphenylamine sulphonate indicator used was that suggested by Allen *et al.* (1974) - the addition of $BaCl_2$ clarifies the colour change.

Determinationsof α-cellulose (via holocellulose), and lignin were made following the methods of Allen *et al.* (1974).

All weights were converted to ash-free, oven-dry weights by the appropriate conversion factors. Where there was sufficient material, two estimations of each of the above components were made from each set of pooled samples.

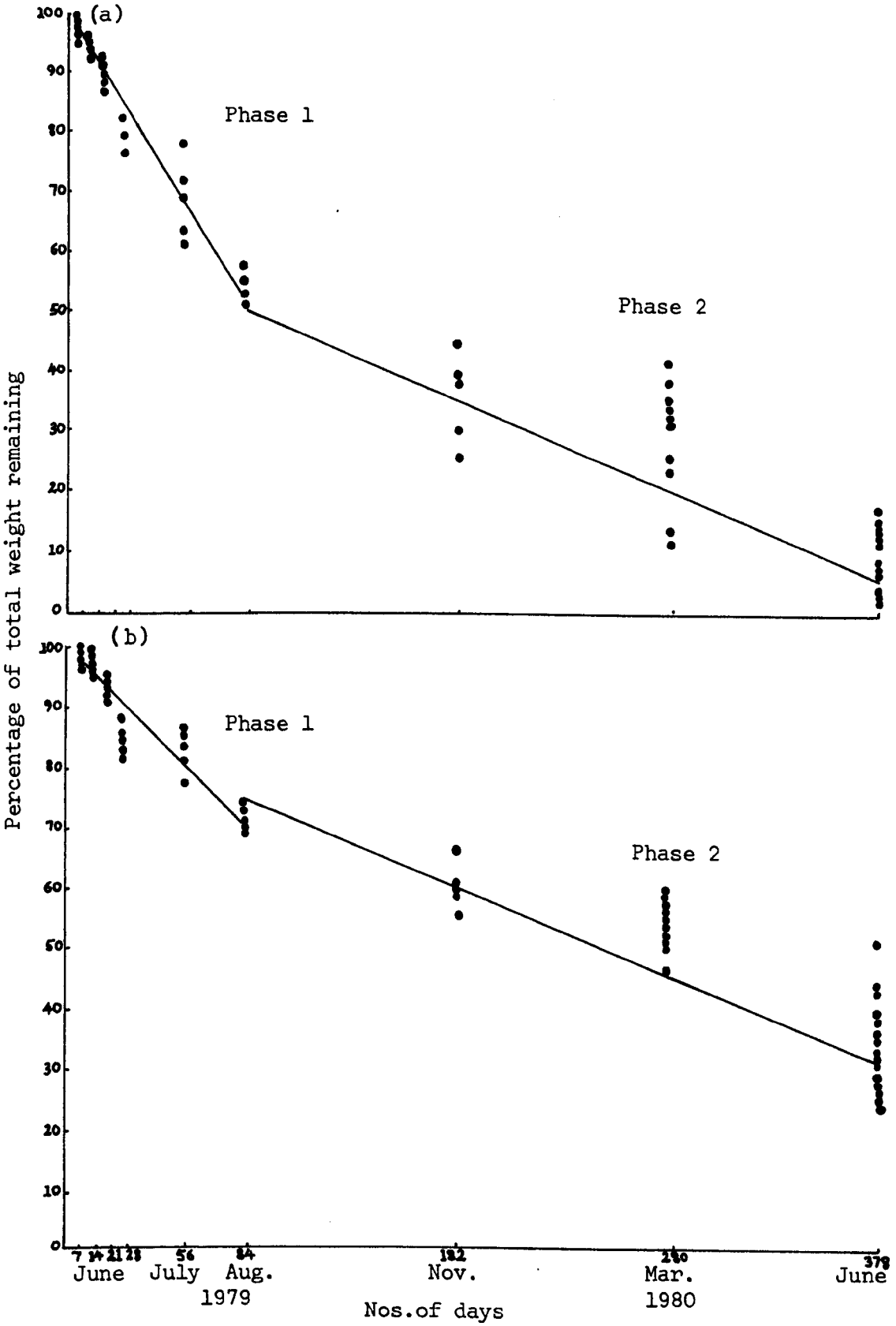

FIG.5:1 Weight loss of *Phragmites* from(a) coarse and(b) fine mesh litter bags.

RESULTS AND DISCUSSION

A. CHEMICAL CHANGES

1). Weight. Fig. 5:1 illustrates the change in weight which occurred in the litter bags during the year-long experiment, expressed as a percentage of the initial weight remaining.

The distribution of points in Fig. 5:1 suggested that there might be at least two phases of (roughly linear) decay with differing rates, these being from June to August and August to June. This division is somewhat arbitrary, and the period from March to June could be regarded as a third phase since an increased rate of decay seems to occur. Assuming two phases, however, regressions of weight remaining against time (in days) were calculated and details are given in Table 5:1; most of the variance can be accounted for by the linear models and r^2 values were significant (F-test, $p < 0.001$). (Strictly speaking, an arcsin transformation of the percentage data should be used to calculate the regression coefficients. However, this does not make any essential difference (see Table 5:1) and interpretation of direct percentage regressions is easier than of transformed data.).

Assuming linearity in the second phase of decay, t_{100}, the time taken for all litter to have disappeared and $\%R_{365}$, the amount remaining after one year, can be estimated from the regression equations. These, together with the decay rates, are summarised in Table 5:2. There was no significant difference between the rates of decay (comparing regression coefficients using a d-test, e.g. Bailey, 1959) for coarse and fine bags during phase two, although litter in the coarse bags did decay faster in the first phase ($0.05 < p < 0.1$). Decay was slower in the second phase compared with the first for both coarse and fine bags ($0.05 < p < 0.1$).

Only three reports have been found where weight loss of *Phragmites*

BAG TYPE	PHASE	n	R^2	R_t*	F	p	Regression Equation
Coarse	1	26	0.943	-0.957	397	<.001	y = 101.29 - 0.57x
	2	34	0.815	-0.757	141	<.001	y = 64.40 - 0.16x
Fine	1	30	0.906	-0.929	270	<.001	y = 99.70 - 0.34x
	2	35	0.806	-0.896	137	<.001	y = 84.69 - 0.13x

TABLE 5:1 Regression parameters for the decay rates of *Phragmites* litter. R_t* is the r-value from a $\sqrt{\arcsin y}$ transformation of the data (see text).

BAG TYPE	PHASE	DECAY RATE (r)	t_{100} (days)	$\%R_{365}$
Coarse	1	0.57	-	-
	2	0.16	404	10
Fine	1	0.34	-	-
	2	0.13	661	37

TABLE 5:2 The decay rate (percentage loss per day), time taken for all litter to disappear (t_{100}) and percentage remaining after one year ($\%R_{365}$) for coarse and fine mesh bags.

litter has been followed, and the rates of decay found in Cop Mere are similar to those reported by Úhlelová (1978), Polunin (1979) and Mason & Bryant (1975). Úhlelová calculated decay rates for *Phragmites* stems in Nesyt fishpond, Czechoslovakia, of 0.20% per day in the summer, and 0.08% per day in the winter (c.f. 0.57% per day and 0.16% per day respectively in this study from coarse bags). Polunin found a loss rate of 0.55% per day of leaf litter in laboratory conditions at 16°C, which is similar to the temperature recorded in the reedbed during summer at Cop Mere. Weight loss of *Phragmites* shoot litter in Alderfen Broad, over a period of about 400 days, was 0.18 and 0.15% per day from coarse and fine mesh bags respectively (Mason & Bryant, 1975).

Mason & Bryant (1975) found no significant differences between the decay rates of *Phragmites* in coarse and fine mesh bags, but they

predicted from the regression lines that after a year more litter would be left in fine mesh bags than coarse bags. They attributed this apparent anomaly to the variation between individual samples adding that "litter in large-mesh bags containing large populations of chironomids appeared very broken down .... The shorter time for decomposition in the large-mesh bags was probably owing to the effect of animals." Similarly in this study more litter was found to be left in the fine bags after one year (37%) than in the coarse mesh bags (10%). However, as was shown above, rate loss from coarse bags was faster than from fine bags in the initial phase and so could account for the greater loss from the former type overall. Polunin (1979) estimated that about 35% litter would be left in his coarse bags after one year, though this was a result obtained for leaves of *Phragmites*, not stems.

The possible role of invertebrates in litter breakdown is discussed in the last section of this chapter.

2). Ash. Percentage ash decreased rapidly in the first eight weeks and then increased for the remainder of the study period (Fig. 5:2a). The initial loss is probably due to leaching of mineral components as found by other workers (Boyd, 1970; Planter, 1970; Howard-Williams & Davies, 1979; Polunin, 1979). The proportions of ash then increased until the end of the study - there was no significant difference ($p > 0.05$, Mann-Whitney U test) at weeks 40 or 54, even though coarse bags apparently contained a relatively higher proportion than did fine bags. Variation between samples and of estimations may be concealing any real differences.

The rise contrasts with the fall inferred by Polunin (1979) from an observed increase in ash-free dry weight of leaves in his study. In fact, from measurements of ash components (K^+, Mg^{2+}, and Ca^{2+} ions),

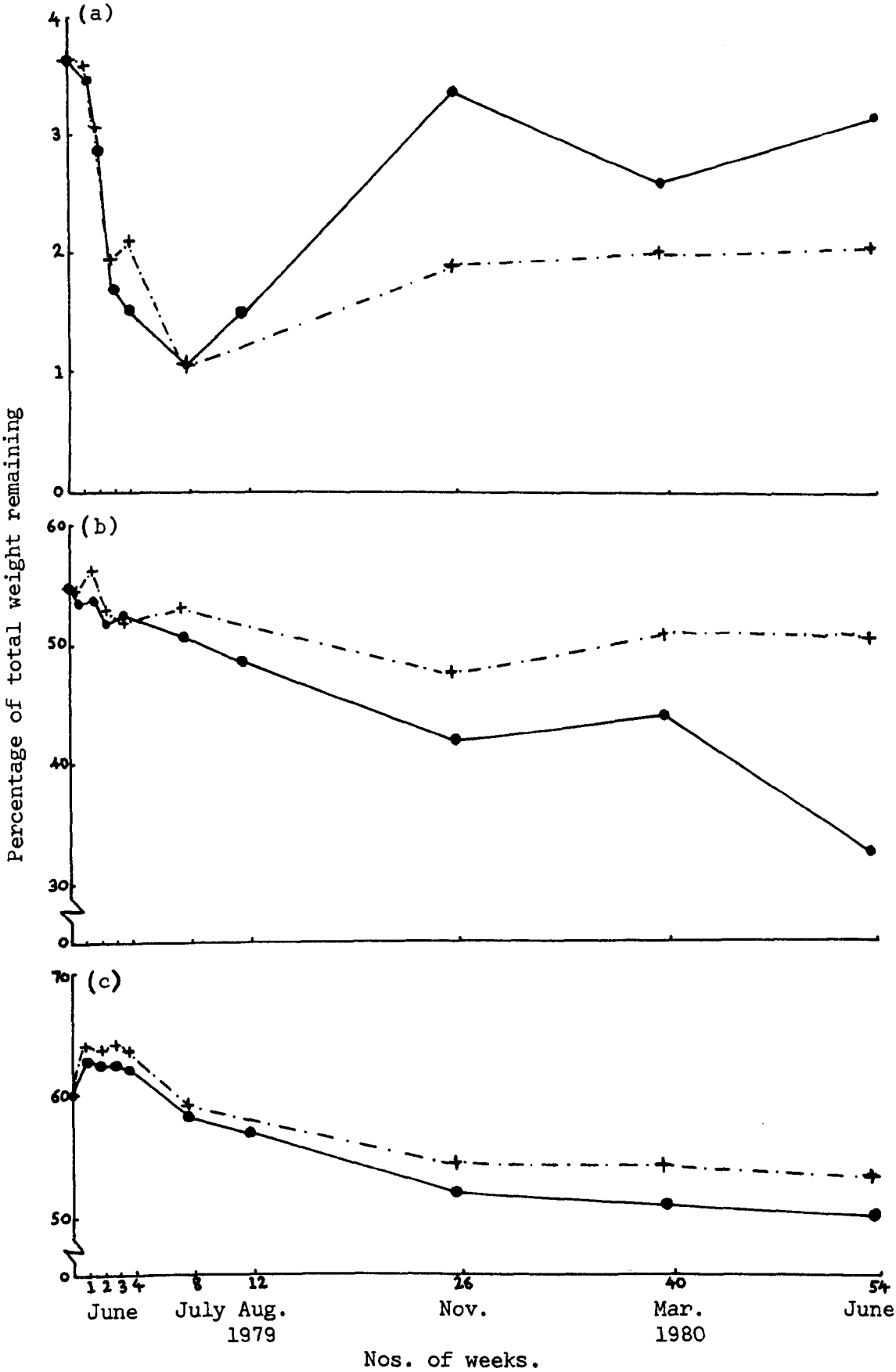

FIG.5:2 Changes in proportions (%) of(a) ash,(b) α-cellulose, (c) lignin. Coarse mesh: ●——●, fine mesh:+---+

his data are variable, Ca^{2+} increasing with time and all three exhibiting considerable fluctuations over the year. Hence, his conclusion that ash-free dry weight increases may not be a valid one.

3). α-Cellulose. A difference between the rates of loss from coarse and fine mesh bags is evident from Fig. 5:2b. There was no significant difference at the 5% level using the Mann-Whitney U test ($p = 0.171$) at 40 weeks, but by 54 weeks the difference between the two mesh sizes was significant ($p = 0.036$). In coarse bags about 30% of the weight is cellulose after one year, in fine mesh bags about 45%, compared with an initial estimate of 55%.

In a woodland stream, Suberkropp *et al.* (1976) found the cellulose levels of oak and hickory leaves to remain around 15-20% through a 32-week study, which suggested a fairly constant processing rate as regards other constituents. The results presented here indicate that cellulose is being broken down and lost faster than some other constituents. This difference is likely considering the two entirely different litter and environmental types of the two studies. Kormondy (1968), following loss of artificial cellulose, found little change over the winter months, but nine months after the start of the study (after spring and summer), 50% of the original weight had disappeared. No sharp increase in the rate of breakdown is evident here, unlike the change observed by Kormondy, but of course the climate is different between the two study sites. Polunin (1979) examined the breakdown of cellulose in the form of filter paper, but found no significant decay.

The greater percentage loss of cellulose from the coarser bags could be due to the presence of greater numbers of invertebrates acting as comminutative agents creating a larger surface area for cellulolytic bacteria and fungi. (However, it is becoming evident

from recent work that possession of cellulase enzymes is not restricted to microbes, worms and molluscs as once seemed to be the case. Monk (1976) found that molluscs and crustaceans have high cellulase activity, while some insects have a lower activity, and Bjarnov (1972) has found carbohydrases in *Chironomus*, *Gammarus* and some Trichoptera larvae. Although gut enzymes may be present, this does not necessarily imply use of them. However, breakdown of cellulose in the bags may be due to the invertebrates directly as well as indirectly.)

Egglishaw (1972) examined cellulose breakdown using cotton and found chytrid fungi to be present within the fibres, which suggests strongly that these could be breaking down the cellulose. No analysis of micro-organisms was done here, but it is likely that *Phragmites* cellulose is attacked primarily by microbes. It is interesting to note that Egglishaw's results show the rate of cellulose decay to be positively correlated with the nitrate concentration of the water, the implication being that the fungi were using the nitrogen for growth, increasing their population and hence the rate of cellulose decomposition.

4). Lignin. It should be noted that lignin is a highly complex compound and its structure is by no means fully understood (Kirk, 1971). The method used for its analysis here is at best a compromise and may not be suitable for litter of this type, so giving spurious results. Consequently, the following discussion should be read with this in mind.

Unlike the other components measured, there is no clear difference in the decomposition rate of lignin between coarse and fine bags, though the former shows slightly more evidence of a higher rate of breakdown throughout (Fig. 5:2c). Differences between bags were significant ($p = 0.028$) at 40 weeks but not at 54 weeks ($p = 0.167$). Although the loss is not large (6-10%), breakdown of lignin seems to be occurring.

This is in contrast to the findings of Suberkropp *et al.* (1976) where the percentage levels rose from about 10 to 25% of the dry weight, and to studies by Polunin (1979) on leaves of *Phragmites* where proportions rose from 5 to 17% during a year. Suberkropp *et al.* (1976) have shown that the accumulation of lignin in the leaf packs is probably due to complexes being formed between nitrogenous compounds (possibly microbial enzymes) and plant phenolics to give resistant, artificial lignin-like compounds, which because of their behaviour during chemical analysis, are recovered in the true lignin fraction thus inflating the estimate. Since the levels of lignin found in this study decrease, there is at least a faster breakdown than accumulation of lignin. Thus formation of complexes may not be occurring. Polyphenols and tannins, present at high concentrations in abscissed leaves from trees, might be at low levels in stems of *Phragmites*, but these compounds were not measured here. Polunin (1979) estimated lignin from an acid-insoluble residue which probably contained other organic compounds, and he worked on leaves of *Phragmites*, not stems; the differences between his results and those in this study are probably a reflection of this.

It is probable that lignin, like cellulose is being broken down enzymatically by microbes; furthermore, once cells are ruptured by microbial attack, loss can increase due to greater exposure and possibly fractional loss into the water.

5). Nitrogen. Two graphs illustrate nitrogen changes; i) percentage of nitrogen remaining relative to other components (Fig. 5:3a) and ii) absolute weights present in the bags (Fig. 5:3b). In both mesh sizes absolute values of nitrogen decrease rapidly over the initial four weeks; after another month levels have risen again before eventually falling in the spring months. The higher weight of nitrogen

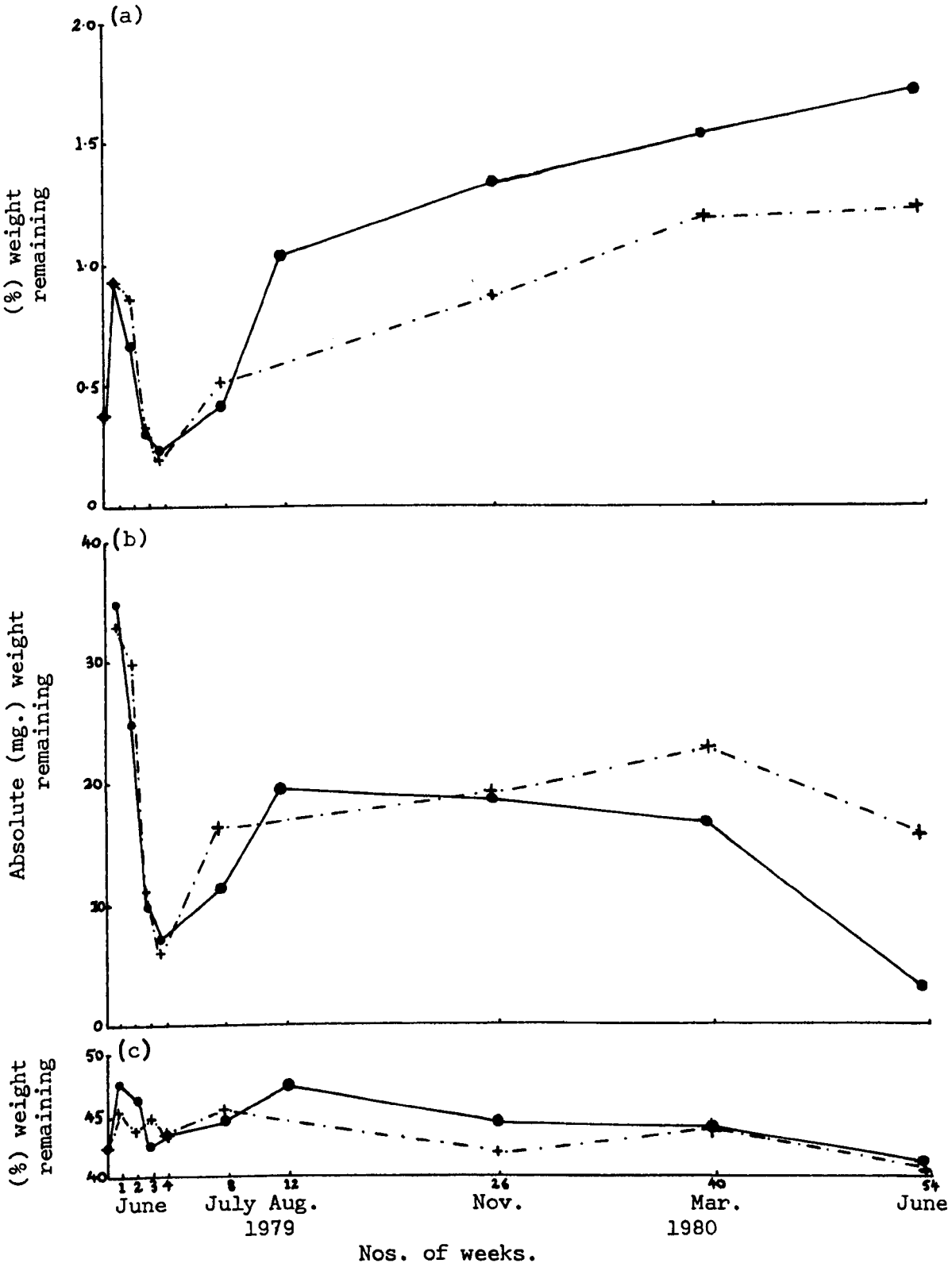

FIG.5:3 Changes in proportions (%) of(a) nitrogen,(c) carbon and absolute weight(b) of nitrogen. Symbols as Fig.5:2.

present in fine compared with coarse bags at the end of the experiment reflects less loss of litter from the former. A similar trend is found initially by plotting percentages of nitrogen, but levels then rise after four to eight weeks and continue to rise through to the end of the experimental period, indicating an accumulation of nitrogen compared with other components. (Differences between mesh sizes for percentage N were almost significant at the 5% level at 40 weeks, $p = 0.057$, and significant at 54 weeks, $p = 0.047$). The increase in proportion of N could be explained by a decrease in other constituents' percentage weight, but will not explain the observed increase of N in absolute weight terms. The initial rise of percentage N over the first week could be due to fast colonisation by microorganisms, followed by a fall due to greater leaching of e.g. soluble amino acids than colonisation by microbes. As time goes on the bacteria and fungi, by immobilising N (Kaushik & Hynes, 1968), increase absolute levels (and percentage levels) until litter weight loss from the bags overshadows any absolute N weight gain and so levels decrease. The observation that from weeks 12 to 40 coarse bags lose N, while fine bags continue gaining in absolute terms, is a reflection that coarse bags are losing more litter than fine bags. This conclusion is supported by the fact that at week 12, when the absolute levels of N begin to fall in coarse bags they have lost about 45% of the litter, whereas the fall in N levels of fine bags does not occur until week 40 at which point 45% of their litter has disappeared.

Levels of N observed here in decaying stems are similar to those reported by other workers for *Phragmites* leaves (Polunin, 1979) and tree leaves (Suberkropp *et al.*, 1976).

6). Carbon. Values of carbon for the litter were similar throughout the period of study - the small-scale changes in proportion of C are

more likely a reflection of the error involved in its analysis by the rapid titration method than any real change. In consequence, little can be said about loss of C (Fig. 5:3c, p.77).

The percentage C in the litter remained around 40% for the whole period; the majority of this organic carbon will originate from cellulose, lignin and other such compounds. The C:N ratio is often considered an important factor in determining the rate of breakdown of litter and susceptibility to attack by invertebrates. A plot of the C:N ratio here will reveal little more than an inverse of the %N plot. However, the ratios vary from about 100:1 initially, 250:1 after 4-8 weeks and then decrease markedly to about 30:1 (Table A5:2 in Appendix). Low ratios are indicative of material more easily assimilable by detritivores, so litter will be of more use to invertebrates as a direct food towards the end of its life.

B. INVERTEBRATES AND *PHRAGMITES* LITTER

1). Non-chironomids. Unfortunately, as mentioned in the Methods, no mesh below 500 µm pore size was available at the start of the experiment. Therefore most chironomids, except larger *Glyptotendipes* spp. and *Camptochironomus tentans* for example, theoretically had free access to the fine mesh bags, though probably restricted to some extent by total body size. Immigration and emigration was also possible for early instars of *Asellus aquaticus* (L.) and other invertebrates, consequently not as much information as had been originally hoped could be gathered from the data.

Changes (in mean numbers of individuals per bag) over the study period show a rapid colonisation of the litter in the first month (Fig. 5:4a), chironomids and *Asellus* making up the bulk, with leeches e.g. *Erpobdella octoculata* (L.), as the main predators (Tables 5:3, 5:4). A sudden drop in numbers seen in the coarse mesh bags at week 8

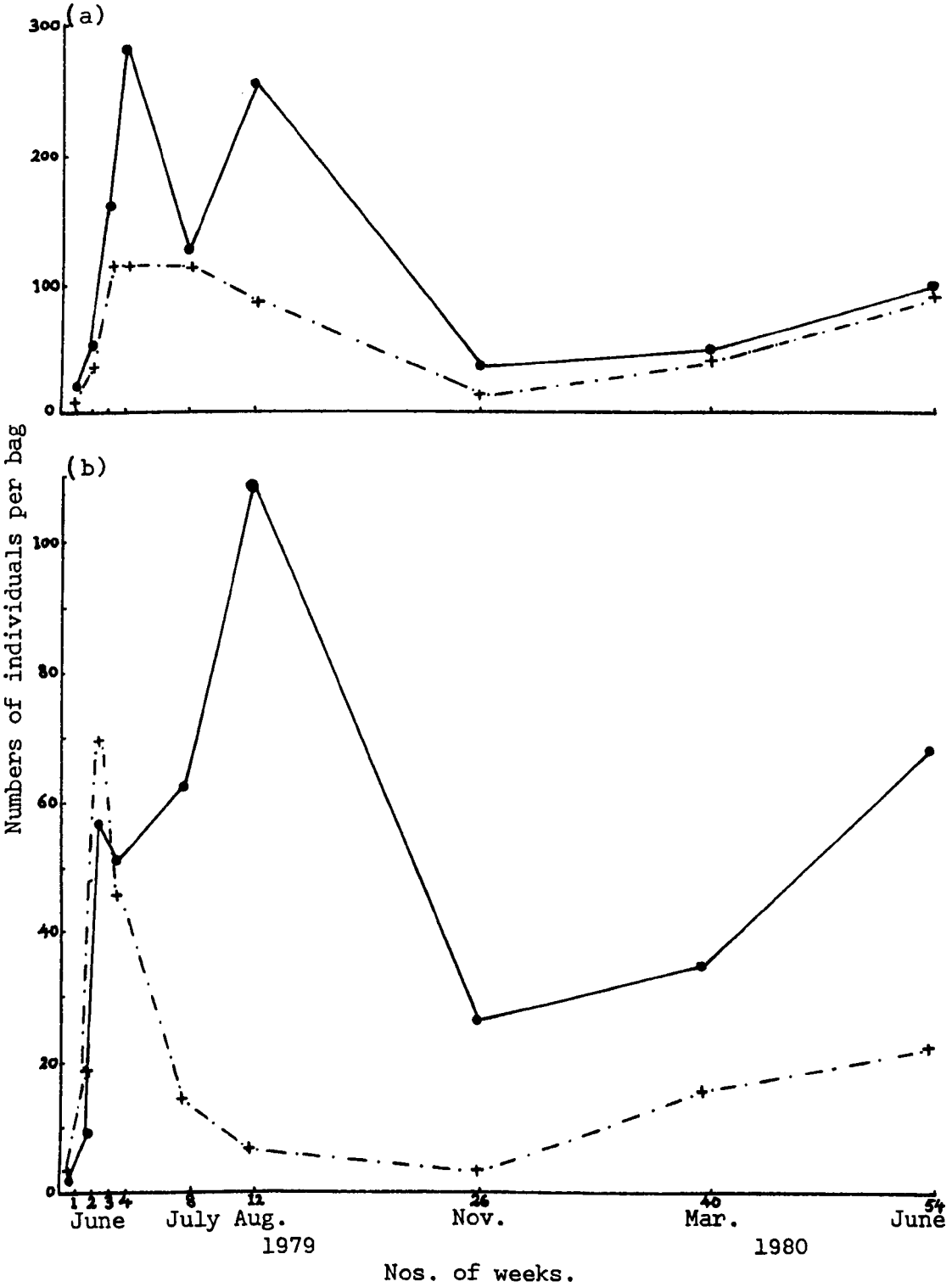

FIG.5:4 Changes in mean numbers of(a) total invertebrates and (b) total chironomid larvae per bag. Coarse mesh:●——●, fine mesh:+·—·—+.

