STUDIES ON THE PREDATORS AND PARASITES OF THREE SPECIES OF LAKE-DWELLING LEECH

THESIS

Submitted in accordance with the requirements of
The University of Liverpool
for the degree of Doctor in Philosophy
by Stuart Mark Spelling

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THIS IS TO CERTIFY that the work here submitted is the result of the candidate's own investigations. Due acknowledgement has been made of any assistance received.

Stuart M. Spelling

I HEREBY CERTIFY that this work has not already been accepted in substance for any degree, and is not being concurrently submitted in candidature for any other degree.

Stuart M. Spelling

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Stuart M. Spelling

......

He told, that to these waters he had come,
To gather leeches, being old and poor:
Employed hazardous and wearisome!
And he had many hardships to endure:
From pond to pond he roamed, from moor to moor;
Housing, with God's good help, by choice or chance;
And in this way he gained honest maintenance.

......

He with a smile did then his words repeat;
And said that, gathering leeches, far and wide
He travelled; stirring thus about his feet
The waters of the pools where they abide.
"Once I could meet them on every side;
But they have dwindled long by slow decay;
Yet still I persevere, and find them where I may."

From 'Resolution and Independence - The Leech Gatherer on the Lonely Moor' by William Wordsworth, 1807.

Summary

In the present study, the incidence and effects of predation and parasitism on three species of lake-dwelling leech, viz. Erpobdella octoculata, Glossiphonia complanata and Helobdella stagnalis were investigated.

A literature survey was carried out,and produced a wide range of studies which reported leeches in the diet of predators. The majority of such records were for fish from lakes and rivers, but a few records from waterfowl were also reported. Simple laboratory experiments demonstrated that a wide range of invertebrate and vertebrate predators may feed on both adult and young leeches. Field collections of these predators were taken and examined,using visual and serological techniques to establish what had been eaten. Positive evidence for predation in the field was provided by this work, but the incidence and intensity of predation was found to be very low. Field experiments, using predator exclusion methods in the stony littoral of a eutrophic lake, were carried out but failed to show any marked changes in leech mortality or population dynamics.

The parasites of leeches collected from fifteen lakes in England and North Wales were surveyed and five species recorded. These parasites were the microsporidians, Nosema herpobdellae and Nosema glossiphoniae, and the trematodes, Apatemon gracilis, Cotylurus cornutus and Cyathocotyle opaca. Only A. gracilis and C. cornutus were previously reported from British leeches. The microsporidian species were re-described, using electron microscopy. Detailed studies on the incidence of the parasites were carried out in leeches from a eutrophic lake, and a limited amount of evidence for parasite-induced host mortality and a reduction in the fecundity of infected leeches was presented.

The findings of the present work are discussed in relation to previous studies on leech populations, and to other mechanisms that may serve to control and regulate these populations. It is concluded that, whilst causing some mortality, predation and parasitism play a minor role in the control and regulation of the leech populations in the stony littoral of eutrophic lakes. It is suggested that the availability of food, particularly to young leeches, may be a more important factor, and certainly one that deserves future attention.

CONTENTS

CHAPTER 1

INTRODUCTION

1.1 Introduction

The problem as to what factors determine the distribution and abundance of species is one that has long taxed biologists and, indeed, forms the definition of the study of ecology as given by Krebs (1978). In this present study, two of the many factors that may affect the distribution and abundance of organisms, namely predation and parasitism are examined in relation to populations of three common species of British lake-dwelling leeches. These factors are further discussed, in relation to other mechanisms which may influence populations, in the final discussion.

Theoretical models of predator/prey interactions have been developed over many years since the original studies of Lotka (1925), Volterra (1926), Thompson (1924) and Nicholson & Bailey (1935). These basic studies on how predator and prey populations interact have been further elaborated by studies such as those of Solomon (1949), who formulated the concept of a functional response to describe changes in the numbers of prey attacked by a predator at different prey densities. Holling (1959,1965) further developed this idea and suggested three types of functional response. In the type I response, the number of prey attacked was predicted in a situation when there was a constant rate of the predator encountering prey. The number of prey attacked increased with density until a threshold was reached, above which there was no further feeding by the predator. In the type II response, the number of attacks per predator showed a negatively accelerating rise to an upper plateau and this occurred when a handling time was introduced into the equations. In the type III response, a sigmoid response curve was obtained and this occurred when elements of learning were introduced into the predator's searching pattern. These theoretical aspects of predator/prey interactions have been further developed by Murdoch (1970), Beddington et al (1976), Hassell (1975), Hassell & May (1974) and Hassell et al (1976), amongst others.

One of the important points to come out of theoretical work, is that numerical responses of predators and prey may occur without the predator exerting any controlling influence on the prey. It is possible that predators may have important effects on prey abundance when prey populations are low, but become unimportant when prey densities are high.

Laboratory experiments have been performed to back up theoretical work. The first detailed studies date back to Gause (1934) who cultured two protozoan populations, Paramecium coudatum and its predator Didinium nasutum. Under the simplest of regimes the predator was found to consume the prey and then starve. When a refuge was introduced, the prey survived and the predators declined to extinction. With more complex conditions, for example with the immigration of prey, stable oscillations of predator and prey could be produced. This phenomenon has been further demonstrated, for example, in the laboratory experiments of Huffaker (1958) and Utida (1957). However, field evidence for predator/prey oscillations is scarce.

Thus, it seems that in laboratory systems, predator/prey interactions can cause regular oscillations in both species. However, such experiments cannot predict which predators in the field would be capable of controlling prey. The only method of demonstrating which predators are important will be to manipulate the interactions in the field, with the most obvious action being to remove the predator and see how the prey responds.

Predators which are capable of disproportionately affecting patterns of prey abundance have been termed as 'keystone species' (Paine, 1966, 1969a, 1969b). In Paine's studies on the rocky intertidal zone of marine habitats, such predators were able to eliminate competition for space between rival prey species. However, Krebs (1978) suggested that 'keystone species' may be rare in aquatic communities. Field experiments carried out by Thorp & Bergey (1981a), using predator exclusion methods, suggested that 'keystone species' were not present in the littoral zone of a freshwater reservoir. It was argued that the development of such species was not possible because of the fact that environmental heterogeneity would reduce predator efficiency; that food web complexity would reduce the community importance of an individual predator species; that resource partitioning of space and food hinders the manipulation of a rate-limiting environmental resource by a single predator species and, further, that predation in such environments may not be extensive enough in time or area to provide sufficient resources to be exploited by a single species. However, the possibility of regulation by a guild of predators was acknowledged, plus the possibility that 'keystone species' might be more important in harsher and less complex habitats.

Most field studies on predator/prey relationships have focused on marine inter-tidal environments. The studies by Paine were mentioned above and other studies include those of Connell(1970), Dayton (1971), Menge (1976), Menge & Sutherland (1976), Sutherland & Karlson (1977). However, there has been some work, and increasingly so in recent years, on the freshwater benthos (Ball & Hayne, 1952; Hayne & Ball, 1956; Hall et al, 1970; Benke, 1976 & 1978; Peckarsky, 1979), and work has started to try to demonstrate the effects of predators on prey populations by using predator exclusion methods. These studies are reviewed in Chapter 4.

The theoretical framework examining how parasites and their hosts interact have also been theoretically and experimentally examined. Indeed, much of the early work on predator/prey interactions concerned the special case of insect parasitoids and their hosts (Nicholson & Bailey, 1935). In recent years, in a series of papers,Anderson (1974, 1978 and 1979), Anderson & May (1978 & 1981), May & Anderson (1978), Crofton (1971) and Anderson & Gordon (1982) this framework has been further elaborated. The role of parasites as biological control agents was reviewed by Anderson (1982).

Basically, it has been found that parasites may sometimes act to regulate and depress their host populations. At its simplest, where the parasite solely influences host survival such that an extra per capita death rate (A) acts on infected hosts, then the condition for regulation is simply that (A) is greater than the host reproductive rate. Further, if infected hosts are unable to reproduce, whether through being killed before breeding or by the pathogen's impact on the reproductive organs, the parasite is always able to regulate the hosts population's growth. One further prediction is that highly pathogenic organisms will exist at low prevalences as a result of the inverse relationship between standing crop (the number of infected hosts) and the rate of turnover (the rate of mortality of infected hosts).

Few field studies have been carried out in sufficient detail to examine the effects of parasites on these population parameters so that the theoretical models can be tested, though Anderson (1982) draws on the materials of Smirnoff (1967), Lacey & Mulla (1977), Gilmore & Tashiro (1966), Pinnock et al (1973) and Zelazny (1973). A general review of the ecological aspects of host/parasite interactions was given in Kennedy (1975).

Studies on the ecology of populations of freshwater leeches have increased in recent years. Early studies were basically interested in the taxonomy of the species, and bibliographies covering these works have been given in Autrum (1936), Mann (1962), Soos (1970), Klemm (1974) and Sawyer (1974). However, apart from the study of Whitehead (1913), these early works largely ignored the ecological aspects of these animals. With the development of the study of ecology in more recent times, population studies have become more fashionable and various 'survey-type' studies were presented in the first half of this century (for example, Ussing 1929; Pawlowski, 1936; Berg, 1938; Brunn, 1938). Perhaps the most important study of this ilk was that of Bennike (1943) who published the results of a survey of Danish leeches from over 200 locations and attempted to relate the distribution of the species to their physico-chemical environment.

Of the fourteen species of leech found in British freshwaters (listed and reviewed in Elliott & Mann, 1979), it has been the free-living aquatic predators that have been given the most attention in recent publications. The commonest of these species are Erpobdella octoculata (L.), Glossiphonia complanta (L.) and Helobdella stagnalis (L.), and it is with these species that this thesis is concerned.

Mann (1953a, 1953b, 1955, 1957a, 1957b & 1961) reported on the distribution and life-history of E. octoculata, G. complanata, H. stagnalis and Erpobdella testacea (Savigny) and reviewed these studies in a book (Mann, 1962). Mann (1964) also produced a key to the British leech species which has since been revised to include a review of the ecological information currently available (Elliott & Mann, 1979). Other work in this country has been carried out in Scotland by Warwick & Mann (1960), and Williams (1961). Elliott (1973a & 1973b) studied the production and life history of E.octoculata in the Wilfen Brook in Cumbria. Learner & Potter (1974) investigated the life history and production of H. stagnalis in a reservoir in South Wales, and Murphy & Learner (1982) carried out a similar study on E. octoculata in the River Ely. Aston & Brown (1975) investigated populations of E. octoculata in the River Trent at sites subject to thermal pollution, and Thompson (1978) studied populations of E. octoculata in gravel pits in Yorkshire.

Further studies, carried out by Dr. J.O.Young and his colleagues at Liverpool University, have collected detailed information on the distribution, life cycles, feeding behaviour and reproductive activity of the three common lake-dwelling leech species (Young 1980, 1981a, 1981b & 1983; Young & Ironmonger 1979, 1980, 1982a & 1982b; Randall et al,1985).

There have also been many ecological studies on leeches from Europe and North America. Perhaps the most important of these, in relation to the present study, were the quantitative studies of

Dall (1979a, 1979b and 1979c) on the leeches of Lake Esrom, Denmark and the studies of Sawyer (1967, 1968 & 1974) on the leeches of Louisiana in the United States.

It is not the purpose of this thesis to collate and present all the existing information on the ecology of these leech species, though detailed discussion of relevant papers is given in later chapters. Good, general reviews of this subject have already been given in Klemm(1974), Sawyer (1974) and Elliott & Mann (1979). However, what is apparent from previous studies is that while detailed ecological information has been collected, there have been few attempts to examine the physico-chemical and biological factors that might influence the distribution and abundance of the species. The exceptions to this being the works of Young and Young & Ironmonger mentioned above. This contrasts with the approach used by workers on freshwater triclad populations (for example, Reynoldson,1958a, 1958b; Reynoldson & Davies, 1970 and Reynoldson & Bellamy 1970, 1971 etc.) who have largely concentrated on this aspect of their ecology.

In a recent thesis on the ecology of leeches and triclads (Ironmonger, 1981), it was concluded that predation by fish and water birds must bear a major responsibility in the mortality of young leeches, and this would seem to re-iterate the point made by Elliott & Mann (1979) who stated that 'little is known about predation on leeches' and suggested that 'when more information is available, there is a high probability that differential mortality from predation will prove to be a major factor in determining the abundance and distribution of each species'.

What is the evidence for these statements? It would seem that the assumption is based on a limited number of dietary records and in the fact that leeches may play a role as intermediate hosts to parasites whose final hosts are fish and waterfowl. Also, no other mechanisms to explain the very high mortality, particularly in young leeches, in the populations have been suggested. In this present study, the predation on and the occurrence of parasites in the three common leech species are examined in order to provide evidence that may help to prove or disprove these statements.

Several lines of investigation have been carried out. Firstly, a literature survey was conducted to establish what records there were for predation on leeches (Chapter 2). The second line of approach was to expose leeches to predators in the laboratory to see which species would eat leeches,if offered them. Although this method would not take into account whether the predators would encounter leeches (or eat them) in the field, it would at least give an indication of what the potential predators were. This was backed up by field collections of vertebrate and invertebrate predators which were examined using visual and serological methods to determine what had been eaten (Chapter 3). These methods, though giving information on both the potential and actual predators of leeches and, perhaps, some indication of the intensity of predation, would not yield information on whether predation had any significant effects upon natural populations. Possible effects might be changes in species composition, density, biomass, production and population dynamics. To study these, at least in part, field manipulations were carried out on leech populations using predator exclusion methods (Chapter 4).

In the second part of the thesis, the parasites of leeches and, in particular, of E. octoculata, G. complanata and H. stagnalis are reviewed and the occurrence of parasites in leeches from local populations surveyed (Chapter 5). Detailed studies on the parasites of leeches, seeking to gain basic ecological data and to find evidence for parasites affecting the population dynamics of their hosts, were carried out on one lake, Crose Mere, and these are described in Chapter 6. Finally, the information collected is reviewed and discussed in relation to previous studies on the populations and life-history strategies of the three leech species.

In the remainder of this chapter, a description of the field sites used in all aspects of this study is given.

1.2 Field Sites

This study included investigations on the leech population of fifteen lakes, ten of which are to be found in the Shropshire-Cheshire Plain, and the remaining five from the Snowdonia region of North Wales. Detailed investigations were carried out on one lake, Crose Mere, in Shropshire, while studies on the remaining lakes concerned surveys for the predators and parasites of leeches. The lakes investigated are listed in table 1.1.

1.2.1 The Shropshire-Cheshire meres

These meres are a group of over sixty meres and pools that occur in clusters on the Shropshire-Cheshire plain. They were formed during the kataglacial phases of the Weichselian glaciation (Boulton & Worsly, 1965; Shotton, 1967), and lie in shallow hollows on the glacial drift. Several are known to have been continuously water-filled since 12,000 B.P. (Beales & Birke, 1973). The range of their morphology suggests that the basins may have several origins and Reynolds(1979) lists five likely possibilities:-

1) Vestigal meltwater lakes, e.g. Fenn's Moss.
2) Kettle Hole lakes, e.g. many Delamere Forest meres.
3) Moraine-dammed hollows, e.g. Crose Mere.
4) Periglacial pingoes, formed by the melting of ice lenses and the collapse of their overlying drift, e.g. Oakhanger Moss.
5) Post-glacial subsidence hollows, formed by the solution of underlying saliferous bedgs, e.g. Budworth Mere.

The ten lakes investigated in this region can readily be split into two groups of five lakes. The Ellesmere group are situated around Ellesmere in North Shropshire and include Crose Mere, while the Knutsford/Delamere group are to be found in North Cheshire. Reynolds (1979) has reviewed the literature concerning the Shropshire-Cheshire meres and summarises the current knowledge concerning their origin, development and present-day ecology. However, studies on the group as a whole are few. Sinker (1962) provided a general ecological background to the North Shropshire Meres, while Tallis (1973) provides some information on the Cheshire sites. Gorham (1957a, b) carried out chemical analyses of the surface waters of a number of meres, and all ten lakes used in this study can be regarded as calcium-rich, productive lakes.

1.2.2 Crose Mere

Crose Mere is a relatively small lake, about 800 metres in length and 300 metres in width, forming a surface area of about 15.2 hectares (Sinker, 1962). Its basin is essentially simple and reaches a maximum depth of 9.2 metres, with a mean depth of 4.8 metres and it has an estimated volume of 7.35×10^5 cubic metres (Reynolds, 1973a).

Surrounding the lake is a clearly defined marginal strip up to 150 metres wide, which suggests an earlier lake level about 3 metres higher than the present level of 86 metres. It was proposed by Hardy (1939) that this could be accounted for by drainage operations in 1864, but Reynolds (1979) suggests that this must be doubted, for a level of 89 metres would have flooded water round to Whattal Moss, lying to the north, which is known to have been a separate basin for many centuries (Eyton, 1854, quoted by Sinker, 1962). In May 1981, during the course of the present study, clearance of the ditch linking Crose Mere to Sweat Mere resulted in a rapid drop of water level by about 350 mm. exposing a wide strip of the littoral zone. The drainage works were intended to improve the pastures bordering the lake, but a drop of only a few centimetres was envisaged by the Nature Conservancy Council at the time the work was carried out. Since the clearance in 1981, and ignoring seasonal fluctuations, the water level appears to have risen again, but has not yet reached its original level. Reynolds (1979) states that the depth of the lake fluctuated between 9.16 - 9.21 metres from January to June/July, but then dropped rapidly to a minimum of 9.08 - 9.10 metres in August and October, a range of 130 mm.

Three small field drains enter the lake on its southern shore, but there are no inflow streams and it seems that the lake acquires most of its water by underground seepage and rainfall. An outflow ditch links Crose Mere to Sweat Mere at its eastern end, and has an estimated average annual discharge of 380,000 cubic metres (Reynolds, 1975a). A detailed account of the hydrology of Crose Mere is given in Reynolds (1975a).

Ironmonger (1981) carried out water analyses on the lake in April 1977, August 1977 and May 1978 and found that calcium ranged between 44.4 - 58.5 mg/l, magnesium 12.2 - 14.3 mg/l, sodium 2 - 3 mg/l, potassium 4 mg/l, chloride 25 - 30 mg/l, sulphate 11 - 17 mg/l, nitrate 1 - 3.4 mg/l, and pH was constant at 7.4. Other water analyses are reviewed in Reynolds (1979), and it is clear that the lake is the richest in ions of the Ellesmere meres. The results of a limited series of water analyses, carried out during this study, are given in chapter 4.

Thermal stratification in the lake has been studied by Reynolds (1975a), who found that the lake became stratified mid May - July and remained so until October, when isothermic mixing was re-established. It seems that unless there are unusual weather conditions, there is only one period of complete mixing per year and, therefore, the lake can be regarded as warm monomictic. In the present study, water temperature was recorded using a continuous temperature recorder (Cambridge Instruments Co.) located in the boathouse mid-way along the northern shore, with the temperature probe submerged to a depth of about 150 cm. The mean weekly water temperatures, together with the range of temperatures recorded are shown in figures 1.1 and 1.2 covering the periods May 1981 to April 1982,and May 1982 to March 1983 respectively.

Light penetration into the lake has been estimated using a Secchi disc by Reynolds (1973a) and the readings rarely exceeded 4 metres, giving a maximum euphotic depth of between 7 - 12 metres. However, much of the time the lake is considerably more turbid, particularly during algal blooms.

The algal and phytoplankton communities have been studied by Griffiths (1925) and Reynolds (1973a, 1973b, 1973c, 1975b, 1976 & 1978). Over 75 species of algae have been recorded in the plankton of Crose Mere (Reynolds,1978). There are usually two major peaks in abundance each year (Reynolds, 1973a). The first, in February to March, is usually dominated by Asterionella formosa (Hassel) or Fragilaria crotonensis (Kitton). In late spring there are then growths of green algae, e.g., Volvox, Eudorina and Pediastrum, followed in summer by the blue-green algae, e.g. Aphanizomenon, Anabaena and Microcystis. These last three genera are responsible for the blooms ('breaks') for which the lake is renowned. Under conditions when the algae produce too many gas vacuoles and there is little water turbulence, all the algae may rise to the water surface to give a dense green scum. There is no evidence that an explosive increase in algal growth occurs prior to the bloom and it is more simply a concentration of the existing algae (Reynolds & Walsby, 1975). The second major peak, in August/ September, is dominated by Ceratium hirundinella (O.F.Müller) with variable proportions of Melosira granulata (Ralfs), A. formosa, F. crotonensis, Microcystis aeruginosa (Kutz) and Coelosphaerium naegelianum (Lemm). The variety of phytoplankton present is regarded by Reynolds (1973b) to be indicative of eutrophic conditions.

The planktonic Rotifera and Entomostraca of Crose Mere have been investigated by Galliford (1960), and Reynolds (1978) presents information on the seasonality of some zooplankters. *Keratella cochlearis* (Gosse) *Kellicottia*, *Asplanchna priodonta* (Gosse) and *Polyarthra* were abundant in March to May, and August to September. *Trichocerca* occurred mainly in summer, while the abundance of *Diaptomus* and *Cyclops* varied throughout the year. *Daphnia hyalina* (Leydig) reached a maximum in mid or late spring.

The littoral vegetation has been described by Sinker (1962) and Reynolds (1979). There are three narrow reed beds, dominated by *Phragmites communis* (Trin.) and *Typha angustifolia* (L.), at the north-west and eastern ends of the lake and along the southern shore. Sinker (1962) also records *Cladium mariscus* (L.), *Scirpus lacustris* (L.) and *Nuphar lutea* (L.) as being abundant.

The littoral fauna has been investigated by Brinkhurst (1960), Kennedy (1961) and Young & Harris (1974). Data on specific groups are to be found in Young (1973) for Microturbellaria, Reynoldson & Bellamy (1970) and Gillham (1976) for the Tricladida, Ironmonger (1981) and Young & Ironmonger (1979, 1980, 1982a & 1982b) for Tricladida and Hirudinea and Macan (1967) for Corixidae. A list of the species recorded from Crose Mere is included in Reynolds (1979), and a list of the species recorded in this present study is presented as parts of chapters 3 and 4.

There is little information available concerning the fish fauna of Crose Mere. Kennedy (1960), on the basis of anglers' reports, lists roach (*Rutilus rutilus* L.), dace (*Leuciscus leuciscus* L.), pike (*Esox lucius* L.), eel (*Anguilla anguilla* L.) and minnows (*Phoxinus phoxinus* L.) as occurring in the mere. In this present study, roach, perch (*Perca fluviatilus* L.), pike, stickleback (*Gasterosteus aculeatus* L.) and tench (*Tinca tinca* L.) were recorded. Fishing on the lake is controlled by the Ellesmere Angling Club, but in recent years Crose Mere has not been a popular angling site.

1.2.3 The North Wales lakes

These are a group of calcium-poor lakes set in mountain valleys surrounded, in the main, by open moorland. The valleys are of pre-glacial origin, though many of the lakes were formed as a result of glaciation (Jehu, 1902; Lewis, 1970; and John, 1971).

Physico-chemical information on the lakes is provided by Jehu (1902), Reynoldson (1958) and in Young & Ironmonger (1979). Reynoldson (1958) surveyed several of the lakes for triclad populations and Seddon (1964) looked at the aquatic vegetation. Davies (1970) collected triclads from some of these lakes, and Brittain (1971) studied the biology and distribution of the Ephemoptera and Plecoptera. Reynoldson & Jacques (1976) investigated the triclad populations from these sites, and both triclad and leech populations from these sites, together with wider ecological information, are described by Young (1981b) and Young & Ironmonger (1982a).

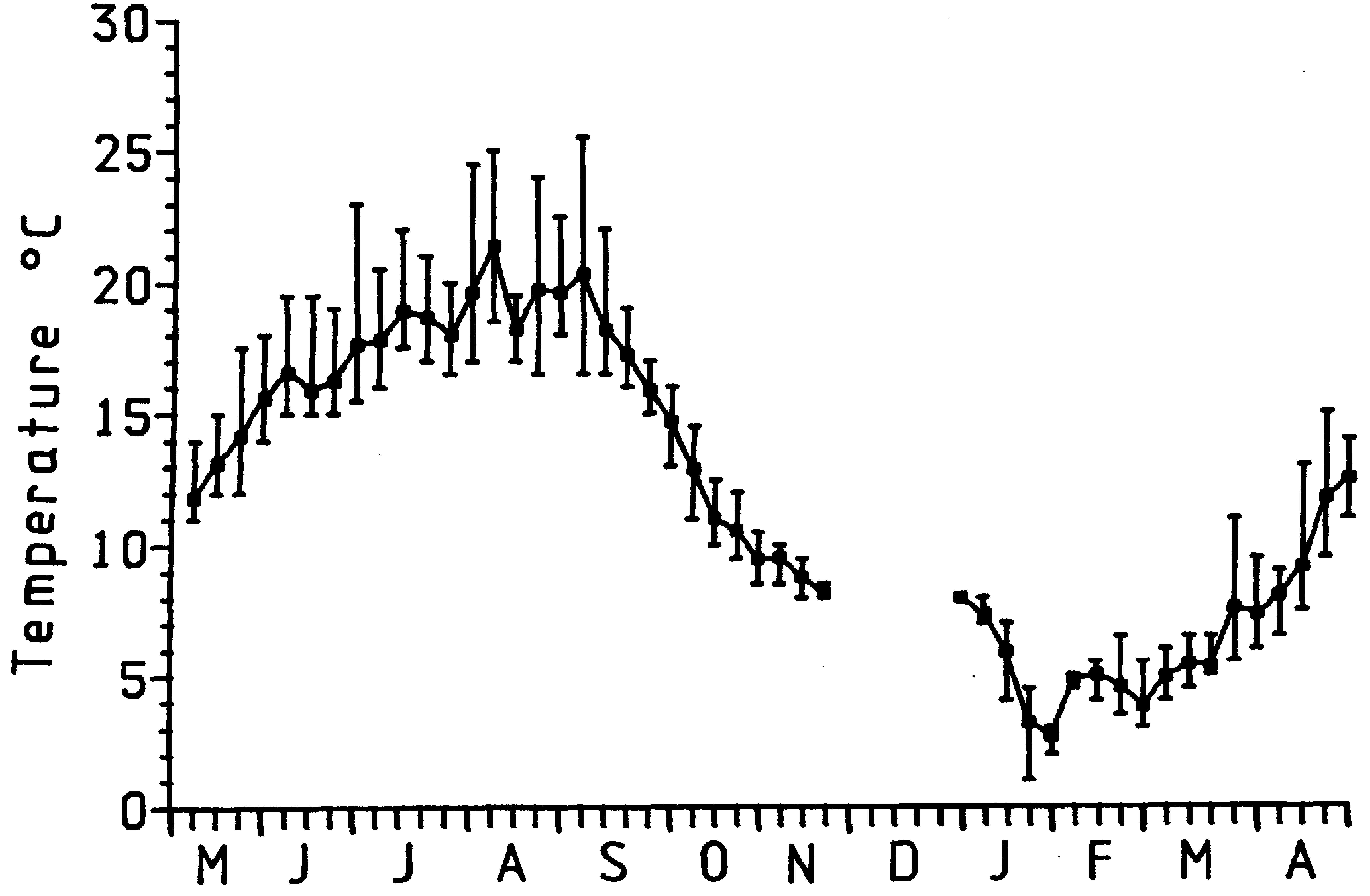


Figure 1.1 The mean weekly water temperature plus the range of temperatures in the littoral zone of Crose Mere. May 1981 to April 1982.

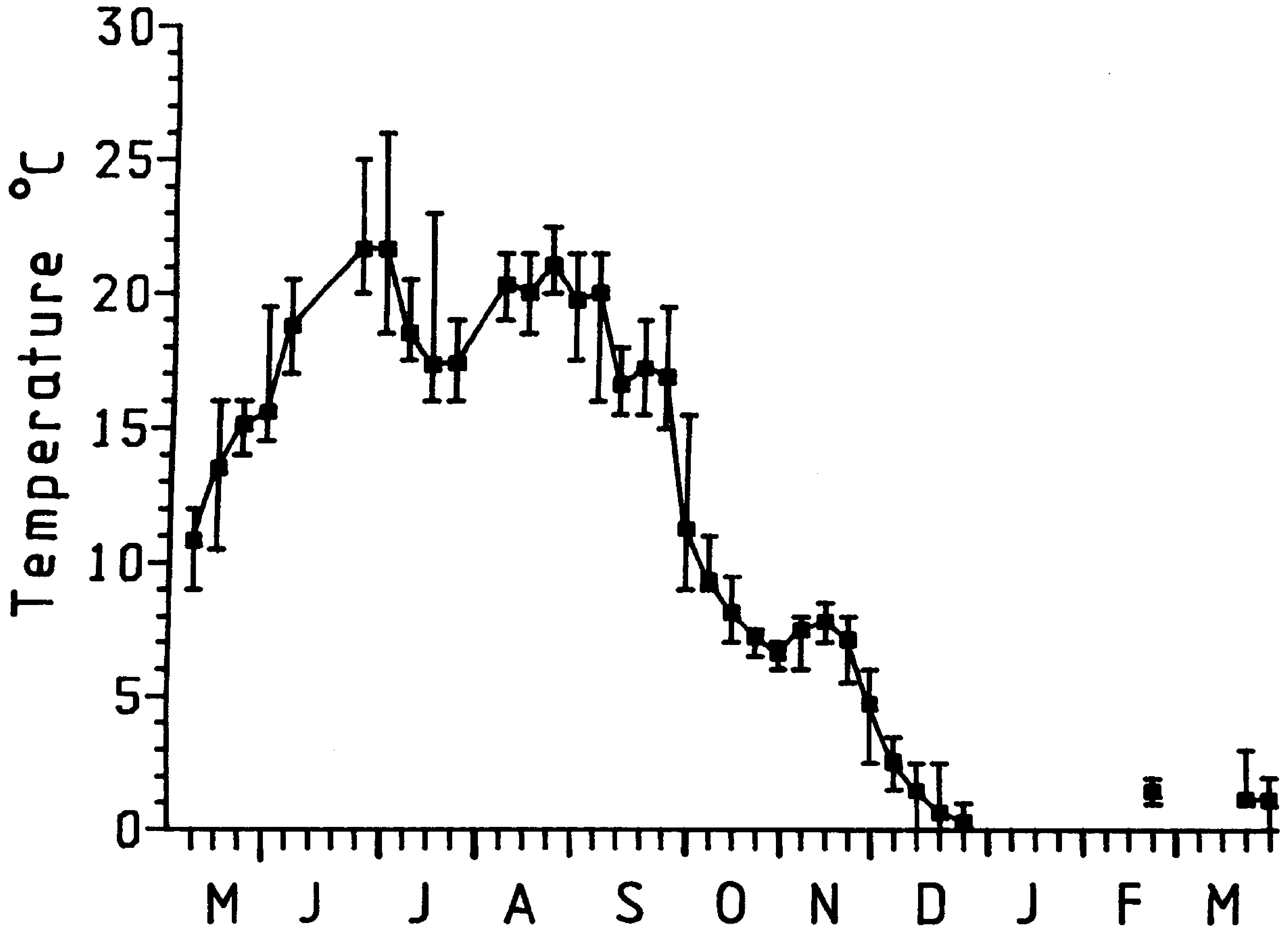


Figure 1.2 The mean weekly water temperature plus the range of temperatures in the littoral zone of Crose Mere. May 1982 to March 1983.

Table 1.1 English and Welsh lakes included in this study

Site	Grid Reference
SHROPSHIRE MERES	
Ellesmere Mere	SJ407350
Newton Mere	SJ425342
White Mere	SJ415330
Cole Mere	SJ434333
Crose Mere	SJ430305
CHESHIRE MERES	
Budworth Mere	SJ657769
Pick Mere	SJ684771
Tabley Mere	SJ723767
Tatton Mere	SJ755802
Petty Pool	SJ619701
NORTH WALES LAKES	
Llyn Gwynant	SH645518
Llyn Dinas	SH615495
Llyn-y-Gadair	SH568522
Llyn Cwellyn	SH560550
Llyn Nantlle Uchaf	SH515530

CHAPTER 2

THE PREDATORS OF LEECHES

A Literature Survey

2.1 Introduction

A general survey of the literature was carried out to establish what records exist of leeches being eaten in field situations. Due to the nature of such studies, the majority of the available literature concerned the diet of fish. However, there have also been several studies reporting on the diet on wildfowl. Dietary studies from invertebrate predators are very scarce and this is partly due to the need to use serological techniques to accurately identify what has been eaten.

The results from a study of this kind need to be interpreted with care for, although the presence of leeches in the diet can be regarded as useful information, their absence may not mean anything at all. It could be that leeches were not present in the habitat sampled, though leeches are of widespread occurrence, or that they were not, or could not be, identified in the study. Similarly, the pattern of records found from differing types of lake and from different species of predator is as much a reflection of the sampling effort on different habitats and species as on any real differences that might exist. For this reason only positive records of leeches in the diet of predators are discussed in any detail.

A further difficulty exists in the multiplicity of ways in which dietary data have been presented in the literature. Methods used include percentage occurrence by number or volume and various points systems. The advantages and disadvantages of these techniques have been described in detail elsewhere (Hynes,1950; Ball,1957; Siddiqui, 1969; Hyslop,1980). The number and volume methods have been the most popular, although the former tends to over-estimate the importance of small items, whilst the latter over-estimates the importance of the larger items. Another technique that has be used is the forage ratio (Hess, 1940), whereby an attempt is made to assess the occurrence of a food item in the diet in relation to its occurrence in the habitat studied (see, for example, Akitoye & Pugh-Thomas, 1981). This kind of study is particularly relevant to the present work, where the aim is to assess the predation pressure on leeches but, unfortunately, these studies have been few and far between.

In this review, the data are presented, where possible, as percentage occurrence by number, i.e. the number of stomachs examined which contained leeches, divided by the number of stomachs which contained food. This was regarded as the best way of bringing together data from such a variety of sources. However, it was not possible to use this calculation in many instances because of the way the authors had presented the results. Where possible, the species of leech found in the study has been given; in the majority of studies, unfortunately, either the leeches were not identified or could not be identified to the specific level.

2.2 Results

2.2.1 Fish

The records of leeches found in the diet of fish are summarised in Table 2.1 for studies on lakes and Table 2.2 for studies on rivers. The records presented are arranged in order of studies from oligotrophic to eutrophic habitats.

Lakes

Leeches have been recorded in the diet of eleven species of fish, from a variety of lakes ranging from oligotrophic habitats such as Llyn Celyn in North Wales to highly eutrophic locations such as Slapton Ley in Devon. In most records, leeches occurred in less than 6% of stomachs examined.

Brown trout (*Salmo trutta* L.) were identified as eating leeches in ten studies on ten different lakes, with *E. octoculata* being identified on three occasions, *H. stagnalis* on one occasion and *Haemopis sanguisuga* L. in only one report. In Loch Leven, Thorpe (1972) recorded leeches being eaten between June and August, but not September. Siddiqui (1969) found leeches in trout from the Welsh lakes, Llyn Celyn in July, September and November, Llyn Cefni in October and from Llyn Tegid (Bala Lake) between January and May and in August and December. Pedley & Jones (1978) recorded *E. octoculata* in the diet of trout in all months except February, July and August for fish from Llyn Dwythwch. In Llyn Alaw, Hunt & Jones (1972) recorded *E. octoculata* in trout between February and August and in October. Moriarty (1963) recorded finding *Haemopis sanguisuga* in three trout taken in June from Poulaphouca Reservoir in Ireland. Macan (1966) recorded *E. octoculata* in brown trout throughout the period of his four-year study on Hodson's Tarn. The highest number in any one fish was six and a total of fortyfive were found in 451 fish examined. Holmes (1960) found several *H. stagnalis* in trout taken in September from Malham Tarn. Hunt & O'Hara (1973) reported *E. octoculata* from rainbow trout (*Salmo gairdneri* Richardson) taken from Llyn Alaw in January. Wilson et al (1974) reported leeches in the diet of both brown and rainbow trout from Blagdon Lake.

The highest over-all occurrence in the diet of trout was in the study of Hunt & Jones (1972) on Llyn Alaw (18.8%). In this study, *E. octoculata* was relatively important in the diet, occuring in 36.4% of fish in March, 28.2% in April, 44.9% in May, 47.1% in June and 100% in July. No other study found the leeches in such a high proportion of fish, though Siddiqui (1969) found that 23% of fish in February, taken from Llyn Tegid, had eaten leeches.

Perch (*Perca fluviatilis* L.) were reported as eating leeches in 14 studies from 11 lakes,with *E.octoculata* being identified in three studies and *H. stagnalis* and *Glossiphonia sp.* each being found in one study. In Loch Leven, Thorpe (1972 & 1977) found leeches in the diet between July and September. Campbell (1955)does not give any seasonal data, but did find leeches in 11% of fish examined. In Llyn Tegid, Ali (1977) found *E. octoculata* and *H. stagnalis* in fish taken in January, between April and July and in September, with most records being for fish in the size range 12-17.9 cm, whilst Chubb (1961) does not report any seasonal data, but did identify *E. octoculata* in the diet. In Poulophouca Reservoir, Moriarty (1963) identified a 'small leech' in one perch in June while, also in Ireland, Healy (1954a) recorded leeches in perch from Lough Clore and Lough Rea, but gave no seasonal data. In two of the numerous studies on Lake Windermere, perch were found to eat leeches. McCormack (1970) found leeches in the perch diet between April and September, while Craig (1978) reported finding *E. octoculata* in fish between March and November. In Smyly's study on Blelham Tarn (1952) a *Glossiphonia sp.* was reported from one perch fry, but the date was not given. In Tatton Mere, Goldspink & Goodwin (1979) reported leeches as forming up to 45% of the diet in July and September, at a time when they observed leeches to be very abundant. In Rostherne Mere, Banks (1970) reported leeches in fish taken in May, June, August, October and November, while in Slapton Ley, Craig (1974) found leeches in the diet in June and August and Bregazzi (1978) reported *E. octoculata* in fish taken in June, July and October. Interestingly, in the latter study, which was a Ph.D. thesis, no records of leeches in the diet of perch were presented in subsequent publications (Bregazzi & Kennedy,1980).

As mentioned above, leeches formed up to 45% of the diet of perch from Tatton Mere (Goldspink & Goodwin,1979). In Craig's (1978) study on Windermere, they reached a 20% occurrence in May and, in Loch Leven, Thorpe (1972) reported leeches as occurring in 23% of fish. However, over-all, leeches were rarely of importance in the diet and in most studies occurred in well under 10% of the fish examined.

Bullhead (Cottus gobio L.) were found to eat leeches in three studies, but the leeches were not identified to a specific level. Smyly (1957) reported leeches in the diet of fish from Rydal Water in January and March while, from Windermere, he found that the larger fish ate leeches in January, April, October and December. Holmes (1965) found that leeches formed approximately 15% of the diet by volume in May and 10% in July, but were not recorded in his fish sample from September.

Stone loach (Nemacheilus barbatula L.) were reported as eating leeches in two studies. Smyly (1955) reported Glossiphonia sp. in fish from Esthwaite, while Holmes (1965) reported leeches in fish from Malham Tarn forming approximately 5% by volume of the diet in May. In neither study was the leech species identified.

Pike (Esox lucius L.) were found to eat leeches in two studies from four different lakes. E. octoculata was identified in one study, but in the remainder, the leeches were unidentified. In Ireland, Healy (1954b) reported pike of between 25 and 50 cm eating leeches. In Lough Glore, 4% of fish in the 45-50 cm. size-group contained leeches, while in Barnagrow Lake, 8% in the 25-30 cm range, 9% in the 30-35 cm range, 3% in the 35-40 cm range, 10% in the 40-45 cm range and 5% in the 45-50 cm range had eaten leeches. In Lough Rea, 25% of fish in the 35-40 cm range and 10% in the 40-50 cm range contained leeches. No season data were given. Banks (1970) reported E. octoculata in pike from Rostherne Mere, but only gave season data for important food items - leeches were not included.

Grayling (Thymallus thymallus L.) were shown to eat leeches in Llyn Tegid by two different workers. Chubb (1961) identified E.octoculata in 11.7% of fish, while Siddiqui (1969) reported leeches in 16.6% of fish, occurring in March, April and August to December. In October and November the % composition reached 75% and 100% respectively. In the same lake,Haram (1968) found Gwyniad (Coregonus clupeoides Lacepede)to eat G. complanata in June and December occurring in 3% and 4% of fish respectively.

Roach (Rutilus rutilus L.) were reported eating leeches in the study of Dunn (1954) on Llyn Tegid. It was found that 25% of larger fish and 2% of smaller fish contained leeches. The leech species was not identified. Rudd (Scardinius erythrophthalmus L.) were found to eat leeches in Llyn Cefni (Siddiqui, 1969) in March (25% of fish) and April (5% of fish). One stickleback (Gasterosteus aculeatus L.) was found to have eaten a leech in Easdale Quarry by Hynes (1950). Wilson et al (1974) also reported leeches in stickleback from Blagdon Lake. In neither study was the leech species identified.

In the following studies on the diet of fish from lakes, leeches were not recorded; Allen (1935, 1938 & 1939) on perch, trout and pike from Windermere, Southern (1935) on trout from Irish Lakes, Munro (1937) on pike from Loch Choin, Frost (1943, 1946a & b and 1977) on minnows, eels, trout, salmon, stone loach, stickleback and char (Salvelinus willughbii Gunther) from Windermere, Campbell (1955 & 1963) on trout from Loch Tummel and Loch Garry, Dunn (1954) on perch, pike, grayling, trout and gwyniad from Llyn Tegid, Ball (1961) on trout from Llyn Tegid, Graham (1960) also on Llyn Tegid trout, Swynnerton & Worthington (1960) on char, trout and perch from Haweswater, McCormack (1965) on perch from Ullswater, Macan (1967b) on trout from Hodson's Tarn, Kennedy & Fitzmaurice (1972) on gudgeon from various Irish lakes, Ali (1973) on roach from Llyn Tegid, Robotham (1977) on spined loach (Cobitis taenia L.) from gravel pits, Westcott (1980) on various fish species from several locations and Allen & Wooten (1984) on stickleback from Llyn Fangoch. This list is not intended to include all the dietary studies carried out on fish from lakes in the British Isles, but rather to give an indication of the range of reports in which leeches were not reported in the diet of the fish being studied.

Rivers

Leeches were recorded in eleven species of fish in twenty rivers and streams from the North of Scotland to the South of England. In only one instance did the % occurrence exceed 10%, and in most cases, it was less than 5%.

Brown trout (S. trutta) were found to eat E. octoculata and H. stagnalis in the study of Neill (1938). Thomas (1962) also reported E. octoculata as being eaten, in his study on the River Teify. The leeches were found in the diet of fish in all months, but the maximum occurrence was only 2.2% in February. He also reported E. octoculata cocoons in the stomachs examined in February, March, August and September but, again, the maximum occurrence was only 0.4%. Pentelow (1932) reported leeches in the diet of fish from the rivers Itchen and Tees, but the species were not identified. Sinha (1965) reported E. octoculata in trout from the River Dwyfach between April and July, occurring in three out of the total fish examined. Salmon (Salmo salar L.) were also reported by Thomas (1962) to eat leeches in the River Teify in the months of April, August, October and December, though the maximum occurrence was only 2%.

Grayling (T.thymallus)were found to eat leeches by Hellawell (1969) who found them in 0.5% of 2+ fish taken from the River Lugg. Radforth (1940) found them to eat Glossiphonia sp. in the River Test and in Derbyshire Rivers, and also reported 1.1% and 4.4% of fish respectively to contain unidentified leeches.

Eel (Anguilla anguilla L.) were found to eat leeches in five studies. In the River Teify, Thomas (1962) found E. octoculata in fish between May and October, with a maximum occurrence of 7.6% in May. In the River Dwyfach, Sinha (1965) found E. octoculata in three fish taken between June and September, while in the River Wen he found that both E.octoculata and H. stagnalis were taken by eels, but does not give any seasonal data. In the River Cam, Hartley (1948) reported a single occurrence of E.octoculata in eels. Chubb (1961) also reports E. octoculata in fish taken from streams feeding Llyn Tegid.

Stone loach (*N. barbatula*) were reported to eat leeches in four studies. Smyly (1955) reported *Glossiphonia sp*. from Black Beck and unidentified leeches from the River Brathay. Morris (1965) reported *E. octoculata* in fish from the River Llafar, but they were only 'occasionally eaten'. Morris (1965) also reported bullhead (*C. gobio*) ate *E. octoculata* and *G. complanata* in the River Llafar, and unidentified leeches were found in fish from Willow Brook. Hartley (1948) reported three occurrences of *E. octoculata* in bullhead from Shepreth Brook. Hyslop (1982) reported leeches in the diet of fish from the River Ouzel.

Leeming (1967) reported chub (*Squalius cephalus* L.) to have eaten *E. octoculata* in the River Welland, while Cragg-Hine (1964) found both *E. octoculata* and *H. stagnalis* in one chub taken in July from Willow Brook. Cragg-Hine (1964) also found *E. octoculata*, *G. complanata* and *H. stagnalis* in dace (*Leuciscus leuciscus* L.) from Willow Brook occurring between November and April and in June, with a maximum of four occurrences in March. He suggested that the leeches were eaten chiefly in the winter months when the water level was high and leeches might be displaced from under stones. Leeming (1967) found *E. octoculata* and *G. complanata* in dace from Wych Brook but they were said not to be important in the diet. Cragg-Hine (1964) also records *E. octoculata* and *H. stagnalis* from perch (*P. fluviatilis*) taken from Willow Brook between April and June, with a total of 16 occurrences.

Bream (*Abramis brama* L.) were found to eat *E. octoculata* in the River Welland by Leeming (1967), who reported them from two fish between 21-40 cm in length. Hynes (1950) found *E. octoculata* and *G. complanata* in two stickleback (*G. aculeatus*)from The Birket, Cheshire, and the remaining species of fish in which leeches have been reported is the record of a *Glossiphonia sp*. in a flounder (*Platichthys flesus* L.) from the lower reaches of the River Tweed (Radforth, 1940).

Studies from rivers which did not find leeches in the diet of fish include those of Slack (1934) on trout from the River Test, Frost (1939) on trout from the River Liffey and Frost & Went (1940) on salmon from the same river, Carpenter (1940)on salmon from the River Dee, Hartley 1947 & 1948) on trout, perch, pike, eel, gudgeon, minnow, dace, roach, stone loach and stickleback from various locations, Frost (1950) on salmon and trout from the River Forss, Cragg-Hine (1964) on roach, eels and pike from Willow Brook, Maitland (1965) on salmon, trout, minnows, stone loach and stickleback from the River Endrick, Elliott (1967) on trout from Walla Brook, Hellawell (1969 & 1972) on dace and roach from tributaries of the River Wye, Mann and Orr (1969) on trout, salmon, bullhead, stickleback and minnow from rivers in Southern England and Mann (1973) on roach from the River Stour.

2.2.2 Waterfowl

Records of leeches in the diet of duck are very rare. Olney (1963) reports one record of E. octoculata and one of H. stagnalis in Teal (Anas crecca L.) taken from a variety of freshwater sites. Olney (1967) reported a single occurrence of H. stagnalis in one out of 16 Mallard (Anas platyrhynchos L.) examined from gravel pits near Sevenoaks in Kent. From the same locality, 2 out of 6 Teal (A. crecca) examined contained H. stagnalis. Cramp & Simmons (1977) report that Goldeneye (Bucephala crangula L.) occasionally eat leaches and that Little Grebe (Tachybaptus rufficollis Pallas) were seen to eat leeches of between 3-5 cm in length (E. octoculata? Haemopis sanguisuga?) rarely, while for the Coot (Fulica atra L.) leeches were 'of little or only local' importance in the diet. Witherby et al (1939) also reported leeches in the diet of Mallard, Goldeneye and Coot, and Elliott & Mann (1979) list herons, swans, ducks and bitterns as eating leeches, though the species consumed and the source of the data is not presented.

2.3 Discussion

What is apparent from this review, is that a wide range of vertebrate predators do eat leeches when they are available, but that,in practice, they are very rarely of anything but minor importance in the diet. A total of sixteen species of fish and eight species of waterfowl were reported to have fed on leeches. In fish from lakes, there were eight instances where leeches exceeded a 16% occurrence in the diet and only two where they occurred in more than 20% of fish. In rivers, there was only one instance where leeches occurred in excess of 10% of fish and, in this case, the sample size was only five.

The number of records and diversity of species that eat leeches, reported in this review, can be regarded as an under-estimate of the true picture for two reasons. Firstly, unlike the more common items recorded in fish diet (e.g. Chironomidae, Asellus, Corixidae etc.), leeches do not possess any hard parts that are readily identifiable. Therefore, they are only likely to be identified if eaten whole and little or no digestion has taken place. This would have the effect of reducing the number of times that leeches were observed in stomach contents, and the effect would be further accentuated in species such as cyprinids which grind down their food for digestion and do not possess a distinct stomach. In the present review, salmonids, perch and pike had over four times the number of records of leeches in the diet than all the cyprinids grouped together. This is just as likely to be a result of the problems in identifying what is eaten by the fish as to any differences in predation. It must also be remembered that diet studies on cyprinids have been less numerous, for exactly the same reasons. In many of the studies outlined above, the identity of the leech was not given. However, this may have been due to grouping all leeches together for convenience rather than any difficulty in identifying the leech species.

A second reason for the number of records being low, is that many authors have tended to present only 'important' items in their diet analysis data and, therefore, many occurrences of leeches being eaten may be hidden in the 'miscellaneous invertebrates' category so often used. It is evident from the records reported above that most of the detailed information has its source in Ph.D. theses from Liverpool University, and not from the subsequent publications. There is probably a lot of detailed information that has not been published.

However, even given that the results are an under-estimate of the occurrence in the diet of fish, it is clear that they are eaten only occasionally and are rarely of any importance in the diet. The seasonal data presented above do not indicate any pattern to when leeches were eaten; they have been recorded in the diet in all months of the year. If anything, there is a tendency for there to be more records from the summer months, when feeding intensity is often highest, but this may reflect the timing of sampling rather than any pattern of feeding.

There is no clear indication of differences between different kinds of water. In the above reports, there was, perhaps, a tendency to find more records from oligotrophic waters but, again, this may be a reflection of the sampling effort and the fact that cyprinids are commoner in eutrophic conditions. Unfortunately, in relation to the present study, there were no published records of predation on leeches in the Shropshire Meres,though Banks (1970) and Goldspink & Goodwin (1979) did report predation from the Cheshire Meres. However, in one unpublished survey carried out at Liverpool Polytechnic (Ookorie, 1971), on The Mere at Ellesmere, perch adults and fingerlings, roach, bream and pike were all found to have eaten leeches, though the % occurrences never exceeded 5%. E. octoculata, E. testacea, G. complanata and H. stagnalis were identified as being eaten in this study, with most of the records being in the spring and summer. These results would tend to re-inforce the general picture of leeches being only occasional items in the diet.

From both lakes and rivers, it seems that E. octoculata was the prevalent species to be identified in the diet of fish. This might be expected both in terms of the fact that the species is far larger than G. complanata or H. stagnalis and, thus, more likely to be noticed by researchers and because the species is more active than the other common leeches and, therefore, perhaps more likely to be taken by fish.

Very few positive records of leeches in the diet of ducks were found, but it is clear that duck will eat them when given the opportunity. The fact that leeches act as second intermediate hosts for parasites of waterfowl (discussed later) emphasises the point, but without more records it is difficult to assess the sort of predation pressure that may be involved. As with fish, there may be a severe problem in identifying leech remains in duck stomachs. In both cases, the use of serological methods to identify stomach contents may give a much higher rate of detection. The use of such techniques is discussed later.

Table 2.1 Positive records of fish predation on leeches from British and Irish lakes

Key:
EO = *Erpobdella octoculata*
HS = *Helobdella stagnalis*
HM = *Haemopis sanguisuga*
GC = *Glossiphonia complanata*
Gsp.= *Glossiphonia* sp.
UN = Unidentified

Lake	Fish Species	Number of stomachs examined	Leech species	Occurrence	Author
Loch Leven	Brown Trout	?	UN	1.6%	Thorpe, J.E. (1972)
	Perch	?	UN	12.9%	Thorpe, J.E. (1972)
	Perch	?	UN	?	Thorpe, J.E. (1977)
Loch Tummel	Perch	47	UN	11.0%	Campbell, R.N. (1955)
Esthwaite	Stone Loach	229	Gsp.	?	Smyly, W.J.P. (1955)
Llyn Celyn	Brown Trout	202	UN	0.5%	Siddiqui, M.S. (1969)
Llyn Cefni	Brown Trout	159	UN	3.8%	Siddiqui, M.S. (1969)
	Rudd	?	UN	5.5%	Siddiqui, M.S. (1969)
Llyn Tegid	Brown Trout	292	UN	4.0%	Siddiqui, M.S. (1969)
	Grayling	104	UN	16.6%	Siddiqui, M.S.
	Grayling	34	EO	11.7%	Chubb, J.C. (1961)

Lake	Fish Species	Number of stomachs examined	Leech Species	Occurrence	Author
Llyn Tegid	Gwyniad	325	GC	?	Haram, O.J. (1968)
	Perch	831	EO + HS	2.6%	Ali, S.S. (1973)
	Perch	644	EO	4.3%	Chubb, J.C. (1961)
	Large Roach	50	UN	25.0%	Dunn, D.R. (1954)
	Small Roach		UN	2.0%	Dunn, D.R. (1954)
Llyn Dwythwch	Brown Trout	378	EO	5.6%	Pedley, R.B. & Jones, J.W. (1978)
Llyn Alaw	Brown Trout	274	EO	18.8%	Hunt, P.C. & Jones, J.W. (1972)
	Rainbow Trout	38	EO	2.6%	Hunt, P.C. & O'Hara K. (1973)
Rydal Water	Bullhead	69	UN	?	Smyly, W.J.P. (1957)
Poulaphouca Reservoir	Perch	312	UN	0.3%	Moriarty, C. (1963)
	Brown Trout	584	HM	0.5%	Moriarty, C. (1963)
Lough Glore	Perch	?	UN	?	Healy, A. (1954a)
	Pike	1991	UN	?	Healy, A. (1954b)

Lake	Fish Species	Number of stomachs examined	Leech Species	Occurrence	Author
Lough Rea	Perch	?	UN	?	Healy, A. (1954a)
	Pike	92	UN	?	Healy, A. (1954b)
Barnagrow Lake	Pike	1019	UN	?	Healy, A. (1954b)
Windermere	Perch	1148	EO	6.0%	Craig, J.F. (1978)
	Perch	947	UN	5.2%	McCormack, J.C. (1970)
	Bullhead	?	UN	?	Smyly, W.J.P. (1957)
Blelham Tarn	Perch Fry	?	Gsp.	?	Smyly, W.J.P. (1952)
Hodson's Tarn	Brown Trout	451	EO	8.2%	Macan, T.T. (1966)
Malham Tarn	Brown Trout	68	HS	5.9%	Holmes, P.F. (1960)
	Bullhead	88	UN	?	Holmes, P.F. (1965)
	Stone Loach	58	UN	?	Holmes, P.F. (1965)
Easdale Quarry	Stickleback	55	UN	2.0%	Hynes, H.B.N. (1950)

Lake	Fish Species	Number of stomachs examined	Leech Species	Occurrence	Author
Tatton Mere	Perch	20	UN	Up to 45%	Goldspink, C.R. & Goodwin, D. (1979)
Rostherne Mere	Perch	1379	UN	?	Banks, J.W. (1970)
	Pike	241	EO	?	Banks, J.W. (1970)
Upholland College lake	Mixed	?	UN	2.6%	Akitoye, C. & Pugh-Thomas, M. (1981)
Slapton Ley	Perch	?	UN	?	Craig, J.F. (1974)
	Perch	807	EO	?	Bregazzi, P.R. (1978)
Blagdon Lake	Brown and Rainbow Trout	?	UN	10.0%	Wilson et al (1974)
	Stickleback	?	UN	<3.0%	Wilson et al (1974)

Table 2.2. Positive records of fish predation on leeches from British Rivers

Key:
EO = *Erpobdella octoculata*
HS = *Helobdella stagnalis*
UN = Unidentified
GC = *Glossiphonia complanata*
Gsp.= *Glossiphonia* sp

River	Fish Species	Number of stomachs examined	Leech Species	Occurrence	Author
River Don	Brown Trout	70	EO + HS	7.1%	Neill, R.M. (1938)
Black Beck	Stone Loach	413	Gsp.	?	Smyly, W.J.P. (1955)
River Brathay	Stone Loach	26	UN	?	Smyly, W.J.P. (1955)
River Llafar	Bullhead	?	EO + GC	?	Morris, V. (1965)
River Teify	Salmon	274	EO	1.0%	Thomas, J.D. (1962)
	Brown Trout	741	EO	1.2%	Thomas, J.D. (1962)
	Eel	155	EO	4.2%	Thomas, J.D. (1962)
Rivers feeding Llyn Tegid	Eel	144	EO	4.1%	Chubb, J.C. (1961)

River	Fish Species	Number of stomachs examined	Leech Species	Occurrence	Author
River Dwyfach	Salmonids	154	EO	1.9%	Sinha, V.R.P. (1965)
	Eels	247	EO	1.2%	Sinha, V.R.P. (1965)
River Wen	Eels	388	EO	2.3%	Sinha, V.R.P. (1965)
	Eels	388	HS	0.5%	Sinha, V.R.P. (1965)
River Lugg	Grayling	?	UN	0.2%	Hellawell, J.M. (1969)
River Test	Grayling	92	Gsp.	4.4%	Radforth, I. (1940)
	Grayling	92	UN	1.1%	Radforth, I. (1940)
Derbyshire Rivers	Grayling	25	Gsp.	8.0%	Radforth, I. (1940)
	Grayling	25	UN	4.0%	Radforth, I. (1940)
River Tweed	Flounder	5	Gsp.	20.0%	Radforth, I. (1940)
River Welland	Chubb	?	EO	?	Leeming, J.B. (1967)
	Bream	70	EO	2.9%	Leeming, J.B. (1967)
River Ouzel	Bullhead	?	UN	2.0%	Hyslop, E.J. (1982)

River	Fish Species	Number of stomachs examined	Leech Species	Occurrence	Author
Willow Brook	Bullhead	?	UN	?	Morris, V. (1965)
	Chubb	170	HS + EO	0.7%	Cragg-Hine, D. (1964)
	Perch	225	HS + EO	8.5%	Cragg-Hine, D. (1964)
	Dace	390	HS + EO + GC	5.1%	Cragg-Hine, D. (1964)
Wych Brook	Dace	?	EO + GC	?	Leeming, J.B. (1967)
	Dace	?	UN	2.4?	Sillah, A.B.S. (1981)
River Itchen	Brown Trout	29	UN	?	Pentelow, F.T.K. (1932)
River Tees	Brown Trout	104	UN	?	Pentelow, F.T.K. (1932)
The Birket	Stickleback	1581	EO + GC	0.1%	Hynes, H.B.N. (1950)
River Cam	Eel	125	EO	0.8%	Hartley, P.H.T. (1948)
Shepreth Brook	Bullhead	84	EO	3.6?	Hartley, P.H.T. (1948)

CHAPTER 3

LABORATORY AND FIELD STUDIES ON THE INCIDENCE AND INTENSITY OF PREDATION ON LEECHES

3.1 Introduction

In the previous chapter it became clear that there were few records of leeches being eaten in field situations, and that what records there were, involved fish and waterfowl predators. There were no records of invertebrates preying on leeches. In this chapter, laboratory and field experiments are described which aim to obtain a broader picture of what might feed on leeches and to what extent predation occurrs in field situations.

To investigate the potential predators of leeches, both adult and young, E. octoculata, G. complanata and H. stagnalis were exposed to likely predators in a series of simple laboratory experiments. Similar such experiments have been carried out by Young & Reynoldson (1965), Davies & Reynoldson (1969) and Young & Ironmonger (1980) in investigating the predators of triclads. Predators were chosen from the Coleoptera, Hemiptera, Trichoptera, Megaloptera, Odonata, Pisces and Amphibia, and the species used are listed as part of tables 3.1 and 3.2.

The problems involved in identifying the remains of soft-bodied animals, such as leeches, in the diets of predators were briefly discussed in the previous chapter. Visual methods of diet identification rely, for such animals, upon the prey being eaten relatively whole, and there to have been little digestive activity. A more accurate way of identifying the prey is to use the chemical reaction of the precipitin test (Proom, 1943) which was identified by Davies (1969a)as bearing potential in identifying the predators of triclads in field situations. The methods has been used successfully in identifying the diet of several fluid-feeding groups, e.g. triclads (Young et al,1964; Reynoldson & Davis, 1970; Pickavance, 1971; Reynoldson & Bellamy, 1975; Reynoldson & Sefton, 1976; Adams, 1979; Reynoldson & Piearce, 1979a & b), corixids (Reynolds, 1975c)and leeches (Young, 1980, 1981a & b).

In the second part of this study, collections of invertebrate predators were made from five chemically-rich, productive lakes in Shropshire, viz. Crose Mere, White Mere, Cole Mere, Newton Mere and The Mere (at Ellesmere), and from five chemically-poor, unproductive lakes from North Wales, viz. Llyn Dinas, Llyn Gwynant, Llyn-y-Gadair, Llyn Cwellyn and Llyn Nantlle. These lakes and their invertebrate populations are described in chapter 1.

The stomach contents of the predators were analysed using a serological method, described below. In addition, samples of fish were obtained from Crose Mere, Shropshire and the stomach contents examined both visually and using the serological method. In using both methods of diet analysis, it was hoped that the problems involved in identifying leeches in the diet of fish using visual methods might be highlighted.

3.2 Methods

3.2.1 Laboratory predation experiments

Each experiment consisted of a single predator being offered one or more leech prey, with each species of leech being tested separately. Insect predators were usually of a late instar size, and non-insect invertebrate and vertebrate predators were of a medium size for the species concerned. Tests were carried out against both adult and young (recently hatched or released) leeches, and a separate series of trials were also performed using leeches from distinct size-groupings.

For tests with invertebrate predators against adult leeches, the experimental regime was as follows. Glass crystallising dishes of 200 ml capacity were three-quarter filled with filtered pond water and an adult leech was placed in each one. The size ranges of leeches used were:

Erpobdella octoculata	20 - 100 mg wet weight
Glossiphonia complanata	10 - 60 mg wet weight
Helobdella stagnalis	5 - 15 mg wet weight

A single predator was added to half of the dishes, the others remaining as controls to check for leeches escaping or dying from causes other than predation. The dishes were covered with a petri-dish lid and examined on each of the following five days. Any dead leeches were removed and replaced. If any leeches were eaten, then a new leech was introduced into the dish, so that there was always a live leech available to be eaten. It was aimed to provide ten experimental and ten control tests for each predator but, in some cases, lesser numbers of predators were available. The experiments were carried out at temperatures ranging between 14 - 20°C and under a summer photoperiod.

A similar regime was used in testing adult leeches against vertebrate predators but, in this case, five leeches were available to each predator on each day of the experiment. In these experiments, larger, plastic experimental containers (50 litres in capacity) were used. In tests on leech young against both invertebrate and vertebrate predators, five leeches per day were again available.

Further experiments were carried out using a smaller range of predators against three weight-groupings within each of the three leech species. These ranges were:

E.octoculata	10 - 25 mg	20 - 50 mg	65 - 80 mg
G. complanata	5 - 15 mg	25 - 35 mg	45 - 55 mg
H. stagnalis	1 - 3 mg	5 - 7 mg	9 - 11 mg

For each particular size of leech, 10 experimental and 10 control crystallising dishes, of 300 ml capacity, were used. All dishes contained leeches, whilst the experimental dishes also had a predator added. A Kruskal-Wallis test was carried out for each leech species versus each predator, to see whether the leech size-grouping affected the numbers of leeches eaten.

The leeches used in the experiments came from Crose Mere field samples and laboratory reared stock. Invertebrate predators were obtained from the Shropshire Meres and local ponds on the Wirral, while vertebrate predators came from fish farms, local ponds and university aquarium stock.

No cover or refuge was provided for the leeches but, in experiments using Odonata, a small piece of plastic mesh was available for the predator to hunt from.

3.2.2 Serological examination of the gut contents of invertebrate and vertebrate predators.

a. Collection

In the productive lakes, samples of invertebrate predators were collected from the undersides of stones in the littoral zone of Crose Mere in 20 monthly samples over the periods April to November 1981 and February 1982 to January 1983. Samples from the four other Shropshire Meres were taken in 16 monthly samples from May to November 1981, April to November 1982 and in January 1983. Samples of predators were also taken by the use of a sweep net from beds of vegetation in 16 monthly samples from all five productive lakes. Eleven monthly samples of carnivorous invertebrates were taken from the stony littoral and vegetation beds from the five unproductive lakes over the period March 1982 to January 1983.

Field samples were immediately sealed in plastic bags and placed in an insulated cold-box containing Frezella packs, for transportation back to the laboratory. The samples were then sorted and the invertebrate predators removed and frozen at a temperature of $-15^{o}C$, for subsequent testing. This whole procedure took only a few hours. The most abundant potential invertebrate predators were species of leeches and triclads, and for each of these species from productive lakes, similar numbers were collected in each of the monthly samples. Further, for each of the species, a range of sizes were collected each month, reflecting their relative proportions in the field. For all other predatory taxa, in both lake types, the numbers collected and tested each month varied according to availability.

Trichoptera, Coleoptera and Corixidae were only identified to the family level prior to freezing. More detailed identification was time-consuming and the important objective was to freeze the specimens as quickly as possible, to stop further digestion of the gut contents. On de-frosting, the animals could no longer be identified, due to their dried and distorted state. However, samples of these groups were taken each month from each of the lakes, for identification purposes, and the species list is given in Appendix A.

Fish were obtained from Crose Mere in five samples taken in May, July and October 1982, and in May and August 1983. Three methods of collection were tried, viz. seine netting, gill netting and the use of traps. It was originally intended to use seine netting alone, this having the advantage of obtaining the fish in a fresh condition. However, the nature of the littoral at Crose Mere, with many submerged tree trunks and obstacles, made this very difficult and, indeed, no fish were caught by this method. The use of traps was also unsuccessful. All fish, therefore, were caught by gill-netting. This method has the disadvantage that the fish may be in the nets for several hours and the stomach contents may become well-digested and, in some cases, the fish may regurgitate the food. However, the method did, at least, catch fish and, in the majority of cases, the fish were in a good condition and alive. On each occasion, a series of nets of mesh size ranging from 1.9 cm to 3.2 cm were combined into 'gangs'. Between two and four of these gangs were then placed at different locations close to the littoral zone in the late afternoon. The nets were hauled in the following morning and the fish removed. The process was then repeated for a further night. The fish, if not dead already, were killed immediately by a blow to the skull and placed in plastic bags within cold-boxes, for transportation to the laboratory.

On arrival at the laboratory, the fish were immediately frozen to a temperature of -15°C for subsequent diet analysis. Samples of stickleback (*Gasterosteus aculeatus* L. and *Pygosteus pungitius* L.) were also obtained during the monthly invertebrate samples, by sweep netting, and these were subject to the same processing as the invertebrate predators. No gill netting was carried out on the unproductive lakes, but minnows (*Phoxinus phoxinus* L.) were taken using sweep nets, and these were processed as above.

b. Preparation of antigens

Leeches were collected from the Shropshire Meres and antigens for each of the three species were prepared using the procedure described by Pickavance (1970) and Young (1980). Homogenised solutions of the leeches, containing 1 gm of leech as wet weight to 1cm^3 of 0.9% saline, were centrifuged to 9000 r.p.m. at a temperature of 4 - 5°C, and the supernatent decanted and stored at -15°C in aliquots of 1cm^3. The protein concentrations for the three antigens were obtained using the Kjeldahl method(Wootten & King, 1956) and were:

E. octoculata : 1.9% protein (W/V)
G. complanata : 1.6% protein (W/V)
H. stagnalis : 1.4% protein (W/V)

c. Preparation of antisera

The anti-leech sera were raised according to the method described in Davies (1969a). For each of the antigens the protein in 6cm^3 were precipitated with potash alum and resuspended in 6cm^3 of 0.9% saline (Proom, 1943). To produce a particular antiserum, a male New Zealand rabbit was given three two-weekly 1cm^3 injections of the precipitated antigen intra-muscularly into each hind limb. Seven days after the last injection, a small sample of blood was taken from the marginal ear vein and, if the titre of the serum was high enough, a full blood sample was taken five days later.

d. Absorption of antisera

Tests for serum specificity and cross-reaction were made using homologous antigens and a range of invertebrate taxa (see list in Young, 1980) collected from the lakes included in the present study. For each anti-leech serum, no cross reactions were obtained for any of the organisms tested, with the exception of weak reactions against the other leech antigens. Thus, it was necessary to remove the cross-reacting antibodies in each antiserum by absorption with cross-reacting antigens. Each antiserum was absorbed first with finely powdered, frozen-dried leech preparation of the species with which it had the greatest cross-reaction and then with the other cross-reacting leech preparation (see Davies,1969a for the technique). The titre of a particular antiserum was expressed as the reciprocal of the highest dilution of the test antigen with which the antiserum gave a positive precipitin reaction. The results obtained were:

E. octoculata	:	32
G. complanata	:	32
H. stagnalis	:	16

i.e. the anti-E. octoculata serum could detect the equivalent of 1/32nd of 1 mg of leech tissue in a test sample etc.

e. Precipitin tests

Precipitin tests were carried out using miniature Ouchterlony plates (Pickavance, 1970; Young, 1980). Other methods of producing the precipitin reaction are described by Davies (1969a). However, the Ouchterlony methods has the advantage of allowing simultaneous tests to be carried out against a series of antigens. Other methods, e.g. the ring or inter-face test (Ascoli,1902; Fornet & Müller, 1908, 1910) and the Oakley-Fulthorpe method (Preer, 1956; Morris, 1964) only allow one test at a time and thus involve greater replication of effort. In the Ouchterlony method (Ouchterlony, 1948) antigens and antibodies diffuse from adjacent wells lined with agar gel and, if a reaction occurs, a precipitate is formed where they meet. The plate is incubated at room temperature for three days.

In the present study, when testing the gut contents of leeches and triclads against anti-leech sera, the gut contents of seven predators were placed in seven of the peripheral wells, and the eighth filled with 0.9% saline, to act as a control. The appropriate anti-leech serum was placed in the central well. For all other potential predators, the gut contents of an individual animal were placed in the central well, the three anti-leech sera placed in separate peripheral wells and the other five filled with 0.9% saline. When investigating fish and the larger invertebrate predators, several samples of the gut contents were used. A positive precipitin reaction indicated that the tested predator had consumed the particular leech species.

Invertebrate predators were defrosted and dissected to remove the gut,where possible, prior to testing. Where dissection was not possible, whole animals were tested. Fish were removed from the freezer, defrosted, measured from the tip of the mouth to the tail fork and weighed. Scales (roach) or opercular bones (perch) were taken for ageing purposes and then the fish were dissected to remove the stomach and intestine.

Several samples of the gut contents were taken and immediately re-frozen for serological study. The remainder of the contents were then examined under water, using a binocular dissecting microscope.

3.3 Results

3.3.1 Laboratory predation experiments

In the control tests, no leeches escaped. However, in both control and experimental tests, several leeches died from unknown causes. These were replaced as soon as the deaths were noted.

The results of the tests using predators against adult and young leeches are presented in tables 3.1 and 3.2. Adult leeches were eaten by most of the predators tested, with the exceptions being Agabus bipustulatus (L.) whose larvae did not eat E. octoculata or G. complanata; Notonecta glauca (L.) which ate none of the leeches (though they readily fed on Tubifex); Polycentropus flavomaculatus (Pictet) which did not eat G. complanata; Limnephilus sp. which did not eat E. octoculata and Coenagrion puella (L.) which did not feed on any of the leeches. The remaining tests were all positive and the large dytiscid beetles, dragonflies and fish were particularly voracious.

Young leeches were eaten by all predators tested, with the exceptions of the four triclad species and three leech species, excepting adult E. octoculata on young E. octoculata, Orectocilus sp. adults which were only tested against H. stagnalis and Perca fluviatilis which, again, were only tests against H. stagnalis. All these predators fed on Tubifex when offered.

The results of tests using the three leech size-groupings are presented in table 3.3 and the Kruskal-Wallis tests in table 3.4. All predators fed on the leeches, but there was a distinct trend to eating more of the smaller size-grouping. Within each test, this was statistically significant, with the exception of Aeshna grandis versus H. stagnalis, where no size effects were indicated. The damselflies Pyrrhosoma nymphula and Sympetrum striolatum and the newt Triturus helveticus had some difficulty in eating the larger leeches and, indeed, did not feed at all on the large E. octoculata size-group.

3.3.2 Serological studies

The results of the various tests on field-collected invertebrate and vertebrate potential predators are given in table 3.5. Because so few positive results were obtained, data from the lakes within each trophic group were combined. Of the substantial number of invertebrates tested, only a few triclads, leeches, damselfly nymphs, Sialis larvae, larvae of polycentropid, psychomyiid and limnephilid caddis flies, larvae and adults of dytiscid beetles and stonefly nymphs were found to have fed on leeches.

The percentage of positive reactions exceeded 1% in only five instances, viz. Sialis feeding on H. stagnalis in productive lakes (1.6%), dytiscid larvae feeding on E. octoculata and H. stagnalis in productive lakes (2.8% and 1.4% respectively) and psychomyiid larvae feeding on E. octoculata and H. stagnalis in productive lakes (1.2% and 2.4% respectively). All positive reactions were obtained in the late spring, summer and early autumn months.

Of the fish tested, none were found to have eaten G. complanata, 0.8% of the three-spined stickleback (G. aculeatus) were found to have eaten H. stagnalis, and 3.2% and 6.3% of perch (P. fluviatilis)and roach (R. rutilus) respectively, were found to have eaten E.octoculata. Ten-spined stickleback (Pygosteus pungitius) and minnows (Phoxinus phoxinus) were not found to eat leeches.

3.3.3 Visual examination of fish diet

The diet of the fish collected from Crose Mere gill netting catches are given in table 3.6 for perch (P.fluviatilis), table 3.7 for roach (R. rutilus) and table 3.8 for pike (E. lucius) and tench (T. tinca). In no instance were any leeches recorded in the diet.

Size-frequency diagrams for perch are given in figure 3.1. In the sample of October 1982, most fish were found to be 4+ year class. In the sample of August 1983, most fish were between 5+ and 8+. Roughly equal numbers of male and female fish were taken.

Perch were found to feed predominantly on Chironomidae and Chaoborus sp. larvae with Corixidae, Asellus and Gammarus being less important, and it is clear that most of the feeding was on open water prey. One large perch was found to have eaten a small perch. Nine out of the 97 fish examined had empty stomachs.

Size-frequency diagrams for roach are presented in figure 3.2. In May 1982, all fish taken were either 5+ or 6+ year-class. In July, a few 4+ and 7+ fish were also taken. In October, a wider variety of age groups were found, ranging from 2+ to 7+ fish. In 1983 most fish taken were between 6+ and 9+ year-classes. Again, roughly equal numbers of male and female fish were collected.

Roach were found to feed frequently on chironomids, with Chaoborus sp. being important in the samples of May and July 1982, but none being found at all in samples after then. In these latter samples, ostracods and Hydracarina were of frequent abundance. Numbers of snails and corixidae were also taken. It seems that the roach were feeding on both open water prey and prey possibly gained from the benthos, or taken in the marginal vegetation. Seventeen out of the 70 fish examined were found to have empty stomachs.

The five pike caught in August 1983 ranged between 33 and 48 cm in length, and all were males. They had fed on *Asellus*, *Gammarus* and Corixidae, but chironomids were the most frequent item. The single specimen of tench that was taken in August 1983 was a male 24 cm in length, and was found to have fed exclusively on copepods and ostracods.

3.4 Discussion

In the previous chapter it became clear, from the literature survey, that there were few records of leeches being predated on in the field by fish and waterfowl predators, and that there were no field observations from invertebrate predators. Laboratory predation experiments have not previously been carried out, though Pearlstone (1972) noted that leeches were never taken by damselfly larvae and Dunn (1952) observed that bullhead (*C. gobio*) did eat leeches in aquaria. Pritchard (1964) did find that leeches were eaten by dragonfly larvae, but this work was concerned with dragonflies rather than the predators of leeches. The experiments described here would seem to suggest that leeches are readily eaten by vertebrate and certain invertebrate predators in the laboratory, but that, in field situations, the incidence of predation is very low.

A wide range of invertebrate predators were found to eat leeches in the laboratory. In those cases, where adult leeches were not eaten, it seems that the size of the leeches were important for, in most cases, the young were eaten. The exceptions to this were the experiments using triclad and leech predators which, with the exception of *E. octoculata* adults eating *E. octoculata* young, were not found to feed on leech young. For adult leeches, it was found *N. glauca* showed little interest in eating, and it is possible that this was due to the leeches remaining inactive in the experimental dishes. *Notonecta* is known to use movement in the water to detect its prey (Giller & McNeill, 1981). However, it was found that *N. obliqua* fed on young *E. octoculata* and *H. stagnalis*, though not on *G.complanata*. Of the three leech species being investigated, *G. complanata* is the least active. The fact that *C. puella* did not take adult leeches would tend to confirm the findings of Pearlstone (1972) but, again, it seems that size is the important factor, for they were found to feed readily on young *G. complanata*. Fish were found to feed readily on all the leeches, the only negative result being that perch (*P. fluviatilis*) did not eat young *Helobdella*, which were probably too small to be noticed.

Experiments using different size-groupings of adult leeches showed convincingly that predators were able to eat more of the smaller leeches, and that large leeches might become partially immune from predation by invertebrates. Neither *Pyrrhosoma nymphula* or *Sympetrum striolatum* were able to eat *E. octoculata* greater than 65 mg. and they ate very few over 35 mg. Also, these same species had difficulty in eating large *G. complanata*. What these experiments did not show, was that the predators had a preference for smaller leeches; the fact that fewer large leeches were eaten could also be explained by the predator becoming more rapidly satiated.

In the field, the majority of the invertebrate predators that were found to feed on leeches, i.e. odonatans, limnephilid larvae, *Sialis* and dystiscid adults and larvae are species that predominantly live in marginal vegetation and, indeed, all positive reactions for these groups, bar one record of *Sialis*, were for animals collected from this habitat. Populations of leeches are high in the stony littoral (Randall, Spelling & Young, 1985), but in this habitat, few positive reactions were found, though triclads, psychomiid and polycentropid caddis were found to have eaten leeches. Serological methods cannot demonstrate cannabalism. However, it was found that there was predation between the different leech species in a very few cases. Wilkialis (1970) and Sawyer (1972) have suggested that recently hatched G. complanata feed on E. octoculata but, in the present study, a sample of young leeches taken in May (n=47) failed to give any positive reactions.

Positive reactions were only recorded during the warmer months of the year when leeches were reproducing and dying (Young and Ironmonger, 1982 and this study), and it is possible that predation was occurring on recently-recruited young and/or moribund or dead adult animals. Unfortunately, the serological technique recorded only the presence of leech material in the guts, with no indication of the size of leech attacked. It is pertinent to mention that no correction factors, to allow for differences in the size of predators, leech species, temperature, etc., were applied to the present data (see Young, 1980) because it was not thought worthwhile in view of the paucity of data obtained, and because of the difficulties in getting some of the potential predators to feed on leeches in the laboratory. The fact that positive results were confined to the warmer part of the year may also have been partly due to the fact that, in the colder months, low temperatures may have resulted in a lowering of the feeding activity by potential predators.

A comparison between the intensity of predation on leeches in productive and unproductive lakes is not easy because of differences in the occurrence of taxa between the two lake types; for example, the tested stonefly nymphs were absent from the productive lakes and three of the triclad species were absent from unproductive lakes. A second reason is the differences in the relative abundance of the taxa between the lake types. For example, *H. stagnalis* and *G. complanata* are sparser in the unproductive than productive lakes. A third reason is the difference in the number of individuals within each taxon that was tested from the two lake types. However, based on the taxa which were recorded as having fed on leeches, the following total percentage positive reactions were obtained:

Productive lakes	*E. octoculata*	0.40% (n=6690)
	G. complanata	0.09% (n=6402)
	H. stagnalis	0.32% (n=6402)
Unproductive lakes	*E. octoculata*	0.29% (n=1726)
	G. complanata	0.00% (n=1948)
	H. stagnalis	0.15% (n=1993)

Because figures are so low, little comment can be made, but values for the same species from the different lake types are similar. The small size of the glossiphoniid populations in the unproductive lakes should be borne in mind in interpretation of the data. In both lake types, the order of predation pressure in decreasing order of magnitude was *E. octoculata*, *H. stagnalis* and *G. complanata*.