Taxon	Date (Week)	7.6.79 (1)	14.6.79 (2)	21.6.79 (3)	28.6.79 (4)	26.7.79 (8)	23.8.79 (12)	30.11.79 (26)	7.3.80 (40)	11.6.80 (54)
Planaria torva		0.2±0.2		0.6±0.2				2.0±1.0	0.9±0.3	0.5±0.2
Stylaria lacustris		0.4±0.4					4.2±1.3			5.3±1.3
Other Oligochaetae							0.2±0.2			0.1±0.01
Erpobdella octoculata		1.4±0.5	11.2±2.4	8.2±2.7	5.7±2.6	1.8±0.2	2.8±1.2	0.6±0.2	1.2±0.3	0.1±0.01
Glossiphonia complanata						0.8±0.4	0.2±0.2	0.2±0.2	0.5±0.3	0.1±0.01
Helobdella stagnalis			2.2±0.9	1.4±0.4			1.2±0.4	0.4±0.2		0.1±0.01
Acroloxus lacustris								0.4±0.2		
Potamopyrgus jenkinsi									0.1±0.01	
Lymnaea peregra							0.2±0.2		0.1±0.01	
Physa fontinalis							0.2±0.2		0.1±0.01	
Pisidium sp.								0.2±0.2	0.2±0.1	0.2±0.1
Planorbis albus			0.2±0.2	0.6±0.2	0.3±0.3	0.6±0.2	9.6±4.0	0.4±0.2	0.4±0.2	
Asellus aquaticus		14.8±3.1	26.0±8.0	89.0±16.0	221.3±44.5	51.6±7.9	117.2±31.9	5.6±1.2	6.5±1.0	20.6±2.8
Gammarus pulex		1.6±0.4	1.4±0.5	2.4±1.0	1.6±1.6	0.8±0.6	1.6±1.2	0.4±0.2	2.8±0.6	1.4±0.9
Caenis sp.										0.1±0.01
Chloeon dipterum				0.2±0.2			0.4±0.2			
Agrypnia pagetana			0.6±0.2	1.0±0.5	2.3±0.7	7.2±1.0	5.8±1.2			0.3±0.2
Athripsodes aterrimus									0.4±0.2	0.8±0.2
Holocentropus picicornis						1.2±0.4	0.8±0.4	0.4±0.2	0.2±0.1	0.4±0.2
Leptoceridae							0.2±0.2			
Mystacides sp.										0.1±0.01
Ceratopogonidae						0.2±0.2				
Dytiscidae(adult)									0.1±0.01	0.1±0.01
Haliplidae(larvae)										0.7±0.20
Chironomidae		1.4±0.5	9.0±1.3	56.6±7.2	51.6±5.7	62.6±5.2	108.8±11.6	26.8±9.7	35.7±3.6	68.9±6.10
TOTALS		19.8±3.68	50.4±7.4	160.0±18.7	282.8±38.8	126.8±11.1	253.4±42.2	37.4±11.0	49.2±3.4	99.8±7.0

TABLE 5:3 Mean number of invertebrates in coarse litter bags. Figures to right of mean are 1 standard error.

Taxon	Date (Week)	7.6.79 (1)	14.6.79 (2)	21.6.79 (3)	28.6.79 (4)	26.7.79 (8)	23.8.79 (12)	30.11.79 (26)	7.3.80 (40)	11.6.80 (54)
Planaria torva				0.2±0.2						0.4±0.2
Stylaria lacustris		1.0±1.0					2.4±1.4			3.3±0.9
Other Oligochaetae							0.4±0.4	0.2±0.2		
Erpobdella octoculata			4.4±0.5	4.2±1.0	7.4±1.3	1.2±0.4	0.8±0.6	0.4±0.4	0.9±0.3	1.1±0.3
Glossiphonia complanata							0.2±0.2	0.2±0.2	0.1±0.01	
Helobdella stagnalis						0.4±0.2	0.2±0.2			0.7±0.4
Potamopyrgus jenkinsi									0.1±0.01	
Physa fontinalis							0.2±0.2			
Pisidium sp.									0.1±0.01	
Planorbis albus					0.2±0.2		0.8±0.4	0.2±0.2	0.6±0.2	0.1±0.01
Asellus aquaticus		1.6±0.4	6.8±1.3	37.0±3.4	58.0±8.6	94.0±8.9	71.6±8.9	5.8±2.5	21.4±4.7	58.5±5.9
Gammarus pulex		0.2±0.2	1.0±0.6	0.4±0.4		0.4±0.4				1.6±0.6
Chloeon dipterum				0.2±0.2						
Sialis lutaria										0.1±0.01
Athripsodes aterrimus									0.1±0.01	
Holocentropus picicornis						1.2±0.6		0.2±0.2		0.2±0.1
Ceratopogonidae		0.4±0.2				0.6±0.2			0.5±0.2	0.1±0.01
Haliplidae (larvae)										0.2±0.01
Chironomidae		3.2±0.6	18.6±2.6	69.4±11.9	45.8±5.1	13.8±3.0	6.4±1.0	3.2±1.6	16.3±2.2	23.4±3.1
TOTALS		6.4±0.7	30.8±4.9	111.4±10.2	111.4±6.5	111.6±9.8	83.0±8.0	10.2±2.4	40.3±4.3	89.8±5.9

TABLE 5:4 Mean numbers of invertebrates in fine litter bags. Figures to right of mean are 1 standard error.

was due to a drop in *Asellus*; the numbers in the fine mesh continued to rise from week 4 to 8 (Tables 5:3, 5:4). This disparity could be due to small instar *Asellus* getting into fine bags, growing and not being able to escape, while movement in and out of large mesh bags is unrestricted, and because of some unknown movement, perhaps breeding, emigration occurred around this time.

Numbers of invertebrates in both bag sizes drop as winter approaches (possibly emigration to more favourable overwintering habitats and/or death if trapped in the bags) and then increase again in the spring and early summer. Numbers after 1 year are about $\frac{1}{2}$-$\frac{3}{4}$ those present in the previous year, and this is probably a reflection of the loss of litter and hence loss of habitat and/or food.

Molluscs were relatively uncommon in fine mesh bags. This is to be expected in view of their size which prevents them entering through the small pores. In the twelfth week numbers increased in coarse bags (Table 5:3) because of an influx of *Planorbis albus* Müll. and then dropped again over winter. The greatest number of species (though not of individuals) was taken in March and this could be an indication of dispersive movement during spring after the winter. More molluscs occurred in the coarse bags overall, but whether this can help to account for more cellulose decay is open to question. Work by Mason & Bryant (1975) has suggested that the rasping of tissue by molluscs, so increasing surface area, increases microbial activity. Undoubtedly this can lead to greater tissue (e.g. cellulose) decomposition. Furthermore, *Lymnaea peregra* (Müll.) and *Ancylus fluviatilis* Müll. (*Acroloxus lacustris* (Linn.), a closely related species, was recorded here) have high cellulase activity (Monk, 1976).

Of the Trichoptera, *Agrypnia pagetana* Curtis was the commonest animal but was excluded entirely from the fine mesh bags. It is a

large caddis and was found to be using *Phragmites* stems as its case inside bags, both as larvae and pupae. If caddis are making use of such stems as cases, then since movement in and out of bags is possible, the weight loss observed for coarse bags could in part be due to caddis larvae - though this might be expected to be offset by immigration.

2). Chironomids. Fourteen genera were represented, the commonest being *Cricotopus*, *Glyptotendipes*, *Limnochironomus* and *Camptochironomus*.

Looking at total chironomids (means per bag) present (Fig. 5:4b,p.80, Tables 5:5,5:6), it can be seen that numbers in the coarse bags increased rapidly to about 100 per bag by August, fell towards winter to 25 and went up in spring to about 70. Numbers in the fine mesh bags peaked around June at 70, fell through August and then increased again in spring to about 20 per bag. From week 8 to 54 inclusive the difference in numbers between mesh sizes is significant ($p = 0.001$, using Mann-Whitney U). This is probably due to larvae being hindered and excluded from entering the fine mesh bags. If they were not, numbers would be expected to be higher than in coarse bags after a year because of the presence of more litter in the fine mesh bags.

Figs. 5:5 and 5:6 show population changes in the bags for the four commoner genera which are now briefly discussed. In general there is good agreement between data presented here for larval populations and those already discussed in the previous two chapters.

Cricotopus sp.

As in previous chapters, larval identification was only taken to genus. Thus *Cricotopus sylvestris*, *C. flavocinctus* and other species have been 'lumped' into the one genus. The former was by far the commoner in emergence traps and it will be assumed that most of the larvae found were of this species. The pattern of colonisation in both bag types was similar (Fig. 5:5) although two peaks (as opposed

Genus	Date (Week)	7.6.79 (1)	14.6.79 (2)	21.6.79 (3)	28.6.79 (4)	26.7.79 (8)	23.8.79 (12)	30.11.79 (26)	7.3.80 (40)	11.6.80 (54)
Procladius	2		0.2±0.2						0.1±0.1	
	3					0.2±0.2				
Corynoneura	3		1.0±0.8	1.2±0.4	0.3±0.3	1.6±0.6				
	4					0.6±0.2				
Cricotopus	2		0.2±0.2	3.2±0.7	5.8±4.2	4.2±1.5	20.4±9.4		1.3±0.7	
	3	1.0±0.5	0.6±0.6	4.0±1.3	0.3±0.3	0.2±0.2	3.0±1.0	0.4±0.2	11.5±2.9	5.9±1.1
	4			0.8±0.5			1.2±1.2		1.8±0.5	1.7±0.5
Microcricotopus	4						0.2±0.2			
Psectrocladius	2			3.6±1.2	5.7±3.5	0.4±0.2				
Cladotanytarsus	3				0.3±0.3			0.2±0.2		
Camptochironomus	1		3.6±1.5	4.0±0.9	10.3±2.9					
	2		0.2±0.2							0.1±0.01
Glyptotendipes	1					17.4±3.0	1.8±1.0		0.9±0.4	13.3±2.3
	2		1.2±0.2	23.0±6.3	12.3±3.2	16.8±4.3	20.4±5.5	3.0±1.6	2.2±0.7	41.3±5.6
	3			0.6±0.2			5.2±1.9	1.2±0.6	0.9±0.3	1.8±0.4
	4	0.4±0.2	0.6±0.2	1.0±0.3	0.3±0.3	0.2±0.2	0.8±0.5	16.0±4.9	6.4±1.3	0.6±0.2
Limnochironomus	2		1.0±0.8	15.2±2.1	16.3±1.2	17.2±1.5	39.8±10.4		1.0±0.3	2.7±0.8
	3					2.2±0.5	9.6±2.7	5.4±3.3	9.5±1.6	1.4±0.4
	4					1.2±0.8	3.8±1.3	0.6±0.2	0.1±0.1	0.2±0.1
Microtendipes	2		0.2±0.2							
Parachironomus	2						0.4±0.2			
	3						0.6±0.2			
Pentapedilum	2						1.0±1.0			
	3						0.4±0.2			
	4						0.2±0.2			
Polypedilum	2		0.2±0.2							
	3					0.4±0.2				
TOTALS		1.4±0.5	9.0±1.3	56.6±7.2	51.6±5.7	62.6±5.2	108.8±11.6	26.8±9.7	35.7±3.6	68.9±6.1

TABLE 5:5 Mean numbers of chironomids in coarse litter bags. Figures to right of genus are instars; figures to right of means are 1 standard error.

Genus	Date (Week)	7.6.79 (1)	14.6.79 (2)	21.6.79 (3)	28.6.79 (4)	26.7.79 (8)	23.8.79 (12)	30.11.79 (26)	7.3.80 (40)	11.6.80 (54)
Procladius	3								0.1±0.01	
Corynoneura	3	0.2±0.2	2.8±1.4	2.2±1.2		0.2±0.2				
Cricotopus	2		2.2±1.0	8.6±2.1	1.2±0.7	1.4±0.4	1.4±0.5		0.6±0.2	2.2±0.6
	3	2.2±0.9	4.2±0.7	3.2±1.2	1.2±0.6				3.2±0.4	1.5±0.4
	4		3.2±1.4	0.2±0.2					0.7±0.3	
Psectrocladius	2			4.6±2.3						
Camptochironomus	1		3.6±1.2	3.4±1.1	2.6±0.7					
	2	0.4±0.2	0.6±0.2	0.8±0.5						
	3							0.2±0.2	0.7±0.4	
	4				0.2±0.2			1.8±0.9	2.4±1.1	0.2±0.01
Endochironomus	4			0.2±0.2					0.3±0.2	0.2±0.01
Glyptotendipes	1					2.4±0.7	0.6±0.6		0.4±0.2	5.3±1.3
	2		1.8±0.4	19.8±4.4	4.6±0.9	2.2±0.7	1.2±0.6		1.2±0.4	6.9±1.6
	3		0.2±0.2	1.8±0.9	0.4±0.2		0.4±0.2	0.4±0.2	1.4±0.4	1.5±0.4
	4				0.2±0.2			0.6±0.4	2.2±0.6	0.8±0.3
Limnochironomus	2			24.6±8.4	18.2±4.2	6.6±1.7	1.6±0.7	0.2±0.2	0.1±0.01	2.7±0.5
	3				17.2±2.6	0.6±0.4	0.6±0.4		2.9±0.6	2.0±0.6
	4					0.2±0.2			0.1±0.01	0.1±0.01
Microtendipes	2	0.2±0.2								
Pentapedilum	2						0.6±0.4			
	3									0.1±0.01
Polypedilum	3	0.2±0.2				0.2±0.2				
TOTALS		3.2±0.6	18.6±2.6	69.4±11.9	45.8±5.1	13.8±3.0	6.4±1.0	3.2±1.6	16.3±2.2	23.4±3.1

TABLE 5:6 Mean numbers of chironomids in fine litter bags. Figures to right of genus are instars; figures to right of means are 1 standard error.

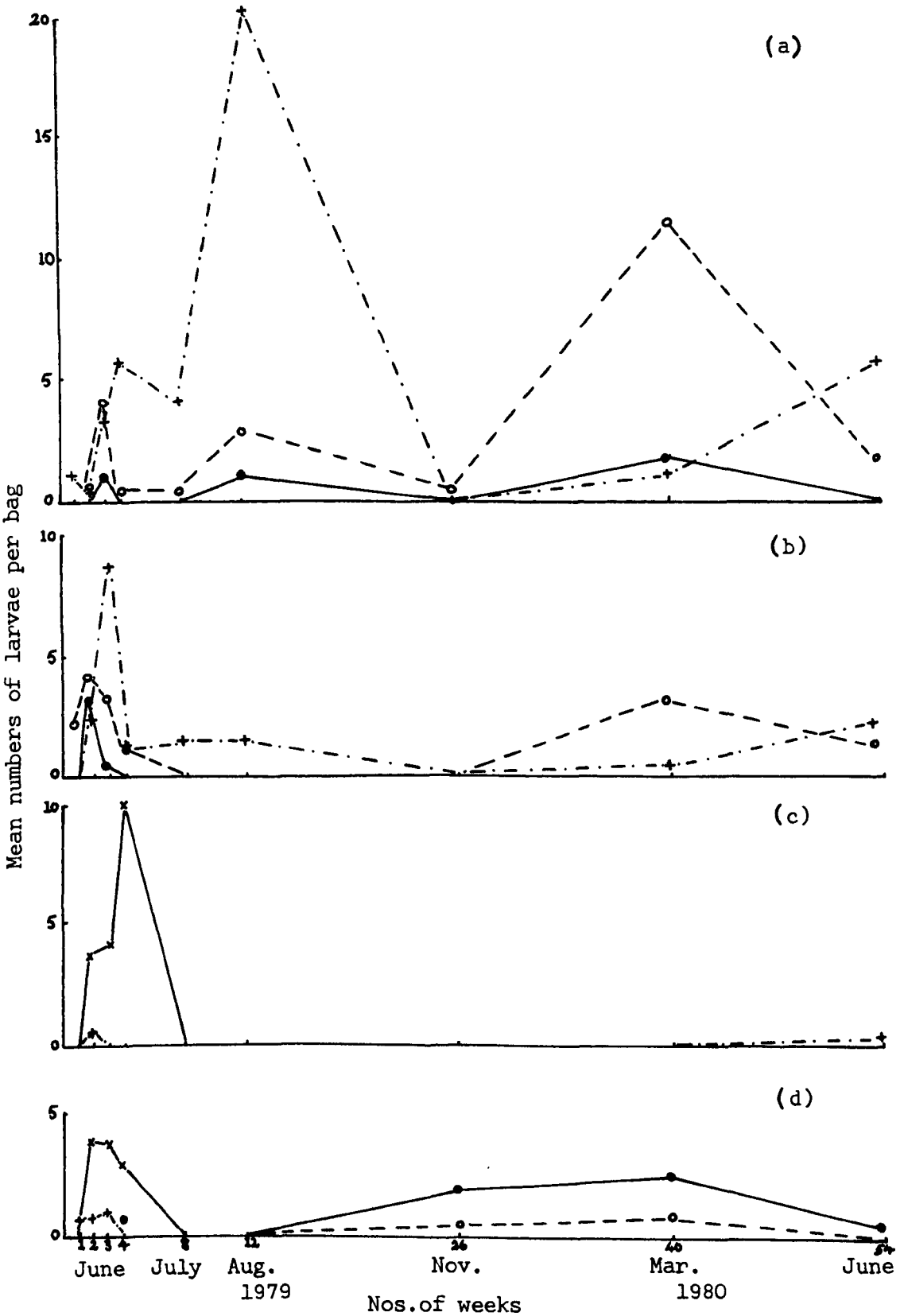

FIG.5:5 Changes in abundance of *Cricotopus* larvae in(a) coarse and (b) fine mesh bags, and *Camptochironomus* larvae in(c) coarse and(d) fine mesh bags. Instars as follows: first (×——×), second (+·—·+), third (o– –o), fourth (●——●).

to one) occurred in the first 3 months in coarse bags. Adult emergence data (chapter 6) show peaks of *C. sylvestris* around weeks 4 and 8 of the litter bag study, accounting for the high numbers of second instars. Larvae appear to spend the winter as third instars, but it is notable that virtually none was found in the November samples. This implies that death or migration away from the bags occurred; this is a similar situation to that found for these larvae on stems (chapter 4). The increase of larvae in the spring suggests they are returning; it is unlikely that any adults would have emerged by March to allow for development of eggs to third instars by the time of sampling, (or that any overwintering eggs, as described in chapter 4, could have developed to third instars by March). *Cricotopus* grazes the epiphytic flora of the stems in the bags and it is possible that the quality/quantity of this deteriorates as winter approaches. The relationships of this species with periphyton on *Phragmites* stems have been discussed in the previous chapter.

Chironomus sp.

Most *Chironomus*-type larvae identified were probably *Camptochironomus tentans* as discussed in the previous chapters. In late June, first instar larvae predominated in both bags and then dropped to zero in coarse bags, while in fine mesh bags third and fourth instars were found throughout the winter and into the next year (Fig. 5:5). The explanation for this may be as follows. First instar larvae disperse upon hatching and search for a suitable substrate on which to settle. Random movements will bring them to the litter bags where some will settle on the stems, possibly building tubes using small detrital material present in the periphyton and begin feeding. Upon moulting into second and third instars it is possible that the larvae need a more solid substratum of sand grains for tube construction (rather

than detrital particles) and so move off to find a new habitat. The head-capsule width of a third instar larva of *Camptochironomus* is about 400-450 µm and its body larger than this (though flexible); thus movement out of a fine meshed bag will be greatly restricted. The trapped larvae become fourth instars some of which probably die and are eaten by detritivores. Small instar larvae were rare in bags in 1980; this could be due to lack of material in the bags, or to the distribution pattern already described in chapter 3; that is, since the litter bags were in the reedbed on the leeward side of the mere, larvae would be carried away from the station.

Limnochironomus sp.

The commonest species found in emergence traps, was *Limnochironomus pulsus* (Walker); larvae were assumed to be this species. Two peaks of larvae occurred in the coarse bags and only one in the fine (Fig. 5:6) as was also found for *Cricotopus* and *Glyptotendipes*. Again, an adult emergence peak occurred around June/July and can account for the rise in second instars then. *Limnochironomus* appears to spend the winter as third instars and unlike *Cricotopus*, some larvae were found in the November samples.

Glyptotendipes sp.

Imagines of *G. pallens* were recorded from traps and it is probable that larvae were of this species. All four instars were clearly represented in the bags and again there were two peaks compared with one in the coarse and fine mesh bags respectively (Fig. 5:6). The majority of larvae spend the winter as fourth instars; the relatively large increase of second instars during March to June 1980 is quite different from the other chironomids and is probably a reflection of the inter-relationship between this species and *Phragmites*. When sorting the bags, it was apparent that virtually all the fourth instars

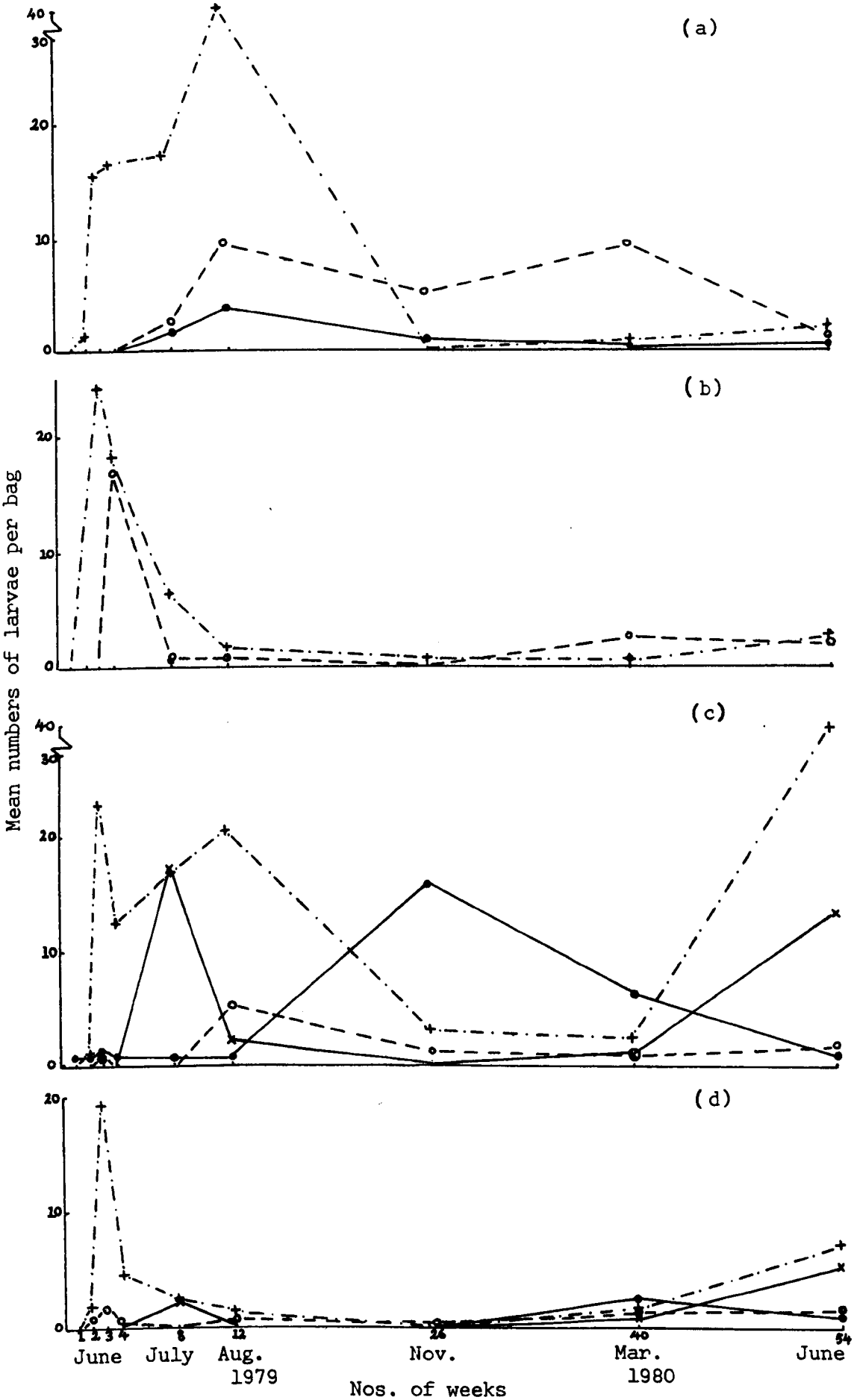

FIG.5:6 Changes in abundance of *Limnochironomus* larvae in(a) coarse and(b) fine mesh bags, and *Glyptotendipes* larvae in(c) coarse and(d) fine mesh bags. Symbols as in Fig.5:5.

found were living within the stems and simple gut preparations revealed a mixture of diatoms and some detrital particles (as found in chapter 4). *Glyptotendipes* larvae appear to use the stems as convenient tubes which would provide some protection from predators, a situation already described from observations on standing stems of *Phragmites*.

GENERAL DISCUSSION

The use of substrata, natural or artificial, to study decomposition and/or colonisation has become an accepted technique, but conclusions drawn from the data must always be viewed with an awareness of their limitations. Leaf packs as used by Petersen & Cummins (1974) and Suberkropp *et al.* (1976) are not as near to the natural situation as is necessarily assumed. For instance, Benfield *et al.* (1979) showed that processing coefficients ranged from fast to slow depending upon the exposure technique employed; pack size may constitute a major factor influencing leaf decay rate. Suberkropp *et al.* (1976) presented evidence that weight loss of packs was not due to fragmentation. However, it is likely that had the stems used in this study been tied together in a bundle, instead of being contained within bags, fragmentation (by caddis larvae for instance) would have constituted a major part of weight loss. Short pieces of broken stem were frequently found inside the bags which would have been lost in an unenclosed system. On the other hand, litter bags have their drawbacks too; Cummins *et al.* (1980) considered leaf packs to give a better indication of processing than leaves enclosed in mesh bags. Also, some chironomid species will have been using the bag material itself as a habitat - *Cricotopus* is likely to have constructed tubes on the mesh. Controls should be set up to assess the contribution to faunal colonisation made by this artificial effect, and indeed, Polunin (1979) found that 'blank bags'

were colonised by macroinvertebrates (though not to such an extent as those containing litter).

The decomposition of stems, as measured by weight loss, seemed to follow a diphasic pattern. There are at least three possible explanations for this, all of which could be operating:

1) The presence of invertebrates. Decay was faster (Phase 1) where there were more invertebrates present, and slowed down during the winter (Phase 2); from March to June 1980, it was possible that the decay rate increased again, and this was concurrent with immigration of animals during the spring. Loss from coarse bags was greater than from fine bags during Phase 1, and since numbers of animals in the coarse bags were greater during this period, it seems reasonable to conclude that the presence of invertebrates contributes towards an increased decay rate, and hence can influence the pattern of decay.

2) Water temperature. When this is higher it increases microbial metabolism, invertebrate activity and consequently decomposition. The greater rate of decay occurred during the summer months when the water temperature was higher.

3) Fast and slow fractions. The presence of fast and slow decomposing fractions in the litter (e.g. soluble carbohydrates cf. lignin) would also contribute towards a diphasic pattern of decay.

It is usual that reports in the literature assume constant decomposition rates described either by linear or exponential decay models (e.g. Petersen & Cummins, 1974; Howard-Williams & Davies, 1979; Polunin, 1979). Where a diphasic pattern is described, the first phase only lasts a month and a linear second phase follows (e.g. Mason & Bryant, 1975; Howard-Williams & Howard-Williams, 1978). In this study the first phase appeared to continue for two to three months before a slower decomposition rate became apparent. Litter breakdown thus

seems to be complex and variable, influenced by several different factors, and it seems likely that estimated decay rates will not be generally applicable but specific to the plant under investigation in the area studied.

It is generally assumed that plant litter needs a period of conditioning by microbial colonisation before it becomes acceptable to invertebrates as a food source. Petersen & Cummins (1974) have demonstrated a difference in the time taken for two species of leaf to be colonised by invertebrates and regarded this as indicative of a selection process by them, dependent upon the differential degree of microbial conditioning of the two leaf types. Although conditioning may be of importance in determining how quickly some invertebrates colonise, the increase and changes in populations of animals observed in this study, and those of Petersen & Cummins (1974) and Polunin (1979) may also be due to other factors not related directly to the conditioning of the litter.

For instance, *Glyptotendipes*, especially in its final instars, was found predominantly in the inside of stems where it was filter-feeding; larvae have evolved a close relationship with stems (see also chapter 4). The caddis, *Agrypnia*, similarly exhibits an association with the *Phragmites*, using it as convenient cases. *Cricotopus* larvae will feed mainly on the periphyton of fallen stems - the algal community would have been present throughout most of the life of the standing and fallen reed, and so conditioning is again probably not of importance in determining colonisation by *Cricotopus*. Animals, such as *Asellus* or *Gammarus*, which ingest the litter itself might be expected to show a lag phase before numbers build up after conditioning has occurred. However, there was no evidence in this study of any delay in colonisation by *Asellus*, or by invertebrates as a whole;

invasion of the litter bags was rapid, maximum numbers being reached after about 1-2 months.

It may be that colonisation and changes in populations were governed more by the season, or specifically the water temperature, than by conditioning. The bags in this study were placed in position in early summer and at this time of year, animal numbers and their activity will be greater than in winter. After the autumn, abundance of animals fell to a minimum during the winter months. Emigration from the bags is possibly a response to temperature, some invertebrates moving from an unpredictable, fluctuating, littoral environment in the winter, either to a more uniform sub-littoral zone or to stem bases and their roots as suggested previously (chapter 4). Increased water temperatures in the spring correlated with increasing numbers of animals in the bags.

The apparent absence of a lag phase before colonisation in this study contrasts with the findings of Petersen & Cummins (1974) and Polunin (1979). The former authors' work was in streams and cannot be easily compared with the present study. Polunin used *Phragmites* leaves, and placed his bags in the water during winter when numbers of animals would have been low. Maximum invertebrate numbers occurred after about 100 days with a peak around July; this compared favourably with the maximum numbers found in this experiment, although at Cop Mere the litter had only been in position for about one to two months. This suggests that the numbers of animals found in litter bags at Cop Mere, and possibly in other studies, is a reflection of the time of year, although a period of conditioning may be necessary for some organisms. In fact Polunin (1979, p.96) summarises his conclusions by saying that "Temporal and spatial variations in macroinvertebrate colonisation emphasises the difficulty of assessing the impact of macroinvertebrates on the process of Reed litter decay in nature".

He is, of course, correct.

In summarising here, however, a number of reasonable conclusions can be drawn as regards the decay of *Phragmites* stems in the littoral zone of Cop Mere.

Weight loss during the year does not occur at a constant rate; two simple linear phases have been recognised (although this may be an oversimplification). The litter remaining at the end of the year consists mainly of lignin and cellulose fractions. The role of invertebrates is likely to be one of comminution, of scraping, chewing and burrowing, all of which increase surface area and hence microbial populations and decomposition rates. Occasionally it will be a role involving enzymatic attack on macromolecules. Chironomids probably do not use the litter directly as a food, but rather as a habitat. Changes in animal numbers and rates of decay are ultimately determined by abiotic, environmental factors (e.g. time of year); proximal factors are more difficult to determine.

Chapter 6

ADULT EMERGENCE FROM COP MERE AND LINFORD

INTRODUCTION

Larval populations in the substratum and those associated with reedstems have been discussed in the previous three chapters. Capture of adult chironomids emerging from the reedbed augments studies of the larval populations, providing information regarding the species which are present, and their abundance and development through the year. Emergence of chironomids from reedbeds at Cop Mere (and Linford) was followed during 1979 and 1980 and the results are presented here.

Previous investigations have been largely concerned with emergence trapping of chironomids from profundal or sub-littoral zones of lakes, reservoirs and occasionally ponds. Rarely have traps been placed in littoral areas amongst emergent vegetation. Paasivirta (1974), in a production study of a Finnish lake, positioned some traps over sparse growth of sedges and rushes. Titmus (1979a) reports that one of his traps was placed over a stand of *Scirpus maritimus* L. in a lagoon area at Linford, Buckinghamshire. Presence of macrophytes in the reservoirs studied by Mundie (1957) and Potter & Learner (1974) was restricted to the margins and consisted primarily of floating-leaved plants. Learner & Potter (1974) monitored emergence from two small, shallow ponds in Hertfordshire; aquatic vegetation again consisted principally of floating-leaved macrophytes, although one pond was surrounded by a swamp of *Sparganium erectum* L.

Emergence has also been followed from pools and ponds in the northern tundra regions (Danks & Oliver, 1972), but these are rather specialised and unique habitats. Driver (1977) trapped adults from sixteen prairie ponds in Central Saskatchewan, Canada. He concluded

that the diveristy of plant species (which is affected by the permanency of the ponds in the summer drought) affects the diversity of chironomid species, the latter increasing from very temporary ponds to permanent ponds.

Thus there is a dearth of information concerning emergence of chironomids from reedbeds. The present chapter is in three sections. The first examines emergence from the *Phragmites* beds at Cop Mere. The second reports on possible differences in emergence that exist between different species of emergent macrophytes, and the third briefly discusses the possible influence of weather on adult emergence. These last two sections use data from samples collected at Linford where there are suitable stands of vegetation for comparison.

SECTION A. COP MERE EMERGENCE

METHODS

Emerging Chironomidae were captured using floating, surface box-traps similar to those used by Morgan *et al.* (1963), but with the modifications described by Titmus (1979). Trap construction was virtually identical to that used by Titmus and details are given by him. The traps differed in that only one sheet of glass was considered necessary (instead of two half-plates), and that these had a slightly smaller surface area (0.09 m^2). Discussions concerning the efficiency of such traps compared with others can be found in Morgan *et al.* (1963) and Potter & Learner (1974); in general it is considered that surface traps are more efficient than submerged ones; they also trap a greater number of individuals and species than submerged traps.

Boltac, a gum resin, was applied to the plate and adults caught in it were carefully removed and stored in acetone for identification. The chironomids were identified using the keys of Pinder (1978) and also Coe (1950).

In 1979, three traps at each station (S1 and S2) were used in the

reedbeds (Fig. 2:2, p. 6), from the beginning of June through to September. Traps were serviced weekly; each was moved slightly from its previous position and also cleaned of algae and invertebrates. Lateral movement of the traps was restricted by tying them to short lengths of cane driven into the substratum.

In 1980, two traps were used at both S1 and S2; additionally, one trap was placed in the open water zone just outside the reedbed at each station (traps OS1 and OS2). Emergence was monitored from April to September.

RESULTS AND DISCUSSION

Total emergence

Large differences in the numbers of imagines caught were often found between individual traps within a particular station, and this must be borne in mind below, where mean values from each station are presented when discussing emergence. Such differences are to be expected because of random variability, variability of the number of reeds contained within a trap, and variability in the abundance of larvae on stems (as found in chapter 4). For the purpose of comparison between the two stations, emergence figures from each trap at each station have been averaged; as shown below:

	1979	1980
means of traps at:	S1 1 + 2 + 3	1 + 2
	S2 4 + 5 + 6	4 + 5

In 1980 traps 3 and 6 were at OS1 and OS2 respectively and have been treated individually. Emergence has been expressed as numbers of adults caught per m^2 per day; raw data are given in Appendix Table A6:1.

Fig. 6:1 shows the pattern for total chironomid emergence for the sampling periods during 1979 and 1980. It is clear that in 1979 the

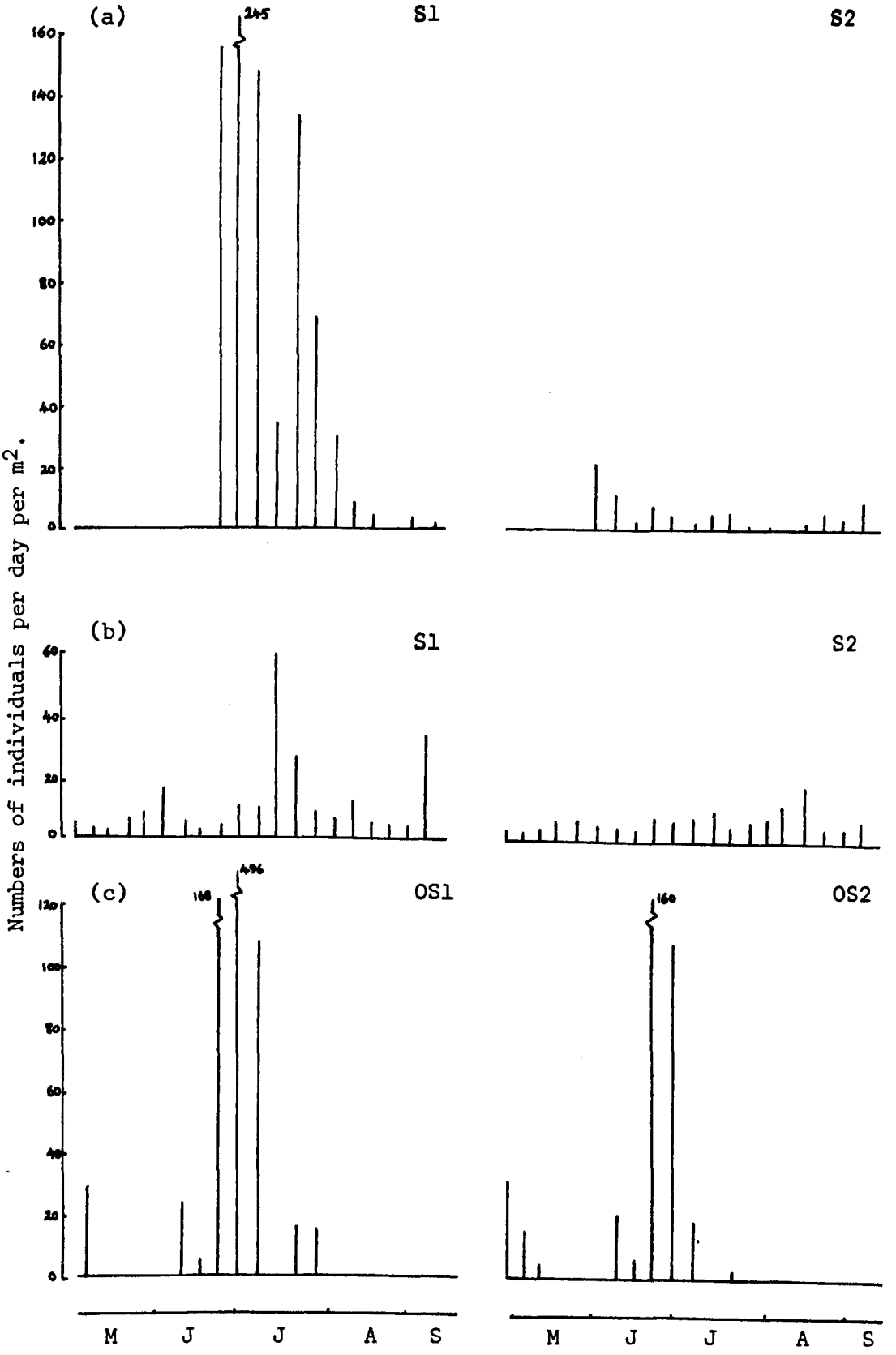

FIG.6:1 Total chironomid emergence at Cop Mere in 1979 (a) and 1980 (b)&(c) from trapping stations indicated.

number of adults at S1 was greater than at S2, and this observation concurs with the results presented in chapter 3 where numbers of larvae in the benthos were higher at S1 than at S2 in 1979. Peak emergence periods at S1 and S2 occurred in June/July (about 150 m^{-2} day^{-1} at S1); in addition a smaller peak occurred in September.

Sampling in 1980 began earlier; however, the pattern was different from that in 1979. Numbers of adults were generally lower throughout the study period, rarely exceeding about 20 m^{-2} day^{-1} at S1 or S2. Peak emergence was not as extended as in 1979, and also occurred later in July; again there was a minor peak in September. As happened in 1979, numbers of imagines emerging at S2 were less during 1980 than at S1. The weather conditions in the early summer of 1980 have already been discussed in chapter 2; they deteriorated at the end of May, with heavier rainfall than in 1979. The poorer climatic conditions at this time may have delayed emergence.

Traps 3 and 6, at open water stations OS1 and OS2, suffered from the exposed conditions and the glass plate was often lost due to strong winds and wave action. This makes comparison between the two stations difficult because of the missing data. However, peak emergence from these traps occurred at the end of June 1980, which was earlier than at S1 or S2. Peak emergence at OS1 was apparently greater than at OS2 (496 cf. 160 m^{-2} day^{-1}); but as discussed below, many of the imagines would have developed from larvae inhabiting filamentous algae collecting under the traps and the differences in numbers between traps may be a reflection of this rather than any real difference between stations.

Specific patterns in emergence from the reedbeds

Individual species and their emergence patterns are listed in Table 6:1 (p.101 & 102); nomenclature is according to Pinder (1978). Emergence from S1, S2 and the open water has been summarised separately

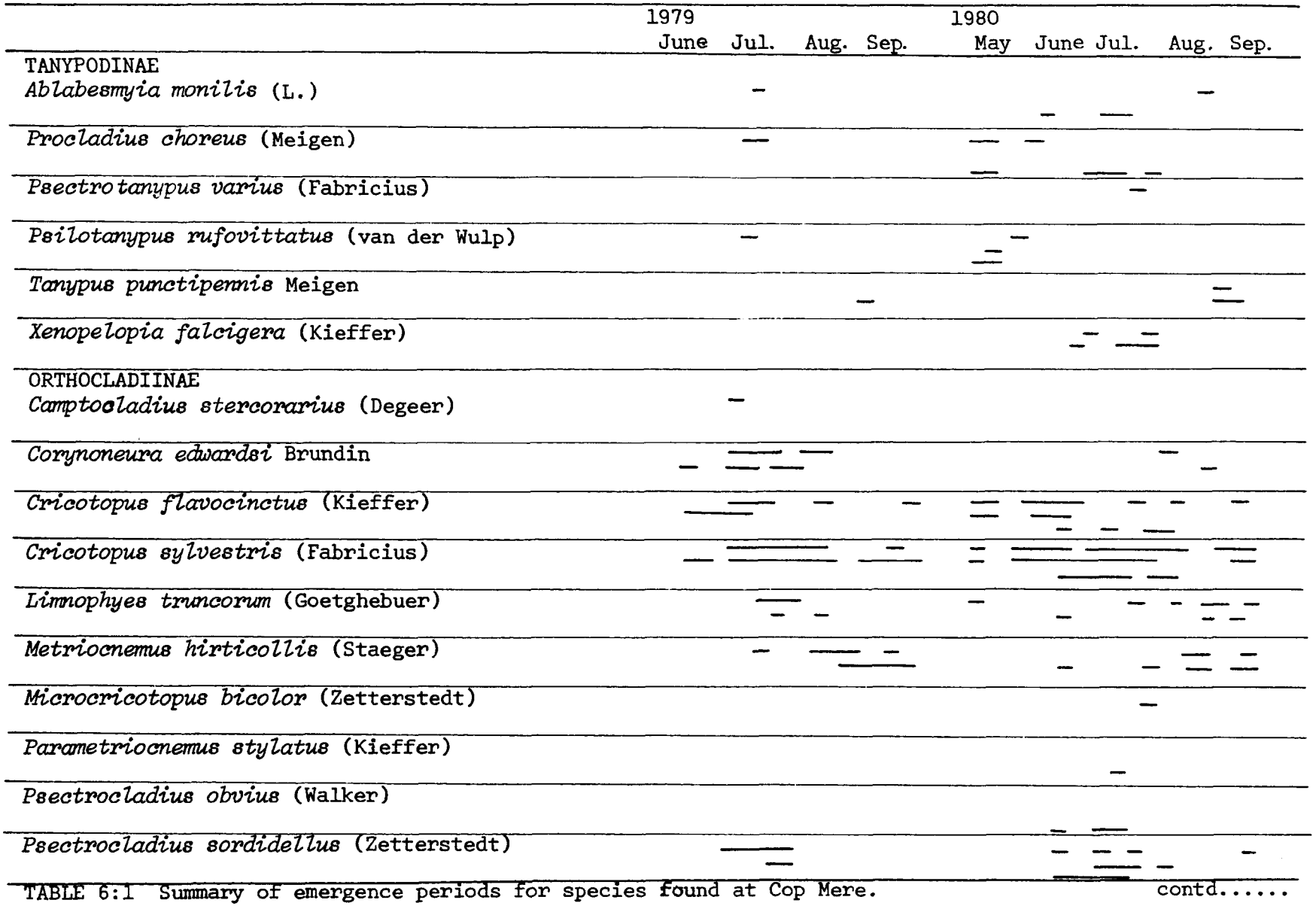

TABLE 6:1 Summary of emergence periods for species found at Cop Mere. contd.....

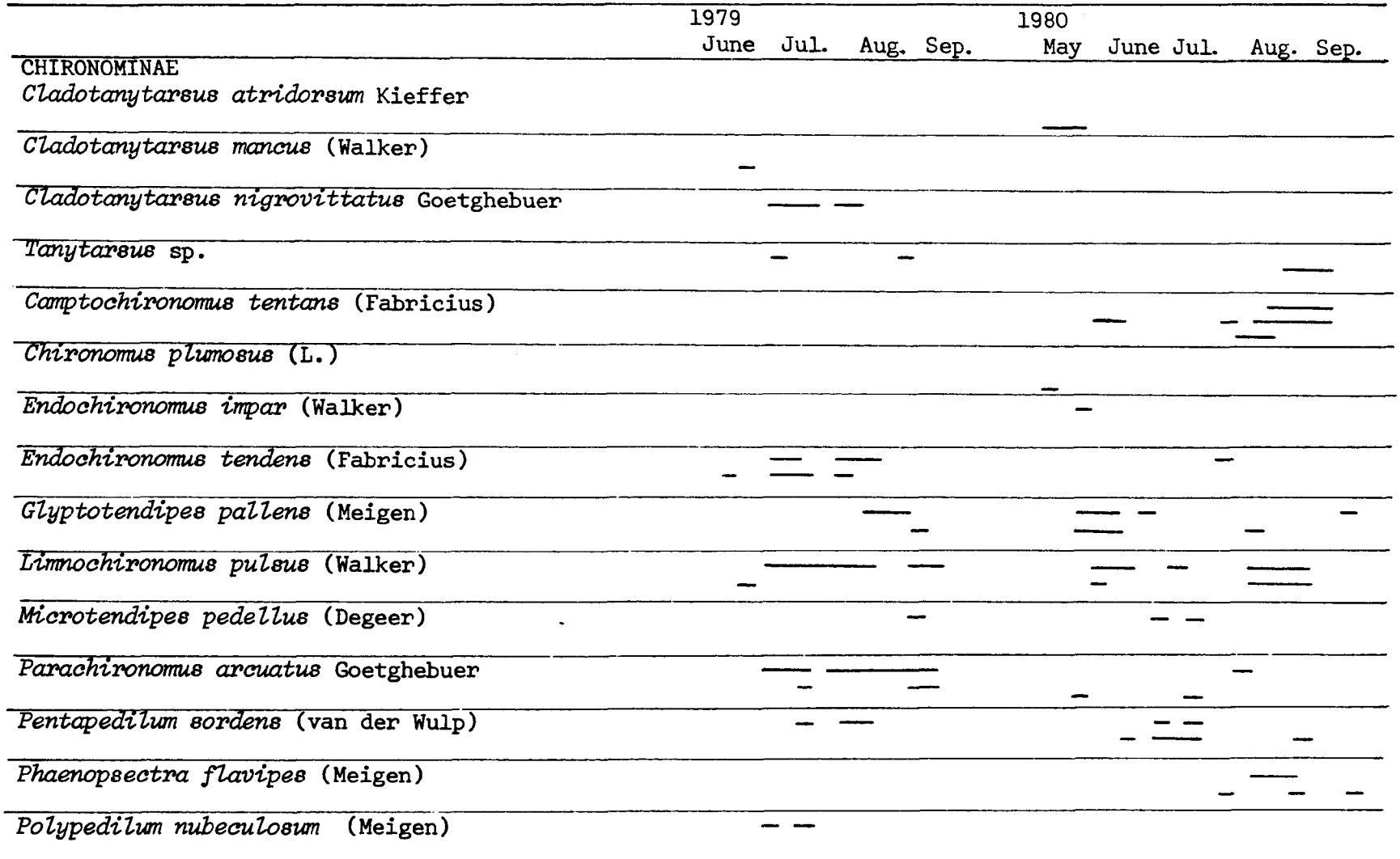

TABLE 6:1 Summary of emergence periods for species found at Cop Mere. Upper line represents emergence at S1 traps, middle line at S2 traps, lower line at open-water traps (OS1 and OS2 combined).

for each set of traps. A total of 31 species were identified during 1979 and 1980; 21 were found in 1979, 24 in 1980 with 17 species common to both years. Most species caught were from traps at S1 in both years.

Nine species were more common than the others present, although there were sometimes considerable inter-year differences in abundance of these species, which are now discussed.

Orthocladiinae

Cricotopus sylvestris

This was the commonest chironomid found in emergence traps; its emergence pattern is given in Fig. 6:2. It appeared to have an extended emergence period throughout the summer, but peaks occurred in July in both 1979 and 1980. An additional peak also occurred in September in both years. Emergence was less in 1980 and also less at S2 than at S1. The earlier start to trapping in 1980 revealed adults flying by April and May. These data correlate quite well with observations on larvae sampled from reedstems during 1980 (chapter 4). *C. sylvestris* may be quadrivoltine here, although emergence was almost continuous and generations may not have been discrete. The species has been described as quadrivoltine and univoltine by Learner & Potter (1974), trivoltine by Mundie (1957) and also bivoltine by Sandberg (1969) in Sweden.

It should be remembered that the differences in numbers of generations exhibited by a species are probably due largely to the different geographical locations of the study sites, where species in southern latitudes are able to pass through more generations a year because of higher temperatures and longer seasons.