The comparison of the diet of fish, using visual and serological methods, indicated that leeches were not readily identified using the former technique and, indeed, no leeches were recorded. Using the latter method, positive reactions were obtained from perch (*P. fluviatilis*), roach (*R. rutilus*) and stickleback (*G. aculeatus*) and this would seem to emphasise the fact that, had serological methods been used in past dietary studies on fish, the number of records of leeches in the diet of fish would be far greater. Westcott (1984) presents a detailed comparison of using different techniques to identify the food of fish. However, in the present study, even the serological technique failed to show anything but a low incidence of predation.

It was not possible, in this study, to investigate the diet of waterfowl in either laboratory or field experiments. The only evidence for feeding on leeches, derived from the literature survey which is presented in the previous chapter, was from the very low number of available diet records and the fact that leeches act as intermediate hosts for duck parasites. It is probable that leeches are not heavily predated upon by these predators, but this remains to be tested. Field experiments where wildfowl (and fish) predators were excluded from leech populations are described in the following chapter.

In conclusion, it would seem that predation on lake-dwelling leeches would be greater from fish than invertebrates; that it might be less on stony shores than in marginal vegetation and that it might be higher on E. octoculata than on the glossiphoniid species. However, the intensity of predation would seem to be very low.

Figure 3.1. Size-frequency data for Crose Mere perch (*P.fluviatilis*)

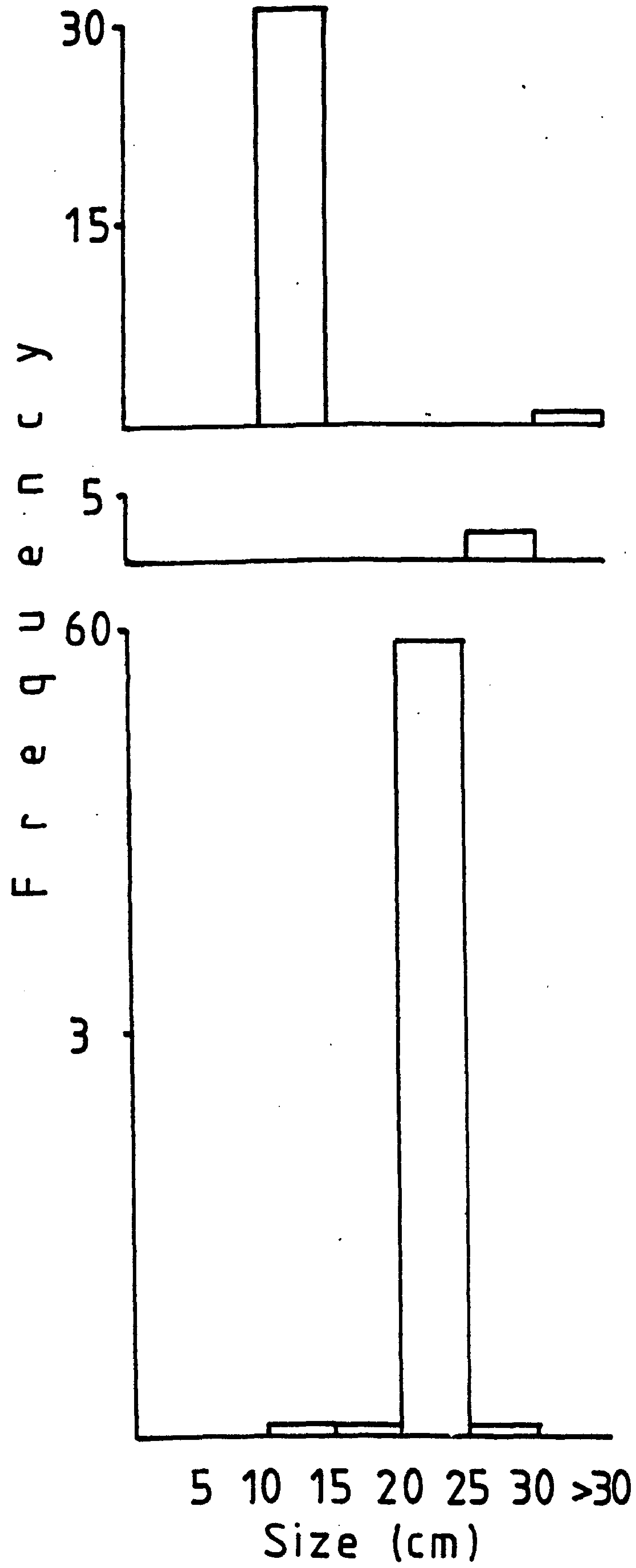


Figure 3.2. Size-frequency data for Crose Mere roach (*R.rutilus*)

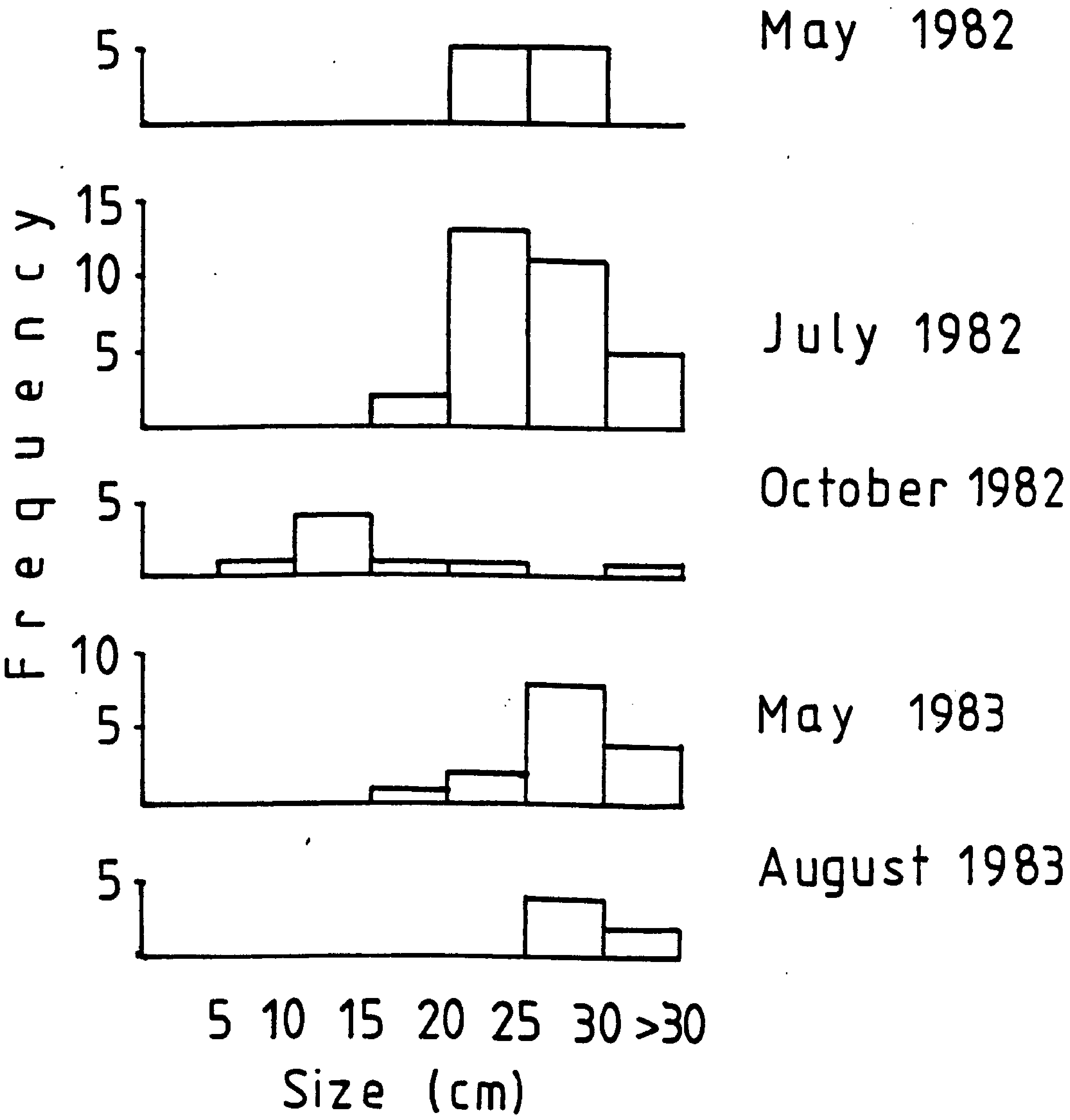


Table 3.1. Laboratory predation experiments. Predation on adult leeches.

Key:- ++ = 50-100% of leeches eaten
+ = 1- 49% of leeches eaten
- = Not eaten
NT = Not tested

Predator	No. of Predators	Erpobdella octoculata (20-100mg)	Glossiphonia complanata (10-60mg)	Helobdella stagnalis (5-15mg)
COLEOPTERA				
Agabus bipustulatus (L.)				
Adults	10	+	+	+
Larvae	10	-	-	+
Dytiscus marginalis (L.)				
Adults	10	++	++	++
Larvae	5	++	NT	+
HEMIPTERA				
Notonecta gluaca (L.)	10	-	-	-
TRICHOPTERA				
Polycentropus flavomaculatus (Pictet)	10	+	-	+
Tinodes waeneri (L.)	1	NT	NT	-
Limnephilus sp.	10	-	+	+
MEGALOPTERA				
Sialis lutaria (L.)	10	++	+	+
ODONATA				
Coenagrion puella (L.)	10	-	-	-
Pyrrhosoma nymphula (Sulzer)	10	+	+	++

Continued

Predator	No. of Predators	*Erpobdella octoculata* (20-100mg)	*Glossiphonia complanata* (10-60mg)	*Helobdella stagnalis* (5-15mg)
ODONATA				
Sympetrum striolatum (Charpentier)	10	+	+	++
Aeshna grandis (L.)	10	++	++	++
Aeshna cyanea (Müll.)	10	++	NT	++
Aeshna juncea (L.)	5	NT	++	NT
PISCES				
Gasterosteus aculeatus (L.)	3	++	++	++
Rutilus rutilus (L.)	10	++	++	++
Perca fluviatilus (L.)	5	++	++	++
Salmo gairdneri (Richardson)	10	++	++	++
Carassius carassius (L.)	3	++	++	++
AMPHIBIA				
Triturus helveticus (Razoumowski)	10	+	+	+

Table 3.2. Laboratory predation experiments. Predation on young leeches.

Key:-
++ = 50-100% of leeches eaten
\+ = 1- 49% of leeches eaten
\- = Not eaten
NT = Not tested

Predator	No. of Predators	Erpobdella octoculata	Glossiphonia complanata	Helobdella stagnalis
TRICLADIDA				
Polycelis nigra (Müll.)	20	-	-	-
Polycelis tenuis (Ijima)	20	-	-	-
Dugesia polychroa (Schmidt)	20	-	-	-
Dendrocoelum lacteum (Müll.)	20	-	-	-
HIRUDINEA				
Erpobdella octoculata (L.)	20	+	-	-
Glossiphonia complanata (L.)	20	-	-	-
Helobdella stagnalis (L.)	20	-	-	-
COLEOPTERA				
Agabus bipustulatus (L.)				
Adults	10	++	NT	++
Larvae	5	++	++	++
Orectochilus sp. Adults	5	NT	NT	-
HEMIPTERA				
Notonecta obliqua (Thurb.)	10	+	-	+

Continued

Predator	No. of Predators	*Erpobdella octoculata*	*Glossiphonia complanata*	*Helobdella stagnalis*
TRICHOPTERA				
Athripsodes albifrons (L.)	8	+	NT	++
Limnephilus sp.	10	+	++	++
Tinodes waeneri (L.)	10	+	NT	+
Polycentropus flavomaculatus (Pictet)	10	+	++	+
MEGALOPTERA				
Sialis lutaria (L.)	10	++	+	+
ODONATA				
Lestes sponsa (Hansemann)	10	++	NT	++
Coenagrion puella (L.)	6	NT	++	NT
Ischnura elegans (Van der Lindens)	6	NT	++	NT
Aeshna grandis (L.)	10	++	NT	++
Aeshna juncea (L.)	10	NT	++	NT
PISCES				
Gasterosteus aculeatus (L.)	3	++	++	++
Carassius carassius (L.)	3	++	++	++
Cyprinus carpio (L.) Fry	5	++	++	++
Perca fluviatilus (L.)	5	NT	NT	-

Table 3.3. Laboratory predation experiments. The % of leeches of different size groups eaten by predators.

Predator	No. of Predators	*Erpobdella octoculata*			*Glossiphonia complanata*			*Helobdella stagnalis*		
		10-25mg	35-50mg	65-80mg	5-15mg	25-35mg	45-55mg	1-3mg	5-7mg	9-11mg
COLEOPTERA										
Agabus bipustulatus (L.) adults	10	16%	11%	12%	20%	17%	13%	58%	33%	21%
ODONATA										
Aeshna grandis (L.)	10	69%	59%	41%	94%	89%	79%	95%	94%	91%
Pyrrhosoma nymphula (Sulzer)	10	16%	1%	0%	19%	13%	3%	75%	79%	26%
Sympetrum striolatum (Charpentier)	10	17%	1%	0%	23%	17%	1%	69%	58%	35%
Amphibia										
Triturus helveticus (Razoumowski)	10	9%	0%	0%	12%	3%	0%	19%	15%	8%

Table 3.4. Laboratory predation experiments. Kruskal-Wallis tests on predation on different size-ranges of leeches.

Values given are the Kruskal-Wallis statistic, with correction made for tied ranks. In each test there were 2 degrees of freedom.

* = $p<0.05$ ** = $p\leq 0.01$ - = not significant

	Erpobdella octoculata	*Glossiphonia complanata*	*Helobdella stagnalis*
COLEOPTERA			
Agabus bipustulatus (L.)	7.404 (*)	7.100 (*)	24.116 (**)
ODONATA			
Aeshna grandis (L.)	22.529 (**)	19.262 (**)	2.679 (-)
Pyrrhosoma nymphula (Sulzer)	26.008 (**)	22.198 (**)	19.605 (**)
Sympetrum striolatum (Charpentier)	25.225 (**)	21.674 (**)	13.147 (**)
AMPHIBIA			
Triturus helveticus (Razoumowski)	24.092 (**)	18.638 (**)	7.740 (*)

Table 3.5. Serology. The diet of invertebrates and vertebrates collected from productive and unproductive lakes.

Key:- EO = Erpobdella octoculata GC = Glossiphonia complanata
HS = Helobdella stagnalis n = sample size
%+ = percentage of positive tests

Predator	Productive Lakes						Unproductive Lakes					
	Anti-EO		Anti-GC		Anti-HS		Anti-EO		Anti-GC		Anti-HS	
	n	%+	n	%+	n	%+	n	%+	n	%+	n	%+
TRICLADIDA												
Polycelis tenuis (Ijima)	840	0.4	840	0.1	840	0.1	-		-		-	
Polycelis nigra (Müll.)	840	0	840	0	840	0	315	0.6	315	0	315	0
Dugesia polychroa (Schmidt)	840	0.4	840	0.1	840	0.1	-		-		-	
Dendrocoelum lacteum (Müll.)	680	0	680	0	680	0	-		-		-	
HIRUDINEA												
Erpobdella octoculata (L.)	-		1192	0.3	1192	0.7	-		377	0	375	0.3
Glossiphonia complanata (L.)	1480	0.7	-		1480	0	107	0	-		49	0
Helobdella stagnalis (L.)	1480	0.2	1480	0	-		107	0	103	0	-	
HYDROZOA												
Hydra sp.	38	0	38	0	38	0	49	0	49	0	49	0

Continued

Predator		Productive Lakes						Unproductive Lakes					
		Anti-EO		Anti-GC		Anti-HS		Anti-EO		Anti-GC		Anti-HS	
		n	%+	n	%+	n	%+	n	%+	n	%+	n	%+
GASTROPODA													
Lymnaea stagnalis (L.)		15	0	15	0	15	0	-		-		-	
Lymnaea peregra (Müll.)		41	0	41	0	41	0	30	0	30	0	30	0
CRUSTACEA													
Gammarus pulex (Schell)		80	0	80	0	80	0	28	0	28	0	28	0
COLEOPTERA													
Dytiscidae	Adults	232	0.4	232	0	232	0.4	112	0	112	0	112	0
	Larvae	71	2.8	71	0	71	1.4	23	0	23	0	23	0
Haliplidae	Adults	30	0	30	0	30	0	7	0	7	0	7	0
Gyrinidae	Adults	41	0	41	0	41	0	-		-		-	
PLECOPTERA													
Chloroperla torrentium (Pictet)		-		-		-		113	0	113	0	113	0.9
Diura bicaudata (Linne)		-		-		-		15	0	15	0	15	0
MEGALOPTERA													
Sialis lutaria (L.)		254	0.8	254	0.4	254	1.6	68	0	68	0	68	0

Continued

Predator	Productive Lakes						Unproductive Lakes					
	Anti-EO		Anti-GC		Anti-HS		Anti-EO		Anti-GC		Anti-HS	
	n	%+	n	%+	n	%+	n	%+	n	%+	n	%+
HEMIPTERA												
Notonecta glauca (L.)	245	0	245	0	245	0	-		-		-	
Nepa cinerea (L.)	31	0	31	0	31	0	-		-		-	
Corixidae	110	0	110	0	110	0	110	0	110	0	110	0
Micronecta poweri (Douglas & Scott)	-		-		-		150	0	150	0	150	0
TRICHOPTERA												
Polycentropidae	132	0.8	132	0	132	0.8	492	0.2	492	0	492	0
Psychomyiidae	82	1.2	82	0	82	2.4	112	0.9	112	0	112	0
Glossomatidae	-		-		-		32	0	32	0	32	0
Phryganeidae	95	0	95	0	95	0	60	0	60	0	60	0
Limnephilidae	337	0.6	337	0	337	0.6	239	0.4	239	0	239	0
Leptocercidae	155	0	155	0	155	0	102	0	102	0	102	0
Molannidae	42	0	42	0	42	0	27	0	27	0	27	0
Sericostomatidae	38	0	38	0	38	0	64	0	64	0	64	0
ODONATA												
Enallagma cyathigerum (Charpentier)	102	1.0	102	0	102	0	95	0	95	0	95	0
Ischnura elegans (Van der Lindens)	26	0	26	0	26	0	10	0	10	0	10	0
Pyrrhosoma nymphula (Sulzer)	-		-		-		20	0	20	0	20	0

Continued

Predator	Productive Lakes						Unproductive Lakes					
	Anti-EO		Anti-GC		Anti-HS		Anti-EO		Anti-GC		Anti-HS	
	n	%+	n	%+	n	%+	n	%+	n	%+	n	%+
DIPTERA												
Tanypodinae	110	0	110	0	110	0	110	0	110	0	110	0
Hydracarina	75	0	75	0	75	0	75	0	75	0	75	0
PISCES												
Perca fluviatilis (L.)	31	3.2	31	0	31	0	-		-		-	
Rutilus rutilus (L.)	48	6.3	48	0	48	0	-		-		-	
Gasterosteus aculeatus (L.)	119	0	119	0	119	0.8	-		-		-	
Pygosteus pungitius (L.)	67	0	67	0	67	0	-		-		-	
Phoxinus phoxinus (L.)	-		-		-		53	0	53	0	53	0

Table 3.6. Fish diet. The percentage occurrence of food organisms found by visual examination in Crose Mere perch (*P. fluviatilis* L.)

	1982			1983	
Samples	May	July	October	May	August
No. of fish	-	-	32	2	63
No. of empty stomachs	-	-	1	0	8
Copepoda	-	-	3.2	-	3.6
Cladocera	-	-	-	-	5.5
Ostracoda	-	-	6.5	-	-
Asellus aquaticus	-	-	45.2	-	14.6
Gammarus pulex	-	-	19.35	-	-
Corixidae	-	-	9.7	50	12.7
Sialis lutaria	-	-	-	-	3.6
Trichoptera	-	-	25.8	-	-
Chaoborus sp.	-	-	71	50	94.6
Chironomidae	-	-	87.1	100	72.7
Oligochaetes	-	-	-	-	1.8
Perca fluviatilis	-	-	-	-	3.6

Table 3.7. Fish diet. The percentage occurrence of food organisms found by visual examination in Crose Mere roach (*R. rutilus* L.)

	1982			1983	
Samples	May	July	October	May	August
No. of fish	10	31	8	15	6
No. of empty stomachs	3	7	5	2	0
Copepoda	14.3	8.3	-	7.7	-
Cladocera	-	-	-	7.7	-
Ostracoda	-	4.2	66.7	15.4	83.3
Hydracarina	-	4.2	33.3	-	33.3
Asellus aquaticus	-	20.8	-	-	-
Gammarus pulex	-	20.8	-	15.4	-
Bythynia tentaculata	-	4.2	-	7.7	-
Potamopyrgus jenkinsi	-	4.2	-	-	-
Planorbis sp.	-	4.2	33.3	15.4	16.7
Valvata piscinalis	-	-	-	-	16.7
Pisidium sp.	14.3	16.7	-	15.4	-
Sphaerium sp.	28.6	12.5	-	-	-
Corixidae	14.3	70.8	-	84.6	50
Sialis lutaria	-	4.2	-	-	-
Trichoptera	-	25	-	15.4	16.7
Chaoborus sp.	42.9	25	-	-	-
Chironomidae	100	37.5	33.3	53.9	50

Table 3.8. Fish diet. The percentage occurrence of food organisms found by visual examination in Crose Mere pike (*E. lucius* L.) and tench (*T.tinca* L.).

Species	Pike	Tench
No. of fish	5	1
No. of empty stomachs	0	0
Copepoda	-	100
Ostracoda	-	100
Asellus aquaticus	20	-
Gammarus pulex	40	-
Corixidae	20	-
Chironomidae	60	-

CHAPTER 4

A FIELD EXPERIMENT TO INVESTIGATE THE OCCURRENCE AND POSSIBLE EFFECTS OF PREDATION ON LEECH POPULATIONS IN THE LITTORAL ZONE OF CROSE MERE

4.1 Introduction

The possible effects of predation on both individual prey species and community structure, under field conditions, are both numerous and varied. As outlined in Chapter 1, predators may theoretically serve to regulate or control the numbers and/or composition of the prey community or, conversely, have little or no effect at all. However, to assess the impact of predation under field conditions is by no means easy and the results of experimentation may be difficult to interpret.

The principle behind most of the experimentation carried out in this research area is to add or remove/exclude predators from a habitat, or part of a habitat, and to attempt to assess what changes occur in the structure and composition of the manipulated communities. The changes to be assessed might include parameters such as prey population density, biomass, growth, mortality, production and life-history characteristics, such as the timing of reproduction and the duration of generations. In addition, the populations of other predators in the community need to be studied because, for example, in a situation where the predator removed was regulating prey abundance, its removal may simply allow another predator species to take over its role. Neither is it sufficient to just study one potential prey species in isolation, for it may be that the removal of a predator will allow the food of the prey species to increase and allow its numbers to rise. In this case the observed increase in the prey population would not be a direct consequence of predator removal. In other words, in order to establish cause and effect relationships in this kind of study it may be necessary to investigate all the species present, and this is often not possible.

Previous experiments in this research field fall broadly into two categories, viz. those in which predators are entirely removed from (or added to) a habitat and those in which prey are protected from predation by means of cages or enclosures. Hayne & Ball (1956) studied benthic communities in two ponds and, by moving fish from one pond to the other, were able to investigate how predation affected zoobenthos productivity. They found that when fish were present the standing crop of benthic species was decreased but had a high rate of production while, when fish were removed, the standing crop was higher but had a lower productivity. Macan (1965 & 1966) followed the effects of fish removal and their subsequent restocking on the fauna of an artificial fish pond. He found that when fish were re-stocked the diversity of species and the range of habitats that they occupied were diminished. For example, Notonecta obliqua Thunb., previously found in open water, was restricted to shallow water with thick vegetation. The leech Erpobdella octoculata, though eaten by fish, showed no numerical or distributional change.

Perhaps the main problem with this approach is that the method used to remove the predator may, in itself, be sufficient to alter the community being investigated. Straskraba (1965) removed fish from a backwater of the River Elbe by means of two treatments of rotenone and this not only removed the fish but also destroyed the invertebrate fauna. When re-established the community structure was different, with a greater abundance of large planktonic species, but it could be argued that this may have been due to the rotenone rather than the removal of predators. Lellak (1966) described similar experiments carried out on the backwaters of the River Elbe whereby the fish and invertebrate fauna were removed by a combination of poisons. The regeneration of the bottom fauna after poisoning and in the absence of fish, led to a different species composition from that found beforehand. Initially, chironomid larvae benefitted from an increased plankton abundance, but rising numbers of planktonic, filter-feeding crustaceans reduced the supply of food to the benthos, and chironomid densities subsequently declined.

The act of adding or removing predators in a habitat has not always been deliberate. Meijering (1970), for example, made use of an unusually high tide, which introduced Gasterosteus aculeatus L. to ponds from which it was previously absent, to observe the effects of predation on the resident cladoceran species. The resting stages of the cladocerans were able to survive the immersion in salt water, but several species were eliminated in the ponds which had G.aculeatus introduced to them.

In the second type of experiment, enclosures or cages are used to exclude predators from a part of the habitat. This has the advantage of allowing experimentation without the large-scale removal of predators and its consequent disturbance to the habitat. It also allows simultaneous comparisons to be made between control and enclosed sites, allowing experiments to be performed relatively quickly and between very similar types of habitat. In the experiments where predators are entirely removed and then re-introduced, it may take several years for the communities to properly re-establish and many other factors, apart from the presence or absence of a predator, may change during that period. In experiments where two separate habitats are studied, one with a predator and the other without, differences between the habitats, perhaps unnoticed by the experimenter, may influence results.

However, enclosure experiments do have their disadvantages, and perhaps the main problem lies in the possible effects of the enclosure itself on the populations being studied. It may be, for example, that inside an enclosure the water-flow may be reduced and this may lower the amount of dissolved oxygen in the water, or perhaps allow the temperature of the enclosed water to rise. Other possible effects of reduced water flow might include altered depositional rates of suspended particles, altered amounts of dissolved nutrients and the promotion of algal growth both on the structure of the enclosure and in the water column enclosed. Thus the physico-chemical environment within an enclosure may differ from control sites. The enclosure may also directly affect the species being investigated if, for example, they are involved in migrations within the habitat or rely upon food species which are also excluded by the enclosures.

Kajak (1977) constructed experimental tubes 0.7 m in diameter and enclosures 2 m^2 in area to investigate the effects of fish predation and other manipulations (for example, the addition of food) on benthos biomass in a lake. The tubes were made from a wire carcass covered in 2 mm mesh nylon netting and were driven into the substratum with about 20 cm rising above the water level. The enclosures were simply areas of the lake bottom fenced with 1 x 1 cm netting. From this and other experiments using larger enclosures (Kajak, 1972) he concluded that benthos biomass was increased in areas protected from fish, but that this was probably due to a change in the planktonic community resulting in better food availability for the benthos, and that the fish themselves caused only small changes in benthos biomass to occur.

Berglund (1968), working on Asellus aquaticus L. in a pond in central Sweden, used enclosures to protect portions of the benthos from trout predation and, furthermore, divided the pond in two, using a large net to produce areas with and without fish. He found that both the abundance and production of Asellus were reduced by predation. Andersson et al (1978), also working on lakes in Sweden, manipulated fish in enclosures some 3 metres in diameter. Enclosures with fish showed reduced benthic and planktonic populations with low water transparency and a high pH. Without the fish the enclosures had higher benthic and planktonic populations and clear water. They likened the addition of fish and its consequences to the process of eutrophication.

Wisniewski (1978) used 60 x 60 cm cages positioned at a depth of 7.5 metres in Lake Snairdy, Poland to manipulate fish and invertebrate populations. He found that the fish decreased the biomass and abundance of the Tubificidae, but increased their productivity by stimulating rapid regeneration of damaged individuals. Worms damaged by foraging vertebrate and invertebrate predators forming some 80% of the littoral population.

Benke (1978), investigating the interspecific interactions of freshwater invertebrates and, in particular, dragonfly larvae, constructed 4 x 4 m pens supported on aluminium poles driven into the bottom mud of a pond. Wooden frames, covered with 14 mm mesh plastic-impregnated steel screening, formed three sides of the pen, the landward side being bounded only by the shore. This construction greatly reduced water flow into the pen, but subsequent physico-chemical comparisons showed little difference between the enclosures and control sites. Much of this work was concerned with interactions between different odonate species, in particular early and late emergents, but the effects of predation on the prey of the odonates, as revealed by diet analysis, was investigated and it was found that the abundance of early-emerging odonates played a role in determining subsequent prey abundance.

Benke et al (1982) used smaller enclosures, consisting of glass aquaria with an aluminium mesh collar, situated on a submerged platform, to further investigate these odonate interactions but also noted that prey abundance was lower in enclosed than in control sites. They suggested that this may have been caused by reduced structural diversity in the enclosures due to the absence of macrophytes, reduced colonisation caused by the structure of the enclosure itself and reduced colonisation due to the enclosures being raised on a platform. Despite a high predation pressure, no firm evidence for a relationship between predator and prey density was found.

Thorp & Bergey (1981a & 1981b) used thirty-six predator-exclusion cages to examine the responses of benthic macro-invertebrates in a reservoir to vertebrate predators and thermal pollution. The cages measured 2 x 2 x 1 m and were placed at a depth of 1 m or less. They comprised black 3 mm mesh netting supported on a frame of aluminium poles; their bottom edge had a flap of steel cloth that, when weighed down with bricks, gave a good seal with the substratum. The cages were sampled at the end of the experimental period using a core sampler and the results suggested that predators played little role in organising the benthic community, with neither diversity nor abundance being conclusively related to predator treatment. No physico-chemical data comparing control and enclosed sites were reported in the study.

Thorp & Cothran (1982), by the use of floating platforms consisting of a styrofoam for buoyancy, which supported wire mesh baskets in which plastic trays containing benthic material were placed, studied the role of dragonfly nymphs in part of the benthic community of a reservoir. This method reduced to a minimum immigration of unwanted invertebrate predators but still allowed immigration of many prey organisms, for example chironomids, through aerial deposition of eggs. Further, because the cages did not need to exclude predators other than dragonfly nymphs, it was possible to use a relatively large mesh size allowing good water flow through the enclosures and reducing potential oxygen tension problems. The results so far reported suggested that there were no significant differences between the experimental microcosms and control samples in either the total density of recorded invertebrates, the density of chironomids or in the number of taxa present.

Fairchild (1982) used six 4 m^2 enclosures, constructed from fibreglass screening attached to wooden frames and sunk into the bottom mud, to assess the effects of foraging by largemouth bass fry on plant-associated invertebrates in a lake. Fry were introduced into three of the enclosures and the population responses recorded. The cladoceran Sida crystallina O.F. Muller declined in the enclosures with fry but increased in control sites. Chironomids and chydorids showed little change. However, from monitoring the invertebrate populations outside the enclosures, it was noted that a rapid decline in density occurred for S. crystallina, and to a lesser extent for chironomids, coinciding with the natural entry of a new school of fry into the lake.

Several other studies, for example those of Dodson (1974), Lynch (1979), Kesler (1981), Neill (1981), Cohu (1982), DeMott and Kerfoot (1982), DeCosta et al (1983) have also used enclosures to study planktonic populations.

Crowley et al (1983) designed and tested an experimental enclosure for use in lentic habitats. The basic design was a cylinder composed of an outer, supporting, chicken-wire frame and on the inside a nylon screen of the desired mesh size. The top and bottom of the cylinder were closed off with plastic lids and the bottom lid was used to contain the natural substratum from the habitat. The size of the cylinder was varied between 10 cm to 43 cm in diameter. Field tests in lentic habitats indicated no enclosure effects on water temperature or oxygen concentration and similar changes in benthos abundance were noted, with few exceptions, for control and enclosed sites.

Another possible experimental variant is to ask the question 'why is a species absent from a particular habitat?' If, when introduced to the habitat the species does not survive, it may be that predation is a contributory cause. Davies (1969b) introduced large numbers of triclads to an unpopulated small weedy pond. He protected some of them in small polythene cylinders and followed the triclad populations inside and outside these cages. He also, simultaneously, used a serological method to investigate the diet of potential predators and found that the unprotected triclads did not survive for long and that they were eaten by damselfly and newt larvae.

Other workers, for example Hall et al (1970), have chosen not to rely upon the vagueries of natural conditions and have used artificially constructed field habitats to investigate the effects of predators. These methods have proved successful, but have the obvious disadvantage that the populations studied may not represent a natural assemblage of species and therefore the results cannot be extrapolated to natural field conditions.

The aims of the present study were to assess the occurence and possible effects of predation by vertebrate predators (fish and waterfowl) on populations of the leeches Erpobdella octoculata, Glossiphonia complanata and Helobdella stagnalis in the stony littoral of Crose Mere. The nature and size of this lake excluded the possibility of removing all the predators and, therefore, enclosures were employed to protect parts of the habitat. To increase the chances of demonstrating any effects of predation on the leech populations, information on as many parameters as possible concerning their populations had to be collected, together with information on the other species present and on any physico-chemical effects caused by the enclosures themselves.

A further purpose in carrying out this field study was to gain additional basic information on the ecology of leeches in Crose Mere and of particular interest were possible differences in the populations from different fractions of the habitat. This is further discussed in section 4.2.2.

The field experiment was carried out in the light of a literature survey reviewing potential leech predators (chapter 2) and in conjunction with field collections from Crose Mere and other lakes of potential predators for diet analysis (chapter 3). It was not possible to obtain wildfowl from Crose Mere for diet analysis, but a species list, provided by the Shropshire Ornithological Society is presented in chapter 6.

4.2 Materials

4.2.1 Enclosures

The nature of the enclosures used in previous studies have been briefly discussed in the introduction to this chapter and it is clear that the design is related to the enclosure's particular purpose and the conditions in which it is to be used. In the present study the requirements of the enclosures were that they should exclude fish and wildfowl predators, keep migration of invertebrates into or out of the enclosures to a minimum, and allow the enclosed areas to remain as undisturbed as possible.

On the north-west shore of Crose Mere are a series of shallow bays caused by erosion of the soft boulder-clays and gravels between bankside trees. Within these bays the water reaches a depth of just less than a metre and on their lakeward side the bottom shelves steeply away. It seemed possible that, by closing off the lakeward side of these bays, large areas of the littoral zone could be enclosed with relatively little construction work or disturbance being necessary.

The materials used to enclose the bays consisted of a fine polypropylene netting (fabric H435. Lining Weavers Ltd., Manchester) of mesh size approximately 1.20 x 0.05 mm, supported on a NETLON plastic frame and held in position in the lake by untreated pine stakes. Plastic garden edging was attached along the bottom edge of the netting so that it could be sunk a few centimetres into the substratum, giving a good seal to the bottom edge. The top edge of the netting was cut to about 15 cm clearance above the water level. Covering the top of the enclosures, and supported by further stakes, was NETLON bean netting, and this was attached in such a way that it could be rolled back to allow access to the bays during sampling.

The basic construction of the enclosures is illustrated in figure 4.1 and photographs of the enclosures in position in Crose Mere are given in figures 4.2 and 4.3.

The polypropylene netting, its NETLON support and the garden edging were pre-fabricated into sections in the laboratory. Joints between the different materials were made with heavy duty staples and then stitched with nylon whipping twine. The pre-fabricated sections were taken to the lake and nailed to the pine stakes on the bankside. The whole construction was then carried out into position in the lake and the pine stakes driven into the substratum until the edging made a good seal with the lake bottom.

Initially, in March 1981, it was decided to construct five enclosures with five associated control sites. Five pairs of bays were selected to cover the length of the north-west shore and the range of substrata present, and one bay in each pair was then enclosed. However, the drainage work described in Chapter 1 resulted in a large drop in water level so that the areas enclosed were greatly reduced.

The only course of action available at the time (apart from abandoning the experiment) was to combine the materials from the five enclosures into two new enclosures, the extra materials being needed to enable the enclosures to extend lakewards out into the hitherto deeper waters. Thus, in 1981, there were just two enclosures and five control sites used in the experiments. In February 1982, the old enclosures were removed and four new ones constructed which, with their associated control sites, gave a total of eight sampling stations along the shore. On the basis of the experience gained in 1981/82 it was found that this number of sampling stations would be the maximum number of sites that could be reasonably handled in the time available.

Because the enclosures were making use of the natural geography of the shoreline, it was not possible to ensure that they were all exactly the same size. The mean area enclosed was 35.2 m^2 with a range of 27.4 m^2 to 39.7 m^2. The depth of water within them reached a maximum of 70 cm, but this value varied with the slight seasonal variations in the lake level.

4.2.2 Sampling methods

A method of sampling was needed that could provide quantitative estimates of leech population density, biomass and mean weight and, in addition, give sufficient information to allow factors such as the timing and intensity of reproduction to be compared between control and enclosed sites. Furthermore, it was desirable to collect information on the other macro-invertebrates present to see whether large-scale changes in their populations occurred.

The methods available for sampling in freshwater habitats are numerous and reflect the variety of habitat types present and the purposes for which the samples are taken. A bibliography of sampling methods is given in Elliott & Tullet (1978) and other recent reviews of methods and samplers are given in Kajak (1971) and Helawell (1978).

Previous studies on leech populations have also used a variety of sampling methods. Elliott (1973a) used a shovel sampler of the type described by Macan (1958) when studying *E. octoculata* in a Lake District stream. Learner & Potter (1974) and Murphy & Learner (1982) used cylinder samplers when studying *H. stagnalis* and *E. octoculata* in a Welsh reservoir and river respectively. Hatto (1968) used roofing slates to sample a population of *Glossiphonia heteroclita* in a small artificial pond, while Ashton & Brown (1975) used black plastic tiles to sample *E. octoculata* in a river. Dall (1979a) described a quantitative method for use on stony substrata which involved sampling from clusters of measured stones and the substratum underneath them. Additional leeches were collected from other stones to supplement data on rarer species. Young & Ironmonger (1982a), working at Crose Mere, sampled from stones measured at the time of sampling, roofing slates and fixed 'quadrats' of measured stones, but largely ignored the underlying substratum.

In the present study, an adapted version of the methods described by Dall (1979a) was adopted. The littoral zone of Crose Mere, in the areas to be sampled, comprises relatively few large stones overlying a compacted substratum of smaller stones, gravel and sand. It was apparent that, because differences could occur between leech populations in these two fractions, both needed to be sampled to provide the accurate data required. The sampling problem was resolved by sampling the two fractions separately; it was then possible to provide estimates for the total populations by using the ratio of one to the other.

For the purpose of this study, a large stone was defined as any stone with its longest axis in excess of 10 cm, and to obtain estimates of its bottom surface area (i.e. the area available for leech colonisation) the simple method described by Müller (1953) and Dall (1979a) of multiplying length by breadth was used. Other workers, for example, Mann (1957a), Calow (1972) and Kovalak (1978) have used more complex and time-consuming methods for estimating stone surface area, but Young & Ironmonger (1982a) found the above method to be suitable for Crose Mere stones, and further found that laboratory calibration of field measurements to be unnecessary. Within each sampling area, being either an open or enclosed bay, four fixed 'quadrats' of measured stones were set up so that the same stones could be sampled on successive occasions. Each 'quadrat' consisted of a series of stones laid from shallow to deep water and with an approximate bottom surface area of $0.1m^2$. Thus, in each bay, a total of $0.4\ m^2$ of stone-bottom area was sampled. The areas of each 'quadrat' from each bay used in 1981 and 1982 are given in Appendix C.

The smaller stones and underlying substratum were sampled by means of trays filled with the natural local substratum. This method has been used successfully by other workers, for example, Moon (1934) and Dunn (1961), and has the advantage of using a known sampling area and enabling good comparisons to be made between different areas under investigation. This was, of course, particularly important in the present study where comparisons between control and enclosed sites, rather than with other studies, were of primary importance. The main disadvantage of the method is that a reasonable time interval may be needed for colonisation (Mundie, 1956) and that they may not attract a typical cross-section of the community being studied. However, again, as comparisons between sites were the main objective, this was not thought to be a major problem.

The trays used were plastic seed trays, with dimensions 36.5 x 21.5 cm, which were filled with the natural substratum of the lake to a depth of 4 cm. This gave a sampling area of 0.0785 m^2 for each tray. All trays had holes drilled in their under-surface and were buried into the lake bottom to allow ready colonisation. Within each of the sampling areas four such trays were located and a period of four weeks was allowed for colonisation before their removal back to the laboratory for examination.

The ratio of large stone-bottom surface area to substratum surface area was estimated by measuring all stones with an axis over 10 cm in each bay. Dall (1979a) used random quadrats to estimate a similar ratio, but in this present study, as the numbers of stones were relatively small, it was feasible to measure them all. By taking the area of each bay, and the bottom surface area of the large stones within it, the substratum:stone ratio could be calculated for each site. The mean value of this ratio, over all bays, was 0.064 (i.e. for every 1 m^2 of substratum there was 0.064 m^2 of stone-bottom surface area). The range of ratios was from 0.04 to 0.10 and the mean ratio for separate control and enclosed sites were 0.60 and 0.70 respectively. It seemed reasonable, accepting the errors involved in estimating stone surface area, that as the ratios in the different bays were so similar, the mean ratio of 0.064 could be used in producing estimates for combined stone and substratum sample data. In effect, the sampling method can be thought of as a stratified sampling procedure with two strata, stones and substratum, and the ratio between them giving their relative weightings.

Sampling Programme

Sampling started one month after the enclosures were first erected, i.e. in April 1981 and was continued on a monthly basis until October

1981. A further sample was then taken in January 1982, before monthly sampling was again commenced in April 1982 and continued to November 1982. A final sample was taken in March 1983. During the periods of leech breeding activity, additional samples were taken from stones to supplement the data relating to reproductive activity.

Treatment of samples in the field.

On each sampling occasion, the following procedure was adopted:-

A. Stone samples

For each of the quadrats, all the stones were carefully lifted and placed over a white-enamelled tray, and the animals on their undersurface removed with a paintbrush into the tray. When all the stones in the quadrat had been cleared, the animals were transferred to a polythene bottle for live transportation back to the laboratory. If *E. octoculata* cocoons were present they were left in place and their numbers recorded. If any *G. complanata* were sitting on eggs they were left undisturbed but their numbers recorded. However, a few such animals were removed to give estimates of the numbers of eggs being brooded.

B. Substratum samples

Each tray containing substratum was lifted and the animals adhering to its underside and outside walls removed with a stiff brush. The trays were then labelled and placed inside separate polythene bags for transportation to the laboratory.

Treatment of samples in the laboratory

On arrival back at the laboratory, all the samples were placed in a 4°C constant temperature room, and the tops of the polythene bottles loosened to allow aeration. If particular bottles were very crowded with animals then the sample would be split into two or more parts. For processing, the bottles were emptied onto an enamelled tray filled with lake water so that the animals could be readily seen. Samples of substratum were emptied onto larger trays and were sorted by hand to remove all the animals. If large numbers of particular groups were present, for example chironomids, then a sub-sample comprising a quarter of the total sample was taken. However, all leeches were always removed.

For each sample, from both stones and substratum, the following data were recorded:-

1. The number of leeches of each species present.
2. The individual wet weight of each leech to the nearest mg. Before weighing, all animals were blotted dry with filter paper, and weights were recorded on a Sartorious micro-balance accurate to 0.001 g.
3. For E. octoculata, the presence or absence of a clitellum. E. octoculata cocoons found on the small stones and gravel in substratum trays were also counted.
4. For G. complanata and H. stagnalis, whether eggs (H. stagnalis) or young (G. complanata and H. stagnalis) were being carried. The numbers of eggs/young being carried by a sub-sample of such leeches were also recorded. In addition, a number of G. complanata and H. stagnalis were examined microscopically so that the presence and number of any eggs in their oviducts could be counted.

5. The numbers and wet weights of all other macro-invertebrates present. Taxa were classified into readily identifiable groups; in some cases this was to the specific level but, for example, no attempt was made to further classify chironomids and oligochaetes. The presence of large numbers of young, newly-hatched animals of all groups was also noted.

Immediately after the samples had been processed, the animals were returned to the lake and replaced in the bays from which they had been taken. Mortality during the sampling procedure was negligible.

In 1981, all trays containing substratum removed in sampling were examined for both leeches and other invertebrates, but this was found to be very time-consuming and so, in 1982 only two out of every four trays from each site were examined for the 'other' species. Leeches were removed, of course, from all trays.

Physico-chemical measurements

On several occasions, measurements of pH, conductivity, dissolved oxygen and temperature were made in the separate bays. Temperature was recorded using a standard 0 - 50°C thermometer while the other parameters were measured using an environmental, multi-probe system (Walden Precision Instruments Ltd.). It was originally intended to carry out these measurements on a regular basis in conjunction with sampling. However, repeated malfunctions of the multi-probe meant that, on several occasions, it was not possible to obtain data. A continuous temperature recorder was installed in a boathouse at one end of the sampled shore and this recorded the water temperature in the littoral zone (see chapter 1).

Substratum samples, for particle size analysis, were taken from each bay in March 1983.

4.2.3 Methods of data analysis

A. Leech data

For the purposes of analysis, the rarer leeches recorded in this study (Theromyzon tessulatum O.F. Müller, Glossiphonia heteroclita L., Hemiclepsis marginata O.F. Müller and Haemopis sanguisuga L.), are included in the 'other groups' section.

Density and biomass

Normality in the data for density and biomass could not be assumed for all samples and the number of replicates for separate control and enclosed sites was, in all cases, less than thirty. Therefore, mean density and biomass were calculated as geometric means with derived confidence limits ($\mathrm{Log}_{10}(x + 1)$), according to the method described in Elliott (1977a). These calculations were made for separate stone and substratum data from control and enclosed sites, and the estimated geometric means for combined stone and substratum data were calculated using the substratum:stone ratio. Comparisons between control and enclosed sites were made using the Mann-Whitney U test (Campbell, 1974).

Mean weight

In most estimates of mean weight, the sample size was in excess of thirty and, therefore, normality was assumed and the arithmetic mean weight with 95% confidence limits was calculated according to the method described in Elliott (1977a). In the few cases where the sample size was less than thirty, the arithmetic means with derived confidence limits ($\mathrm{Log}_{10}(X)$) were expressed (again, see

Elliott 1977a). Where homogeneity of variances was not disproved by an F test, comparisons between the two sample fractions and between control and enclosed sites were made using t test; otherwise the d test, described in Bailey (1959) was employed.

Growth and mortality

In those periods where the growth rate or mortality rate was thought to be constant, the following regression equation was applied to the data, and its fit tested using a t test:-

$$\mathrm{Ln}\ Y = RX + \mathrm{Ln}\ Q$$

where X is time, measured in days, and Y either geometric mean density or arithmetic mean weight. Comparisons between the slopes of the regression equations (R) were made using an analysis of covariance (Snedecor & Cochran, 1980).

Production

The methods available for estimating secondary production are reviewed in Edmonson & Winberg (1971). In previous studies on leech populations Mann (1971) used the Allen curve method (Allen, 1951) to estimate the production of E. octoculata, G. complanata and H.stagnalis, while Elliott (1973a) used both the Allen curve and the instantaneous growth-rate method of Ricker (1946) for E. octoculata. Learner & Potter (1974) and Murphy & Learner (1982) working with H. stagnalis and E. octoculata used the instantaneous growth-rate method, while Dall (1976b) used the product of the instantaneous growth-rate and the mean number of leeches present during the sampling interval to calculate production for E. octoculata and E. testacea. In the present study, both the Allen curve and instantaneous growth-rate methods were employed.

In the Allen curve method, production is estimated as the area under a weight/survivorship curve in which mean individual weight and the numbers in the cohort are the respective x and y axes. The method has the advantage of allowing irregularities caused by sampling error to be smoothed out in calculating production. In addition, if estimates of the number of young entering a population from cocoon counts or fecundity data are available, then by including this on the graph, the production that occurs before the young are picked up by sampling can be estimated. However, if there is much irregularity in the weight/survivorship data, then it may be difficult to decide upon the correct shape of the curve to be fitted.

The instantaneous growth-rate method uses the formula

$$p = \bar{B} . G$$

where $\bar{B}$ is the mean population biomass during the sampling period and G is the instantaneous growth-rate, defined as

$$G = \mathrm{Ln}\ \bar{W}_{t1} - \mathrm{Ln}\ \bar{W}_{t0}$$

where $\bar{W}_{t0}$ and $\bar{W}_{t1}$ are the mean individual weights at the beginning and end of the sampling interval. The method is adapted for use with species that reproduce with cohorts rather than continuously and makes the assumption that the mortality rate is constant between sampling intervals.

For Allen curve estimates, arithmetic mean weight was plotted against geometric mean density, while for the instantaneous growth-rate method, arithmetic mean weight and geometric mean biomass were used. These were thought to be the best estimates of the parameters for this study. In other studies, various combinations of arithmetic and geometric means have been employed and will naturally affect the estimates produced.

Various adaptations of the basic methods described above had to be employed, and these are described in the relevant results sections for each species.

Turnover rate, defined as

$$TR = \frac{P}{\bar{B}}$$

where p = production and $\bar{B}$ is the mean biomass during the interval investigated, was also calculated. The ratio expresses the periodic addition to existing biomass, and has gained popularity in recent publications. Waters (1969) suggested that the ratio, when applied to the whole life of a cohort would remain constant in a given situation, and that the ratio usually lies between 2.5 - 5.

Other groups

For species or groups other than the common leeches, geometric mean density with $Log_{10}(X + 1)$ confidence limits and geometric mean biomass with $Log_{10}(X + 1)$ confidence limits were calculated for separate stone and substrate sample data and total geometric means calculated using the substratum:stone ratio. Density and biomass in control and enclosed sites were compared by Mann-Whitney U tests.

Unless otherwise stated, a 5% probability level was used in all statistical tests. Where given, variation around the mean was always expressed as the 95% confidence interval.

Figure 4.1. The basic design of the Crose Mere enclosures.

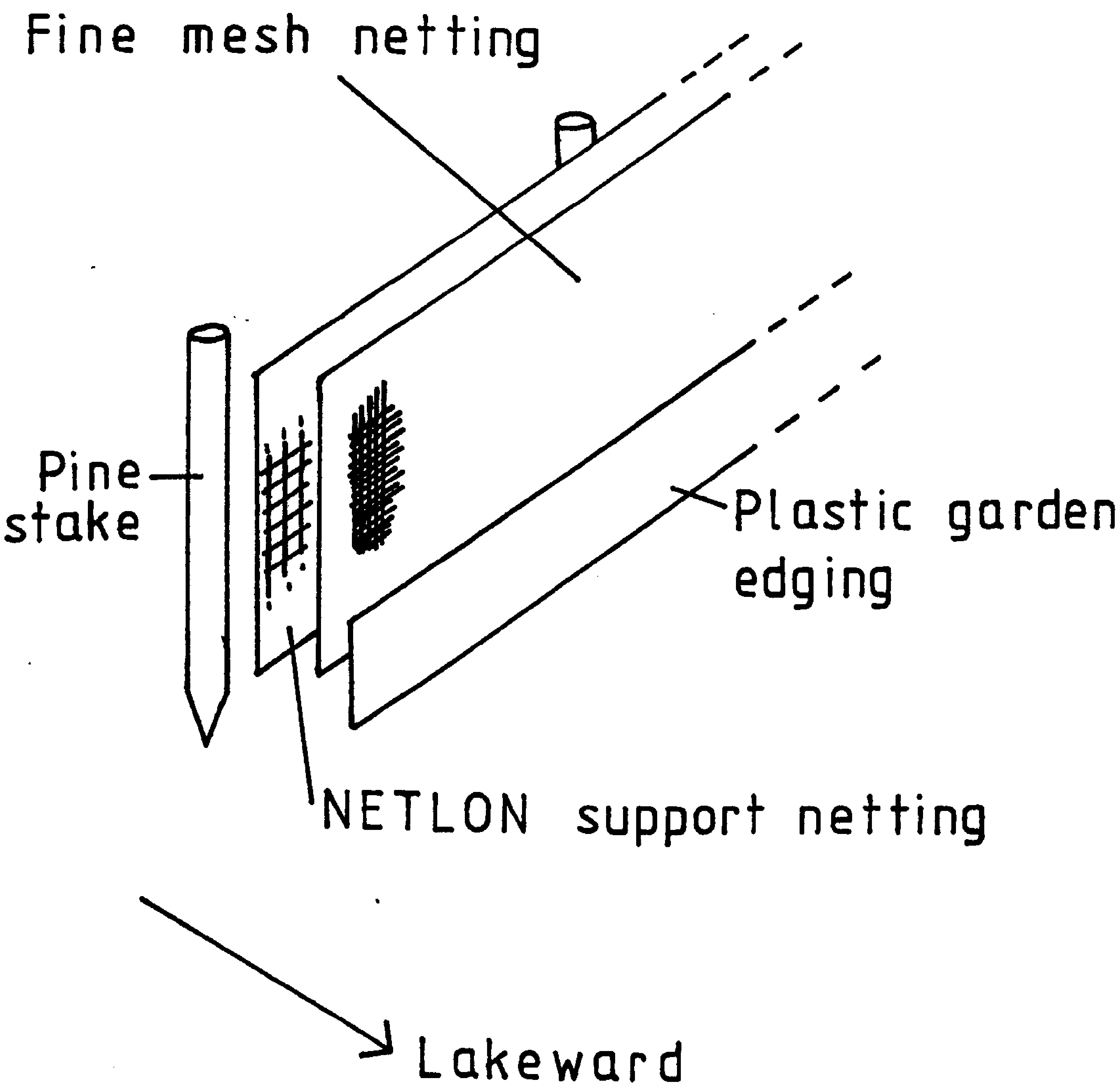


Figure 4.2. An experimental enclosure in position in Crose Mere

Figure 4.3. An experimental enclosure in position in Crose Mere

4.3 Results

4.3.1 Erpobdella octoculata

During the course of this experiment a total of 6147 leeches was collected from the lake. From weight-frequency histograms it was possible to split them into three distinct cohorts. The 1980/81 cohort, present at the time sampling commenced in April 1981, the 1981/82 cohort, the offspring of the 1980/81 generation and the 1982/83 cohort, the offspring of the 1981/82 cohort.

4.3.1.1 Density

The data showing geometric mean densities with 95% confidence limits for separate stone and substratum samples from control and enclosed sites are illustrated in figures 4.4 and 4.5. In all samples the majority of the leech population was to be found in the substratum and, within each cohort followed, the proportion on the stones was at a minimum from after hatching to reach a maximum during the breeding season from May to July.

For the 1980/81 cohort, the proportion of leeches on the stones was 1.2% and 2.5% for control and enclosed sites respectively in April 1981. In control sites, this increased steadily through May and June to reach a maximum of 16.8% in July. In enclosed sites, no rise occurred until July 1981, when a maximum of 40.5% was reached. In control sites, the density in the gravel decreased during the period April 1981 to July 1981 while it rose on the stones. In enclosed sites, densities fluctuated, but showed a decrease in the substratum and rise on the stones between June and July 1981.

For the 1981/82 cohort, the proportion on the stones was 1.2% and 1.9% for control and enclosed sites respectively in September 1981. In May 1982, the proportions were 3.4% and 4.9% respectively, and in August 1982 maximum values of 11.1% and 20.0% were reached. The young leeches first appeared in July 1981, both on stones and in the substratum, and their numbers increased to a maximum on the stones in October 1981, and to a maximum in the substratum in September 1981 in control sites and October 1981 in enclosed sites. Between May and June 1982 the density decreased in the substratum and increased on the stones in control sites, but in enclosed sites only a decrease in the substratum occurred.

For the 1982/83 cohort, 6.2% of the leeches were on the stones in control sites and 2.7% in enclosed sites in September 1982, and these proportions decreased to 2.7% and 1.2% respectively by the last sample in March 1983. The young leeches first appeared in July 1982 in both stone and substratum samples, and maximum densities occurred in September 1982 in both samples from both control and enclosed sites.

The data comparing total geometric mean densities, stone sample densities with 95% confidence limits and substratum sample mean densities with 95% confidence limits for control and enclosed sites are given in figures 4.6, 4.7 and 4.8 The results of Mann-Whitney U tests, comparing densities in control and enclosed sites are given in table 4.1.

For the 1980/81 cohort, overall densities decreased between April and May 1981 in both control and enclosed sites, coinciding with the lowering of the lake level mentioned earlier. The mean densities then fluctuated until August 1981 when the entire generation died out. No significant differences between control and enclosed sites occurred until August 1981, when there were significantly more leeches on the stones in control sites. The densities in the substratum did not differ significantly.

Significant differences in density between control and enclosed sites occurred on the stones in August and September 1982, when the density was higher in control sites, and in the substratum in March 1983 when the densities were higher in enclosed sites.

4.3.1.2 Biomass

The data showing the geometric mean biomass with 95% confidence limits for separate stone and substratum samples from control and enclosed sites are presented in figures 4.9 and 4.10. In common with the density data, the highest proportion of the biomass was always in the substratum.

In the 1980/81 cohort, the proportion of the biomass on stones in control sites rose from 0.8% in April 1981 to a maximum of 26% in July 1981, while in enclosed sites the proportions were 1.7% and 47.9% respectively. In both control and enclosed sites biomass increased between May and June 1981 on both stones and in the substratum, and continued to increase in the substratum in August.

In the 1981/82 cohort, the proportion of the biomass on stones in control sites was 1.4% in September 1981, 3.8% in May 1982 and reached a maximum of 22.7% in June 1982, while the proportions in control sites in the corresponding months were 3.4%, 4.8% and 6.2% respectively.

In the 1982/83 cohort, the biomass on stone samples in control sites was 9.1% in September 1982 and had decreased to 1.2% by the last sample in March 1983, while in enclosed sites the respective proportions were 2.0% and 0.2%.

The data comparing total geometric mean biomass, stone sample mean biomass with 95% confidence limits and substratum sample mean biomass with 95% confidence limits for control and enclosed sites are given in figures 4.11, 4.12 and 4.13. The results of Mann-Whitney U tests, comparing biomass in control and enclosed sites are given in table 4.2.

For the 1980/81 cohort, in both control and enclosed sites, overall biomass decreased between April and May 1981 and then rose to a maximum in August 1981 of 11.5 $g.m^{-2}$ and 4.1 $g.m^{-2}$ respectively. Significant differences in biomass between control and enclosed sites occurred in August 1981 in both stone and substratum samples.

For the 1981/82 cohort, overall biomass rose with increasing numbers of young entering the population and reached a peak in September 1981 of 2.8 $g.m^{-2}$ in control sites, and in October 1981 of 4.9 $g.m^{-2}$ in enclosed sites. Biomass then decreased over the winter months before starting to rise again after the sample in April 1982, reaching a peak of 1.5 $g.m^{-2}$ in control sites in June 1982; in enclosed sites a second peak occurred between May and July 1982, but was at a maximum of 0.8 $g.m^{-2}$ in May. Significant differences between control and enclosed sites occurred in September 1981, January 1982 and June 1982 in stone samples. There were no significant differences in the substratum samples.

In the 1982/83 cohort, overall biomass rose with the increasing population size and peak in both control and enclosed sites in September 1982 with values of 0.6 $g.m^{-2}$ and 1.4 $g.m^{-2}$ respectively. Overall biomass then declined until November 1982 but by the last sample in March 1983, another slight rise had occurred in enclosed sites, while in control sites biomass had continued to decline. The final figures for March 1983 were 0.1 $g.m^{-2}$ and 0.8 $g.m^{-2}$ for control and enclosed sites respectively. Significant differences in biomass between control and enclosed sites occurred in August 1982 in the stone samples, and in September 1982, November 1982 and March 1983 in substratum samples.

4.3.1.3 Growth

Figures 4.14 and 4.15 present the size-structure of leeches from separate stone and substratum samples from control and enclosed sites. The size-structure of leeches from combined stone and substratum sample data for control and enclosed sites are presented in figure 4.16. Figures 4.17 and 5.18 present the arithmetic mean individual weights with 95% confidence limits for separate stone and substratum samples from control and enclosed sites. The results of t and d tests, comparing stone sample versus substratum sample mean individual weights for control and enclosed sites are given in table 4.3.

For the 1980/81 cohort in control sites, mean individual weights in stone samples rose from 26.8 mg in April 1981 to a peak of 144.7 mg in June 1981 and then declined until August. In the substratum the mean weight was 22.3 mg in April and rose to a peak of 90.9 mg in August. The mean individual weight on the stones was significantly higher than mean weight in the substratum samples from May 1981 to August 1981. In enclosed sites the mean weight in stone samples was 25.9 mg in April 1981 and reached 131.2 mg in June 1981 before declining. In the substratum mean individual weight increased from 20.2 mg in April 1981 to a peak of 79.5 mg in July 1981 and then declined. The mean individual weights on stones were significantly higher than in the substratum in samples from June to August 1981.

For the 1981/82 cohort in control sites, the mean individual weights in stone samples rose from 4.6 mg in July 1981 to 17.9 mg in April 1982 and then sharply increased to a peak of 175.9 mg in June 1982 before declining. In the substratum,mean individual weights were 2.9 mg in July 1981, 10.1 mg in April 1982 and increased to a peak of 103.8 mg in July 1982 before declining. Significant differences between stone and substratum samples occurred in October 1981, January 1982 and in all samples from May to July 1982. In enclosed sites, mean individual weights on the stones rose from 3.7 mg in July 1981 to 7.0 mg in January 1982 and rose rapidly from April to June 1982 when it reached a maximum of 116.8 mg. In substratum samples,mean weight rose from 2.2 mg in July 1981 to 12.7mg in April 1982, and then increased rapidly to a peak of 84.1 mg in July 1982. The mean individual weight on stones was significantly higher in September 1981 and in samples from April to July 1982.

For the 1982/83 cohort in control sites, mean individual weights on the stones rose from 5.3 mg in July 1982 to 17.9 mg in March 1983, and in the substratum samples from 2.8 to 30.8 mg for the same months. Mean weights on the stones were significantly higher than in the substratum in August and November 1982. In enclosed sites, mean individual weight rose from 4.7 mg to 38.8 mg on stones and from 3.8 mg to 32.1 mg in the substratum between July 1982 and March 1983, and significant differences between stone and substratum samples occurred only in November 1982.

The data comparing arithmetic mean individual weights from combined stone and substratum sample data, stone sample mean weights with 95% confidence limits and substratum sample mean weights with 95% confidence limits for control and enclosed sites are given in figures 4.19, 4.20 and 4.21. The results of t and d tests comparing weights in control and enclosed sites for separate stone and substratum sample data are given in table 4.4, and regression equations describing the growth of the cohorts are given in table 4.5.

For the 1980/81 cohort, mean individual weights for leeches from combined stone and substratum data rose from 22.3 mg in April 1981 to a peak of 94.3 mg in July 1981 in control sites, and from 20.3 mg to 94.1 mg in enclosed sites. The mean weight was significantly higher in oontrol sites than in enclosed sites in July 1981 in stone samples and August 1981 in substratum samples.

For the 1981/82 cohort, mean individual weight rose from 2.9 mg in July 1981 through 10.1 mg in April 1982, and reached a maximum of 105.9 mg in July 1982 in control sites. In enclosed sites the mean individual weight was 2.2 mg in July 1981, 9.6 mg in April 1982 and at a maximum of 85.1 mg in July 1982. The mean weights were significantly higher in control sites than in enclosed sites in the stone samples of October 1981 and June and July 1982. The reverse was true in September 1981 and April 1982. The only significant difference in substratum samples occurred in January 1982 when the mean weight was higher in enclosed sites.

In the 1982/83 cohort, mean individual weight increased from 2.8 mg in July 1982 to 30.4 mg in March 1983 in control sites and from 3.8 mg to 32.3 mg in enclosed sites. The mean weight was significantly higher in enclosed sites than in control sites in the substratum sample of November 1982. There were no other significant differences.

The results from attempts to fit the equation $\mathrm{Ln}\ Y = RX + \mathrm{Ln}\ Q$ to the growth rates in different periods of the life-cycle (see table 4.5) indicated that the growth rate was relatively high between the time of hatching to October of the same year, was lower over the winter months and then rose again from April until the leeches bred. Where comparisons were possible this pattern was repeated in each of the generations followed. However, although the correlation between weight and time was always high, a significant fit of the data to the regression equation was only achieved for the 1980/81 cohort from enclosed sites in the period April to July 1981.

When the same regression equation was fitted to the data for the 1981/82 cohort covering the period from July 1981 to July 1982, a significant fit was achieved for both control and enclosed sites, suggesting that the growth-rate could be regarded as constant from birth to breeding.

4.3.1.4 Reproduction

The data showing the size structure of breeding and non-breeding leech populations from separate stone and substratum samples for control and enclosed sites, and the size structure of breeding and non-breeding leeches from combined stone and substratum sample data in control and enclosed sites were given in figures 4.14, 4.15 and 4.16.

In control sites breeding in the 1980/81 cohort started in May 1981 when 27.5% of leeches in stone samples and 4.4% in substratum samples had a clitellum. In June these figures rose to 89.3% and 43.0% respectively, and further increased to 98.9% and 100% in July 1981. Breeding ended after the August sample and all the leeches in the cohort died out. Breeding in the 1981/82 generation started in June 1982 when 86.5% of the leeches in stone samples and 61.8% in substratum samples had a clitellum. In July 1982 these figures had increased to 100% and 94.1% respectively. No leeches bore a clitellum in August 1982 and the cohort had died out before the sample in September 1981.

In enclosed sites, breeding of the 1980/81 cohort started in May 1981 when 15.2% of leeches in stone samples had a clitellum but no breeding animals were found in substratum samples. In June 1981, 88.6% of leeches in stone samples and 43.0% in substratum samples had a clitellum and these figures increased to 100% and 91.3% respectively in August 1981. Breeding in the 1981/82 cohort started in June 1982, when 56.5% of leeches in stone samples and 61.9% in substratum samples had a clitellum. These figures increased to 100% and 81.8% respectively in July, but by August 1982 only three leeches of this cohort were present in samples and none were present in the September 1981 sample.

The overall pattern of breeding was very similar in control and enclosed sites. In May 1981, 5% of leeches in control sites and 1.9% in enclosed sites had a clitellum. The figures for June 1981 were 46.1% and 39.1%,for July 99.9% and 61.1% and for August 96.2% and 9.14% respectively. In the following year 63.6% and 61.6% of leeches were breeding in June, 94.5% and 81.8% were breeding in July and 100% and 100% were breeding in August in control and enclosed sites respectively.

The data for cocoon production in control and enclosed sites are given in table 4.6. The results of Mann-Whitney U tests comparing the densities of cocoons in control and enclosed sites for separate stone and substratum samples are given in table 4.7.

In July 1982 a sample of sixty cocoons containing eggs and sixty cocoons containing young were examined from each of control and enclosed sites. The mean number of eggs per cocoon was 5.8 in control sites and 5.9 in enclosed sites and there was no significant difference between these values ($t = 0.217$ with 118 d.f.). The mean number of young per cocoon was 5.4 in control sites and 5.5 in enclosed sites and, again, the difference was not significant ($t = 0.326$ with 118 d.f.).

In addition to these counts, thirty five cocoons from each sampling site were examined and the numbers that were sterile or damaged recorded. In control and enclosed sites 10.0% and 9.3% respectively of the cocoons were found to be sterile and, in addition, a further 12.1% and 12.8% respectively were found to be broken. This gave a total of 22.1% of cocoons which were not viable in both control and enclosed sites.

In the summer of 1981, the maximum numbers of cocoons, 1715.8 m^{-2}, found in control sites was nearly four times the number, 444.9 m^{-2}, in enclosed sites. From the maximum number of leeches found breeding in this period, the estimated number of cocoons produced by each leech was 12.3 in control sites and 7.3 in enclosed sites. Assuming 22.1%(based on the 1982 data above) of the cocoons were not viable then the number of young estimated to have entered the population in the summer of 1981 was 7177.5m^{-2} in the control and 1899.4m^{-2} in the enclosed sites. In the summer of 1982, the maximum number of cocoons was 393.0 m^{-2} in control sites and 363.3 m^{-2} in enclosed sites. The estimated number of cocoons produced by each breeding leech was 12.4 in the control and 14.3 in the enclosed sites, and an estimate 1643.8 young m^{-2} in control sites and 1542 young m^{-2} in enclosed sites entered the population during the summer.

The number of cocoons found in control sites was significantly higher than in enclosed sites in the stone samples of June, July and August 1981 and in August 1982. The same was true in the substratum samples from September 1981.

4.3.1.5 Mortality

The data describing mortality are given in table 4.8 and the regression equations covering the periods when density declined were given in section 4.3.1.1.

In 1981, 97.2% of the young produced in the summer in control sites had died by October, while 86.3% had died in enclosed sites. By July 1982, 99.8% and 99.1% of the populations had died respectively. The regression equations gave a significant fit to the data and suggested that the mortality rate was constant between October 1981 and July 1982. An analysis of covariance suggested that the mortality rates were not significantly different between control and enclosed sites ($F = 2.520$ with 1,8 d.f.) during this period.

In 1982, 98.2% and 96.9% in control and enclosed sites respectively of the new cohort had died by October and this mortality had increased to 99.4% and 98.0% by the last sample in March 1983. The regression equations (see section 4.3.1.1) did not give a significant fit to the data for this cohort.

4.3.1.6 Production

Data illustrating the rate of biomass production, and calculated using the instantaneous growth-rate method, for leeches sampled between April 1981 and March 1983 are presented in figure 4.22.

Using the instantaneous growth-rate method of calculating production, the annual production of the 1981/82 cohort calculated for the period 30th July 1981 to 18th August 1982, and ignoring the negative production of post-reproductive leeches in August 1982, was 2.7 $g.m^{-2}$ in control and 3.1 $g.m^{-2}$ in enclosed sites. The mean biomass over the same period was 1.1 $g.m^{-2}$ in control and 1.6 $g.m^{-2}$ in enclosed sites, giving turnover rates ($\frac{P}{B}$ ratio) of 2.5 and 2.0 respectively. The rate of biomass production was high during the period when new young were being added to the population, lower over the winter months when negative production occurred in control sites, and higher again during the period of pre-reproductive growth.

The data presented above do not include any estimates of the production contributed by the large number of young which, on the basis of cocoon data, were thought to have entered the population but were never recorded in samples. In the summer of 1981, over 7000 young . m^{-2} in control sites and nearly 2000 young . m^{-2} in enclosed sites were estimated to have entered the population, but the maximum numbers recorded in samples were 203.7 m^{-2} and 260.9 m^{-2} respectively. If these 6800 and 1750 missing young had grown just 1 mg before dying then a production of approximately 6.8 $g.m^{-2}$ and 1.8 $g.m^{-2}$ would have occurred and this would form a very high proportion of the total production for the cohort. However, because the animals were not recorded in samples, it is not known whether they grew before death or simply died without putting on weight. For the above reasons, two sets of production estimates are therefore presented. The data presented above are based on calculations on the leeches actually recorded in samples. Estimates based on calculations incorporating the missing young are given below. The true value of production for the cohorts will lie somewhere between these two values.

The missing young were incorporated into the estimates as follows. The number of young that should have hatched by the July sample was calculated from the number of cocoons present in June 1981. Hatching time at the temperature of the lake during this period was estimated at approximately 28 days (i.e. the sampling interval), from the data presented in Young & Ironmonger (1982b). This procedure was repeated to estimate the number of young that should have hatched by the times that the August and September samples were taken. Production and mean biomass were then calculated as if the young were present in samples and had entered the population with a mean weight of 0.3 mg (from the data presented in Ironmonger, 1981).

On this basis, the production for the 1981/82 cohort was estimated at 10.4 $g.m^{-2}$ in control sites and 8.2 $g.m^{-2}$ in enclosed sites. The mean biomass over the life-span of the cohort was 1.3 $g.m^{-2}$ in control and 1.6 $g.m^{-2}$ in enclosed sites, giving turnover rates of 8.0 and 5.1 respectively.

In using the Allen curve method of estimating production, a similar problem occurs. By including the estimated number of young produced on the graph, the assumption is also made that some growth occurs in the young before they die, though the amount of growth will depend on the shape of the curve used. Therefore, two estimates are again presented: the production estimated from the area under the curve not including the young, and from the curve including the young.

The Allen curves for the 1981/82 cohort from separate control and enclosed sites are presented in figures 4.23 and 4.24.

In control sites, production, not including the young, was estimated at 3.6 $g.m^{-2}$ and including the young at 13.6 $g.m^{-2}$. In enclosed sites the figures were 3.5 $g.m^{-2}$ and 5.3 $g.m^{-2}$ respectively. Using the mean annual biomass data presented above, turnover rates of between 3.4 and 10.5 were obtained in control sites for estimates not including young and including young respectively, while in enclosed sites the respective rates were 2.3 and 3.3.

It can be seen from figure 4.22 that, at the times when the separate cohorts do overlap, the 'outgoing' cohort are in a state of very low or even negative production. For this reason the estimates presented are essentially equivalent to annual estimates for the population as a whole.

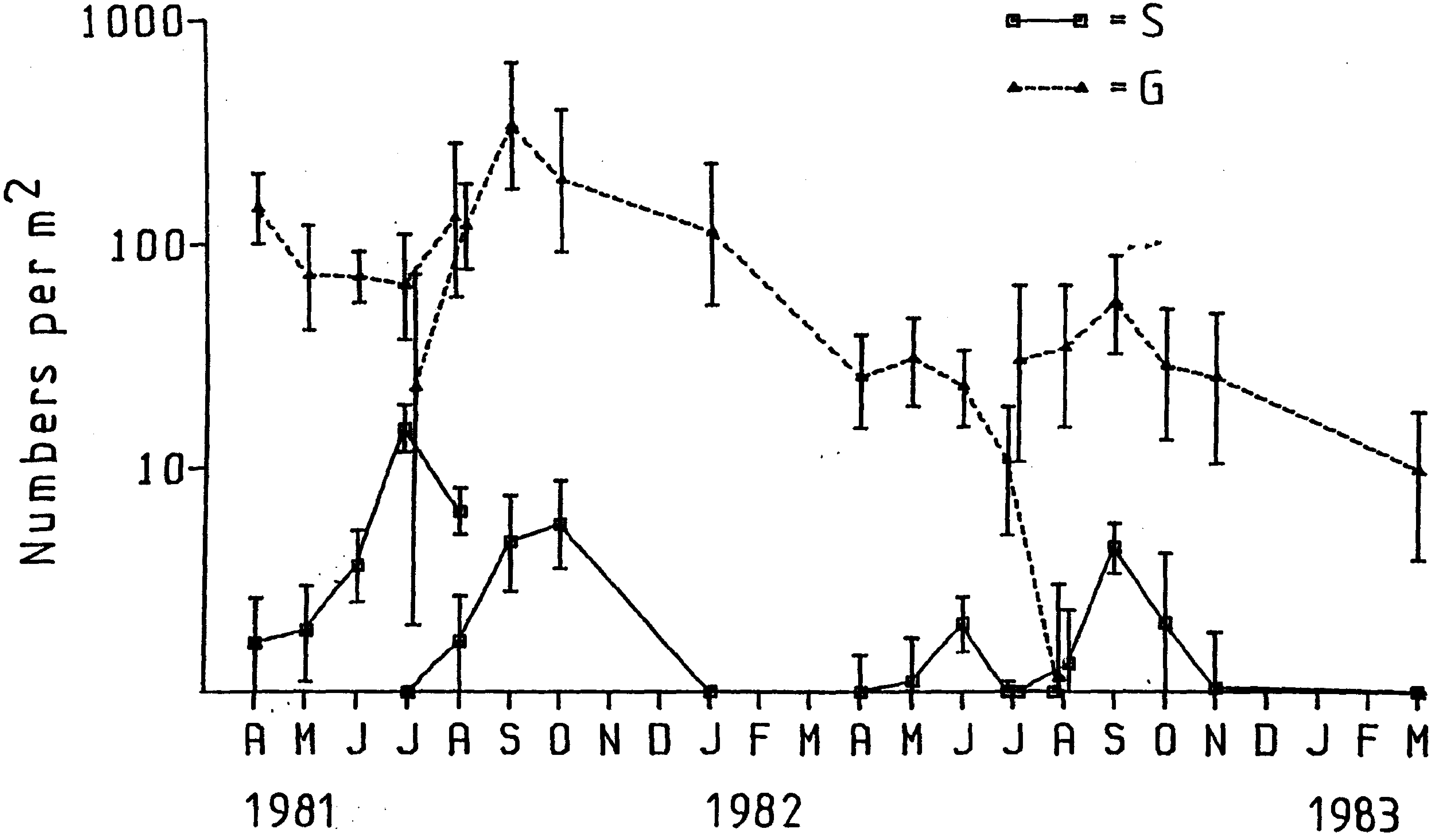


Figure 4.4. *Erpobdella octoculata*. Geometric mean density ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from control sites.

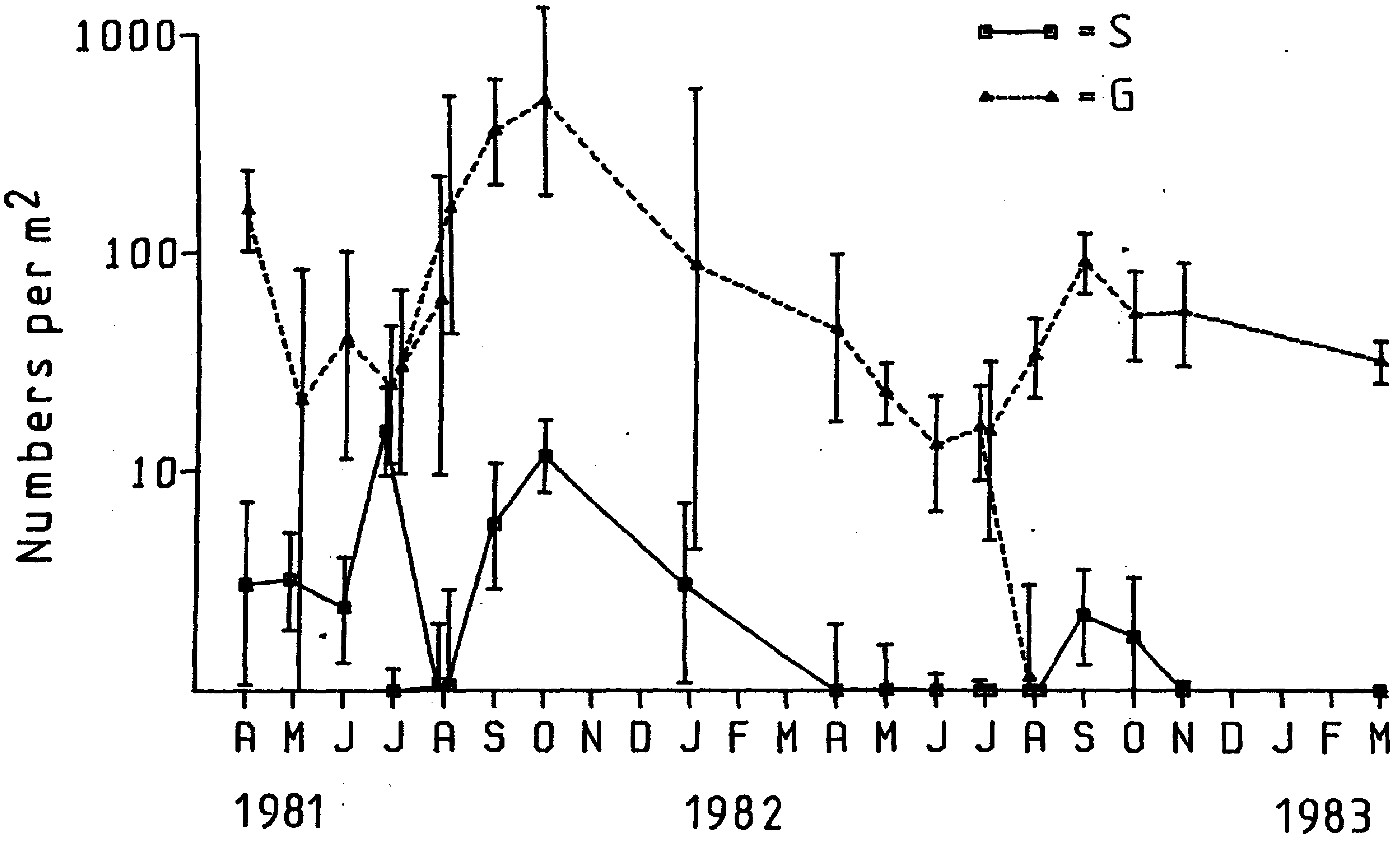


Figure 4.5. Erpobdella octoculata. Geometric mean density ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from enclosed sites.