Cricotopus flavocinctus

Adults appear to be flying earlier than *C. sylvestris*, though the pattern is different between S1 and S2 and between years (Fig. 6:3,

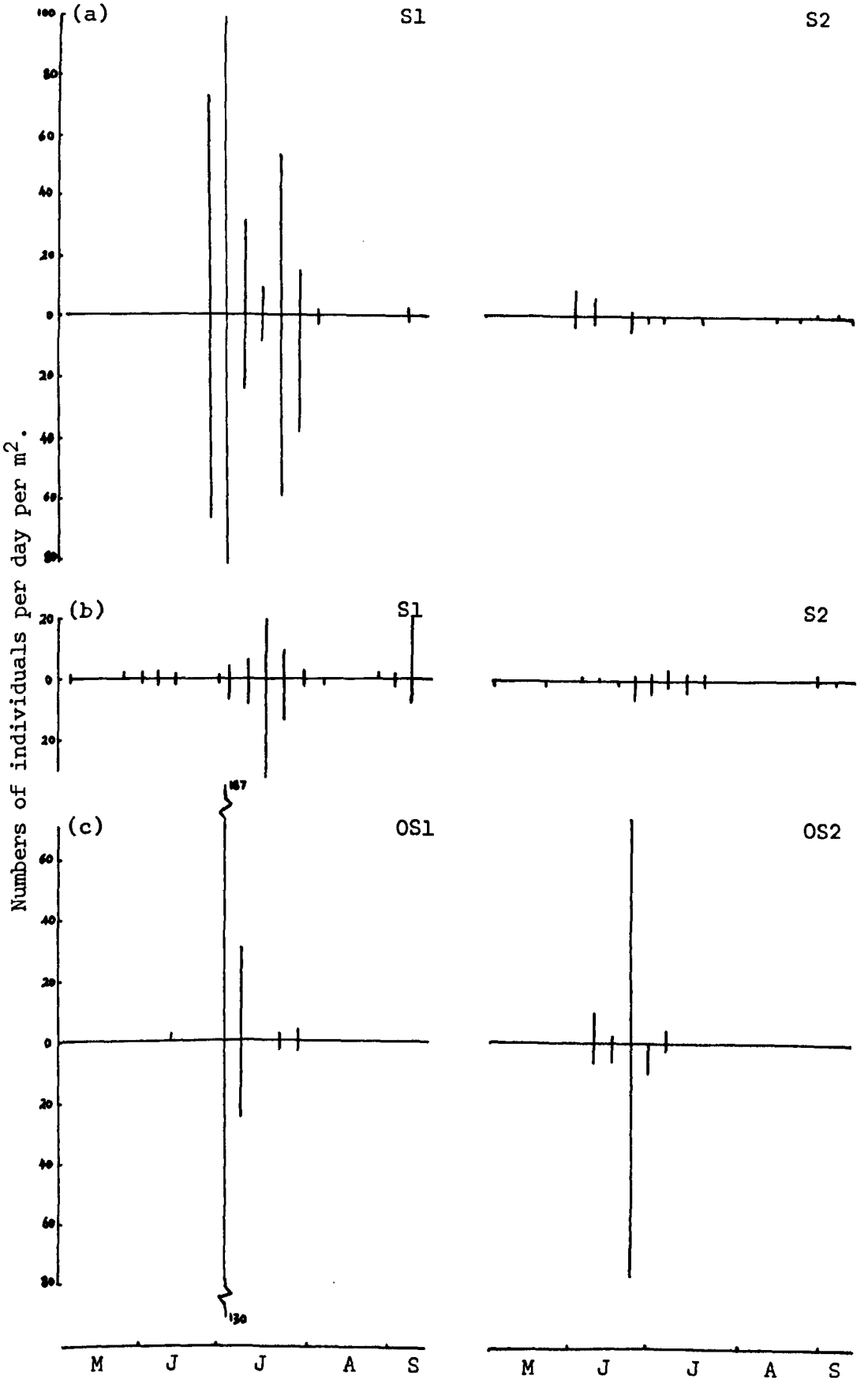

FIG.6:2 Emergence of *C.sylvestris* at Cop Mere in 1979 (a) and 1980 (b)&(c) from trapping stations indicated. Males are plotted above the axis, females below the axis.

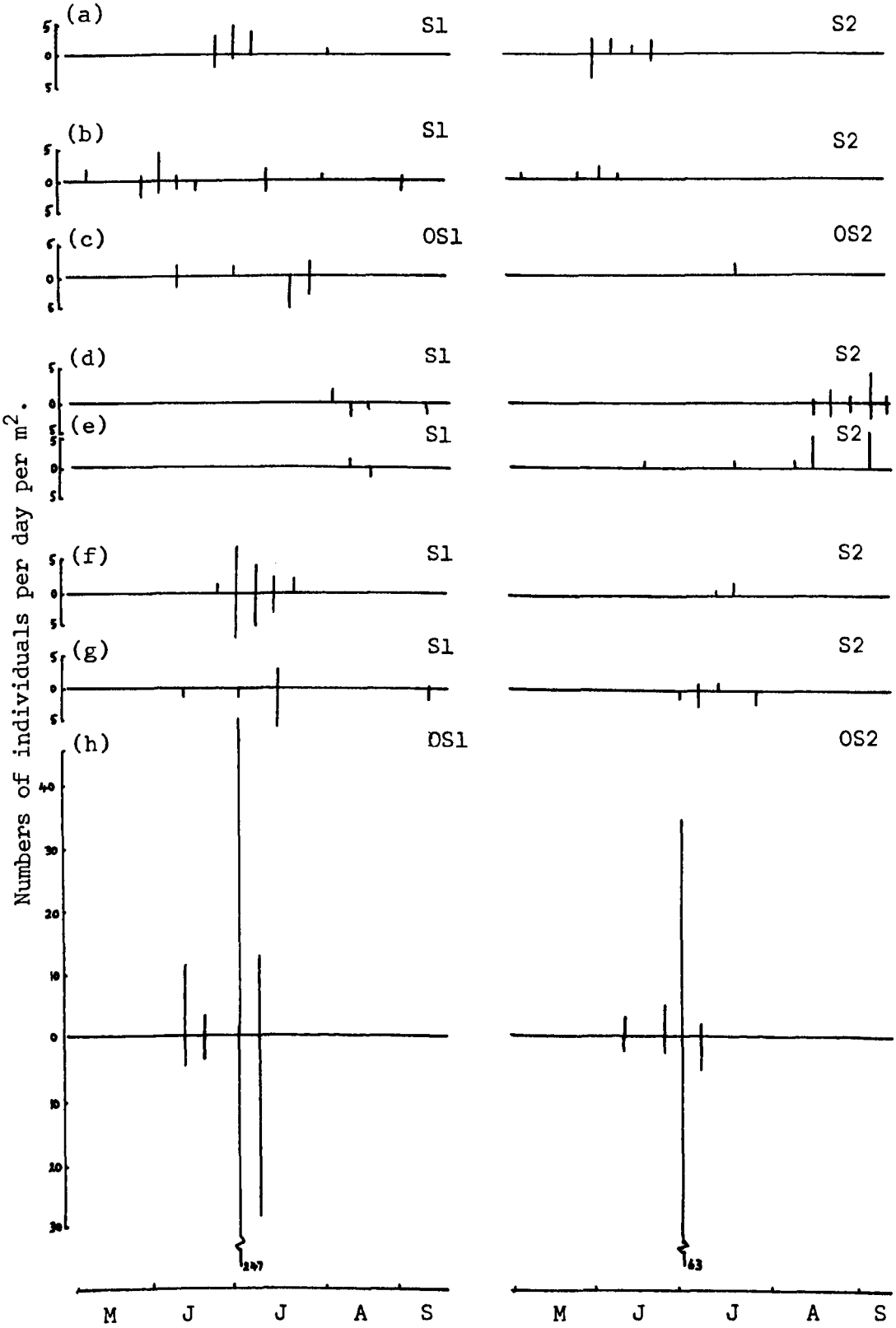

FIG.6:3 Emergence of *C.flavocinctus* at Cop Mere in 1979 (a) and 1980 (b)&(c), *M.hirticollis* in 1979 (d) and 1980 (e),*P.sordidellus* in 1979 (f) and 1980 (g)&(h), from trapping stations indicated. Males are plotted above the axis, females below the axis.

p.105). Sampling at S1 was not started until three weeks after S2 in 1979, and adults were probably present at both stations during this period. After June, adults were caught only at S1 in 1979. In contrast, no adults were taken during late June or early July 1980. Interpretation is difficult because of the low numbers trapped, but it is possible that the species has two or three generations a year. The life-history of *C. flavocinctus* seems to be mentioned in the literature only by Learner & Potter (1974) who record it as bi- or trivoltine.

Limnophyes truncorum

Numbers of this species were low; from Table 6:1 (p.101 & 102), it can be seen that most adults were caught in July 1979 or August 1980. Since some individuals were also captured in April and May 1980, it is likely that the species is bivoltine. There seems to be no reference to this species in the literature. Mundie (1957) recorded an undetermined member of the genus; Learner & Potter (1974) identified *Limnophyes prolongatus* (Kieffer) and *L. pulsillus* Eaton from the ponds they studied, and the former was thought to be bivoltine. Driver (1977) found *L.* cf. *vunalis* more commonly in temporary and semi-permanent ponds, where the latter contained emergent macrophytes.

Metriocnemus hirticollis

This species was commonest in both years during August and September; some adults were also trapped in June and July (Fig. 6:3). Compared with other chironomids it appears to have a later emergence period and was probably uni- or bivoltine. Learner & Potter (1974) considered it to be bi- or quadrivoltine.

Psectrocladius sordidellus

This species appeared to have a more discrete emergence period (in June/July) than other midges (Fig. 6:3). Emergence was greater

at S1 than at S2 in 1979; emergence during 1980 was sparse at both stations. A small emergence in September 1980 suggests that the species is possibly bivoltine. This is in agreement with data from larval populations on reedstems in chapter 4, though its peculiar temporal pattern in the larval stage has already been noted there. Sandberg (1969) found this species to be uni- or bivoltine as did Learner & Potter (1974).

Chironominae

Camptochironomus tentans

For the reason that this was the only common *Chironomus*-type adult trapped, larvae of the *C. 'plumosus'* complex found in samples were designated as this species. However, in spite of the considerable larval abundance, especially during 1980, very few adults were captured (only a few individuals per trap, or about 20-50 m^{-2}). As already described in chapter 3, adults of *C. tentans* were not found in traps during 1979 (Table 6:1, p.101 & 102); in 1980 the majority were caught in August, though they were also flying in late May and early June (Table 6:1). From analysis of the larval data and adult emergence it is probable that the species is bivoltine. *C. tentans* has been recorded from the reservoir studied by Potter & Learner (1974) and also the two ponds they sampled (Learner & Potter, 1974).

Glyptotendipes pallens

Similarly, this species was common in larval samples, but not as frequently found in traps as might have been expected. It had a similar emergence pattern to that of *C. tentans*, i.e. periods in May and in August/September (Table 6:1) and thus is bivoltine. Learner & Potter (1974) classed this species (*G. glaucus* Meigen in their paper) as uni- or bivoltine.

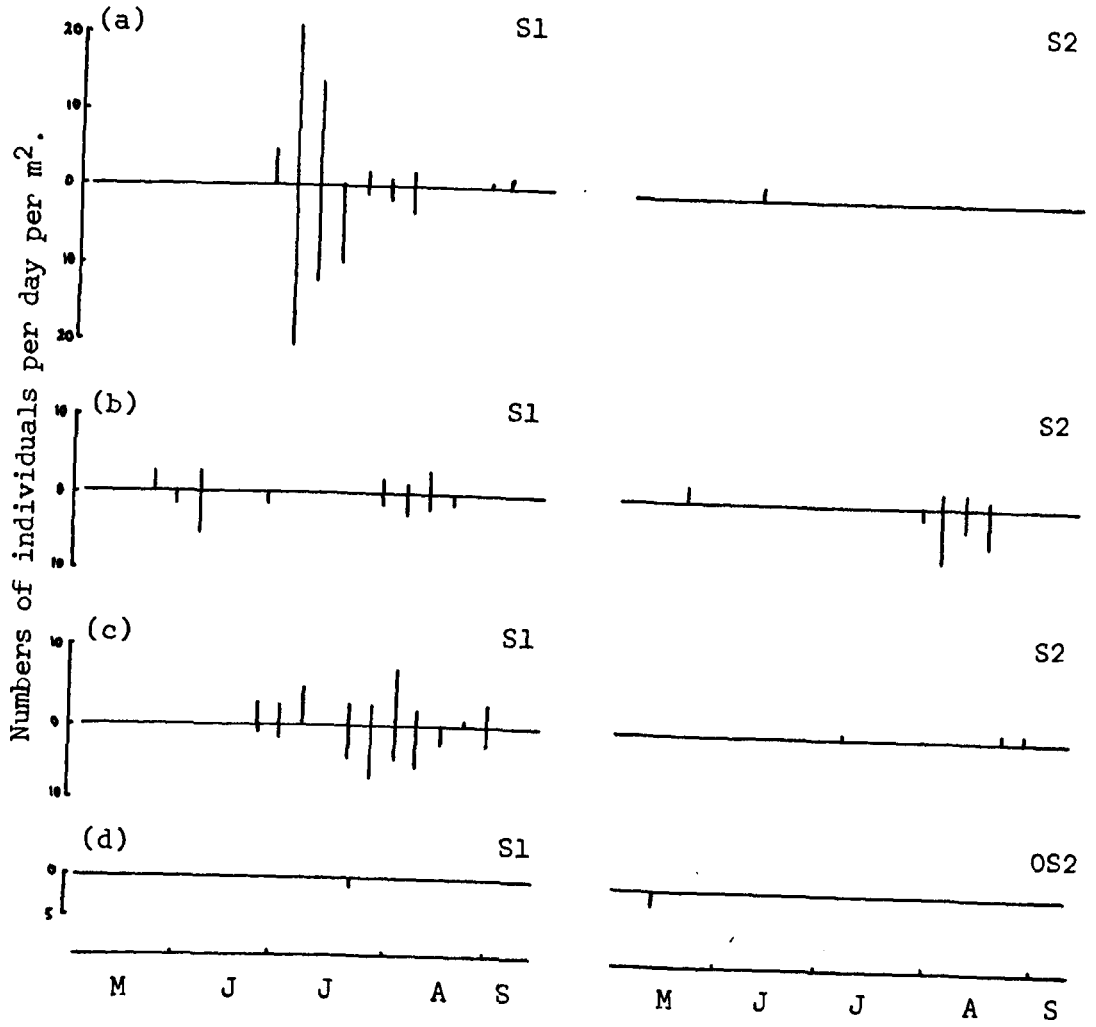

FIG.6:4 Emergence of *L.pulsus* at Cop Mere in 1979 (a) and 1980 (b), and *P.arcuatus* in 1979 (c) and 1980 (d) from trapping stations indicated. Males are plotted above the axis, females below the axis.

Limnochironomus pulsus

In common with the other chironomids, this species exhibited a later emergence period in 1980 than 1979, at both S1 and S2 (Fig. 6:4). Peak emergence was earlier in 1979 in July, and only at S1; in 1980 the peak occurred in August at lower densities at both S1 and S2. An earlier emergence in May indicates the species bivoltine. Potter & Learner (1974) recorded *L. pulsus* from Eglwys Nunydd Reservoir where it was bivoltine, and it was also found by Mundie (1957).

Parachironomus arcuatus

The species was very rare in 1980, compared with the emergence at

S1 in 1979 (Fig. 6:4). Its flight period at S1 occurred from June to September with no clear peaks, emergence being seemingly continuous. Imagines were virtually absent at S2 in 1979. Learner & Potter (1974) recorded the related species *L. parilis* as possibly quadrivoltine.

Species Emergence from the open water traps

During their operation in 1980 the two traps sampled 11 species (Table 6:1, p.101 & 102). Again, the most abundant species was *Cricotopus sylvestris*, but its peak emergence occurred about two weeks earlier here than in the reedbeds. Imagines would have arisen mostly from larvae living in the algal mats prevalent in the early summer which tended to get caught under the traps. The other abundant species were also the Orthocladiinae - *Psectrocladius sordidellus* was common and to a lesser extent so was *P. obvius* (Table 6:1). Both could have come from the mats of algae. Mundie (1957) reports that *Cricotopus* larvae were common in *Cladophora* around the margins of the reservoirs. Potter & Learner (1974) similarly noted that *Cricotopus* larvae can be carried into traps with blue-green algal blooms.

The Tanytarsini were represented predominantly by *Cladotanytarsus atridorsum* at OS1 and OS2 in late April/early May 1980 (Table 6:1). In contrast, *C. nigrovittatus* was not found in open water traps and was taken in reedbed traps during July 1979 but not in 1980 (Table 6:1). This genus has not been reported from littoral zones before, but is usually recorded from sub-littoral and profundal zones (e.g. Mundie, 1957; Potter & Learner, 1974).

The Tanypodinae were commonly represented in open water traps more than in reedbeds. *Procladius choreus* and *Psilotanypus rufovittatus* were common in late April/early May and the former also in July. *Ablabesmyia monilis* was also more common outside the reedbed than in it. Other workers have also recorded these species from sub-littoral and

profundal zones (e.g. Mundie, 1957; Potter & Learner, 1974; Titmus, 1979 a).

The main difference between the faunal assemblage from traps in the reedbed and those in the open water areas at Cop Mere was the greater number of species found in the former. This can probably be accounted for by the greater habitat diversity in the reedbed.

SECTION B. EMERGENCE FROM SIX DIFFERENT MACROPHYTES

In the previous sections it was noted that differences existed within the same stand of *Phragmites*, and also that the two areas of the reedbed at Cop Mere exhibited differences in species and abundance both intra- and inter-yearly. It was thought desirable to compare the emergence from the *Phragmites* bed at Cop Mere with that at another site to see what, if any, differences there might be. Additionally, does emergence of chironomids differ in abundance or species composition between different species of emergent aquatic macrophytes?

There is no suitable area of Staffordshire where stands of different species of reeds occur in any large quantity within the same lake. However, it proved possible to obtain samples of adults from six species of macrophytes within a lagoon area of a reclaimed gravel pit at Linford, Buckinghamshire. The ecology of midges in the sub-littoral and deeper waters of the gravel pit habitat has been studied by Titmus (1979), but he did not sample the chironomid population emerging from vegetated littoral zones, except for one trap in one year situated over a stand of *Scirpus maritimus*. Details of the gravel pit at Linford are given in Titmus (1979) and it is not necessary to repeat the information here.

METHODS

Emergence was monitored from six species of reed during the summers

of 1979 and 1980 (April to August). Two traps were placed in stands of each reed-type and Fig. 2:6 (p.14) indicates the actual positions of the traps at Linford within the gravel pit lagoon area. Table 6:2 below summarises the details of the positions of the 12 traps. Note that traps L5 and L8 and L2 and L10 were in different stands of their

TRAP	PLANT SPECIES	POSITION
1, 9	*SPARGANIUM ERECTUM* L. (Bur reed)	in same stand
2, 10	*SCIRPUS MARITIMUS* L. (Sea-Club Rush)	in different stands
3, 11	*TYPHA LATIFOLIA* L. (Reedmace)	in same stand
4, 12	*CAREX RIPARIA* Curt. (Pond Sedge)	in same stand
5, 8	*GLYCERIA MAXIMA* (Hartm.) Holmberg (Reed Grass)	in different stands L5 moved into lagoon in 1980
6, 7	*PHRAGMITES AUSTRALIS* (Cav.) Trin. ex Steud. (Common Reed)	in same stand

TABLE 6:2 Positioning of traps at Linford, 1979 and 1980

respective species; also that trap L5 was repositioned inside the lagoon area in 1980, rather than adjacent to Black Horse Lake.

The traps used at Linford were slightly larger (0.1 m^2 surface area) but trap operation was similar to that in Cop Mere. They were positioned over cut reedstems and plates removed weekly during 1979, but every 2 or 3 days in 1980. This increased frequency of sampling enabled analysis of the possible influence of weather on emergence and is described in the next section. Traps were repositioned every 2 weeks. Emergence was monitored for 16 weeks each year.

In order to check whether the substratum differed greatly between stands, sediment analysis was carried out as already described in chapter 2.

RESULTS AND DISCUSSION[1]

Comparison of species of chironomid associated with different macrophytes

The primary concern of Section B is to consider any differences in total emergence or species composition between the six species of reed sampled at Linford; there will be no detailed consideration of the emergence periods of individual species. Table 6:3 summarises the data from Linford, listing the species of chironomid found and indicating their emergence periods. A total of 52 species were identified during 1979 and 1980, the Orthocladiinae being the most numerous in terms of abundance, although the Chironomini had most species represented. The commonest chironomids trapped were *Cricotopus flavocinctus*, *C. sylvestris* and *Limnophyes truncorum*; all three were present at high densities throughout the season. At certain times *Corynoneura edwardsi* and *C. scutellata* were also abundant. The commonest of the Chironomini were *Chironomus cingulatus*, *Parachironomus arcuatus* and *Pentapedilum sordens*; the last named was at very high densities in *Sparganium* during July 1980.

The percentage of the total numbers represented by each subfamily did not differ considerably between reed types; however, *Carex* and *Glyceria* appeared to have had the least number of species (Table 6:4, p.116). There did not seem to be any specific association between a chironomid species and a particular macrophyte, except perhaps for *Pentapedilum sordens* which was found more commonly on *Sparganium*, *Scirpus* and *Phragmites*.

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1 Owing to the substantial amount of raw data (i.e. the numbers of males and females of each chironomid species for each sampling occasion from each reed trap in 1979 and 1980), they cannot be reduced effectively for inclusion in the Appendix; they are available on request. However, the total numbers of imagines on each sampling occasion from each reed trap have been included in Appendix Table A6:2 since these data are discussed in greater detail than are the chironomid species themselves.

	1979 May	June	Jul.	Aug.	1980 May	June	Jul.	Aug.
TANYPODINAE								
Ablabesmyia monilis (L.)		–	–			—		——
Clinotanypus nervosus (Meigen)				—		—		
Guttipelopia guttipennis (van der Wulp)							—	
Procladius choreus (Meigen)	——	——	——	——	——	——	——	——
Psectrotanypus varius (Fabricius)			–				——	—
Psilotanypus lugens (Kieffer)					—			
Tanypus punctipennis Meigen		– –	——		–		—	——
Tanypus vilipennis (Kieffer)		–						–
Trissopelopia longimana (Staeger)			— —					
Xenopelopia falcigera (Kieffer)								—
ORTHOCLADIINAE								
Acricotopus lucens (Zetterstedt)	——	——						
Bryophaenocladius aestivus Brundin					—		— —	
Corynoneura edwardsi Brundin	——	——	——	——	—	—	——	——
Corynoneura scutellata Winnertz				—			—	——
Cricotopus flavocinctus (Kieffer)	—	——	——	——		——	——	——
Cricotopus obnixus (Walker)	–	–	—					
Cricotopus sylvestris (Fabricius)	——	——	——	——	–	——	——	——
Limnophyes truncorum (Goetghebuer)	——	——	——	——	——	——	——	——

TABLE 6:3 Summary of emergence periods for species found at Linford.

contd.....

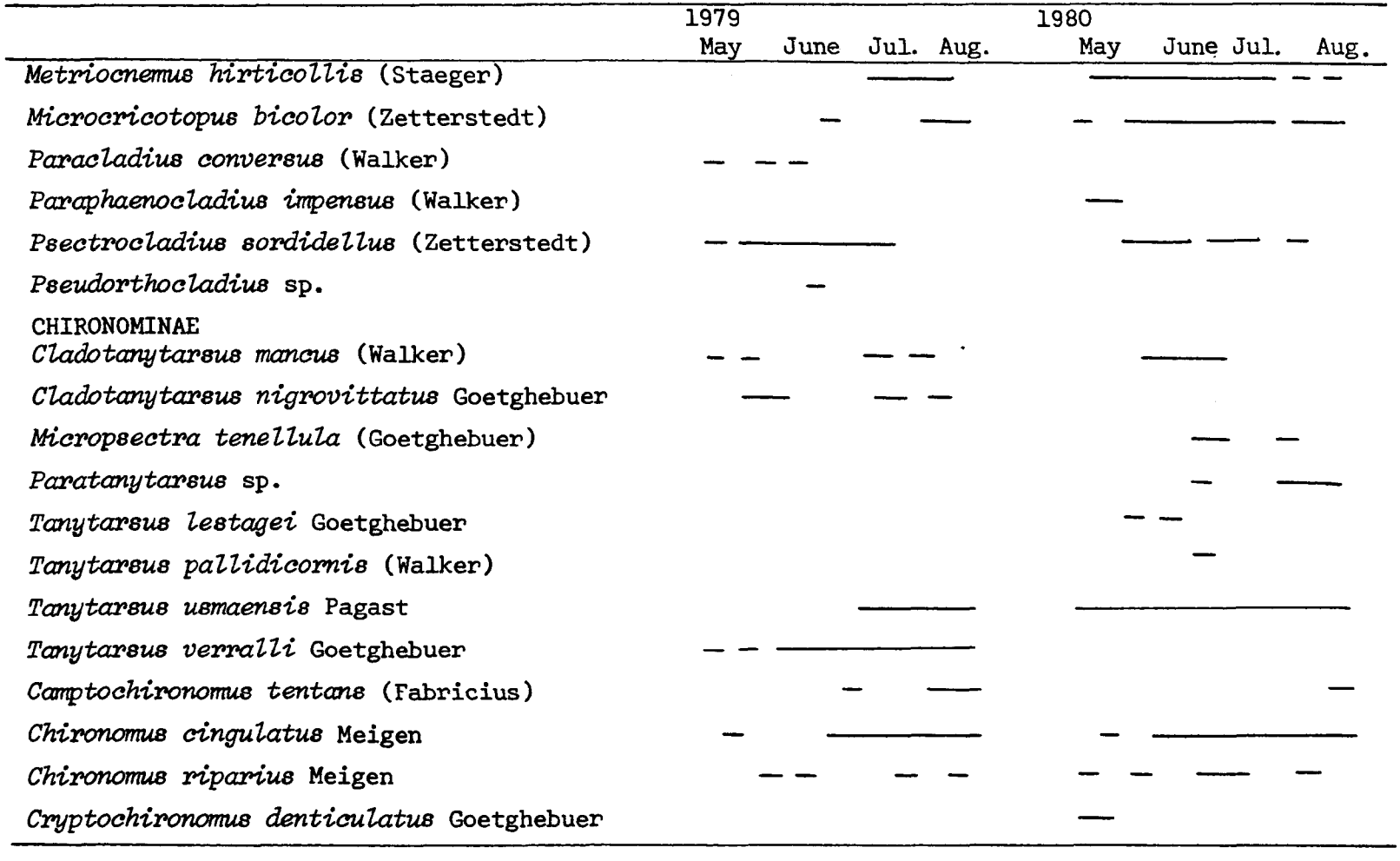

TABLE 6:3 Summary of emergence periods for species found at Linford. ....contd.....

	1979 May	June	Jul.	Aug.	1980 May	June	Jul.	Aug.
Endochironomus impar (Walker)		———	———		———	———	———	
Endochironomus tendens (Fabricius)	———	———	———		———	———	———	
Glyptotendipes foliicola Kieffer					—			
Glyptotendipes gripekoveni (Kieffer)	–		—	– –		–	— –	——
Glyptotendipes mancunianus(Edwards)				–		– –	———	———
Glyptotendipes pallens (Meigen)			–	——				—
Limnochironomus pulsus (Walker)							—	–
Microtendipes nitidus (Meigen)						———		
Microtendipes pedellus (Degeer)		———	———				–	———
Parachironomus arcuatus Goetghebuer	———	———	———		———	———	———	
Parachironomus parilis (Walker)	—	—					–	
Parachironomus tenuicaudatus (Malloch)						——		—
Pentapedilum sordens (van der Wulp)	– –	———	———		—	———	———	
Phaenopsectra flavipes (Meigen)		–	———			—	———	
Polypedilum acutum Kieffer						–	——	
Polypedilum nubeculosum (Meigen)		———			–	——	—	

TABLE 6:3 Summary of emergence periods for species found at Linford.