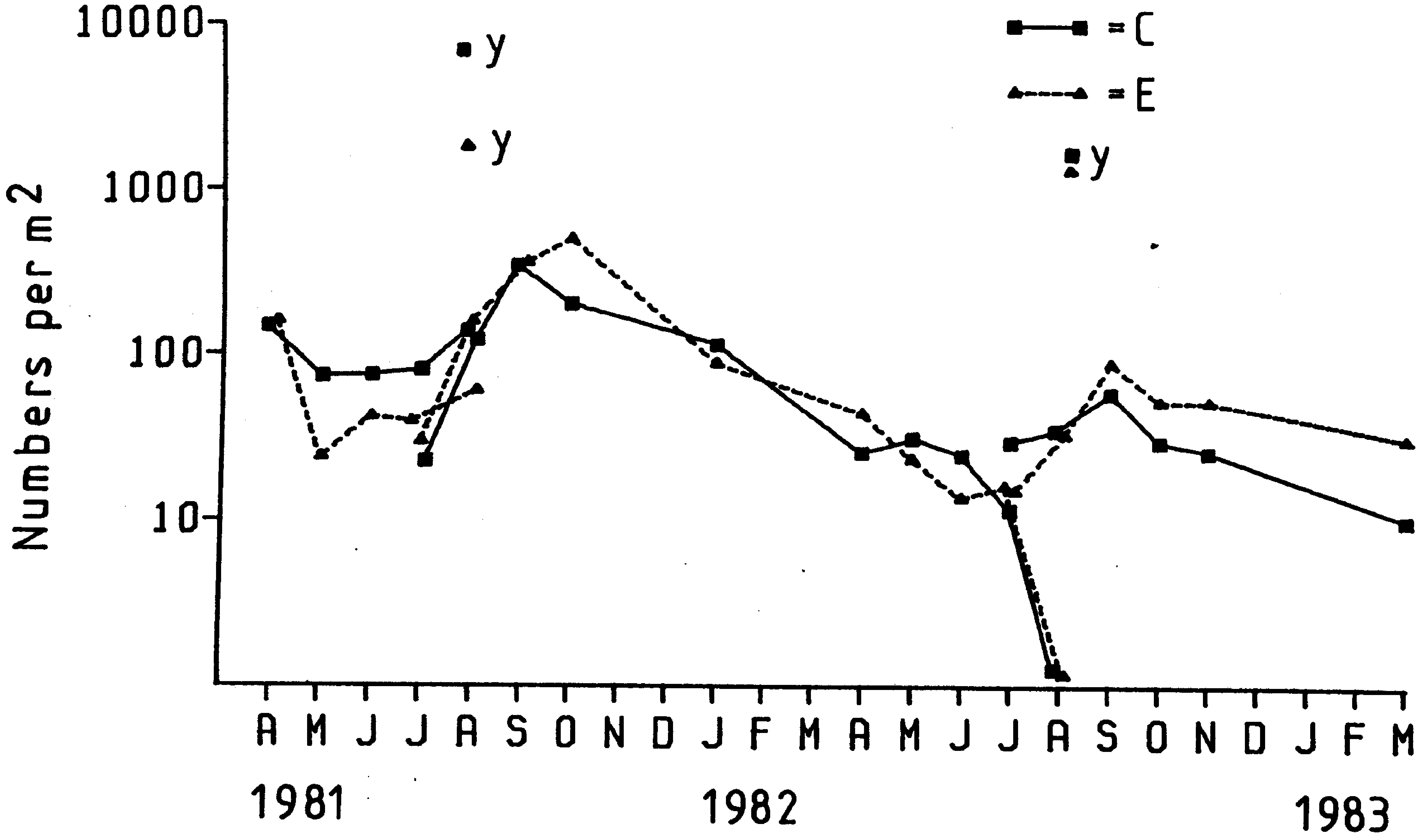


Figure 4.6. Erpobdella octoculata. Total geometric mean density for each cohort from combined stone and substratum sample data and the estimated number of young (y) entering the 1981/82 and 1982/83 cohorts in control (C) and enclosed (E) sites.

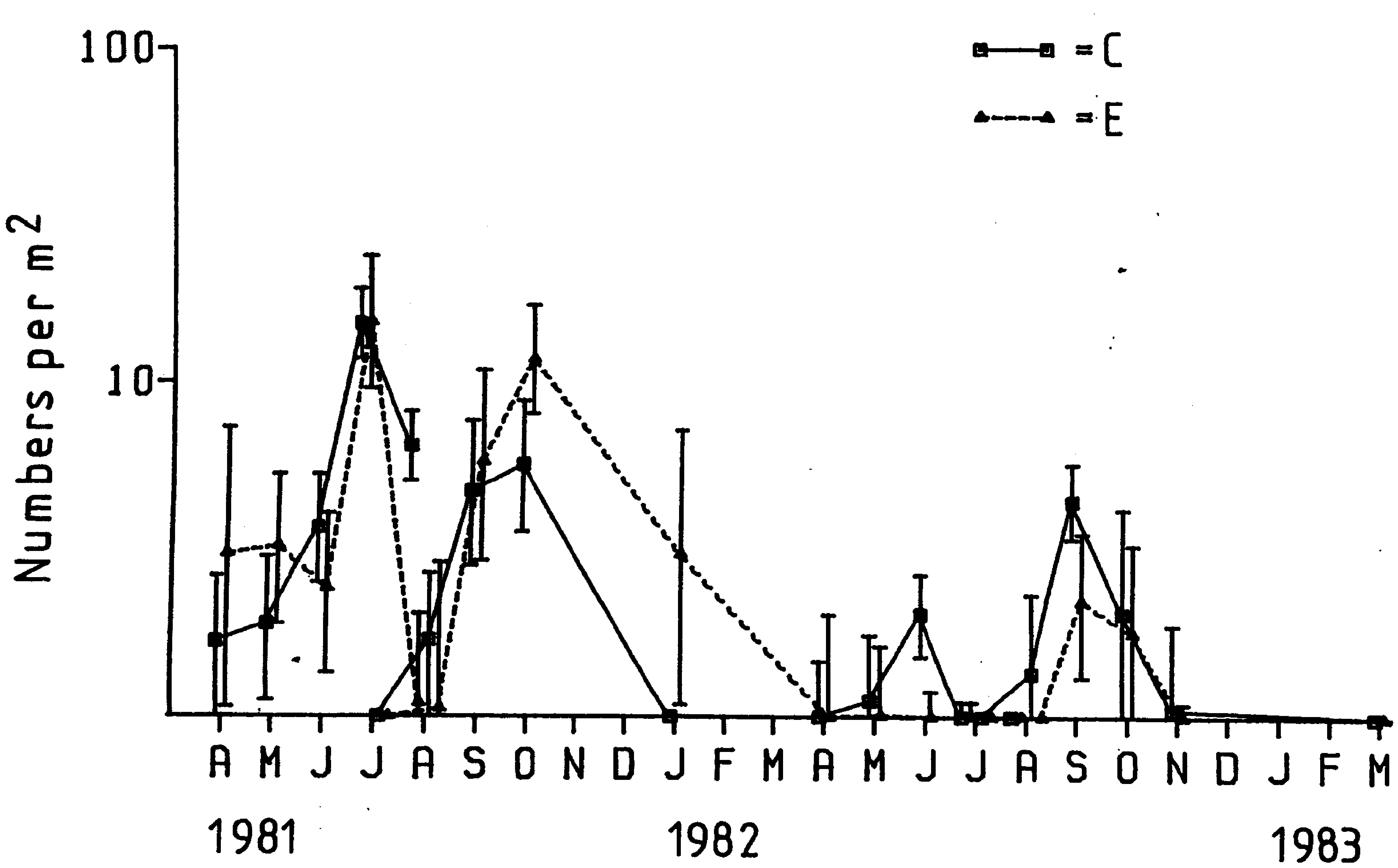


Figure 4.7. *Erpobdella octoculata*. Geometric mean density ± 95% confidence limits for each cohort in stone samples from control (C) and enclosed (E) sites.

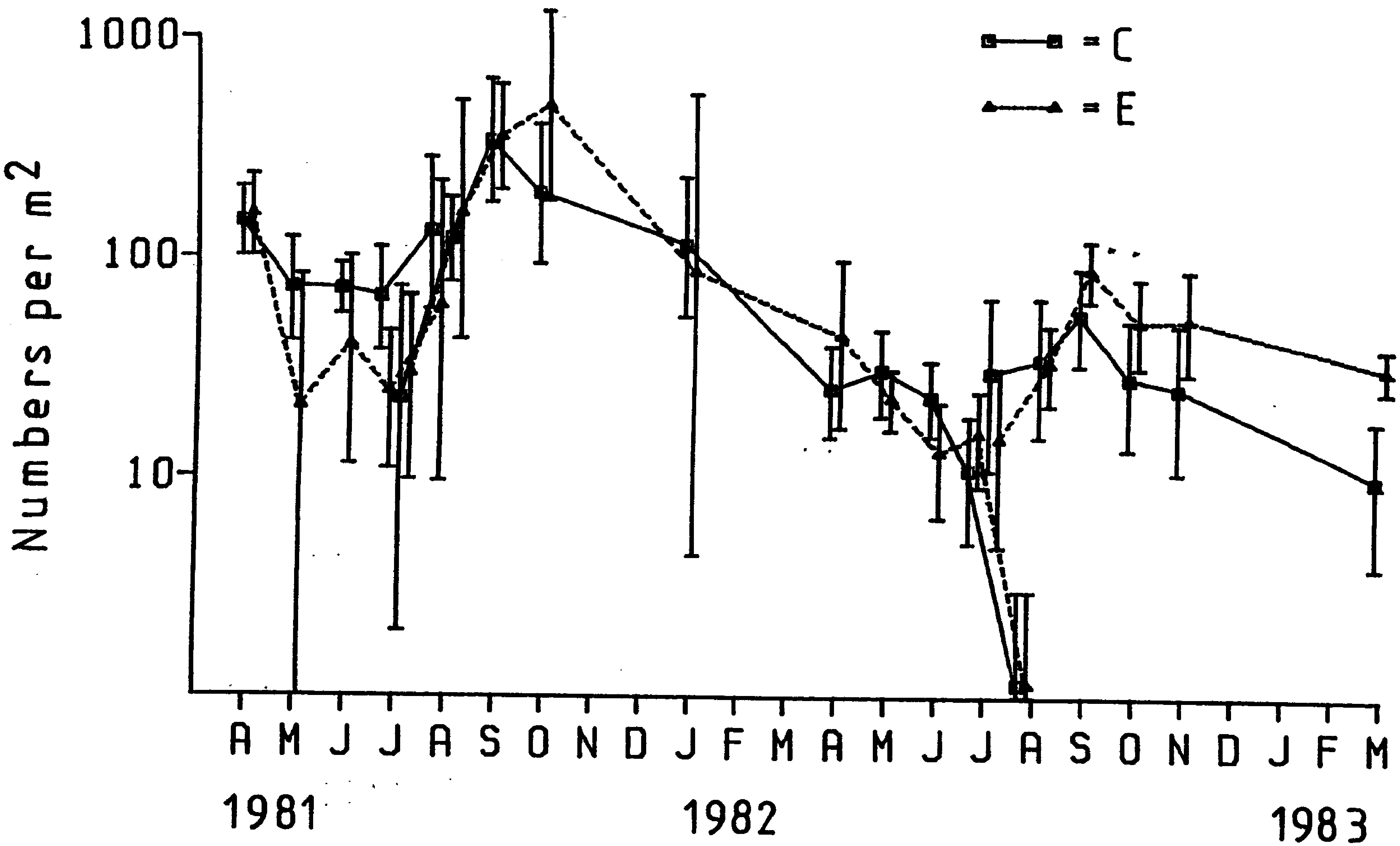


Figure 4.8. Erpobdella octoculata. Geometric mean density $\pm$ 95% confidence limits for each cohort in substratum samples from control (C) and enclosed (E) sites.

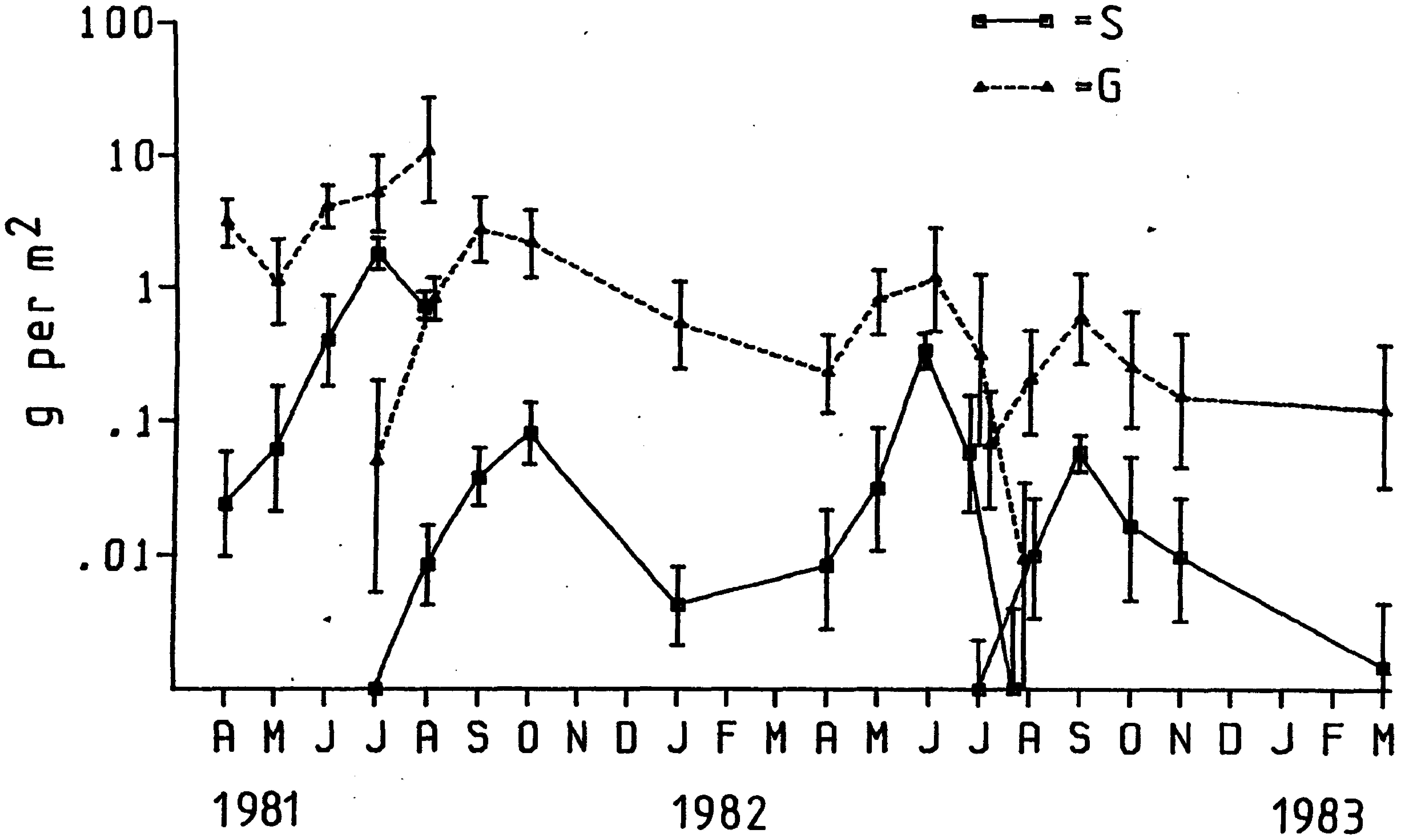


Figure 4.9. Erpobdella octoculata. Geometric mean biomass ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from control sites.

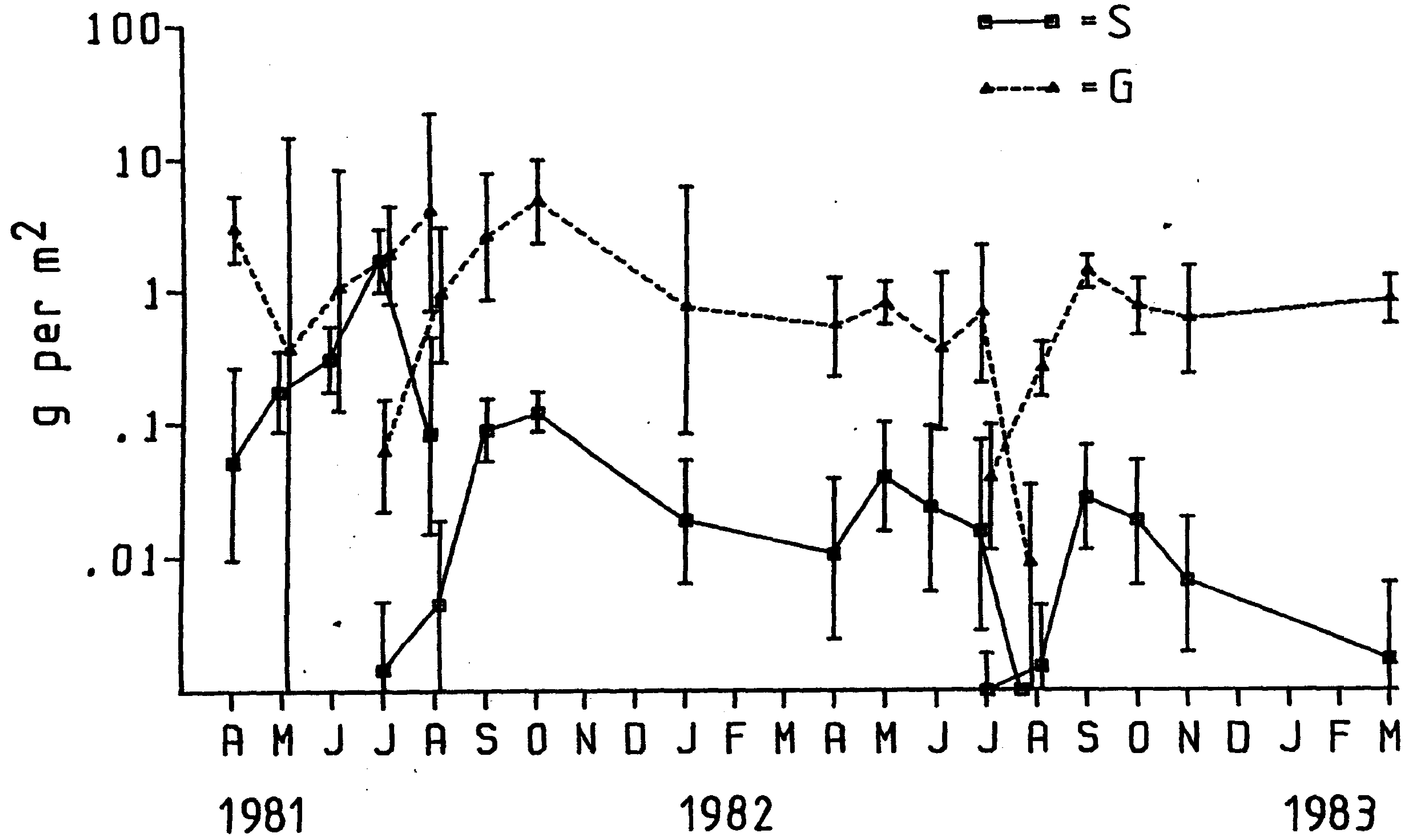


Figure 4.10. Erpobdella octoculata. Geometric mean biomass ± 95% confidence limits for each cohort from separate stone (S) and substratum (G) samples from enclosed sites.

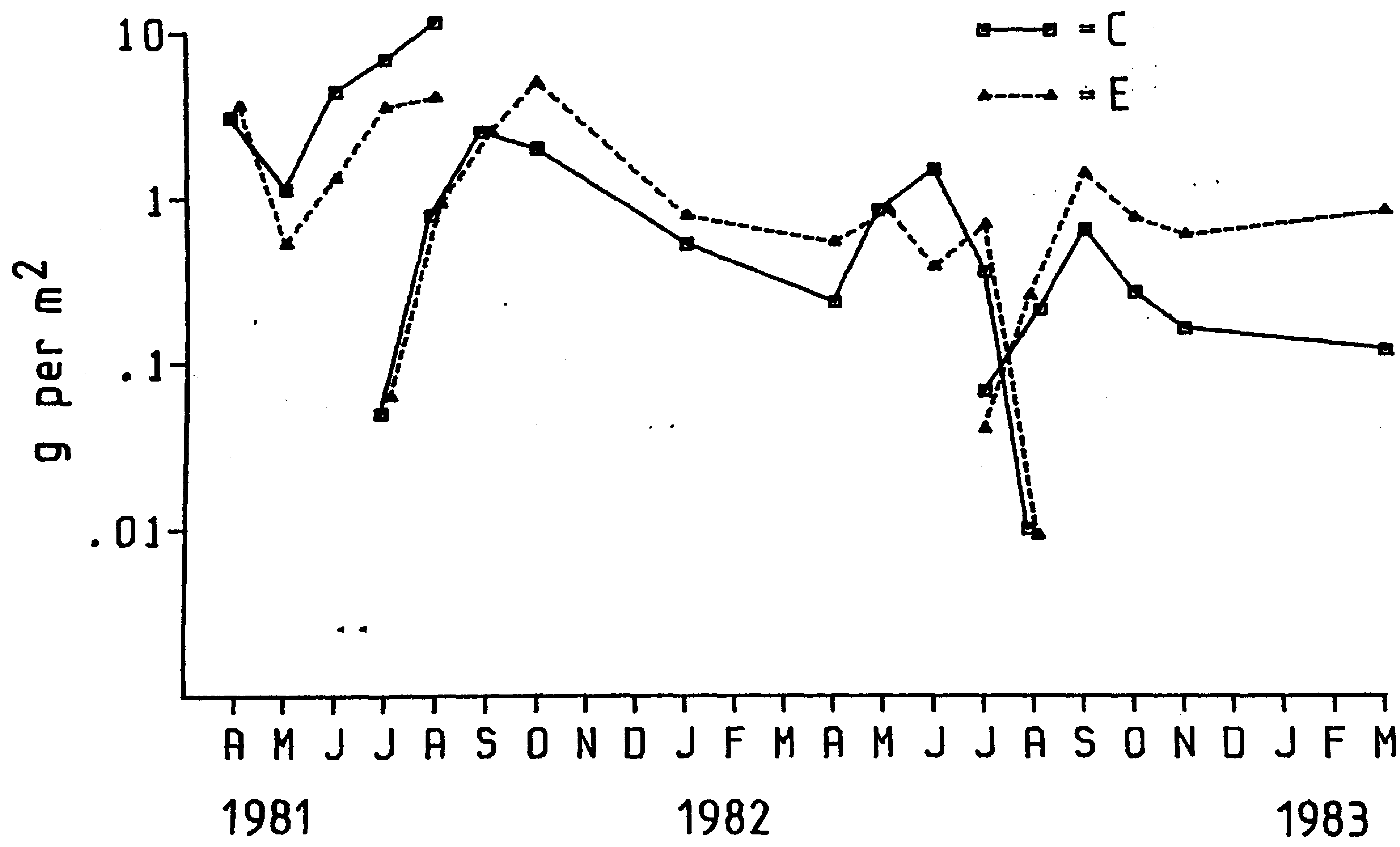


Figure 4.11. Erpobdella octobulata. Total geometric mean biomass for each cohort from combined stone and substratum sample data in control (C) and enclosed (E) sites.

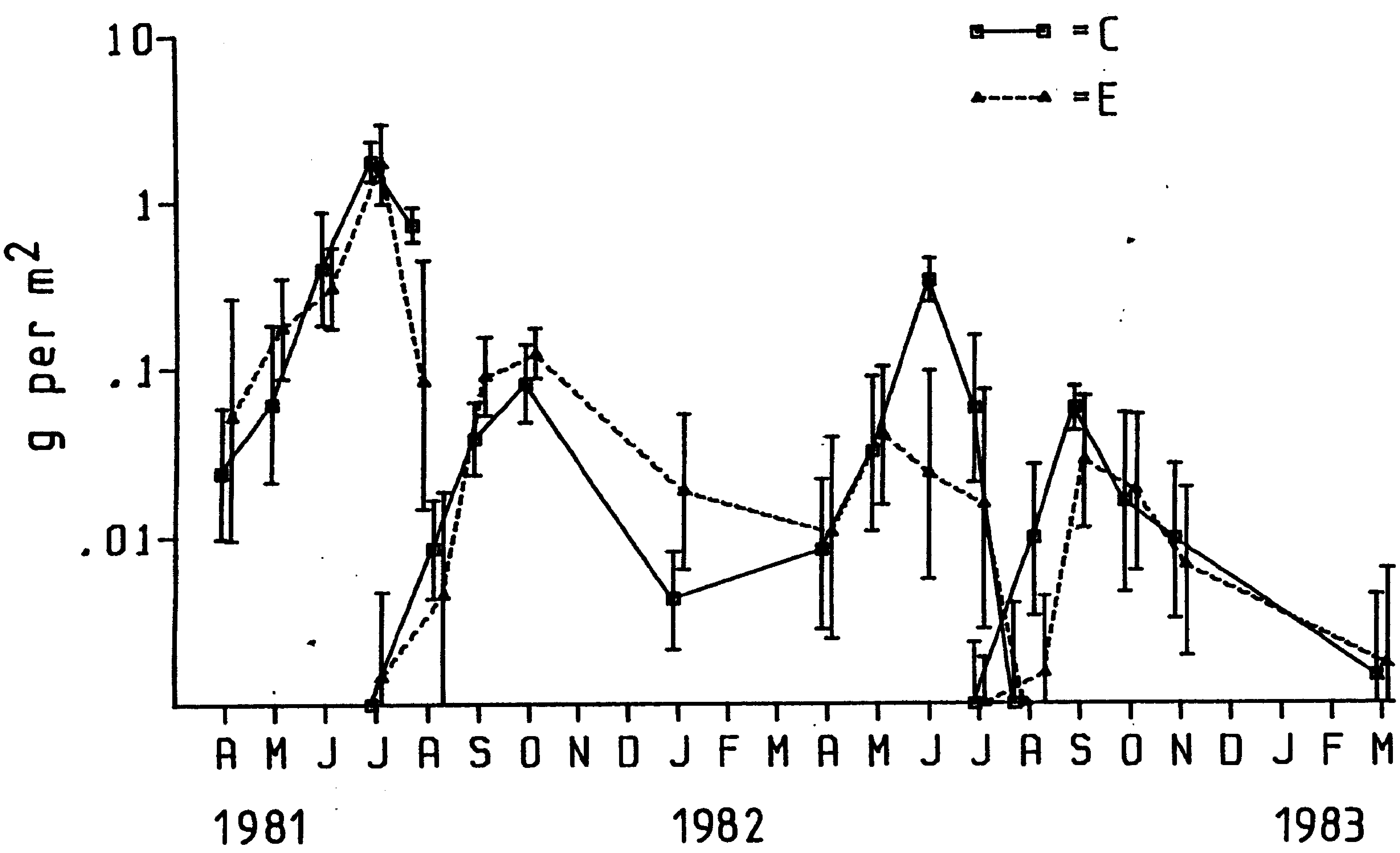


Figure 4.12. Erpobdella octoculata. Geometric mean biomass ± 95% confidence limits for each cohort in stone samples from control (C) and enclosed (Ē) sites.

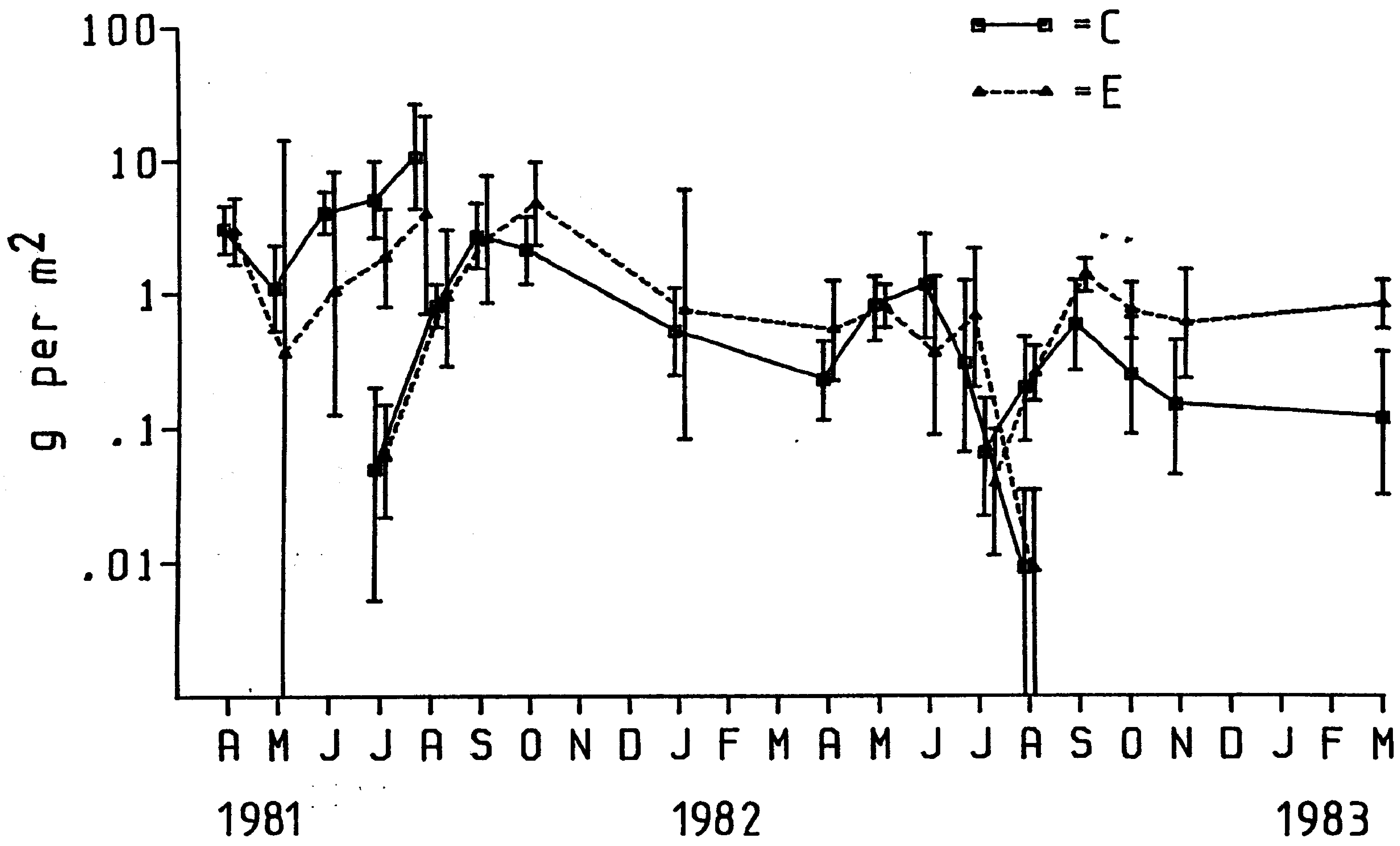
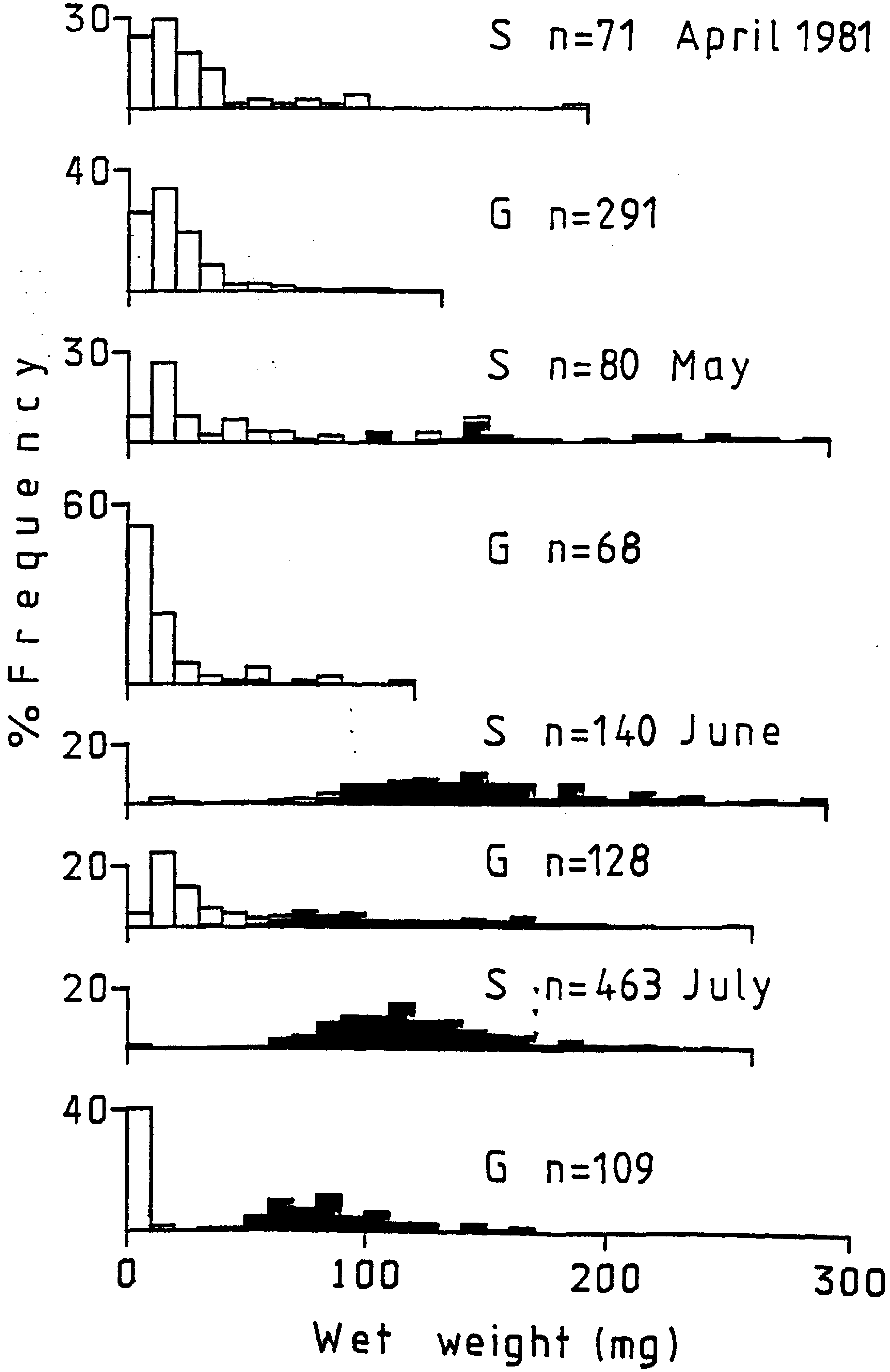


Figure 4.13. Erpobdella octoculata. Geometric mean biomass ± confidence limits for each cohort in substratum samples from control (C) and enclosed (E) sites.

Figure 4.14. Erpobdella octoculata. The size-structure of breeding (shaded) and non-breeding (clear) leech populations from stone (S) and substratum (G) samples in control sites between April 1981 to March 1983.



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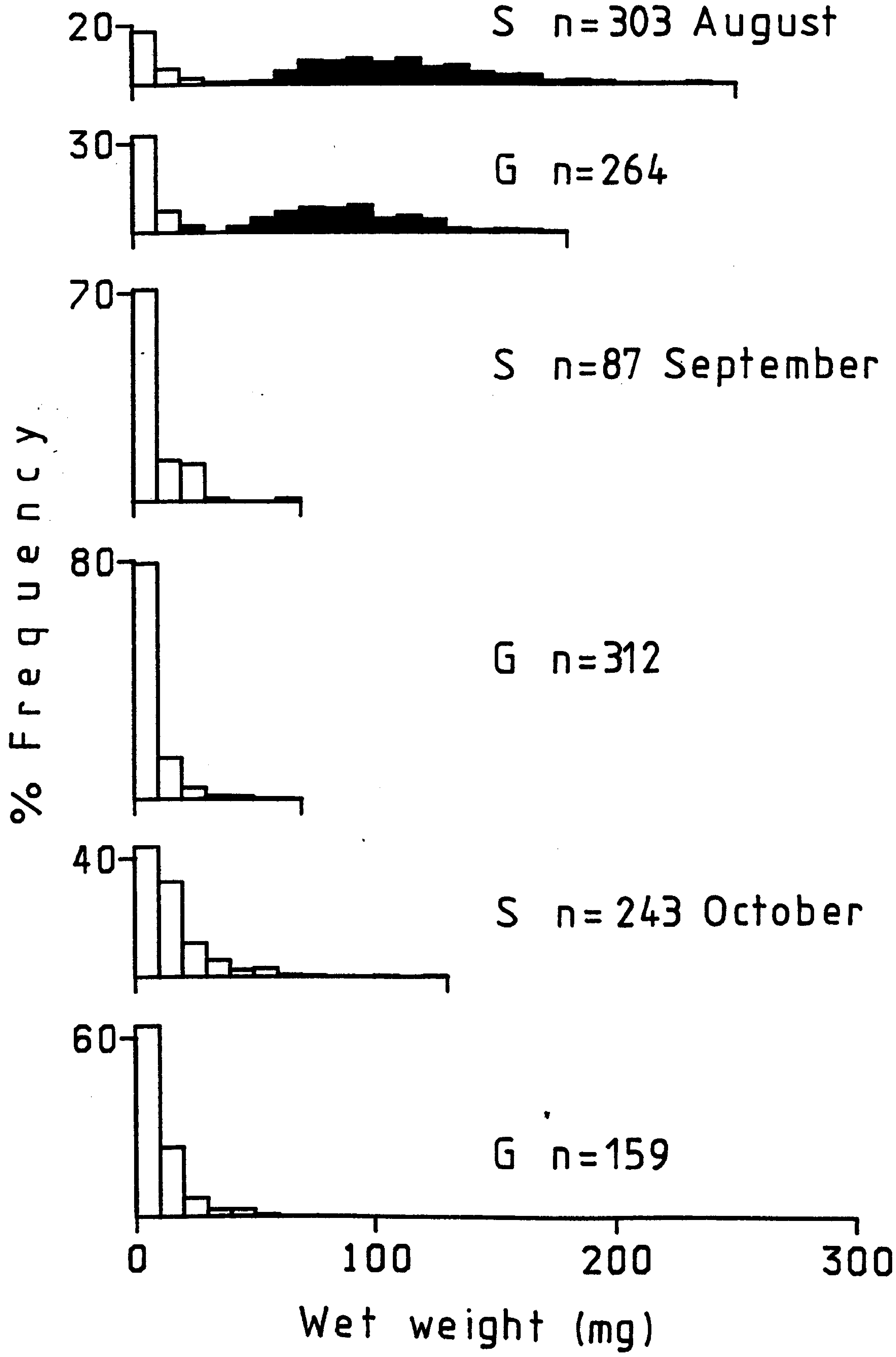
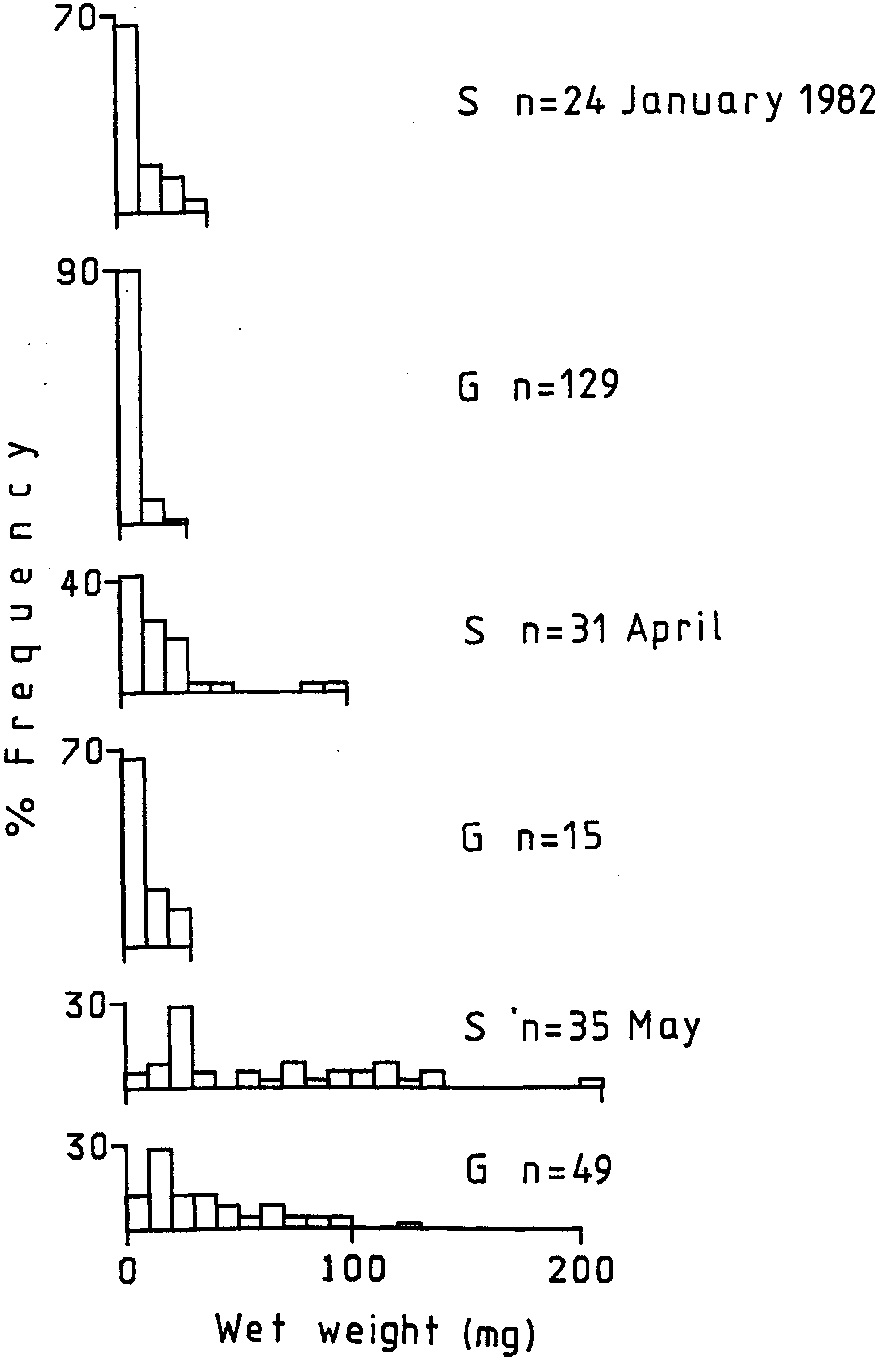
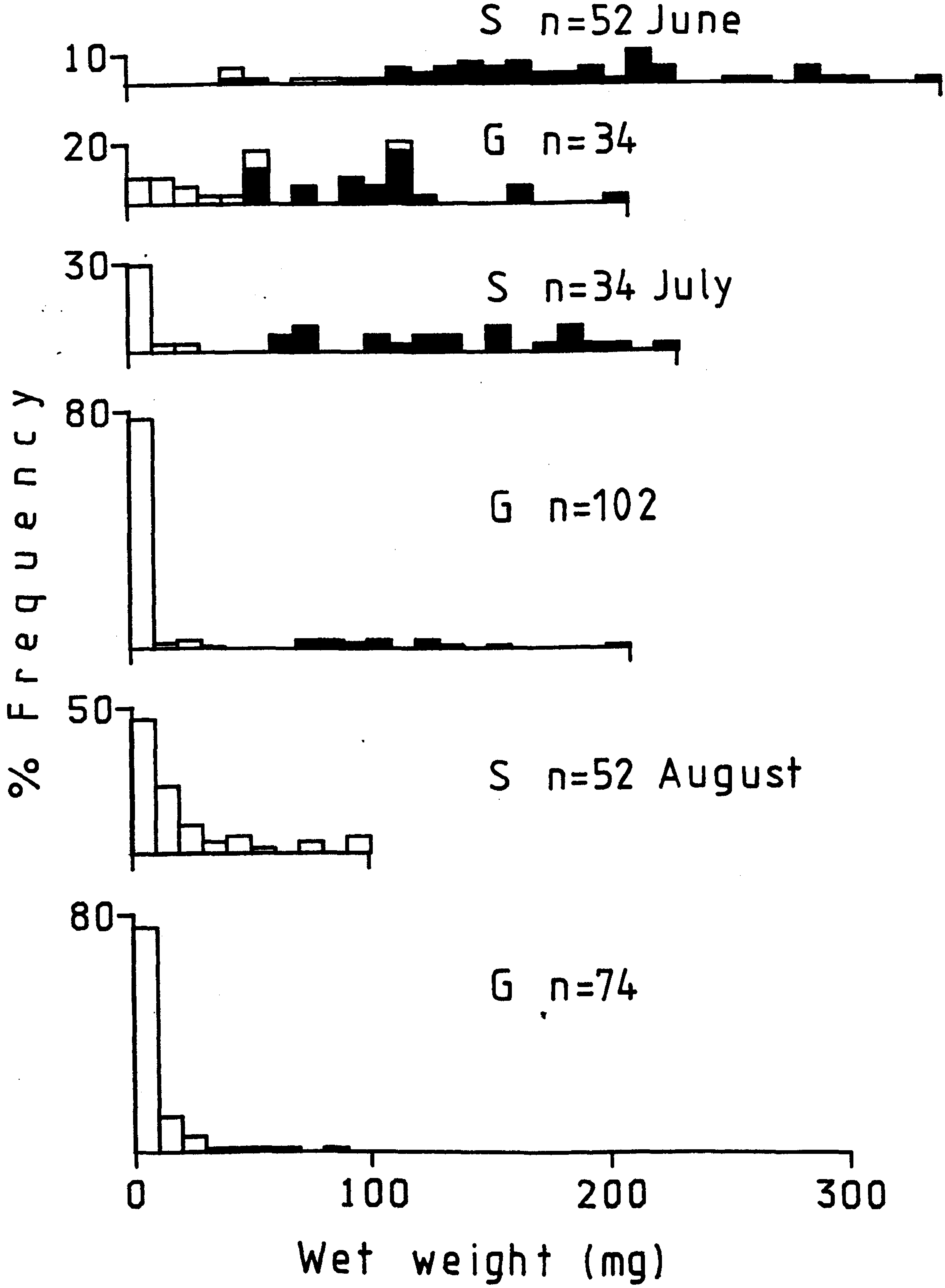

20
S n=303 August
30
G n=264
70
S n=87 September
80
G n=312
40
S n=243 October
60
G n=159
% Frequency
0
100
200
300
Wet weight (mg)

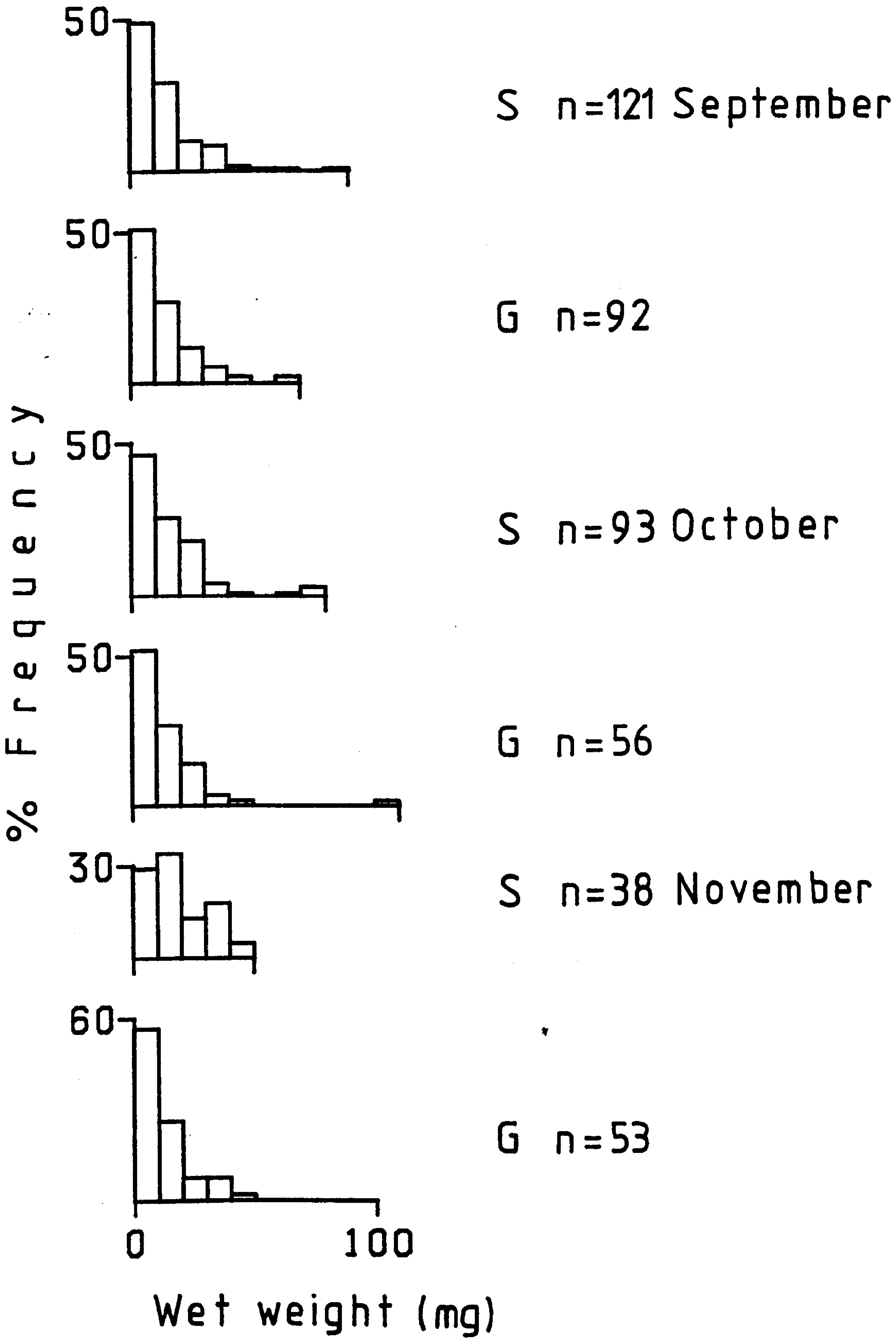
Continued


70
S n=24 January 1982
90
G n=129
40
S n=31 April
70
G n=15
30
S n=35 May
30
G n=49
% Frequency
0
100
200
Wet weight (mg)

Continued


S n=52 June
10
G n=34
20
S n=34 July
30
80
G n=102
S n=52 August
50
80
G n=74
% Frequency
0
100
200
300
Wet weight (mg)

Continued


50
S n=121 September
50
G n=92
50
S n=93 October
50
G n=56
30
S n=38 November
60
G n=53
% Frequency
0
100
Wet weight (mg)

Continued

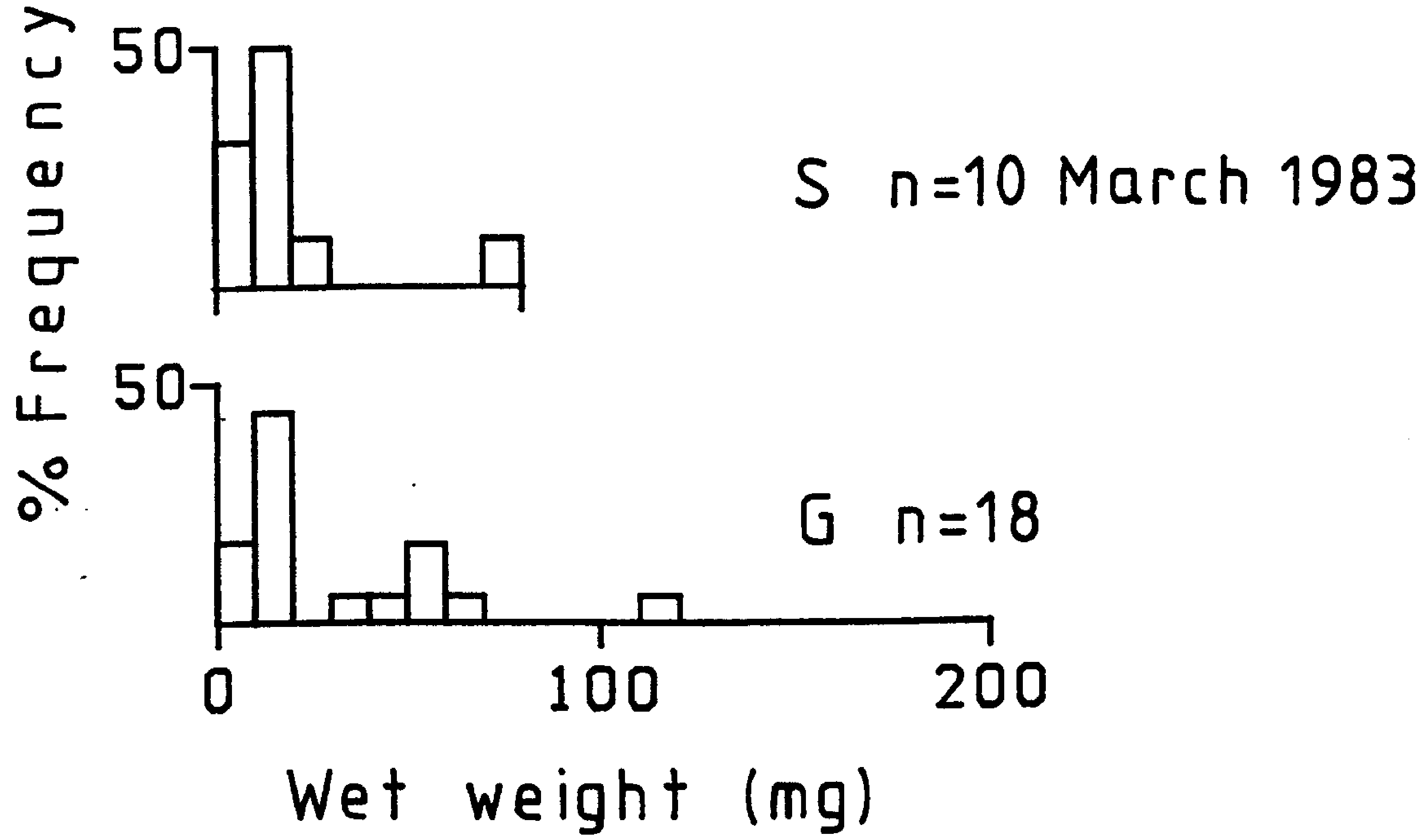
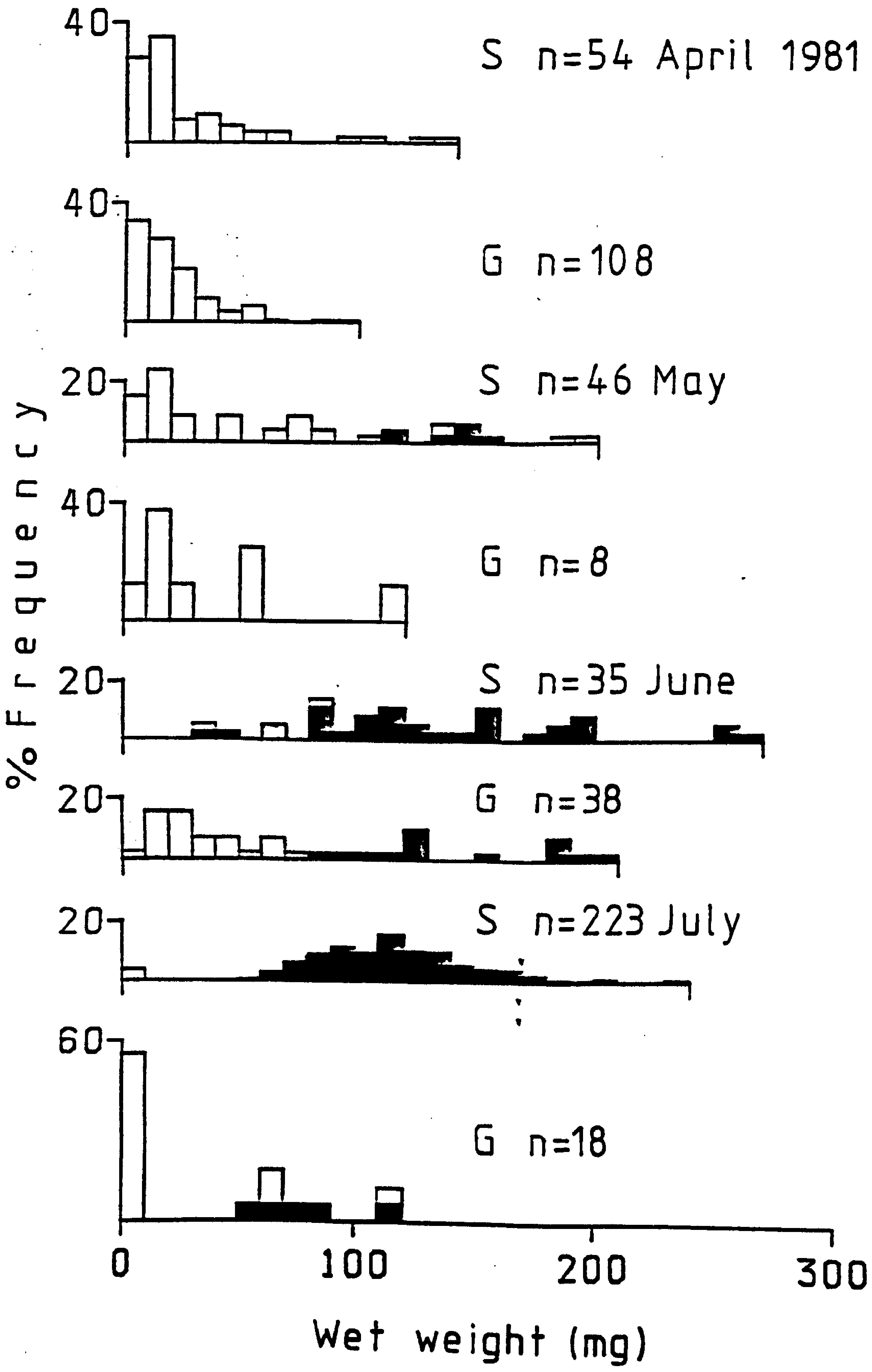

% Frequency
50
S n=10 March 1983
50
G n=18
0
100
200
Wet weight (mg)

Figure 4.15. Erpobdella octoculata. The size-structure of breeding (shaded) and non-breeding (clear) leech populations from stone (S) and substratum (G) samples in enclosed sites between April 1981 to March 1983.



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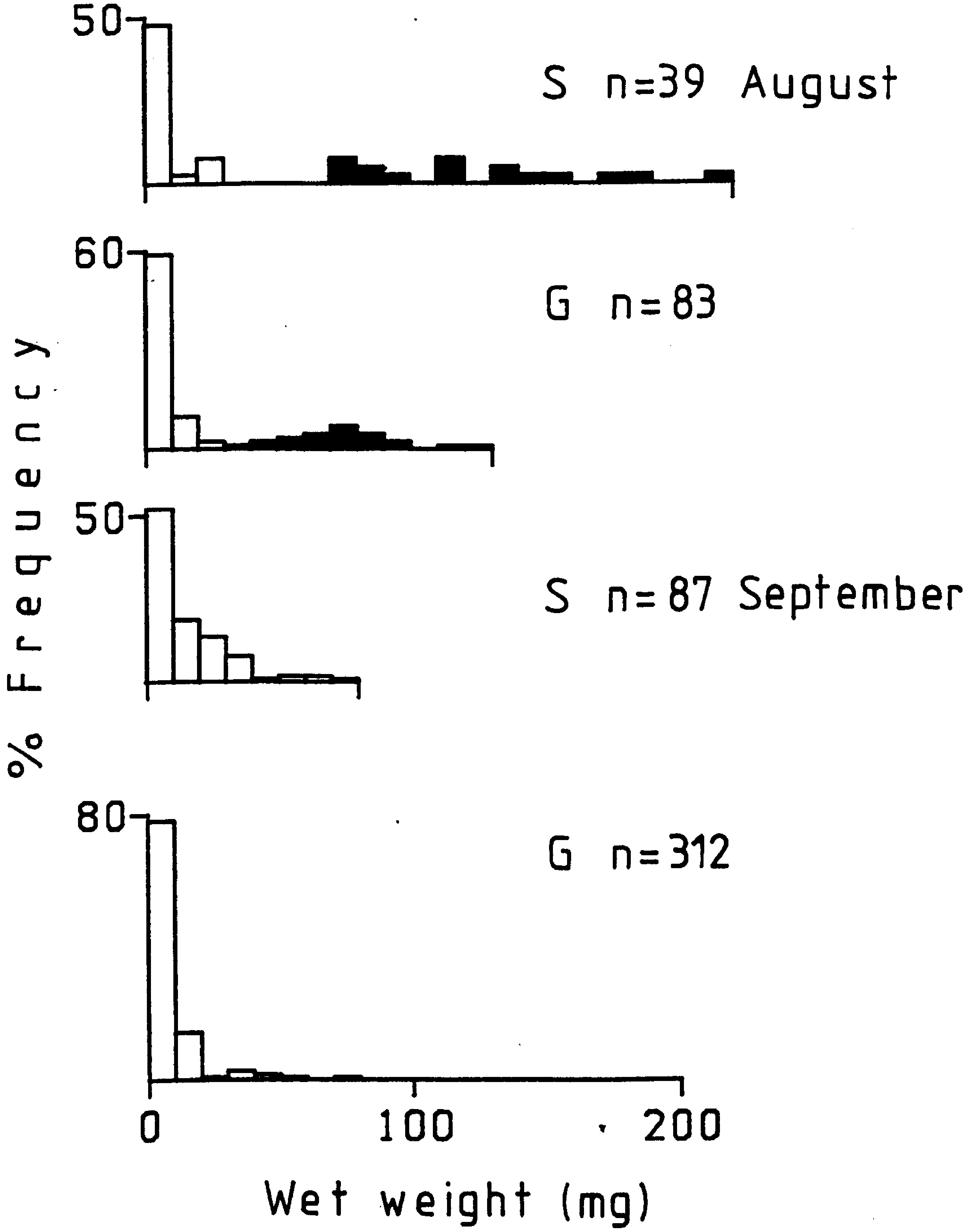
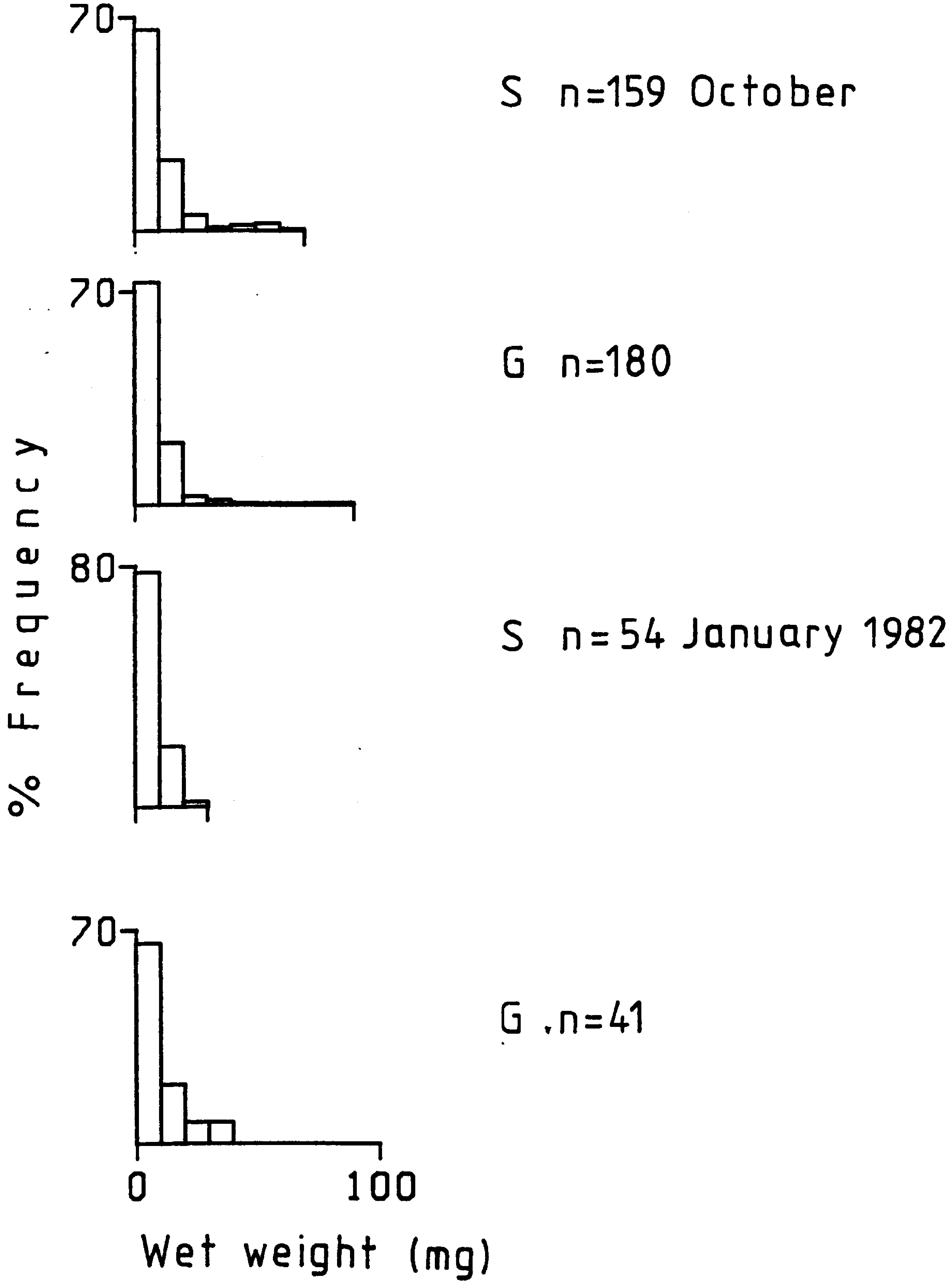
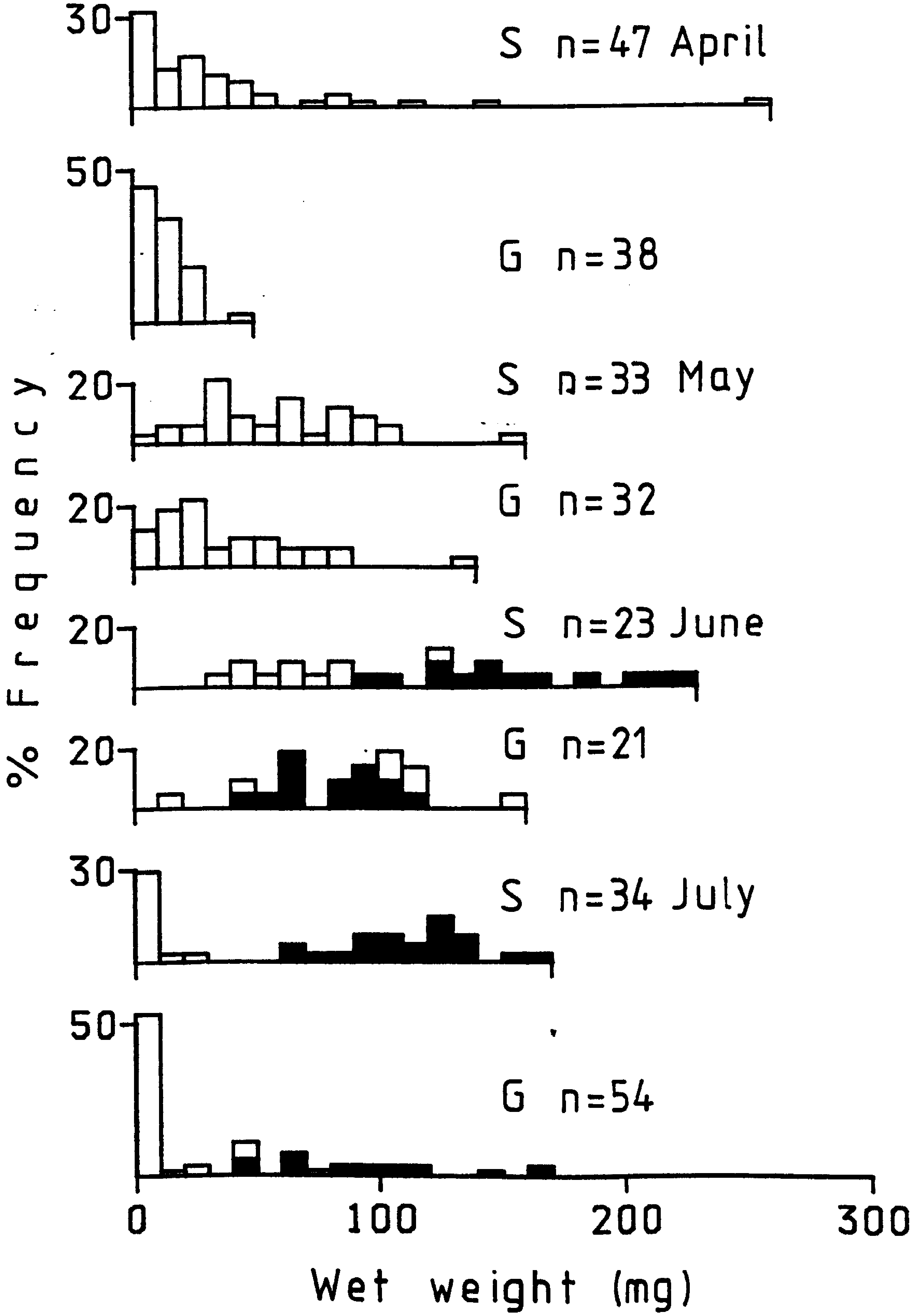

50
S n=39 August
60
G n=83
50
S n=87 September
80
G n=312
% Frequency
0
100
200
Wet weight (mg)

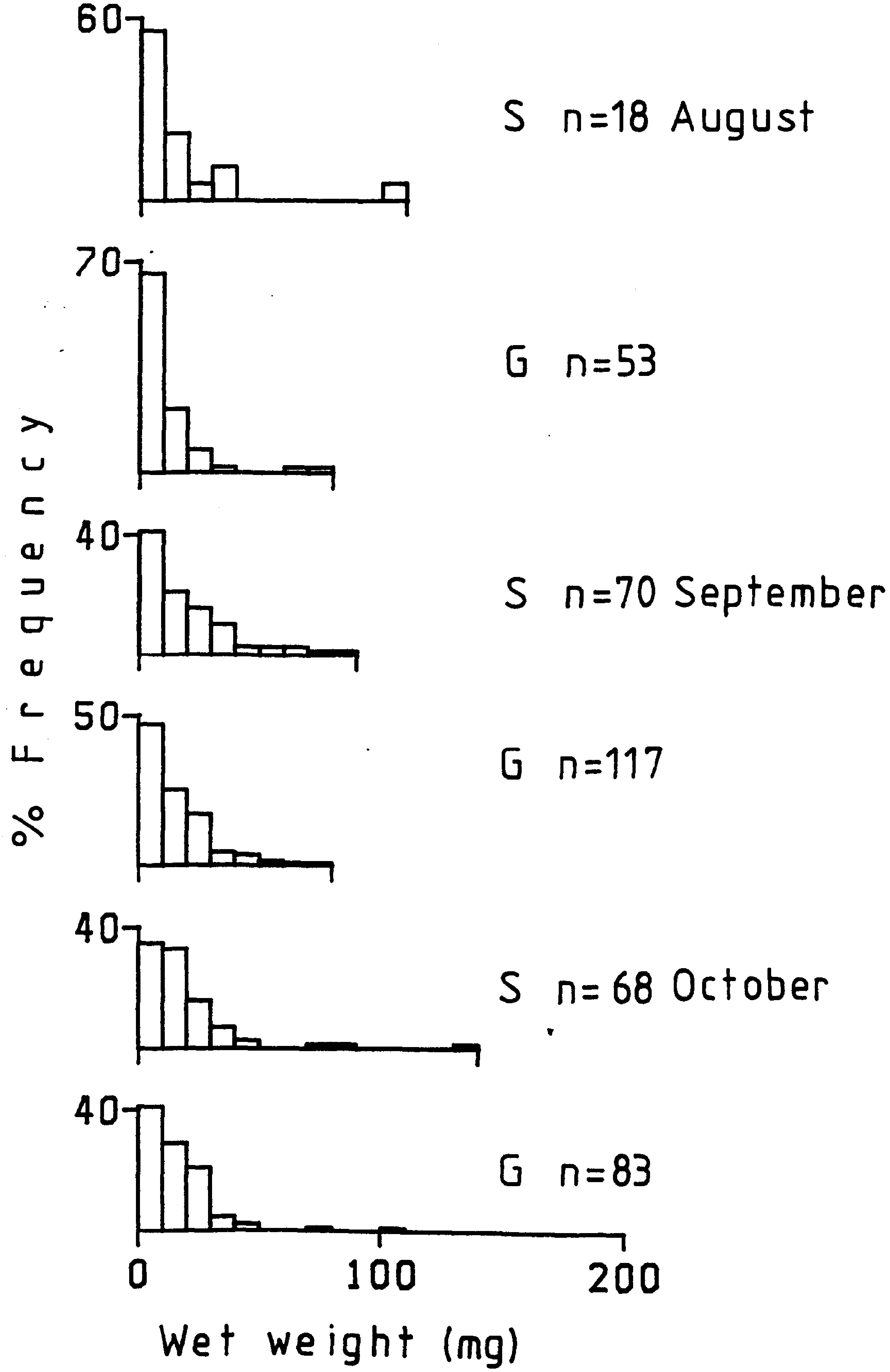
Continued


70
S n=159 October
70
G n=180
80
S n=54 January 1982
70
G .n=41
% Frequency
0
100
Wet weight (mg)

Continued


30
S n=47 April
50
G n=38
20
S n=33 May
20
G n=32
20
S n=23 June
20
G n=21
30
S n=34 July
50
G n=54
% Frequency
0
100
200
300
Wet weight (mg)

Continued


60
S n=18 August
70
G n=53
40
S n=70 September
50
G n=117
40
S n=68 October
40
G n=83
% Frequency
0
100
200
Wet weight (mg)

continued

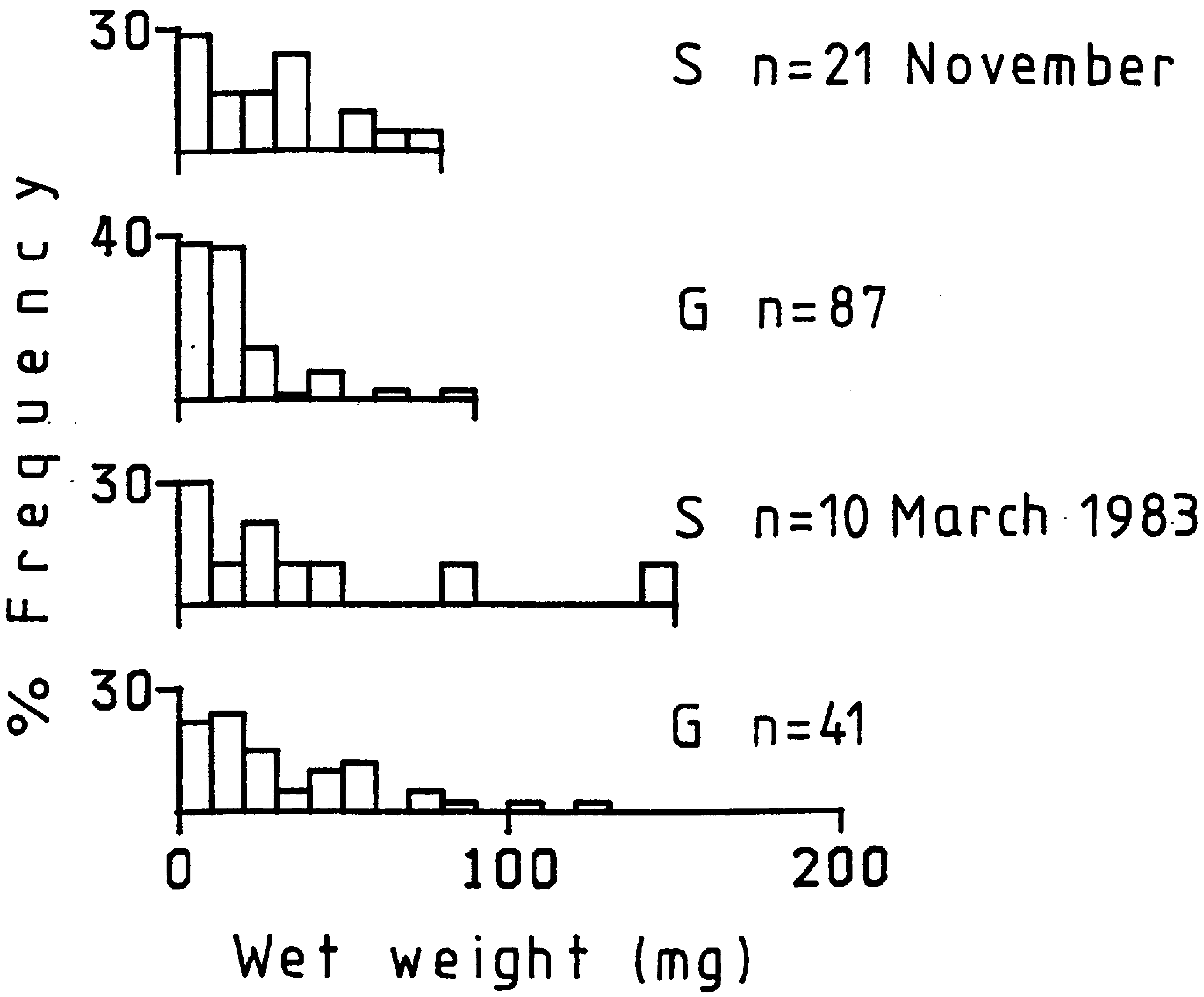
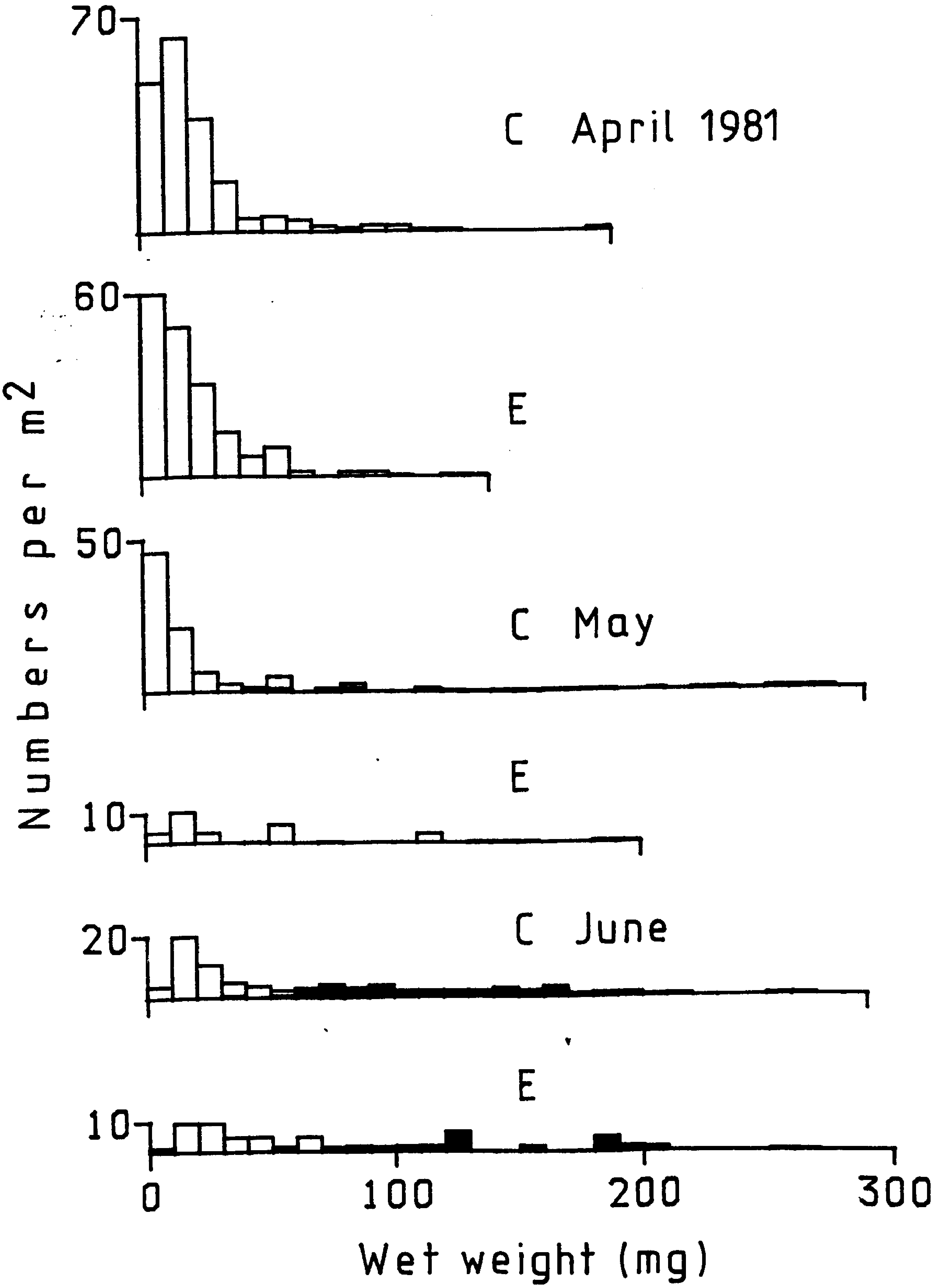

30
S n=21 November
40
G n=87
30
S n=10 March 1983
30
G n=41
% Frequency
0
100
200
Wet weight (mg)

Figure 4.16. Erpobdella octoculata. The size-structure of breeding (shaded) and non-breeding (clear) leech populations from combined stone and substratum sample data in control (C) and enclosed (E) sites.



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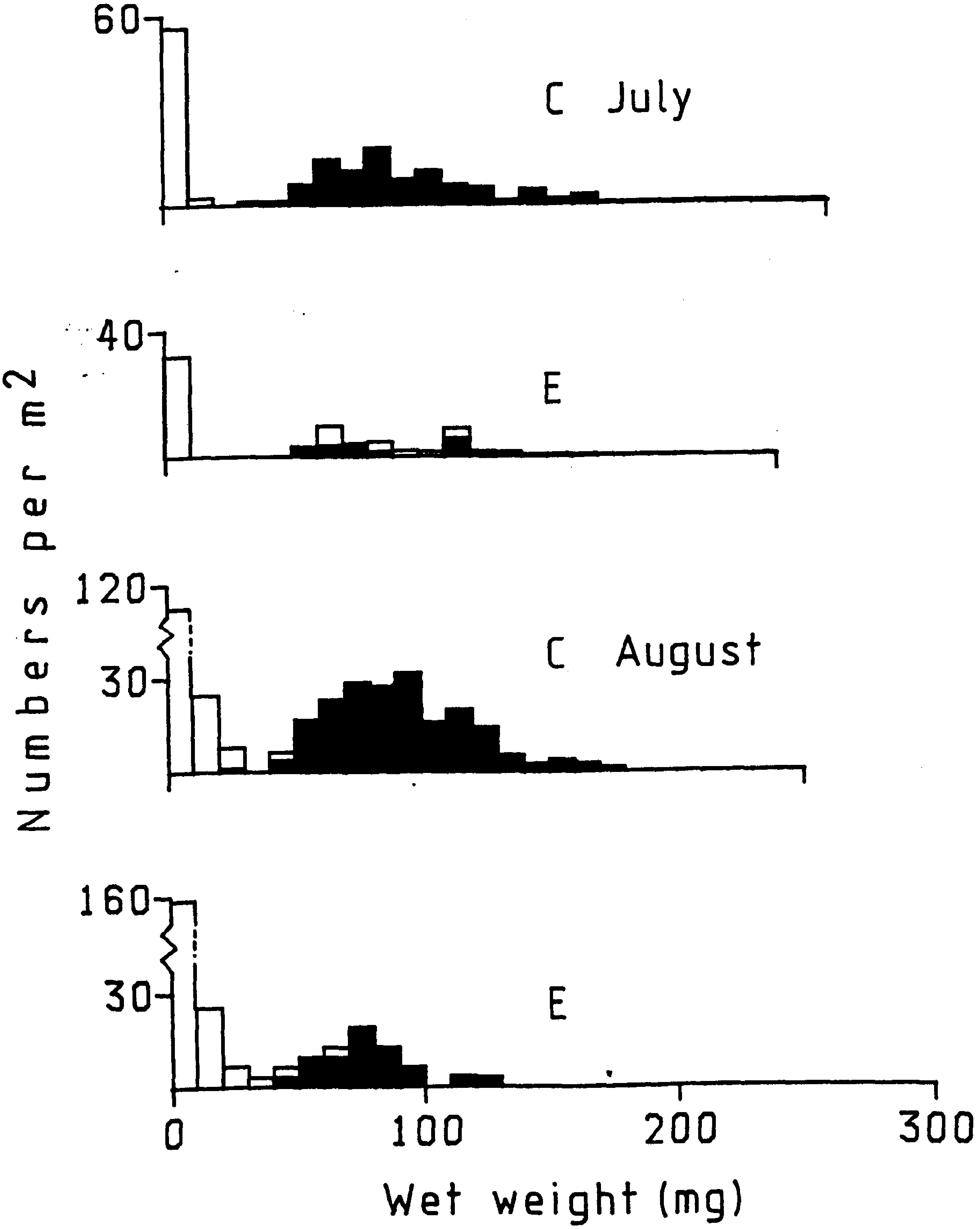
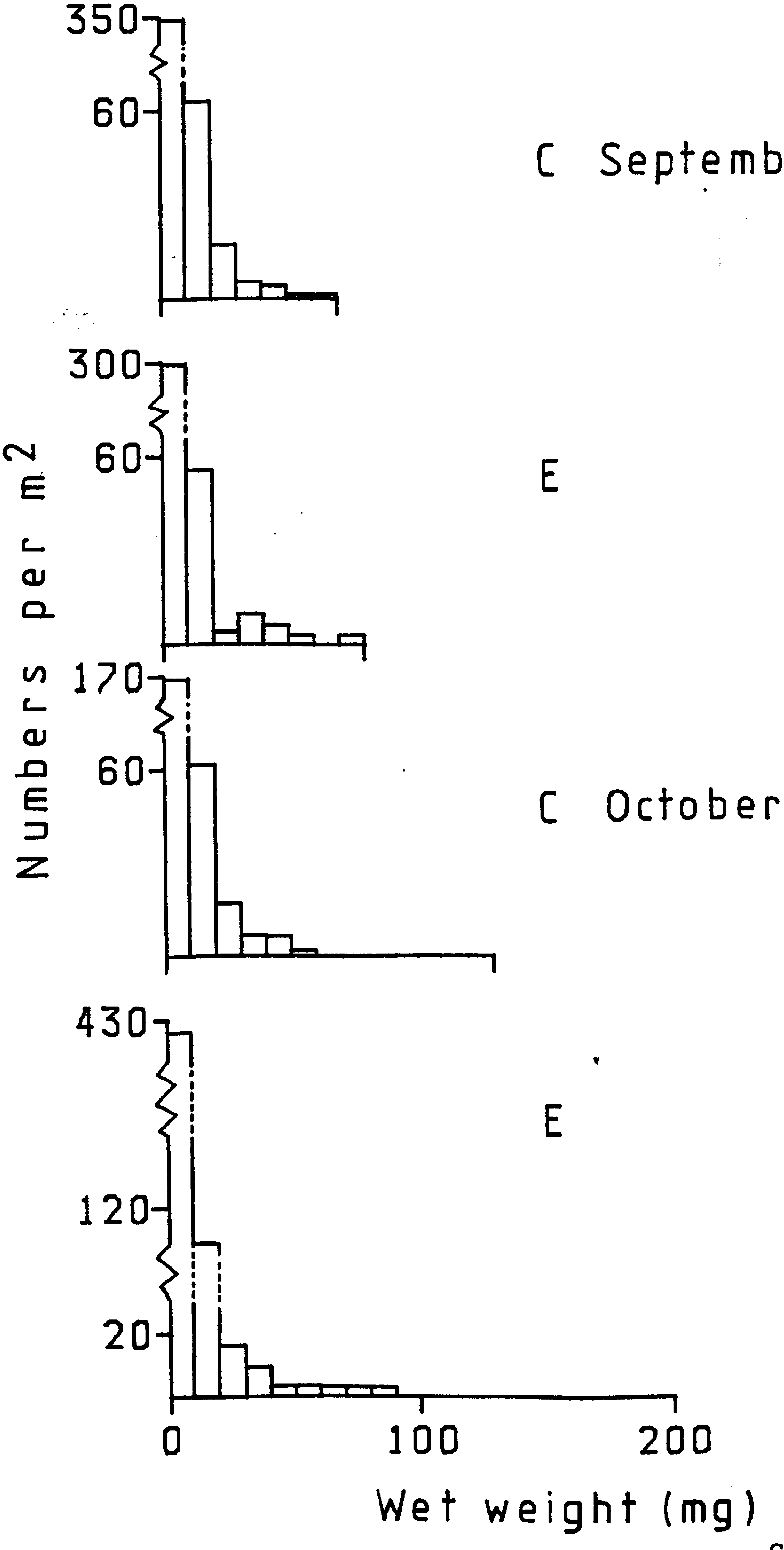
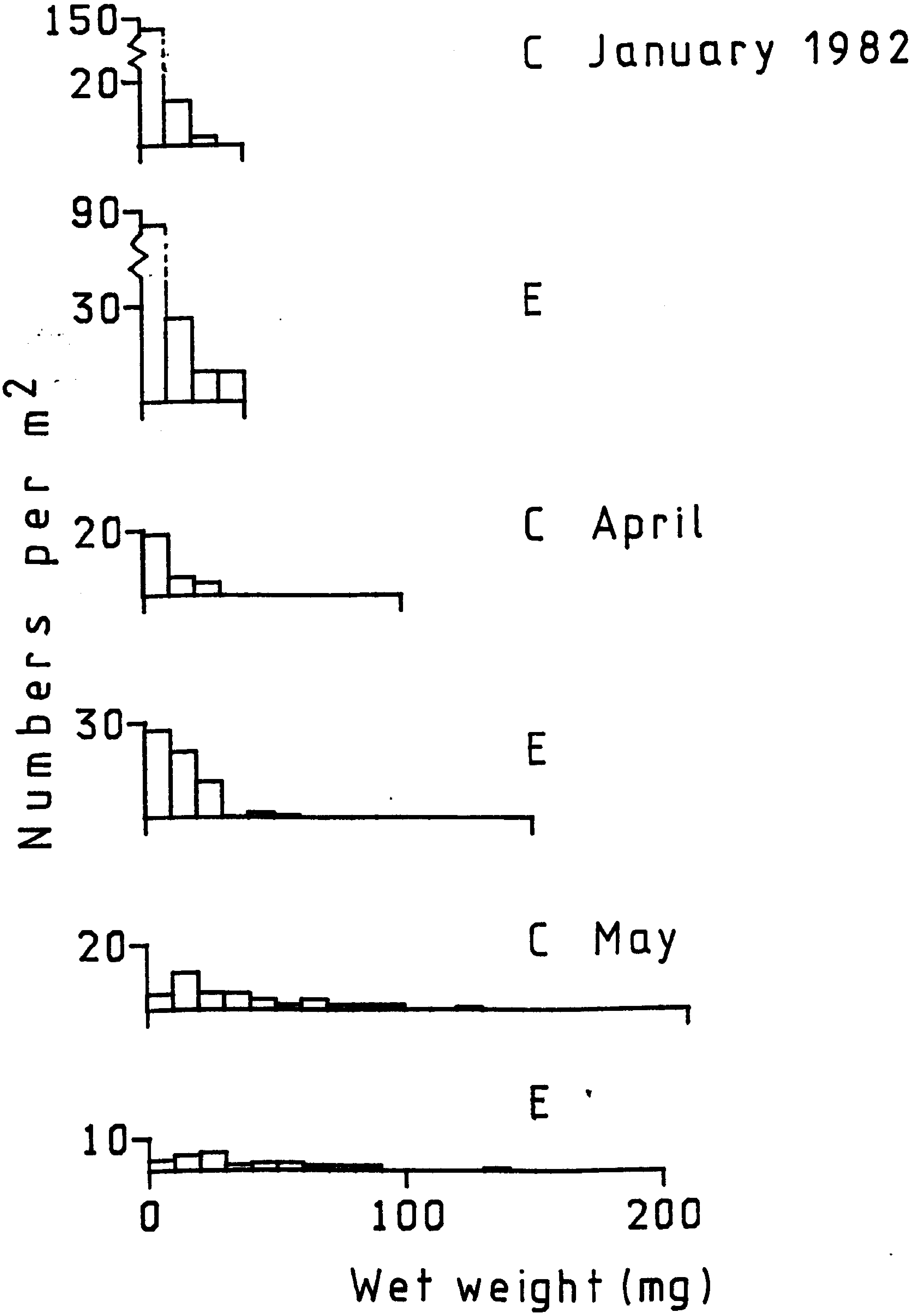

60
C July
40
E
Numbers per m^2
120
30
C August
160
30
E
0
100
200
300
Wet weight (mg)

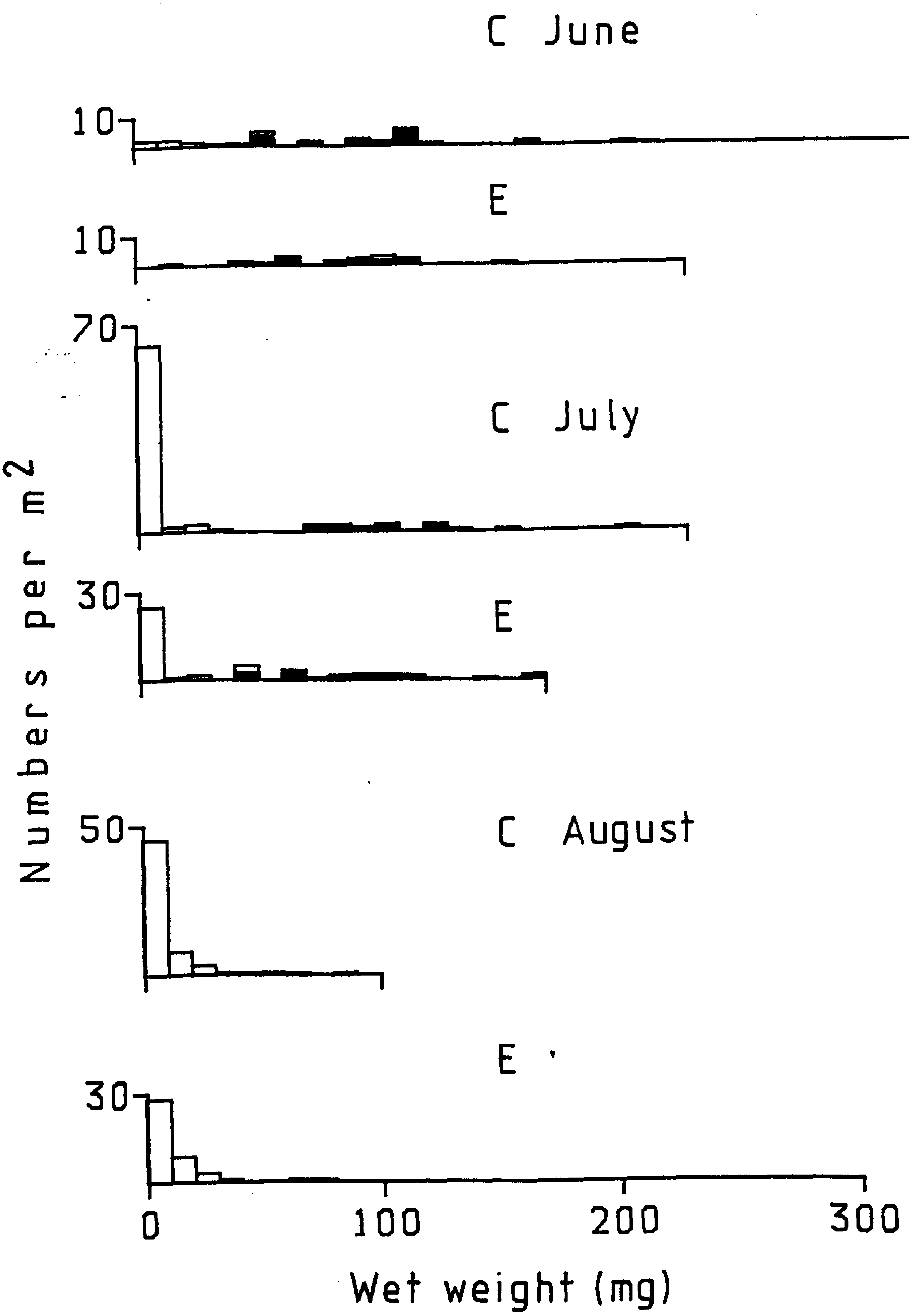
Continued


350
60
C September
300
60
E
170
60
C October
430
120
20
E
Numbers per m^2
0
100
200
Wet weight (mg)

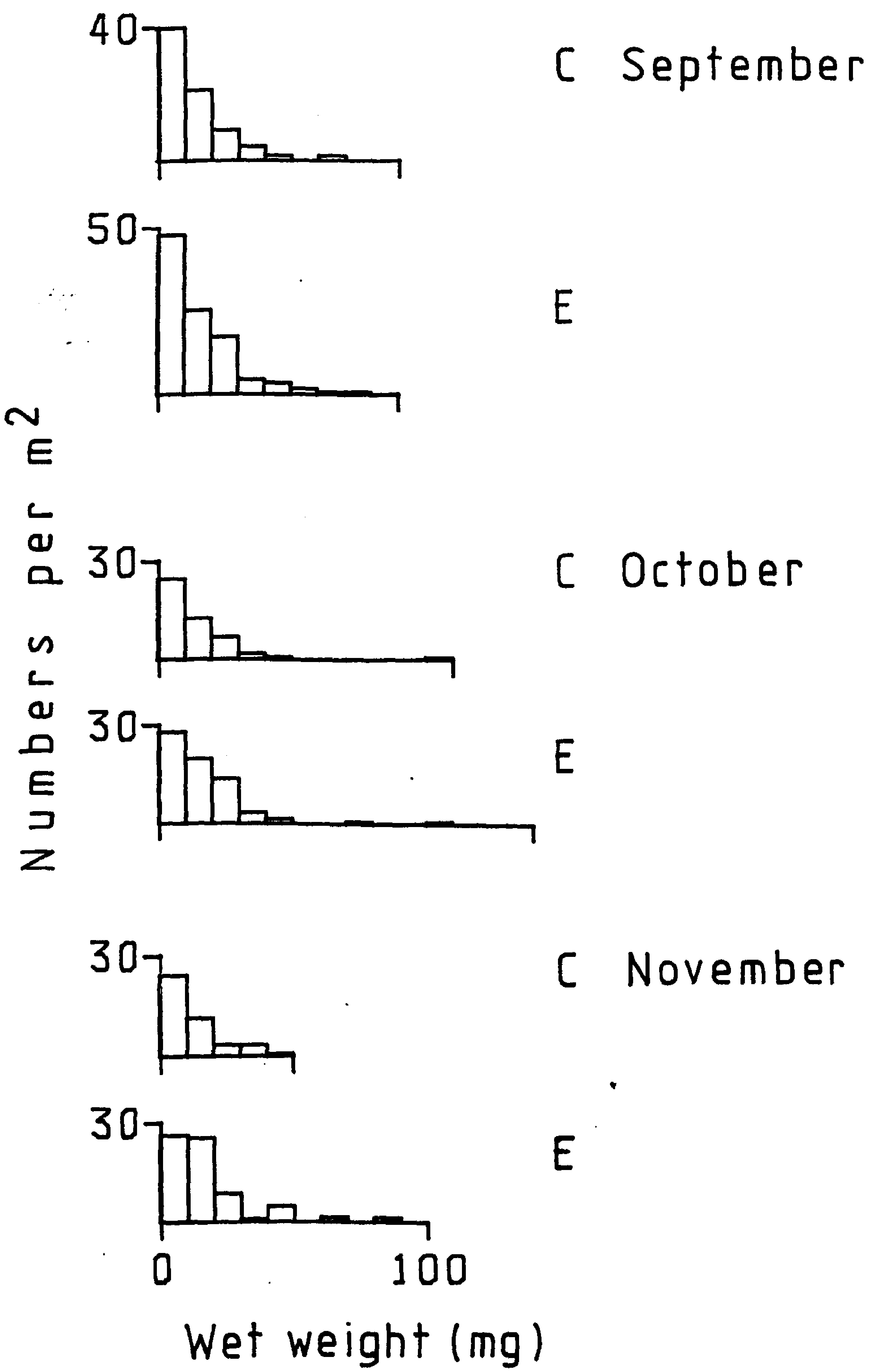
Continued


C January 1982
150
20
90
30
E
C April
20
30
E
C May
20
E
10
0
100
200
Wet weight (mg)
Numbers per m²

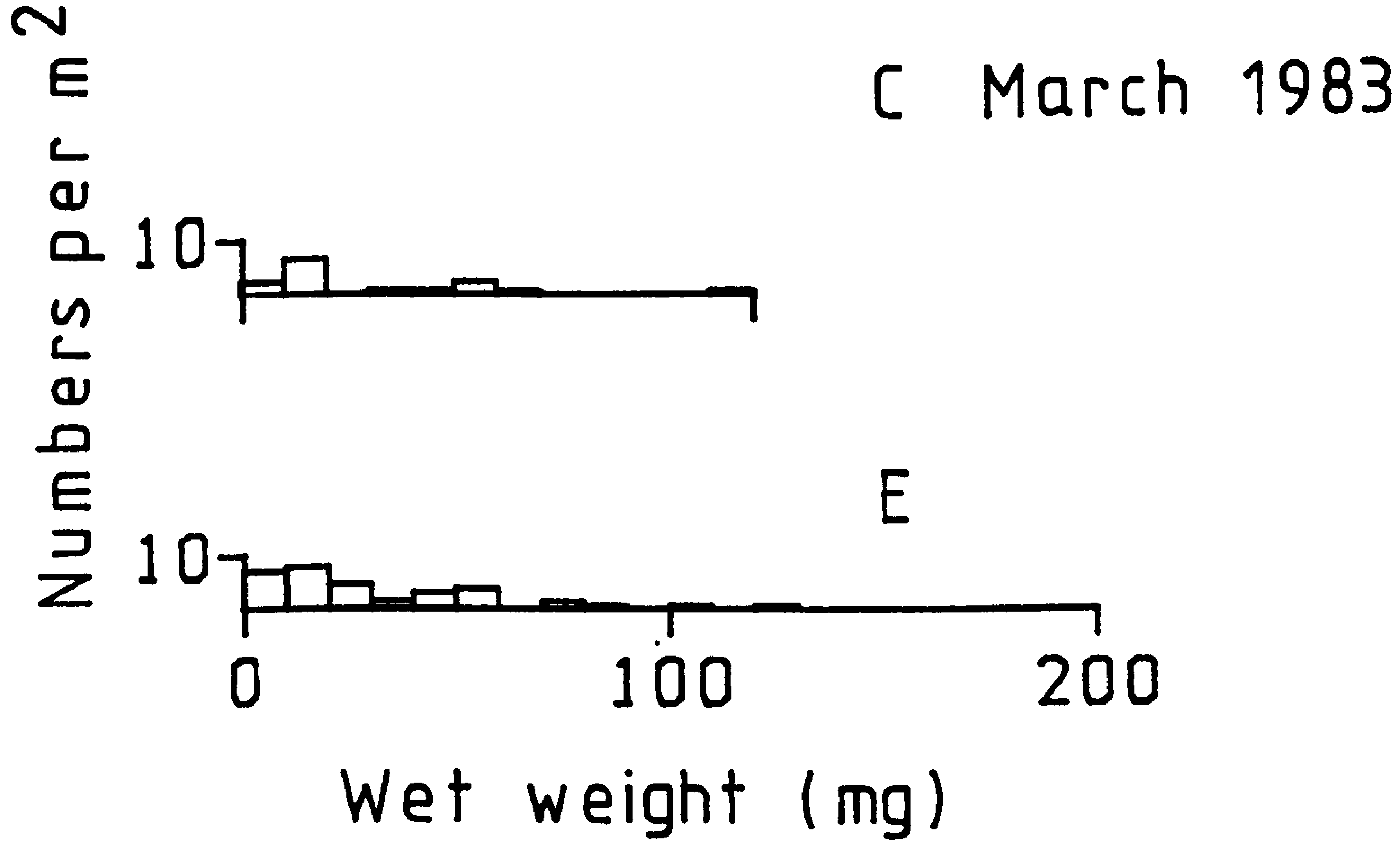
Continued


C June
10
E
10
70
C July
30
E
C August
50
E
30
0
100
200
300
Wet weight (mg)
Numbers per m2

Continued


40
C September
50
E
30
C October
30
E
30
C November
30
E
0
100
Wet weight (mg)
Numbers per m2

Continued


C March 1983
E
Numbers per m^2
10
10
0
100
200
Wet weight (mg)

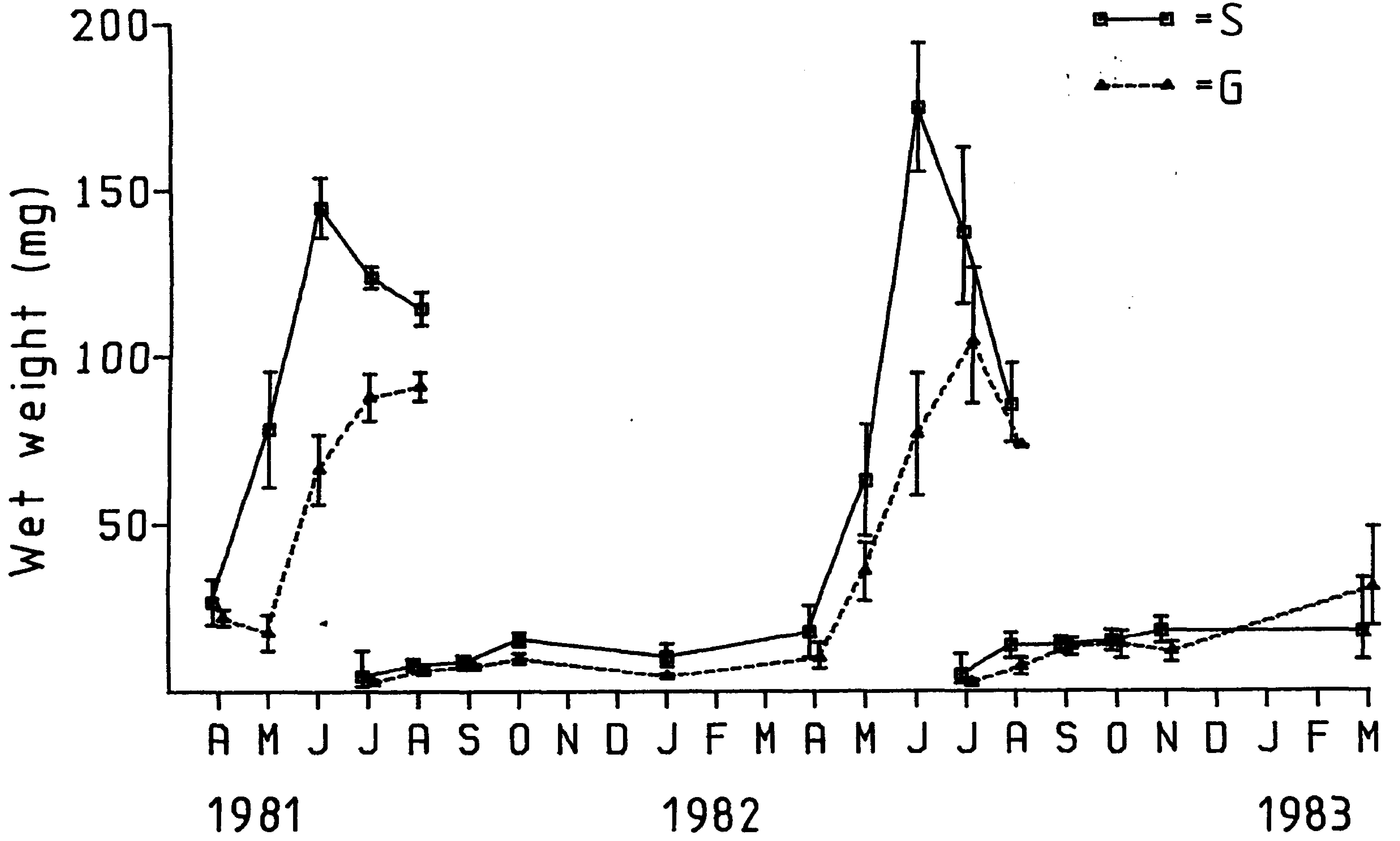


Figure 4.17. *Erpobdella octoculata.* Arithmetic mean individual weights ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from control sites.

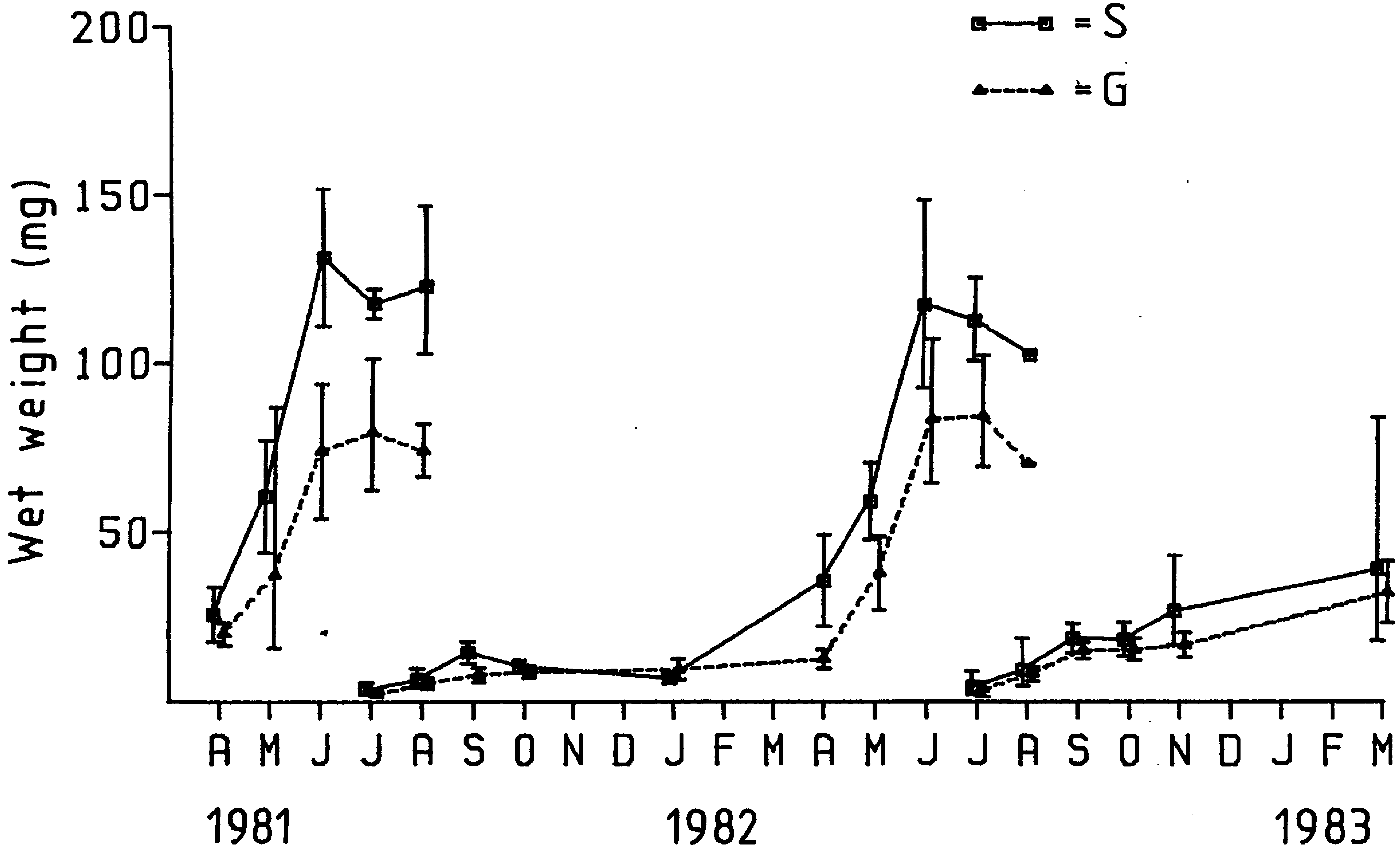


Figure 4.18. <u>Erpobdella octoculata.</u> Arithmetic mean individual weights ± 95% confidence in limits for each cohort in separate stone (S) and substratum (G) samples from enclosed sites.

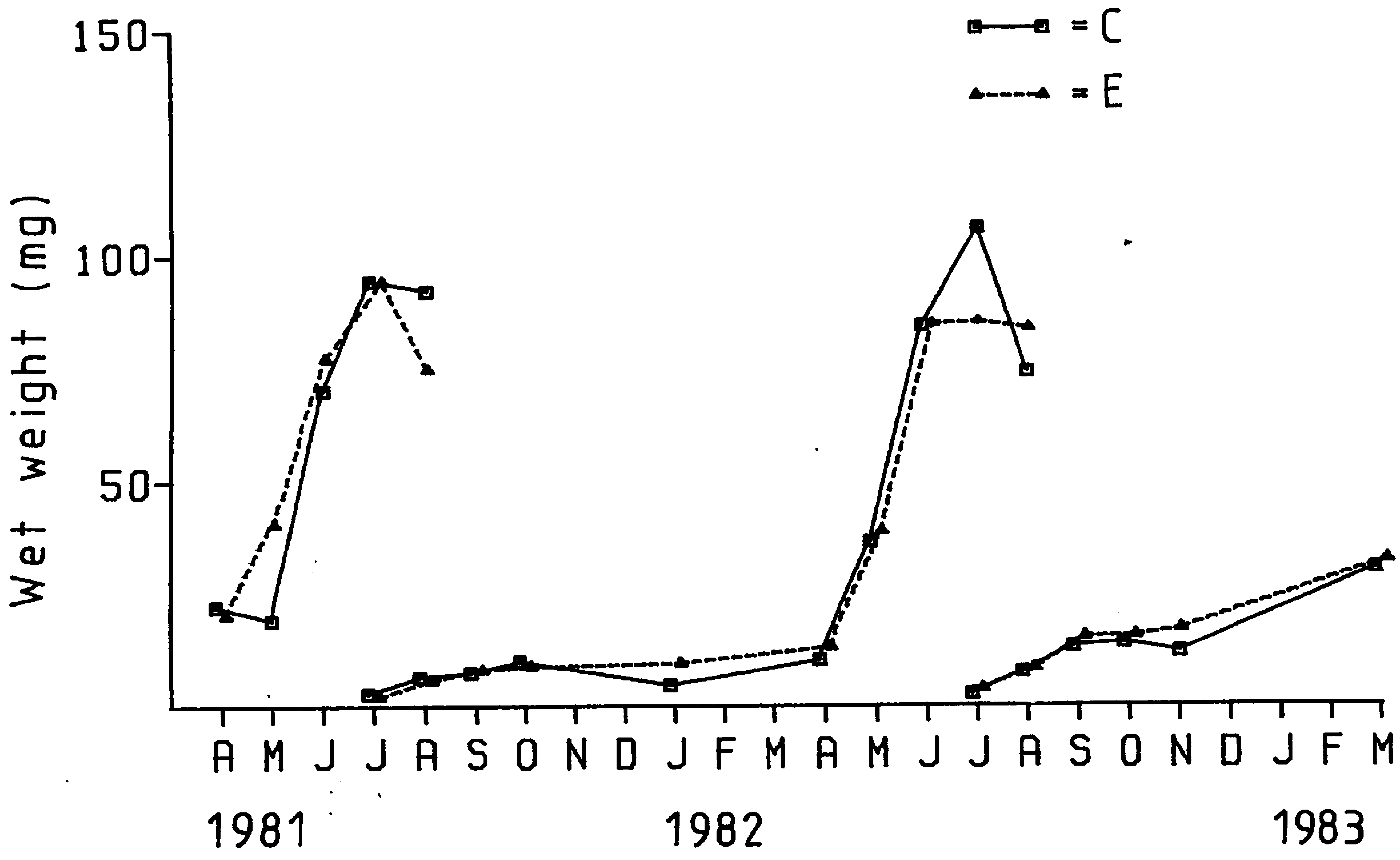


Figure 4.19. Erpobdella octoculata. Arithmetic mean individual weights for each cohort from combined stone and substratum sample data in control (C) and enclosed (E) sites.

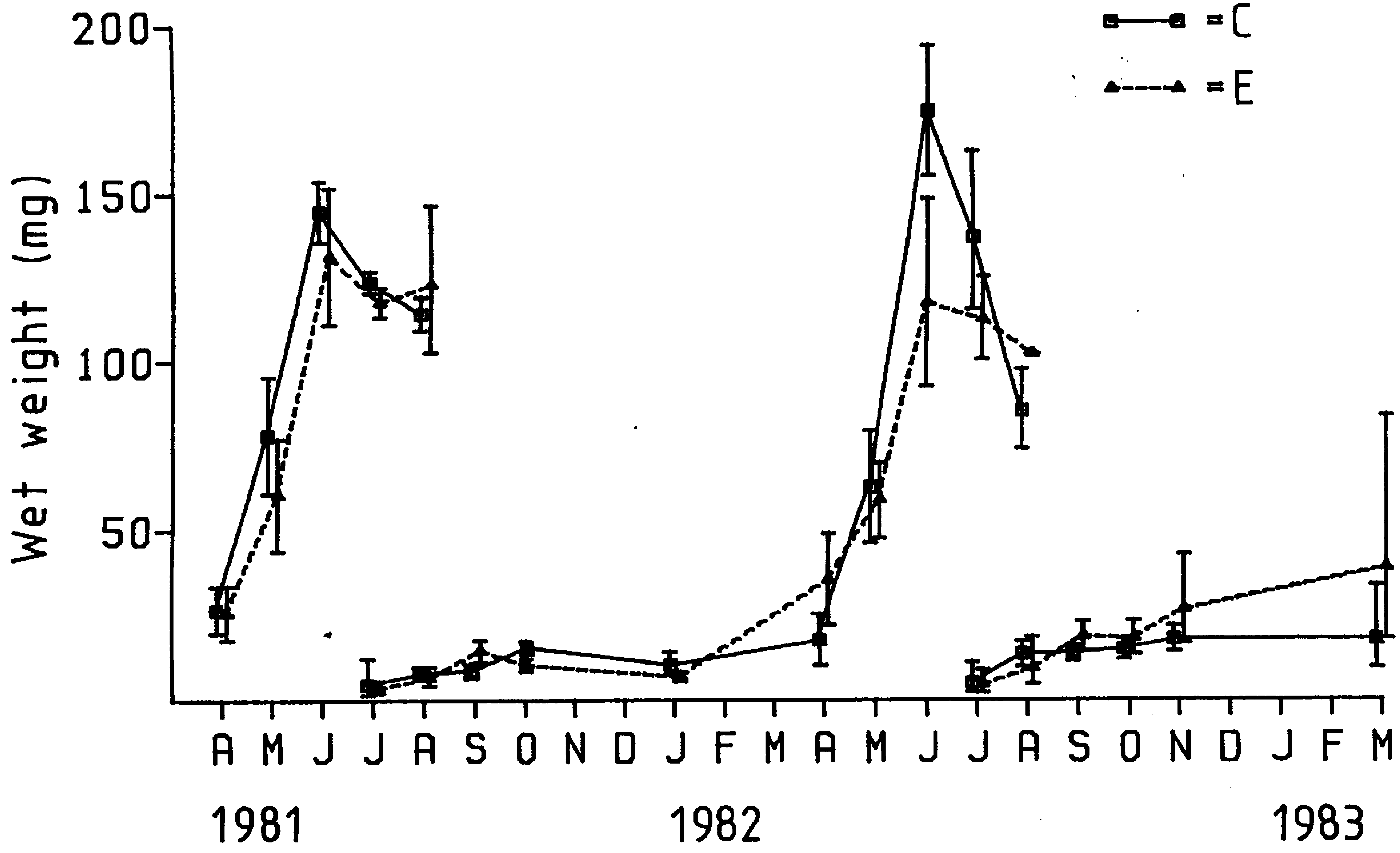


Figure 4.20. Erpobdella octoculata. Arithmetic mean individual weights ± 95% confidence limits for each cohort in stone samples from control (C) and enclosed (E) sites.

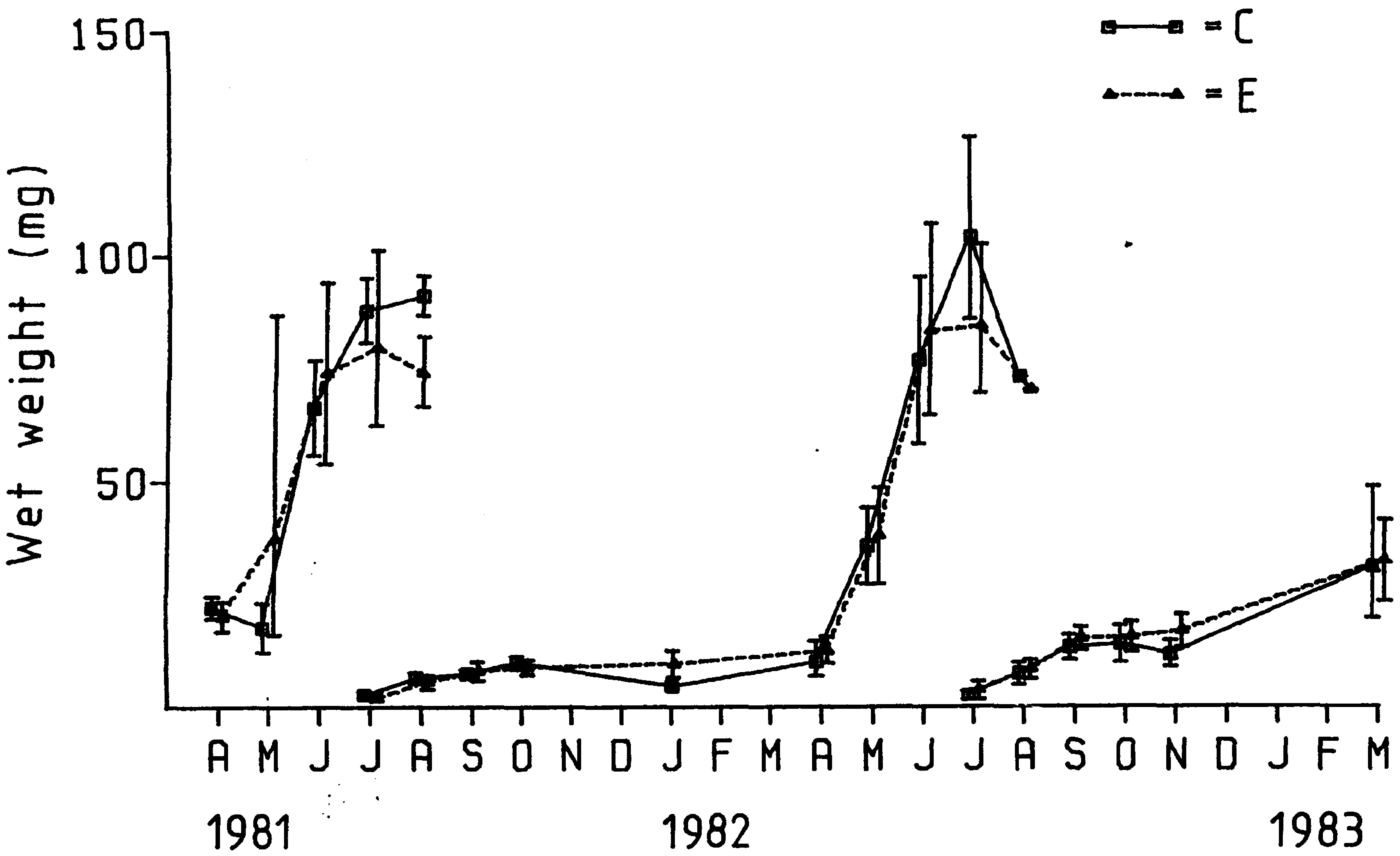


Figure 4.21. <u>Erpobdella octoculata.</u> Arithmetic mean individual weights ± 95% confidence limits for each cohort in substratum samples from control (C) and enclosed (E) sites.

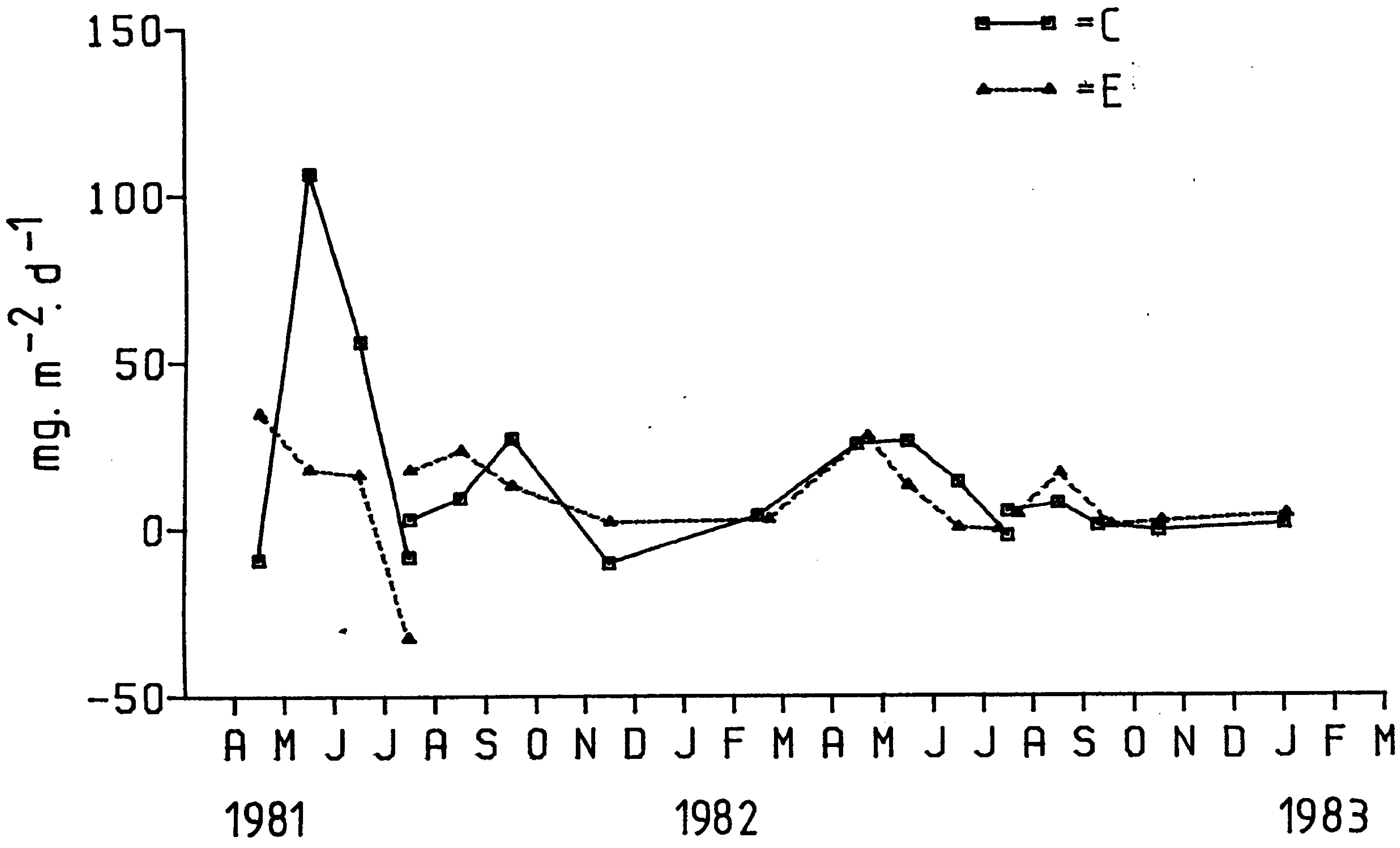


Figure 4.22. <u>Erpobdella octoculata.</u> The rate of biomass production for leeches of cohort in control (C) and enclosed (E) sites.

Figure 4.23. Erpobdella octoculata. The Allen curve for the 1981/82 cohort in control sites.

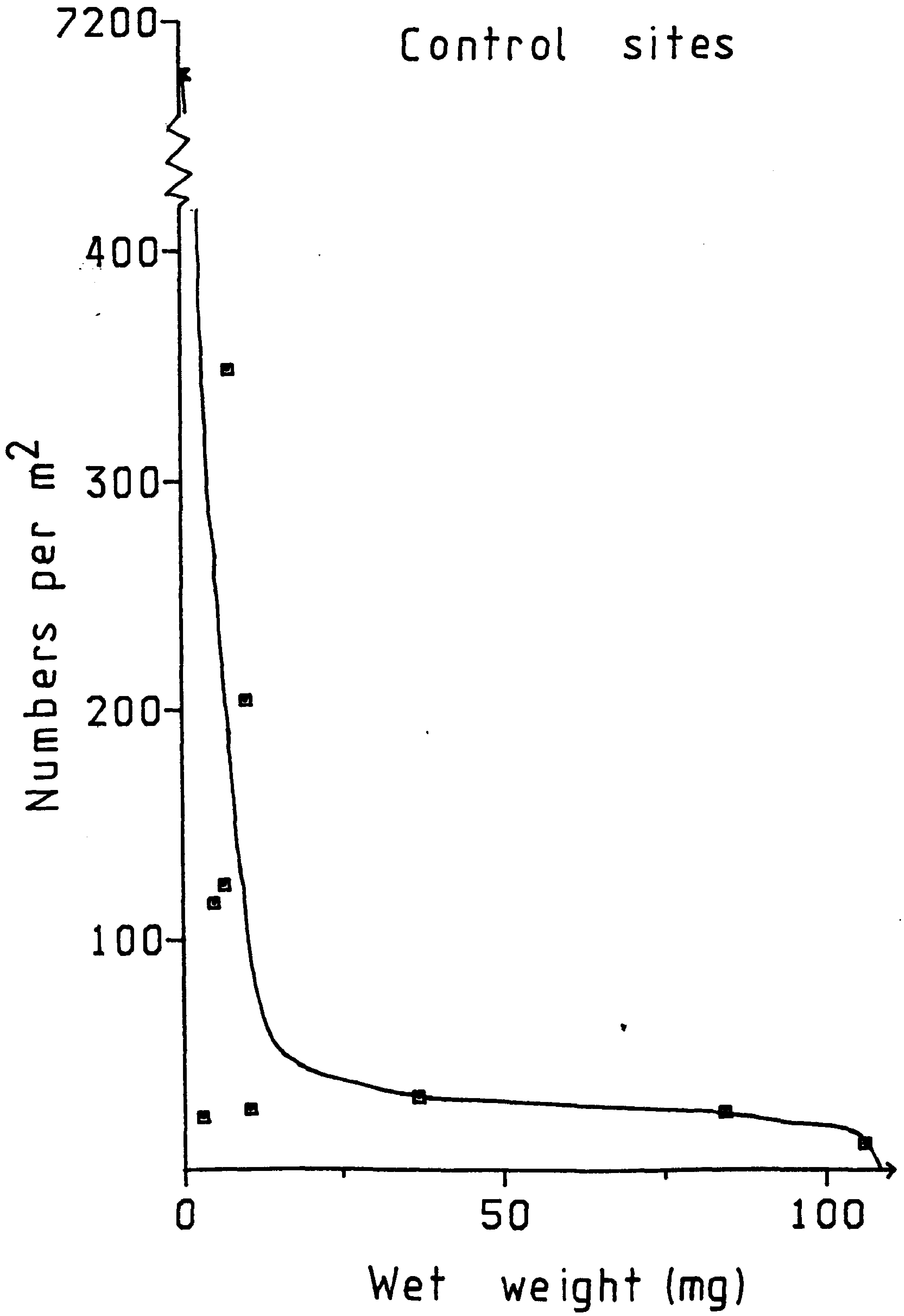


Figure 4.24. Erpobdella octoculata. The Allen curve for the 1981/82 cohort in enclosed sites.

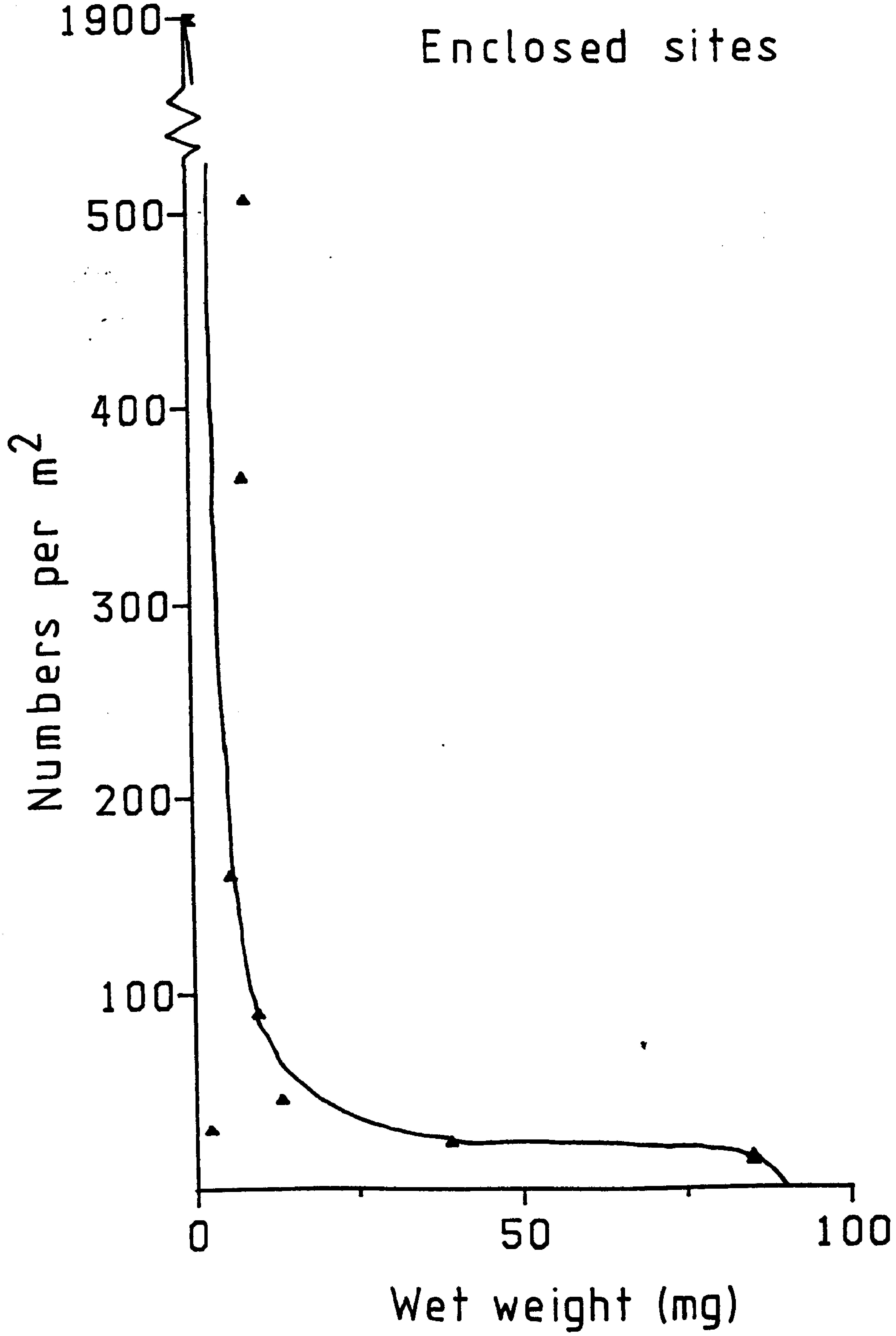


Table 4.1. *Erpobdella octoculata*. Mann-Whitney U tests comparing densities in stone (S) and substratum (G) samples between control and enclosed sites.

		U1	U2	N1	N2	Sig
1980/81 cohort						
1981						
April	S	51	109	20	8	-
	G	71.5	88.5	20	8	-
May	S	57.5	102.5	20	8	-
	G	33.5	6.5	10	4	-
June	S	112.5	47.5	20	8	-
	G	101.5	58.5	20	8	-
July	S	80.5	79.5	20	8	-
	G	34	6	10	4	-
August	S	159	1	20	8	$p<0.05$
	G	30	10	10	4	-
1981/82 cohort						
1981						
July	S	41	103	18	8	-
	G	15	25	10	4	-
August	S	98	62	20	8	-
	G	15.5	24.5	10	4	-
September	S	31.5	48.5	10	8	-
	G	20	16	9	4	-
October	S	41.5	118.5	20	8	-
	G	5.5	26.5	8	4	-
1982						
January	S	33	127	20	8	$p<0.05$
	G	21	19	10	4	-
April	S	122	134	16	16	-
	G	21.5	34.5	7	8	-
May	S	139.5	116.5	16	16	-
	G	146	110	16	16	-
June	S	197.5	42.5	15	16	$p<0.05$
	G	166	90	16	16	-
July	S	133	107	16	15	-
	G	99	141	16	15	-
August	S	145	111	16	16	-
	G	128	128	16	16	-

Continued

1982/83 cohort

		U1	U2	N1	N2	Sig
1982						
July	S	124	116	16	15	-
	G	141	99	16	15	-
August	S	187	69	16	16	$p<0.05$
	G	128.5	127.5	16	16	-
September	S	193.5	62.5	16	16	$p<0.05$
	G	82.5	157.5	16	15	-
October	S	138	118	16	16	-
	G	88.5	167.5	16	16	-
November	S	156	100	16	16	-
	G	78	162	15	16	-
1983						
March	S	136.5	119.5	16	16	-
	G	33	223	16	16	$p<0.05$

Table 4.2. *Erpobdella octoculata*. Mann-Whitney U tests comparing biomass in stone (S) and substratum (G) samples between control and enclosed sites.

		U1	U2	N1	N2	Sig
1980/81 cohort						
1981						
April	S	53.5	106.5	20	8	-
	G	81.5	78.5	20	8	-
May	S	65	95	20	8	-
	G	28	12	10	4	-
June	S	115	45	20	8	-
	G	98	62	20	8	-
July	S	73	71	18	8	-
	G	34	6	10	4	-
August	S	159	1	20	8	$p<0.05$
	G	3	37	10	4	$p<0.05$
1981/82 cohort						
1981						
July	S	40.5	103.5	18	8	-
	G	19	21	10	4	-
August	S	97	63	20	8	-
	G	16.5	23.5	10	4	-
September	S	13.5	66.5	10	8	$p<0.05$
	G	19.5	16.5	9	4	-
October	S	67	93	20	8	-
	G	5	27	8	4	-
1982						
January	S	33.5	126.5	20	8	$p<0.05$
	G	16	24	10	4	-
April	S	110	146	16	16	-
	G	14.5	41.5	7	8	-
May	S	129	127	16	16	-
	G	130	126	16	16	-
June	S	218	22	15	16	$p<0.05$
	G	169.5	86.5	16	16	-
July	S	138	102	16	15	-
	G	113.5	126.5	16	15	-
August	S	144.5	111.5	16	16	-
	G	129	127	16	16	-

Continued

		U1	U2	N1	N2	Sig
1982/83 cohort						
1982						
July	S	132.5	107.5	16	15	-
	G	135.5	104.5	16	15	-
August	S	193	63	16	16	$p<0.05$
	G	130	126	16	16	-
September	S	146	110	16	16	-
	G	64	176	16	15	$p<0.05$
October	S	136	120	16	16	-
	G	82	174	16	16	-
November	S	137.5	116.5	16	16	-
	G	70.5	185.5	16	16	$p<0.05$
1983						
March	S	125	131	16	16	-
	G	52.5	203.5	16	16	$p<0.05$

Table 4.3. Erpobdella octoculata. T and d tests comparing mean individual weights between stone and substratum samples for control (C) and enclosed (E) sites.

		F	(v1,v2)	Sig	Test	(d.f.)	Sig
1980/81 cohort							
1981							
April	C	1.998	(70,290)	*	d= 1.339	(87)	-
	E	2.850	(53,107)	*	d= 1.314	(72)	-
May	C	12.240	(79, 67)	*	d= 6.616	(93)	$p<0.001$
	E	2.546	(45, 7)	*	d= 1.556	(14)	-
June	C	1.220	(127,139)	-	t=11.350	(266)	$p<0.001$
	E	1.050	(37, 34)	-	t= 4.077	(71)	$p<0.001$
July	C	1.698	(456, 62)	*	d= 9.114	(94)	$p<0.001$
	E	1.886	(213, 7)	-	t= 3.270	(220)	$p<0.001$
August	C	1.952	(223,151)	*	d= 6.896	(373)	$p<0.001$
	E	5.207	(15, 22)	*	d= 4.362	(19)	$p<0.001$
1981/82 cohort							
1981							
July	C	1.194	(5, 45)	-	t= 0.766	(50)	-
	E	2.596	(8, 9)	-	t= 1.832	(17)	-
August	C	1.376	(78,111)	-	t= 1.454	(189)	-
	E	1.416	(22, 59)	-	t= 0.569	(81)	-
September	C	1,400	(86,311)	*	d= 1.080	(122)	-
	E	1.911	(89,116)	*	d= 3.313	(156)	$p<0.005$
October	C	3.011	(242,158)	*	d= 4.421	(394)	$p<0.001$
	E	1.060	(158,179)	-	t= 1.229	(337)	-
1982							
January	C	4.465	(23,128)	*	d= 3.279	(25)	$p<0.005$
	E	3.599	(40, 53)	*	d= 1.593	(57)	-
April	C	7.666	(30, 14)	*	d= 1.824	(42)	-
	E	25.303	(46, 37)	*	d= 3.372	(51)	$p<0.001$
May	C	2.706	(34, 48)	*	d= 2.963	(52)	$p<0.005$
	E	1.177	(32, 31)	-	t= 2.748	(63)	$p<0.001$
June	C	1.802	(51, 33)	*	d= 7.402	(83)	$p<0.001$
	E	3.253	(22, 20)	*	d= 2.472	(35)	$p<0.025$
July	C	1.658	(21, 17)	-	t= 2.380	(38)	$p<0.025$
	E	2.158	(21, 21)	*	d= 2.863	(37)	$p<0.001$
August	C	2.881	(1, 4)	-	t= 1.334	(5)	-
	E		n too small				

Continued

		F.	(v1,v2)	Sig	Test	(d.f.)	Sig
1982/83 cohort							
1982							
July	C	2.351	(11, 83)	*	d= 1.249	(12)	-
	E	1.338	(11, 31)	-	t= 0.449	(42)	-
August	C	1.509	(46, 71)	-	t= 2.833	(117)	$p<0.01$
	E	2.397	(16, 50)	*	d= 0.388	(21)	-
September	C	1.090	(120, 91)	-	t= 0.368	(211)	-
	E	1.884	(69,116)	*	d= 1.459	(113)	-
October	C	1.018	(55, 92)	-	t= 0.410	(147)	-
	E	1.866	(67, 82)	*	d= 0.971	(120)	-
November	C	1.293	(37, 52)	-	t= 2.655	(89)	$p<0.001$
	E	1.649	(20, 86)	-	t= 2.373	(106)	$p<0.025$
1983							
March	C	1.824	(17, 9)	-	t= 1.287	(26)	-
	E	2.308	(9, 40)	*	d= 0.469	(11)	-

Table 4.4. *Erpobdella octoculata*. T and d tests comparing mean individual weights between control and enclosed sites for separate stone (S) and substratum (G) samples.

		F.	(v1,v2)	Sig	Test	(d.f.)	Sig
1980/81 cohort							
1981							
April	S	1.010	(53, 70)	-	t= 0.256	(123)	-
	G	1.411	(290,107)	*	d= 1.029	(226)	-
May	S	1.946	(79, 45)	*	d= 1.472	(118)	-
	G	2.471	(7, 67)	*	d= 1.544	(8)	-
June	S	1.210	(34,139)	-	t= 1.299	(173)	-
	G	1.050	(37,127)	-	t= 0.683	(164)	-
July	S	1.277	(456,213)	*	d= 2.189	(466)	$p<0.05$
	G	1.418	(62, 7)	-	t= 0.785	(69)	-
August	S	1.229	(15,223)	*	d= 0.788	(17)	-
	G	2.171	(151, 22)	*	d= 3.872	(38)	$p<0.001$
1981/82 cohort							
1981							
July	S	1.904	(5, 8)	-	t= 0.128	(13)	-
	G	4.139	(45, 9)	*	d= 1.281	(28)	-
August	S	1.131	(78, 22)	-	t= 0.764	(100)	-
	G	1.164	(111, 59)	-	t= 0.747	(170)	-
September	S	2.531	(89, 86)	*	d= 2.941	(151)	$p<0.005$
	G	1.854	(116,311)	*	d= 0.464	(165)	-
October	S	1.969	(242,158)	*	d= 3.726	(397)	$p<0.001$
	G	1.442	(179,158)	*	d= 0.931	(336)	-
1982							
January	S	2.756	(23, 53)	*	d= 1.850	(31)	-
	G	5.831	(40,128)	*	d= 3.213	(44)	$p<0.005$
April	S	4.611	(46, 30)	*	d = 2.314	(70)	$p<0.025$
	G	1.397	(37, 14)	-	t= 0.986	(51)	-
May	S	2.232	(34, 32)	*	d= 0.376	(60)	-
	G	1.031	(31, 48)	-	t= 0.336	(79)	-
June	S	1.508	(51, 22)	-	t= 3.445	(73)	$p<0.001$
	G	2.723	(33, 20)	*	d= 0.575	(53)	-
July	S	3.438	(21, 21)	*	d= 2.117	(32)	$p<0.05$
	G	1.041	(21, 17)	-	t= 1.651	(38)	-
August	S		n too small				
	G		n too small				

Continued

		F.	(vl,v2)	Sig	Test	(d.f.)	Sig
1982/83 cohort							
1982							
July	S	1.081	(11, 11)	-	t= 0.239	(22)	-
	G	1.625	(35, 83)	*	d= 0.880	(46)	-
August	S	1.220	(46, 16)	-	t= 1.150	(62)	-
	G	1.938	(71, 50)	*	d= 0.515	(121)	-
September	S	1.925	(69,120)	*	d= 1.968	(111)	-
	G	1.113	(116, 91)	-	t= 1.050	(207)	-
October	S	1.822	(67, 92)	*	d= 1.142	(118)	-
	G	1.042	(55, 82)	-	d= 0.582	(137)	-
November	S	3.116	(20, 37)	*	d= 1.769	(27)	-
	G	2.443	(86, 52)	*	d= 2.229	(138)	$p<0.05$
1983							
March	S	4.423	(9, 9)	*	d= 1.388	(13)	-
	G	1.050	(40, 17)	-	t= 0.166	(57)	-

Table 4.5. *Erpobdella octoculata*. Regression equations for arithmetic mean weight (mg) plotted against time (days) for data from control (C) and enclosed (E) sites.

Equation: $\ln Y = RX + \ln Q$ H_o: slope = 0

		R ± 95% C.I.	Q	t (d.f.)	Sig
1980/81 cohort					
April 1981 to	C	0.0169 ± 0.0245	2.8581	2.967 (2)	-
July 1981	E	0.0159 ± 0.0090	3.0917	7.590 (2)	$p<0.05$
1981/82 cohort					
July 1981 to	C	0.0142 ± 0.0157	1.2465	3.903 (2)	-
October 1981	E	0.0167 ± 0.0219	1.0314	3.285 (2)	-
October 1981 to	C	-0.0002 ± 0.0627	2.0864	0.033 (1)	-
April 1982	E	0.0022 ± 0.0125	2.1434	2.198 (1)	-
April 1982 to	C	0.0234 ± 0.0244	2.6585	4.131 (2)	-
July 1982	E	0.0191 ± 0.0247	2.8847	3.329 (2)	-
1982/83 cohort					
July 1982 to	C	0.0164 ± 0.0242	1.3275	2.921 (2)	-
October 1982	E	0.0148 ± -.0202	1.5571	3.154 (2)	-
October 1982 to	C	0.0059 ± 0.0277	2.4954	2.690 (1)	-
March 1983	E	0.0050 ± 0.0059	2.7181	10.727 (1)	-

		R ± 95% C.I.	Q	t (d.f.)	Sig
1981/82 cohort					
July 1981 to	C	0.0080 ± 0.0043	1.2627	4.448 (7)	$p<0.005$
July 1982	E	0.0084 ± 0.0030	1.2273	6.562 (7)	$p<0.001$

Table 4.6. *Erpobdella octoculata*. The total geometric mean densities of cocoons recorded in the summers of 1981 and 1982 from control (C) and enclosed (E) sites.

	C	E
1981		
June	176.62	78.29
July	958.17	366.24
August	1715.78	444.94
September	1625.64	285.13
1982		
June	36.91	21.78
July	171.75	148.91
August	272.36	233.24
September	392.95	361.29

Table 4.7. *Erpobdella octoculata*. Mann-Whitney U tests comparing the densities of cocoons in control and enclosed sites for separate stone (S) and substratum (G) samples.

		U1	U2	N1	N2	Sig
1981						
June	S	128.5	31.5	20	8	$p<0.05$
	G	112	48	20	8	-
July	S	131	29	20	8	$p<0.05$
	G	32	8	10	4	-
August	S	132	28	20	8	$p<0.05$
	G	34	6	10	4	-
September	S	-	-	-	-	-
	G	37	3	10	4	$p<0.05$
1982						
June	S	168	72	15	16	-
	G	153.5	102.5	16	16	-
July	S	177.5	78.5	16	16	-
	G	113	127	16	15	-
August	S	194	62	16	16	$p<0.05$
	G	114.5	141.5	16	16	-
September	S	165	91	16	16	-
	G	123	117	16	15	-

Table 4.8. *Erpobdella octoculata*. Mortality data for the 1981/82 and 1982/83 cohorts from control (C) and enclosed (E) sites.

	1981/82 cohort		1982/83 cohort	
	C	E	C	E
Maximum density of cocoons (.m $^{-2}$)	1715.8	444.9	393.0	361.3
1. Estimated number of young produced (. m $^{-2}$)	7177.5	1899.4	1643.8	1542.3
2. Density of leeches in October (. m $^{-2}$)	203.8	260.9	30.2	48.3
3. Density of leeches in March (. m $^{-2}$)	-	-	10.1	31.1
4. Density of leeches in July (.m $^{-2}$)	11.7	16.3	-	-
Mortality between points 1-2 above	97.2%	86.3%	98.2%	96.9%
Mortality between points 1-3 above	-	-	99.4%	98.0%
Mortality between points 1-4 above	99.8%	99.1%	-	-

4.3.2 Glossiphonia complanata

During the course of this experiment a total of 12,335 leeches were collected from the lake. From weight-frequency data it was possible to split them into four cohorts. When sampling commenced in April 1981, the bimodal frequency distribution suggested that two cohorts were present; the leeches born in 1979 and surviving into their second year and the leeches born in 1980 and over-wintering for the first time. A new cohort appeared in May 1981, the offspring of the over-wintering leeches, and a second new cohort appeared in May 1982. These cohorts remained sufficiently distinct to enable them to be identified throughout the experiment and are hereafter referred to as the 1979/81, 1980/82, 1981/83 and 1982/84 cohorts.

In the graphs presented below, data for stone and substratum samples and for control and enclosed sites are presented on separate graphs. However, graphs for comparison are plotted on the same page. This was necessary because the two-year lifespan of the cohorts for this species would render combined graphs too complex to comprehend. For the E.octoculata data presented above, the one-year lifespan of the cohorts enabled combined graphs to be plotted. The 1979/81 G. complanata cohort was only present in the sample of April 1981 and is not included in some of the following graphs.

4.3.2.1 Density

The data showing geometric mean densities with 95% confidence limits for separate stone and substratum samples from control and enclosed sites are illustrated in figures 4.25 and 4.26.

For the 1979/81 cohort, in both control and enclosed sites, all leeches were to be found in the stone samples in April 1981.

For the 1980/82 cohort, 5.3% in control sites and 5.5% in enclosed sites, of the leeches were to be found on the stones in April 1981. These proportions increased to a peak of 20.2% in enclosed sites in June 1981 and to 10.7% in July 1981 in control sites. Little other pattern was discernible in the data, however, and by the samples of January and April 1982, leeches were only to be found in stone samples. Apart from the sample of September 1981, the proportion on the stones in enclosed sites was higher than in control sites.

The 1981/83 cohort first appeared in May 1981 in both stone and substratum samples when 13.4% in control sites and 22.3% in enclosed sites of the leeches were to be found on the stones. These proportions then varied between 3.4% and 20.8% in control sites and between 6.4% and 23.1% in enclosed sites but showed little discernible pattern, and no large-scale movements between the fractions were observed. In all samples, except those of June and July 1981 and May and June 1982 the proportion of leeches on the stones in enclosed sites was higher than in control sites.

The 1982/84 cohort first appeared in June 1982 when 21.3% in control sites and 13.6% in enclosed sites of the leeches were to be found in stone samples. These proportions then declined and varied between 3.9% to 11.2% in control sites and 6.4% to 13.1% in enclosed sites and, again, no obvious patterns were detected in the data. There was little difference in the proportions on the stones between control and enclosed sites.

The data comparing total geometric mean densities, stone sample densities with 95% confidence limits and substratum sample mean densities with 95% confidence limits between control and enclosed sites are given in figures 4.27, 4.28 and 4.29. The results of Mann-Whitney U tests, comparing densities in control and enclosed sites, are given in table 4.9.

For the 1980/82 cohort, the estimated total density of leeches in April 1981 was $103.5 m^{-2}$ in control sites and $279.1\ m^{-2}$ in enclosed sites. The regression equation $\text{Ln } Y = RX + \text{Ln } Q$, when applied to the period April 1981 to January 1982 for separate control and enclosed site data, indicated that during this time a constant decrease in density occurred.

Control sites: $R = -0.021 \pm 0.006$ $p<0.001$
$Q = 5.479$

Enclosed sites: $R = -0.022 \pm 0.007$ $p<0.001$
$Q = 6.209$

The cohort was still present in April 1982 but had entirely died out by May 1982. Mann-Whitney U tests indicated significant differences in density between control and enclosed sites in the samples of April 1981 to August 1981 from stone samples and in April 1981 and August 1981 from substratum samples. In these cases, the density was higher in enclosed rather than in control sites. In the remaining samples there were no significant differences.

In the 1981/83 cohort, the total density of leeches rose from $4.9\ m^{-2}$ in control sites and $5.2\ m^{-2}$ in enclosed sites in May 1981 to a peak of $216.0\ m^{-2}$ in September 1981 in control sites and $332.0\ m^{-2}$ in August 1981 in enclosed sites. The densities then declined and the regression equation $\text{Ln } Y = RX + \text{Ln}Q$, when applied to the period August 1981 to March 1983 for separate control and enclosed site data, indicated that the rate of decline could be regarded as constant.

Control sites: $R = -0.008 \pm 0.002$ $p<0.001$
$Q = 5.673$

Enclosed sites: $R = -0.007 \pm 0.002$ $p<0.001$
$Q = 5.353$

In both control and enclosed sites and in both stone and substratum samples, a sharp dip in density occurred between April and May 1982,i.e. during the breeding period. However, the confidence limits suggest that this may have been due just to sampling error. Mann-Whitney U tests indicated that the density in substratum samples from control sites was higher than in enclosed sites in October 1981, and that the reverse was true in stone samples in January 1982. However, for the rest of the two-year lifespan of the cohort there were no other significant differences between control and enclosed sites.

In the 1982/84 cohort, the density of leeches rose from 28.7 m^{-2} in control sites and 28.1 m^{-2} in enclosed sites in June 1982 to reach a maximum of 104.3 m^{-2} in control sites and 81.9 m^{-2} in enclosed sites in September 1982. The densities then remained more or less constant until the last sample of March 1983. The regression equation $\text{Ln } Y = RX + \text{Ln } Q$ did not indicate a significant relationship between density and time during the period August 1982 to March 1983.

Control sites:	$R = 0.000 \pm 0.001$	$p>0.05$
	$Q = 4.582$	
Enclosed sites:	$R = 0.002 \pm 0.005$	$p>0.05$
	$Q = 4.169$	

Mann-Whitney U tests indicated that the densities were significantly higher in substratum samples from control sites than in substratum samples from enclosed sites in July and August 1982. There were no other significant differences.

4.3.2.2 Biomass

The data showing geometric mean biomass with 95% confidence limits for separate stone and substratum sample data from control and enclosed sites are presented in figures 4.30 and 4.31.

For the 1980/82 cohort, 6.4% in control sites and 5.2% in enclosed sites of the leech biomass was present in stone samples in April 1981. These proportions then varied between 3.6% in August 1981 to 31.9% in September 1981 in control sites,and between 5.7% in August 1981 and 25.6% in July 1981 in enclosed sites. In the two samples at the end of the cohort, January and April 1982, all the biomass was present in the stone samples.

In the 1981/83 cohort, 13.4% in control sites and 22.3% in enclosed sites of the biomass was present in stone samples in May 1981. In control sites the proportion then fluctuated between 2.4% in November 1982 and 31.2% in May 1982, while in enclosed sites the proportion varied between 4.2% in June 1981 and 31.8% in January 1982. In most samples the proportion on the stones was higher in enclosed than in control sites.

In the 1982/84 cohort, 20.1% in control sites and 10.3% in enclosed sites of the biomass was on the stones in June 1982. In control sites the proportions then varied between a maximum of 13.8% in April 1982 to 3.3% in March 1983. In enclosed sites the maximum of 13.3% occurred in October 1982 and the minimum of 7.8% in November 1982.

The data comparing total geometric mean biomass, stone sample biomass with 95% confidence limits and substratum sample mean biomass with 95% confidence limits between control and enclosed sites are given in figures 4.32, 4.33 and 4.34 respectively. The results of Mann-Whitney U tests, comparing biomass between control and enclosed sites are given in table 4.10.

For the 1980/82 cohort in control sites, the estimated total biomass in April 1981 was 10. $g.m^{-2}$, while in enclosed sites the corresponding value was 3.4 $g.m^{-2}$. In control sites, the biomass increased to a peak of 1.7 $g.m^{-2}$ in June 1981 and then declined so that by the last sample in which the cohort was present, i.e. April 1982, the biomass present was just 0.007 $g.m^{-2}$. In enclosed sites, biomass decreased between April and July 1981 and then rose to a maximum of 4.1 $g.m^{-2}$ in August 1982 before declining to 0.003 $g.m^{-2}$ in April 1982. Mann-Whitney U tests suggested significant differences between control and enclosed sites in April 1981, May, June, July and August 1981 for stone samples in April, August and September 1981 for substratum samples. In all cases, the biomass was higher in enclosed sites.

For the 1981/83 cohort, the total biomass present when the cohort first appeared in May 1982 was 0.005 $g.m^{-2}$ in both control and enclosed sites. The biomass then quickly rose to a maximum of 4.1 $g.m^{-2}$ in September 1981 in control sites and to 5.2 $g.m^{-2}$ in August 1981 in enclosed sites. Biomass then declined over the rest of the lifespan of the cohort. However, a sharp decline followed by a recovery occurred during the breeding season of 1982 (April-May) and this corresponded with the drop and recovery of density mentioned in section 4.3.2.1. At the end of the cohort, the biomass present in control sites was 0.028 $g.m^{-2}$ while the corresponding value in enclosed sites was 0.032 $g.m^{-2}$. Mann-Whitney U tests indicated differences between control and enclosed sites in August and October 1981 and January 1982 for stone samples only. In these cases biomass was higher in enclosed sites.