Reed	(Trap)	Nos. species	Percentage Tanypodinae	Orthocladiinae	Tanytarsini	Chironomini
1979						
Sparganium	(1)	20	2	55	8	35
	(9)	14	1	82	1	16
Scirpus	(2)	25	2	53	8	37
	(10)	21	2	31	12	55
Typha	(3)	21	1	52	29	18
	(11)	22	5	67	12	16
Carex	(4)	17	4	70	3	23
	(12)	18	6	74	3	17
Glyceria	(5)	19	3	74	2	21
	(8)	18	5	56	8	31
Phragmites	(6)	23	5	53	3	39
	(7)	26	4	50	4	42
1980						
Sparganium	(1)	24	2	54	10	34
	(9)	27	3	40	3	54
Scirpus	(2)	32	2	84	1	13
	(10)	29	2	70	7	21
Typha	(3)	21	3	79	6	12
	(11)	24	2	81	8	9
Carex	(4)	23	2	60	14	24
	(12)	26	4	42	28	26
Glyceria	(5)	20	1	61	27	11
	(8)	18	1	57	17	25
Phragmites	(6)	18	16	66	3	15
	(7)	26	8	53	13	26

TABLE 6:4 Numbers of species of chironomid found in each reed-type at Linford during 1979 and 1980, together with percentages of each subfamily or tribe represented in total number of individuals caught.

		Numbers of individuals (m^{-2})			
		1979		1980	
Reed	(Trap)	Total	Mean	Total	Mean
Sparganium	(1)	1570	2450	5090	9910
	(9)	3330		14730	
Scirpus	(2)	8450	6270	12420	8935
	(10)	4090		5450	
Typha	(3)	1890	2700	3990	4460
	(11)	3510		4930	
Carex	(4)	4680	3245	3010	3235
	(12)	1810		3460	
Glyceria	(5)	8780	5430	3290	2780
	(8)	2080		2270	
Phragmites	(6)	5230	5085	2890	2950
	(7)	4940		3010	

TABLE 6:5 Total numbers and mean numbers of chironomids caught during sampling period in 1979 and 1980 from each reed-type.

Differences in abundance between the reed-types

The variability exhibited between reed types in terms of the numbers and species of chironomids emerging from each is in part due to the factors mentioned previously for Cop Mere, i.e. variation in the number of stems contained within each trap and differences in larval abundances between stems. In addition, some data are missing, often during peak emergence times, owing to trap destruction or plate loss.

As shown in chapter 2 there did not seem to be any major differences between the substrata within the reedbeds, and it is unlikely that any small differences between substrata contributed to the large-scale variability seen.

Table 6:5 presents the total numbers of midges and mean number emerging from each reed type in 1979 and 1980. Figs. 6:5 to 6:9 show the total emergence pattern during the two years from each reed species. Raw data are given in Appendix Table A6:2. Interpretation of these results has to be considered carefully in view of the inter-trap and inter-year variability.

Monthly totals of emergent imagines were calculated for each trap. On comparing these totals for replicate traps within the same reed (e.g. traps L1 & L9), no significant differences ($p > 0.05$) were found between the replicate traps for any of the six reeds during 1979 or 1980.

Therefore monthly totals from both traps within a reed type were grouped and treated as one sample. The six samples resulting were then compared using a Kruskall-Wallis analysis of variance (Siegel, 1956) to test the null hypothesis that no difference existed between mean numbers of imagines caught from the six different reed species. For both 1979 and 1980 the 'H' values were not significant ($p > 0.05$) and so the null hypothesis could be accepted.

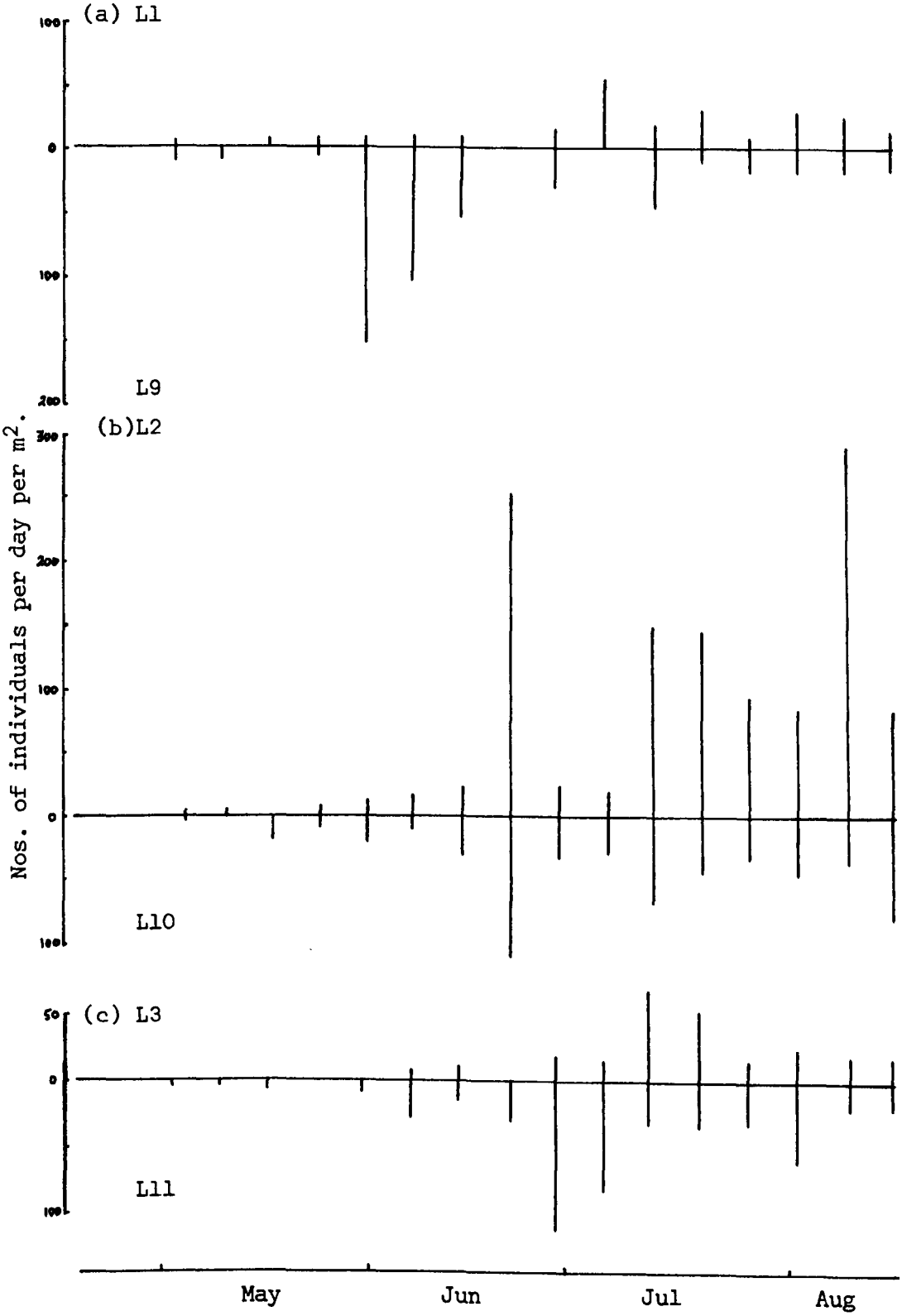

FIG.6:5 Total Chironomidae Emergence at Linford in 1979 from *Sparganium* (a), *Scirpus* (b) and *Typha* (c). Replicate traps indicated above and below the axis.

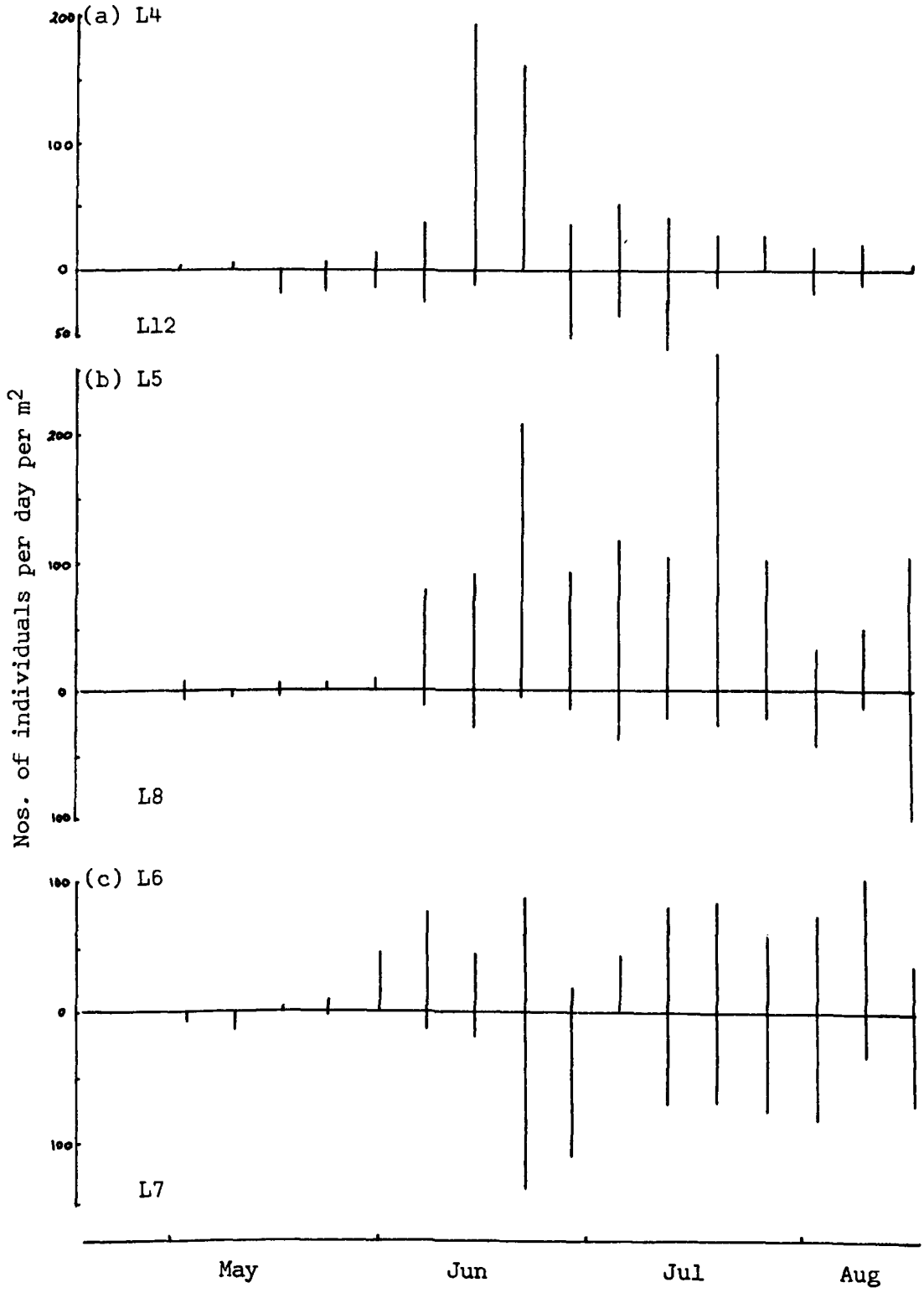

FIG.6:6 Total Chironomidae Emergence at Linford in 1979 from *Carex* (a), *Glyceria* (b) and *Phragmites*(c). Format as in Fig.6:5.

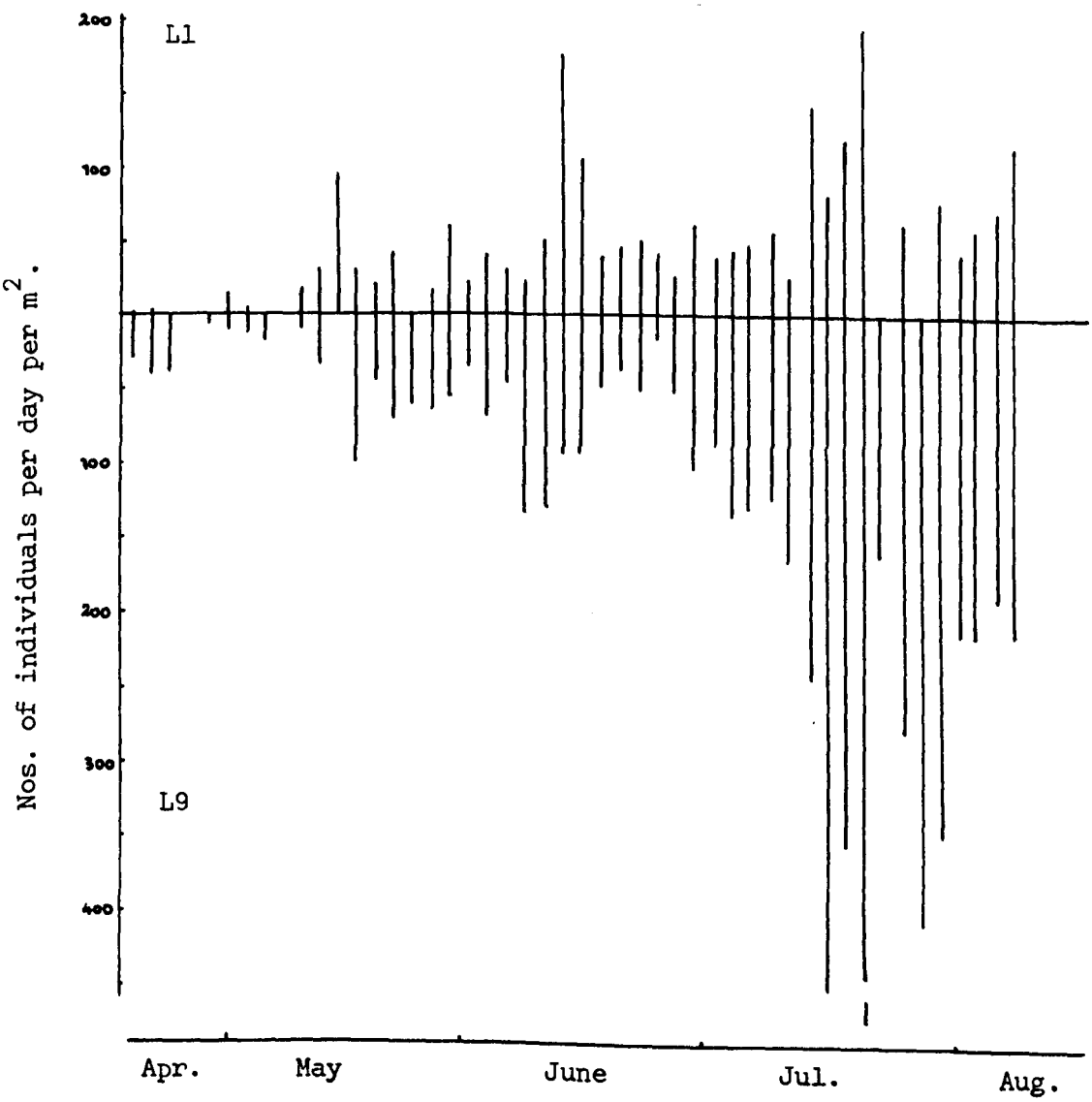

FIG.6:7 Total Chironomidae Emergence at Linford in 1980 from *Sparganium*. Format as in Fig.6:5.

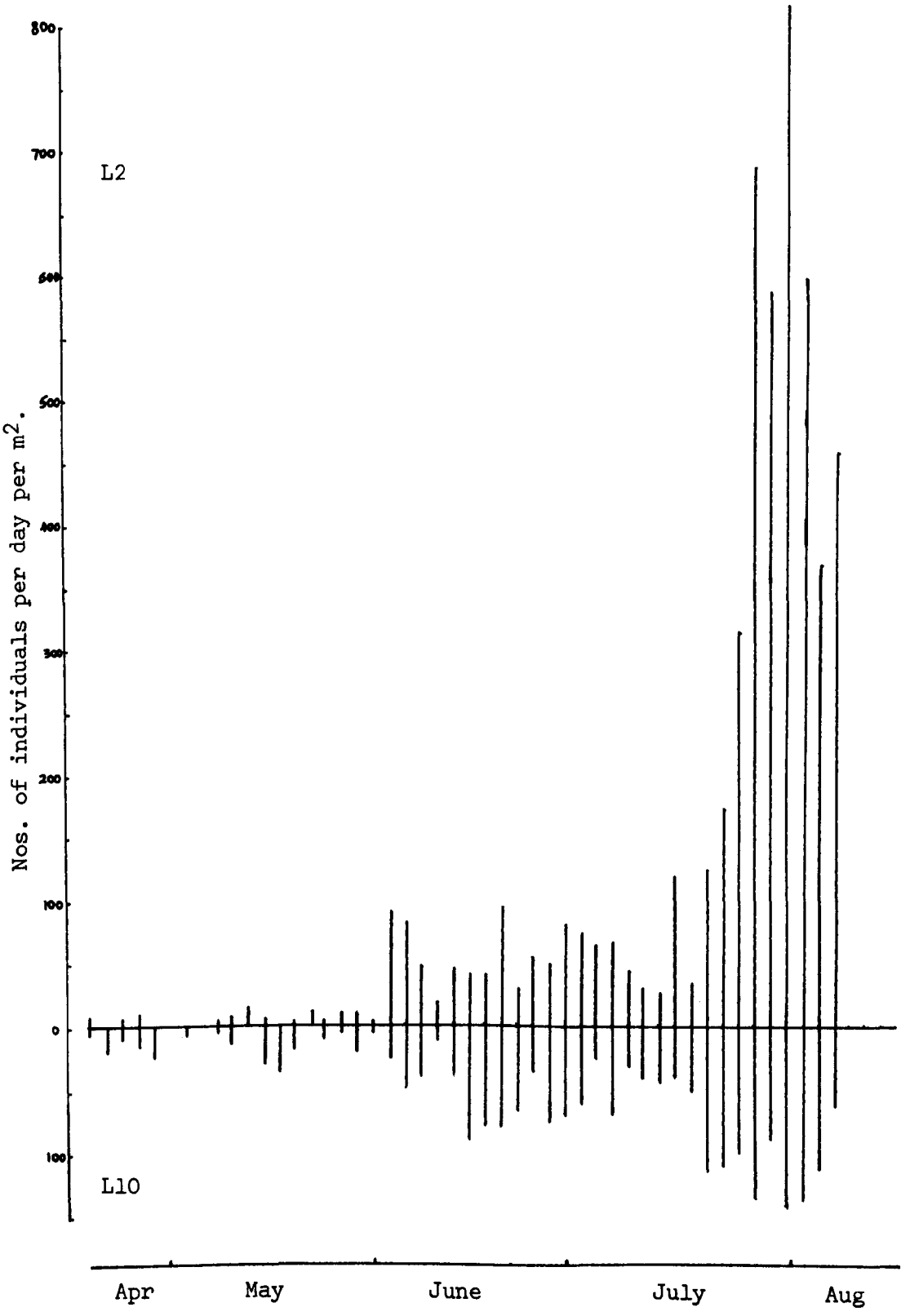

FIG.6:8 Total Chironomidae Emergence at Linford in 1980 from *Scirpus*. Format as in Fig.6.5.

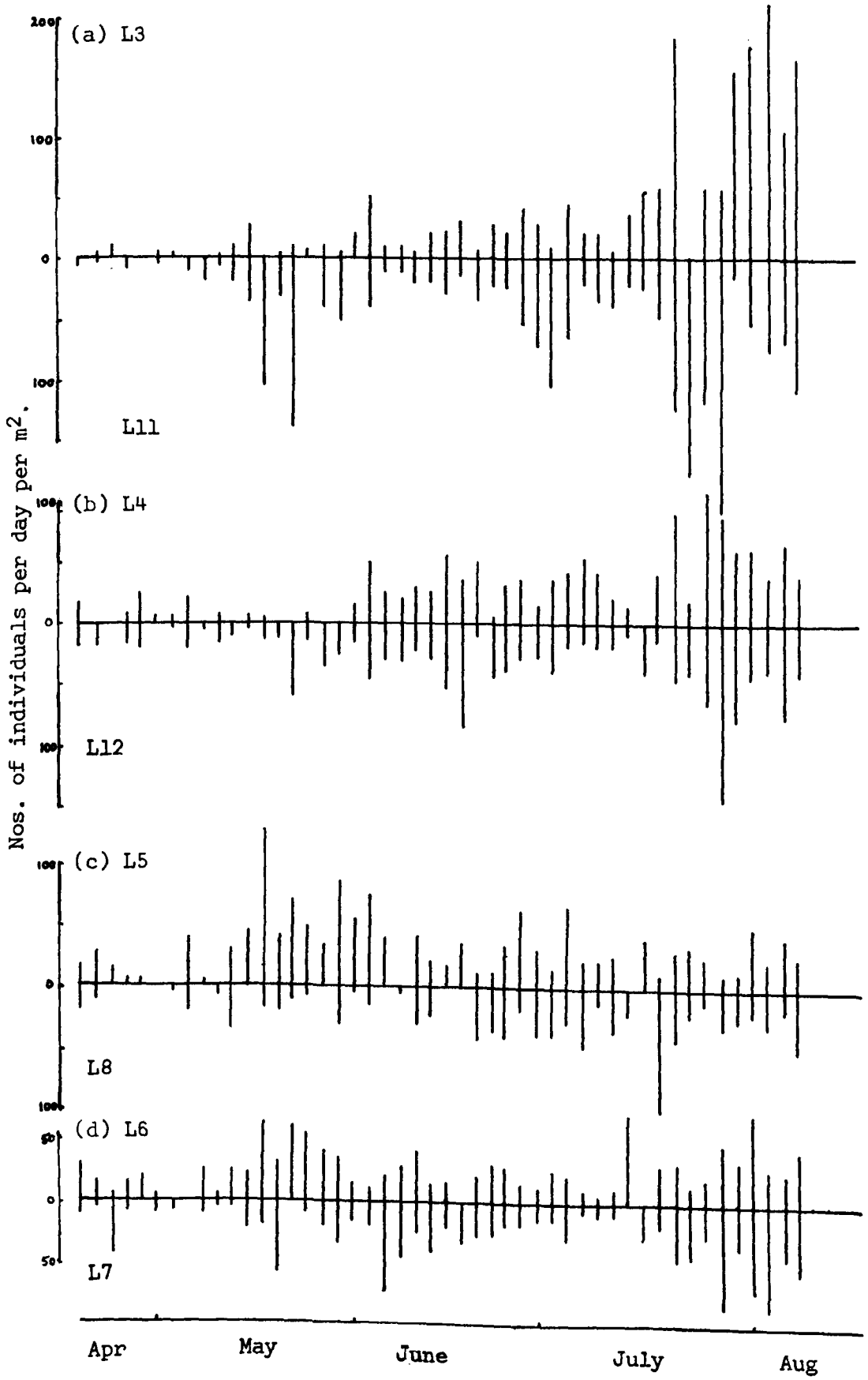

FIG.6:9 Total Chironomidae Emergence at Linford in 1980 from *Typha*(a), *Carex*(b), *Glyceria*(c) and *Phragmites*(d). Format as in Fig.6:5.

Thus, despite the apparently large differences in total emergence from the reed types during 1979 and 1980, (e.g. *Scirpus* in both years), these are not significant.

Emergence from *Phragmites* at Cop Mere and Linford

Owing to the lack of reported studies of emergence from *Phragmites* or other reedbeds, it is not possible to make many observations about the generality of the results presented here. However, some indication may be gained by comparing *Phragmites* beds at Cop Mere and Linford.

At S1 in Cop Mere in 1979 and 1980, peak emergence and total emergence were similar to that at Linford. In 1980 emergence was less than in 1979 at both sites, as the following table shows:

	YEAR	TRAPPING PERIOD	NUMBERS EMERGING
COP MERE S1 mean of 3 traps	1979	13 weeks	5960 m^{-2}
	1980	20 weeks	1606 m^{-2}
LINFORD mean of 6 & 7	1979	16 weeks	5085 m^{-2}
	1980	16 weeks	2950 m^{-2}

TABLE 6:6 Abundance of chironomids emerging from *Phragmites* at Cop Mere and Linford, 1979 and 1980

The number of species found in Cop Mere and Linford *Phragmites* beds were 29 and 36 respectively, although out of a total of 43 species in two years, only 22 were common to both sites. In general, genera at Linford were represented by more than one species, e.g. *Parachironomus arcuatus*, *P. parilis* and *P. tenuicaudatus*. Linford had more representatives of the Chironominae than Cop Mere - the less sandy nature and greater organic content of substrata in the benthos at Linford (chapter 2) may favour the larger, generally detritivorous Chironominae. The Orthocladiinae, many of which are associated with

the reedstems themselves, e.g. *Cricotopus, Psectrocladius, Limnophyes, Metriocnemus,* were common to both sites. Any differences in fauna might be expected, given the contrasting nature of the two sites and their differing geographical locality.

SECTION C. ENVIRONMENTAL FACTORS AFFECTING EMERGENCE

The emergence pattern of adult midges often showed large fluctuations over short periods at Cop Mere and Linford. It has already been noted previously that climatic conditions possibly affected larval distribution and also delayed emergence. This section briefly examines environmental factors (the weather) affecting emergence, to see if the short-term fluctuations could be accounted for by weather conditions.

METHODS

The samples analysed were those taken at Linford during 1980, that is 48 samples over a period of 16 weeks. The meteorological data were obtained from the station at Silsoe, about 25 Km from Linford. The relative importance of each of the five factors examined on numbers of chironomids emerging was assessed using a backward elimination procedure for multiple regression as described in Pollard (1977). The calculations involved were carried out using a multiple regression programme available at Keele Computer Centre.

The numbers of flies present in each trap on any one sampling occasion represented the sum of emergence, not only from part of the day of servicing (the time of servicing during the day varied), but also from the previous 2 or 3 days' emergence. Thus, an average value (per day) of each independent variable (except VI) for the 2 or 3 days prior to servicing was calculated and compared with the average emergence (numbers per day) during this period. Emergence from all six reed types was summed and the mean daily emergence used as the dependent variable in the regression equation. The independent

Regression equation	Residual sum of squares R_{ss}	Term removed	Increase in R_{ss}	F
V1+V2+V3+V4+V5	3560411	V1	1343690	$F_{1,42}=15.85$
		V2	21433	$F_{1,42}=0.25$
		V3	27520	$F_{1,42}=0.33$
		V4	58935	$F_{1,42}=0.70$
		V5	13042	$F_{1,42}=0.15$
V1	3756441	-	-	$F_{1,46}=97.04$

TABLE 6:7 Summary of steps in the backward elimination procedure (see text for explanation of symbols).

variables used were: V1) number of days since the start of the trapping period (i.e. the end of April), V2) average daily hours of sunlight, V3) average daily wind speed, V4) average minimum temperature and V5) average maximum temperature.

RESULTS AND DISCUSSION

Table 6:7 gives a summary of the calculations involved in determining the 'best' regression equation by the backward elimination procedure. For instance if variable V1 were removed from the model, the increase in the residual sum of squares is large and significant ($F = 15.85$, $p < 0.001$), indicating that this variable is important. On the other hand, removing V5 results in a low increase of residual sum of squares and this is not significant ($F = 0.15$, $p > 0.05$), indicating the factor not to be of importance to the regression equation. Therefore, from the first stage model (number of emerging flies (y) = V1 + V2 + V3 + V4 + V5) the next (and final) model can be written as y = V1, since removing any of the other variables does not result in a significant increase in the residual sum of squares. Thus V1, number of days since the start of the trapping period, is the single most important factor determining the time of emergence of midges. These conclusions support those of Mundie (1957) and Titmus

(1979). However, in contrast to the latter author, no significant correlation was found between sunlight and emergence.

GENERAL DISCUSSION

From the data presented here it would seem that the reedbed environment supports a chironomid fauna somewhat different from that in open water zones, there tending to be more Orthocladiinae species in the reeds, although large numbers of the Orthocladiinae may occur in the open water zones where there are suitable substrata, e.g. algal mats, as shown by the greater emergence from open water traps containing algae.

A comparison of adults sampled from the open water zones of the gravel-pit at Linford by Titmus (1979a) with those species taken from the reedbeds in this study indicates that the Orthocladiinae were commoner in the latter (Table 6:8). Similarly, the studies of Mundie (1957) and Potter & Learner (1974) show fewer species of the Orthocladiinae relative to the Chironomini in open water zones (Table 6:8).

TAXA	Reedbeds[1]	Open water[2]	Eglwys Nunydd[3] (open water)	KPER[4] (open water)
TANYPODINAE	10	9	4	4
ORTHOCLADIINAE	14	9	6	5
CHIRONOMINI	20	24	17	15
TANYTARSINI	8	5	7	6
TOTAL	52	47	34	30

TABLE 6:8 A comparison of the species found in the reedbeds at (1) Linford, and open water zones at (2) Linford (Titmus, 1979a), (3) Eglwys Nunydd Reservoir (Potter & Learner, 1974) and (4) Kempton Park East Reservoir (Mundie, 1957).

Obvious differences were the presence of *Cryptochironomus* spp. and

Einfeldia spp. in open waters at Linford and their absence from reedbeds (except for the occasional individual) and the presence of smaller Tanytarsini (*Paratanytarsus* sp., *Micropsectra* sp.) within the reedbeds. *Metriocnemus hirticollis*, common in the reedbeds was entirely absent from open-water samples of Titmus. The differences are almost undoubtedly due to the reedstem habitat in the littoral zone.

A number of factors contributed to the trap variability at Cop Mere and Linford. 'Sampling errors' are often difficult to avoid. Although traps are protected to a degree from the strong wind and wave action, reedstems are often found growing up inside them and in doing so pushing against the plate. Surface boxtraps also present an ideal roosting place for moorhens and ducks; some traps at Cop Mere were capsised by such 'vandals'. Larvae such as *Cricotopus* will build tubes on the traps and efficient cleaning is essential to prevent inflatory abundance estimates. Larval density varies from stem to stem and no attempt was made at standardising the number of stems contained within a trap. Stem density also varies between different plant stands.

Numbers of emerging adults might be expected to vary from different reeds given that stem morphology (and thus surface area) and stem density of a reeds species will differ. For example, *Scirpus* has a branched stem in contrast with that of *Phragmites*. Although no statistical difference in abundance of emerging midges between the six reed types was shown, emergence from *Scirpus* in both years and from *Sparganium* in 1980 was greater than from the others - stem morphology and density are likely to be important factors in determining larval and adult abundance.

It was shown above that the number of days since trapping started is an important factor determining emergence, due to the number of day-degrees experienced by the larvae (Mundie, 1957). Emergence seemed

to be delayed at Cop Mere in 1980, and fewer adults were caught that season. As noted in chapter 2, the air temperature maximum did not occur until August 1980 compared with July in 1979. Titmus (1979) has proposed that emergence began earlier in 1976 compared to 1975 in the gravel pit at Linford because of higher air temperatures during the earlier part of 1976; similarly, emergence could have been delayed at Cop Mere in 1980 because of lower air temperatures during May to July. However, water temperatures during May and June were slightly higher in 1980 (Fig. 2:2, chapter 2), although the rise from May to July was not as steep as in 1979. Despite this, it is possible that the critical number of total day-degrees required for larval maturation was not reached until later in 1980, thus delaying emergence (although no data are available for the early months of 1979). Food supply may also be adversely affected by lower temperatures early in the season, e.g. fewer diatoms, so contributing to retarded development of larvae feeding on it, and hence delaying emergence.

Not only was peak emergence delayed in 1980, but the total number of emerging imagines was also reduced (Table 6:6, p. 123). As reported in chapter 2, heavy rainfall occurred from May to June 1980 and therefore mortality of chironomid adults during this period is likely to have been particularly high; swarming and oviposition would also have been less. Jónasson (1970) has reported that emergence of *Chironomus anthracinus* Zetterstedt was reduced in "rough weather", and the poorer conditions during early summer 1980 probably affected emergence adversely, possibly through unknown inhibitory effects on pupal development or the emergence process itself. In consequence, larval populations of the next (summer) generation would have been lower and so subsequent adult emergence during the later summer months reduced.

Emergence was also slightly earlier at OS1 and OS2 than at S1 and S2 in 1980. The predominant genera in the open water traps were *Cricotopus* and *Psectrocladius* living in the floating algal mats. Surface water temperatures may have been greater in the open water compared to those in the reedbed due to shading by *Phragmites* in the latter, (although no comparative data are available) and the slight differences may have contributed to enhancement of larval development in the open water zone, resulting in an earlier emergence.

Thus, although onset of emergence is largely a function of the rate of larval development caused by water temperatures over the long term, it can also be affected on a short-term basis. Differences in water temperature between habitats (e.g. open-water compared to reedbeds), rainfall and rough weather can enhance or retard emergence; additionally, heavy rainfall or windy conditions can act as mortality factors and reduce numbers of larvae and adults in subsequent generations.

Chapter 7

FINAL DISCUSSION

The data presented and discussed in the previous pages have been the product of a survey of the reedbed habitat, largely at Cop Mere, aimed at providing some information concerning the ecology of chironomids living there. Ecology can be defined as "the scientific study of the interactions that determine the distribution and abundance of organisms" (Krebs, 1972). In other words where are the chironomids found, how many occur there and how is it that they occur there? This study has been concerned principally with answering the first two of these questions; explanations of the last can be provided upon the evidence from the survey, and future experimental studies can either verify or refute these conclusions. The results of this investigation have been discussed previously in the appropriate chapters and the intention in this final chapter is to present a general summary of chironomid ecology within the reedbeds at Cop Mere, and briefly, that at Linford.

Unlike most other meres in the Shropshire-Cheshire plain, Cop Mere is shallow, does not stratify during the summer months and can be regarded as having no profundal zone, the open-water being sub-littoral. The littoral margins of the mere support quite extensive *Phragmites* reedbeds in the south-eastern part, grading landwards into marginal marsh vegetation. Elsewhere, the littoral zone has sparse stands of emergent macrophytes or is influenced by allochthonous input from overhanging trees. The substratum of the littoral, and much of the sub-littoral, is sandy in nature, with little silt or clay and the organic content is very low (< 1%). The nature of the sediments in the littoral is, therefore, similar to that at Newton Mere and Crose Mere, two meres of the Shropshire-Cheshire plain studied intensively by

Tait-Bowman (1976). However, the substrata of the profundal zones (and often sub-littorals) of other lakes reported in the literature are usually of a fine mud 'ooze' (Tait-Bowman, 1976; Carter, 1976; Titmus, 1979). It might be expected that burrowing, tubiculous larvae could construct tubes in such sediments more easily than in coarser (e.g. sand) substrata, especially if they were small species or small instars. For instance, Edgar & Meadows (1969) found that larvae of *Chironomus riparius* could not build tubes from sand, but preferred algal material. Furthermore, the nature of such fine sediments will be largely of detrital origin, a source of more food than that of relatively inert sand particles. Therefore, perhaps the sub-littoral at Cop Mere, composed largely of coarser particles might be expected to have a lower density of larvae than corresponding zones in other lakes. The sub-littoral of the mere was not examined thoroughly, but data from emergence trapping showed that very few Chironominae (a group which, by and large contains tubiculous, detritivorous larvae) were present (chapter 6). The majority of species caught were Orthocladiinae, living in floating algae. Occasional hand-net samples of the benthos of the sub-littoral mostly caught larvae of *Camptochironomus tentans*, and it has been noted previously that this species is common in shallow, warm-water lakes (Sadler, 1935). Within Cop Mere this chironomid is ubiquitous, being found in the substratum of the sub-littoral and reed-bed littoral, also associated with decaying stem litter and occasionally found on standing stems of *Phragmites* (in both these last two cases mostly as early instars). Its particular prevalence in Cop Mere contrasts with its absence from other meres examined in a general survey by Tait-Bowman (1976), where she only found it in Crose Mere at low densities (20 per m^2). Its predominance at Cop Mere may be due to a tolerance of warmer temperatures and to its large size, which enables

it to burrow effectively in the coarse, particulate sediments.

Within the reedbed, a series of core samples revealed that the total population of *Camptochironomus* larvae in the benthos exhibited a contagious dispersion, i.e. the larvae were clumped. The clumping of the population as a whole masked an underlying random dispersion of fourth instars, probably because the greater number of aggregated third instars caused bias in the overall determination of the spatial pattern. Different instars have been shown to have different dispersion patterns (Shiozawa & Barnes, 1977), as have different species (Titmus & Badcock, 1981). This is due to a combination of factors, e.g. the influence of food availability, distribution of larvae from an original point source (e.g. egg mass) and habitat heterogeneity. It is, for instance, possible that smaller instars of *Camptochironomus* can live among the matted root systems of the *Phragmites* whilst larger, fourth instars cannot. Thus the dispersion of the third instars will be influenced by plant stem dispersion. Or, as larvae become older and larger, competition for space increases, resulting in a more randomly dispersed population. 'Territories' of larvae will also affect pattern (Edgar & Meadows, 1969). Rougharden (1977) has concluded that patchiness is an inevitable consequence simply of distribution (e.g. larval movement) in a randomly fluctuating environment. On a large scale this is probably true for *Camptochironomus*. As discussed in chapter 3, the marked increase in larval density (to about 3000 - 4000 per m^2) in the reedbed at S1 and S2 in June 1980 was thought to be due to water movements caused by (unpredictable) heavy rain and prevailing westerly winds towards the end of May.

The abundance of *Camptochironomus* at S1 and S2 during 1980 contrasts with the situation in the summer and autumn of 1979. During this period *Glyptotendipes* larvae (at densities of between 100 - 6000

per m^2) predominated at S1, although other chironomids were present (e.g. *Camptochironomus*, *Limnochironomus*, *Microtendipes*) while there were very few larvae of any genus at S2. The low density of larvae at S2 is attributed partly to the proximity of S1 to the outflow and the calmer conditions of the summer months of 1979 when less aerobic conditions in the benthos at S2 may have been unfavourable for larvae other than tolerant ones (e.g. *Camptochironomus*). The decrease in diversity observed in summer 1980 at S1 has been suggested to be partly due to displacement of other larvae by larger *Camptochironomus*, in a manner similar to that reported by Cantrell & McLachlan (1977) for other chironomids.

Other studies have also revealed marked changes in abundance and diversity of chironomid populations from one year to the next. For instance, in the sandy littoral area of Loch Leven, Maitland & Hudspith (1974) noted that *Endochironomus* larvae completely disappeared during their three year study period. They could give no reasons for its extinction. Similarly, populations of *Glyptotendipes* decreased while *Stictochironomus* increased - this they attributed possibly to a change in food availability during this time. It would seem from studies such as this, and the present one at Cop Mere, that relatively short-term large fluctuations occur in the abundance of larval chironomid populations. The exact reasons are not always clear, but could be caused by, for example, weather or food variability from one season to the next.

As mentioned above *Glyptotendipes* larvae were the commonest in benthic samples in 1979. Like *Camptochironomus*, *G. pallens* is ubiquitous in Cop Mere, being found in cores and on decaying, fallen stems and standing ones in high numbers. As determined from analysis of their guts, *Glyptotendipes* larvae are primarily filter-feeders,

passage of water through their tubes being caused by irrigation movements (Walshe, 1951). As final instars, their tubes are commonly inside stems; either fallen ones or the tops of broken, standing stems. These instars are quite large and by exploiting these niches they probably escape predation pressures acting on larvae outside stems. These larvae are opportunistic, also being found inside empty caddis cases on the outside of stems.

In contrast to the predominance of the larger Chironominae in the reedbed benthos, the standing stems of *Phragmites* support a flourishing epifloral and epifaunal community, the latter being composed of large numbers of the Orthocladiinae. It is a dynamic community which changes with season and breeding cycles. When water temperatures rise during the spring and summer, the increase in metabolic, growth and reproductive rates result in a build-up of algal populations on the stems as discussed in chapter 4. Consequently, there may be local migrations of some organisms, e.g. molluscs, to the stems to feed on the developing periphyton. Chironomid larvae, especially *Cricotopus*, *Glyptotendipes* and *Psectrocladius* also became very common on reedstems during the summer months but they were not all grazing the periphyton; the stems of *Phragmites* represent different resources to different larvae. *Glyptotendipes*, being primarily a filter-feeder, would select stems mainly as a base for the construction of its tubes - when supported higher in the water column, they can exploit a greater volume of water for extraction of food. Data for *Psectrocladius* were odd and it is difficult to draw any conclusions regarding their distribution, except that they were commonly found on stems during the summer. Additionally, like *Cricotopus*, they inhabit algal mats floating in the water and two species of *Psectrocladius* were taken from this habitat - why only *P. sordidellus* was recorded from the reedbed is not known. *Cricotopus*

is a grazer and there were usually greater numbers of this genus on older stems, (which generally had more periphyton on them), than on younger stems. In December, there were more third instar larvae on young stems, which by this time had more periphyton than older stems. This suggests that *Cricotopus* larvae are attracted to stems with denser algal growth. However, the data do not support the conclusion of Mason & Bryant (1975a) that larvae are responsible for the fall-off in periphyton density observed on stems (see chapter 4). Other factors may be more important, such as a decrease in light intensity in the water due to the increase in stem density during spring growth.

Other chironomid larvae present tended to be smaller species, and were generally only found during the summer months. The epiflora cover on the stems, especially dense in the warmer months, would be expected to be a rich source of food and also shelter for the large numbers of larvae occurring during the summer. For example, *Procladius* larvae would be feeding on small crustaceans (Titmus & Badcock, 1981) and perhaps also chironomids (Kajak & Dusoge, 1970). *Corynoneura* is also errant although detritivorous. *Metriocnemus* larvae are semi-terrestrial and might be expected to be common in a reedbed where they can live on the stems near to the water surface. Other larvae are tubiculous (e.g. *Pentapedilum*, *Endochironomus*), living among the filamentous algae on the stems, either filter-feeding or grazing.

During the winter, there are very few larvae on the stems. It is thought that there is migration of the larvae down to the base of the stems, rather than to the substratum itself, possibly as an avoidance of the harsh winter conditions which appertain higher in the water column and as a response to a drop in food quality/quantity on the stems. The latter possibility was also suggested by Mason & Bryant (1975a); there was evidence in this study that *Cricotopus*

larvae move to younger stems in the winter where the quantity (and quality?) of periphyton was greater than on old stems by December. Future studies should aim to determine the factors responsible for the fall in numbers on the stems - whether it is due to a drop in temperature, food quality, mortality or a combination of all three.

Phragmites not only provides a habitat and food source when standing, but as the results from chapter 5 show, many invertebrates colonise decaying, fallen stems lying in the benthos. Rates of decay of organic material are important since they determine how quickly the various component molecules and ions are returned to the ecosystem. Furthermore, the decomposition rate is partly responsible for the speed of ecological succession. In a typical hydrosere succession (water → reedbed → marsh → dry land) a very slow decay rate of plant matter (e.g. reeds) will lead to the build-up of organic material, causing infilling and enhancing successional stages.

The chemical composition of the plant will in part determine how quickly it disappears. By purely physical means, some soluble components will be lost quickly (e.g. leaching of soluble fractions); larger, refractory molecules will disappear less easily. Micro-organisms can break down organic matter by enzymatic attack, and additionally some macroinvertebrates, e.g. molluscs, can degrade litter by chemical means (Monk, 1976). However, the majority of invertebrates act on the litter through comminution (e.g. *Asellus*), scraping (e.g. molluscs) and burrowing (e.g. chironomids), all of which increase the surface area available for further enzymatic attack.

The litter itself is probably not used directly as a food source by chironomid larvae, except when it becomes fragmented to such an extent that it is eaten by particle-feeding detritivores such as *Camptochironomus*. The epiphytic flora on the fallen stems provides

food for grazing *Cricotopus*, as has been seen previously on erect stems. *Glyptotendipes* larvae were commonly found inside the stems where they would be filter feeding, as already described above for standing stems. Other larvae variously use the stems as cover, as a food source (indirectly) and as bases for tube construction. Consequently, it is considered that the changes in abundance of chironomid larvae on the fallen stems are likely to be more due to seasonal variations in the populations caused by reproduction, than to any other specific response to the litter as it changes its quality through decomposition. Changes in abundance of other invertebrates feeding directly on the litter (e.g. *Asellus*) may be influenced more by the changing composition of the litter as it decays. However, there was no apparent correlation between animal numbers on the litter and changes in chemical composition, and again changes in abundance are probably due more to breeding cycles.

In chapter 5 it was suggested that macroinvertebrates play an important role in determining the rate of decay of *Phragmites* stems, because of the greater amount of litter remaining in fine mesh bags (where larger macroinvertebrates such as *Asellus* and *Gammarus* were restricted in their access) compared with coarse mesh bags. The increased weight loss from coarse mesh bags contrasts with that found by Mathews & Kowalczewski (1969) and Kaushik & Hynes (1971) where no increase in weight loss of tree leaves occurred when animals were allowed access, and the former authors considered that macroinvertebrates do not play a significant role in decomposition of plant litter in water. On the other hand, Mason & Bryant (1975), working on *Typha* and *Phragmites* litter in the Norfolk Broads, concluded that invertebrates do increase the breakdown rate of litter. This would seem to be the most sensible conclusion, given that comminution and fragmentation by

animals increases the surface area available for microbial attack and hence increases the rate of decay of the litter.

Of the final amount of litter remaining in coarse and fine mesh bags after a year (10% and 30% of the initial weight respectively), most was in the form of lignin and cellulose. It was found that lignin was being broken down, which is in contrast to the two other investigations on the compound in freshwater (Suberkropp *et al.*, 1976; Polunin, 1979) where proportions of lignin increased. This difference might be due to the different nature of the litter under examination in all three cases, and a reflection of the methods of chemical analysis used.

In this study it was apparent that weight loss of the litter did not occur at a constant rate - instead two phases were recognised, with decay being faster during the summer months. A combination of factors probably accounted for this pattern, the principal ones being the numbers of invertebrates present, water temperature (both being greater in the summer) and the presence of slow and fast decomposing fractions in the litter. Therefore, in contrast with the conclusions about litter breakdown in various species by some workers (e.g. Petersen & Cummins, 1974; Howard-Williams & Davies, 1979), decay of *Phragmites* stem litter does not follow a simple linear or exponential decay model. Here, as in such studies as Mason & Bryant (1975) or Howard-Williams & Howard-Williams (1978), decay was at least diphasic and this type of pattern may in fact be more applicable to litter breakdown than has been previously assumed.

Larval chironomids inhabiting the various niches within the reedbed develop and mature, giving rise to adult populations during the warmer months of the year. It was pointed out in chapter 6 that errors inherent in the sampling method using emergence traps, such as

varying stem density, larval density per stem or larvae being carried into the traps on floating algae, lead to difficulties in the interpretation of abundance estimates and in following emergence patterns of imagines. In future studies some of this variability could be reduced by standardising the stem number per trap. The results of the emergence trapping aided identification of the larval chironomids and also supplemented the data obtained from cores and other sampling methods. Indeed, some forms were only recorded in the adult data (e.g. *Xenopelopia falcigera, Camptocladius stercorarius*) and others were rarely found in larval samples (e.g. *Metriocnemus hirticollis, Parachironomus arcuatus*). Conversely, there were considerably fewer imagines of *Camptochironomus tentans* or *Glyptotendipes pallens* caught in traps than would be expected from their great larval abundance. Trap avoidance could be a partial explanation for this; the pupae are large and perhaps strong-enough swimmers to avoid the surface of the water under the trap if conditions there were inhibitory for any reason. Such behaviour has been suggested previously by Potter & Learner (1974).

Reedbeds offer a much greater habitat diversity (the benthos, standing and fallen stems) than do open water areas, and so it would be expected that more species would be present. At Cop Mere this was the case, where 31 species of adult chironomid were found in the reedbeds and 11 in the open water traps. Individuals of the Orthocladiinae were particularly numerous (*Cricotopus sylvestris, Psectrocladius sordidellus* and others) which is not surprising considering the close association between larvae and reedstems seen previously.

Although numbers of species at Cop Mere were greater from the reedbed zone, it is difficult to compare the numbers of individuals

emerging from the reeds and open water areas because of trap losses from the latter. However, much of the adult biomass in the open water traps was contributed by *Cricotopus* and *Psectrocladius* which originated from larvae living in floating algal mats. As mentioned previously, the numbers of tubiculous larvae may be reduced at Cop Mere because of the sandy nature of the substratum, and hence emergence is less than in corresponding zones in other lakes where, for instance, tubiculous and detritivorous larvae of the Chironominae may be more abundant.

Numbers of imagines recorded from other areas of open water where surface-traps were used are generally greater than from the reedbeds at Cop Mere. For example, Learner & Potter (1974) estimated an emergence of 11,000 - 16,000 adults per m^2 per year from two ponds in Hertfordshire, and Morgan & Waddell (1961) recorded similar densities from the eutrophic Loch Dunmore in Scotland. In the present study, during restricted sampling periods of 13 weeks in 1979 and 20 in 1980, 5960 per m^2 and 1606 per m^2 were captured respectively from the *Phragmites* reedbed at S1. At Linford over 16 weeks in both 1979 and 1980, totals of 5085 and 2950 individuals per m^2 respectively were trapped from *Phragmites*. However, although emergence from the reedbeds is less than from open water areas at previous sites studied, the sampling period here was shorter and the sites are probably not directly comparable due to their differing physical characteristics. More quantitative data are required from stations within the same site before any firm conclusions are made concerning differences in biomass of adult midges from between reedbeds and open water zones.

In terms of abundance of imagines emerging from a *Phragmites* reedbed, the results from Cop Mere are comparable to those at Linford where total emergence over the season was similar. Species diversity was greater at Linford and this was probably owing to the differing

nature of the substratum and geographical location.

The rate of larval development (governed by the number of day-degrees that the larvae experience) was considered to be the most important factor influencing emergence of imagines from the reedbeds, from analysis of the data obtained at Linford. This is in agreement with previous workers (Mundie, 1957; Titmus, 1979). Additionally, short-term (e.g. daily) variations in numbers of emerging adults could be caused by small-scale temperature differences within a lake (e.g. between the reedbed and the open water). Other factors may also contribute to the observed fluctuations, e.g. sunlight (Titmus, 1979), although this was not considered to be important in this study. Jónasson (1970) claimed that *Chironomus anthracinus* emergence is reduced in "rough weather", and Weerekoon (1956) reported that oviposition and swarming was reduced in this species during windy conditions. Certainly heavy rain or wind could act on the imagines, killing them or reducing swarming and oviposition, and possibly the poor summer weather of 1980 was in part responsible for the observed decrease in adult emergence compared with 1979 (since subsequent larval populations during the summer of 1980 would have been reduced if imagines had suffered heavy mortality during the earlier part of the season).

Emergence from six different reed types at Linford was monitored during the summers of 1979 and 1980. Within the same pool complex at Linford it might be expected that species would be more or less "universally" distributed with small-scale random variability. This seemed to be the case, with no particular specific associations between chironomids and the different reeds. However, because of the nature of the reed plant, i.e. its surface area, morphology and stem density, differences might be expected in the numbers of midges emerging. Although no statistical difference between reed types was shown in the

total numbers emerging over the two summers, there was an indication that *Scirpus* (and possibly *Sparganium* in 1980) yielded greater numbers than the other reed species. Stricter sampling procedure (e.g. standardising the number of stems per trap) is required before concluding that one reed type produces a greater emergence than another.

The Game Conservancy at Linford was interested in the results of the emergence monitoring from the six reeds, since they are investigating methods for reclamation of gravel-pits for use as wildfowl reserves. Ducks require adequate nesting sites and a supply of invertebrate food. Young ducklings need a high protein diet for survival and growth (Street, 1978) and this is provided by invertebrates. Since young mallards are unable to dive and feed on benthic organisms, they rely heavily on emerging insects, especially the Chironomidae (Lees & Street, 1973). Hence, enhancement of emergence would decrease mortality caused by starvation; reedbeds offer an answer not only because they encourage chironomid emergence, but also because they provide nesting sites. If a large chironomid emergence were required, it is probably better to plant those reeds with a high stem density and stem surface-area, e.g. *Scirpus*. However, a high stem density may restrict access to larger birds and this has to be taken into consideration.

Reedbeds, in this study *Phragmites*, by their very nature provide an entirely different habitat to that of the open water zones. Cop Mere differs from most other reedbeds, e.g. the Norfolk Broads, because of the sandy substratum and generalisations should be made with caution. However, because most of the larvae will be associated with the reed-stems, the results are likely to be generally applicable although the exact species assemblages will differ according to the geographical location. Larvae present in the substratum at Cop Mere are mainly

Camptochironomus tentans and *Glyptotendipes pallens*, the former predominating in 1980 largely due to distribution of larvae by water movements under the influence of wind and rain into the reedbeds. Dead stems, fallen and decaying in the benthos provide additional habitat diversity on the floor of the reedbed, supporting a varied community, including chironomid larvae which utilise them as a habitat and indirectly as a food source. Erect stems provide a further habitat, for filter-feeders and grazers (e.g. *Glyptotendipes* and *Cricotopus* respectively) and large populations are supported on them. This large herbivore population must be important in the trophic web within the reedbed community providing a link between the algae and secondary consumers. In the reedbed much of the adult population is contributed by the Orthocladiinae, many of which originate from the stems. At Cop Mere the Chironominae are poorly represented, in contrast to Linford and this is probably due to the more organic nature of the substratum at Linford.