For the 1982/84 cohort the biomass in June 1982, when the cohort first appeared in samples, was 0.039 $g.m^{-2}$ and 0.042 $g.m^{-2}$ in respective control and enclosed sites. In control sites biomass reached a maximum of 2.1 $g.m^{-2}$ in November 1982 and then declined slightly to 2.0 $g.m^{-2}$ in March 1983. In enclosed sites biomass continued to rise until March 1983, reaching a maximum of 2.6 $g.m^{-2}$. Mann-Whitney U tests indicated that in March 1983 the biomass in stone samples from enclosed sites was significantly higher than in stone samples from control sites. No other significant differences were indicated.

4.3.2.3 Growth

Figures 4.35 and 4.36 present the size structure of leeches from separate stone and substratum samples from control and enclosed sites. The size structure of leeches from combined stone and substratum sample data for control and enclosed sites are presented in figure 4.37. Figures 4.38 and 4.39 present the arithmetic mean individual weights with 95% confidence limits for separate stone and substratum samples from control and enclosed sites. The results of t and d tests, comparing stone sample versus substratum sample mean individual weights for control and enclosed sites are given in table 4.11. In the majority of samples mean weight was higher for leeches on the stones than for leeches in substratum samples.

In the 1980/82 cohort in control sites, mean weight in stone samples rose from 11.9 mg in April 1981 to a maximum of 65.7 mg in April 1982 while in the substratum the mean weight was 10.8 mg in April 1981 and a maximum of 59.1 mg in October 1981. In enclosed sites mean weight in stone samples was 10.8 mg in April 1981 and reached a maximum of 65.4 mg in October 1981 before declining to 56.7 mg in April 1982. In the substratum mean weight was 12.4 mg in April 1981 and a maximum of 58.7 mg in October 1981. T and d tests indicated that the mean weight was significantly higher for leeches on the stones in May 1981 in control sites and in May, June, July and September 1981 in enclosed sites.

In the 1981/83 cohort, leeches were first recorded from samples in May 1981 with a mean weight of 1.0 mg. In stone samples from control sites, the mean weight increased to 23.6 mg by January 1982 and then declined to 17.3 mg in May 1982. After this, the mean weight rose quickly and reached a maximum of 70.0 mg in March 1983. In substratum samples the mean weight rose to 19.8 mg in October 1981, declined to a nadir of 14.5 mg in May 1982 and then increased to a maximum of 75.4 mg in November 1982. In enclosed sites the mean weight in stone samples in January 1982 was 28.9 mg in May 1982 17.6mg and a maximum of 77.9 mg in March 1983. In substratum samples the mean weight was 23.1 mg in January 1982 and a maximum of 77.7 mg in November 1982. T and d tests indicated that mean weight was significantly higher on the stones in October 1981 and in January, April and June 1982 in control sites and in July 1981 and January, April and June 1982 in enclosed sites. In June 1981, when the young leeches would be leaving the adults, mean wight was significantly higher in substratum samples in both control and enclosed sites.

In the 1982/84 cohort, the mean weight of leeches in stone samples from control sites as 1.3 mg in June 1982 and rose to a maximum of 27.6 mg by March 1983. In substratum samples, mean weight in June 1982 was 1.6 mg and rose to a maximum of 22.0 mg in November 1982. In stone samples from from enclosed sites, mean weight in June 1982 was 1.1 mg and had reached 34.3 mg by March 1983. In substratum samples the mean weight in June 1982 was 1.7 mg and had reached 29.3mg by March 1983. T and d tests showed that in June 1982 the mean weight was significantly higher in substratum samples in both control and enclosed sites. In August, September and November 1982 and March 1983 the mean weight was significantly higher on stones in enclosed sites and the same was true in March 1983 in control sites.

The data comparing the estimated arithmetic mean individual weights from combined stone and substratum sample data, stone sample mean weights with 95% confidence limits and substratum sample mean weights with 95% confidence limits for control and enclosed sites are given in figures 4.40, 4.41 and 4.42. The results of t and d tests comparing weights in control and enclosed sites are given in table 4.12.

In the 1980/82 cohort, overall mean weight rose from 10.9 mg in April 1981 to 65.7 mg in April 1982 in control sites and from 12.3 mg in April 1981 to 64.5 mg in January 1982 in enclosed sites. T and d tests indicated significant differences between mean weights in control and enclosed sites in April, June and July 1981 from both stone and substratum samples. In each case the weights were higher in enclosed sites.

In the 1981/83 cohort, the mean weight rose after hatching to 19.8 mg in October 1981 and then declined to 14.5 mg in May 1982 in control sites. In enclosed sites the respective figures were 27.9 mg and 17.2 mg. After May, the weights rapidly increased to reach a maximum in November 1982 of 75.4 mg in control sites and 77.7 mg in the enclosed sites. T and d tests indicated that weights were significantly higher in control sites in July 1981 for substratum samples and higher in enclosed sites in August, September and October 1981 and January 1982 for both stone and substratum samples. In October 1982, the same was true of stone samples alone.

In the 1982/84 cohort, the mean weight in June 1982 was 1.5 mg in control sites and 1.6 mg in enclosed sites. In control sites a maximum of 22.1 mg was achieved in November 1982 and in enclosed sites the peak of 29.7 mg occurred in March 1983. T and d tests indicated that the weights were significantly higher in enclosed sites in June, August, September, October and November 1982 and March 1983 in leeches from stone samples and in July and October 1982 and March 1983 in leeches from substratum samples.

The regression equations describing growth in different periods within each cohort are presented in table 4.13. After hatching in April/May the growth rate of the new young was high until September and then remained low over the winter months. In May of the following year the growth rate increased again and was high until October/November before again declining over winter.

In the 1980/82 cohort, which was starting its second year in April 1981, the regression equations suggested that the growth-rate was constant between April 1981 to October 1981. An analysis of covariance indicated that there was no significant difference between the growth-rate in control and enclosed sites (F=0.707 with 1,10 d.f.). Between October 1981 and April 1982 there was no relationship between weight and time.

In the 1981/83 cohort, the growth-rate of the newly-hatched young was constant between June and September 1981 and there was no significant difference between control and enclosed sites (F=0.368 with 1,4 d.f). Between September 1981 and May 1982 there was no significant relationship between weight and time. However, between May and November 1982 a significant relationship was again established. During this period the growth-rate was lower than in the initial period of growth after release from the adults and the growth-rates were the same in control and enclosed sites (F=0.349 with 1,10 d.f.). The growth-rate in this period was similar to that in the 1980/82 cohort for leeches of the same age. However, in control sites, the variance around the point estimates of the slopes was significantly different between data from these two periods (F=14.322 with 5,5 d.f. p<0.01). In enclosed sites the variances (F=2.199 with 5,5 d.f.) and slopes (F=2.218 with 1,10 d.f.) were not significantly different. Between November 1982 and March 1983 no growth occurred in either control or enclosed sites, but as only two samples covered this period a regression equation could not be fitted.

In the 1982/84 cohort, the growth-rate of the newly-released young was constant between June and September 1982 and there was no significant difference between control and enclosed sites (F=0.002 with 1,4 d.f.). There was also no significant difference between the growth-rates of these young and the young in the 1981/83 cohort (control sites: F=0.162 with 1,4 d.f. and enclosed sites: F=0.967 with 1,4 d.f.) during this period. Between September 1982 and March 1983 little or no growth occurred and there was no significant relationship between weight and time.

4.3.2.4 Reproduction

In 1981, breeding data were only collected for leeches taken in stone samples at the times of the monthly samples. Additional samples, also from stones only, yielded further information on fecundity.

On 22nd April 1981, when sampling commenced, 39.7% of leeches on the stones in control sites and 36.7% of leeches on stones in enclosed sites were sitting on eggs. A further 15.1% in control sites and 29.0% in enclosed sites still had eggs in their oviducts, giving a total of 54.8% breeding in control sites and 65.7% breeding in enclosed sites. A sample of 21 leeches revealed that the mean number of eggs per breeding leech was 21.8 ± 2.9.

In an additional sample, taken on 8th May,18.4% of leeches in control sites (n=38) and 17.7% of leeches in enclosed sites (n=79) were sitting on eggs. A further 55.3% in control sites and 59.5% in enclosed sites were carrying young, giving total breeding estimates of 73.7% in control sites and 77.2% in enclosed sites. A further sample of leeches taken from either end of the sampling shore revealed that the mean number of eggs per breeding leech was 23.3 ± 2.1 (n=32) and the mean number of young per leech was 19.0 ± 2.1 (n=31).

By 27th May no leeches were still brooding eggs and only 4.0% were carrying young. No breeding leeches were observed after this date.

From the maximum proportion of leeches found breeding, the maximum number of mature leeches present during the breeding period and the mean number of eggs per breeding leech (from the data of 8th May, above) the estimated maximum recruitment of young into the population was 1776.5 m^{-2} in control sites and 5020.6 m^{-2} in enclosed sites. This assumes that all eggs hatched successfully.

In 1982, breeding data were collected from stone and substratum samples at the time of the monthly samples. Additional samples from stones only yielded further information on fecundity.

No leeches brooding eggs were observed on 15th April 1982. However, 95.5% of the leeches on stones in control sites and 93.9% on stones in enclosed sites had eggs in their oviducts. In the substratum 85.2% in control sites, and 88.9% in enclosed sites, of the leeches had eggs in their oviducts. From the density data for separate stone and substratum samples, this gave an estimated 86.2% breeding in control sites and 82.3% breeding in enclosed sites. The mean number of eggs in oviducts was 31.7 ± 2.4 (n=89) in control sites and 36.9 ± 3.1 (n=86) in enclosed sites and this difference was statistically significant ($d=2.585$ with 160 d.f. $p<0.05$).

In an additional sample, taken on 27th April from outside the main sampling area, 92.1% of leeches were sitting on eggs and 2.6% still had eggs in their oviducts (n=38). The mean number of eggs per breeding leech was 26.8 ± 3.8 (n=35). Another sample on 6th May showed that 7.5% of leeches were sitting on eggs and 67.9% had young (n=53). The mean number of young per breeding leech was 25.3 ± 4.5 (n=36). A few leeches still had eggs in their oviducts.

On the 12th May, 21.2% of leeches on stones in control sites and 23.9% on stones in enclosed sites still carried young. In the substratum, the figures were 2.9% and 15.8% for respective control and enclosed sites. From the density data, this gave a total of 7.7% breeding in control sites and 18.3% breeding in enclosed sites. The mean number of young per breeding leech was 24.6 ± 18.9 (n=11) in control sites and 20.5 ± 9.8 (n=11) in enclosed sites and there was no significant difference between these values ($d=0.640$ with 13 d.f.). By the 20th May, few leeches still carried young. The mean number per breeding leech was 7.0 ± 2.7 (n=25) and obviously most of the young had already left the adults.

From the maximum proportion of leeches found breeding in monthly samples, the maximum number of mature leeches present during the breeding period and the mean number of eggs per breeding leech (from the data of 27th April, above), the estimated maximum recruitment of young into the population was 2219.8 m^{-2} in control sites and 1450.6 m^{-2} in enclosed sites.

4.3.2.5 Mortality

The data describing mortality are given in table 4.14 and the regression equations covering the periods when the rate of mortality was constant were given in section 4.3.2.1.

The mortality rates in the first few months of the leech's life-span were very high. In the 1981/83 cohort, 87.8% in control sites and 96.5% in enclosed sites of the leeches released during breeding had died by September 1981. By the time these leeches were in their first breeding season, mortality had increased to 94.6% and 98.6% respectively and by their second breeding season in 1982, the mortality had reached 99.8% and 99.9% in respective control and enclosed sites. 2.9% in control sites and 4.9% in enclosed sites of the leeches which survived to April of their first year went on and survived to the breeding season of their second year. In the 1980/82 cohort, 0.5% in control sites and 0.1% in enclosed sites of the leeches present in April 1981 survived to the breeding season of April/May 1982.

In the 1982/84 cohort, 95.3% in control sites and 94.4% in enclosed sites of the new young had died by September 1982 and then little or no further mortality occurred until the last sample of March 1983.

The regression equations given in section 4.3.2.1 suggested that, for the 1980/82 cohort, the mortality rate was constant between April 1981 and January 1982 and an analysis of covariance suggested that there was no difference in this rate between control and enclosed sites ($F=0.085$ with 1,12 d.f.). In the 1981/83 cohort, the mortality rate was constant between August 1981 to March 1983 in both control and enclosed sites and there was no significant difference between their respective rates ($F=0.169$ with 1,22 d.f.). In the 1982/84 cohort, there was no significant relationship between density and time during the period August 1982 to March 1983.

4.3.2.6 Production

Data illustrating the rate of biomass production, and calculated using the instantaneous growth-rate method, for leeches sampled between April 1981 and March 1983 are presented in figure 4.43.

Using the instantaneous growth-rate method of calculating production, the annual production of all leeches present between April 1981 and April 1982 was 4.0 $g.m^{-2}$ in control sites and 8.9 $g.m^{-2}$ in enclosed sites. The mean biomass over this period was 2.3 $g.m^{-2}$ in control sites and 1.6 $g.m^{-2}$ in enclosed sites giving turnover rates of 1.8 and 3.7 respectively. Between April 1982 and March 1983, the production of all leeches was 2.3 $g.m^{-2}$ in both control and enclosed sites. The mean biomass was 1.6 $g.m^{-2}$ in both control and enclosed sites giving a turnover rate of 1.4.

In the 1980/82 cohort, production between April 1981 and April 1982 was 1.3 $g.m^{-2}$ in control sites and 3.1 $g.m^{-2}$ in enclosed sites. The mean biomass was 0.5 $g.m^{-2}$ in control sites and 1.1 $g.m^{-2}$ in enclosed sites giving respective turnover rates of 2.6 and 2.8.

In the 1981/83 cohort, production between May 1981 and April 1982 was 2.7 g.m.$^{-2}$ in control sites and 5.8 g.m^{-2} in enclosed sites. The mean biomass present during this period was 2.0 g.m^{-2} and 1.5 g.m^{-2} respectively giving turnover rates of 1.4 and 3.9. Between April 1982 and March 1983 the production was 0.6 g.m^{-2} in control sites and 0.7 g.m^{-2} in enclosed sites with a mean biomass of 0.3 g.m^{-2} in both control and enclosed sites. The turnover rates were 2.0 and 2.3 respectively.

In the 1982/84 cohort, production between 1982 and March 1983 was 1.7 g.m^{-2} in control sites and 1.6 g.m^{-2} in enclosed sites. The mean biomass was 1.5 g.m^{-2} in control sites and 1.6 g.m^{-2} in enclosed sites, giving turnover rates of 1.1 and 1.0 respectively.

The above data are based on the leeches actually recorded in samples. However, this may lead to an under-estimate of the production for two reasons. Firstly, it ignores the possible production by the large number of young that were never found in samples. Secondly, the maximum density of each new cohort continued to rise after breeding had finished. In the 1981/83 cohort, the maximum density in control sites occurred in September 1981 and in enclosed sites in August 1981, while breeding had finished in May. In the 1982/83 cohort, maximum densities occurred in September 1982 in both control and enclosed sites and, again, breeding had finished in May. As the breeding season was short and well-defined, the number of leeches present at these maxima must also have been present at the end of the breeding season, though for some reason they were not sampled. Therefore, it seems reasonable to include them in the estimates of production and this was done as follows. In the 1981/83 cohort in control sites, for example, a maximum density of 216 m^{-2} occurred in September 1981. These leeches must also have been present at the end of the breeding season in May 1981 and are therefore included in the estimates of biomass and mean weights for that month. Production was then calculated using the instantaneous growth-rate method for the period May to September, and then incorporated into the cohort and annual estimates. The same method was used for enclosed sites and for both control and enclosed sites in the 1982/83 cohort.

The remaining problem is the production by young leeches which never appeared in samples. In the 1981/83 cohort in control sites, 1776.5 m^{-2} were estimated to have entered the cohort, but the maximum density recorded was just 216.0 m^{-2} in September 1981. In the *Erpobdella octoculata* data (section 4.3.1.6) the young were incorporated into production estimates using both cocoon density and hatching data, for each month during the breeding season. For *Glossiphonia complanata* breeding took place over just one month and so the mortality of the young must have occurred somewhere between May and the maximum density recorded in September. However, it is not known whether the mortality rate was constant over this period or, if not, where the mortality occurred. It is, therefore, perhaps best to assume that most of the missing young died soon after hatching, without significant addition to the production of the cohort, and only to adjust the production estimates with the young known to have survived until the maximum densities were reached.

On this basis, the annual production of all leeches present between April between April 1981 and April 1982 was 9.4 $g.m^{-2}$ in control sites and 14.9 $g.m^{-2}$ in enclosed sites. The mean biomass over the same period was 2.9 $g.m^{-2}$ in both control and enclosed sites, giving respective turnover rates of 3.2 and 5.1. Between April 1982 and March 1983, production was 4.1 $g.m^{-2}$ in control sites and 3.8 $g.m^{-2}$ in enclosed sites. The mean biomass was 1.6 g.m in control sites and 1.7 g.m in enclosed sites, giving turnover rates of 2.6 and 2.2 respectively.

In the 1981/83 cohort, production between May 1981 and April 1982 was 8.1 $g.m^{-2}$ in control sites and 11.7 $g.m^{-2}$ in enclosed sites. The mean biomass was 2.7 $g.m^{-2}$ in control sites and 1.9 $g.m^{-2}$ in enclosed sites, giving turnover rates of 3.0 and 6.2 respectively.

In the 1983/84 cohort, production between June 1982 and March 1983 was 3.4 $g.m^{-2}$ in control sites and 3.2 $g.m^{-2}$ in enclosed sites. The mean biomass was 1.6 $g.m^{-2}$ in control sites and 1.7 $g.m^{-2}$ in enclosed sites giving turnover-rates of 2.1 and 1.9 respectively.

The Allen curves for the 1981/83 cohort from separate control and enclosed site data are given in figures 4.44 and 4.45. Because the maximum densities recorded did not coincide with the minimum mean weights, and because negative production occurred over the winter months, i.e. a loss of weight, there is a wide scatter of points. The smoothed lines fitted, therefore, are somewhat arbitary and the estimated recruitment of young have not been included in the data set. Production in control sites was estimated at 4.6 $g.m^{-2}$ and at 5.4 $g.m^{-2}$ in enclosed sites. It should be noted that this is production over two years, the life-span of the cohort, and not an annual estimate.

Figure 4.25. Glossiphonia complanata. Geometric mean density ± 95% confidence limits for the different cohorts in separate stone (S) and substratum (G) samples from control sites.

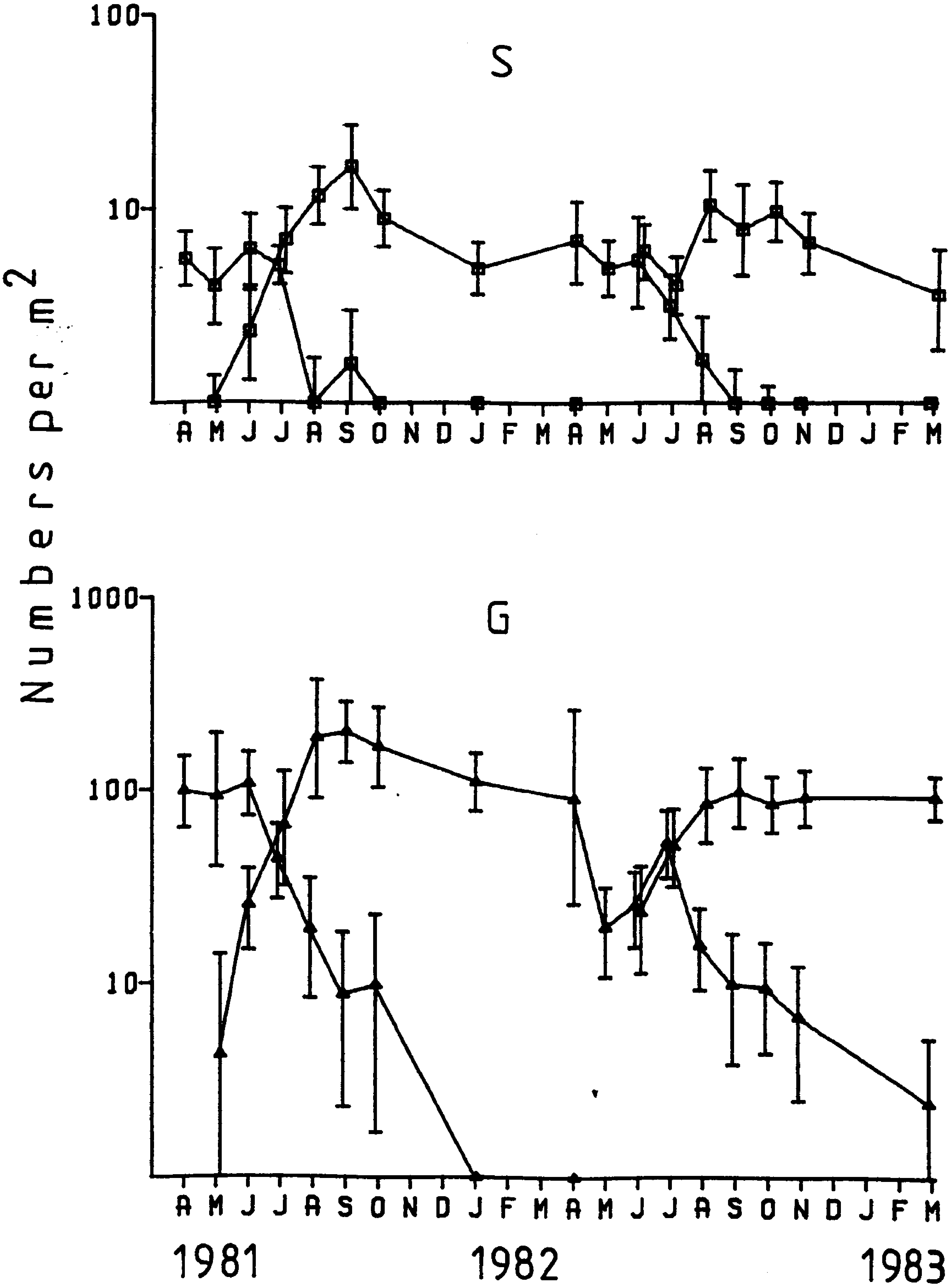
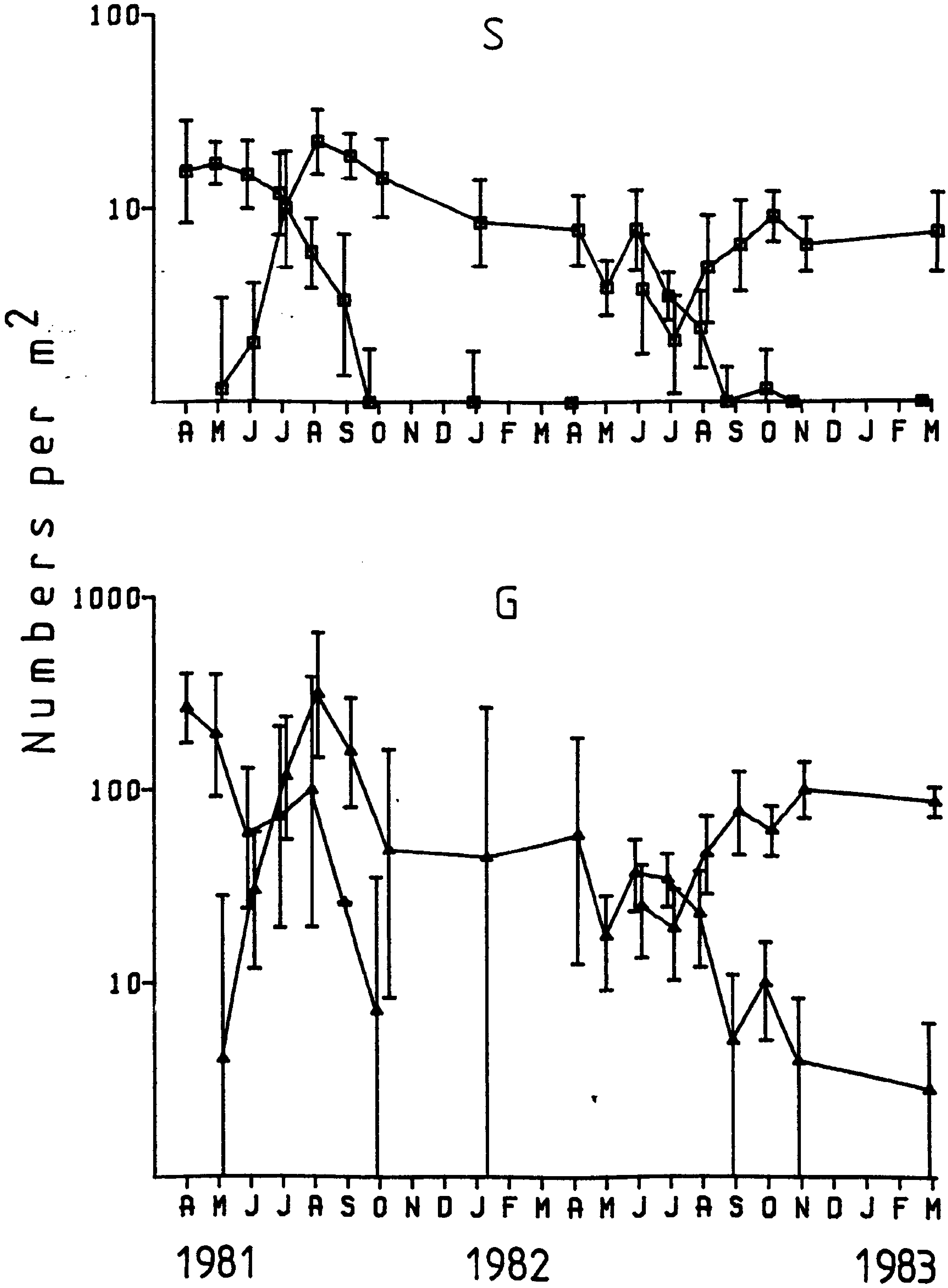


Figure 4.26. Glossiphonia complanata. Geometric mean density ± 95% confidence limits for the different cohorts in separate stone (S) and substratum (G) samples from enclosed sites.



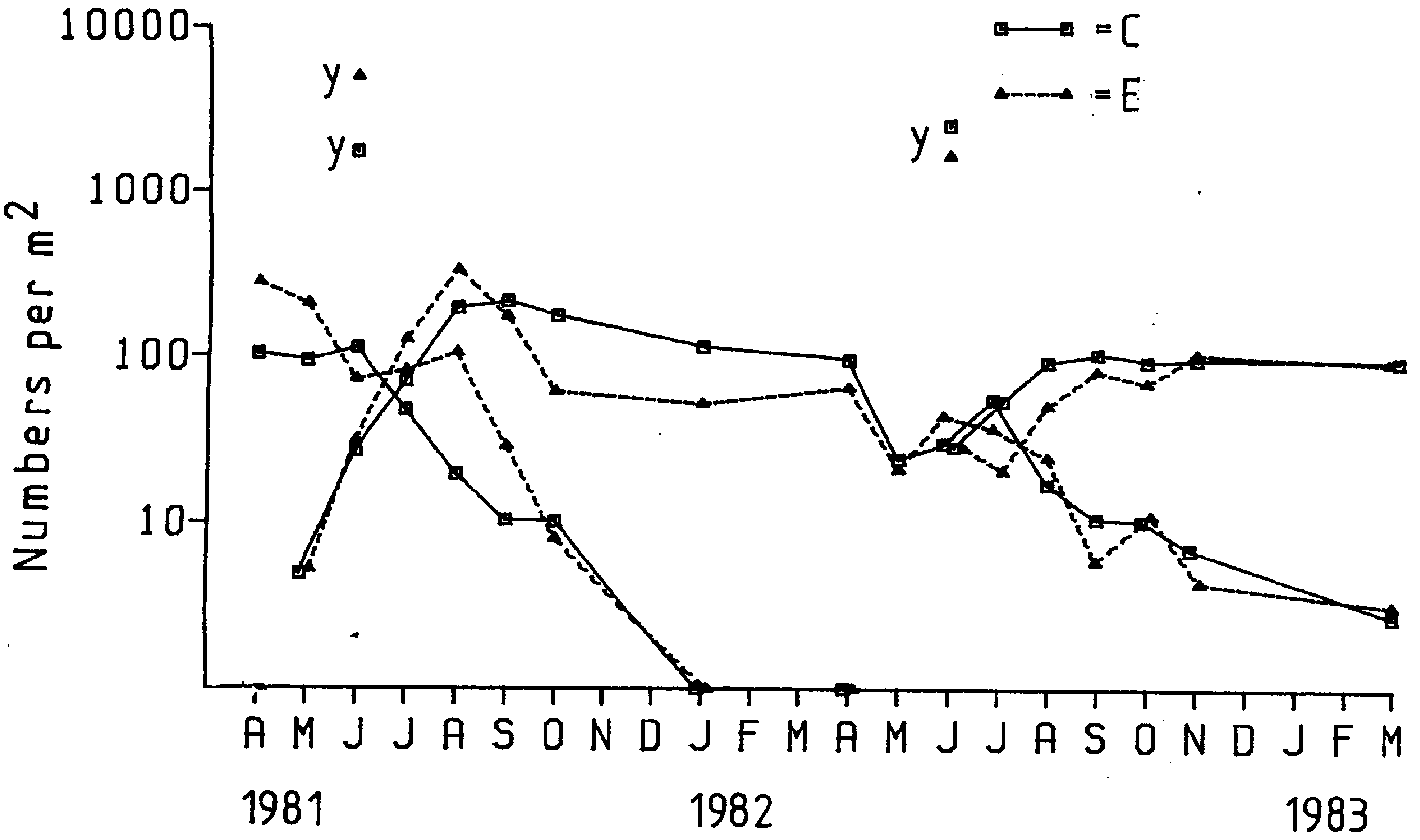


Figure 4.27. Glossiphonia complanata. Total geometric mean density for the different cohorts from combined stone and substratum sample data and the estimated number of young (y) entering the 1981/83 and 1982/84 cohorts in control (C) and enclosed (E) sites.

Figure 4.28. Glossiphonia complanata. Geometric mean density with 95% confidence limits for the different cohorts in stone samples from control (C) and enclosed (E) sites.

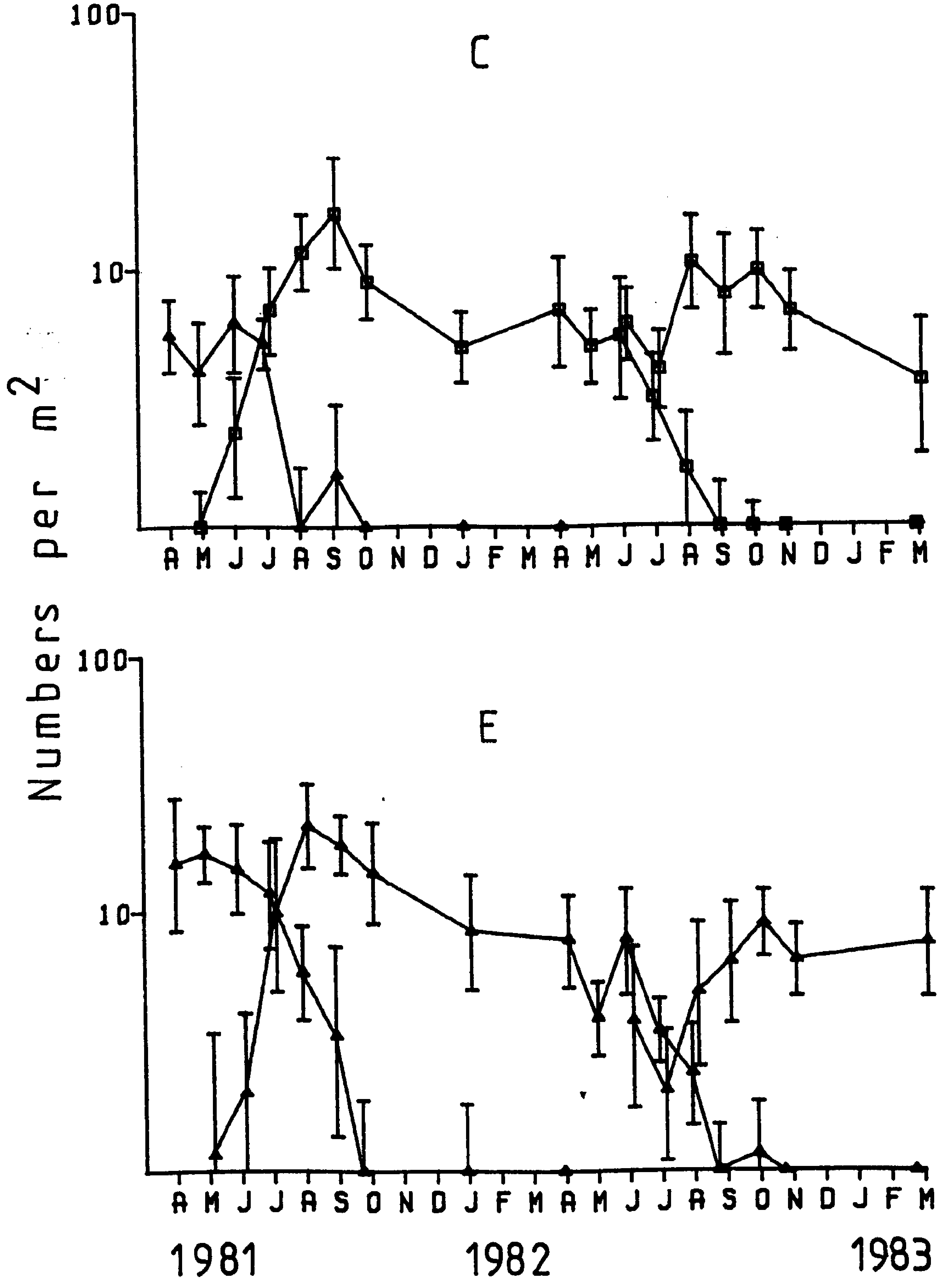


Figure 4.29. Glossiphonia complanata. Geometric mean density with 95% confidence limits for the different cohorts in substratum samples from control (C) and enclosed (E) sites.

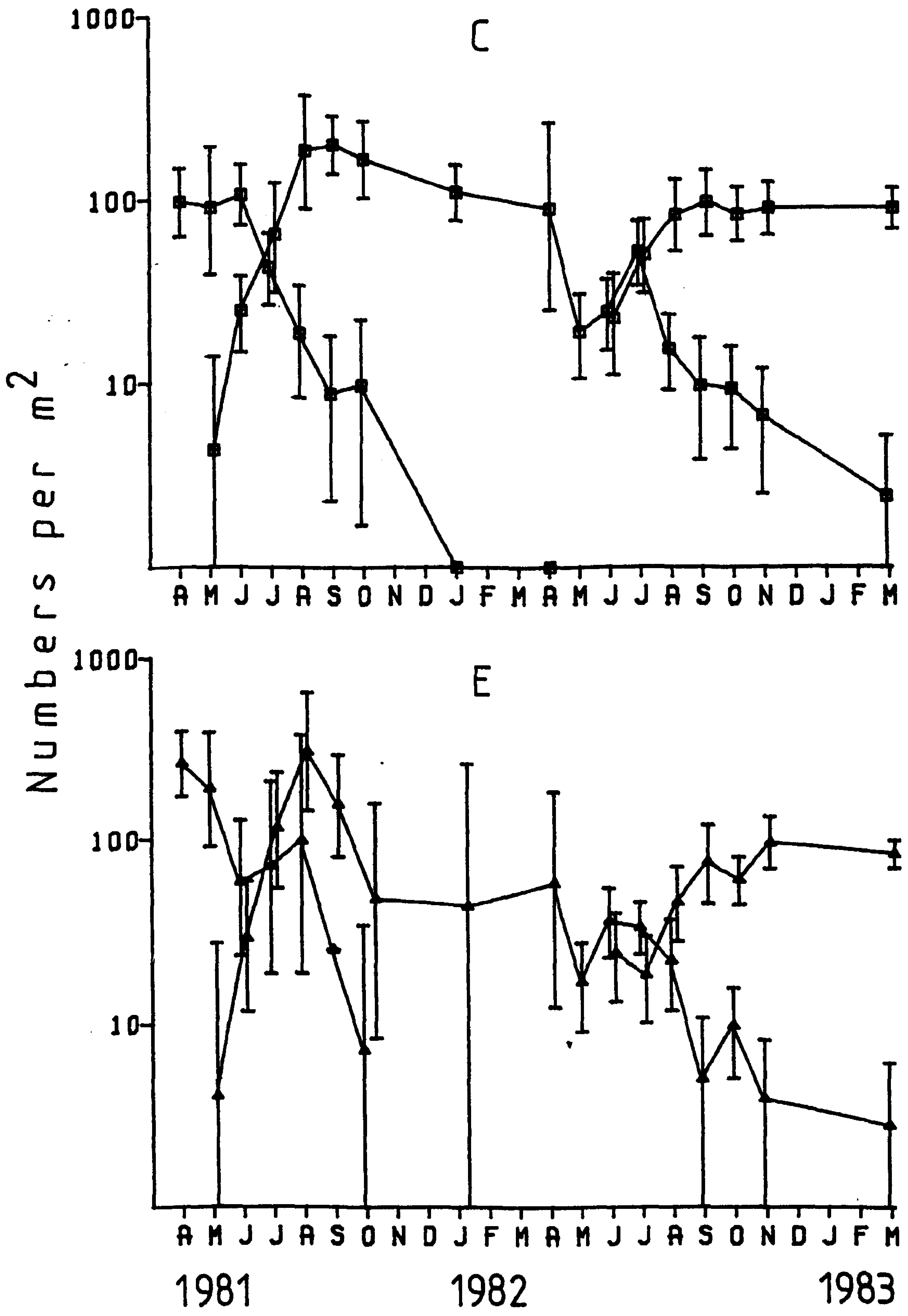


Figure 4.30. Glossiphonia complanata. Geometric mean biomass ± 95% confidence limits for the different cohorts in separate stone (S) and substratum (G) samples from control sites.

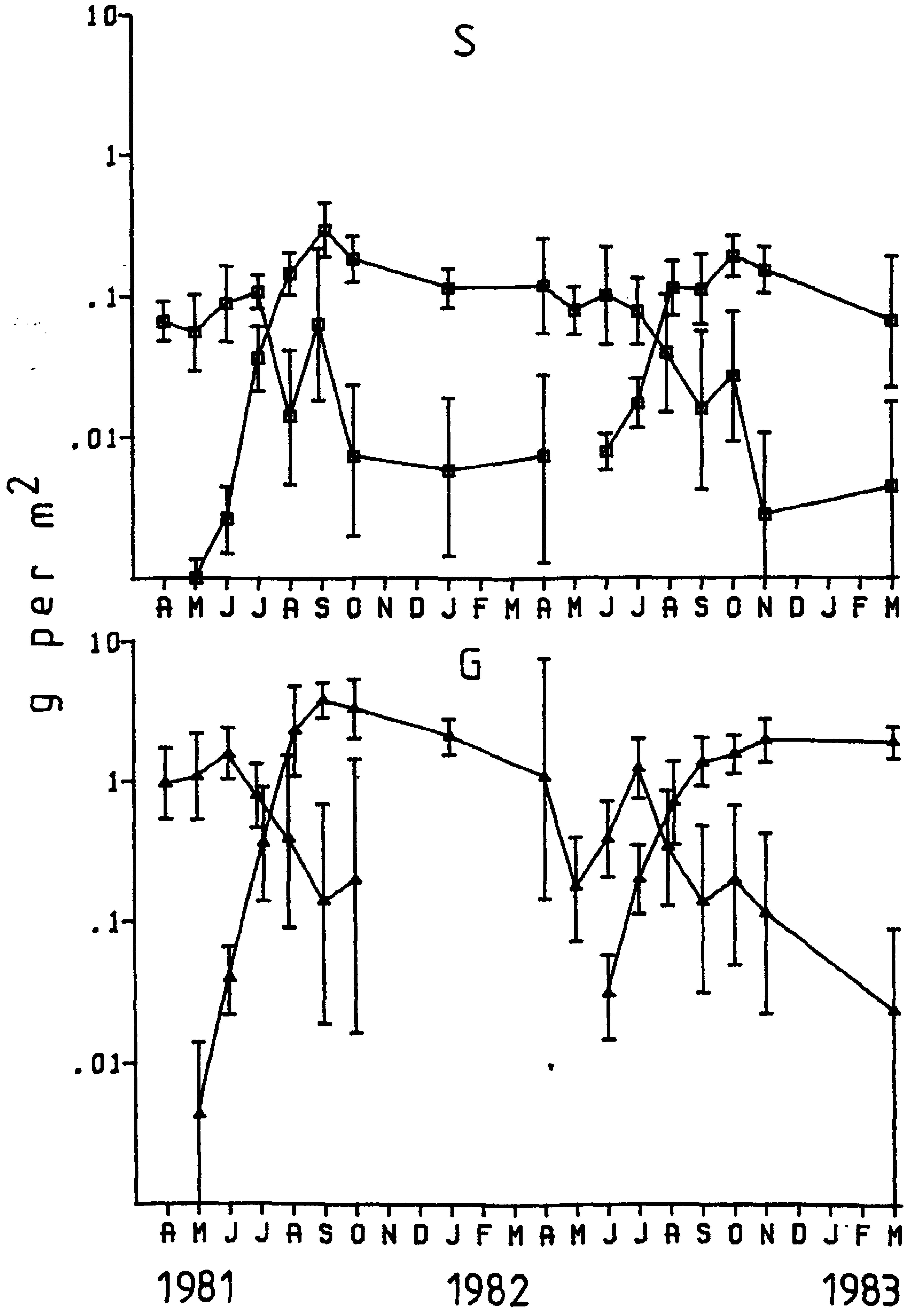
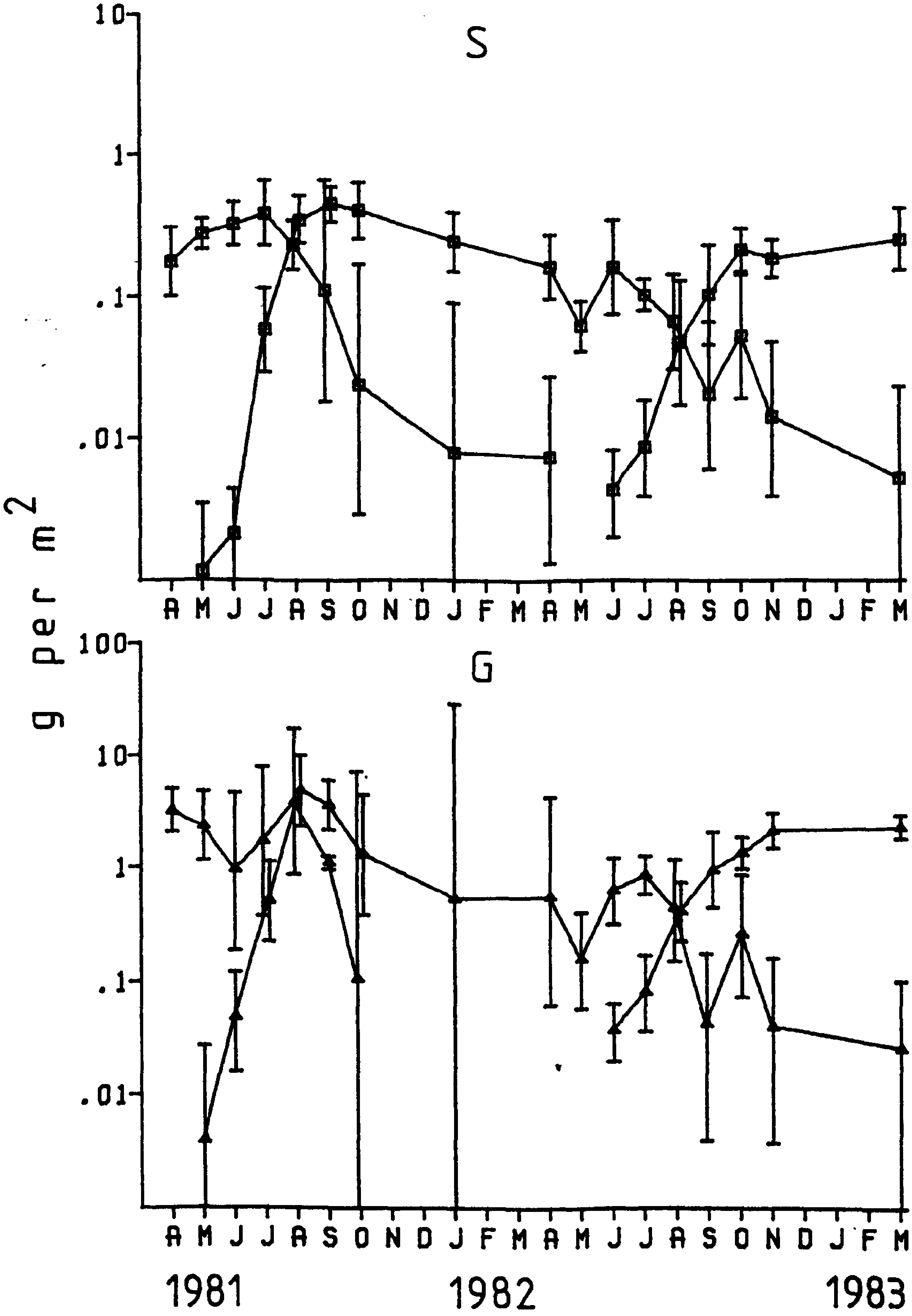


Figure 4.31. Glossiphonia complanata. Geometric mean biomass ± 95% confidence limits for the different cohorts in separate stone (S) and substratum (G) samples from enclosed sites.



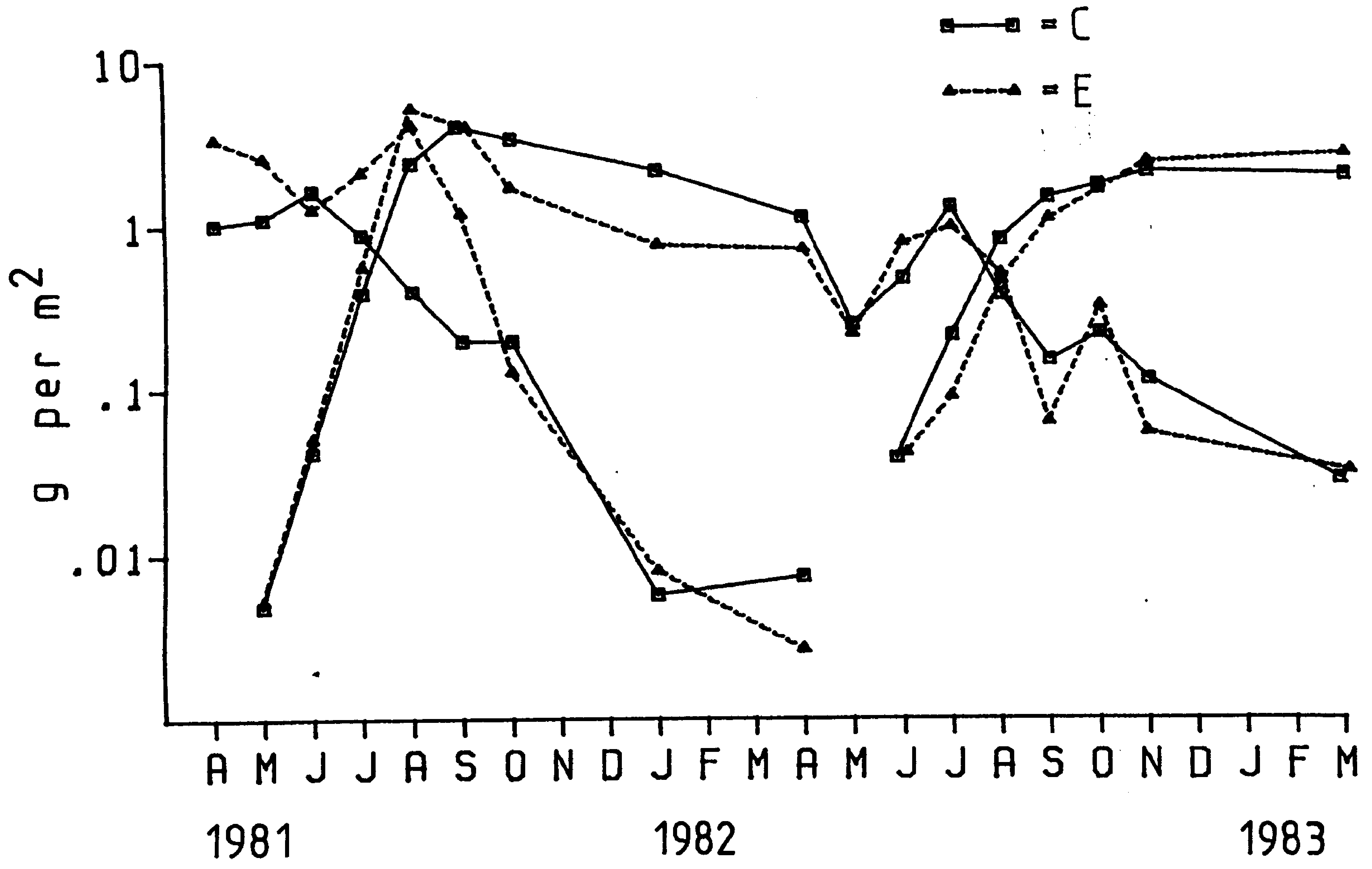


Figure 4.32. Glossiphonia complanata. Total geometric mean biomass for the different cohorts from combined stone and substratum sample data in control (C) and enclosed (E) sites.

Figures 4.33. Glossiphonia complanata. Geometric mean biomass ± 95% confidence limits for the different cohorts in stone samples from control (C) and enclosed (E) sites.

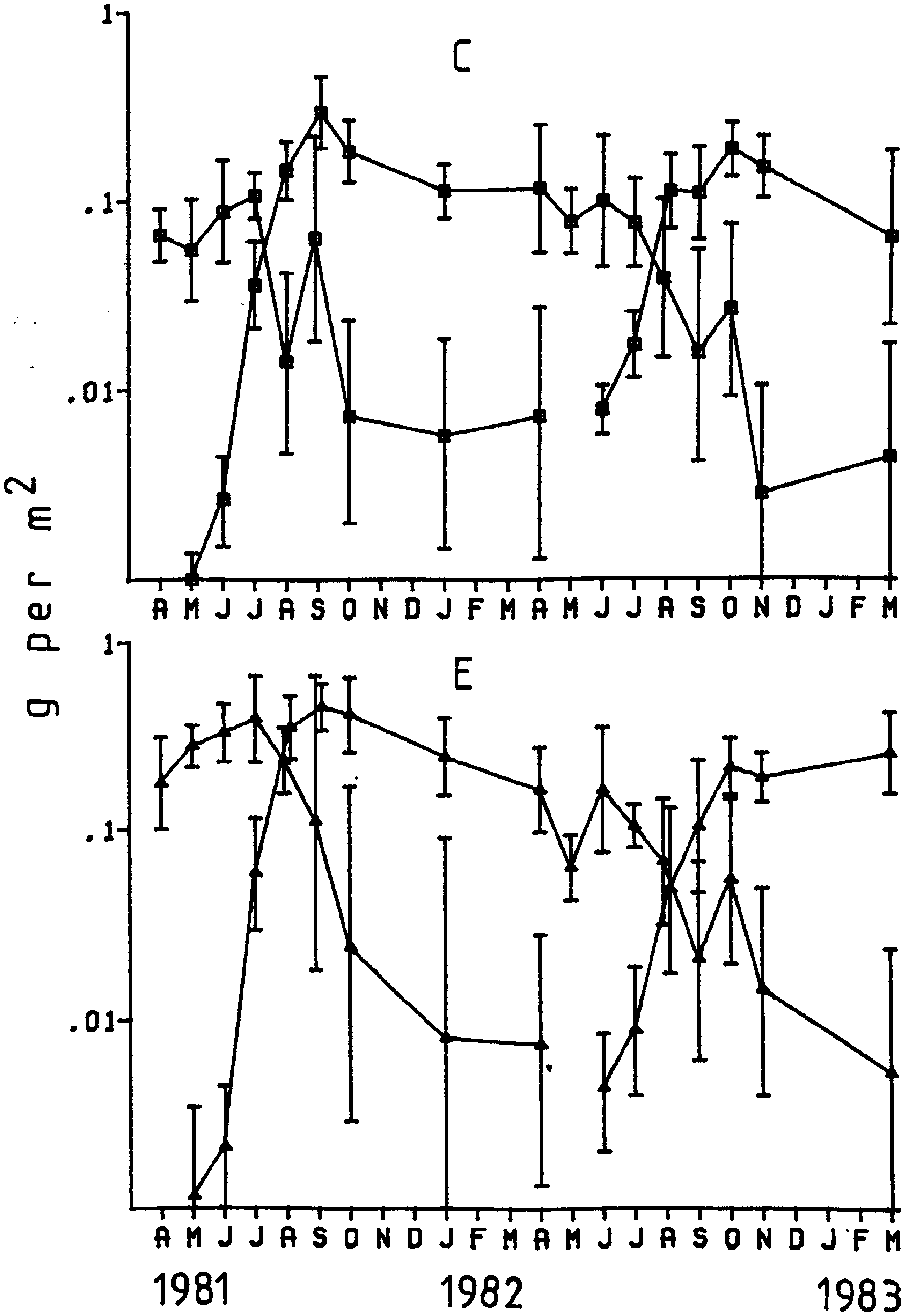


Figure 4.34. Glossiphonia complanata. Geometric mean biomass ± 95% confidence limits for the different cohorts in substratum samples from control (C) and enclosed (E) sites.

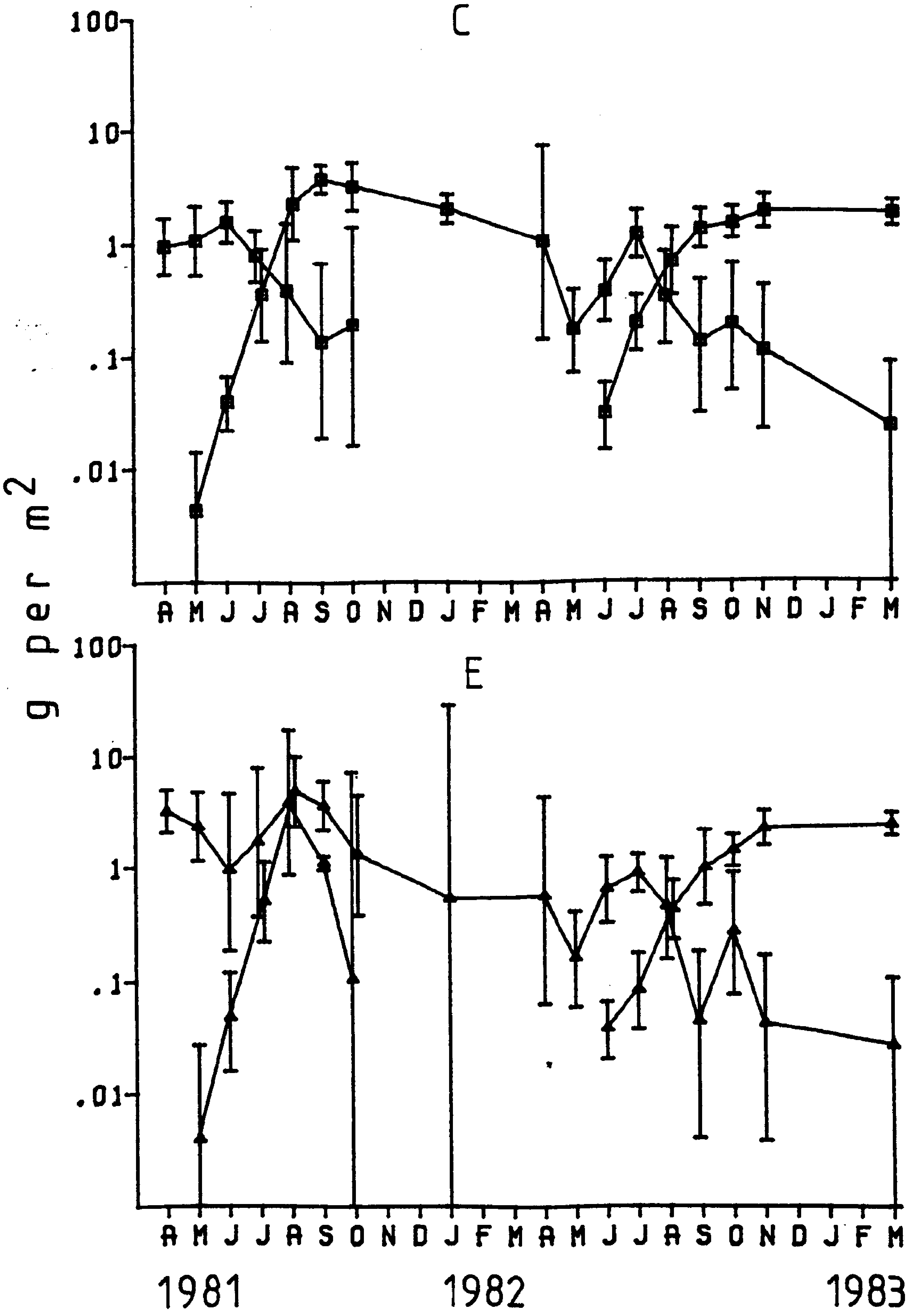
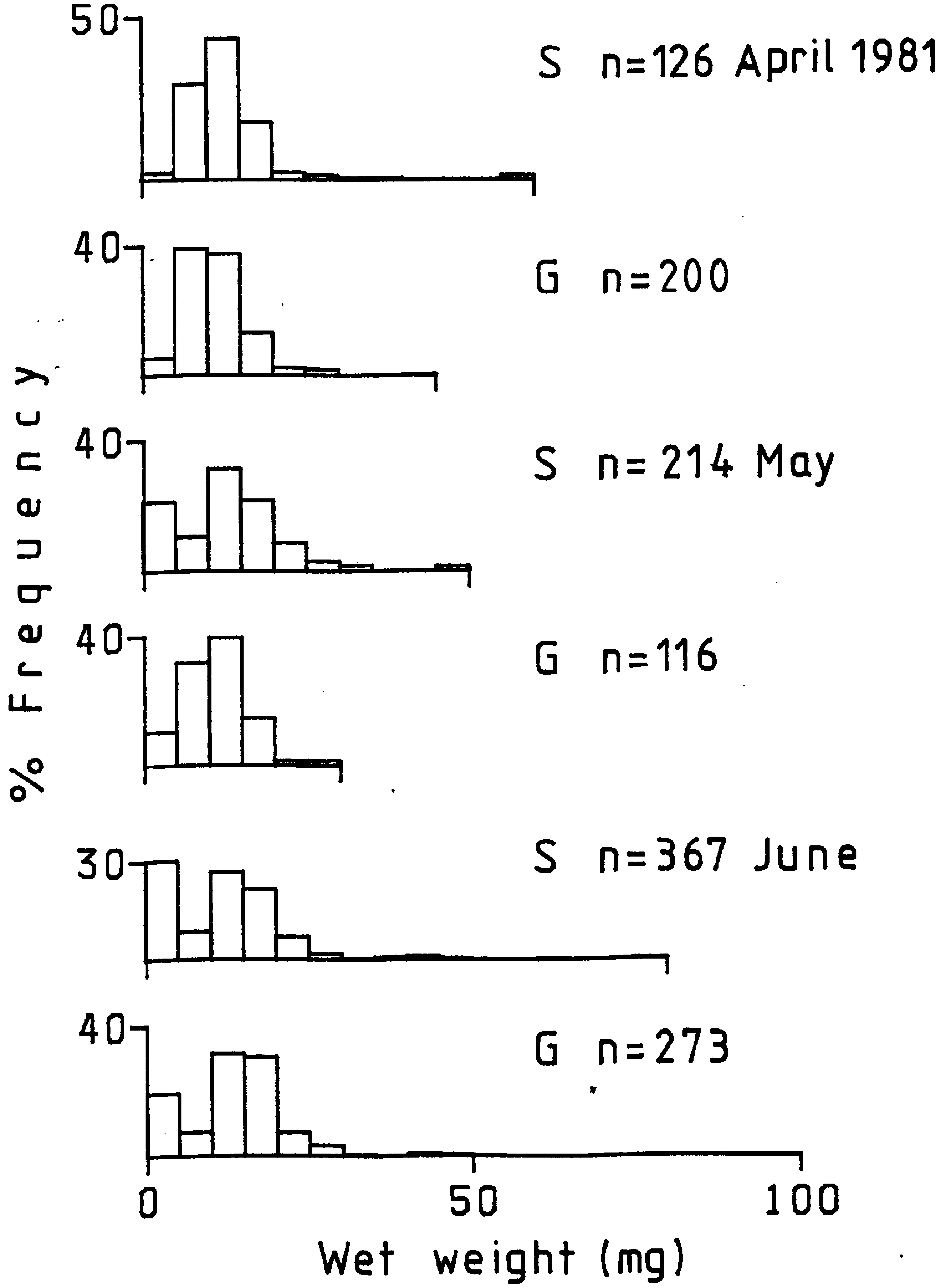


Figure 4.35. Glossiphonia complanata. The size-structure of leech populations from stone (S) and substratum (G) samples in control sites between April 1981 to March 1983.



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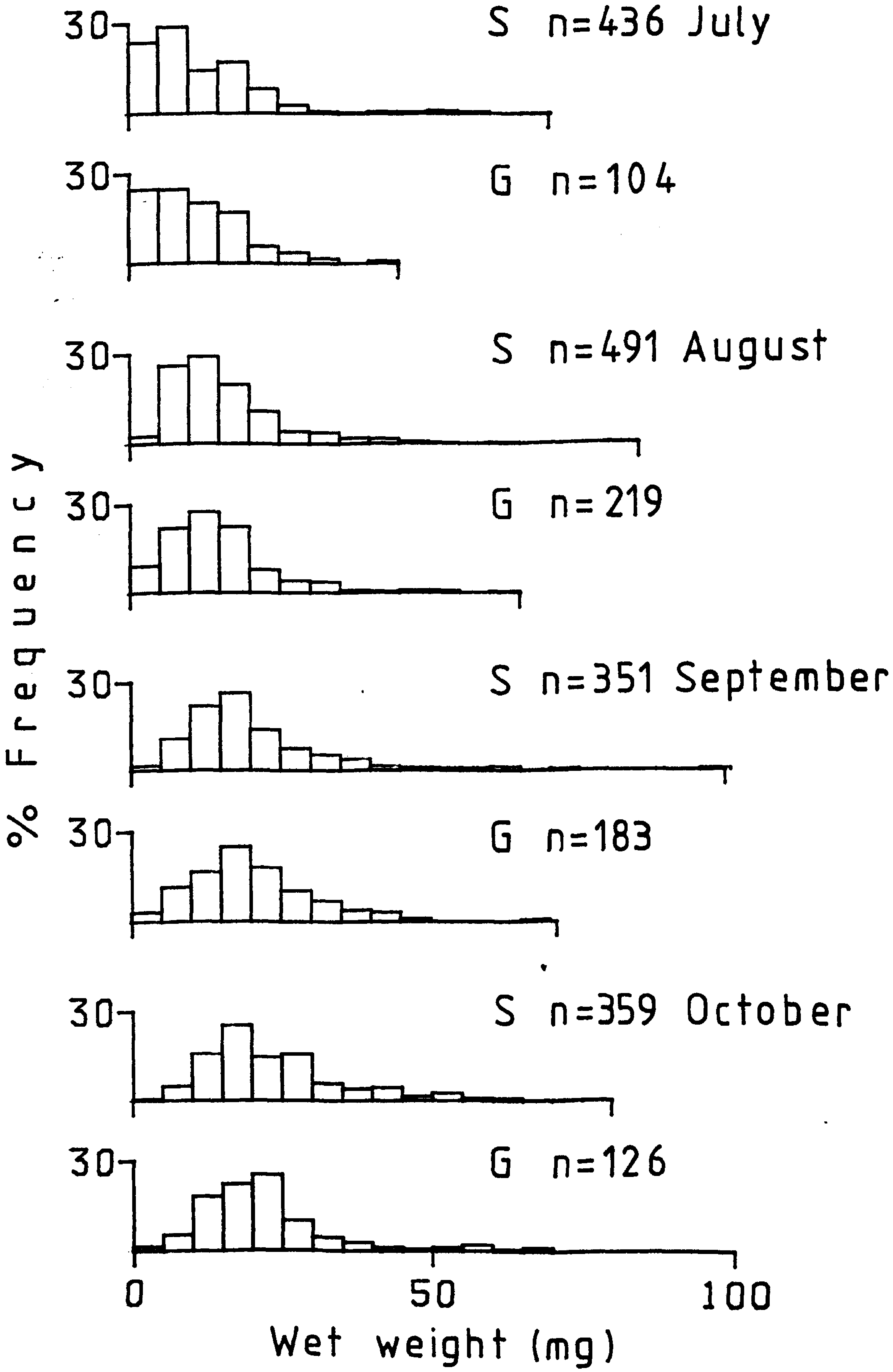
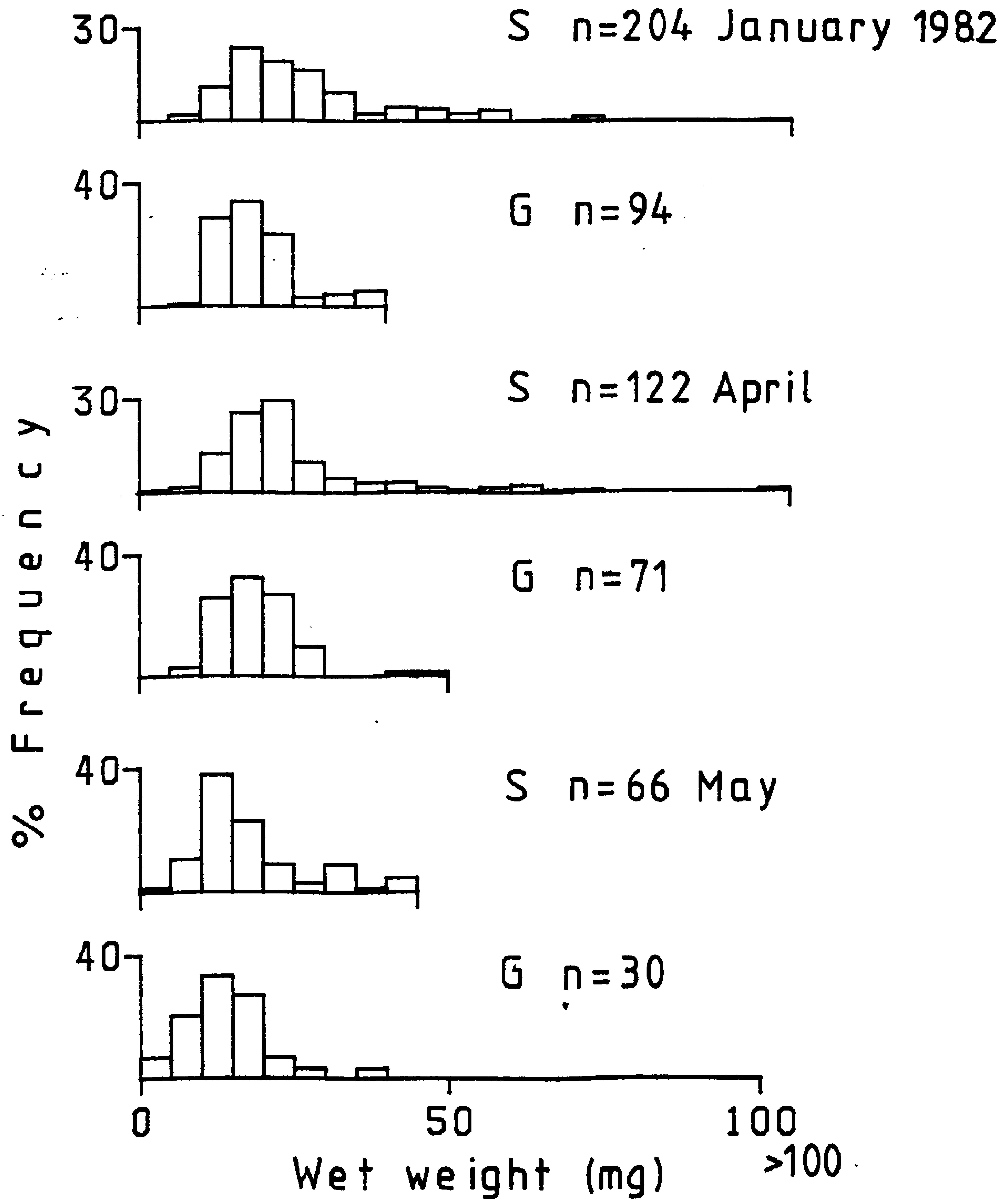
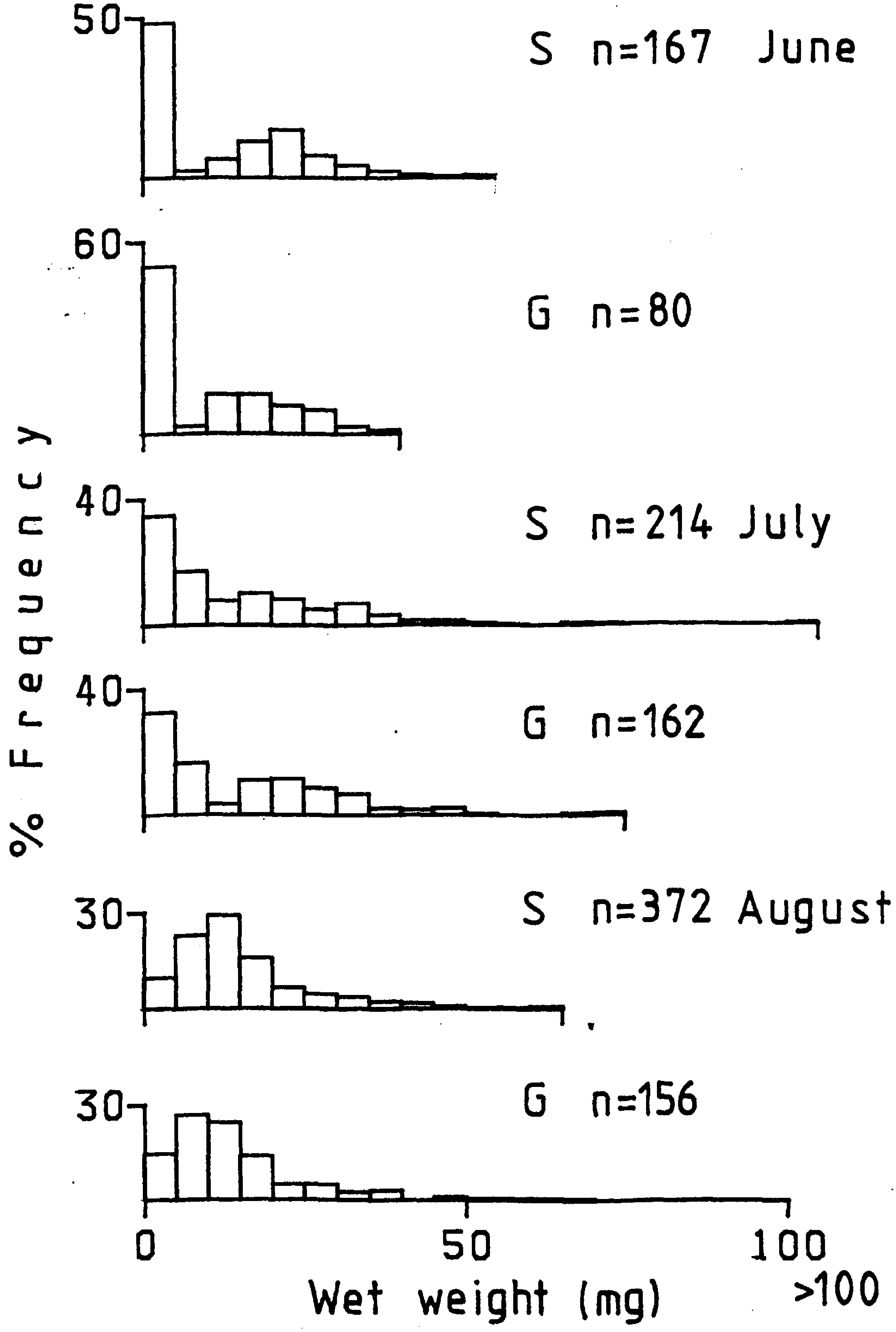

30
S n=436 July
30
G n=104
30
S n=491 August
30
G n=219
30
S n=351 September
30
G n=183
30
S n=359 October
30
G n=126
% Frequency
0
50
100
Wet weight (mg)

Continued


30
S n=204 January 1982
40
G n=94
30
S n=122 April
40
G n=71
40
S n=66 May
40
G n=30
% Frequency
0
50
100
>100
Wet weight (mg)

Continued


50
S n=167 June
60
G n=80
40
S n=214 July
40
G n=162
30
S n=372 August
30
G n=156
% Frequency
0
50
100
>100
Wet weight (mg)

Continued

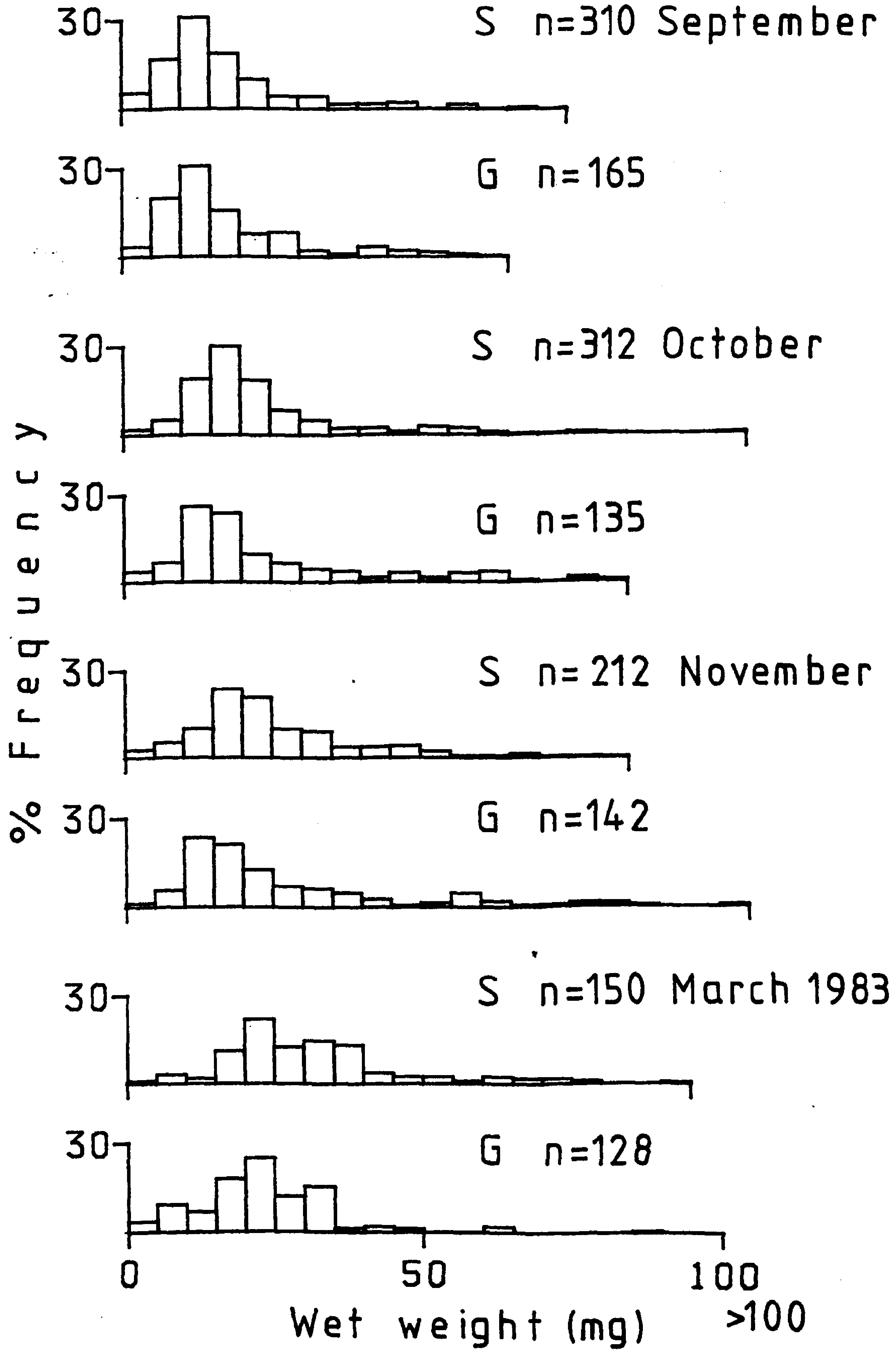
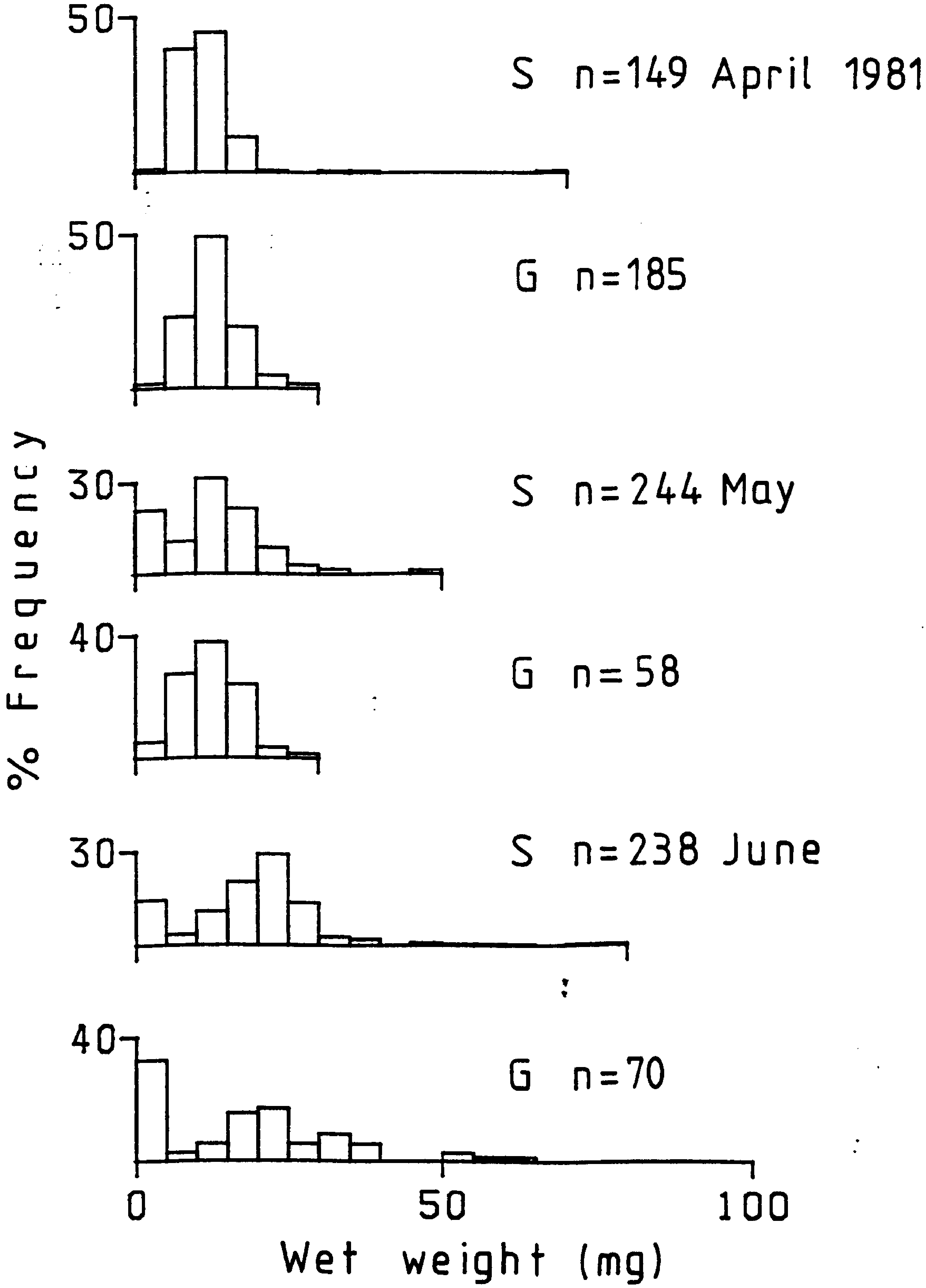

30
S n=310 September
30
G n=165
30
S n=312 October
30
G n=135
30
S n= 212 November
30
G n=142
30
S n=150 March 1983
30
G n=128
% Frequency
0
50
100
>100
Wet weight (mg)

Figure 4.36. Glossiphonia complanata. The size-structure of leech populations from stone (S) and substratum (G) samples in enclosed sites between April 1981 to March 1983.