The reedbed is an integral part of the lake ecosystem and represents that stage in the lake's ontogeny where infilling is occurring which will lead in time to dry land. This is of concern in some quarters, where conservationists are keen to maintain the *status quo*, e.g. in the Norfolk Broads or some SSSI's. Successful management practices, however, demand a knowledge of the system, both in terms of the biology of the plants and also their associated fauna; all too often a 'stable' ecosystem has been detrimentally affected through mismanagement owing to a lack of knowledge of the community. Chironomids, being among the most abundant invertebrates present in reedbeds, are necessarily important to the community there. An understanding of how they fit into the trophic structure, and how important they are in reedbed ecology should be of help to those who are concerned with the management of

reedbeds for conservation purposes, fishing and wildfowl breeding. This study hopefully provides a framework on which to build future research aimed at producing reasonable scientific theories to enable predictions to be made concerning the various natural or man-made pressures on reedbeds.

SUMMARY

1. Populations of chironomids in *Phragmites* reedbeds at Cop Mere, Staffordshire were studied during 1979 and 1980. The mere is shallow (2.7 m maximum depth) but has a relatively large surface area (16.8 ha) compared with most meres in the Shropshire-Cheshire plain. It does not stratify, oxygen levels were high in the waters of the reedbed (90-100%) and conductivity (3.7-4.75 S m^{-1} x 10^4) and pH levels (7.8-8.5) were similar to other meres.

2. The sediments of the reedbed benthos are mainly sand (> 90%) and have a low organic content (< 1%); the benthos, however, is overlain by decaying, fallen reedstems.

3. Core samples of the benthos at two different stations in the reedbeds (at S1 and S2) showed that during the summer months of 1979, total larval density of chironomids at S1 was greater than that at S2 (7000-10,000 m^{-2} cf. 0-300 m^{-2}). During the winter of 1979 and during 1980, densities at both stations were similar (1000-5000 m^{-2}).

4. More genera were found in S1 benthic samples in summer 1979 (maximum 13) than at S2 (maximum 3); the predominant chironomid at S1 was *Glyptotendipes* at a density of 100-6000 m^{-2}. The majority of larvae were members of the Chironominae. During 1980, fewer genera were found at S1, and the predominant genus during the summer and remaining months of the year was *Camptochironomus*, at high densities (3000-4000 m^{-2}). Its presence and abundance in the reedbed during 1980 was thought to be due to distribution of early instar larvae by prevailing winds and increased water movements because of poor weather conditions at the end of May.

5. The spatial dispersion of the total larval population of *Camptochironomus* at S2 was contagious. Third instars were also shown

to be clumped, but fourth instars were randomly dispersed.

6. The most abundant chironomids on standing reedstems were larval *Cricotopus*. These were grazers and more common on those stems where there was greater periphyton growth (generally on 'older' stems). Of the other 10 genera, *Glyptotendipes* and *Psectrocladius* larvae were particularly abundant. The former is primarily a filter-feeder, showed no preference for old or young stems, and larvae were often found living inside the tops of broken stems or empty caddis cases. *Psectrocladius* larvae were grazers, but showed no stem preference; they were only found on stems during the summer months.

7. It did not seem likely that the fall in periphyton density on the stems in early summer was primarily due to grazing by chironomid larvae.

8. Litter bag studies revealed that decaying, fallen *Phragmites* stems were a suitable habitat for larval chironomids (e.g. *Glyptotendipes*) and served as an indirect food source (e.g. *Cricotopus* grazing the epiflora). Fourteen genera were recognised, the commonest being *Cricotopus*, *Glyptotendipes*, *Limnochironomus* and *Camptochironomus*.

9. Weight loss of stem litter over a period of a year did not occur at a constant rate. Two phases of linear decay were recognised, loss being faster in the summer months than during the winter. Breakdown of litter was enhanced by the presence of macroinvertebrates. The proportions of ash and nitrogen, after an initial decrease, rose during the rest of the study period. Those of α-cellulose and lignin decreased.

10. Emergence of imagines at Cop Mere was monitored during the summers of 1979 and 1980. Peak emergence occurred in June/July 1979 at about 150 m^{-2} day^{-1} at S1 (and 10-20 m^{-2} day^{-1} at S2). In 1980, peak emergence was low at both S1 and S2 (about 20-50 m^{-2} day^{-1}) and occurred slightly later. The lower and delayed emergence was thought to be due

to the poor weather during the early summer of 1980.

11. A total of 31 species were identified from the emergence traps. *Cricotopus sylvestris* was abundant in both years and the Orthocladiinae were the most numerous chironomids caught. Despite their abundance as larvae in the reedbed, imagines of *Camptochironomus tentans* and *Glyptotendipes pallens* were relatively uncommon. Eleven species were caught from open water traps, the commonest being *C. sylvestris* and *Psectrocladius* spp.

12. In a comparison of 6 reed species in a lagoon area of a gravel pit at Linford, emergence was statistically the same from all reedbeds during 1979 and 1980. However, emergence from *Scirpus maritimus* showed a tendency to be greater than the others in both years; this may be a real difference, possibly due to its larger stem surface-area than some of the other reeds.

13. Total emergence over the sampling periods was similar from *Phragmites* reedbeds both at Linford and Cop Mere, though numbers of species were less at Cop Mere (29) than at Linford (36). This is due to the differing geographical locality and contrasting nature of the sediments of the reedbeds.

14. Analysis of emergence data from Linford (by a multiple regression procedure) suggested that onset of emergence is governed primarily by the rate of larval development.

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APPENDIX

	28.6.79										12.7.79										26.7.79									9.8.79							
Core No:	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8
Pr 3		1		1						1		1							1	2																	
4		2		1								1						1		2																	
Cr 2														1	2	1			1	1																	
3														2	1																						
4												2								1																	
Ps 4																	1																			
Cl 4		3	3	1		2				2	11		9	5	2	2	2	3		5			2						1							
Ta 4						1				2																										
Ca 2				1																						1										
4	1																																			
Cry 3		1	1			1																														
4																	2	1		1				1												
En 3											3					2							1													
4												1																								
Gl 2			1	1		4				4	1	1			1		1		1	2																
3	1	10	2	9	3	8	2		3	8	15	3	11	14	5	9	13	16	9	6	1	4	1		2		7	1	2			1			1	
4		2		3		2	2	2		2	4			2	2	2	2	3			1		2	5	6	2	7	1	7	2	3		2	4	3	3	1
Li 3				1						1	2		2			1															1					
4		1	5	1						5	1					1																				
Mi 4																1																				
Pa 2														1																1						
Po 2							1			1																										
3	1						1								1								1													

	6.9.79					23.	11.10.79									30.11.79								29.1.80							20.2.80						
Core No:	1	2	3	4	5	1	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	1	2	3	4	5	6	7
Pr 3																											1										
Ca 2	1					1																															
3	1	1		1	1			1						2	1	1	1					2	1		2	1		1	1		2	1	1			2	1
4			1	1				1	1				2	1	1	1		3	1		1			2	1			1	1			1		1	1		1
Cry 3																										1											
Gl 3							1														1																
4								1	1		4	1	1							1	2	3					1	2	1	1					1	1	
Li 4							1			1				1	1																						
Mi 3															1																						

TABLE A3:1 Numbers of larvae in each core at sampling date shown from Station One, 1979 - 1981. contd.....

		7.3.80								18.4.80			21.5.80				26.6.80									30.7.80								3.9.80				
Core No:		1	2	3	4	5	6	7	8	1	2	3	1	2	3	4	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5
Cr	4																						1																
																																	1						
Cl	4												1	1																									
Ca	2												1				5	4	2	1		1	2	9	12													
	3				1	1			1	1	1	1					26	1	2	5	5		2	10	3	3	2			1									
	4		1		1		1		1	1					1	1										3		1	2	1	2	1	2	1	1			1	1
Gl	4	1						1																														
Po	3			1																																		

		15.10.80									11.11.80										15.12.80									29.1 81							
Core No:		1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8
Cr	2																															1					
Ca	2														1												1										
	3	1	1		1	1	2		1	2				1	3		3				3	3	1			3	2	2	2			1		1	1		
	4	1		2	4	1		1		1	1	1	1	1		5	2	3	1	4	1	1	1	2	2	2		4	3	1	1	1	2	1	2		2
Gl	2												1																								
	3						1									1																						
	4												1		1																					1		
Mi	2																				1																
	4																1																				

TABLE A3:1 Numbers of larvae in each core from Station One at sampling date shown, 1979 - 1981. Figures next to genus are instars. Key to genera: Pr- *Procladius*, Cr- *Cricotopus*, Ps- *Psectrocladius*, Cl- *Cladotanytarsus*, Ta- *Tanytarsus*, Ca- *Camptochironomus*, Cry-*Cryptochironomus*, En- *Endochironomus*, Gl- *Glyptotendipes*, Li- *Limnochironomus*, Mi-*Microtendipes*, Pa- *Paratendipes*, Po- *Polypedilum*.
Ten cores were taken on each occasion but those with no larvae in them have been omitted from the table.

	28.6.79				23.9	11.10	30.11.79					29.1.80				20.2.80						7.3.80				21.5.80			26.6.80								
Core No:	1	2	3	4	1	1	1	2	3	4	5	1	2	3	4	1	2	3	4	5	6	1	2	3	4	1	2	3	1	2	3	4	5	6	7	8	9
Cr 2	1																				1																
3																											2										
4			1																								1										
Ca 2					1																							1	14	6	6	12	4	11	7	1	
3						1	1				1	2		1		1													9	4	10	12	3	11	8	7	7
4				1				1						2	3			1	1			2		1	1	1	1			3	2	3					1
Cry 3														1																							
Gl 2		1																														1	1	2	1		
3																	1																				
4										1			1							1																	
Li 3									1																							1					
Mi 2									1																												
4																							1														

	30.7.80										3.9.80										15.10.80										11.11.80								
Core No:	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9
Tan 3														1																								
Cr 4															2	1																						
Ca 2	1						1			3	2					1		1	1											1				6		1	1		
3		5	7		3	2		1	2	28	1	2	1	3	2	3	1	1	4	4		6	1	2	1	1	2	3	2	4	1	6	1	16	2	4	4	2	4
4	1	8	2	1	5	2		2	4	8		2		3	3	7	5		10	3	3	3	2	5		1	1	2		2	2	1	2	1	2	3	1	2	3
Gl 2																		1																		2		
3																								1		1				1								
4																						1	2							1	1			1		1			

	15.12.80										29.1.81									
Core No:	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Ca 2													1							
3	4	3	3	2	2	1	5	1	1	5	1	1	4	2	1	7	9	3	2	3
4	4	1			6		3	2		4	3	2	2	1	4	3	5	1	3	1
En 3			2																	
Gl 3			1								1						1			1

TABLE A3:2 Numbers of larvae in each core at sampling date shown from Station Two, 1979 - 1981. Figures next to genus are instars. Key as in Table A3:1 and also: Tan - *Tanypus*.

	PERIPHYTON		LARVAE	
	OLD	YOUNG	OLD	YOUNG
JAN	0.47 (0.06)		0.02 (0.01)	
FEB	0.94 (0.05)		0.03 (0.01)	
MAR	0.87 (0.06)		0.11 (0.02)	
APR	4.11 (0.25)		0.03 (0.01)	
MAY	11.21 (0.71)	5.23 (0.37)	0.27 (0.11)	0.02 (0.01)
JUN	4.97 (0.46)	1.79 (0.20)	0.39 (0.07)	0.17 (0.02)
JUL	3.52 (0.29)	0.61 (0.11)	1.22 (0.17)	0.44 (0.07)
AUG	2.44 (0.22)	0.25 (0.05)	0.22 (0.04)	0.07 (0.02)
SEP	2.39 (0.23)	0.37 (0.06)	0.36 (0.04)	0.07 (0.01)
OCT	1.66 (0.14)	0.46 (0.07)	0.40 (0.08)	0.14 (0.02)
NOV	1.53 (0.13)	0.51 (0.04)	0.23 (0.06)	0.09 (0.02)
DEC	0.86 (0.09)	1.08 (0.09)	0.15 (0.04)	0.15 (0.02)

TABLE A4:1 Density of periphyton (mg cm^{-2}) and chironomid larvae (nos.cm^{-2}) on old and young *Phragmites* stems during 1980. Numbers in parentheses represent one standard error.

	OLD				YOUNG			
	First	Second	Third	Fourth	First	Second	Third	Fourth
JAN								
FEB		0.002 (0.001)						
MAR		0.002 (0.001)						
APR		0.001 (0.001)	0.001 (0.001)					
MAY			0.002 (0.001)					
JUN	0.025 (0.01)	0.062 (0.02)	0.013 (0.01)		0.005 (0.01)	0.028 (0.01)	0.007 (0.001)	
JUL	0.001 (0.001)	0.018 (0.01)	0.013 (0.01)	0.002 (0.001)		0.005 (0.001)	0.006 (0.001)	0.001 (0.001)
AUG		0.007 (0.001)	0.004 (0.001)			0.002 (0.001)	0.001 (0.001)	
SEP	0.007 (0.001)	0.004 (0.001)	0.006 (0.001)	0.004 (0.001)		0.011 (0.01)	0.006 (0.001)	0.003 (0.001)
OCT		0.012 (0.01)	0.002 (0.001)	0.002 (0.001)	0.003 (0.001)	0.007 (0.001)	0.005 (0.001)	0.007 (0.001)
NOV		0.001 (0.001)				0.004 (0.001)		
DEC				0.003 (0.001)		0.003 (0.001)		

TABLE A4:2a Density of *Glyptotendipes* larvae on old and young stems (nos.cm^{-2}) during 1980. Numbers in parentheses represent one standard error.

	OLD			YOUNG		
	Second	Third	Fourth	Second	Third	Fourth
JAN	0.012 (0.01)	0.005 (0.01)				
FEB	0.023 (0.01)	0.005 (0.01)				
MAR	0.020 (0.01)	0.074 (0.01)	0.014 (0.01)			
APR		0.001 (0.01)	0.027 (0.01)			
MAY	0.154 (0.11)	0.158 (0.08)	0.031 (0.01)	0.016 (0.01)	0.003 (0.01)	0.005 (0.01)
JUN	0.109 (0.03)	0.087 (0.02)	0.076 (0.03)	0.068 (0.01)	0.026 (0.01)	0.016 (0.01)
JUL	0.743 (0.13)	0.217 (0.02)	0.179 (0.03)	0.235 (0.04)	0.094 (0.02)	0.047 (0.01)
AUG	0.150 (0.03)	0.057 (0.01)	0.005 (0.01)	0.036 (0.01)	0.025 (0.01)	0.002 (0.01)
SEP	0.033 (0.01)	0.085 (0.01)	0.219 (0.03)	0.007 (0.01)	0.013 (0.01)	0.019 (0.01)
OCT	0.364 (0.07)	0.005 (0.01)	0.003 (0.01)	0.094 (0.02)		
NOV	0.155 (0.04)	0.068 (0.03)		0.069 (0.01)	0.018 (0.01)	
DEC	0.116 (0.04)	0.025 (0.01)		0.101 (0.02)	0.053 (0.01)	

TABLE A4:2b Density of *Cricotopus* larvae on old and young stems (nos.cm^{-2}) during 1980. Numbers in parentheses represent one standard error.

	OLD				YOUNG		
	First	Second	Third	Fourth	Second	Third	Fourth
JUN	0.017 (0.02)	0.017 (0.02)	0.001 (0.001)	0.003 (0.001)	0.007 (0.001)	0.007 (0.001)	0.007 (0.001)
JUL		0.001 (0.001)	0.021 (0.01)	0.013 (0.01)	0.012 (0.01)	0.018 (0.01)	0.013 (0.01)
AUG		0.001 (0.001)	0.001 (0.001)	0.001 (0.001)			
SEP							
OCT		0.014 (0.01)			0.023 (0.01)		

TABLE A4:2c Density of *Psectrocladius* larvae on old and young stems (nos.cm^{-2}) during 1980. Numbers in parentheses represent ±one standard error.

Planaria torva (Mull)	Pla
Stylaria lacustris (L)	Sty
Erpobdella octoculata (L)	Erp
Glossiphonia complanata (L)	Glo
Helobdella stagnalis (L)	Hel
Acroloxus lacustris (L)	Acr
Lymnaea peregra (Mull)	Lym
Physa fontinalis (L)	Phy
Planorbis albus Mull.	Plab
Potamopyrgus jenkinsi (Smith)	Pot
Asellus aquaticus (L)	Ase
Agrypnia pagetana Curtis	Agr
Athripsodes aterrimus (Stephens)	Ath
Cyrnus sp.	Cyr
Holocentropus picicornis (Stephens)	Hol
Hydroptilidae sp.	Hyd
Mystacides longicornis (L)	Mys
Tinodes waeneri (L)	Tin
Haliplidae (larvae)	Hal
Ceratopogonidae	Cer
Psychodidae	Psd
Corynoneura sp.	Cor
Cricotopus sp.	Cri
Metriocnemus sp.	Met
Psectrocladius sp.	Pse
Camptochironomus sp.	Cam
Endochironomus sp.	End
Glyptotendipes sp.	Gly
Limnochironomus sp.	Lim
Microtendipes sp.	Mic
Pentapedilum sp.	Pen
Polypedilum sp.	Pol
Procladius sp.	Pro

TABLE A4:3 List of invertebrates occurring on *Phragmites* stems during 1980, with key to Tables A4:4, A4:5 on right.

	January															February																				
STEM:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Sty																	1																		
Acr	2	2											4				2	1	4		1					1	3			2	3				1
Ase											1																								
Ath		1																																	
Cri	2		2			1		1			1		2				2	1	2	3	1	1			1	2			4			1	1		
	3			1				1			1										2	1									1			1	
Gly	2																									1									

	March																				April																
STEM:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Hel											1																													
Acr	2			3			1	1	2		1			4	3	1	2	2	2	3											1			1			1			
Cer																									1															
Pro	2							1																																
Cri	2			1	2	2	1					1		1	1	2		1	3																					
	3	2	2	4	3		3	3	3	4	5		2	5	6	1		5	11	1	3													1						
	4			1			1	1	1		1				2		3		1		1	1	6	4	1	1		1	1	2	1	1			1			1	1	
Gly	2																1							1															
	3																							1															
Lim	3																																1						

TABLE A4:4 Numbers of invertebrates occurring on OLD stems during 1980. contd.....

		May									June												July																				
STEM:		1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Pla															1																													
Sty		3	3	3	6	2	9	2	6	6	10		3		16	5	1	1	4	2	1	3	2	7	1	4	4		1		1	3		10	10	3	3	7	15	7	18	3	7
Erp											1																			1			1		1						1			1
Hel																								1																				
Phy								1																																			
Plab		2			3	1																		1							1		1						1			
Pot							1																			1																	
Ase			1		2						4				6		1						2										1	1								
Ath					1																												1									
Cyr																											1	1													1		
Hyd																																	1	1		1	1					1
Mys																	1																										
Tin					1																												1									
Hal													1		2																												
Cer							1	1		1	1																																
Cri	2	46	2		1	2	2	3	7	4	1		5	4	4		4	3	3	6	6	5	17	15	6	2	38	76	60	33	11	30	32	1	33	56	60	21	22	31	25	33	33
	3	4	4	1	7	4	6	2	2	3	2		2	4	4	5	2	9	7	2	4	2	5	4	3	6	22	12	11	11	5	10	5	3	9	14	14	9	5	10	6	18	11
	4	1		2	1	1	3	4	2		2	1	1	1	3	1		19	4	1	1	2	9	4		1	7	14	8	2	3	10	4	1	8	9	27	4	5	9	10	19	10
Met	3															1																											
Pse	2													1													1																
	3												1													1	1	1		1			1	2	2	1	1	2	1	4			
	4																		1								2		2					1		1	1	1		2	2		
Cam	2																		1																								
	3																		1																								
Gly	1													1	1	1		1	2		2	2	2																				1
	2											1		5	15		3	2	3		5	1		1		2					1		1	2	1		1				1		5
	3					1									4		1	2	1							1	1	1	1				1		2			1	1			2	
	4																																	1									
Lim	2																							1				1	1			1	1				1				1	1	1
	3																																	1	1								
Mic	2				1																																					
Pen	2																	1																									

TABLE A4:4 Numbers of invertebrates occurring on OLD stems during 1980. ....contd.....

		August																					September																					
STEM:		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Pla		2																																									
Sty					4								1					1					4								2	2		2	3			2				
Erp																	1									1																	
Glo			1																																							
Lym																																									1	
Phy										1																																
Plab									1	1																																
Ase																1						1					2						2					1				
Hyd												1																														
Tin						1																																			
Psy																																				1					
Cor	4											1														1																
Cri	2	8	10	2	4	3	5	16	22	1	5	22	10	5	1	2	1	5	5	6	9	2	4	3		2		2	1		1		1	3			1		1		1
	3	10	3	1	4	1		1	4	2	2	12				1	2	1	1	3	4	2	1	2		6	1	2	4	4	2	4	1	6	2	4	2	1	8	4	3
	4	1			1							1									1	2	9	2	7	6	9	5	18	13	10	10	2	11	8	7	2	11	13	3	5
Met	3																														1					1						
Pse	2				1																																				
	3											1																														
	4							1																																		
End	3																		1																							
Gly	1																					2				1	1							1								
	2	1								1							1	1			2			1	1									1								
	3					1						4																		1				2							
	4																																	1					1		1
Lim	2																									1								1								

TABLE A4:4 Numbers of invertebrates occurring on OLD stems during 1980. ....contd....

	October																				November																						
STEM:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Sty																						1																				
Acr				2							2	2					1																								2
Plab																1										1															
Hol																																				1				
Cri	2	26	37	3	5	39	6	17	28	20	30	5	2	6	8	11	18	5	7	5	5	1	6	16	10	1	11	21		3	1	15	12		6	2		4		6	4
	3										1					1	2						1	14	2		9	13			1	7	2	2	1		1			3	
	4			1						1																															
Pse	2	3	5			4																																			
Gly	2	1				1	1				3								1	1																				1	
	3										1						1																								
	4									1																															

	December																			
STEM:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Acr					1														1	
Ase							1						1							
Agr						1													1	
Cri	2	1	6	2	2	6		12			1	3	30		8		1	1	2	15
	3		2		1	2		2	2				2		2					6
Gly	4		1															1		
Lim	2			1						1										

TABLE A4:4 Numbers of invertebrates occurring on OLD stems during 1980. Key to names can be found in Table A4:3, together with naming authorities.

	May										June													
STEM:	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Pla	1			1		2																		
Sty	14	12	16	13	4	5	4	9	6	12	2	4		1	6	3		1	2	1	5		1	
Glo				1																				
Hel				1				1																
Acr								1	1															
Plab		2	1				2	1	1	1				1										
Pot						1				1														
Ase			2	1		1		1		2		1											3	
Tin									1															
Cri 2		1		1		2	1				1		3	4	3	3	4	5	6	2	3	3	4	
3					1							1	1		3	1	2		1	1	3	1	2	
4				1					1					1	2	2	1				1	2		1
Pse 2														2					1					1
3																			2				1	1
4											1													
Gly 1													1	1	1				1					
2											1	4			1					1	2	6	3	
3												1	1		1	1					1			
Pen 4														1									1	

	July																			August																			
STEM:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Pla						1																																	
Sty	2	1	1	2			6				7	4	4		1		5	10	3						1														
Erp	1	1		2		2						1						1								1			1								1		
Glo	1	1																												1									
Hel						2						2															1												
Plab		1						1			1		1						1			1			1		1		2								1		
Pot																															1							
Hol																1																							
Hal																															1							

TABLE A4:5 Numbers of invertebrates occurring on YOUNG stems during 1980. contd....

July (contd.)																				
STEM:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
Cri	2	12	35	5	11	5	11	17	6	14	25	6	4	10	4	1	8	5	3	28
	3	12	11	4	6	1	6	1	1	3	16	2	2	2	1	1	4	2		14
	4	2	7	1	1	1	1	2	2	1	2	3		7	1		3	1	1	6
Pse	2	2	1						2		4									2
	3	1	2		3				1	1	1		1	2		2			1	1
	4	1	1		3		1				1		3	1						
Gly	2	2										1		1						
	3	2			1					1										1
	4				1															
Pen	4				1													1		

August (contd.)																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	2	2		7	1			2	4	8	1		1	2		3		3	1	1
				2	3	1	1	2		9	3			2			1	1	4	
				1										1						

September																					
STEM:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Pla											1									
Sty	1							3	1		2		2		1		2		2	
Erp						2					1									
Glo									1											
Hel															1					
Acr			1	1				3	1								1			
Plab			1										1							
Ase	1	1																1		
Hol																				
Psd	1																			
Cer						1														

October																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
										1										
					1	1	1				2	1		1			3	1		
					1		1													
						1														

TABLE A4: 5 Numbers of invertebrates occurring on YOUNG stems during 1980. ....contd....

		September (contd.)																				October (contd.)																			
STEM:		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Cor	3																	1																								
Cri	2				1	1	1			1	1										1	3	1	1	7	3	4	2	4	2	1	2	3	4	4	1	2	5	7		8
	3						1	1	2		1								1	1	3																				
	4	3	1				1				1	3			1				1	2	4																				
Pse	2																					1		1				2	2		1	3		1	2				2	1	
Gly	1		1																			1						1			1			1				1			
	2	1					2		1	1	1	1				1					1												1	1				1			1
	3		1			1				1		1					1									1	1				1	1									
	4	2					1							1										1			1				2		1								
Lim	2											1			1		3																								

		November																				December																			
STEM:		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Sty																				1																						
Acr			1		1					1										1			1		1			1														
Cri	2	3	3	4	2	4	1	4	6	2	1	2	3	2	3				2	3	11	1	9	4	9	3	5	11		2		5	4	4	8	3		3	2	1	10
	3	1	4		1				4							1					5		1	2	2	1	4	4	2	1	3	4	2		4	1		2	1	1	1
Gly	2												1				1						1										1								
Lim	2																															1									

TABLE A4:5 Numbers of invertebrates occurring on YOUNG stems during 1980. Key to names can be found in Table A4:3, together with naming authorities.

TABLE A5.1 Initial and Final Weights of Phragmites stem litter, and percentage remaining in bags (1979-1980). All weights are ash-free, oven-dry. (*final weight is air-dry because sample lost in grinder).

COARSE BAGS								FINE BAGS							
Date (WEEK)	INITIAL WEIGHT	FINAL WEIGHT	%R	Date (WEEK)	INITIAL WEIGHT	FINAL WEIGHT	%R	Date (WEEK)	INITIAL WEIGHT	FINAL WEIGHT	%R	Date (WEEK)	INITIAL WEIGHT	FINAL WEIGHT	%R
7.6.79 (1)	4.08	4.06	99.51	30.11.79 (26)	4.27	1.91	44.73	7.6.79 (1)	4.00	3.94	98.50	30.11.79 (26)	3.72	2.01	54.03
	3.61	3.51	97.22		3.73	1.43	38.34		3.51	3.44	98.01		3.55	2.20	61.97
	3.29	3.18	96.66		3.85	1.00	25.97		3.61	3.55	98.34		3.21	1.89	58.88
	3.56	3.47	97.47		3.85	1.17	30.39		3.33	3.28	98.50		3.60	2.14	59.44
	4.07	3.95	97.05		3.68	1.46	39.68		3.28	3.20	97.56		3.80	2.50	65.79
14.6.79 (2)	3.29	3.07	93.31	7.3.80 (40)	4.15	1.73	41.69	14.6.79 (2)	3.42	3.27	95.61	7.3.80 (40)	3.56	2.04	57.30
	4.09	3.92	95.84		4.00	0.46	11.50		3.56	3.46	97.19		3.48	1.95	56.03
	3.77	3.57	94.69		3.85	1.36	35.32		3.58	3.49	97.49		3.26	1.70	52.15
	3.81	3.66	96.06		3.63	1.38	38.02		3.87	3.78	97.67		3.38	1.83	54.14
	4.16	-	-		3.83	1.30	33.94		3.73	3.63	97.32		3.57	1.67	46.78
21.6.79 (3)	3.90	3.59	92.05		4.30	0.95	22.09	21.6.79 (3)	3.41	3.13	91.79		4.09	2.28	55.75
	3.72	3.35	90.05		3.90	0.48	12.31		3.64	3.38	92.86		3.21	1.65	51.40
	4.09	3.79	92.67		4.35	1.43	32.87		3.58	3.34	93.30		3.89	2.06	52.96
	3.07	2.68	87.30		4.32	1.34	31.02		4.06	3.84	94.58		3.79	2.09	55.15
	3.68	3.29	89.40		4.03	1.02	25.31		3.82	3.51	91.88		3.86	2.24	58.03
28.6.79 (4)	3.59	-	-		3.39	0.43	12.68	28.6.79 (4)	3.39	2.77	81.71		3.81	1.29	33.86
	3.30	2.63	79.70		4.07	0.44	10.81		3.64	3.14	86.26		4.18	1.38	33.01
	3.89	3.23	83.03		3.31	0.42	12.69		3.27	2.77	84.71		3.87	0.97	25.06
	3.15	2.45	77.78		3.01	0.01	0.27		3.70	3.29	88.92		3.60	0.97	26.94
	3.56	-	-		3.73	0.45	12.06		3.55	3.03	85.35		3.39	0.75	22.12
26.7.79 (8)	3.70	2.70	72.97	11.6.80 (54)	3.31	0.48	14.50	26.7.79 (8)	4.19	3.49	83.29	11.6.80 (54)	4.28	1.51	35.28
	3.44	2.15	62.50		3.54	0.16	4.52		3.71	2.82	76.01		3.40	0.84	24.71
	3.70	2.90	78.38		3.47	0.01	0.20		4.23	3.60	85.11		4.15	1.42	34.22
	3.56	2.49	69.94		3.09	0.42	13.59		3.71	3.05	85.21		3.70	1.05	28.38
	3.34	2.06	61.68		3.71	0.23	6.20		3.44	2.77	80.52		3.95	1.73	43.80
23.8.79 (12)	4.12	2.32	56.31		3.72	0.17	4.57	23.8.79 (12) *	3.52	2.71	68.78		4.41	2.26	51.25
	2.98	-	-		4.08	0.01	0.20		3.90	3.18	72.77		4.25	1.65	38.24
	3.62	1.87	51.66		4.48	0.01	0.20		3.40	2.77	72.70		4.16	1.84	44.23
	3.60	1.87	51.94		3.87	0.19	4.91		3.86	3.11	71.99		3.82	1.52	39.79
	3.95	2.24	56.71		3.18	0.01	0.28		3.55	2.82	70.85		3.70	1.16	31.35

Coarse Mesh.

SAMPLE NO.	%Ash	%Cell.	%Lignin	%N	%C	C:N ratio
Initial	3.57 (.33)	54.5 (1.1)	59.9 (.15)	0.38 -	42 (1)	111.1
Week 1	3.47 (.04)	53.6 (1.5)	62.9 (.15)	0.95 (.05)	47 (1)	49:1
2	2.87 (.06)	53.1 (.6)	62.5 (.7)	0.69 (.12)	46 (1)	67:1
3	1.70 (.02)	51.8 (1.4)	62.4 (.05)	0.29 (.09)	42 (-)	145:1
4	1.54 (-)	52.4 (1.2)	62.1 (.45)	0.24 (.02)	43 (-)	179:1
8	1.06 (.12)	50.5 (1.95)	58.1 (.60)	0.45 (.13)	44 (1.5)	244:1
12	1.50 (.03)	48.2 (1.2)	56.8 (.60)	1.03 (.02)	47 (1.5)	46:1
26	3.37 (.65)	41.3 (1.25)	51.7 (.15)	1.33 (.05)	44 (-)	33:1
40	2.62 (.45)	43.8 (3.2)	51.3 (.76)	1.49 (.07)	45 (1.5)	30:1
54	3.15 (-)	32.1 (.25)	50.2 (-)	1.71 (.02)	41 (-)	24:1
Fine Mesh						
Week 1	3.55 (.02)	54.4 (1.05)	64.5 (.2)	0.95 (.03)	45 (.5)	48:1
2	3.05 (.1)	56.9 (2.7)	63.9 (-)	0.85 (.01)	43 (-)	51.1
3	1.88 (.45)	53.0 (2.2)	64.4 (.05)	0.32 (.18)	44 (1.5)	138:1
4	2.12 (.01)	51.6 (.85)	63.6 (.20)	0.18 (.12)	43 (-)	239:1
8	1.06 (.01)	53.4 (2.05)	59.0 (.05)	0.51 (.04)	45 (-)	88:1
26	1.90 (.18)	47.5 (.4)	54.5 (.2)	0.88 (.01)	42 (.5)	48:1
40	2.07 (.10)	51.8 (7.4)	54.9 (.67)	1.18 (.09)	44 (.9)	38:1
54	2.08 (.31)	51.4 (4.6)	53.7 (.54)	1.23 (.06)	41 (.3)	34:1

TABLE A5:2 Mean proportions (%) of components of *Phragmites* litter present per bag. Figures in parentheses represent one standard error.

SAMPLE NO.	Litter weight	Nitrogen weight
Coarse Mesh.		
Week 1	3634 (163)	34.5 (1.54)
2	3555 (179)	24.9 (1.23)
3	3340 (188)	9.7 (0.54)
4	2770 (236)	6.7 (0.28)
8	2460 (159)	11.07 (0.72)
12	1896 (201)	19.53 (2.07)
26	1394 (159)	18.68 (2.24)
40	1145 (131)	17.07 (1.96)
54	228 (50)	3.92 (0.08)
Fine Mesh.		
Week 1	3482 (129)	32.73 (1.22)
2	3526 (86)	29.97 (0.73)
3	3440 (117)	11.01 (0.37)
4	3000 (103)	5.4 (0.18)
8	3146 (170)	16.36 (0.89)
26	2148 (103)	18.9 (0.90)
40	1951 (73)	22.81 (0.75)
54	1356 (107)	16.19 (1.18)

TABLE A5:3 Mean weights (mg.) of litter and nitrogen remaining per bag. Figures in parentheses represent one standard error.

NITROGEN ANALYSIS: MIXED INDICATOR USED FOR KJELDHAL DISTILLATION.

(i) Conway Indicator: 66 mg of bromocresol green

33 mg of methyl red

Make up in 100 mls 95% ethanol.

(ii) Boric acid Indicator (to make 2 litres):

Dissolve 40 g AR Boric acid crystals in 1400 mls hot distilled water. Cool solution. Put into 2 litre volumetric flask. Add 40 mls Conway indicator soln. (above). Add 400 mls 95% ethanol. Add 0.05M NaOH until a faint green colour is obtained when 1 ml of solution is added to 1 ml of tap water. Make up to the mark.

TABLE A5.4a Numbers of invertebrates in each litter bag : Coarse Mesh. (Figures to right of Chironomidae represent instars)

DATE	7.6.79					14.6.79					21.6.79					28.6.79					26.7.79					23.8.79					30.11.79					7.3.80										11.6.80									
WEEK	1					2					3					4					8					12					26					40										54									
TAXA \ BAG NO.	22	23	24	25	26	6	7	8	10	11	27	28	29	30	31	12	13	14	15	16	47	48	49	50	51	1	2	3	4	5	52	53	54	55	56	32	33	34	35	36	37	38	39	40	41	17	18	19	20	21	42	43	44	45	46	57	58	59	60	61
Planaria torva		1										1	1	1																	1		4	5	3		1		1	2	2						1				1	2	2			1				
Stylaria lacustris			2																							2	9	4	2	4																5	4	4	6	6	20	1	3	5	4	12	1	2		6
Erpobdella octoculata	1	2	1		3	8	20	6	12	10	18	6	10	4	3	1	6	1	10	1	1	2	2	2	2	2	1																																1
Glossiphonia complanata																					1			2	1			6	5	1		1		1	1			2	1	2	1	2	2	2						1		1						
Helobdella stagnalis							5	2	3	1	2	1	2	2												2			1					1							2		1	2						1								
Acroloxus lacustris																											2	1	1			1			1																	1				
Potamopyrgus jenkinsi																																1		1																				
Lymnaea peregra																																							1																
Physa fontinalis																												1									1																	
Pisidium sp.																														1									1																
Planorbis albus						1					1	1	1					1			1	1		1		20								1			1				1					1	1					1				
Asellus aquaticus	25	9	17	8	15	40	40	35		15	80	65	152	68	80	40	134	280	250	60	30	35	68	65	60	235	2	18	1	7				2		1	1			1		1													
Gammarus pulex	2	2	1		2	2	1	1	3			5	4		3				5		3				1	6	77	111	115	48	5	3	5	10	5	5	4	10	11	5	9	2	10	4	5	22	17	17	21	11	45	42	10	9	25	25	14	12	14	25
Caenis sp.																												2			1			1		7	5		2	3	1	2	2	3	3					14	4				2		1
Cloeon dipterum														1												1																										1			1				
Sialis lutaria																												1																							1					
Agrypnia pagetana						1		1		1	3	1			1		3	3	1		6,p	9,p	4,p	7	6,p	7	2	2,4p	7	4																					3		1							
Athripsodes aterrimus																																				1		2			1								1	1	1	1			2	1	2	2	
Holocentropus picicornis																					1		2	1	2		1	2	1					2		1	1										1	1			1					2		1
Leptoceridae sp.																								1		1																									1						
Mystacides longicornis																																																		1							
Ceratopogonidae																					1																																					
Nytiscidae																																						1													1						
Haliplidae																																																		2	1		1		2			2	1	1				
Procladius sp. 2										1																																																		
3																							1																																			
Corynoneura sp. 3								4		1	2	1	1	2					1		1	4	1	1	1																																		
4																						1	1		1																																	
Cricotopus sp. 2								4			4	3	3	5	1		14	1	2		4	10	1	2	4	11	14	16	4	57										1	7	2			3	15	6	11	7	4	3	4	7	2		13	4	3	6	3
3	3	1		1						3	7	1	4	1	7	1	1			1	1	1				2	1	5	1	6	1	1				2	14		7	4	7	22	27	19	13			3		1	3	1	4	1		6	2	3		1
4											2	2																		6						1	5	2	2			1	2	3	2													
Microcricotopus sp. 3																										1																															
Psectrocladius sp. 2											8	3	2	4	1	3	12	5			1		1																																			
Cladotanytarsus sp. 3																			1															1																					
Camptochironomus sp. 1						2		4	9	3	4	5	2	7	2		5	15	11																																						
2										1																																															
3																																																									
4																																																									
Glyptotendipes sp. 1																					8	17	19	27	16	1	3			5						1	1			3	3		1		4	7	16	30	3	15	2	8	13	15	27	5	24	17	13
2						1	2		2	1	47	15	24	12	17	8	12	7	18	11	10	15	7	21	31	20	6	19	40	17		1	3	2	9	1		1	4		5		4	1	6	64	55	86	73	64	21	33	25	27	36	20	32	25	22	26
3													1	1	1											10	1	9	1	5		1	2		3		1			1		2	2	2	1		1	1		3	3	1	1		1		2	4	4	4
4		1	1				2	1			2	1		1	1		1				1						2		1	1	5	17	23	5	10	9	4	9	12	6		4	5	12	3	2		1		1	1					2	1	1
Limnochironomus sp. 2						4	1				6	18	14	28	10		18	17	14	12	15	14	22	16	19	56	22	54	59	8						1	2	2		1	1		2	1			3	2	1	3	5	2	4	12	3	1		2	2	
3																					2	1	4	2	2	16	7	16	5	4		6	2	1	18	10	6	9	9	6	21	2	11	11	10		3	4		3	4	1		1	1		3			1
4																						4	2			2	6	7	4			1		1	1						1								1	1				1				
Microtendipes sp 3									1																																																	
Parachironomus sp. 2																										2																															
3																										3																															
Pentapedilum sp. 2																														5																											
3																														2																											
4																														1																											
Polypedilum sp. 2										1																																																
3																					2																																					

TABLE A5.4b Numbers of invertebrates in each litter bag : Fine Mesh. (Figures to right of Chironomidae represent instars)

DATE		7.6.79					14.6.79					21.6.79					28.6.79					26.7.79					23.8.79				
WEEK		1					2					3					4					8					12				
TAXA / BAG NO.		62	63	64	65	67	95	96	97	98	99	85	86	87	88	89	70	71	72	73	74	115	116	117	118	119	90	91	92	93	94
Planaria torva																1															
Stylaria lacustris				5																							8		1	2	1
Other oligochaetae																											2				
Erpobdella octoculata							6	4	3	4	5	7	2	5	2	5	10	5	10	8	4	1	1	2	2				1	3	
Glossiphonia complanata																															1
Helobdella stagnalis																							1			1					1
Potamopyrgus jenkinsi																															
Physa fontinalis																												1			
Pisidium sp.																															
Planorbis albus																			1								1	2		1	
Asellus aquaticus		2	1	1	1	3	10	7	5	3	9	28	40	45	42	30	50	80	60	30	70	105	100	95	110	60	41	92	81	63	81
Gammarus pulex						1	3				2				2								2								
Cloeon dipterum												1																			
Sialis lutaria																															
Athripsodes aterrimus																															
Holocentropus picicornis																								2	1	3					
Ceratopogonidae			1	1																			1	1	1						
Haliplidae																															
Procladius sp.																															
Corynoneura sp.	3					1	8	1	1	1	3	1	7	1	1	1								1							
Cricotopus sp.	2						6	2	1		2	13	4	11	12	3	1		4	1			2	1	2	2	3	1	2	1	
	3	2	3		5	1	4	4	2	5	6	7	5	2	2			1	2		3										
	4						1	1	6	1	7		1																		
Psectrocladius sp.													2	13	6	2															
Camptochironomus sp.	1						7	5	1	4	1	6	2	6	2	1	3	1	1	4	4										
	2							1	1	1			2			2															
	3																														
	4																				1										
Endochironomus sp.												1																			
Glyptotendipes sp.	1																					4	2	3	3			3			
	2						2	3	2	1	1	27	16	12	11	33	2	3	4	5	9	3	4		2	2			1	2	3
	3									1		4		4	1					2										1	1
	4																				1										
Limnochironomus sp.	2											48	18	1	17	39	35	14	15	13	14	6	10	1	10	6	1	4	2	1	
	3																18	12	11	25	20		1		2			1		2	
	4																						1								
Microtendipes sp.				1																											
Pentapedilum sp.	2																											2	1		
Polypedilum sp.	3			1																				1							

DATE		30.11.79					7.3.80.										11.6.80														
WEEK		26					40										54														
TAXA / BAG NO.		75	76	77	78	79	110	111	112	113	114	120	121	122	123	124	80	81	82	83	84	100	101	102	103	104	105	106	107	108	109
Planaria torva																			1							3	1				1
Stylaria lacustris																		3	1	3	3	3	3	12	2	7			1	8	3
Other oligochaetae					1																										
Erpobdella octoculata				2				2	1		1			2	2	1			1	2	1	2		2	1	1		3			4
Glossiphonia complanata		1										1																			
Helobdella stagnalis																			5					2		2		1		1	
Potamopyrgus jenkinsi												1																			
Physa fontinalis																															
Pisidium sp.								1																							
Planorbis albus		.1					1	1	2	1					1																
Asellus aquaticus		15	3	7	2	2	21	13	12	53	42	25	11	12	13	12	20	20	50	50	55	60	65	75	90	50	50	70	100	40	90
Gammarus pulex												7	3											5		1	1		5	2	
Cloeon dipterum																															
Sialis lutaria												1																			
Athripsodes aterrimus										1																					
Holocentropus picicornis					1																		1		1						1
Ceratopogonidae							1				1											1			1						
Haliplidae																						2	1								
Procladius sp.									1																						
Corynoneura sp.	3																														
Cricotopus sp.	2						1	1				1	2	1			2			2	2	3	9	4	2	2	2	2		1	2
	3						6	4	3	3	2	3	4	4	2	1	1					1	2	3	1	4	3	3		1	3
	4							2		1	1	2				1															
Psectrocladius sp.																															
Camptochironomus sp.	1																														
	2																														
	3				1								1		3	3															
	4	1		1	2	5	1		1				6		9	7									1				2		
Endochironomus sp.									1				2														1			2	
Glyptotendipes sp.	1										1		1		1	1	11	12		15	12	4	4	2	2	1	1	1	6	6	3
	2						4		1	2	1		1	2	1		12	18	2	22	5	3	4	1	4	2	7	4	11	5	4
	3				2		3	3	2				1	2		3	2	2		4	2		2	2	1		3		5		
	4				1	2	6	2		3		3	3	4		1					1	1	1		1			1	2		5
Limnochironomus sp.	2				1							1					1	2		5	2	5	6	1	5	4	2	2	1		4
	3						6	1	2	1	3	4	6	2	2	2		7	1	4	2		1	3	1	1	2			6	2
	4													1																1	
Microtendipes sp.																															
Pentapedilum sp.	2																														1
Polypedilum sp.	3																														

1979	Station 1					Station 2				
	1	2	3	mean	s.e.	4	5	6	mean	s.e.
7.6							24	17	20.5	3.5
14.6							17	5	11.0	6.0
21.6							2	0	1.0	1.0
28.6	100	265	138	167.7	49.9	3	9	15	9.0	3.5
5.7	108	291	336	245.0	69.9	9	3	2	4.7	2.2
12.7	77	262	103	147.3	57.9	2	2	3	2.3	0.3
19.7	53	41	12	35.3	12.2	3	7	5	5.0	1.2
26.7	99	66	237	134.0	52.4	5	7	-	6.0	1.0
2.8	50	50	108	69.3	19.3	0	0	3	1.0	1.0
9.8	41	31	14	28.7	7.9	0	0	2	0.7	0.7
16.8	5	11	-	5.3	3.9	0	0	0	0.0	0.0
23.8	7	7	0	4.7	2.3	3	3	0	2.0	1.0
30.8	0	5	0	1.7	1.7	5	11	2	6.0	2.7
6.9	3	7	5	5.0	1.2	0	5	6	3.7	1.8
13.9	2	2	5	3.0	1.0	7	5	14	8.7	2.7
20.9	0	0	2	0.7	0.7	3	2	2	2.3	0.3

1980	Station 1				Station 2				OS1	OS2
	1	2	mean	s.e.	4	5	mean	s.e.	3	6
30.4	3	6	4.5	1.5	0	5	2.5	2.5	-	31
7.5	2	2	2.0	0.0	0	3	1.5	1.5	31	14
14.5	0	2	1.0	1.0	0	5	2.5	2.5	-	3
21.5	12	2	7.0	5.0	2	11	6.5	4.5	-	-
28.5	3	14	8.5	5.5	2	9	5.5	3.5	-	-
4.6	29	6	17.5	11.5	3	3	3.0	0.0	-	2
11.6	7	2	4.5	2.5	3	3	3.0	0.0	24	20
18.6	5	2	3.5	1.5	2	3	2.5	0.5	6	6
25.6	5	2	3.5	1.5	3	12	7.5	4.5	168	160
2.7	17	6	11.5	5.5	5	9	7.0	2.0	496	108
9.7	9	15	12.0	3.0	7	9	8.0	1.0	108	19
16.7	49	71	60.0	11.0	5	14	9.5	4.5	-	-
23.7	14	39	26.5	12.5	3	5	4.0	1.0	15	2
30.7	5	12	8.5	3.5	3	9	6.0	3.0	14	-
6.8	5	11	8.0	3.0	15	0	7.5	7.5	-	-
13.8	6	17	11.5	5.5	15	7	11.0	4.0	-	-
20.8	5	5	5.0	0.0	22	14	18.0	4.0	-	-
27.8	6	3	4.5	1.5	7	3	5.0	2.0	-	-
3.9	3	7	5.0	2.0	3	6	4.5	1.5	-	-
10.9	12	52	32.0	20.0	7	6	6.5	0.1	-	-

TABLE A6:1 Total emergence of chironomids ($m^{-2}day^{-1}$) and mean number per trap (±1 standard error) at Cop Mere for week ending as shown, during 1979 and 1980.
- signifies trap destroyed.

TRAP:	1	9	2	10	3	11	4	12	5	8	6	7
1979												
4.5	4	11	4	4	0	7	4	0	9	6	0	4
11.5	0	9	3	0	0	4	7	1	_	4	0	11
18.5	7	-	1	24	0	14	-	16	9	3	4	-
25.5	7	4	6	14	4	0	7	14	7	-	9	-
1.6	6	153	11	21	-	10	17	14	11	1	4	-
8.6	10	104	17	10	9	26	33	24	73	7	76	11
15.6	7	51	21	31	9	11	191	14	90	27	46	17
22.6	-	-	251	110	-	33	160	-	209	3	90	131
29.6	16	31	24	31	20	117	38	48	91	10	23	110
6.7	51	-	20	27	17	83	54	31	116	38	46	-
13.7	16	43	150	67	71	36	43	58	107	17	81	71
20.7	30	10	144	43	57	33	31	6	261	16	87	67
26.7	7	16	91	34	19	33	26	-	101	20	64	77
3.8	26	17	86	44	30	58	18	14	33	38	76	80
10.8	24	11	290	33	20	17	18	10	44	10	104	31
17.8	14	14	86	84	14	18	4	-	104	97	37	71
1980												
21.4	-	27	7	7	-	7	17	17	17	20	30	10
23.4	5	40	-	20	5	5	-	20	30	10	15	5
25.4	-	40	5	10	10	-	-	-	15	-	5	45
28.4	-	-	10	17	-	10	7	17	7	-	17	10
30.4	-	5	-	25	-	-	25	20	5	-	20	-
2.5	15	10	-	-	5	5	5	-	-	-	5	10
6.5	5	10	-	8	3	-	5	3	-	3	-	7
7.5	-	20	-	-	-	10	20	20	40	20	-	-
9.5	-	5	5	5	-	20	-	5	5	-	25	10
12.5	20	10	7	13	3	7	7	13	-	7	7	3
14.5	35	30	15	-	10	20	-	10	30	35	25	5
16.5	95	-	5	30	25	35	5	5	45	-	20	25
19.5	27	103	-	37	-	107	3	13	130	17	63	20
22.5	20	37	3	20	3	33	-	13	40	20	33	60
23.5	40	70	10	-	10	140	-	60	70	10	60	-
27.5	-	58	3	10	7	-	7	15	47	7	55	10
29.5	15	65	10	5	10	40	-	35	35	-	40	20
31.5	60	55	10	20	5	50	-	25	85	30	35	35
2.6	30	35	5	5	20	-	15	15	55	5	15	15
4.6	40	70	90	25	50	35	50	45	75	15	10	20
6.6	30	45	80	50	10	10	25	30	40	-	20	75
9.6	20	133	47	40	10	10	23	30	-	3	27	43
11.6	50	130	20	10	5	20	30	20	40	30	40	25
13.6	180	90	45	40	20	20	25	30	20	25	15	40

TABLE A6:2Total emergence of chironomids ($m^{-2}day^{-1}$) from each trap at Linford (for period ending as shown) during 1979 and 1980. - signifies trap destroyed.

contd.....

.....contd....

TRAP:	1	9	2	10	3	11	4	12	5	8	6	7
1980												
16.6	103	90	40	90	20	30	57	53	17	-	17	20
18.6	35	50	40	80	30	15	35	85	35	-	-	35
20.6	40	35	95	80	5	35	50	10	10	45	20	30
23.6	53	50	30	67	27	23	7	43	10	37	30	27
25.6	40	15	55	35	20	25	30	40	35	40	25	20
27.6	25	50	50	75	40	55	35	30	60	20	15	20
30.6	60	97	83	70	30	70	17	27	30	40	10	17
2.7	35	90	75	60	10	105	35	40	15	40	25	15
4.7	30	135	65	25	45	65	40	20	65	30	20	30
7.7	47	127	67	67	20	20	53	17	20	50	10	7
9.7	55	110	45	30	20	35	40	20	20	15	5	10
11.7	25	170	30	40	5	40	20	20	25	35	10	10
14.7	137	240	27	43	37	23	13	10	-	23	73	-
16.7	80	450	120	40	55	25	-	40	40	-	-	30
18.7	120	355	35	50	55	50	40	15	10	100	30	20
21.7	190	913	127	113	183	127	90	47	30	43	33	47
23.7	-	160	175	110	-	180	15	40	35	20	15	45
25.7	60	280	315	100	55	120	110	65	25	10	20	25
28.7	-	410	687	137	57	210	87	147	13	33	50	83
30.7	75	350	585	80	155	15	60	80	15	25	35	35
1.8	40	215	815	145	175	55	60	45	50	20	75	70
4.8	57	217	597	137	213	77	37	40	23	30	30	83
6.8	80	190	365	115	105	70	65	75	45	15	25	45
8.8	105	215	455	65	165	110	40	40	25	50	45	55

TABLE A6:2 Total emergence of chironomids ($m^{-2}day^{-1}$) from each trap at Linford (for period ending as shown) during 1979 and 1980. - signifies trap destroyed.