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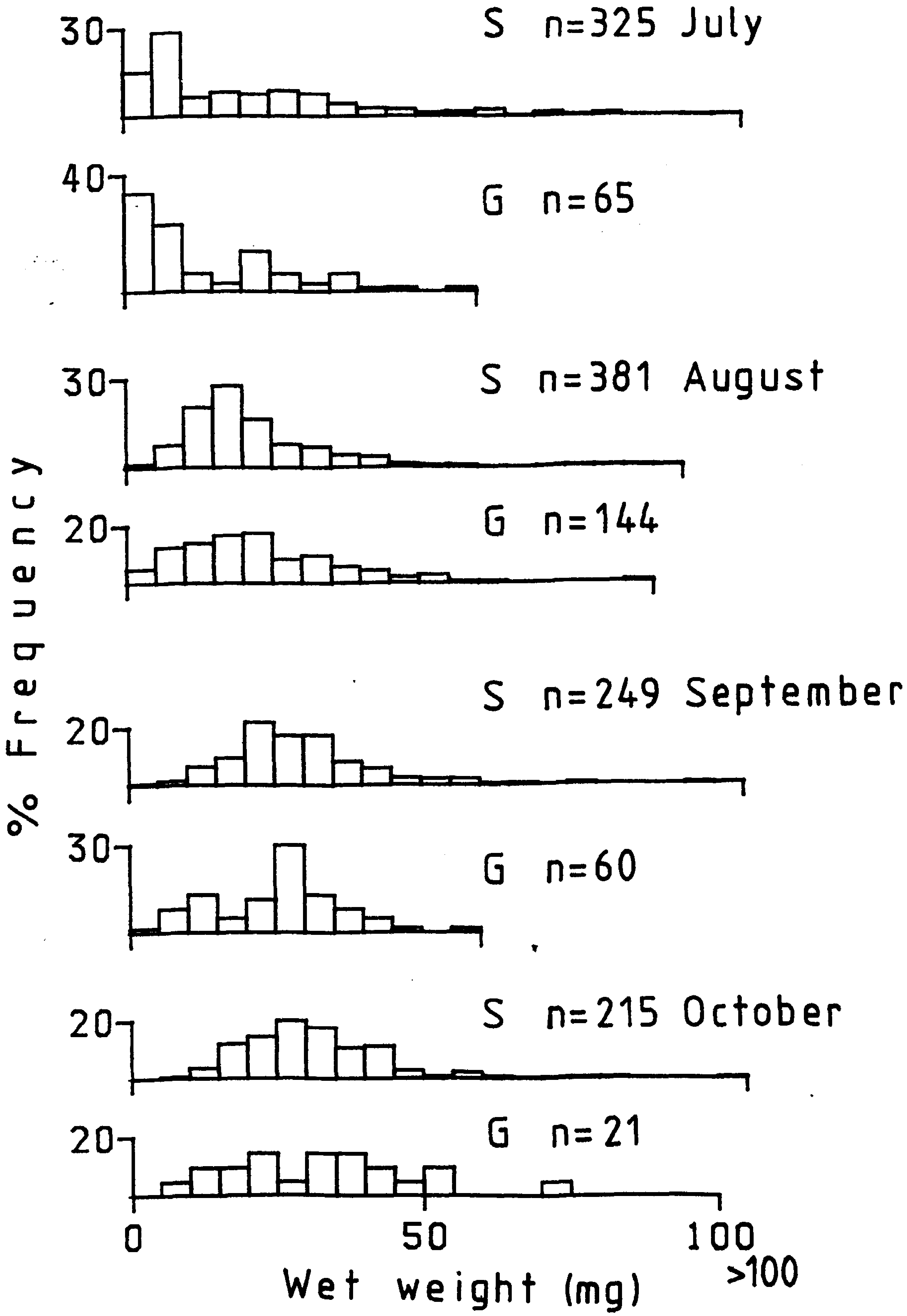
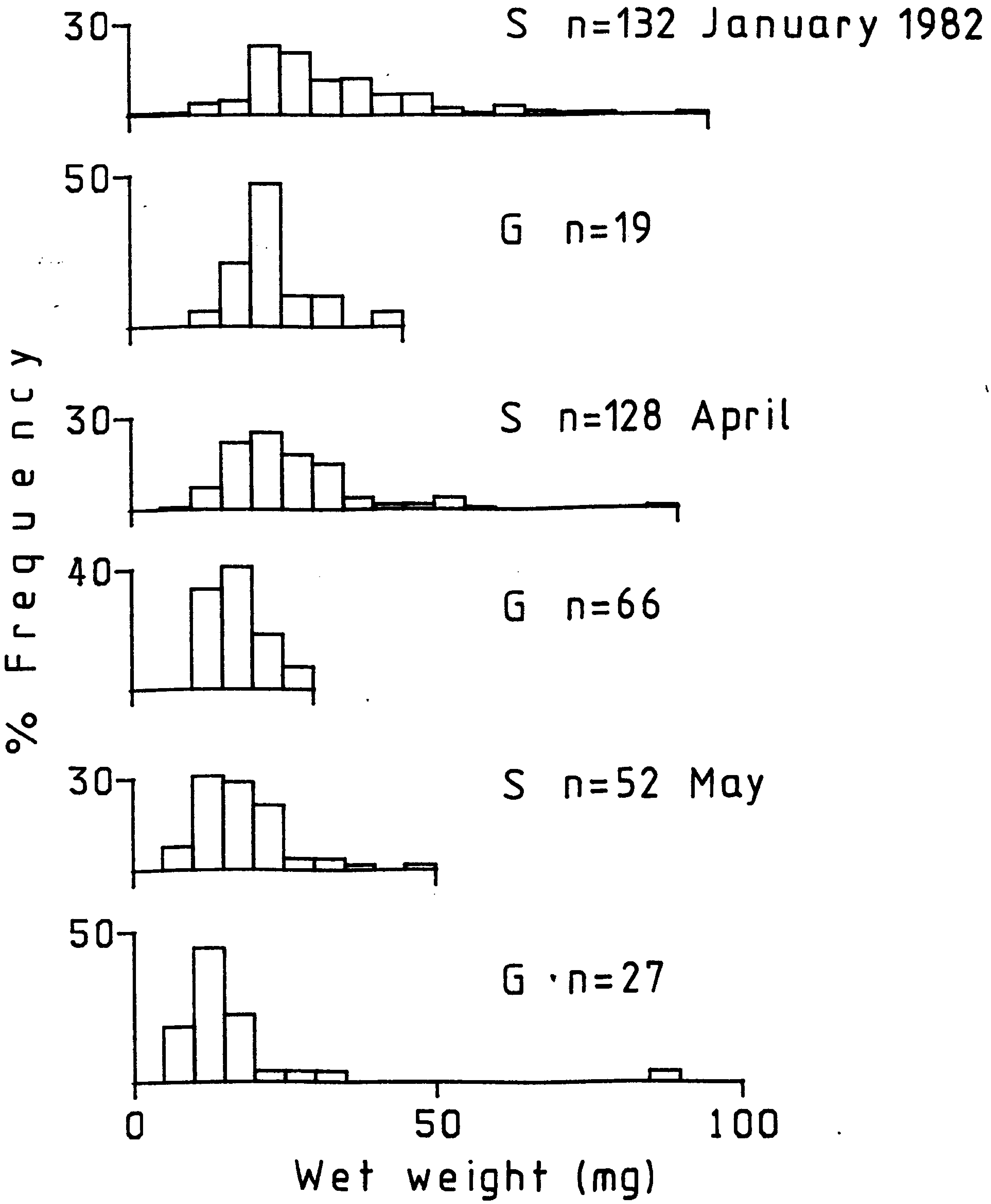
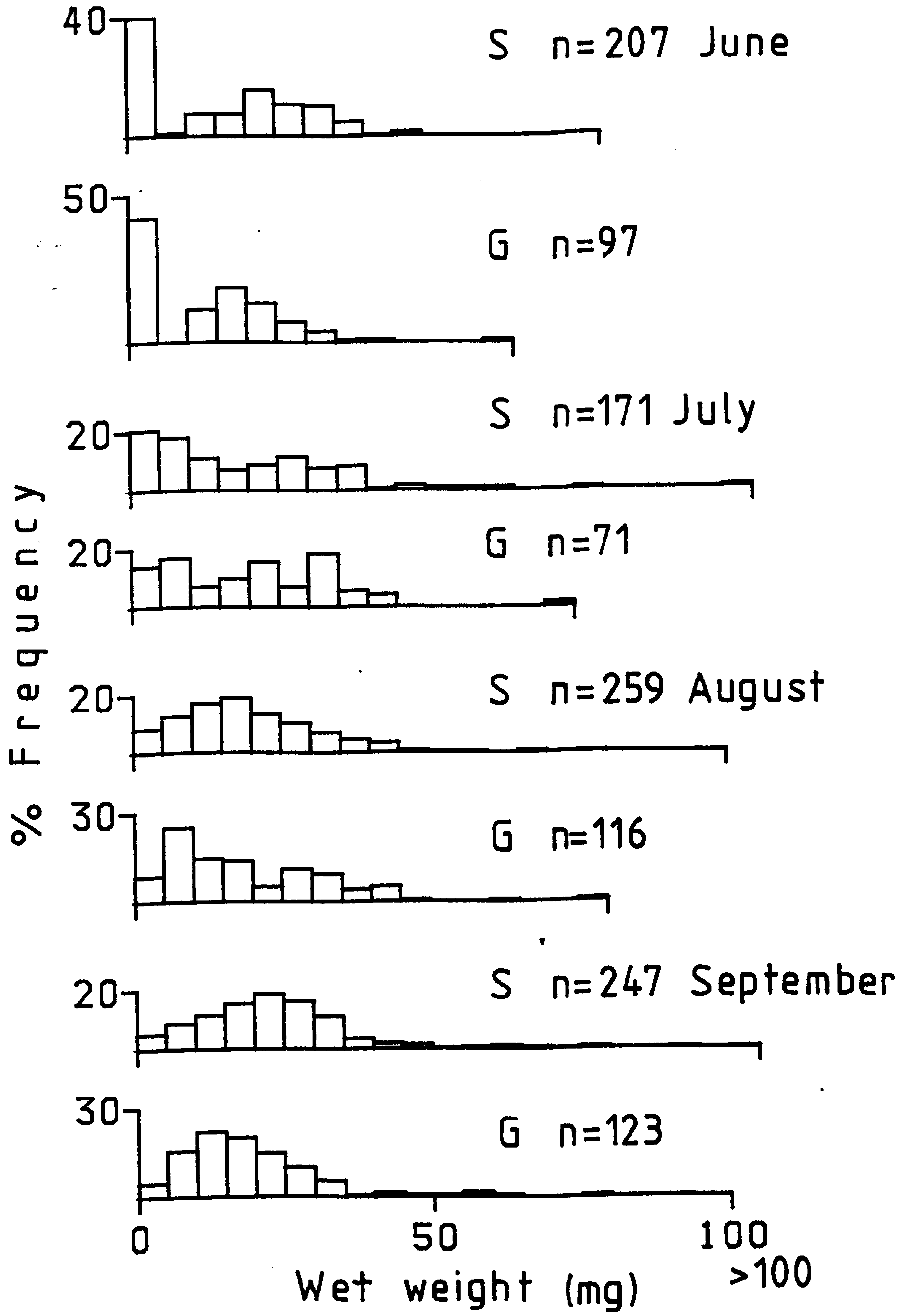

30
S n=325 July
40
G n=65
30
S n=381 August
20
G n=144
20
S n=249 September
30
G n=60
20
S n=215 October
20
G n=21
0
50
100
>100
Wet weight (mg)
% Frequency

Continued


30
S n=132 January 1982
50
G n=19
30
S n=128 April
40
G n=66
30
S n=52 May
50
G n=27
0
50
100
Wet weight (mg)
% Frequency

Continued


S n=207 June
40
G n=97
50
S n=171 July
20
G n=71
20
S n=259 August
20
G n=116
30
S n=247 September
20
G n=123
30
% Frequency
0
50
100
>100
Wet weight (mg)

Continued

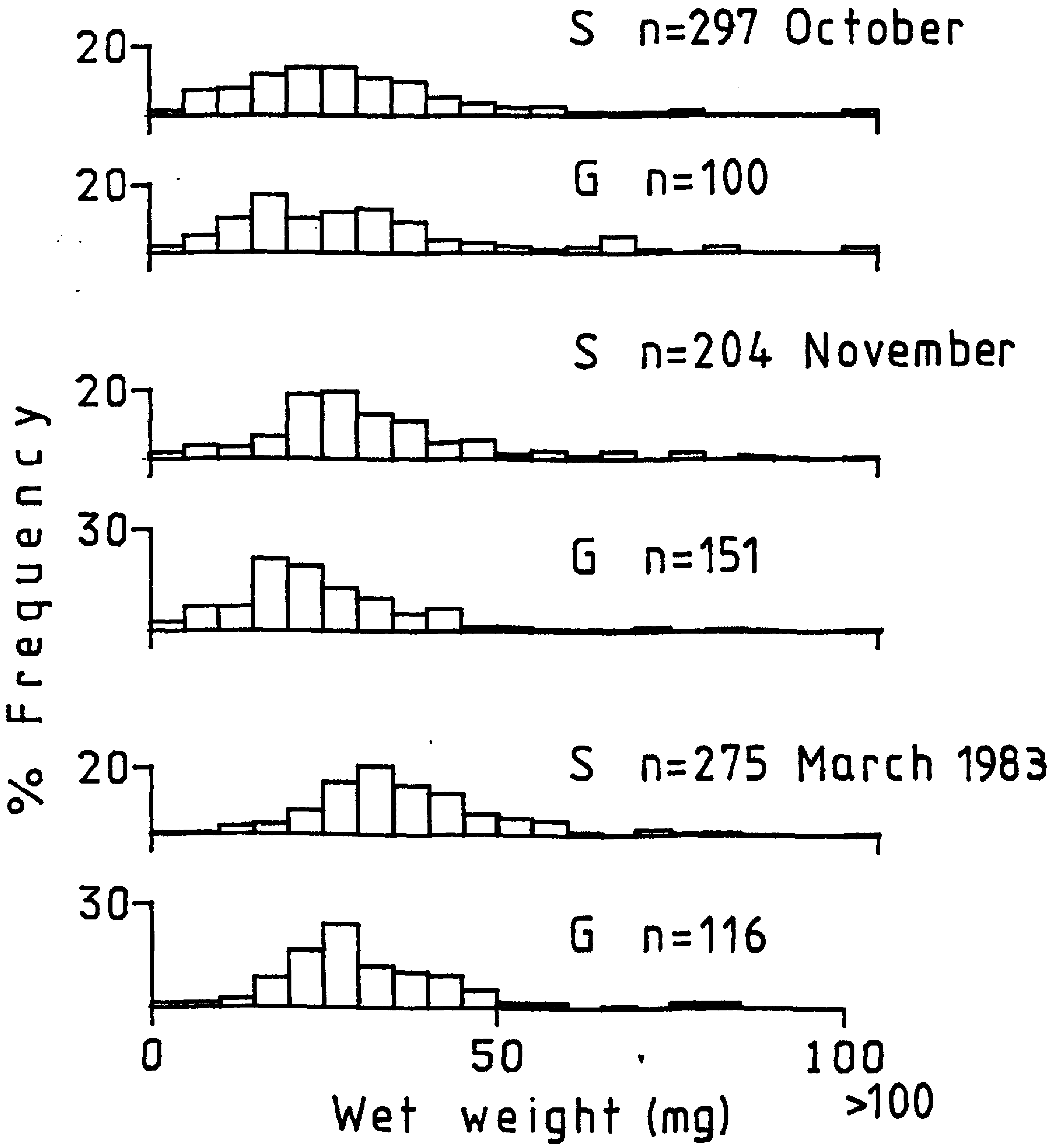
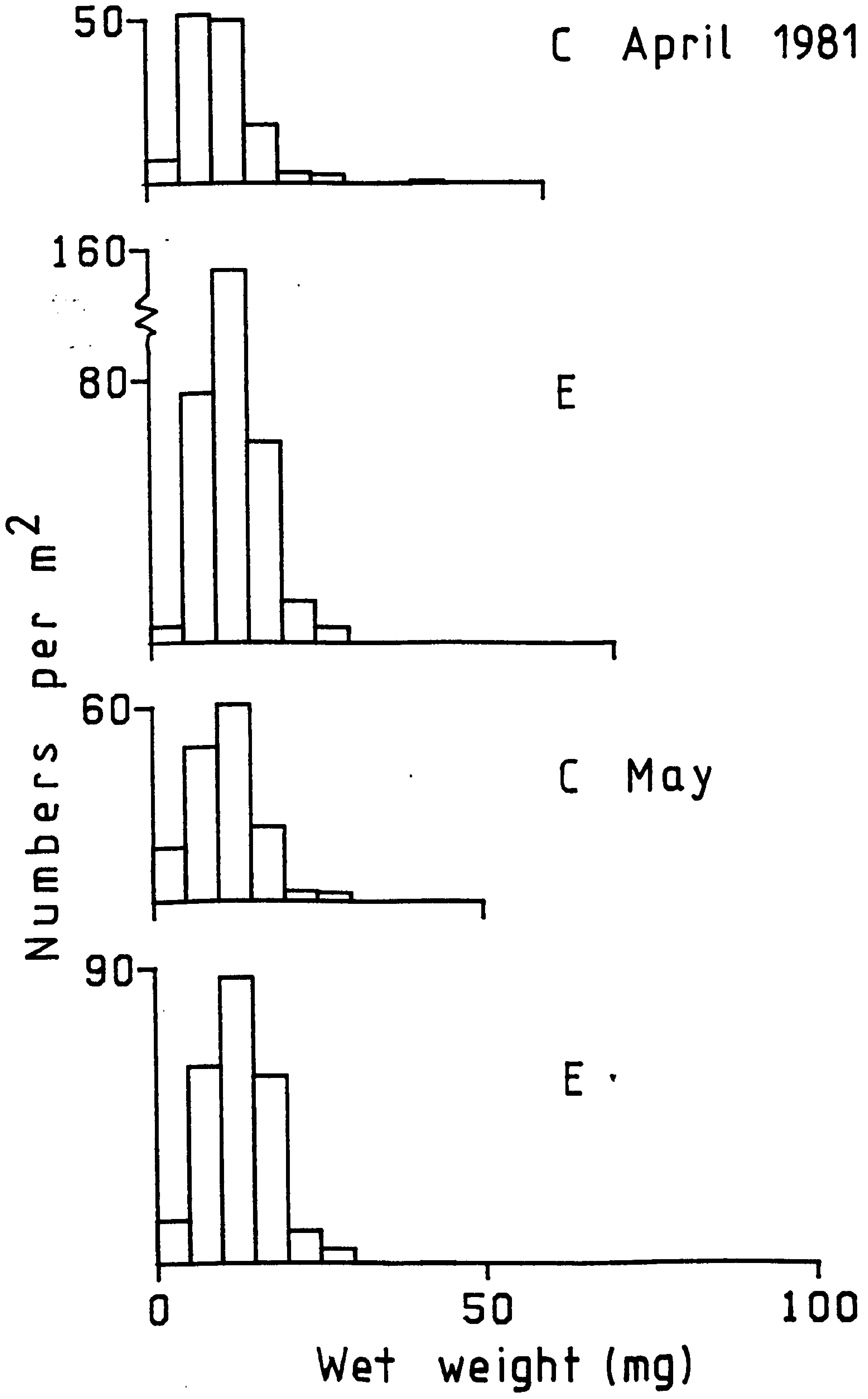
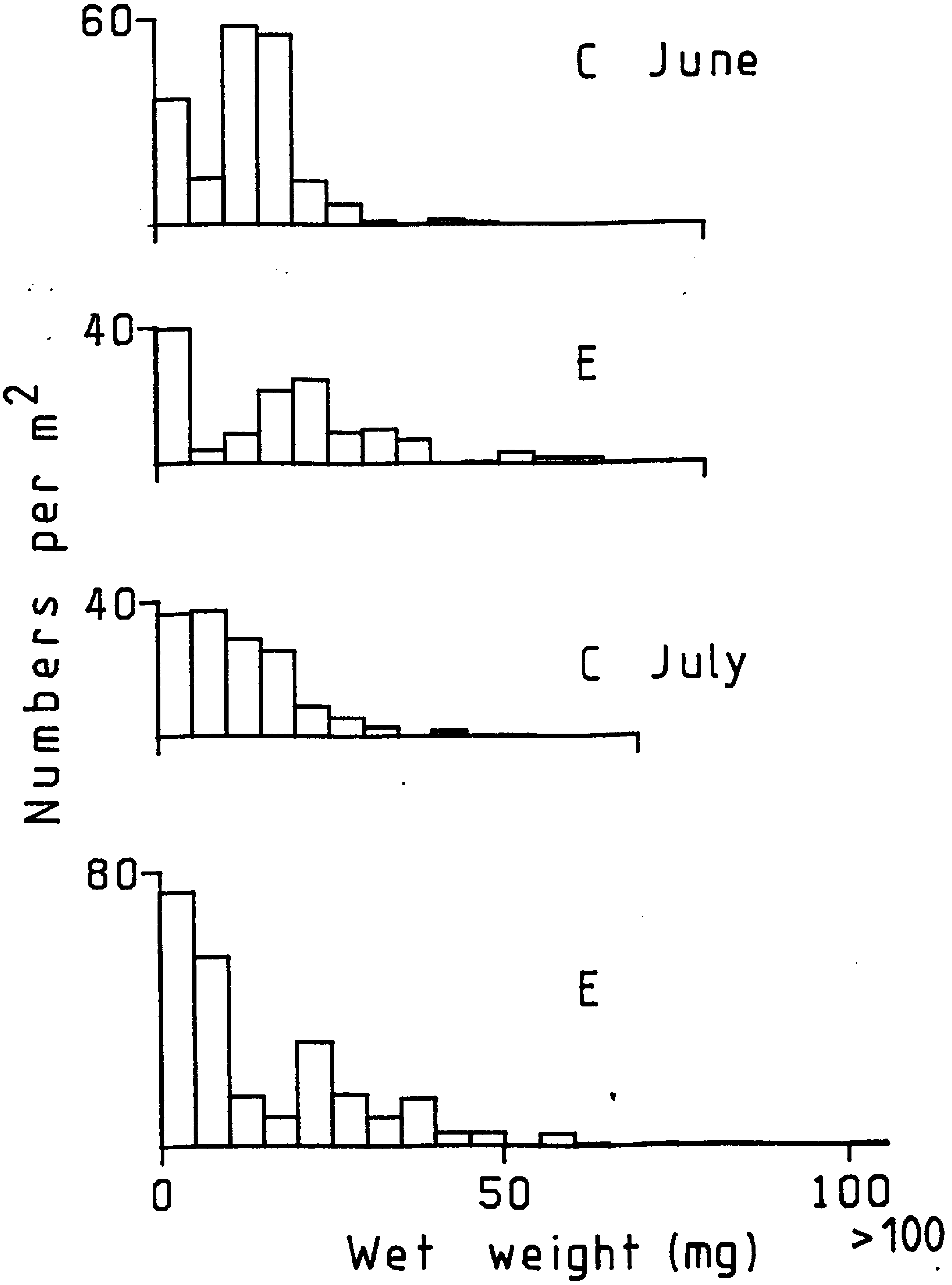

S n=297 October
20
G n=100
20
S n=204 November
20
G n=151
30
S n=275 March 1983
20
G n=116
30
% Frequency
0
50
100
>100
Wet weight (mg)

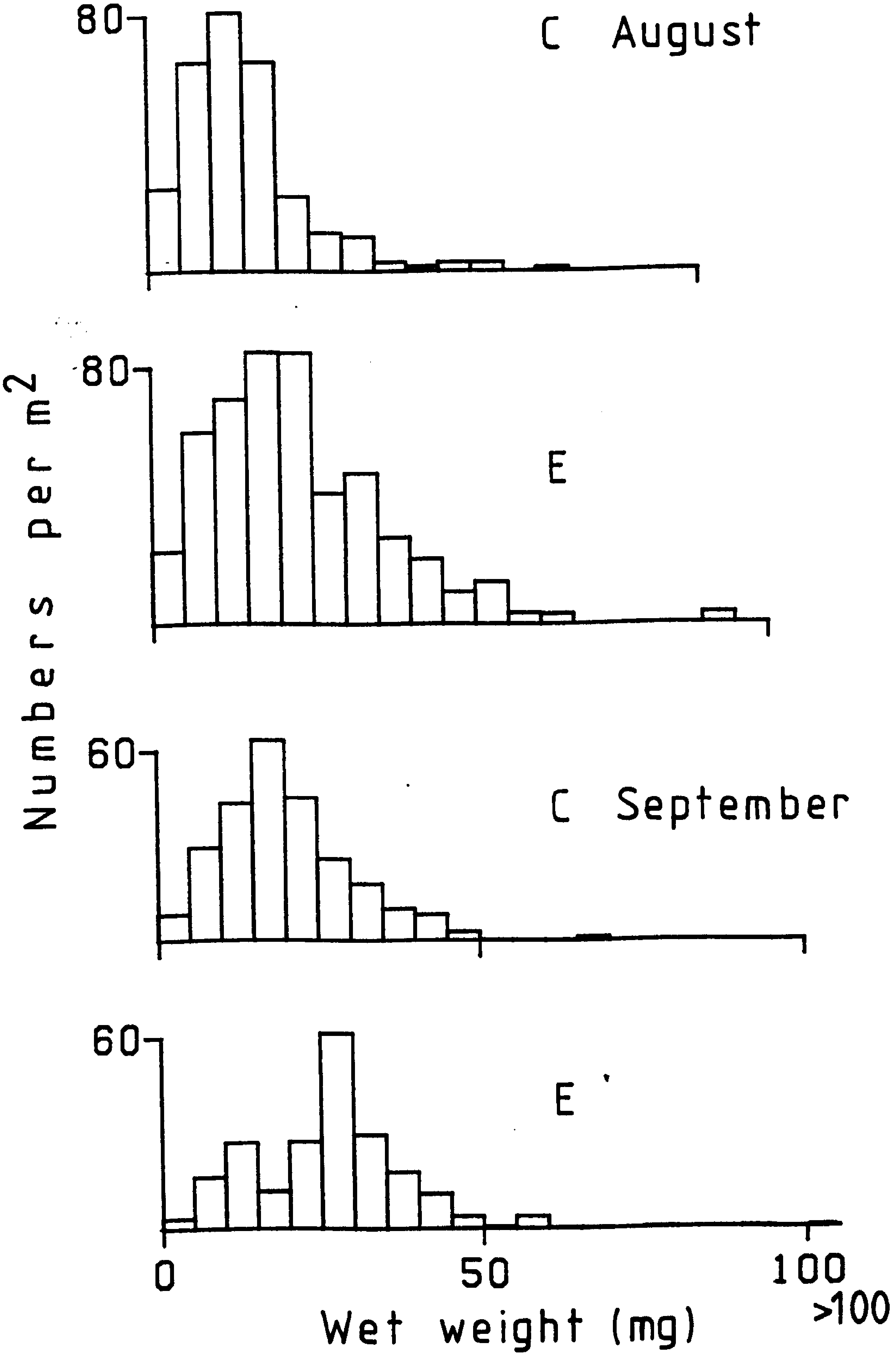
Figure 4.37. Glossiphonia complanata. The size-structure of leech populations from combined stone and substratum sample data in control (C) and enclosed (E) sites between April 1981 to March 1983.



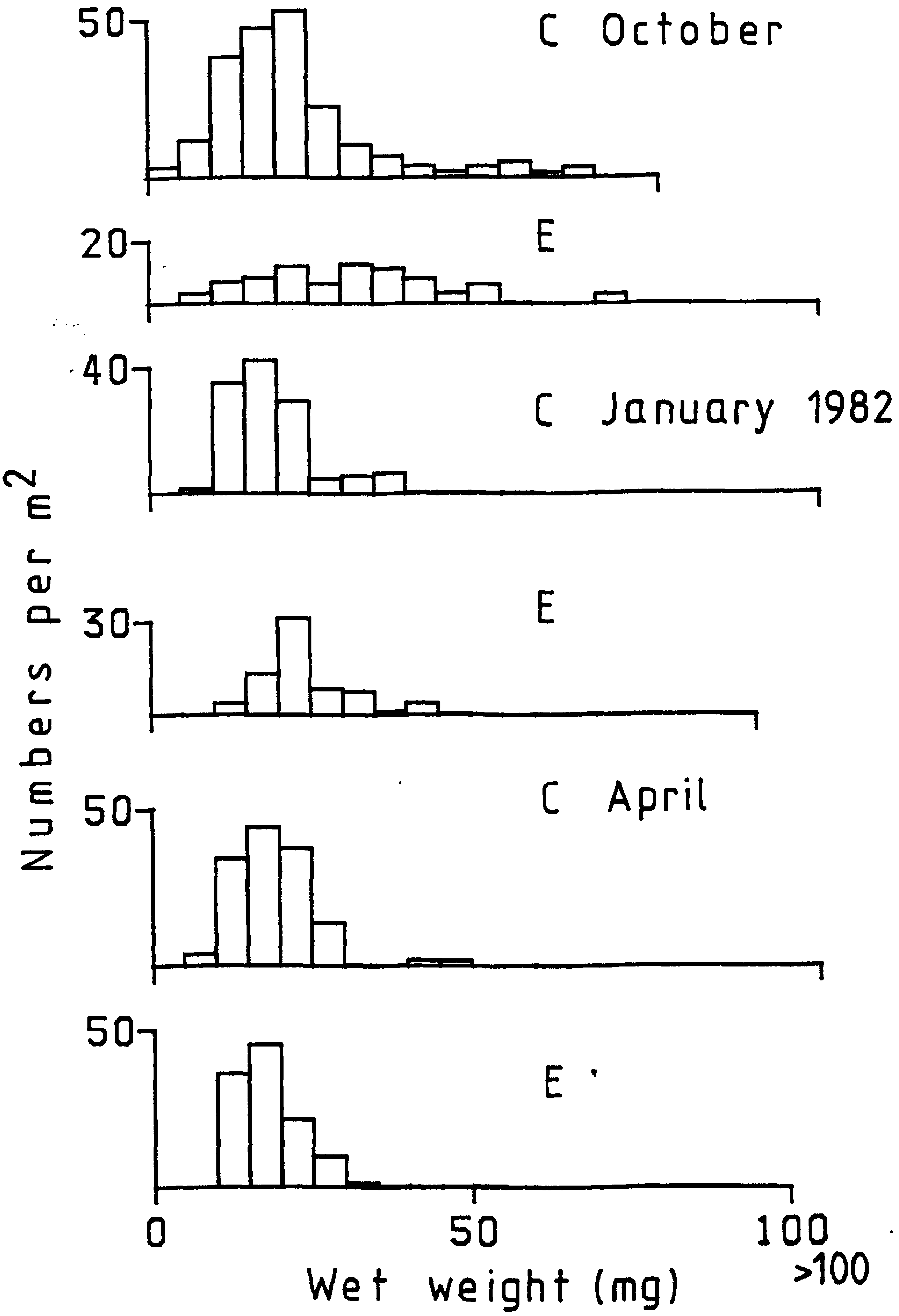
Continued


60
C June
40
E
Numbers per m²
40
C July
80
E
0
50
100
>100
Wet weight (mg)

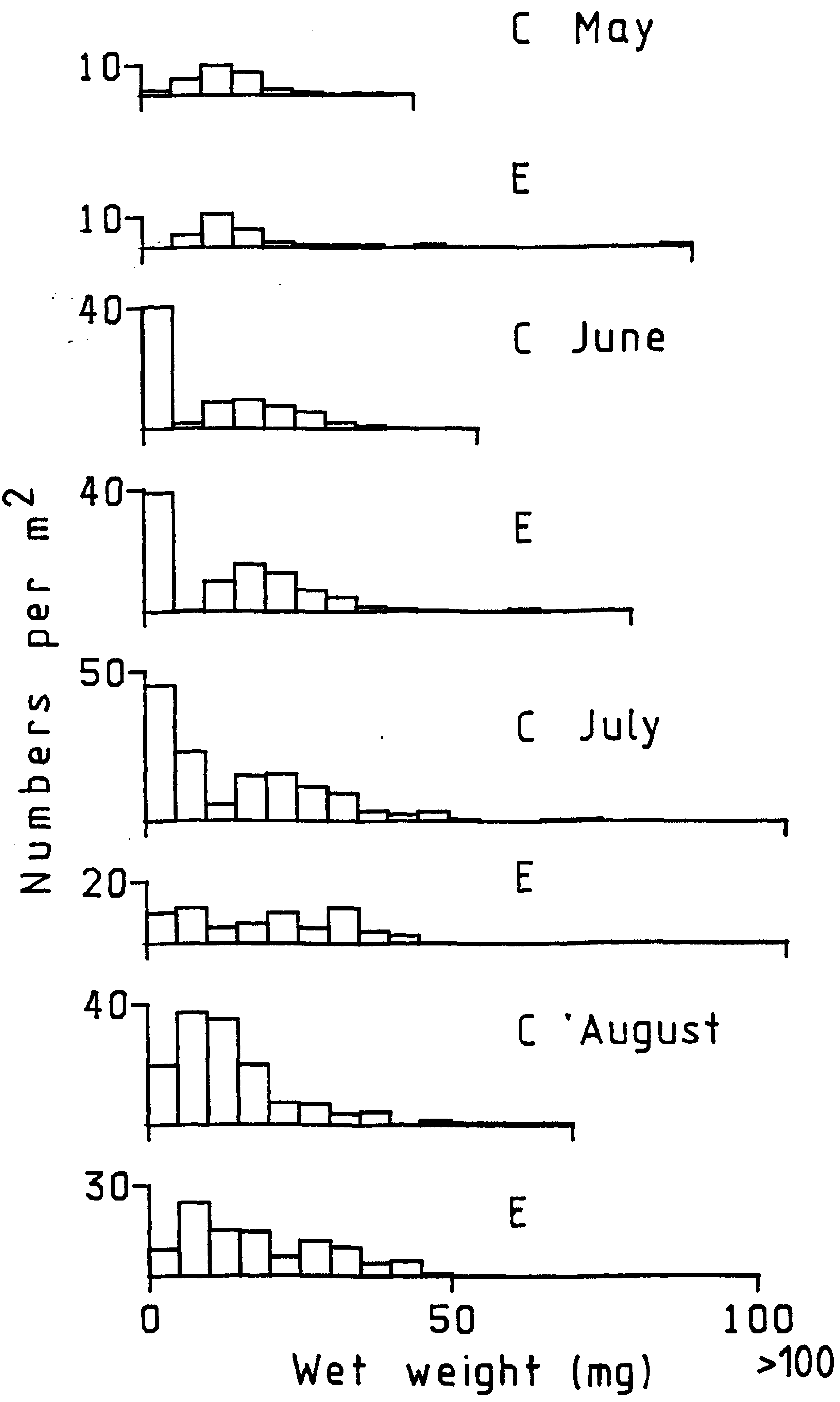
Continued


80
C August
80
E
60
C September
60
E
Numbers per m^2
0
50
100
>100
Wet weight (mg)

Continued


50
C October
20
E
40
C January 1982
30
E
50
C April
50
E
Numbers per m^2
0
50
100
>100
Wet weight (mg)

Continued


C May
10
E
10
C June
40
40
E
Numbers per m^2
50
C July
20
E
40
C 'August
30
E
0
50
100
>100
Wet weight (mg)

Continued

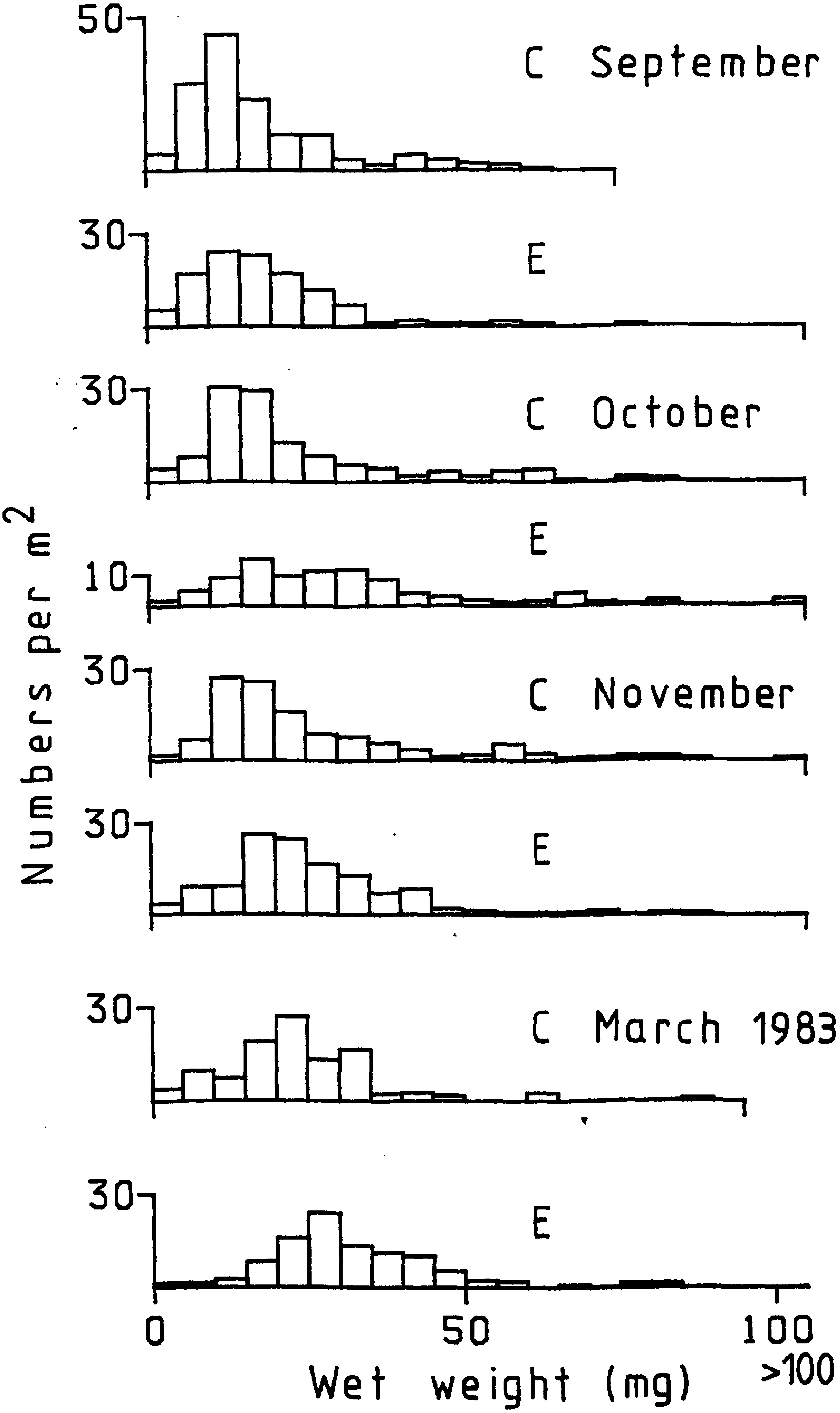

50
C September
30
E
30
C October
E
10
30
C November
30
E
30
C March 1983
30
E
0
50
100
>100
Wet weight (mg)
Numbers per m2

Figure 4.38. Glossiphonia complanata. Arithmetic mean individual weights $\pm$ 95% confidence limits for the different cohorts in separate stone (S) and substratum (G) samples from control sites.

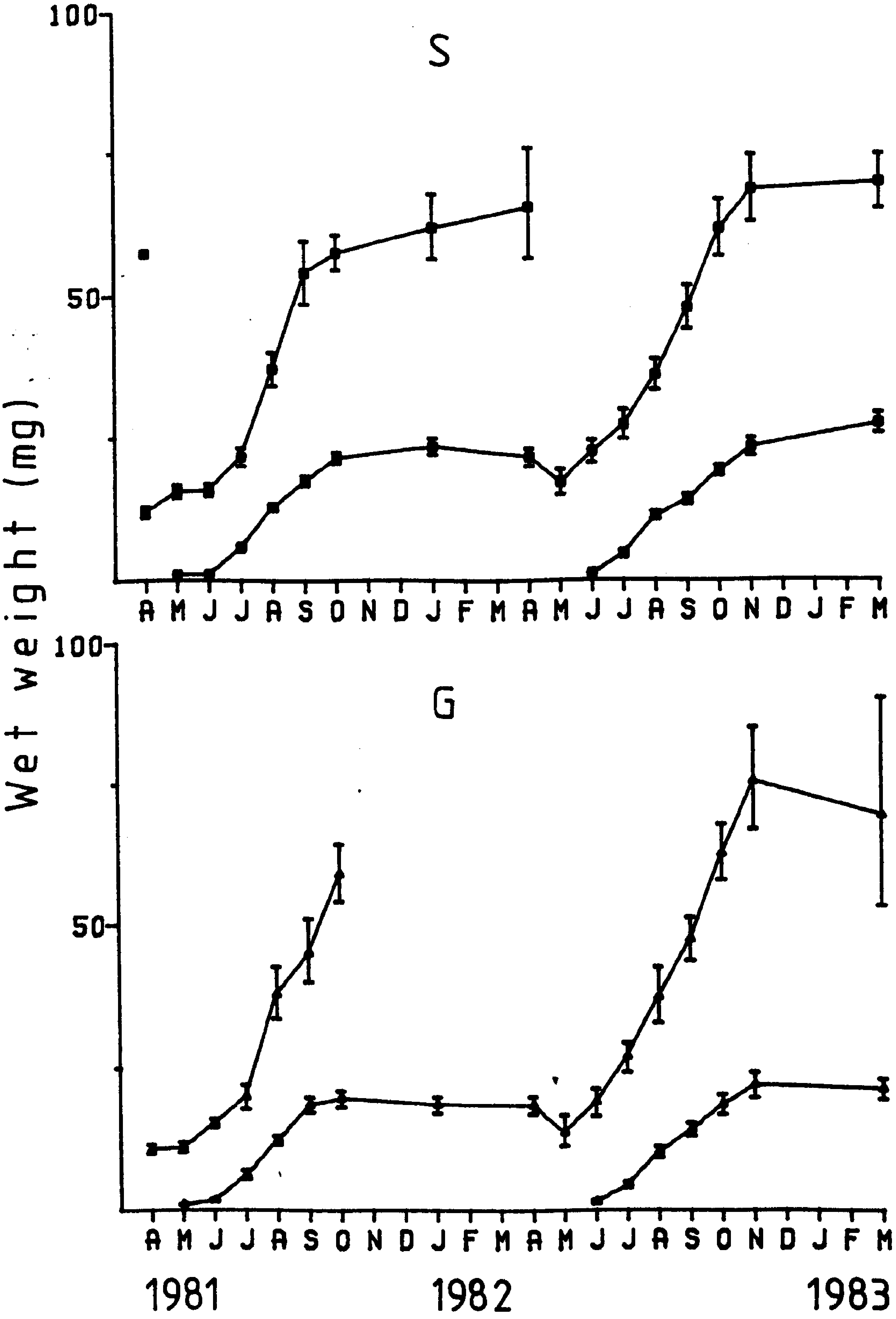
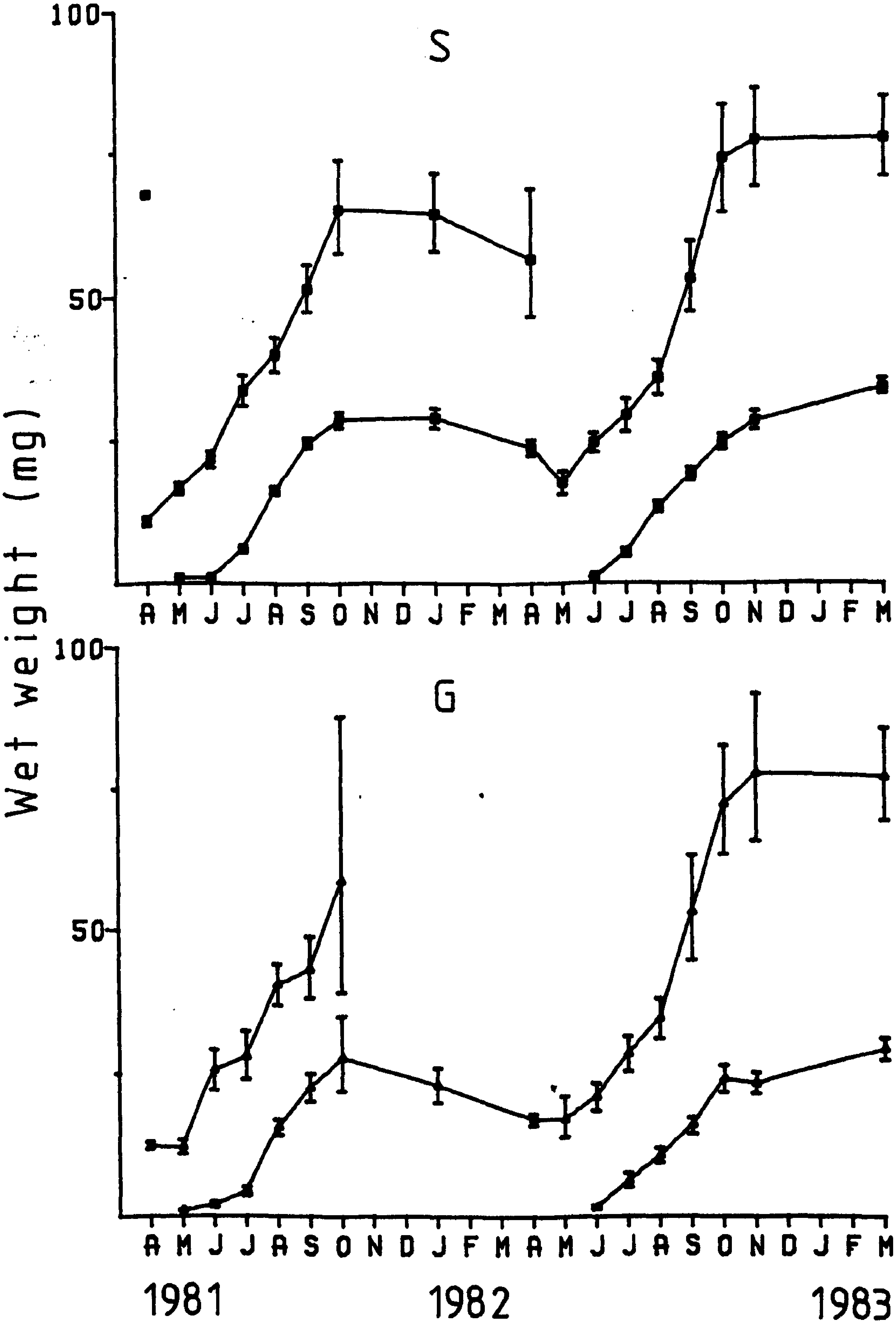


Figure 4.39. Glossiphonia complanata. Arithmetic mean individual weights ± 95% confidence limits for the different cohorts in separate stone (S) and substratum (G) samples from enclosed sites.



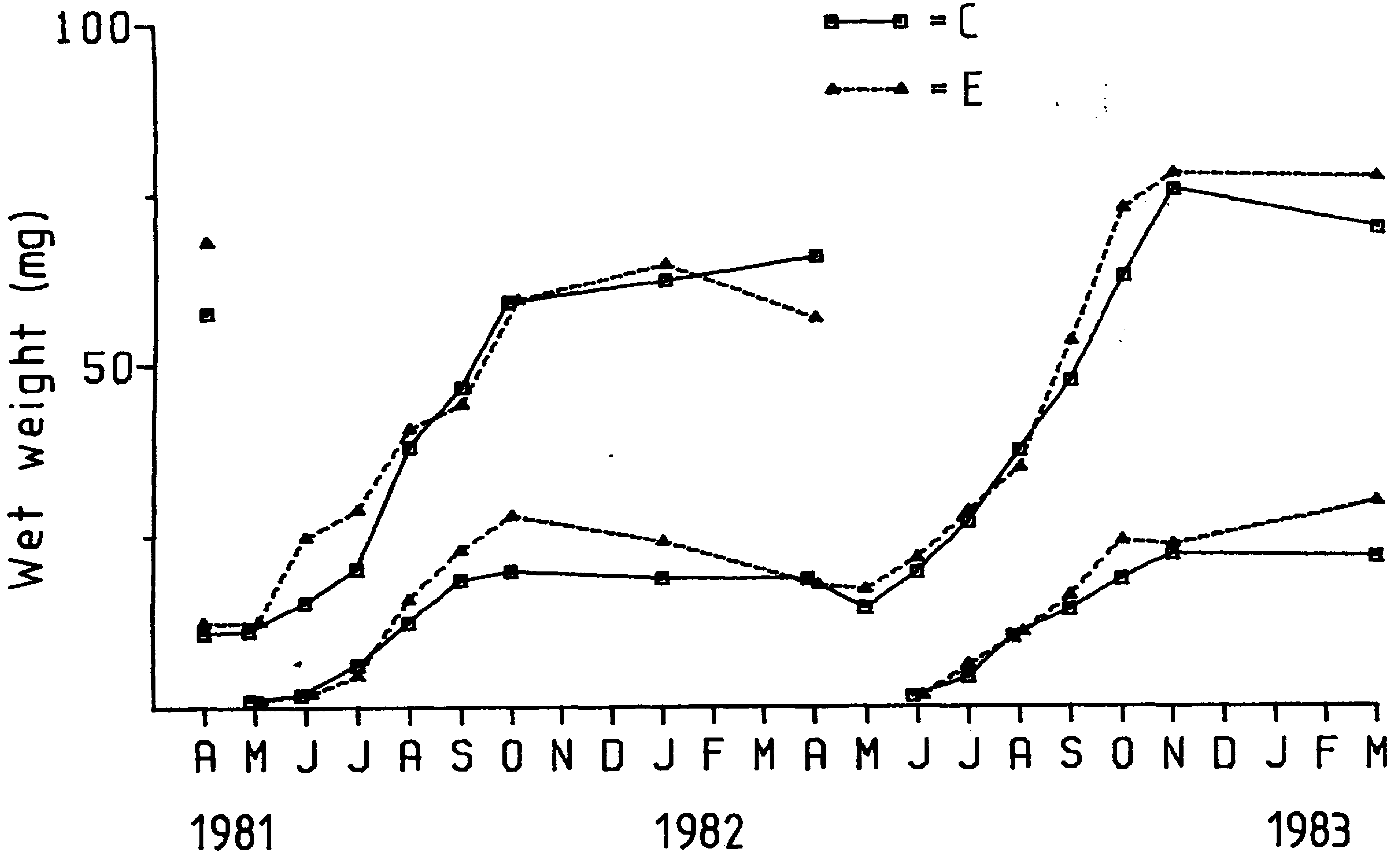


Figure 4.40. Glossiphonia complanata. Arithmetic mean individual weights for the different cohorts from combined stone and substratum sample data in control (C) and enclosed (E) sites.

Figure 4.41. Glossiphonia complanata. Arithmetic mean individual weights ± 95% confidence limits for the different cohorts in stone samples from control (C) and enclosed (E) sites.

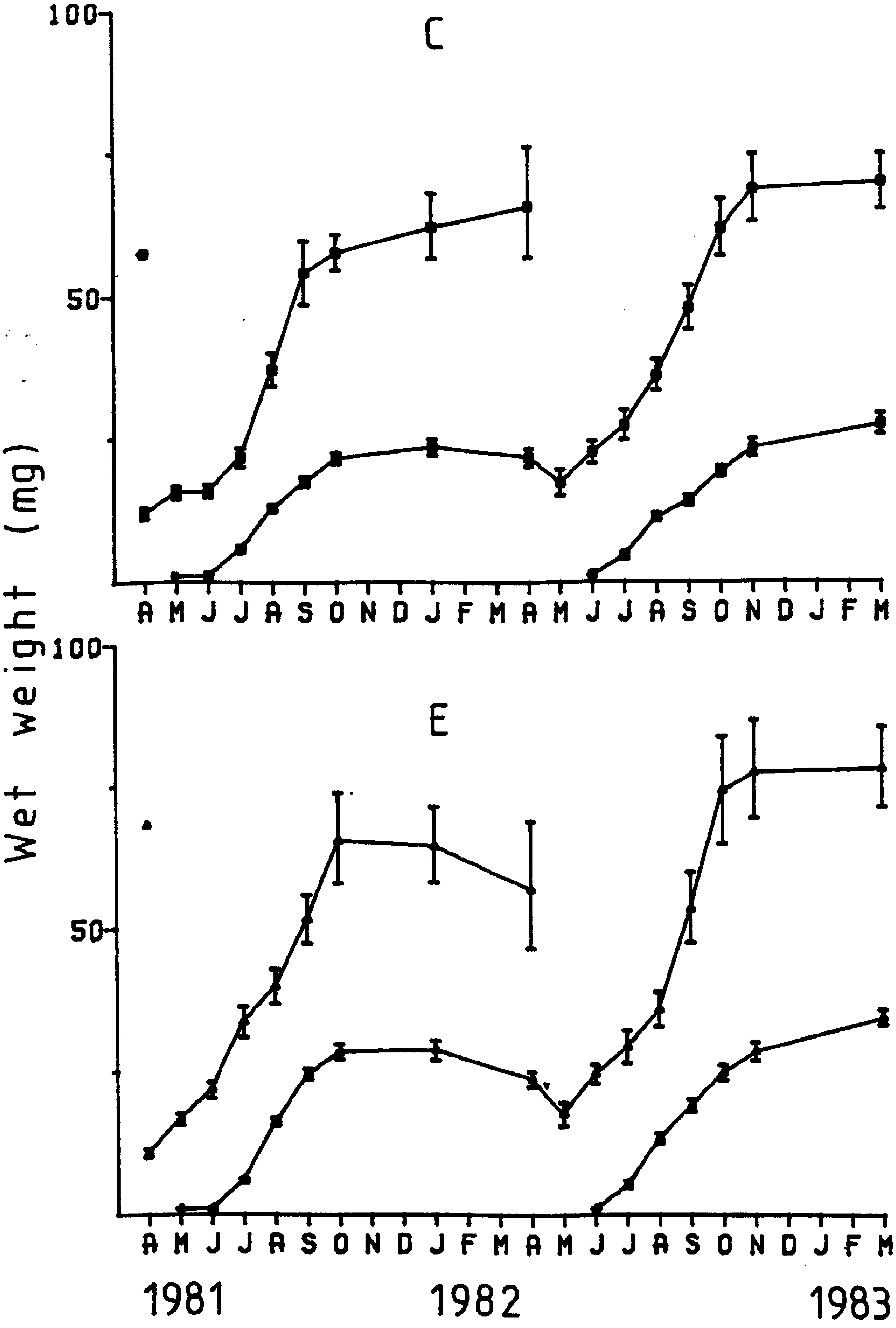


Figure 4.42. Glossiphonia complanata. Arithmetic mean individual weights ± 95% confidence limits for the different cohorts in substratum samples from control (C) and enclosed (E) sites.

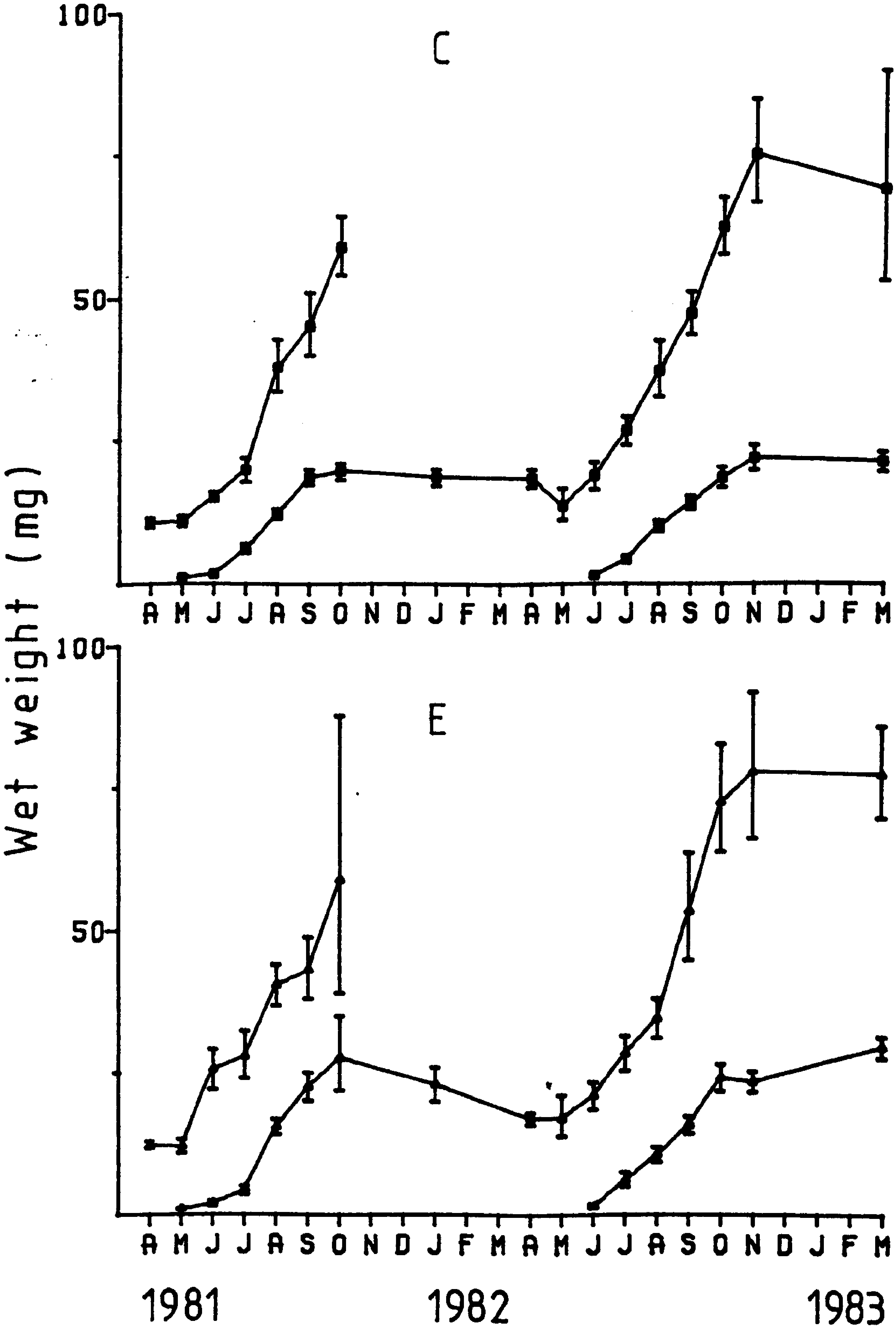


Figure 4.43. Glossiphonia complanata. The rate of biomass production for leeches of the separate cohorts in control (C) and enclosed (E) sites.

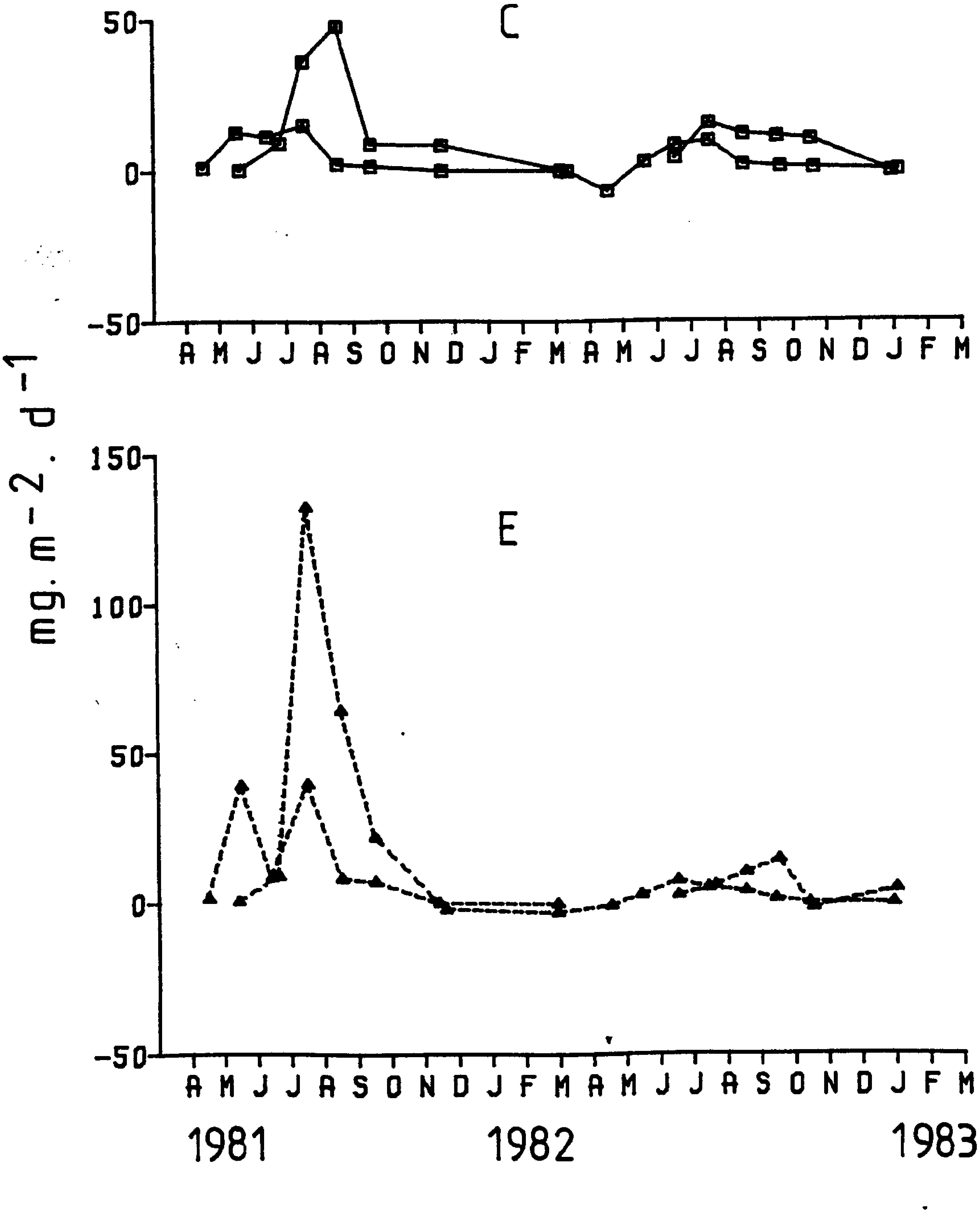


Figure 4.44. <u>Glossiphonia complanata.</u> The Allen curve for the 1981/83 cohort in control sites.

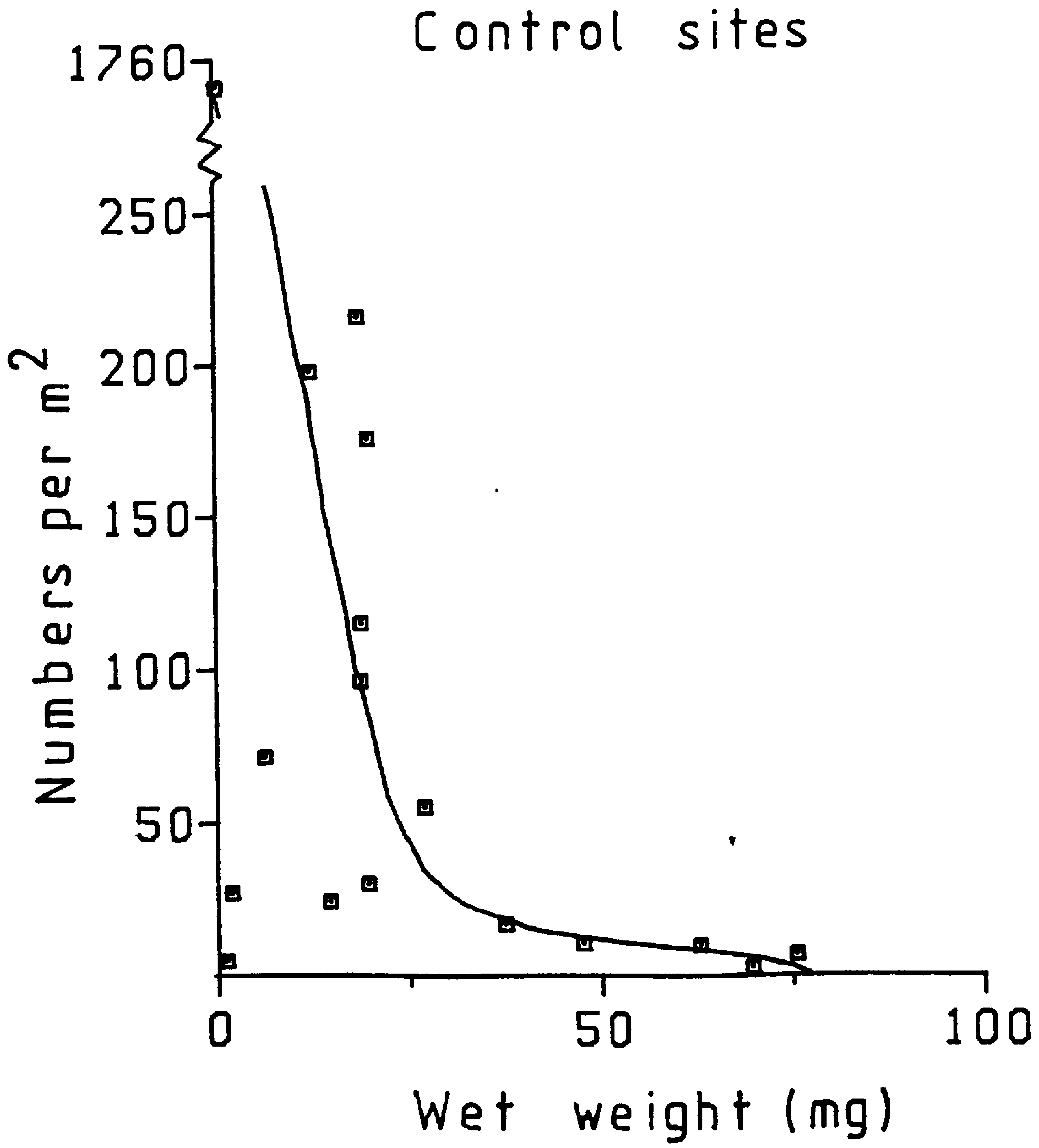


Figure 4.45. <u>Glossiphonia complanata.</u> The Allen curve for the 1981/83 cohort in enclosed sites.

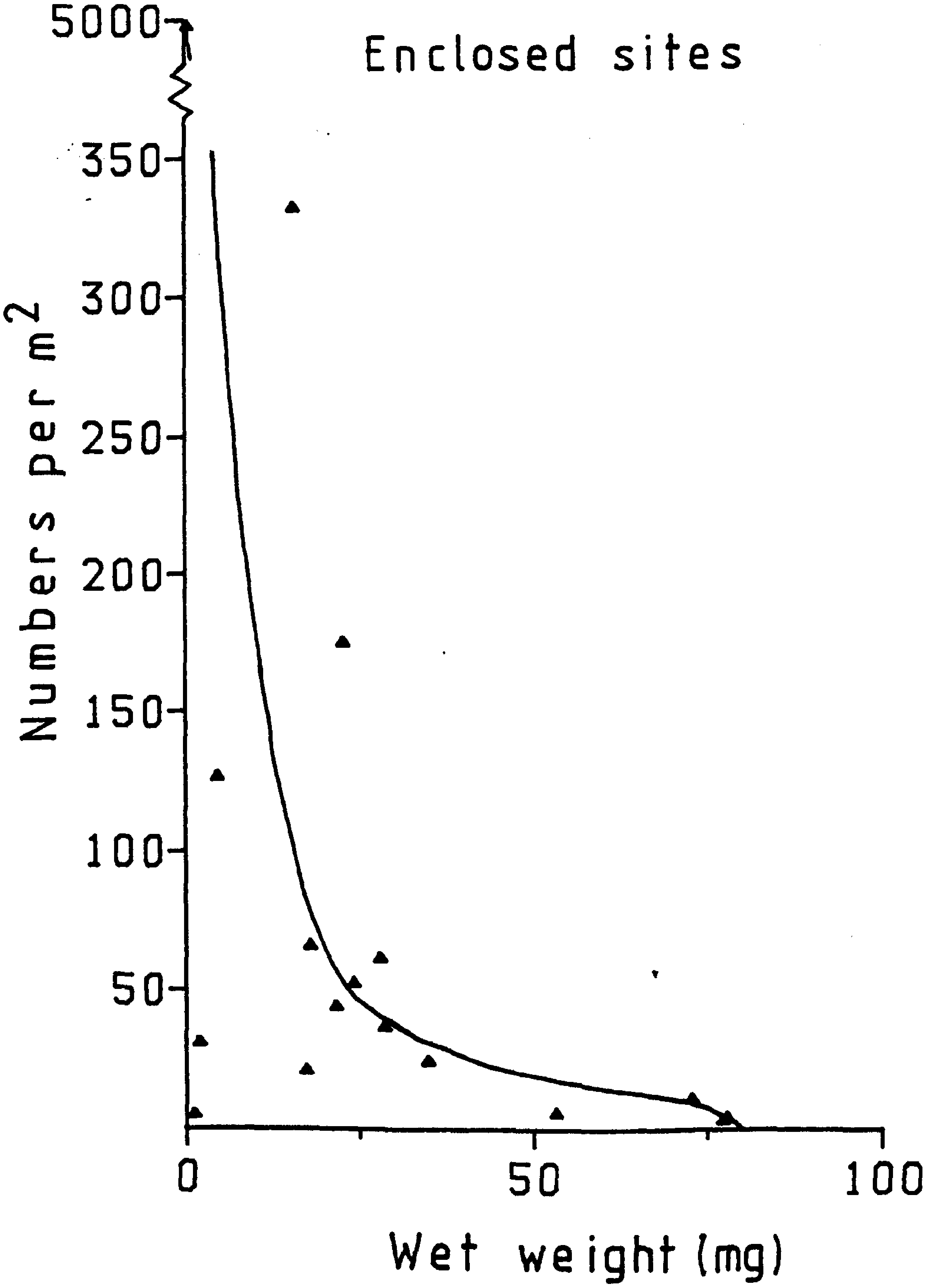


Table 4.9. *Glossiphonia complanata*. Mann-Whitney U tests comparing densities in stone (S) and substratum (G) samples between control and enclosed sites.

		U1	U2	N1	N2	Sig
1979/81 cohort						
1981						
April	S	78	82	20	8	-
	G	80	80	20	8	-
1980/82 cohort						
1981						
April	S	25.5	134.5	20	8	$p<0.05$
	G	24.5	135.5	20	8	$p<0.05$
May	S	2.5	157.5	20	8	$p<0.05$
	G	10.5	29.5	10	4	-
June	S	30	130	20	8	$p<0.05$
	G	111.5	48.5	20	8	-
July	S	18.5	141.5	20	8	$p<0.05$
	G	11.5	28.5	10	4	-
August	S	10	150	20	8	$p<0.05$
	G	4.5	35.5	10	4	$p<0.05$
September	S	18	62	10	8	-
	G	6	34	10	4	-
October	S	59	101	20	8	-
	G	18	14	8	4	-
1982						
January	S	68.5	91.5	20	8	-
	G	20	20	10	4	-
April	S	145.5	110.5	16	16	-
	G	28	28	7	8	-
1981/83 cohort						
1981						
May	S	65	95	20	8	-
	G	19.5	20.5	10	4	-
June	S	91	69	20	8	-
	G	71	89	20	8	-
July	S	52	108	20	8	-
	G	11	29	10	4	-

Continued

		U1	U2	N1	N2	Sig
1981						
August	S	41.5	118.5	20	8	-
	G	14.5	25.5	10	4	-
September	S	33	47	10	8	-
	G	26.5	13.5	10	4	-
October	S	52	108	20	8	-
	G	29.5	2.5	8	4	$p<0.05$
1982						
January	S	38	122	20	8	$p<0.05$
	G	34.5	5.5	10	4	-
April	S	121.5	134.5	16	16	-
	G	33.5	22.5	7	8	-
May	S	157	99	16	16	-
	G	139	117	16	16	-
June	S	88	152	15	16	-
	G	89	167	16	16	-
July	S	117.5	138.5	16	16	-
	G	163.5	76.5	16	15	-
August	S	129.5	126.5	16	16	-
	G	101.5	154.5	16	16	-
September	S	127	129	16	16	-
	G	147.5	92.5	16	15	-
October	S	104	152	16	16	-
	G	126.5	129.5	16	16	-
November	S	89	167	16	16	-
	G	151.5	104.5	16	16	-
1983						
March	S	126	130	16	16	-
	G	126	130	16	16	-
1982/84 cohort						
1982						
June	S	150.5	89.5	15	16	-
	G	122.5	133.5	16	16	-
July	S	180	76	16	16	-
	G	186.5	53.5	16	15	$p<0.05$
August	S	163.5	92.5	16	16	-
	G	192.5	63.5	16	16	$p<0.05$

Continued

		U1	U2	N1	N2	Sig
1982						
September	S	145	111	16	16	-
	G	136.5	103.5	16	15	-
October	S	140	116	16	16	-
	G	174	82	16	16	-
November	S	135	121	16	16	-
	G	121	135	16	16	-
1983						
March	S	84.5	171.5	16	16	-
	G	135.5	120.5	16	16	-

Table 4.10. *Glossiphonia complanata*. Mann-Whitney U tests comparing biomass in stone (S) and substratum (G) samples between control and enclosed sites.

		U1	U2	N1	N2	Sig
1979/81 cohort						
1981						
April	S	77	83	20	8	-
	G	80	80	20	8	-
1980/82 cohort						
1981						
April	S	7	153	20	8	$p<0.05$
	G	13	147	20	8	$p<0.05$
May	S	2	158	20	8	$p<0.05$
	G	9	31	10	4	-
June	S	11	149	20	8	$p<0.05$
	G	82	78	20	8	-
July	S	9	151	20	8	$p<0.05$
	G	9	31	10	4	-
August	S	6.5	153.5	20	8	$p<0.05$
	G	4	36	10	4	$p<0.05$
September	S	17.5	62.5	10	8	-
	G	5	35	10	4	$p<0.05$
October	S	55	105	20	8	-
	G	17	15	8	4	-
1982						
January	S	67	93	20	8	-
	G	20	20	10	4	-
April	S	150	106	16	16	-
	G	28	28	7	8	-
1981/83 cohort						
1981						
May	S	65	95	20	8	-
	G	19.5	20.5	10	4	-
June	S	93	67	20	8	-
	G	73	87	20	8	-
July	S	51.5	108.5	20	8	-
	G	19	21	10	4	-

Continued

		U1	U2	N1	N2	Sig
1981						
August	S	29	131	20	8	$p<0.05$
	G	9	31	10	4	-
September	S	23	57	10	8	-
	G	20	20	10	4	-
October	S	32	128	20	8	$p<0.05$
	G	27	5	8	4	-
1982						
January	S	30	130	20	8	$p<0.05$
	G	30	10	10	4	-
April	S	112.5	143.5	16	16	-
	G	35	21	7	8	-
May	S	151.5	104.5	16	16	-
	G	138	118	16	16	-
June	S	85.5	154.5	15	16	-
	G	78	178	16	16	-
July	S	95	161	16	16	-
	G	151	89	16	15	-
August	S	132.5	123.5	16	16	-
	G	105.5	150.5	16	16	-
September	S	118	138	16	16	-
	G	143	97	16	15	-
October	S	86	170	16	16	-
	G	116	140	16	16	-
November	S	84	172	16	16	-
	G	150	106	16	16	-
1983						
March	S	118.5	137.5	16	16	-
	G	123	133	16	16	-
1982/84 cohort						
1982						
June	S	154.5	85.5	15	16	-
	G	115.5	140.5	16	16	-
July	S	157	99	16	16	-
	G	165	75	16	15	-
August	S	153	103	16	16	-
	G	169	87	16	16	-

Continued

		U1	U2	N1	N2	Sig
1982						
September	S	125.5	130.5	16	16	-
	G	134	106	16	15	-
October	S	115	141	16	16	-
	G	142.5	113.5	16	16	-
November	S	104	152	16	16	-
	G	117.5	138.5	16	16	-
1983						
March	S	67	189	16	16	$p<0.05$
	G	95	161	16	16	-

Table 4.11. Glossiphonia complanata. T and d tests comparing mean individual weights between stone and substratum samples for control (C) and enclosed (E) sites.

		F.	(v1,v2)	Sig	Test	(d.f.)	Sig
1979/81 cohort							
1981							
April	C	n too small					
	E	n too small					
1980/82 cohort							
1981							
April	C	1.042	(199,123)	-	t=1.923	(322)	-
	E	1.151	(147,184)	-	t=3.245	(331)	$p<0.005$
May	C	2.438	(168,108)	*	d=6.697	(276)	$p<0.001$
	E	2.720	(218, 55)	*	d=5.556	(141)	$p<0.001$
June	C	2.332	(255,220)	*	d=0.802	(444)	-
	E	1.588	(46,202)	*	d=2.024	(60)	$p<0.05$
July	C	2.754	(167, 37)	*	d=1.462	(89)	-
	E	2.786	(169, 25)	*	d=2.389	(50)	$p<0.05$
August	C	1.013	(46, 17)	-	t=0.257	(63)	-
	E	1.517	(80, 38)	-	t=0.209	(118)	-
September	C	3.356	(31, 8)	-	t=1.669	(39)	-
	E	4.884	(53, 7)	*	d=2.623	(20)	$p<0.05$
October	C	1.367	(20, 7)	-	t=0.484	(27)	-
	E	2.661	(13, 2)	-	t=0.682	(15)	-
1982							
January	C	no leeches in substratum					
	E	no leeches in substratum					
April	C	no leeches in substratum					
	E	no leeches in substratum					
1981/83 cohort							
1981							
May	C	all leeches the same weight					
	E	all leeches the same weight					
June	C	2.309	(51,110)	*	d=5.187	(72)	$p<0.001$
	E	10.721	(22, 34)	*	d=3.782	(25)	$p<0.001$
July	C	1.246	(65,267)	-	t=1.124	(332)	-
	E	1.061	(38,154)	-	t=3.710	(192)	$p<0.001$

Continued

		F.	(v1,v2)	Sig	Test	(d.f.)	Sig
1981							
August	C	1.084	(200,443)	-	t=0.968	(643)	-
	E	1.461	(104,299)	*	d=0.771	(157)	-
September	C	1.206	(173,318)	-	t=1.439	(491)	-
	E	1.323	(51,239)	-	t=1.728	(290)	-
October	C	1.386	(337,117)	*	d=2.167	(238)	p<0.05
	E	1.589	(17,200)	-	t=0.370	(217)	-
1982							
January	C	2.042	(186, 93)	*	d=5.071	(250)	p<0.001
	E	1.683	(118, 18)	-	t=2.597	(136)	p<0.05
April	C	1.516	(112, 70)	*	d=2.945	(170)	p<0.01
	E	2.815	(120, 65)	*	d=7.723	(183)	p<0.001
May	C	1.581	(65, 29)	-	t=1.923	(94)	-
	E	1.404	(51, 25)	-	t=1.849	(76)	-
June	C	1.549	(85, 37)	-	t=2.247	(122)	p<0.05
	E	1.188	(123, 55)	-	t=2.408	(178)	p<0.05
July	C	1.241	(94, 79)	-	t=0.310	(173)	-
	E	1.935	(96, 43)	*	d=0.492	(113)	-
August	C	1.478	(22, 55)	-	t=0.471	(77)	-
	E	1.628	(75, 37)	-	t=0.516	(112)	-
September	C	1.897	(28, 16)	-	t=0.162	(44)	-
	E	2.219	(29, 8)	-	t=0.012	(37)	-
October	C	1.999	(23, 14)	-	t=0.223	(37)	-
	E	2.143	(37, 14)	-	t=0.235	(51)	-
November	C	4.014	(10, 7)	*	d=1.381	(15)	-
	E	1.605	(14, 6)	-	t=0.031	(20)	-
1983							
March	C	2.191	(3, 12)	-	t=0.094	(15)	-
	E	5.538	(17, 4)	-	t=0.129	(21)	-
1982/84 cohort							
1982							
June	C	1.505	(41, 80)	-	t=2.225	(121)	p<0.05
	E	2.715	(40, 82)	*	d=4.448	(55)	p<0.001
July	C	1.571	(118, 81)	*	d=0.524	(195)	-
	E	1.155	(26, 73)	-	t=1.415	(99)	-
August	C	1.021	(132,315)	-	t=1.896	(447)	-
	E	1.214	(182, 77)	-	t=3.326	(259)	p<0.005

Continued

		F.	(vl,v2)	Sig	Test	(d.f.)	Sig
<u>1982</u>							
September	C	1.083	(148,278)	-	t=0.032	(426)	-
	E	1.181	(218,111)	-	t=3.257	(329)	p<0.005
October	C	1.432	(119,287)	*	d=0.774	(192)	-
	E	1.026	(258, 84)	-	t=0.576	(342)	-
November	C	1.250	(130,203)	-	t=1.105	(333)	-
	E	1.093	(188,143)	-	t=4.218	(331)	p<0.001
<u>1983</u>							
March	C	1.268	(136,123)	-	t=4.908	(259)	p<0.001
	E	1.084	(256,110)	-	t=4.112	(366)	p<0.001

Table 4.12. Glossiphonia complanata. T and d tests comparing mean individual weights between control and enclosed sites for separate stone (S) and substratum (G) samples.

		F.	(v1,v2)	Sig	Test	(d.f.)	Sig
1979/81 cohort							
1981							
April	S	n too small					
	G	n too small					
1980/82 cohort							
1981							
April	S	1.269	(123,147)	-	t= 1.991	(270)	p<0.05
	G	1.523	(199,184)	*	d= 3.183	(377)	p<0.005
May	S	1.189	(218,168)	-	t= 1.285	(386)	-
	G	1.065	(55,108)	-	t= 1.487	(163)	-
June	S	1.332	(202,255)	-	t= 6.968	(457)	p<0.001
	G	4.935	(46,220)	*	d= 5.641	(50)	p<0.001
July	S	2.747	(169,167)	*	d= 7.608	(278)	p<0.001
	G	2.715	(25, 37)	*	d= 3.477	(38)	p<0.005
August	S	1.865	(80, 46)	*	d= 1.360	(119)	-
	G	1.246	(38, 17)	-	t= 0.834	(55)	-
September	S	1.019	(31, 53)	-	t= 0.779	(84)	-
	G	1.483	(8, 7)	-	t= 0.556	(15)	-
October	S	4.895	(13, 20)	*	d= 1.667	(17)	-
	G	2.515	(2, 7)	-	t= 0.094	(9)	-
1982							
January	S	1.239	(16, 12)	-	t= 0.503	(28)	-
	G	none in substratum					
April	S	1.029	(6, 8)	-	t= 1.246	(14)	-
	G	none in substratum					
1981/83 cohort							
1981							
May	S	All leeches the same weight					
	G	All leeches the same weight					
June	S	2.680	(110, 34)	-	d= 1.121	(95)	-
	G	1.732	(22, 51)	-	t= 0.640	(73)	-
July	S	1.578	(267,154)	*	d= 0.609	(381)	-
	G	1.852	(65, 38)	*	d= 3.348	(98)	p<0.005

Continued

		F.	(v1,v2)	Sig	Test	(d.f.)	Sig
1981							
August	S	1.020	(443,299)	-	$t=7.974$	(742)	$p<0.001$
	G	1.321	(104,200)	-	$t=4.367$	(304)	$p<0.001$
September	S	1.047	(318,239)	-	$t=10.995$	(557)	$p<0.001$
	G	1.048	(51,173)	-	$t=3.005$	(224)	$p<0.005$
October	S	1.055	(337,200)	-	$t=8.421$	(537)	$p<0.001$
	G	2.087	(17,117)	*	$d=2.865$	(20)	$p<0.01$
1982							
January	S	1.048	(186,118)	-	$t=4.821$	(304)	$p<0.001$
	G	1.159	(18, 93)	-	$t=2.645$	(111)	$p<0.01$
April	S	1.196	(112,120)	-	$t=1.948$	(232)	-
	G	2.221	(70, 65)	*	$d=1.570$	(123)	-
May	S	1.532	(65, 51)	-	$t=0.155$	(116)	-
	G	1.361	(29, 25)	-	$t=0.421$	(54)	-
June	S	1.124	(123, 85)	-	$t=1.424$	(208)	-
	G	1.465	(55, 37)	-	$t=1.151$	(92)	-
July	S	1.286	(96, 94)	-	$t=1.020$	(190)	-
	G	1.212	(79, 43)	-	$t=0.733$	(122)	-
August	S	1.735	(75, 55)	*	$d=0.167$	(130)	-
	G	1.386	(22, 37)	-	$t=0.973$	(59)	-
September	S	3.220	(29, 28)	*	$d=1.392$	(46)	-
	G	2.754	(8, 16)	*	$d=1.281$	(11)	-
October	S	4.562	(37, 23)	*	$d=2.305$	(56)	$p<0.05$
	G	4.256	(14, 14)	*	$d=1.717$	(20)	-
November	S	6.633	(14, 7)	*	$d=1.624$	(20)	-
	G	1.030	(6, 10)	-	$t=0.299$	(16)	-
1983							
March	S	3.172	(17, 12)	*	$d=1.876$	(28)	-
	G	3.825	(3, 4)	-	$t=1.189$	(7)	-
1982/84 cohort							
1982							
June	S	1.848	(80, 82)	*	$d=2.276$	(147)	$p<0.05$
	G	1.025	(41, 40)	-	$t=0.541$	(81)	-
July	S	1.089	(73,118)	-	$t=1.587$	(191)	-
	G	1.976	(26, 81)	*	$d=2.764$	(35)	$p<0.05$
August	S	1.280	(182,315)	-	$t=3.698$	(497)	$p<0.001$
	G	1.032	(77,132)	-	$t=0.427$	(209)	-

Continued

		F.	(vl, v2)	Sig	Test	(d.f.)	Sig
1982							
September	S	1.514	(218,278)	*	d= 6.684	(415)	p<0.001
	G	1.184	(111,148)	-	t= 1.738	(259)	-
October	S	1.769	(258,287)	*	d= 6.464	(476)	p<0.001
	G	1.204	(84,119)	-	t= 3.718	(203)	p<0.001
November	S	1.031	(203,188)	-	t= 4.278	(391)	p<0.001
	G	1.407	(130,143)	*	d= 0.855	(256)	-
1983							
March	S	1.015	(256,136)	-	t= 5.826	(392)	p<0.001
	G	1.188	(110,123)	-	t= 6.038	(233)	p<0.001

Table 4.13. *Glossiphonia complanata*. Regression equations for arithmetic mean weight (mg) plotted against time (days) for data from control (C) and enclosed (E) sites.

Equation: $\mathrm{Ln}\ Y = RX + \mathrm{Ln}\ Q$ H_0: slope = 0

		R ± 95% C.I.	Q	t (d.f.)	Sig
1980/82 cohort					
April 1981 to October 1981	C	0.011 ± 0.003	2.166	9.269 (5)	$p<0.001$
	E	0.009 ± 0.002	2.433	10.881 (5)	$p<0.001$
October 1981 to January 1982	C	0.001 ± 0.001	4.077	8.493 (1)	-
	E	0.000 ± 0.009	4.113	0.245 (1)	-
1981/83 cohort					
June 1981 to September 1981	C	0.028 ± 0.028	0.782	6.418 (2)	$p<0.05$
	E	0.031 ± 0.018	0.668	7.688 (2)	$p<0.05$
September 1981 to May 1982	C	-0.001 ± 0.002	2.981	1.504 (3)	-
	E	-0.002 ± 0.002	3.271	2.717 (3)	-
May 1982 to November 1982	C	0.008 ± 0.001	2.682	31.466 (5)	$p<0.001$
	E	0.008 ± 0.001	2.795	15.666 (5)	$p<0.001$
1982/84 cohort					
June 1982 to September 1982	C	0.025 ± 0.017	0.545	6.615 (2)	$p<0.05$
	E	0.025 ± 0.020	0.701	5.361 (2)	$p<0.05$
September 1982 to March 1983	C	0.002 ± 0.005	2.795	1.558 (2)	-
	E	0.003 ± 0.005	2.926	2.438 (2)	-

Table 4.14. *Glossiphonia complanata*. Mortality data for the 1980/82, 1981/83 and 1982/84 cohorts from control (C) and enclosed (E) sites.

	1980/82 cohort		1981/83 cohort		1982/84 cohort	
	C	E	C	E	C	E
1. Estimated number of young produced (. m^{-2})	-	-	1776.5	5020.6	2219.8	1450.6
2. Density of leeches in September of their first year (. m^{-2})	-	-	216.0	175.2	104.3	81.9
3. Density of leeches in April of their first year (. m^{-2})	103.5	279.1	96.1	65.8	93.3	91.9
4. Density of leeches in September of their second year (. m^{-2})	10.5	28.9	10.6	5.9	-	-
5. Density of leeches in April of their second year (. m^{-2})	0.5	0.4	2.8	3.2	-	-
Mortality between points 1-2 above	-	-	87.8%	96.5%	95.3%	94.4%
Mortality between points 1-3 above	-	-	94.6%	98.6%	95.8%	93.7%
Mortality between points 1-4 above	-	-	99.4%	99.9%	-	-
Mortality between points 1-5 above	-	-	99.8%	99.9%	-	-
Mortality between points 3-4 above	89.9%	89.7%	85.5%	91.1%	-	-
Mortality between points 3-5 above	99.5%	99.9%	97.1%	95.2%	-	-

4.3.3 *Helobdella stagnalis*

In this part of the work, a total of 24,002 leeches were collected from the lake. From weight frequency histograms these leeches were identified as belonging to three cohorts. When sampling commenced in April 1981 all leeches were thought to be the offspring of animals which had bred the previous year, and it was not feasible to distinguish between possible spring and summer broods. During 1981, two peaks in breeding activity occured, giving rise to spring and summer broods of young. These broods remained distinct until October 1981 and the survivors of both broods then formed the over-wintering population. In 1982, two peaks of breeding activity again occurred, giving rise to spring and summer broods which remained distinct until October 1982. These leeches then formed the over-wintering population which was last sampled in March 1983.

The above groups are hereafter referred to as the over-wintering 1980/81 cohort, the 1981/82 cohort, divided into spring and summer broods and the over-wintering population, and the 1982/83 cohort, divided into spring and summer broods and the over-wintering population.

For ease of presentation, in most of the following graphs, data from spring and summer broods of young were combined and separate graphs plotted to cover the periods when the two broods were distinct.

4.3.3.1 Density

The data showing geometric mean densities with 95% confidence limits for separate stone and substratum samples from control and enclosed sites are illustrated in figures 4.46 and 4.47.

In the 1980/81 cohort in control sites, the proportion of leeches on the stones increased from 1.9% in May 1981 to 60.0% in July. In enclosed sites the proportion rose from 7.2% in May to 52.3% in July. During this period in control sites, density increased on the stones and decreased in the substratum between May and July. In enclosed sites density decreased in both fractions during this period, but the rate of decrease was higher in the substratum.

In the spring brood of the 1981/82 cohort in control sites, the proportion of leeches on the stones declines from 29.8% in June 1981 to 7.3% in August. In enclosed sites the decline was from 24.8% in June to 7.0% in August. In the summer brood of the 1981/82 cohort the proportion on the stones decreased from 13.2% in August 1981 to 4.2% in September in control sites, and from 10.5% to 4.4% in enclosed sites over the same period. In January 1982, 0.9% in control and 4.7% in enclosed sites of the over-wintering leeches were on the stones. Between May and June 1982 the proportion increased from 8.7% to 42.8% in control sites and from 10.9% to 38.5% in enclosed sites, and during this period the density of leeches rose on the stones and decreased on the substratum in both control and enclosed sites.

In the spring brood of the 1983/83 cohort in control sites the proportion of leeches on the stones declined from 13.1% in June 1982 to 4.6% in July. In enclosed sites the decline was from 12.1% in June to 4.2% in July. In the summer brood of the 1982/83 cohort the proportion of leeches on the stones decreased from 18.6% to 9.7% between August and September in control sites. In enclosed sites a slight rise occurred from 7.4% in August to 8.3% in September. By March 1983, 12.% in control sites and 0.8% in enclosed sites of the over-wintering leeches were on the stones.

The data comparing total geometric mean density, total geometric mean density of spring and summer broods, stone sample densities with 95% confidence limits and substratum sample mean density with 95%

confidence limits are given in figures 4.48, 4.49, 4.50 and 4.51. The results of Mann-Whitney U tests, comparing densities in control and enclosed sites, are given in table 4.15.

In April 1981 the density of the 1980/81 cohort in control sites was 342.6 m^{-2}, and 410.5 m^{-2} in enclosed sites. The density in control sites decreased until September 1981 when the cohort died out. In enclosed sites, density declined until July and then appeared to rise in August before the cohort died out after the sample in September 1981. However, the wide confidence limits during this period suggested that this apparent rise could be due to sampling error.

The regression equation $\ln Y = RX + \ln Q$, when applied to the period April to August 1981 for separate control and enclosed sites suggested that during this time a constant decrease in density occurred.

Control sites: $R = -0.037 \pm 0.025$ $p<0.05$
$Q = 6.445$

Enclosed sites: $R = -0.026 \pm 0.017$ $p<0.05$
$Q = 6.174$

Significant differences in density between control and enclosed sites occurred in May, July and August 1981 in stone samples, and in all cases the density was higher in enclosed sites. No significant differences were recorded in substratum samples or in the remainder of the stone samples for this cohort.

The spring brood of the 1981/82 cohort first appeared in June 1981 and in control sites the density of leeches rose from 70.8 m^{-2} in June to 198.6 m^{-2} in August. In enclosed sites, the density in June was 90.4 m^{-2} and a maximum of 378.2 m^{-2} occurred in September. The summer brood appeared in August 1981 with a density of 86.9 m^{-2} in control and 216.2 m^{-2} in enclosed sites. By September 1981, the density in control sites had risen to 192.8 m^{-2} but had declined to 142.6 m^{-2} in enclosed sites. In the sample of October 1981 the two broods were no longer distinct and the numbers now declined until the sample of October 1982, when no leeches belonging to this cohort were recognised.

The regression equation $\ln Y = RX + \ln Q$ when applied to the period September 1981 to June 1982, suggested that the decrease in density during this period could be regarded as constant.

Control sites: $R = -0.012 \pm 0.005$ $p<0.005$

$Q = 6.350$

Enclosed sites: $R = -0.014 \pm 0.006$ $p<0.005$

$Q = 6.164$

However, from figure 4.48 it seemed that the rate of decline was lower in the period September 1981 to April 1982 than between April and July 1982.

No significant differences in density between control and enclosed sites in either stone or substratum samples were recorded when the spring and summer broods were distinct. However, in the over-wintering population differences in the stone samples occurred in June, July and August 1982, and in substratum samples in January and May 1982. In all cases the density was higher in control sites.

The spring brood of the 1982/83 cohort appeared in June 1982 and in control sites the density of leeches rose from 107.9 m^{-2} in June to a maximum of 229.2 m^{-2} in July and then declined. In enclosed sites, the maximum density of 93.1 m^{-2} occurred in June and declined thereafter.

The summer brood appeared in August 1982 and the density in control sites rose from 92.7 m^{-2} in August to 166.5 m^{-2} in September. In enclosed sites the respective densities were 44.7 m^{-2} and 126.2 m^{-2}. By October 1982, the two broods were not distinct and the over-all density declined to 94.1 m^{-2} in control sites and to 89.2 m^{-2} in enclosed sites in March 1983.

The regression equation $\text{Ln } Y = RX + \text{Ln } Q$, when applied to the period September 1982 to March 1983 suggested that the rate of decrease in density was constant.

Control sites $R = -0.005 \pm 0.004$ $p<0.05$
$Q = 5.430$

Enclosed sites: $R = -0.004 \pm 0.004$ $p<0.05$
$Q = 5.189$

In the spring brood, the density in control sites was significantly higher than in enclosed sites in both stone and substratum samples in July 1982 and in stone samples only, in August and September 1982. In the summer brood the density was significantly higher in control sites in stone samples from August 1982. In the remainder of samples for this cohort, there were no other significant differences.

4.3.3.2 Biomass

The data showing geometric mean biomass with 95% confidence limits for separate stone and substratum sample data from control and enclosed sites are presented in figures 4.52 and 4.53.

In the 1980/81 cohort the proportion of the leech biomass on the stones rose from 1.8% in May 1981 to 83.7% in July in control sites and from 9.2% to 73.1% in enclosed sites for the same months.

In the spring brood of the 1981/82 cohort the proportion of the biomass on the stones in control sites rose from 23.0% in June 1981 to 32.8% in July, and then declined. In enclosed sites in June, the proportion was 33.0% and thereafter decreased. In the summer brood, the proportion was 10.5% in control sites and 9.3% in enclosed sites in August 1981 and after this, decreased. In January 1982, the proportions were 1.0% and 4.1% for respective control and enclosed sites and then rose from 10.8% in May 1982 to 64.1% in June in control sites and from 11.5% to 51.7% in enclosed sites.

In the spring brood of the 1982/83 cohort, the proportion on the stones was 12.4% in control sites and 11.9% in enclosed sites in June 1982 and decreased to 6.1% and 4.3% respectively by July. In the summer brood, the proportions were 17.3% and 7.2% for control and enclosed sites in August 1982 and 9.9% and 8.7% respectively in September. By the last sample of March 1983 the proportion of the biomass on the stones was 1.0% in control sites and 0.6% in enclosed sites.

The data comparing total geometric mean biomass, total geometric mean biomass for spring and summer broods, stone sample mean biomass with 95% confidence limits and substratum sample mean biomass with 95% confidence limits are given in figures 4.54, 4.55, 4.56 and 4.57. The results of Mann-Whitney U tests, comparing biomass between control and enclosed sites are given in table 4.16.

In the 1980/81 cohort in April 1981, the mean biomass was 2.0 $g.m^{-2}$ in control sites and 2.6 $g.m^{-2}$ in enclosed sites. The biomass then decreased rapidly and no leeches of this cohort were present by October 1981. The mean biomass was significantly higher in enclosed sites in stone samples only in May and August 1981, but in all other samples for this cohort, there were no significant differences.

In the spring brood of the 1981/82 cohort the biomass in control sites increased from 0.071 $g.m^{-2}$ in June 1981 to 1.2 $g.m^{-2}$ in September, and in enclosed sites from 0.095 $g.m^{-2}$ to 3.4 $g.m^{-2}$ in the same months.

In the summer brood, the biomass in August 1981 was 0.1 $g.m.^{-2}$ in control sites and 0.3 $g.m^{-2}$ in enclosed sites and had increased to 0.5 $g.m^{-2}$ in control sites and 0.4 $g.m^{-2}$ in enclosed sites by September. The mean biomass in both control and enclosed sites for the combined broods then decreased at a relatively slow rate until June 1982, before a rapid decline to the end of the cohort.

The biomass in enclosed sites was significantly higher in the spring brood in September 1981 in substratum samples, but there were no other significant differences during the time when the broods were distinct. In the over-wintering population, the biomass was significantly higher in enclosed sites from stone samples in October and significantly higher in control sites in the substratum samples of May 1982 and the stone samples of June and August 1982. There were no other significant differences.

In the spring brood of the 1982/83 cohort, the biomass was 0.1 $g.m^{-2}$ in both control and enclosed sites in June 1982 and had reached 0.8 $g.m^{-2}$ in control sites and 0.5 $g.m^{-2}$ in enclosed sites by September. In the summer brood, biomass increased between August and September 1982 from 0.1 $g.m^{-2}$ to 0.6 $g.m^{-2}$ in control sites and from 0.1 $g.m^{-2}$ to 0.4 $g.m^{-2}$ in enclosed sites. Over-all biomass then declined and by March 1983 was at 0.5 $g.m.^{-2}$ in control sites and 0.4 $g.m^{-2}$ in enclosed sites. In the spring brood, the biomass was significantly higher in control sites in the stone and substratum samples of July 1982 and in the stone samples only of August and September. In the summer brood, the biomass was significantly higher in control sites in the stone samples of August 1982, and the same was true in the substratum samples of November 1982 for the over-wintering population. There were no other significant differences.

4.3.3.3 Growth

Figures 4.58 and 4.59 present the size-structure of leeches from separate stone and substratum samples from control and enclosed sites. The size-structure of leeches from combined stone and substratum sample data for control and enclosed sites are presented in figure 4.60. Figures 4.61 and 4.62 present the arithmetic mean individual weights with 95% confidence limits for separate stone and substratum samples from control and enclosed sites. The results of t and d tests, comparing stone sample versus substratum sample mean weights for control and enclosed sites are given in table 4.17.

For the 1980/81 cohort in control sites,the mean individual weight on the stones rose from 6.6 mg to 18.8 mg between April and August 1981, and in the substratum, from 5.9 mg to 15.8 mg. In enclosed sites, the corresponding rise was from 6.5 mg to 16.4 mg on the stones and from 6.3 mg to 17.4 mg in the substratum. In control sites the mean weight on the stones was significantly higher than in the substratum in the samples of April, May, June and August 1981. In enclosed sites, the mean weight on the stones was significantly higher in May and June 1981.

In the spring brood of the 1981/82 cohort, the mean weight in June 1981 in control sites was 1.0 mg for leeches both on the stones and in the substratum. In enclosed sites, the mean weight was 1.0 mg on the stones and 1.1 mg in the substratum. By September 1981 in control sites, the mean weight had reached 7.8 mg on the stones and 7.2 mg in the substratum. In enclosed sites the weights were 9.9 mg on the stones and 9.2 mg in the substratum. In the summer brood,the mean weight in August 1981 in control sites was 1.2 mg for leeches on the stones and 1.6 mg for leeches in the substratum. In enclosed sites, the mean weight was 1.1 mg on the stones and 1.3 mg in the substratum. In September 1981, the mean weight in control sites had reached 2.3 mg on the stones and 2.5 mg in the substratum. In enclosed sites, the mean weights were 2.9 mg in both stone and substratum samples. By April 1982, the mean weight of the combined broods was 6.3 mg on the stones and 5.0 mg in the substratum in control sites, and 6.9 mg on the stones and 4.8 mg in the substratum in enclosed sites. The mean weight now increased rapidly and by July 1982 had reached 13.3 mg in both stone and substratum samples in control sites and 14.1 mg on the stones and 11.3 mg in the substratum in enclosed sites.

In the spring brood, the mean weight was significantly higher on the stones than in the substratum in the samples of July and August 1981 for enclosed sites and in September 1981 for control sites. In the summer brood, the same was true in August and September 1981 in control sites and in August only for enclosed sites. For the overwintering population, the mean weight was higher on the stones in both control and enclosed sites for all samples between October 1981 and June 1982.

In the spring brood of the 1982/83 cohort, the mean weight of leeches in June 1982 was 1.3 mg on both the stones and in the substratum in control sites,and 1.3 mg on the stones and 1.2 mg in the substratum in enclosed sites. By September 1982, in control sites the mean weight had reached 10.6 mg on the stones and 9.9 mg in the substratum. In enclosed sites the weights were 9.8 mg on the stones and 9.6 mg in the substratum. In the summer brood, the mean weight in August 1982 in control sites was 1.3 mg for leeches on the stones and 1.4 mg for leeches in the substratum. In enclosed sites, the mean weight was 1.3 mg for both leeches on the stones and in the substratum. In September 1982, the mean weight in control sites had reached 3.8 mg for leeches both on the stones and in the substratum,and in enclosed sites the mean weights were 3.7 mg on the stones and 3.2 mg in the substratum. By March 1983, the mean weight of the combined broods was 5.3 mg on the stones and 5.1 mg in the substratum on control sites and 5.1 mg on the stones and 4.9 mg in the substratum in enclosed sites.

In the spring brood, the mean weight of leeches was significantly higher on the stones in July and August 1982 for control sites and in August only for enclosed sites. In the summer brood, the same was true in August 1982 in control sites and September in enclosed sites. For the over-wintering population the mean weight was higher on the stones in October 1982 in control sites and November 1982 in enclosed sites.

The data comparing the estimated arithmetic mean individual weights from combined stone and substratum sample data, the mean weights of the spring and summer broods, stone sample mean weights with 95% confidence limits and substratum sample mean weights with 95% confidence limits for control and enclosed sites are given in figures 4.63, 4.64, 4.65 and 4.66. The results of t and d tests comparing mean weights between control and enclosed sites are given in table 4.18.

In the 1980/81 cohort, over-all mean weight rose from 5.9 mg to 16.1 mg in control sites, and from 6.3 mg to 17.3 mg in enclosed sites between April and August 1981. The mean weight was significantly higher in control sites in stone samples of August 1981 only and higher in enclosed sites in the stone samples of May and June and the substratum samples of August 1981.

The mean weight of the spring brood rose from 1.0 mg to 7.2 mg in control sites,and from 1.0 mg to 9.2 mg in enclosed sites between June and September 1981. Between August and September 1981 the mean weight of the summer brood rose from 1.5 mg to 2.5 mg in control sites and from 1.3 mg to 2.9 mg in enclosed sites. In the over-wintering population little further growth occurred until May 1982, when growth was again rapid and by August 1982, the mean weights had reached 16.9 mg in control sites and 15.5 mg in enclosed sites. In the spring brood, the mean weight was significantly higher in enclosed sites in the stone samples of July 1981 and the stone and substratum samples of August and

September 1981. In the summer brood, the mean weight was significantly higher in control sites in both stone and substratum samples taken in August 1981. In September 1981, however, the mean weight of leeches was significantly higher in enclosed sites in both stone and substratum samples. In the over-wintering population, the mean weight was significantly higher in enclosed sites in stone and substratum samples in October 1981. For the rest of the cohort, there were no significant differences.

In the spring brood of the 1982/83 cohort, mean weight rose from 1.3 mg to 10.0 mg in control sites and from 1.2 mg to 9.6 mg in enclosed sites between June and September 1982. Between August and September 1982, the mean weight of the summer brood rose from 1.4 mg to 3.8 mg in control sites and from 1.3 mg to 3.3 mg in enclosed sites. In the over-wintering population, little further growth occurred and by March 1983 the mean weight was 5.1 mg in control sites and 4.9 mg in enclosed sites. The mean weight was significantly higher in control sites in the spring brood from stone samples in September 1982, in the summer brood from substratum samples in September 1982 and in the over-wintering population from substratum samples in November 1982. In all other samples for this cohort, there were no other significant differences.

The regression equations describing growth in different periods within each cohort are given in table 4.19. In general, growth-rates were initially high after release from the adults, low over the winter and high again from the following April to the end of the cohort.

In the 1980/81 cohort, the regression equation suggested that the growth-rate was constant between April and August 1981, and an analysis of covariance indicated that there was no significant difference in the rates between control and enclosed sites ($F=0.129$ with 1,7 d.f.).

In the 1981/82 cohort between June and September 1981, the growth-rate was constant in enclosed sites, but the regression equation did not give a significant fit to the data in control sites. Between September 1981 and April 1982 there was no significant relationship between weight and time, but between April and September 1982 a constant growth-rate occurred in both control and enclosed sites. The analysis of covariance indicated that the growth-rates were not significantly different between control and enclosed sites ($F=0.875$ with 1,8 d.f.). On comparing the growth-rates during this period with those found in the 1980/81 cohort, it was found that the rate was significantly higher in control sites ($F=6.995$ with 1,7d.f. $p<0.05$), but did not differ significantly in enclosed sites. When the regression equation was applied to the whole lifespan of the cohort, from June 1981 to September 1982, a significant result was again obtained and there was no difference in the rates between control and enclosed sites.

In the 1982/83 cohort, no significant relationships between weight and time were found.

4.3.3.4 Reproduction

Table 4.20 presents the proportions of H. stagnalis breeding in monthly samples taken during 1981 and 1982. The data summarising the production of eggs, cocoons and young are given in table 4.21.

During 1981, breeding data were only collected for leeches from stones at the times of the main samples.

In April 1981, for the 1980/81 cohort of leeches, a total of 44.8% in control sites and 44.7% in enclosed sites were breeding. Most of the breeding leeches still had eggs in their oviducts, though a few carried eggs in cocoons. On 27th May 1981, no leeches still had eggs in their oviducts, and few were carrying cocoons. However, 22.9% in control sites and 35.0% in enclosed sites of leeches were carrying young. On 30th June, leeches with eggs in oviducts, carrying eggs in cocoons and carrying young were recorded in both control and enclosed sites and a total of 41.9% in control sites and 70.0% in enclosed sites were breeding. On 30th July 1981, no leeches still had eggs in their oviducts, a few still carried eggs in cocoons, but most breeding leeches were carrying young and a total of 63.4% in control sites and 58.4% in enclosed sites were breeding. On the 26th August, only leeches carrying young were recorded. The number of eggs in oviducts was significantly higher in enclosed than in control sites for leeches sampled on 22nd April ($t=2.223$ with 29 d.f $p<0.05$), and the reverse was true for the number of young carried in June 1981 ($d=2.605$ with 17 d.f. $p<0.05$). There were no other significant differences between control and enclosed sites.

For the spring brood of the 1981/82 cohort, leeches carrying eggs in oviducts and in cocoons were recorded on 30th July 1981, when a total of 14.9% in control sites and 38.3% in enclosed sites were breeding. On 26th August, only one leech carrying eggs in cocoons was recorded and 7.3% in control sites and 5.3% in enclosed sites were carrying young. The number of eggs in oviducts, on 30th July was significantly higher in enclosed sites ($t=3.370$ with 5 d.f. $p<0.05$), though the sample size was very small. There were no other significant differences between control and enclosed sites in either the number of eggs in cocoons or the number of young being carried.

From the above data, it seemed that the over-wintering 1980/81 cohort bred in two pulses. Breeding leeches were found between April and May, but then there was a break with no leeches having eggs in their oviducts. However, leeches with eggs in their oviducts were again recorded at the end of June. In order to estimate the maximum proportions found breeding in each of these two pulses were used and employed as follows.

In control sites, for example, 44.8% of the leeches were breeding in April 1981. The density at this time was 342.6 m^{-2}, giving a total of 153.5 breeding leeches from m^{-2}. This meant that 189.1 leeches per m^{2} had not bred. In the second breeding pulse, a maximum of 63.4% of the leeches were found breeding, giving a further 119.9 breeding animals per m^{2}. Thus, out of the initial density of 342.6 m^{-2}, in April 1981, a maximum of 273.4 m^{-2} of the leeches may have bred (79.8%). From the maximum mean number of eggs found in oviducts (20.9 . breeding leech) the maximum number of young produced by this cohort was estimated at 5714.1 m^{-2}.

Of the spring brood of young, some 14.9% were found breeding in control sites on 30th July. The density of young at this time was 127.7 m^{-2}, giving a total of 19.0 breeding leeches per m^{2}. The mean number of eggs in oviducts was 10.4 giving an estimated production of 197.6 young per m^{2}. Thus, the maximum total number of leeches entering the 1981/82 cohort in control sites was 5911.7 m^{-2}.

Using the same method of calcuation and the same assumptions for leeches from enclosed sites, 83.4% of the over-wintering population bred, giving rise to 9140.9 young per m^{2}. In the spring brood, 38.3% were found breeding on 30th July, giving rise to 2329.3 young per m^{2}. Thus, the maximum total number of leeches entering the 1981/82 cohort in enclosed sites was 11470.2 young per m^{2}.

In 1982, data for breeding were obtained for leeches from both stone and substratum samples from control and enclosed sites at the times of the monthly samples. Additional samples, from stones only, were taken to assist in interpreting the pattern of breeding, but these data were not used for estimates of fecundity.

On 15th April 1982, a total of 19.4% in control sites and 29.9%, in enclosed sites, of the leeches were carrying eggs in their oviducts. The proportions breeding in the substratum were approximately equal (control sites) or greater (enclosed sites) than the proportions breeding on the stones. On 6th May, an additional sample (n=51) revealed that 82.4% of leeches on the stones were carrying eggs in cocoons, and that a further 7.8% still had eggs in their oviducts. In the monthly sample of 12th May, a total of 37.9% in control sites, and 33.3% in enclosed sites, of the leeches were breeding. Most of these leeches were carrying eggs in cocoons, although leeches with eggs in oviducts and carrying young were also recorded. The proportions breeding, for all breeding states, were higher for leeches from stone samples than for leeches in substratum samples.

An intermediate sample, taken on 2nd June (n=43), showed that no leeches had eggs in their oviducts and that all of the breeding leeches were carrying young.

On the 18th June, for the 1981/82 cohort, a total of 16.7% in control sites and 15.6% in enclosed sites, of the leeches were breeding and leeches with eggs in oviducts, eggs carried in cocoons and carrying young were recorded. However, no breeding leeches were found in substratum samples. On 21st July, 67.8% in control sites and 68.6% in enclosed sites of the leeches were breeding, and the majority of these were carrying young. The proportions breeding on the stones and in the substratum were approximately equal.

There were no significant differences between control and enclosed sites in the mean numbers of eggs in oviducts, eggs carried in cocoons, or young carried per breeding leech.

For the spring brood of the 1983/83 cohort, leeches carrying eggs in oviducts, eggs in cocoons and young, were recorded on 21st July 1982, when 7.5% in control sites and 12.3% in enclosed sites of the leeches were breeding. The proportion of breeding was higher on the stones than in the substratum. On the 18th August, only leeches carrying young were recorded and no breeding leeches were found in substratum samples. There were no significant differences between control and enclosed sites in the mean numbers of eggs in oviducts, eggs carried in cocoons or young carried per breeding leech.

From the above data, again, it seemed that the over-wintering cohort bred in two pulses. Leeches with eggs in their oviducts were found from 15th April to 12th May. No such leeches were present on 2nd June, but leeches with eggs in their oviducts were again found from 18th June to 21st July. Therefore, the estimates of the number of young produced by this cohort were made using the same calculations and assumptions as for the 1981 breeding data.

Using the same calculations as for the 1980/81 over-wintering cohort, of the over-wintering 1981/82 cohort in control sites, some 80% of the leeches were thought to have bred, giving rise to 1527.9 young per m^2. In the spring brood, 7.5% were breeding on 21st July and were estimated to have produced 209.1 young per m^2. Thus the maximum number of leeches entering the 1982/83 cohort in control sites was 1737.0 m^{-2}. For the over-wintering 1982/83 cohort in enclosed sites, 79.1% of the leeches were thought to have bred, producing 1316.3 young per m^2. In the spring brood, 12.3% were breeding on 21st July and were estimated to have produced 144.3 young per m^2. Thus the maximum number of leeches entering the 1982/83 cohort in enclosed sites was 1460.6 m^{-2}.

The pattern of breeding described above is summarised in figure 4.67.

4.3.3.5 Mortality

The data describing mortality are given in table 4.22 and the regression equations covering the periods when the rate of mortality was constant were given in section 4.3.3.1.

The mortality rate in the first few months of the leech's life-span was high. In the 1981/82 cohort, 93.3% in control sites and 95.4% in enclosed sites of the young thought to have entered the population had died by September 1981. By the following April, this mortality had increased to 98.5% in control and 99.4% in enclosed sites, and by August 1982 very few leeches of this cohort were still alive.

In the 1982/83 cohort, the recruitment into the population was thought to be much lower than in the previous year and this was reflected in a lower rate of mortality in the first few months. By September 1982, 85.4% in control sites and 86.7% in enclosed sites of the young had died. The mortality had increased to 94.6% in control sites to 93.9% in enclosed sites by the last sample of March 1983.

The regression equations given in section 4.3.3.1 suggested that, for the 1980/81 cohort, the rate of mortality was constant between April and August 1981 in both control and enclosed sites. An analysis of covariance indicated that the rates did not differ significantly between control and enclosed sites ($F=1.477$ with 1,6 d.f.). In the 1981/82 cohort, the mortality rate was constant between September 1981 to July 1982 in both control and enclosed sites and there was no significant difference between their respective rates ($F=0.257$ with 1,10 d.f.). In the 1982/83 cohort, between September 1982 and March 1983, the mortality rates were also constant and there was no difference between the rates in control and enclosed sites ($F=0.669$ with 1,4 d.f.).

4.3.3.6 Production

Data illustrating the rate of biomass production, and calculated using the instantaneous growth-rate method, for all leeches samples between April 1981 and March 1983, and for the separate spring and summer broods are presented in figures 4.68 and 4.69.

Using the instantaneous growth-rate method of calculating production, the annual production of all leeches present between April 1981 and April 1982 was 1.7 $g.m^{-2}$ in control sites and 2.7 $g.m^{-2}$ in enclosed sites. The mean biomass over this period was 1.1 $g.m^{-2}$ in control sites and 1.3 $g.m^{-2}$ in enclosed sites, giving turnover rates of 1.6 and 2.1 respectively. Between April 1982 and March 1983, production by all leeches was 1.6 $g.m^{-2}$ in control sites and 0.8 $g.m^{-2}$ in enclosed sites. The mean biomass over this period was 0.7 $g.m^{-2}$ in control sites and 0.5 $g.m^{-2}$ in enclosed sites, giving turnover rates of 2.3 and 1.6 respectively.

In general, the rate of biomass production was high at the beginning of each cohort, was low or even negative in the autumn and winter, and then rose again before the cohort died out.

In the 1981/82 cohort, being the only cohort to be sampled over its entire life-span, total production was 1.0 $g.m^{-2}$ in control sites and 2.0 $g.m^{-2}$ in enclosed sites. The mean biomass for the cohort was 0.6 $g.m^{-2}$ in control sites and 0.8 $g.m^{-2}$ in enclosed sites, giving turnover rates of 1.7 and 2.5 respectively.

In common with data for _Erpobdella octoculata_ and _Glossiphonia complanata_, the above results do not include the possible production by the large number of young which were thought to have entered the population, but which were never recorded in samples. However, unlike the _G. complanata_ results, the population density of _Helobdella stagnalis_ did not continue to rise after breeding had stopped and, therefore, it seems likely that the missing young died soon after hatching. For this reason no attempt has been made to include them in the production estimates.

The Allen curves for the 1981/82 cohort from separate control and enclosed sites are given in figures 4.70 and 4.71. In common with the G. complanata results, the maximum density did not coincide with the minimum mean weights (due to prolonged recruitment), and negative production occurred in the autumn and winter. This gave rise to a wide scatter of points and, therefore, the smoothed curves fitted were, again, somewhat arbitrary. However, production was estimated at 1.6 $g.m^{-2}$ in control sites and 1.5 $g.m^{-2}$ in enclosed sites.

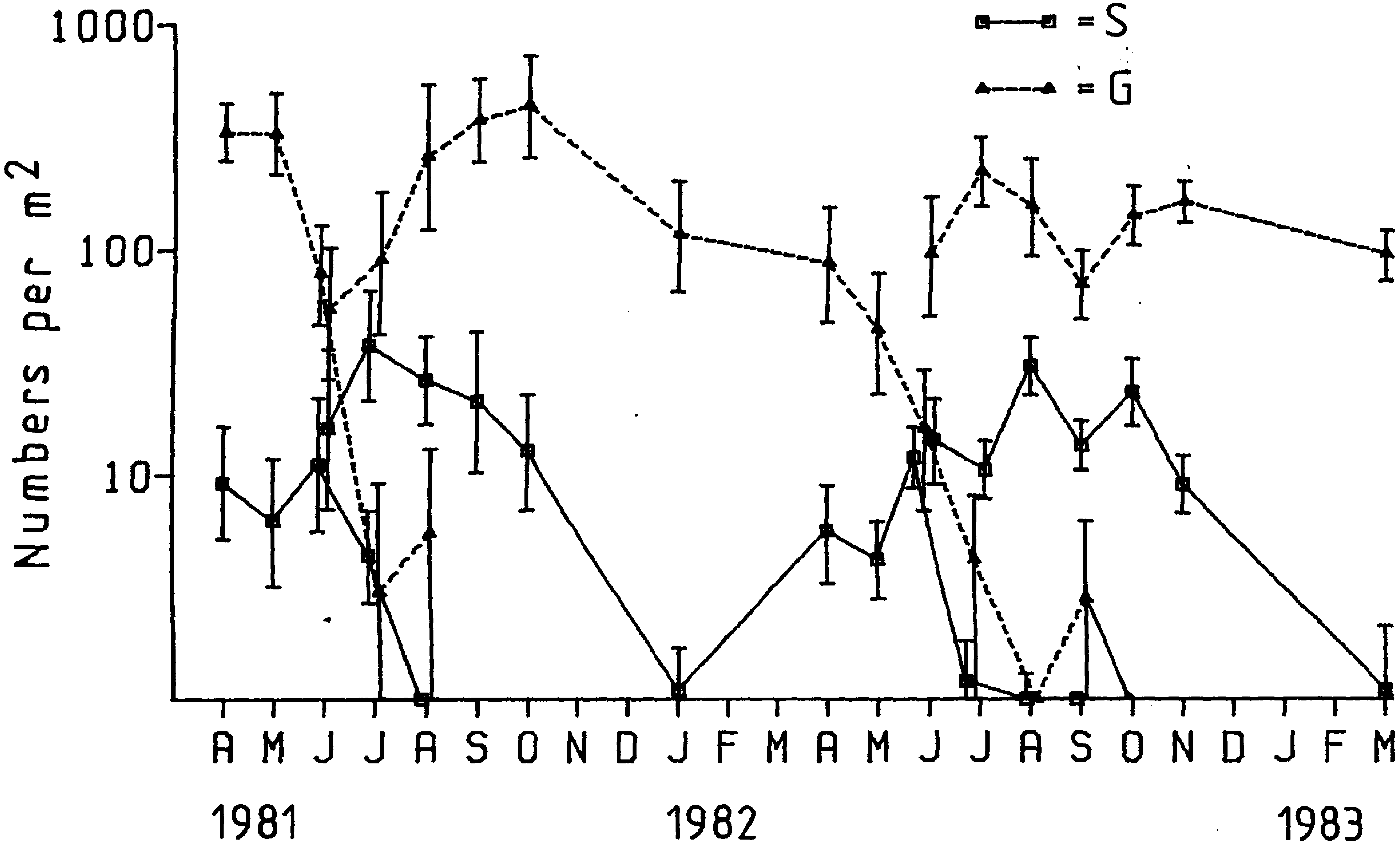


Figure 4.46. Helobdella stagnalis. Geometric mean density ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from control sites (spring and summer broods of young combined).

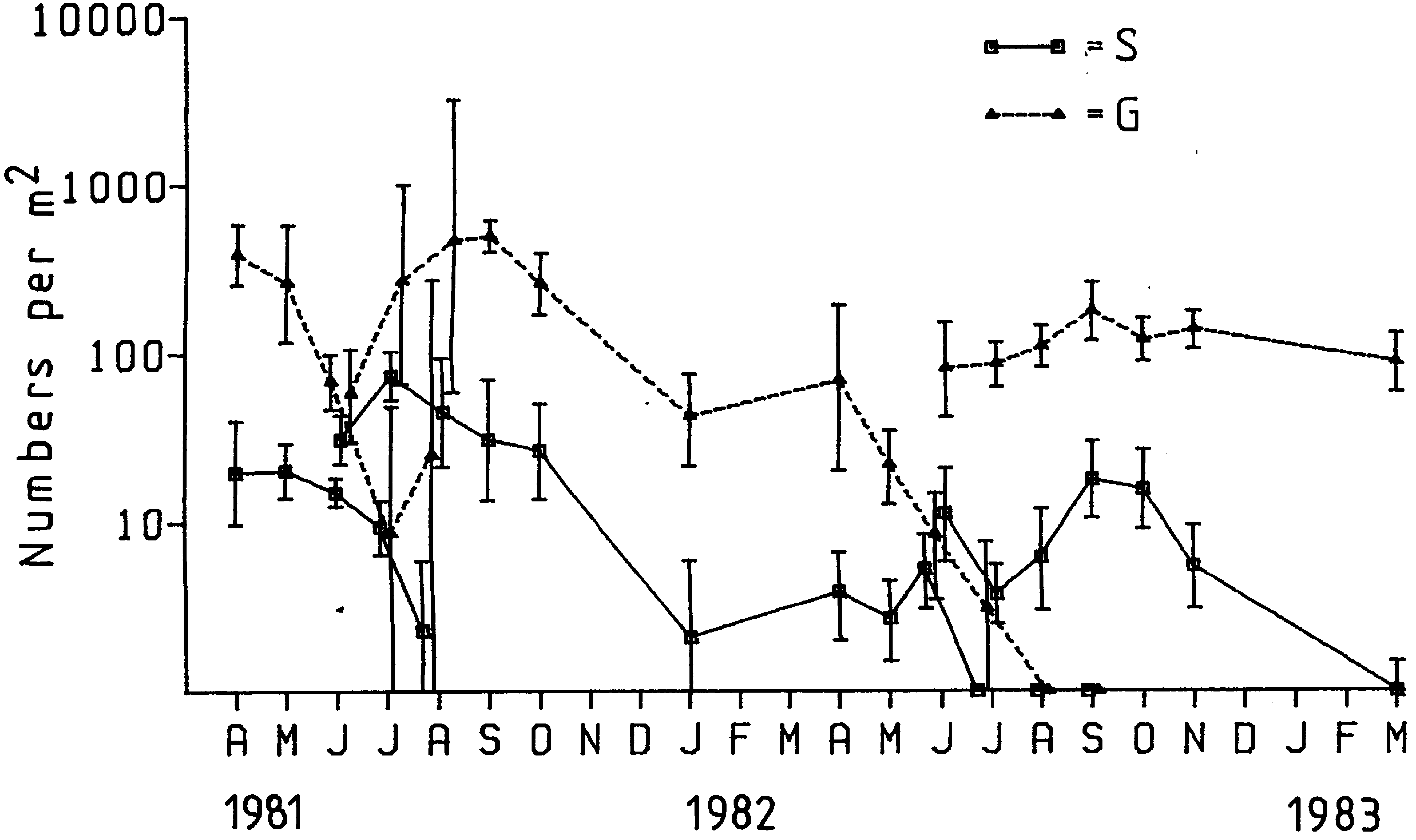


Figure 4.47. Helobdella stagnalia. Geometric mean density ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from enclosed sites (spring and summer broods of young combined).

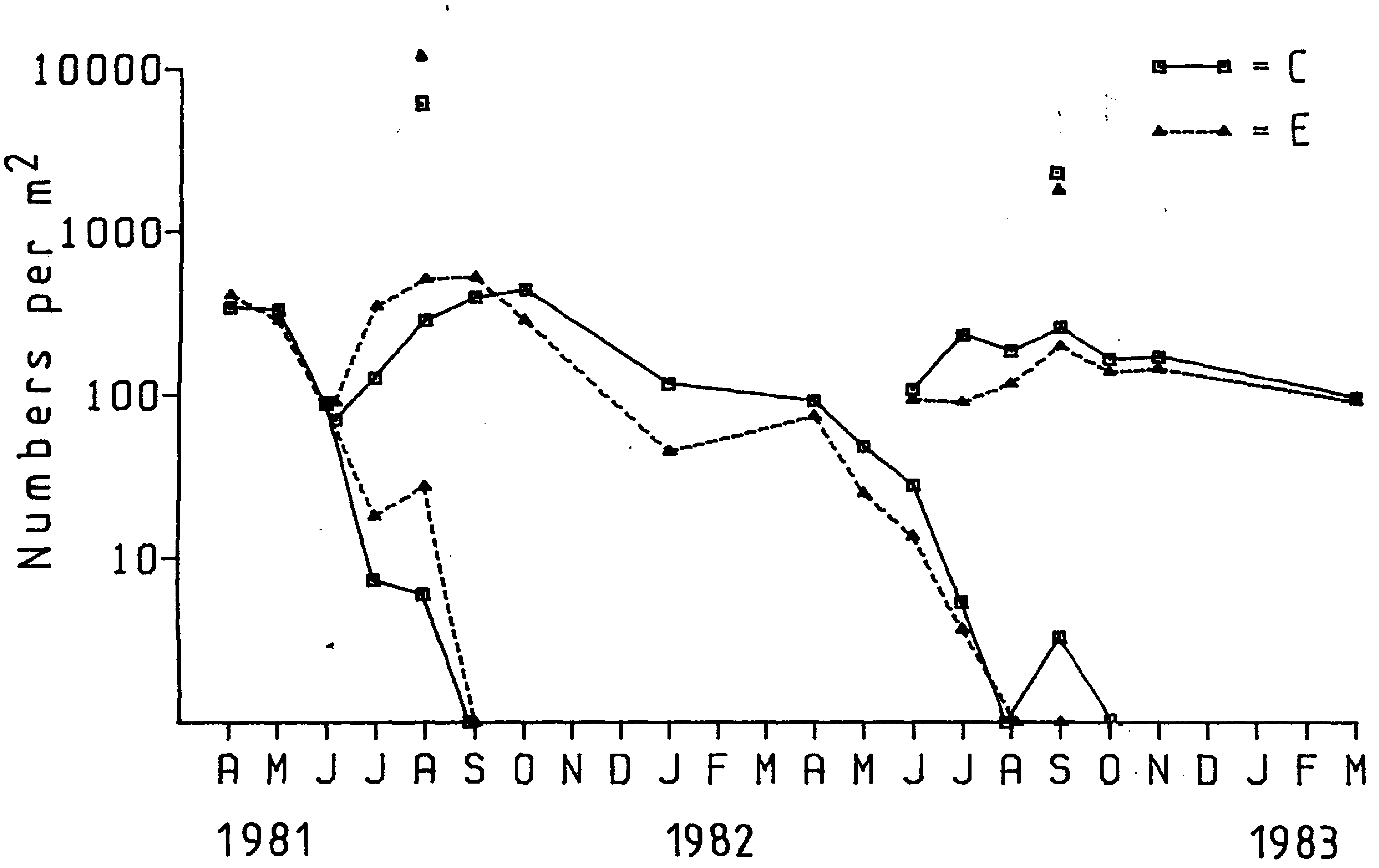
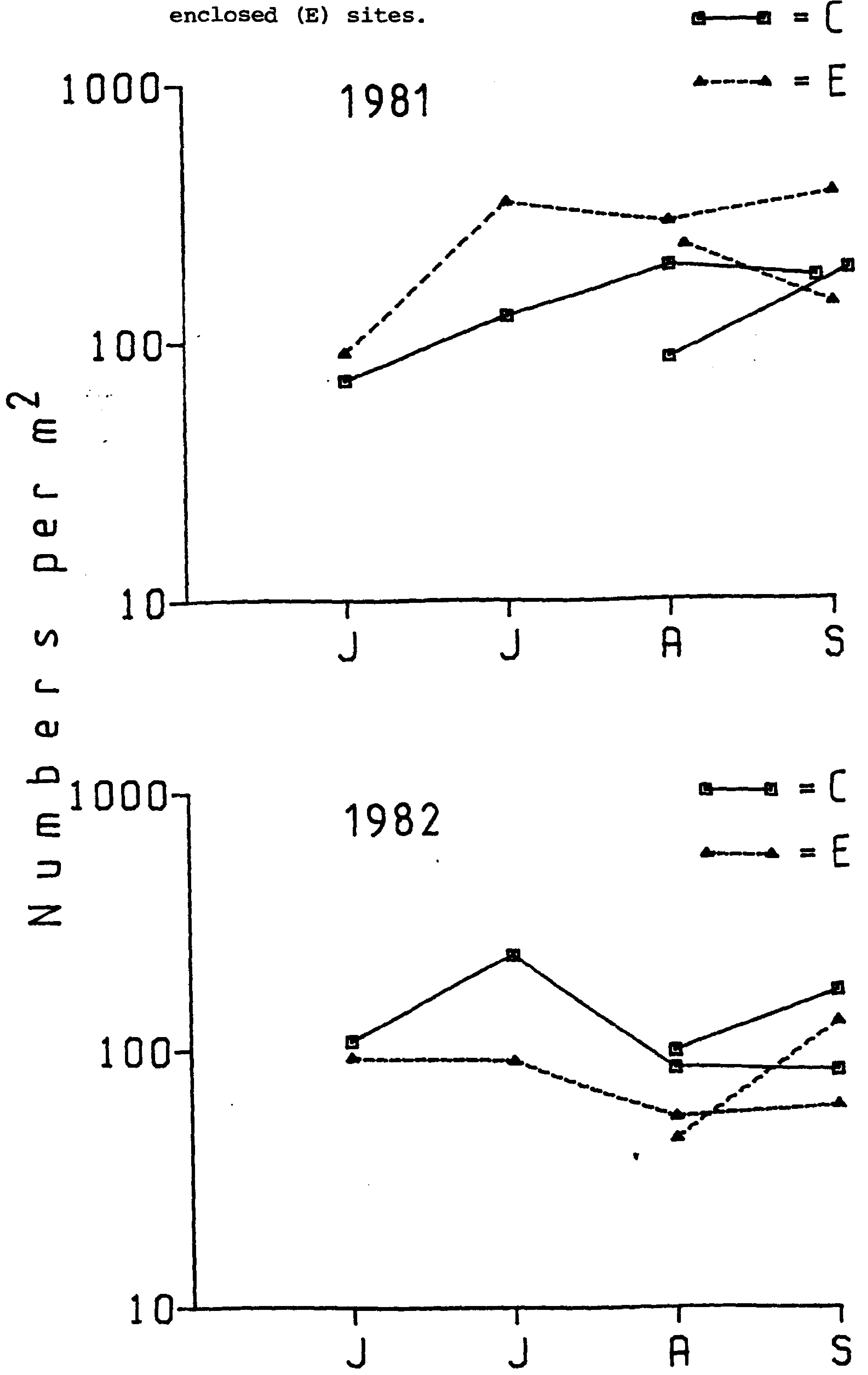


Figure 4.48. *Helobdella stagnalis*. Total geometric mean density for each cohort from combined stone and substratum sample data and the estimated number of young (y) entering the 1981/82 and 1982/83 cohorts in control (C) and enclosed (E) sites (spring and summer broods of young combined.

Figure 4.49. Helobdella stagnalis. Total geometric mean density from combined stone and substratum samples for the spring (June onwards) and summer (August onwards) broods of young in 1981 and 1982 for control (C) and enclosed (E) sites.



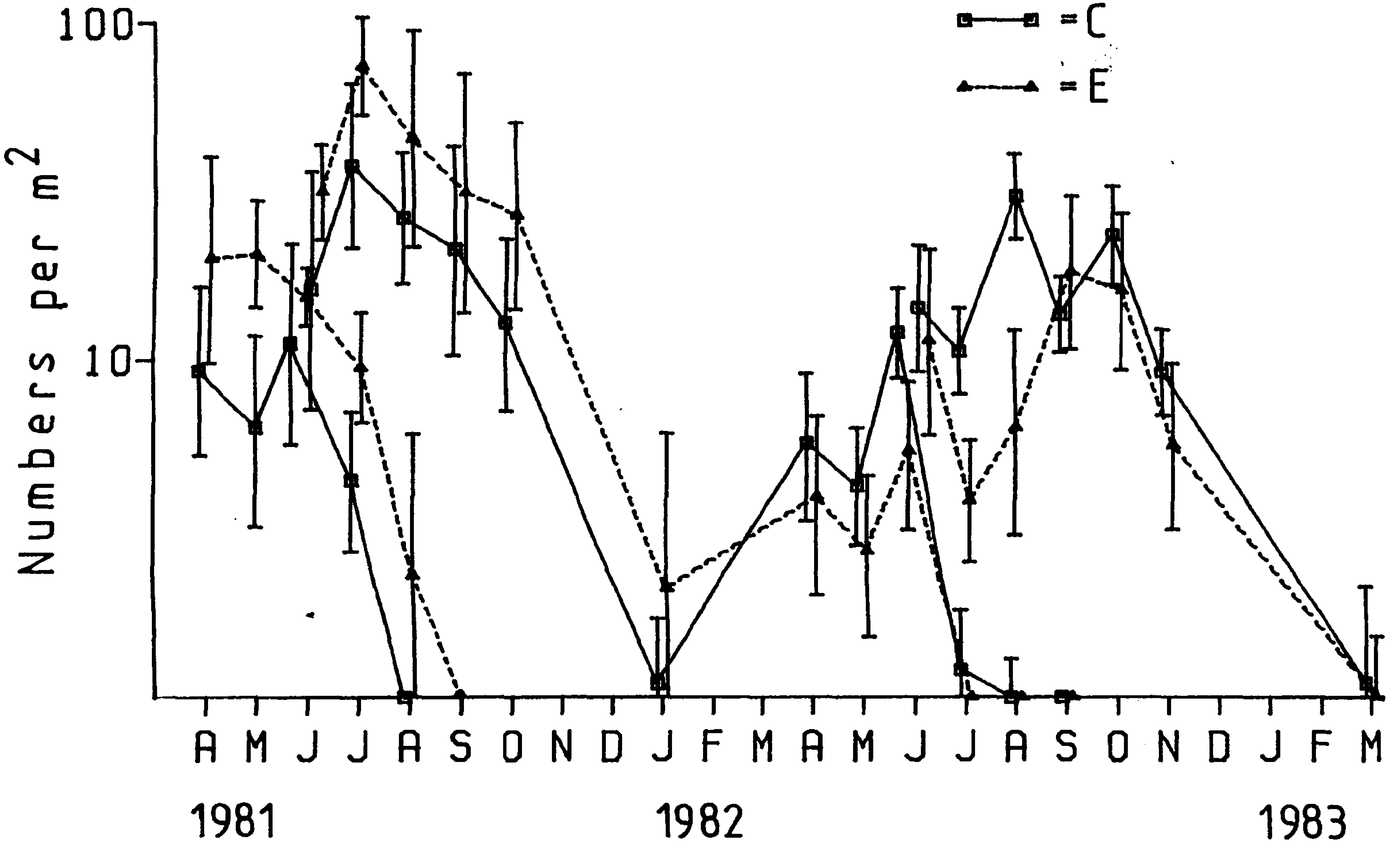


Figure 4.50. Helobdella stagnalis. Geometric mean density ± 95% confidence limits for each cohort in stone samples from control (C) and enclosed (E) sites (spring and summer broods of young young combined).

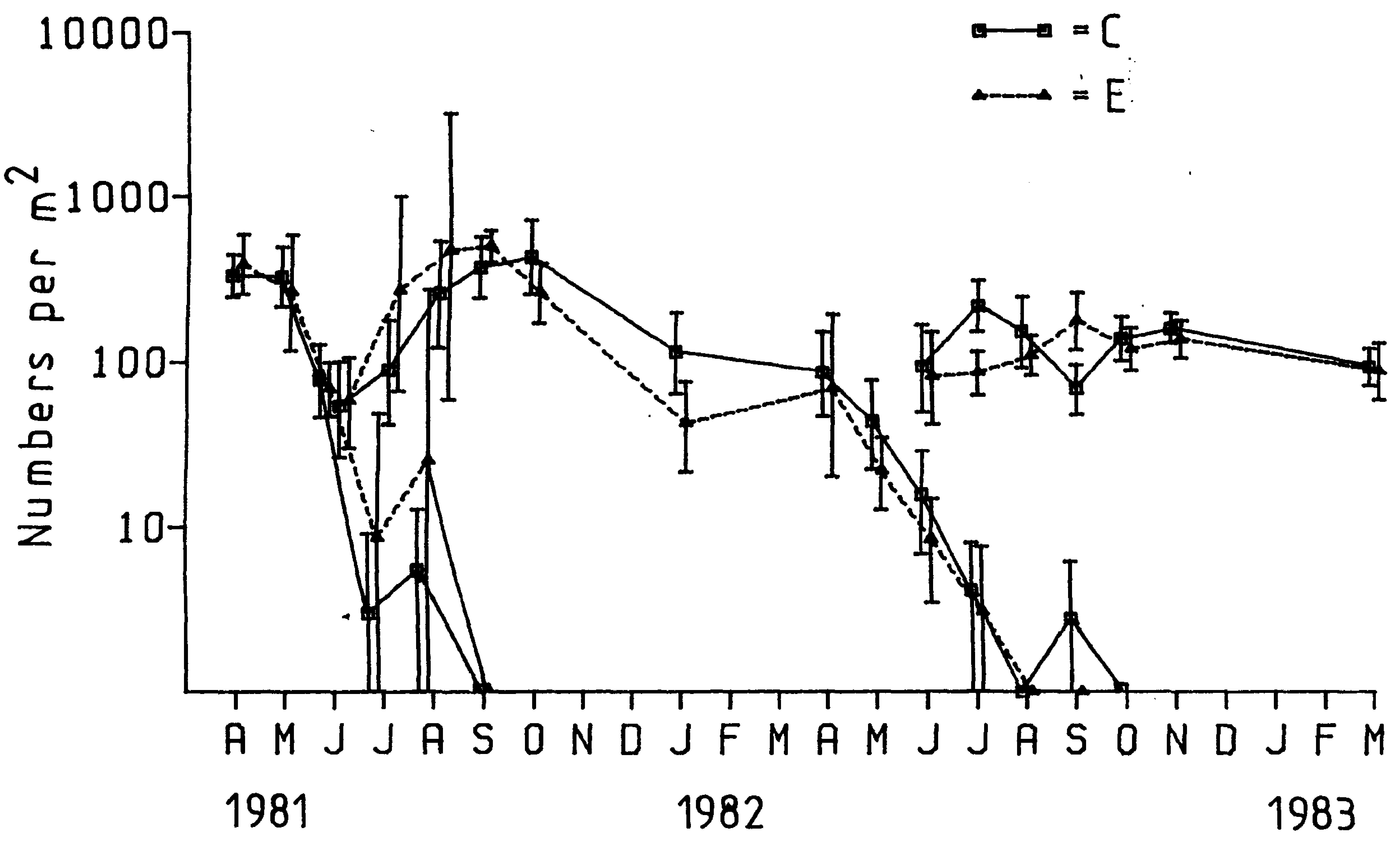


Figure 4.51. Helobdella stagnalis. Geometric mean density $\pm$ 95% confidence limits for each cohort in substratum samples from control (C) and enclosed sites (E) (spring and summer broods of young combined).

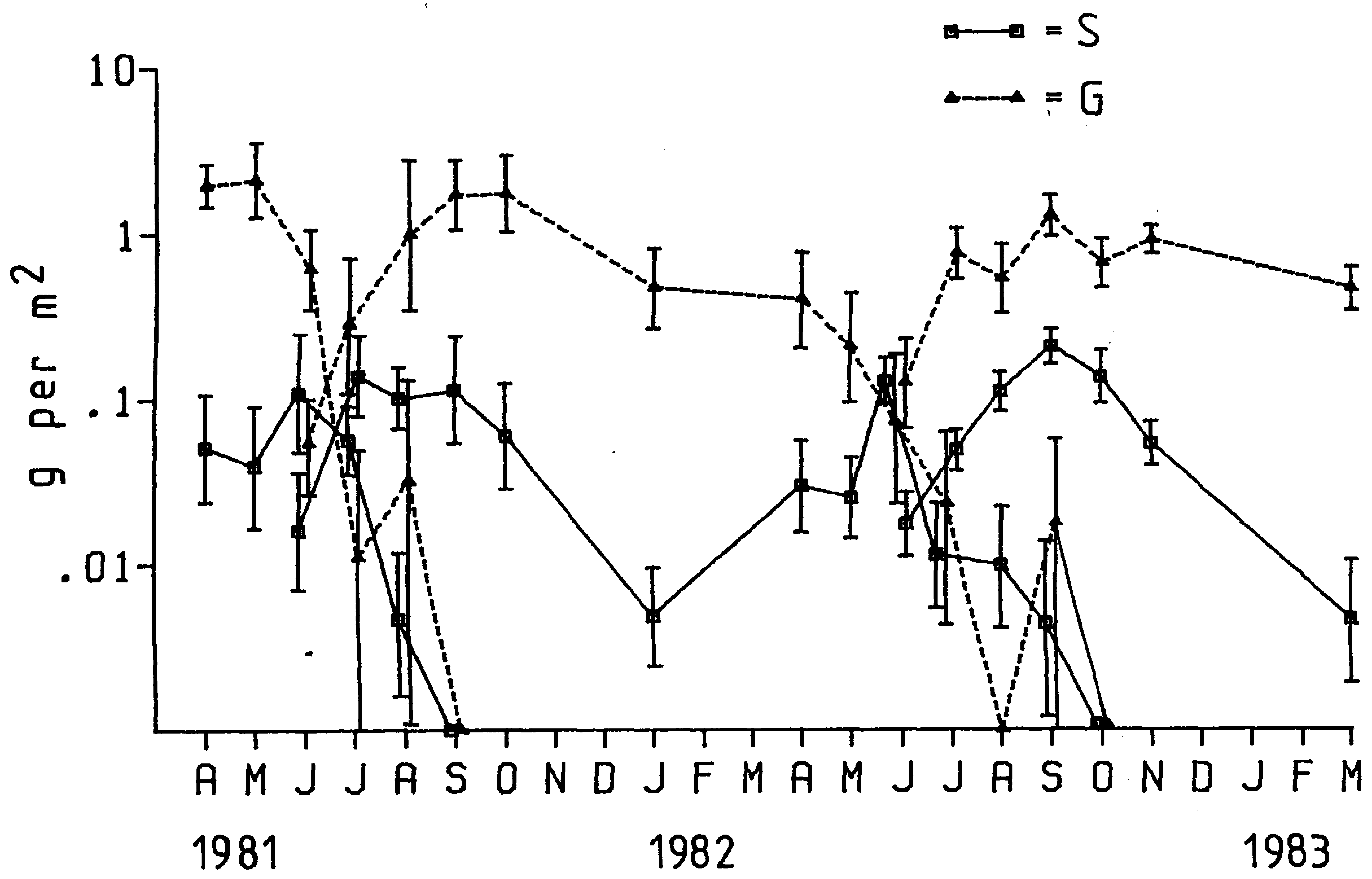


Figure 4.52. <u>Helobdella stagnalis</u>. Geometric mean biomass ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from control sites (spring and summer broods of young combined).

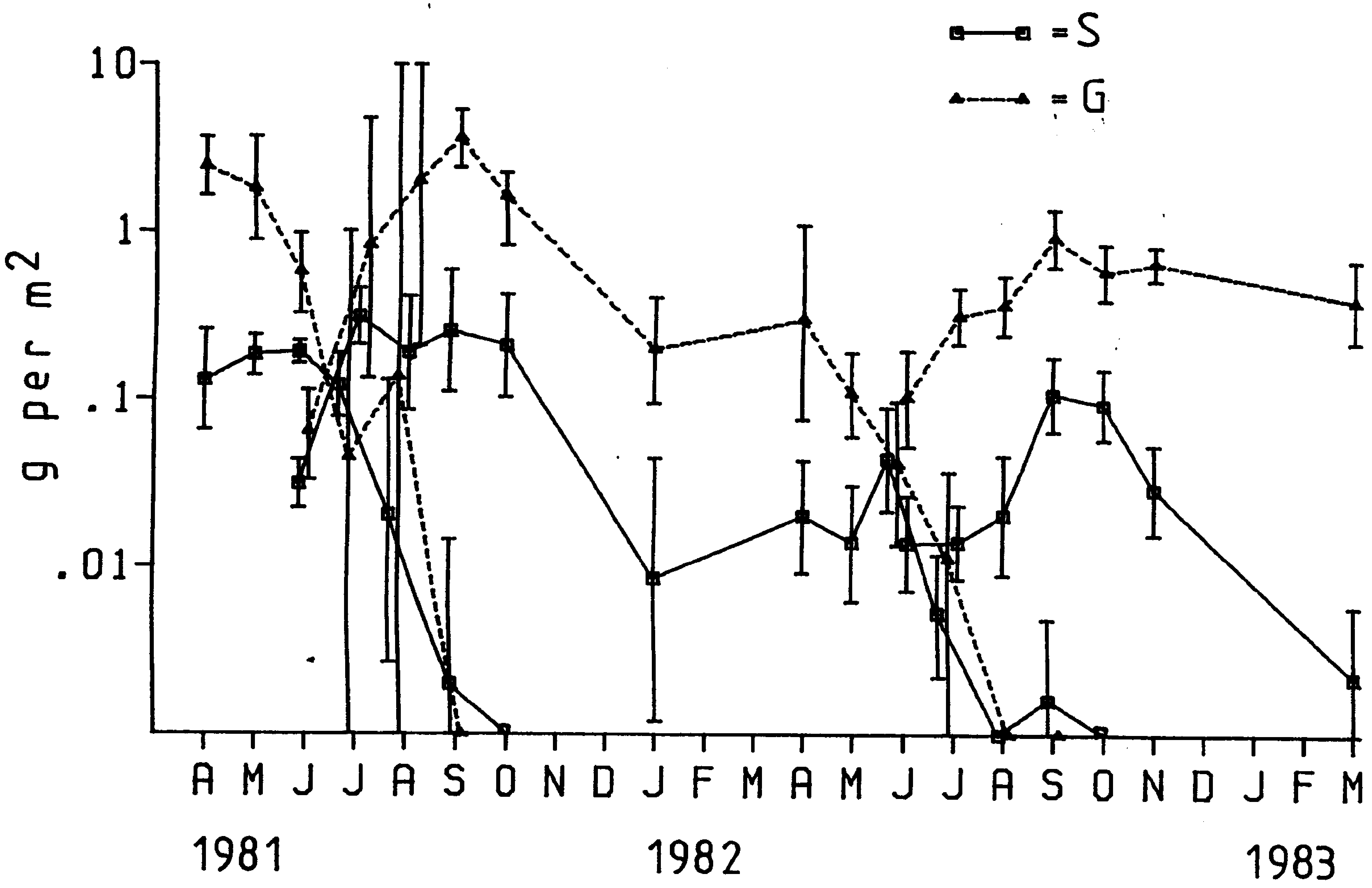


Figure 4.53. Helobdella stagnalis. Geometric mean biomass ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from enclosed sites (spring and summer broods of young combined).

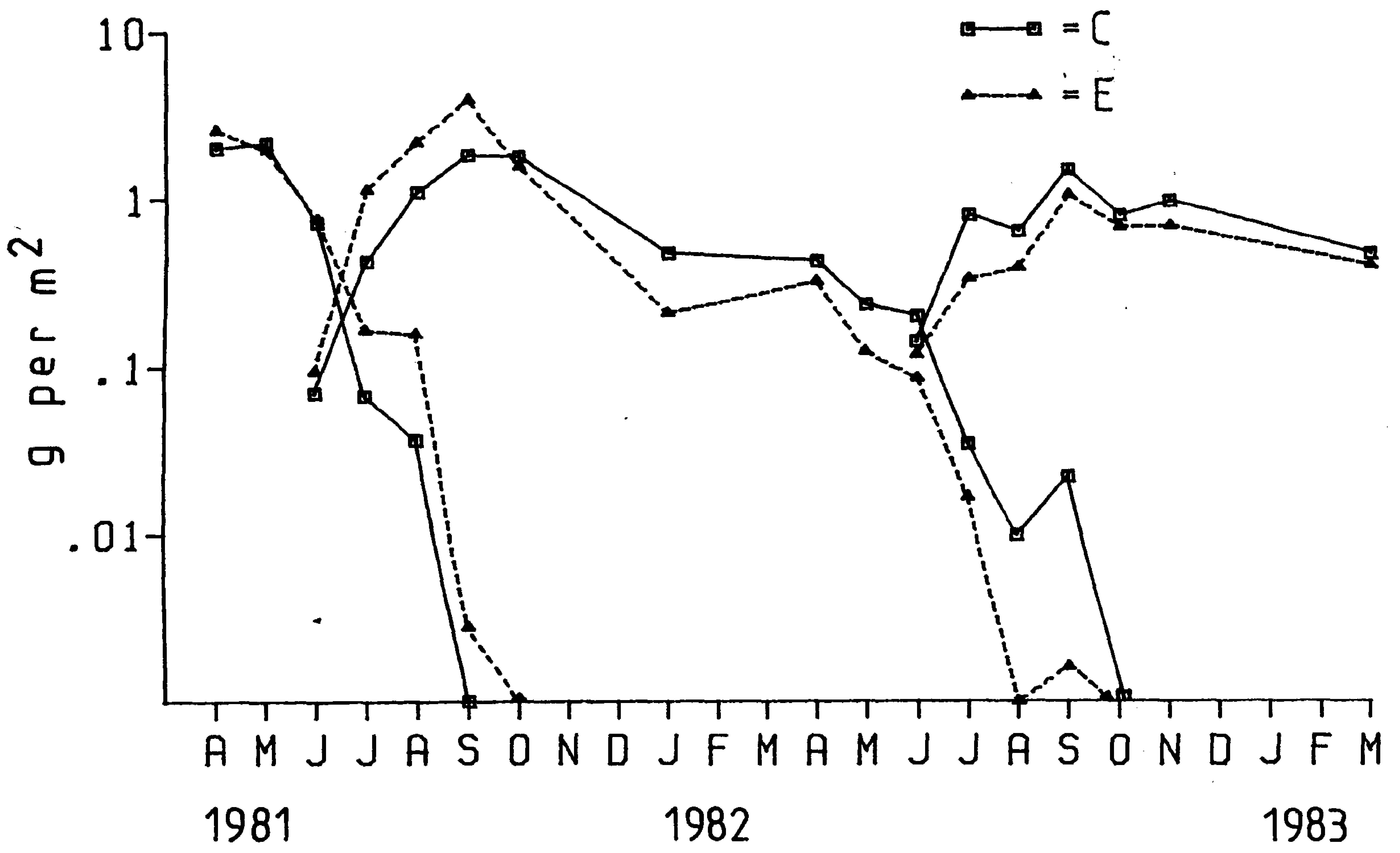
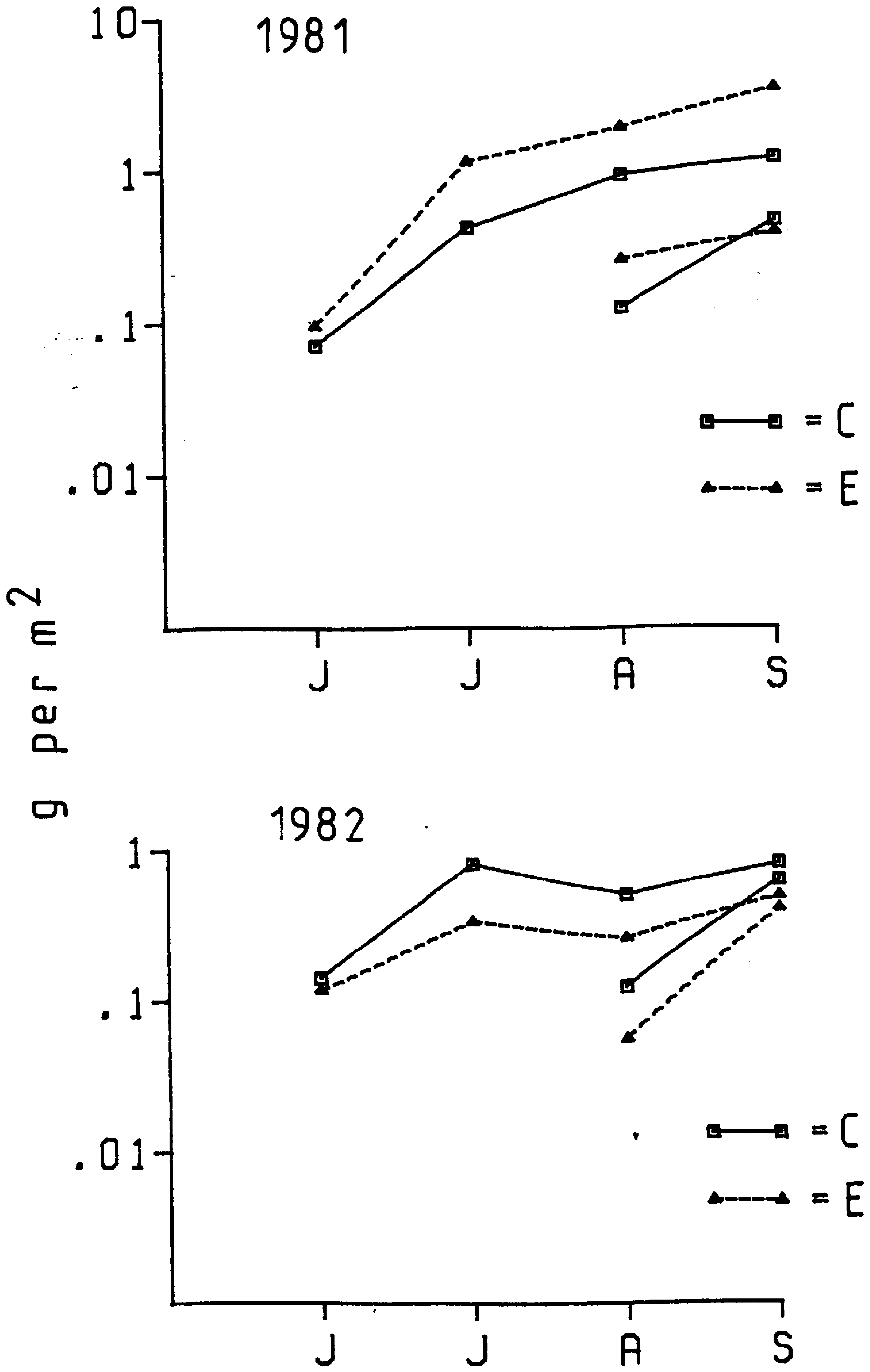


Figure 4.54. Helobdella stagnalis. Total geometric mean biomass for each cohort from combined stone and substratum sample data in control (C) and enclosed (E) sites (spring and summer broods of young combined).

Figure 4.55. Helobdella stagnalis. Total geometric mean biomass from combined stone and substratum sample data for the spring (June onwards and summer (August onwards) broods of young in 1981 and 1982 for control (C) and enclosed (E) sites.



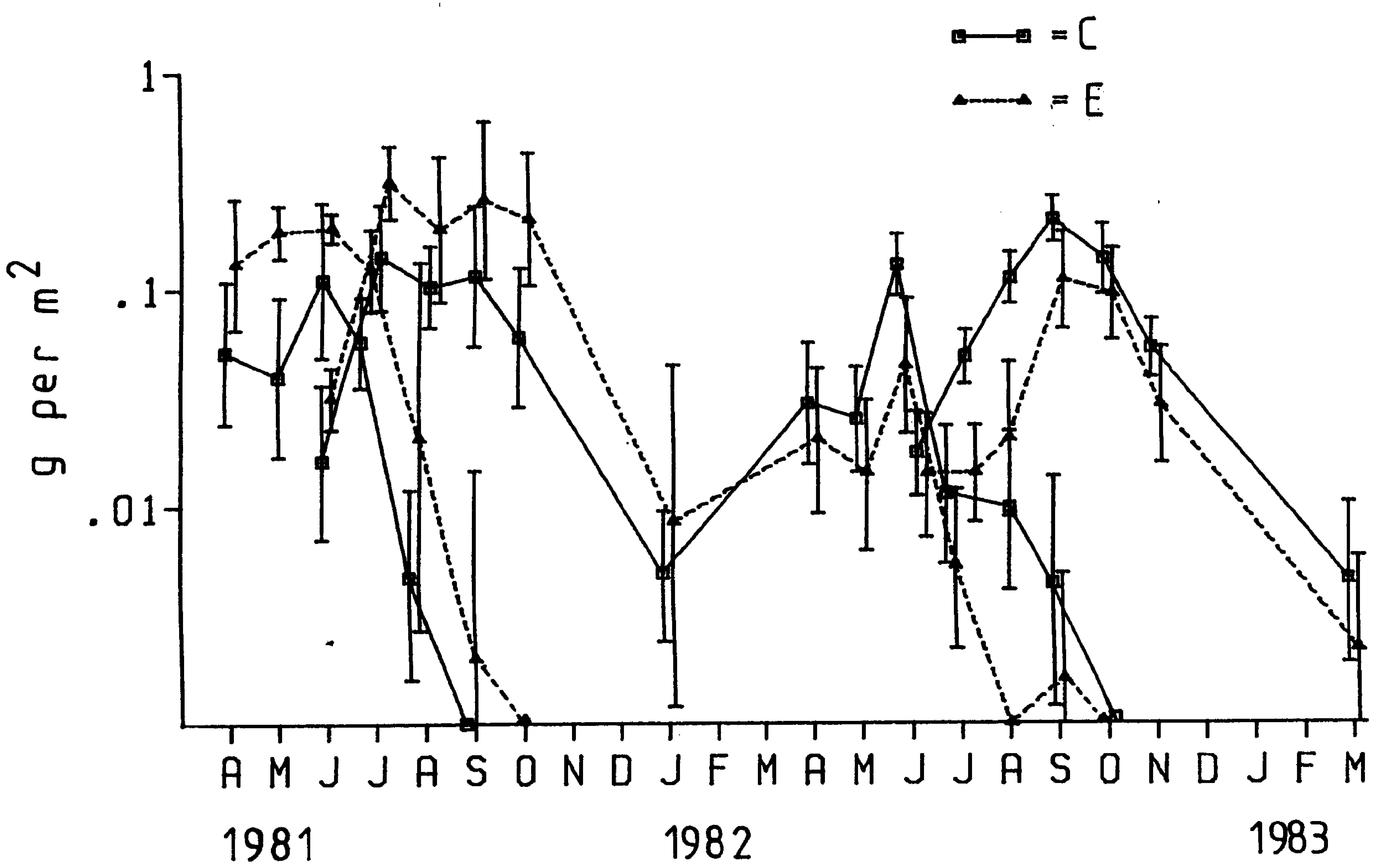


Figure 4.56. Helobdella stagnalis. Geometric mean biomass ± 95% confidence limits for each cohort in stone samples from control (C) and enclosed (E) sites (spring and summer broods of young combined).

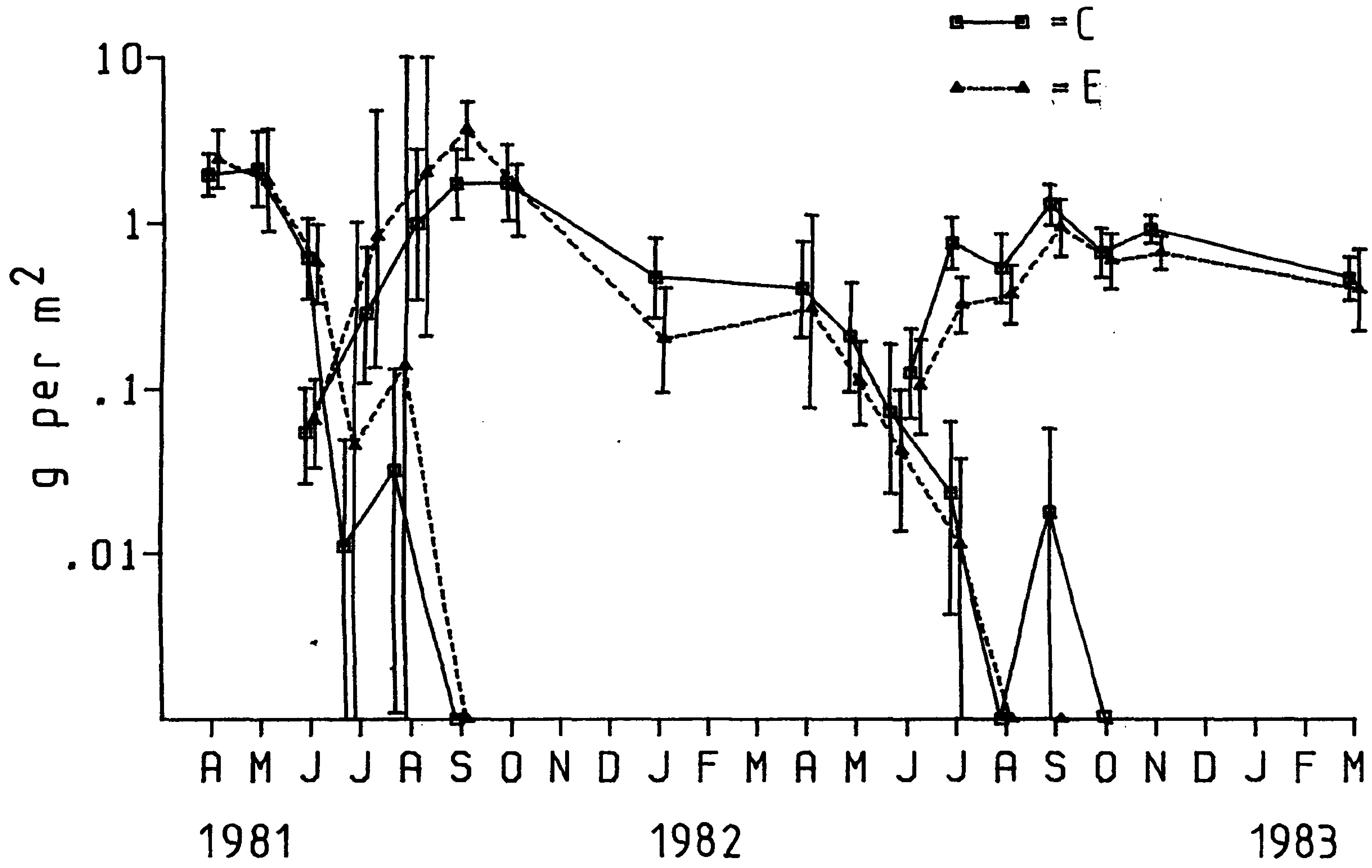
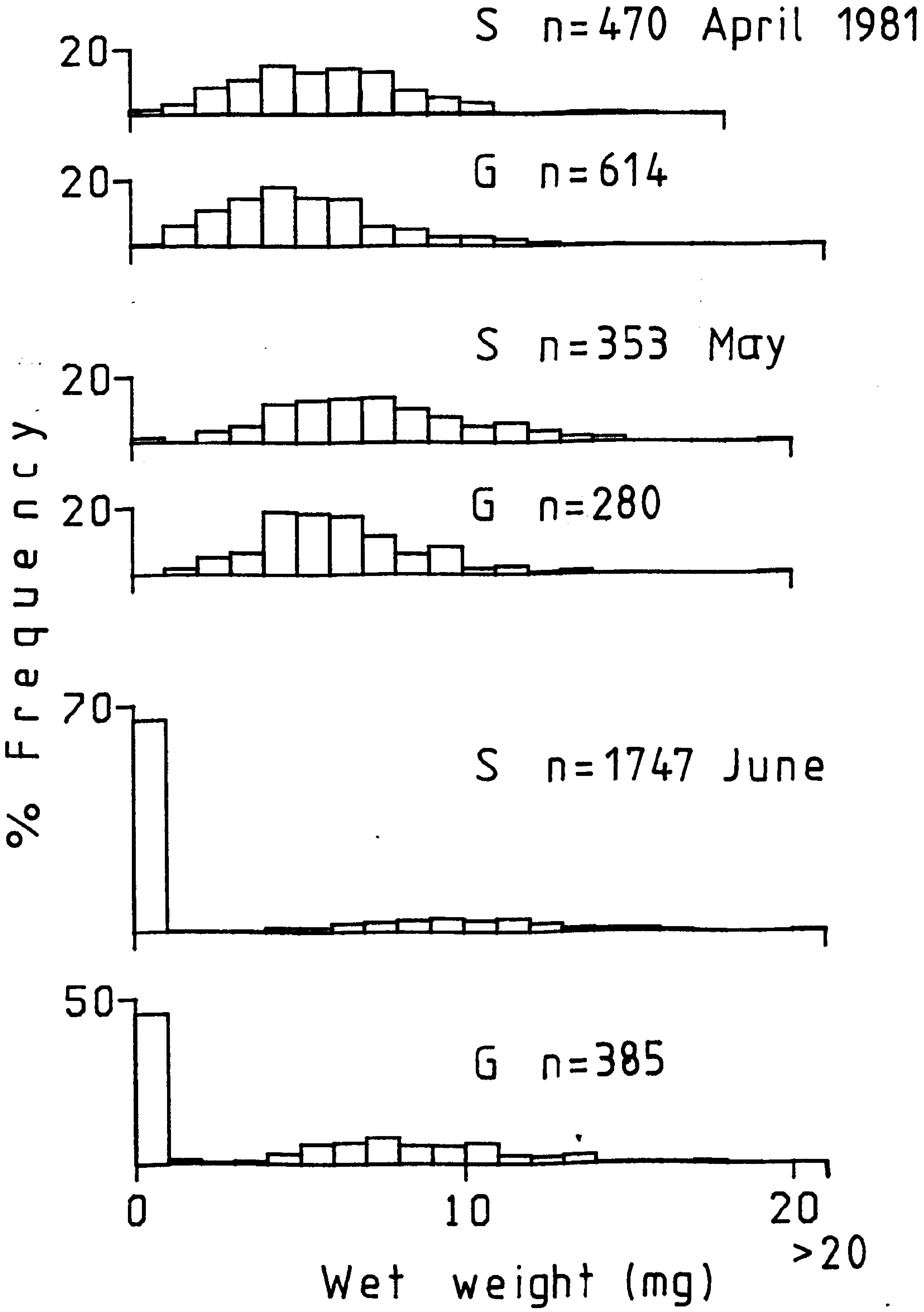


Figure 4.57. Helobdella stagnalis. Geometric mean biomass $\pm$ 95% confidence limits for each cohort in substratum samples from control (C) and enclosed (E) sites (spring and summer broods of young combined).

Figure 4.58. Helobdella stagnalis. The size-structure of leech populations from stone (S) and substratum (G) samples in control sites between April 1981 to March 1983.



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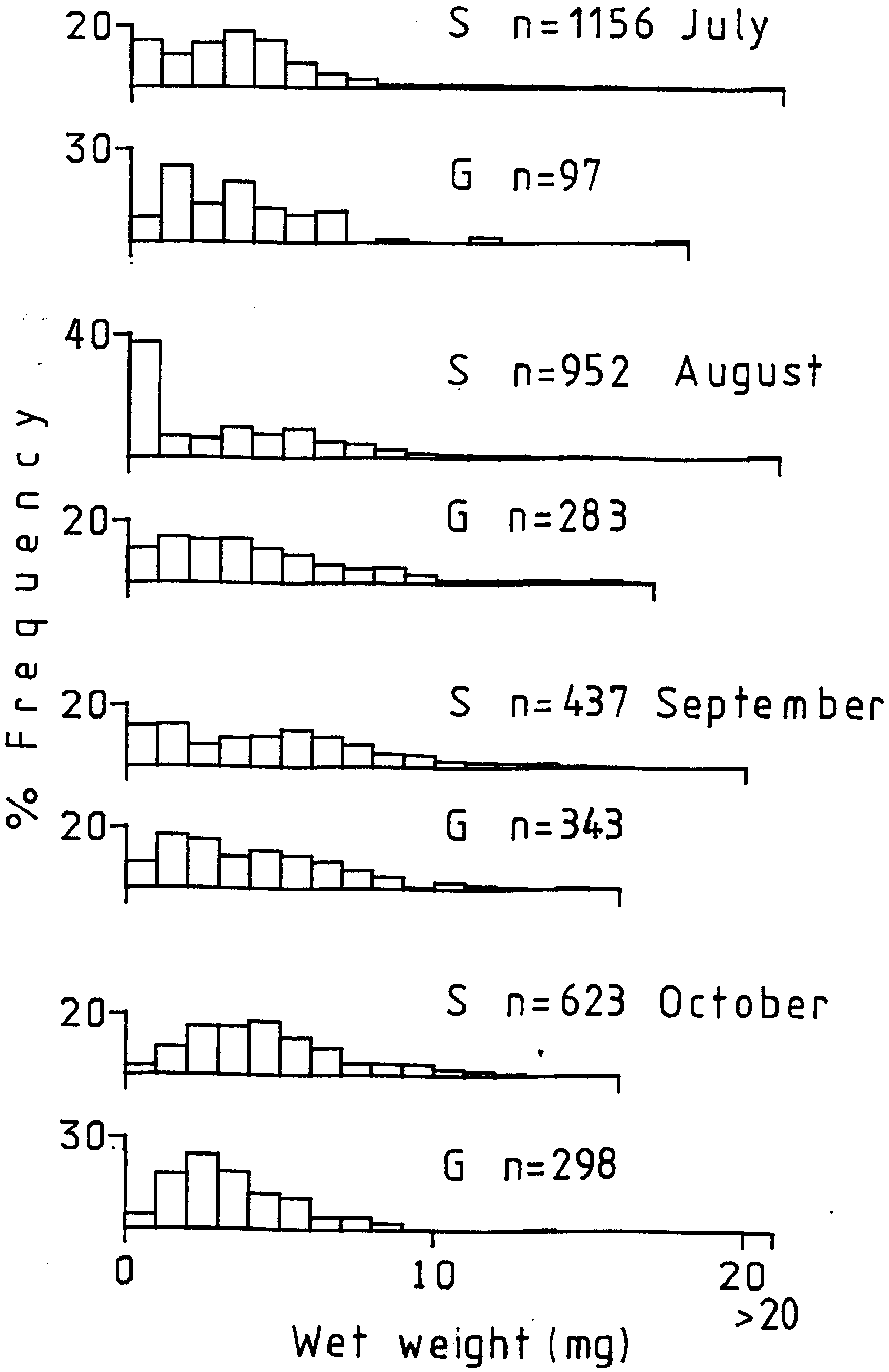
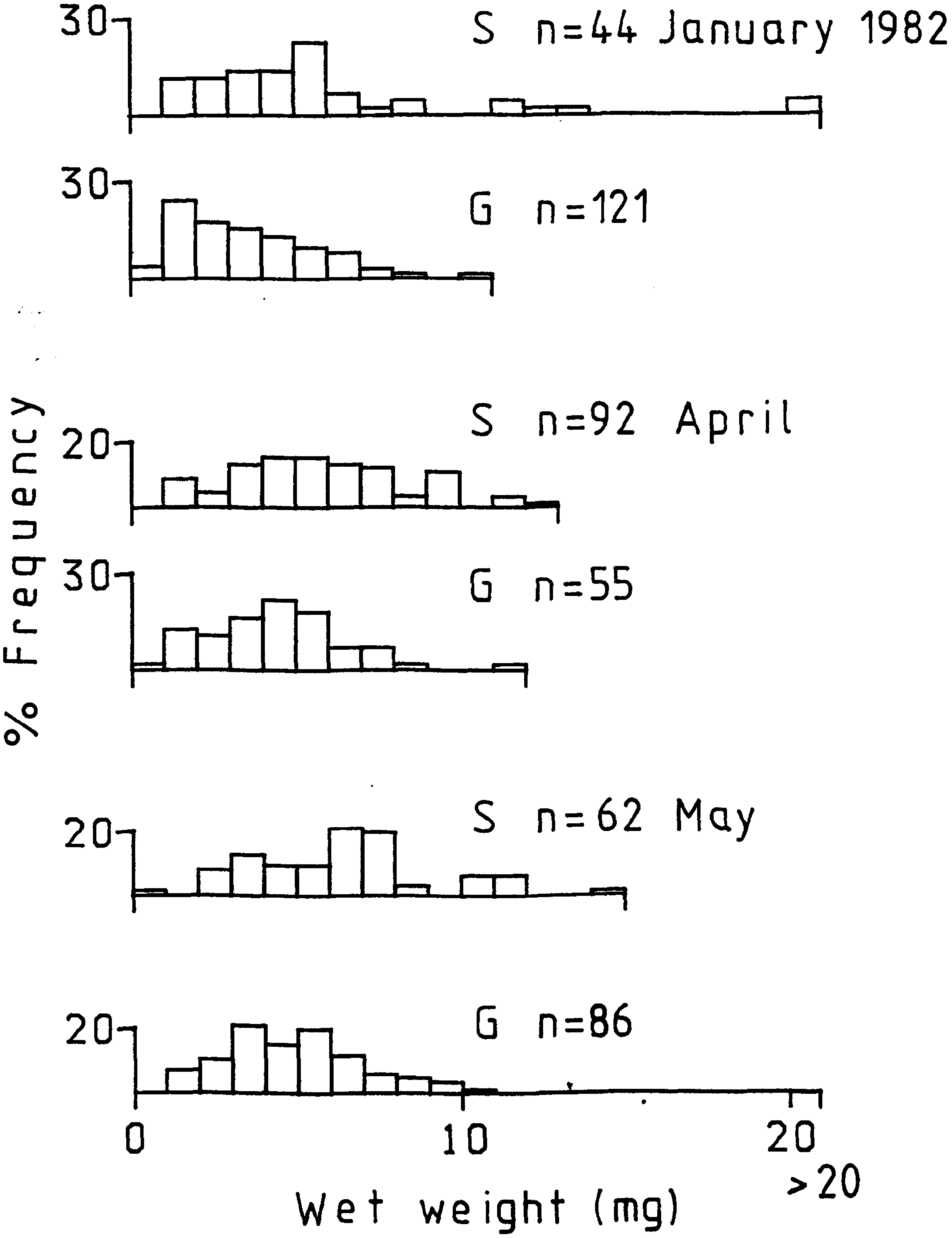
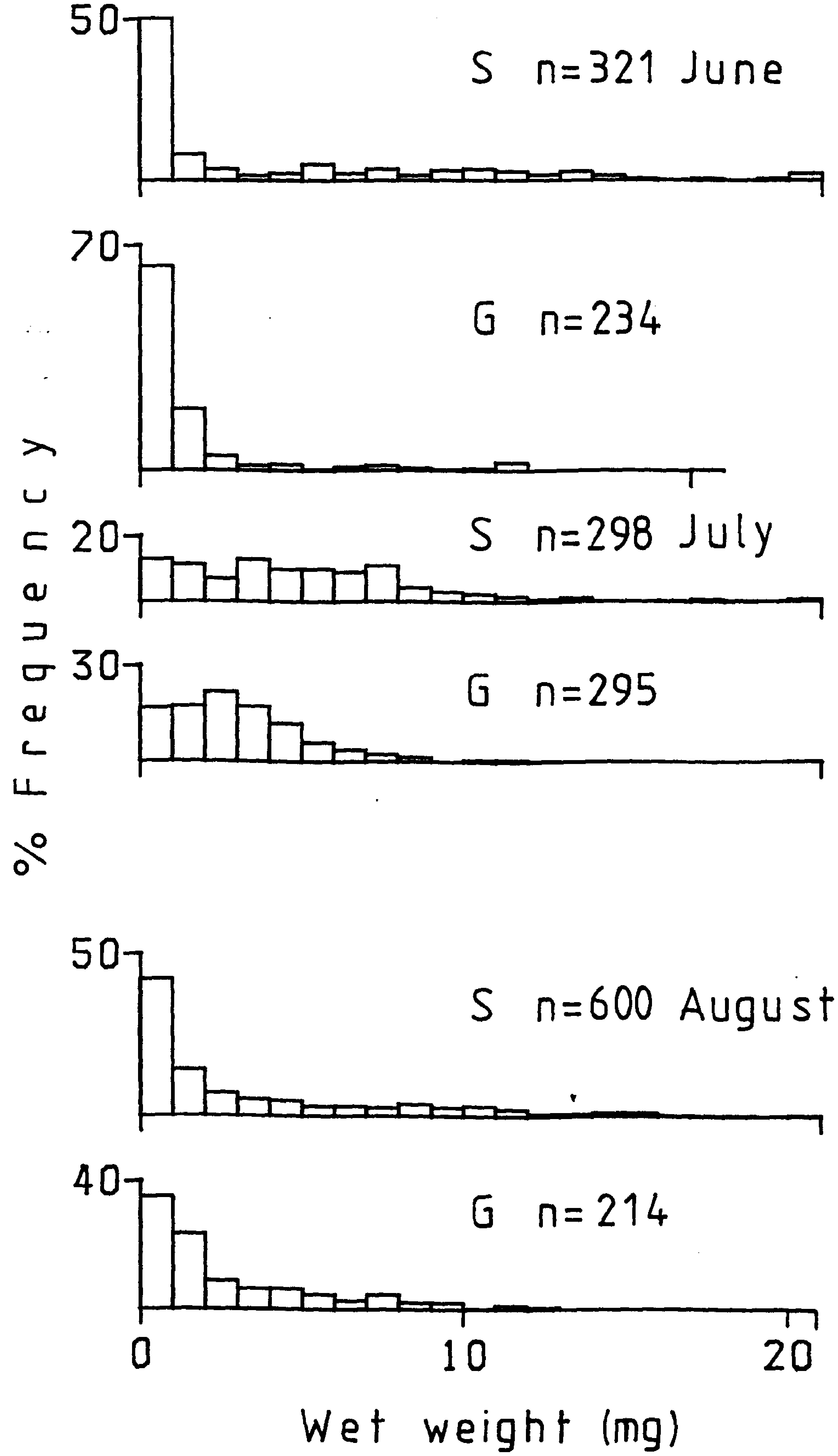

20
S n=1156 July
30
G n=97
40
S n=952 August
20
G n=283
20
S n=437 September
20
G n=343
20
S n=623 October
30
G n=298
% Frequency
0
10
20
>20
Wet weight (mg)

Continued


30
S n=44 January 1982
30
G n=121
% Frequency
20
S n=92 April
30
G n=55
20
S n=62 May
20
G n=86
0
10
20
>20
Wet weight (mg)

Continued


50
S n=321 June
70
G n=234
20
S n=298 July
30
G n=295
% Frequency
50
S n=600 August
40
G n=214
0
10
20
Wet weight (mg)

Continued

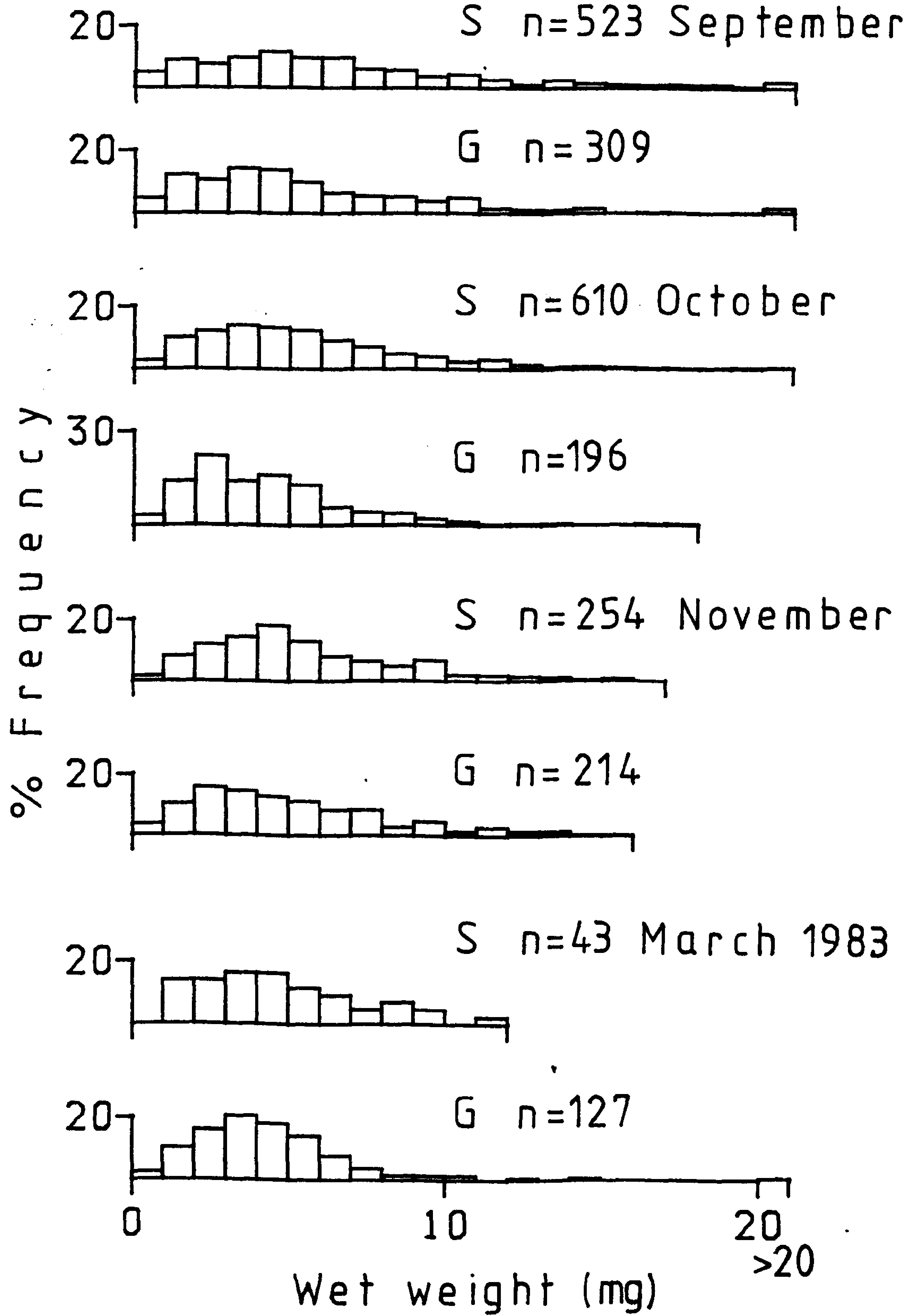
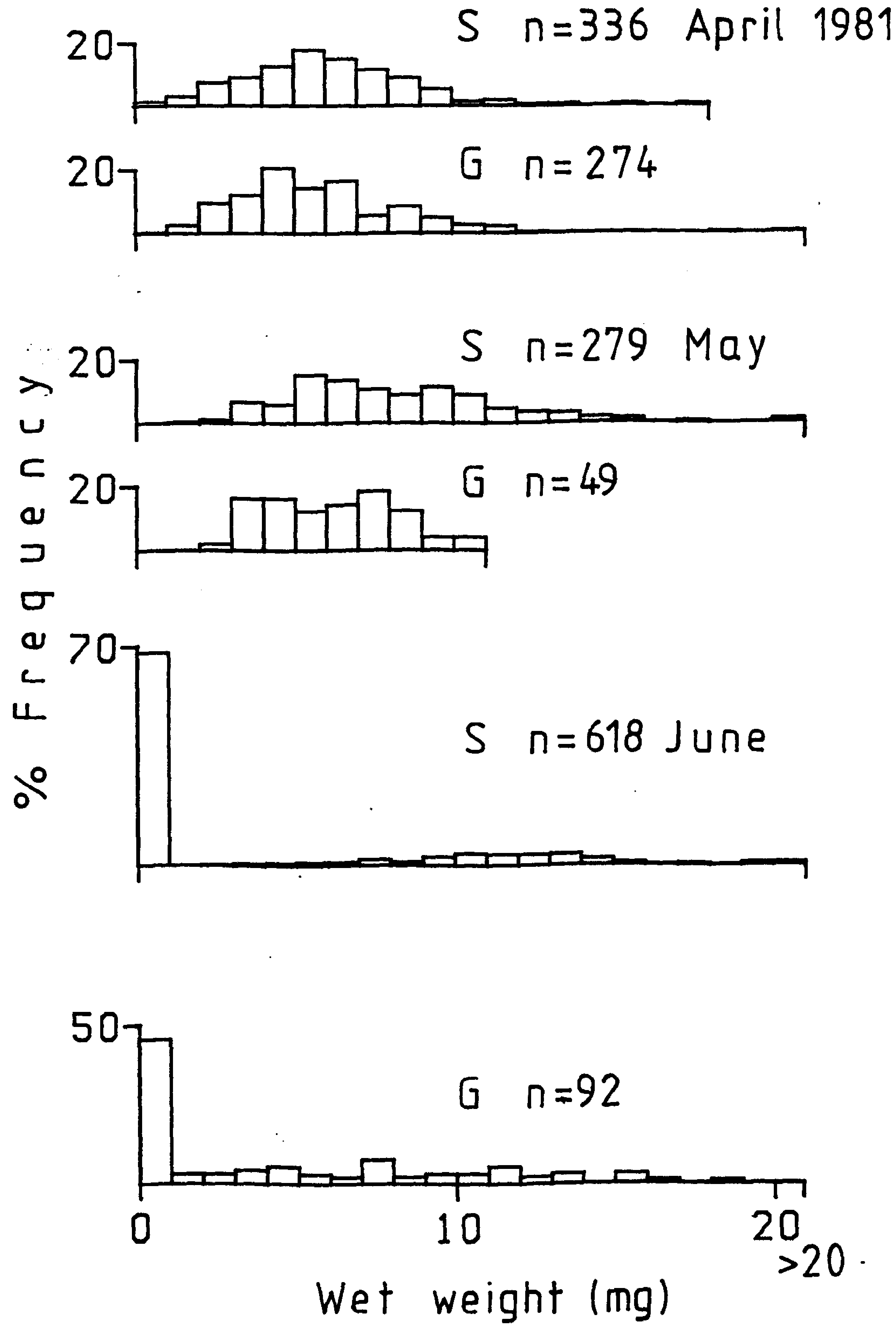

20
S n=523 September
20
G n=309
20
S n=610 October
30
G n=196
20
S n=254 November
20
G n=214
20
S n=43 March 1983
20
G n=127
% Frequency
0
10
20
>20
Wet weight (mg)

Figure 4.59. Helobdella stagnalis. The size-structure of leech populations from stone (S) and substratum (G) samples in enclosed sites between April 1981 to March 1983.



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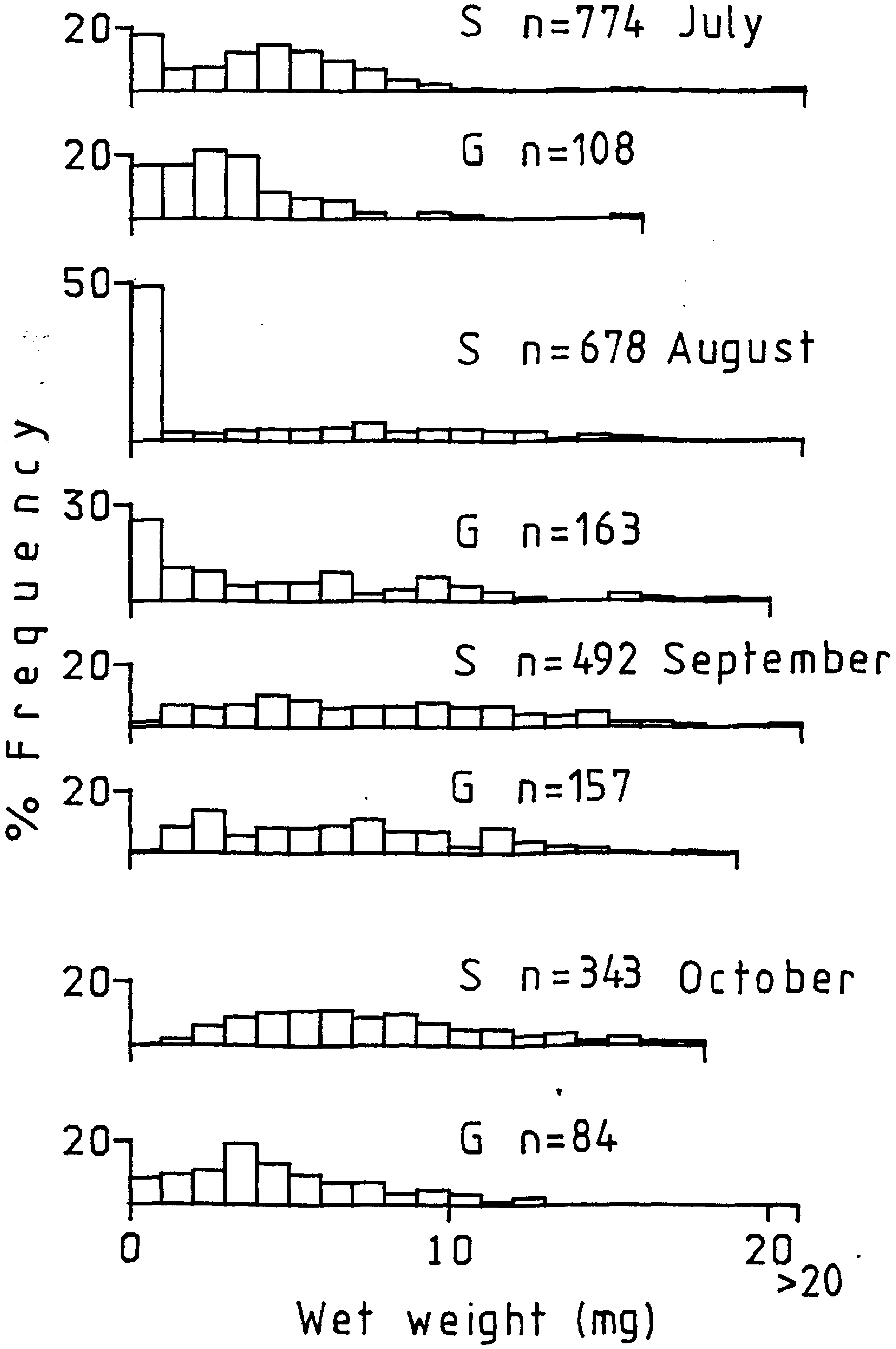
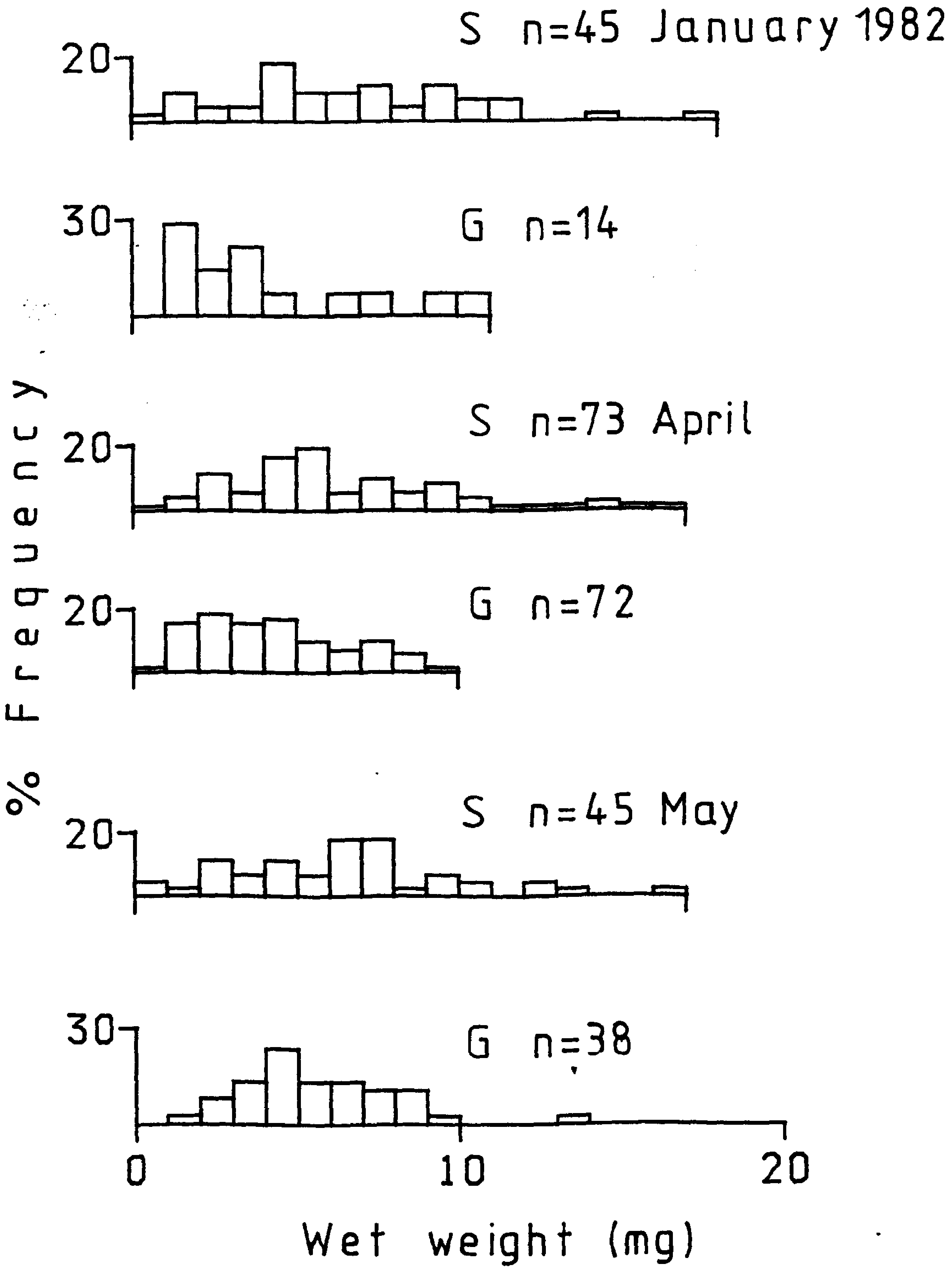
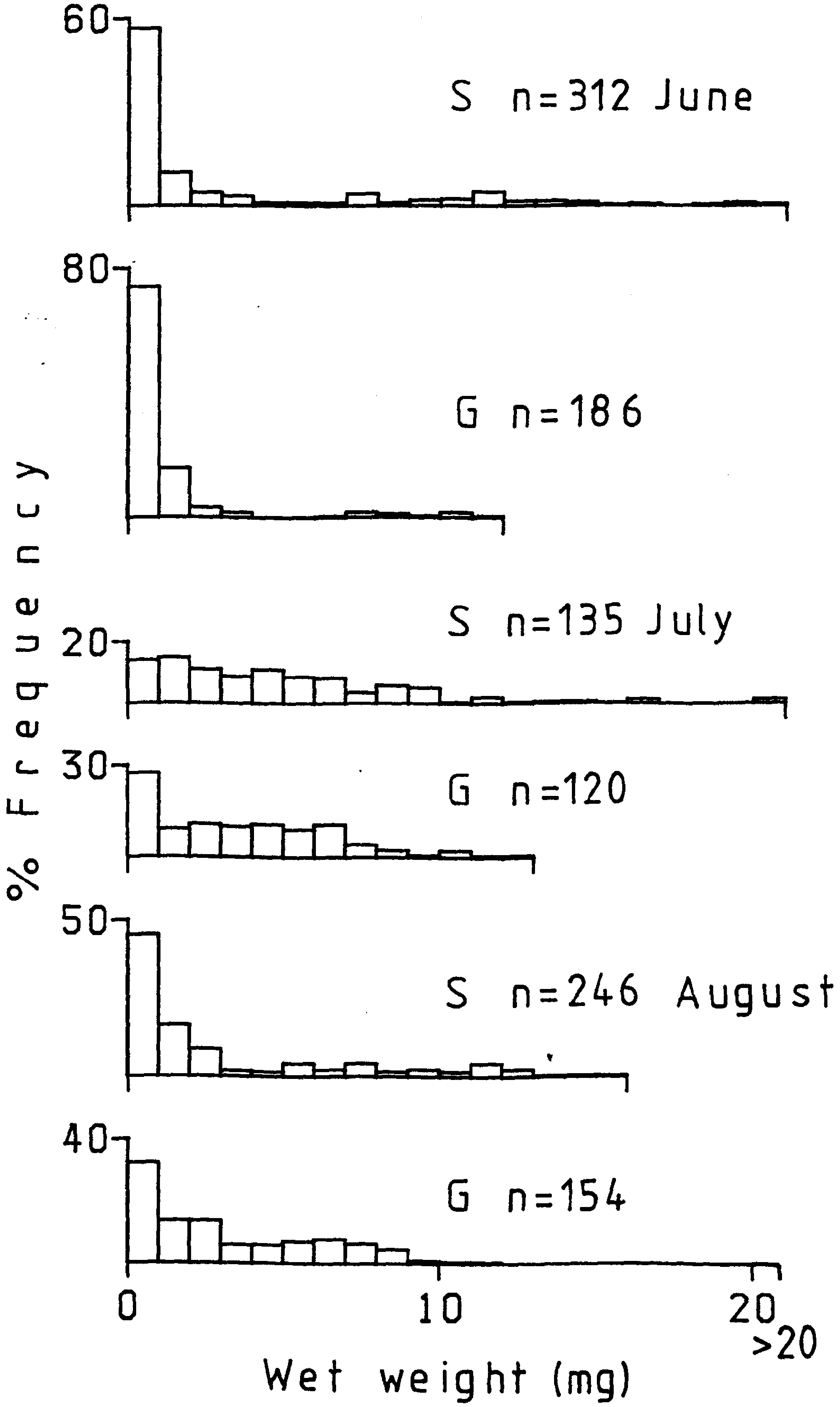

S n=774 July
G n=108
S n=678 August
G n=163
S n=492 September
G n=157
S n=343 October
G n=84
20
20
50
30
20
20
20
20
% Frequency
0
10
20
>20
Wet weight (mg)

Continued


S n=45 January 1982
20
G n=14
30
S n=73 April
20
G n=72
20
S n=45 May
20
G n=38
30
% Frequency
0
10
20
Wet weight (mg)

Continued


60
S n=312 June
80
G n=186
S n=135 July
20
30
G n=120
50
S n=246 August
40
G n=154
% Frequency
0
10
20
>20
Wet weight (mg)

Continued

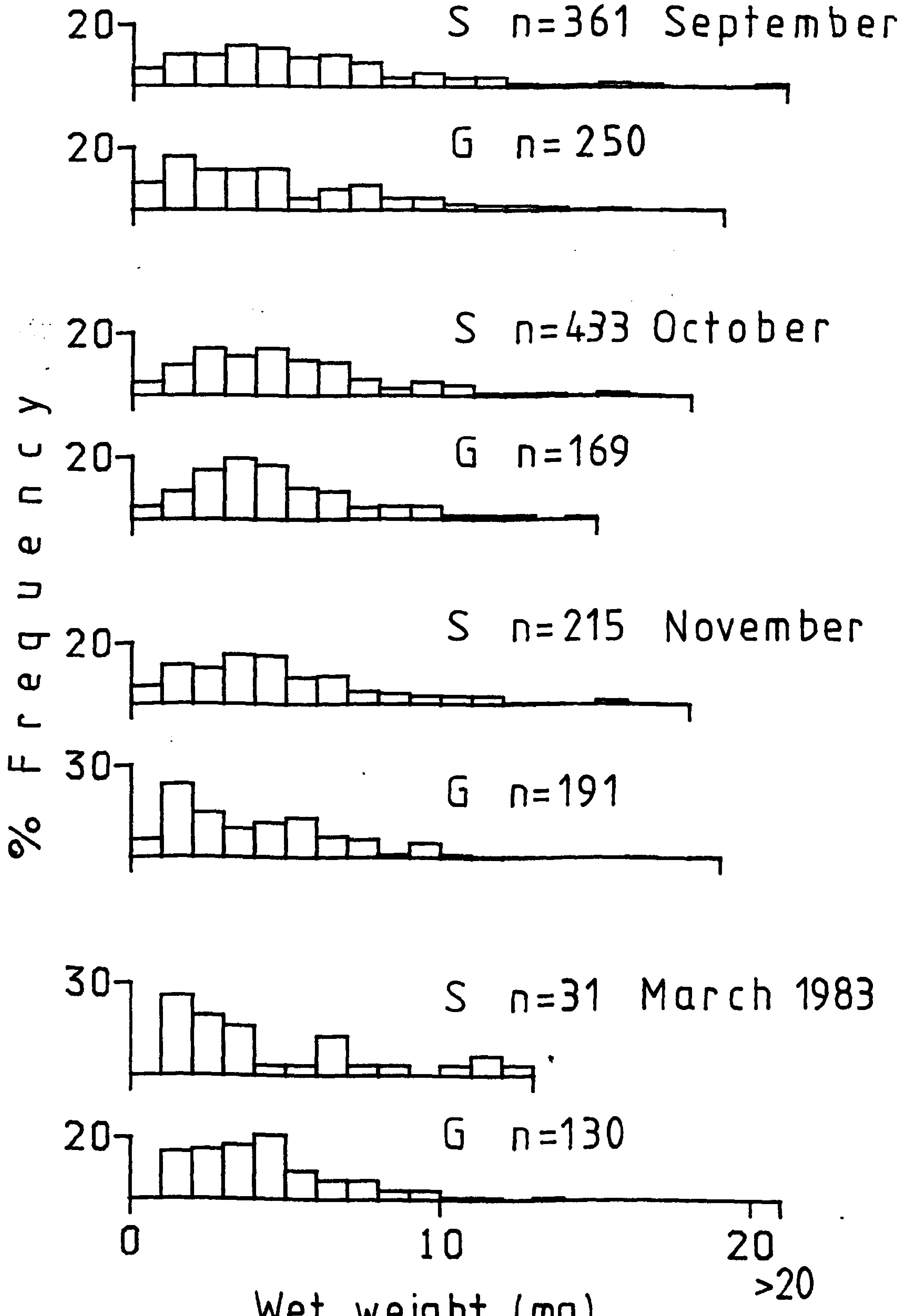
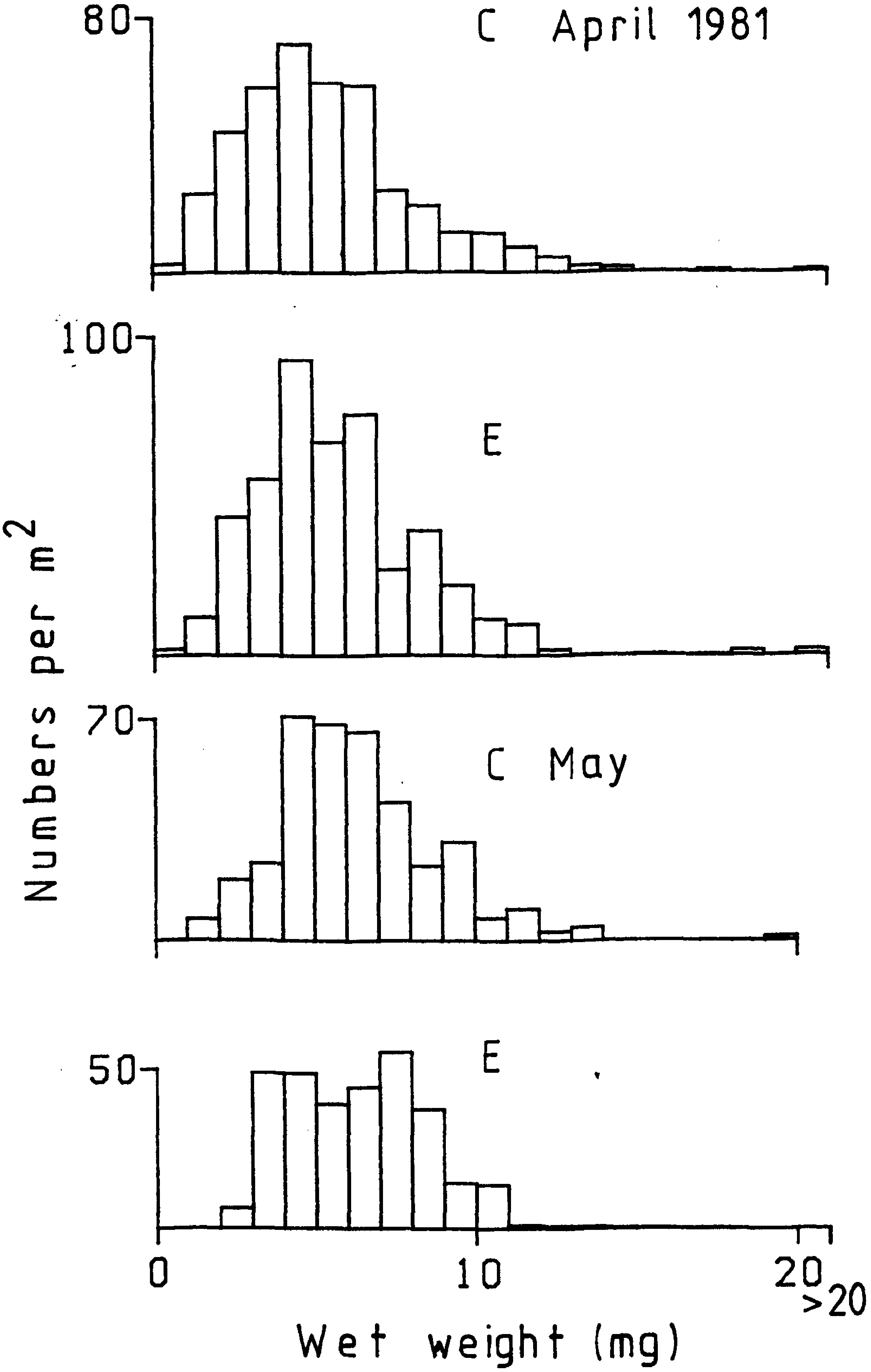

20
S n=361 September
20
G n= 250
20
S n=433 October
20
G n=169
20
S n= 215 November
30
G n=191
30
S n=31 March 1983
20
G n=130
% Frequency
0
10
20
>20
Wet weight (mg)

Figure 4.60. Helobdella stagnalis. The size-structure of leech populations from combined stone and substratum sample data in control (C) and enclosed (E) sites between April 1981 to March 1983.



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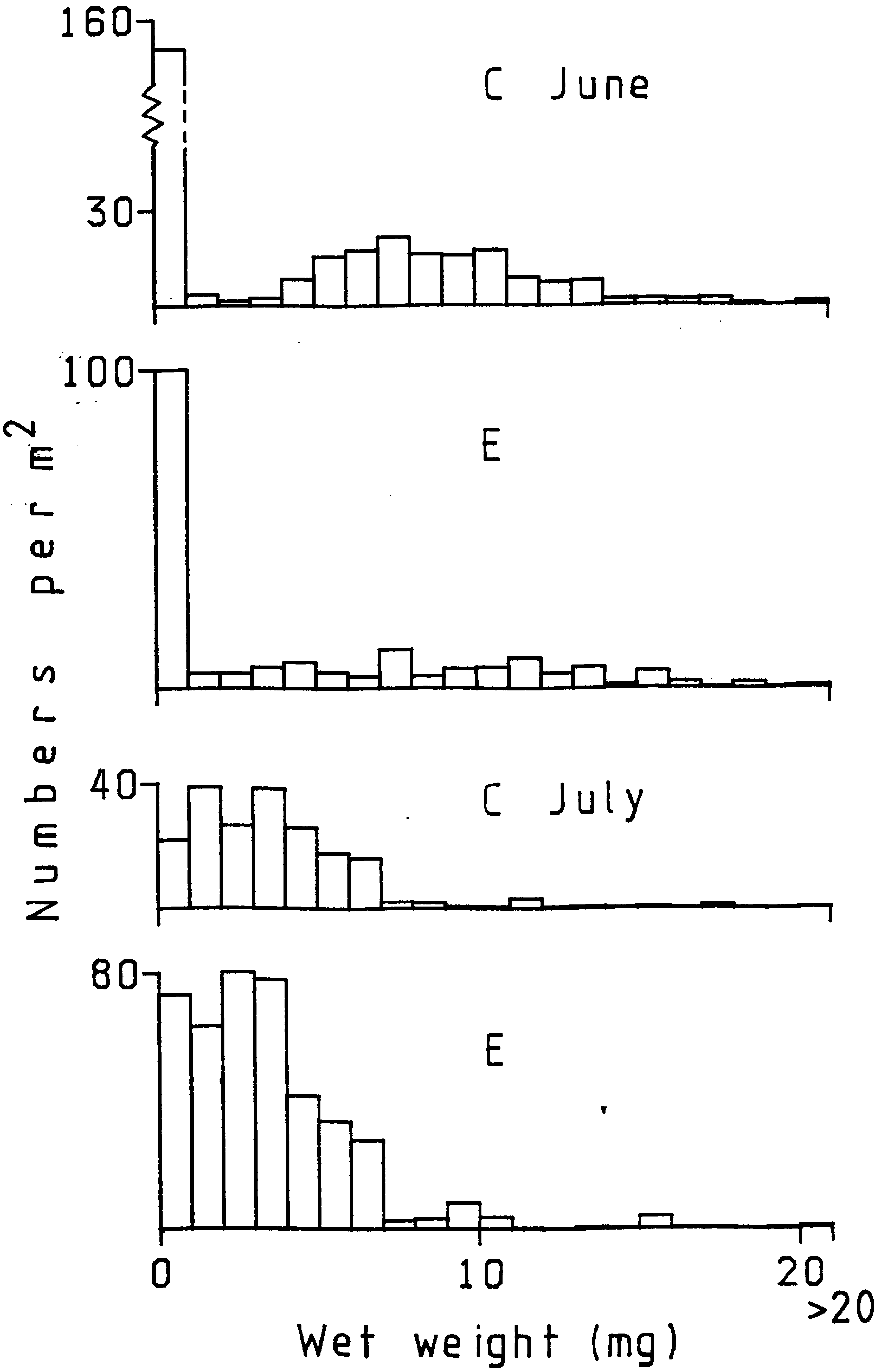
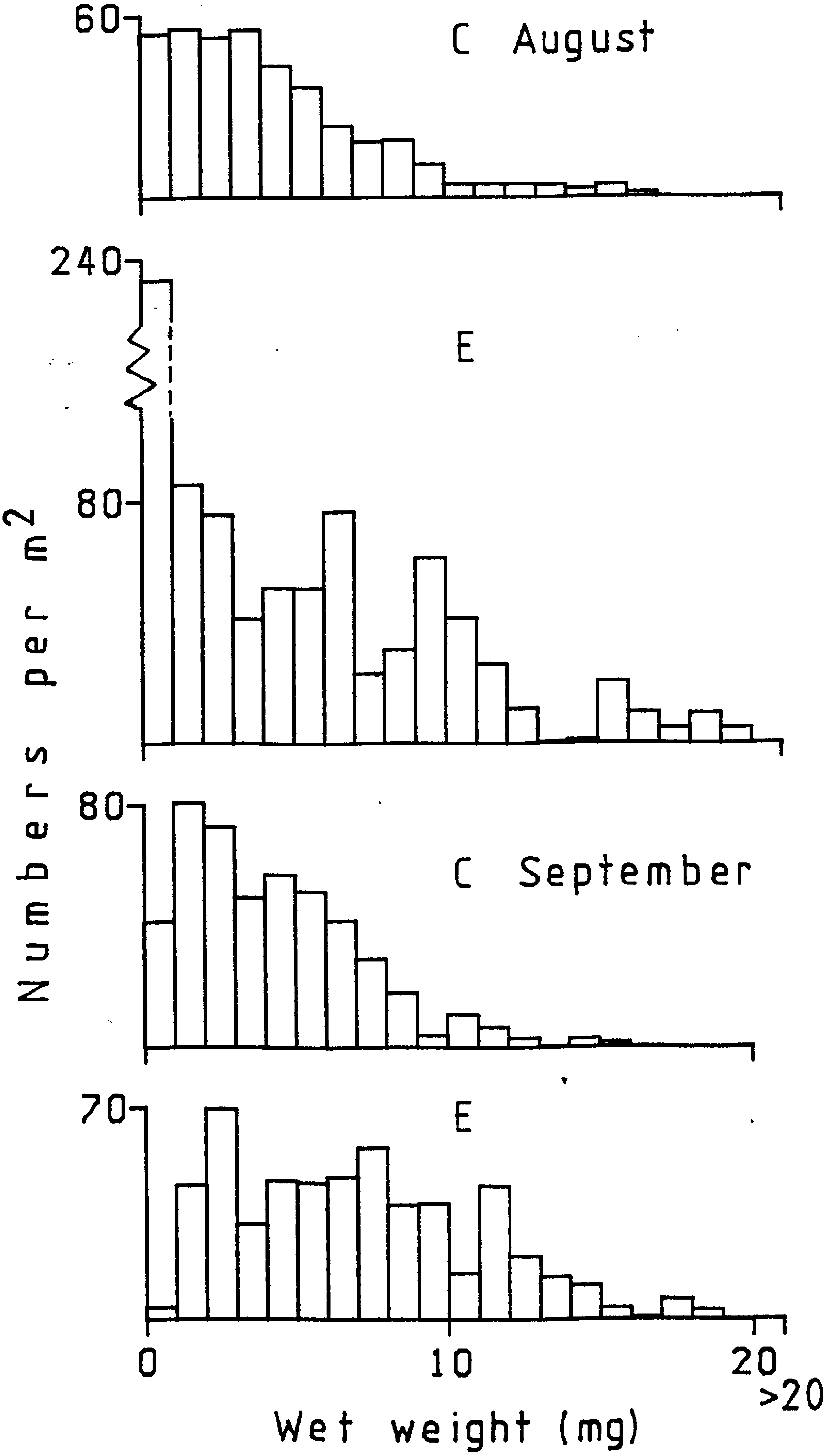
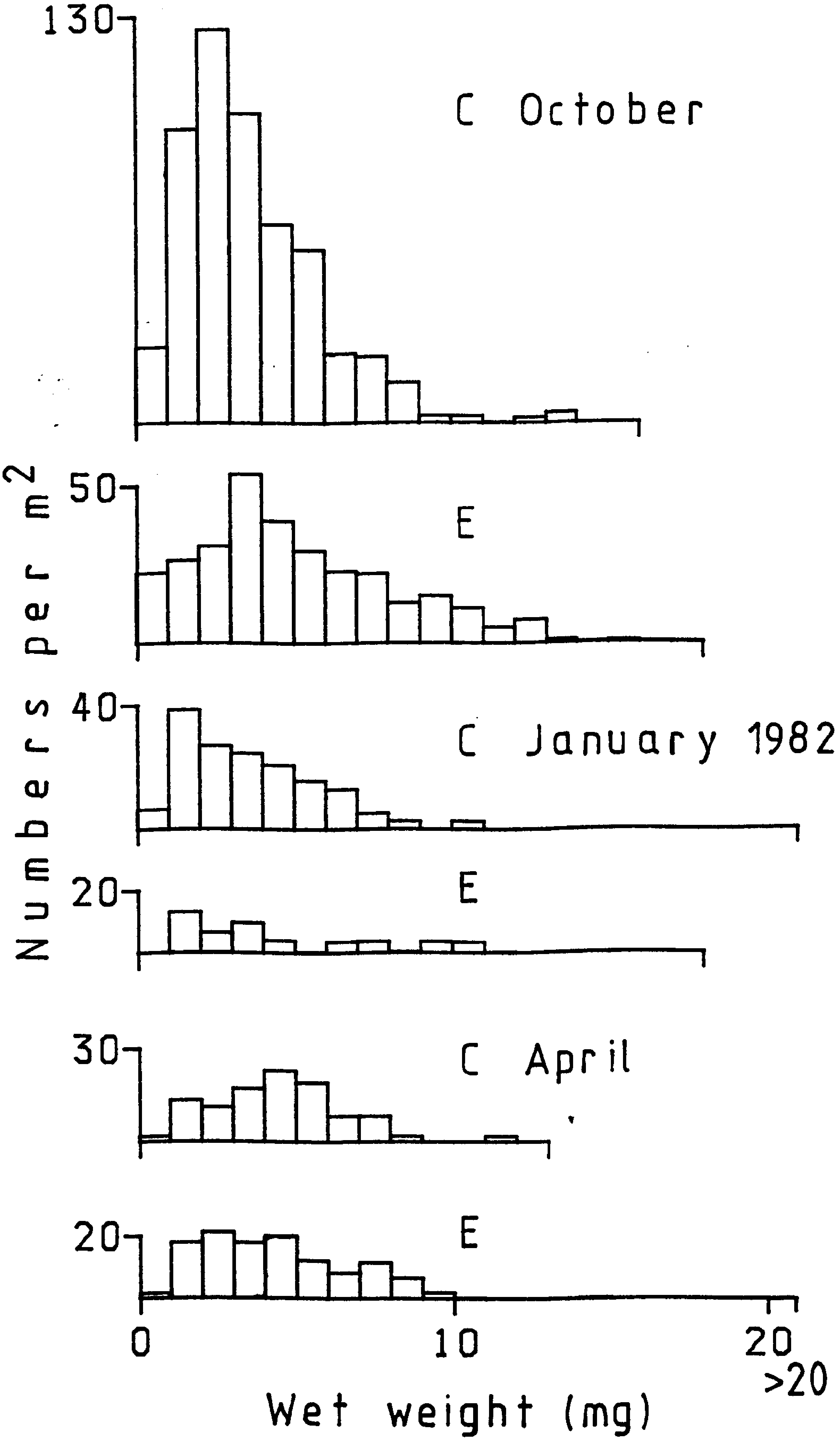

160
30
C June
100
E
40
C July
80
E
Numbers per m^2
0
10
20
>20
Wet weight (mg)

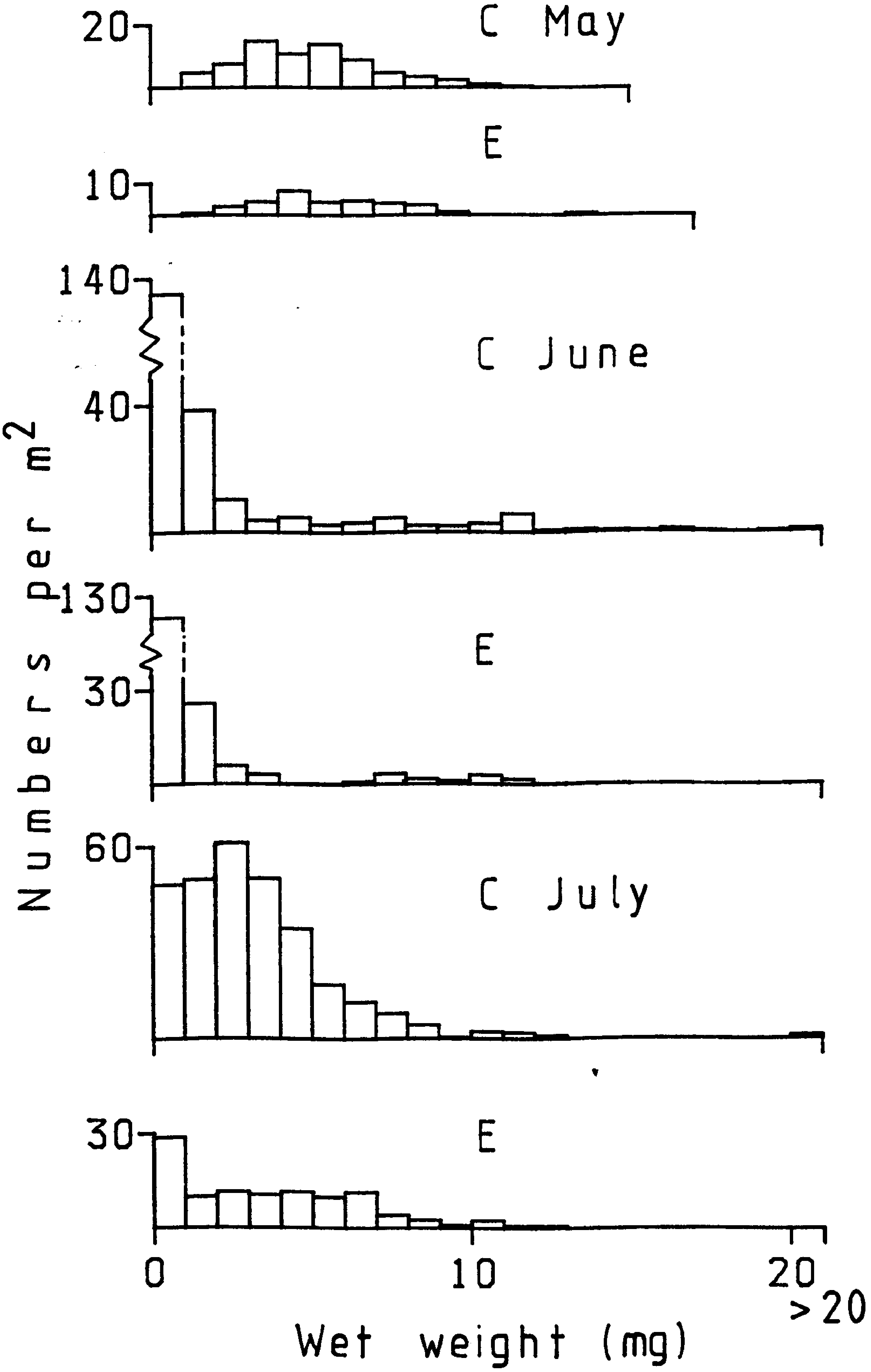
Continued


60
C August
240
E
80
80
C September
70
E
Numbers per m^2
0
10
20
>20
Wet weight (mg)

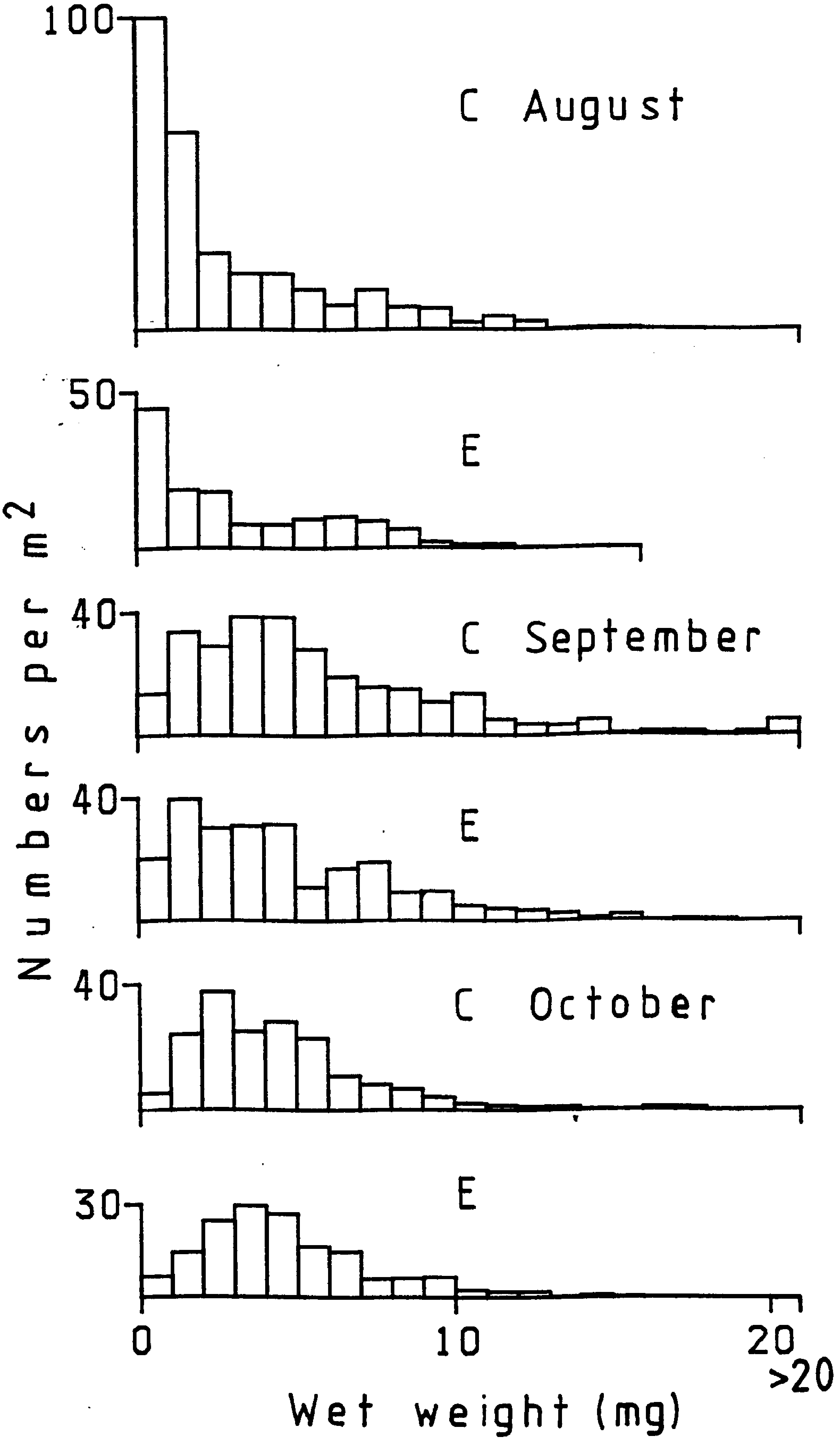
Continued


130
C October
50
E
40
C January 1982
20
E
30
C April
20
E
Numbers per m^2
0
10
20
>20
Wet weight (mg)

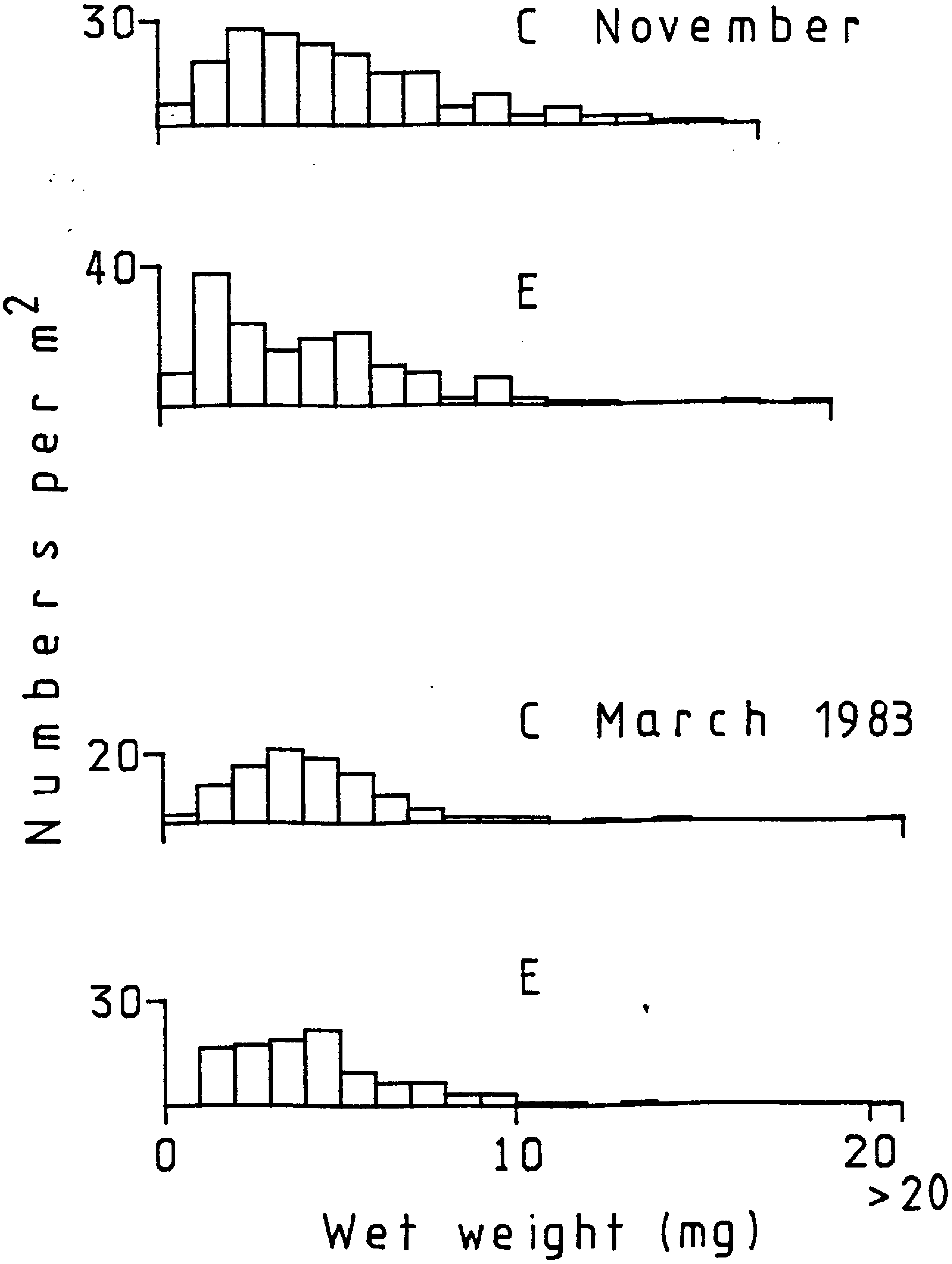
Continued


C May
20
E
10
C June
140
40
E
130
30
C July
60
E
30
Numbers per m^2
0
10
20
>20
Wet weight (mg)

Continued


100
C August
50
E
40
C September
40
E
40
C October
30
E
Numbers per m^2
0
10
20
>20
Wet weight (mg)

Continued


C November
30
E
40
C March 1983
20
E
30
Numbers per m^2
0
10
20
>20
Wet weight (mg)

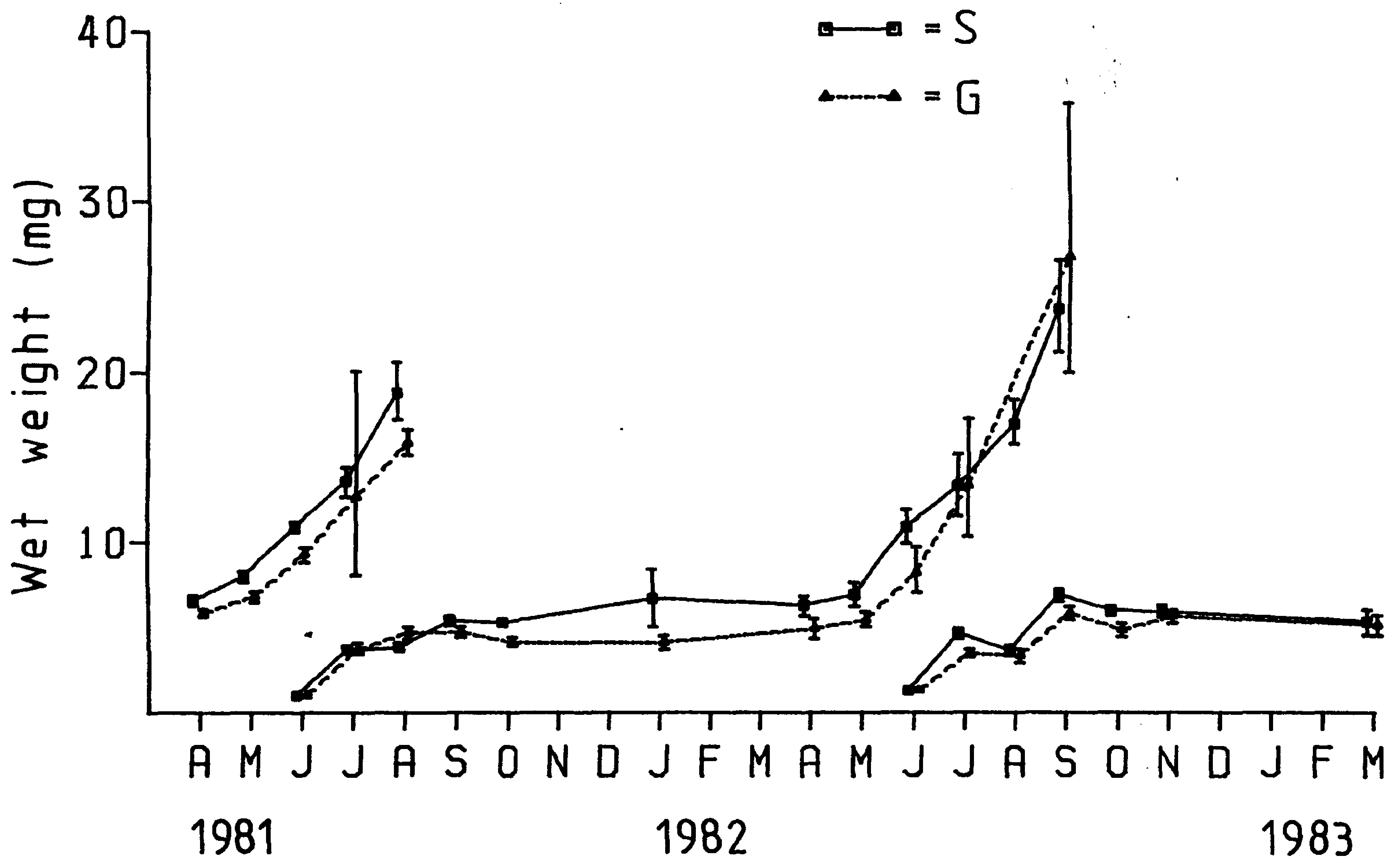


Figure 4.61. Helobdella stagnalis. Arithmetic mean individual weights ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from control sites (spring and summer broods of young combined).

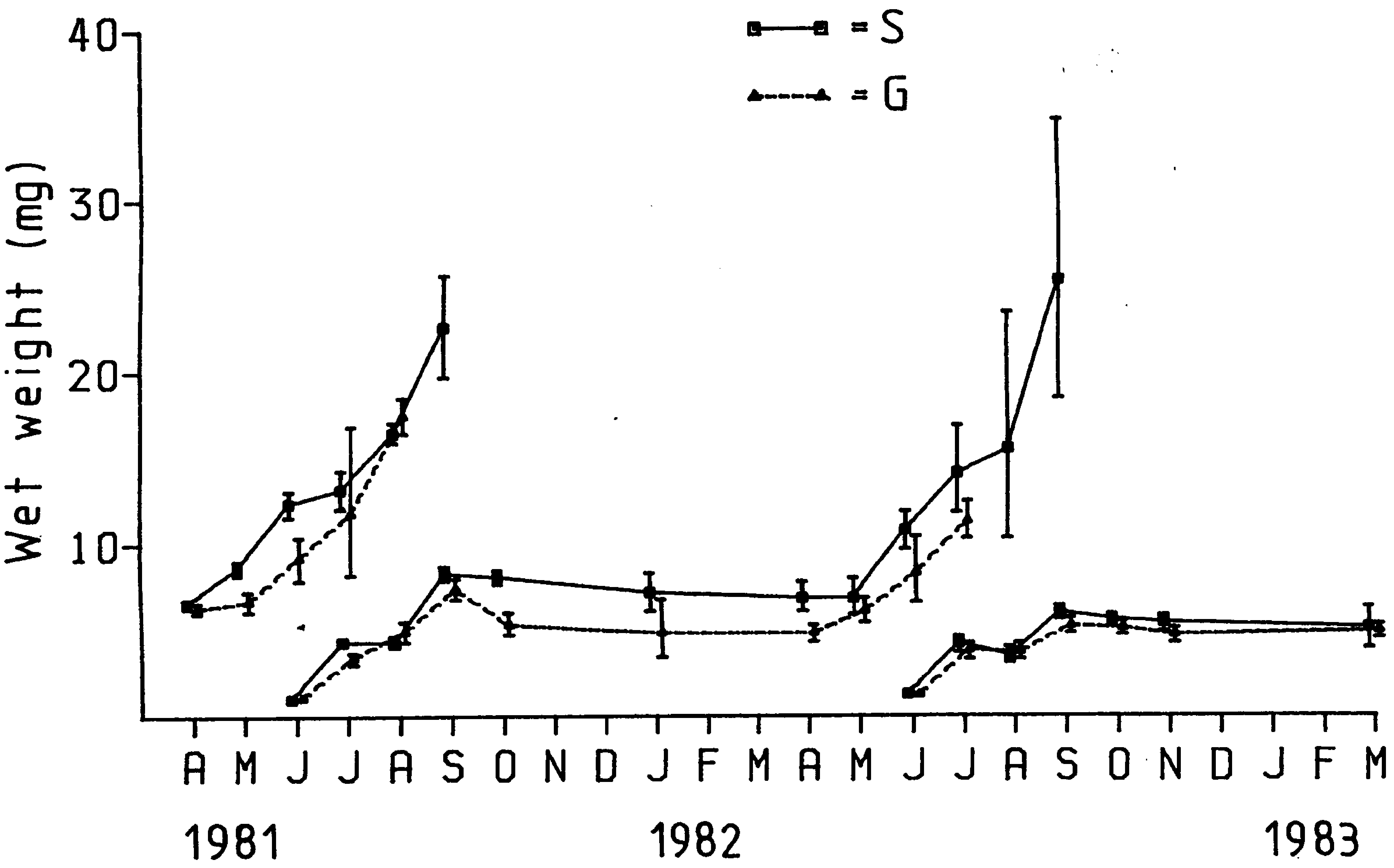


Figure 4.62. *Helobdella stagnalis*. Arithmetic mean individual weights ± 95% confidence limits for each cohort in separate stone (S) and substratum (G) samples from enclosed sites (spring and summer broods of young combined).

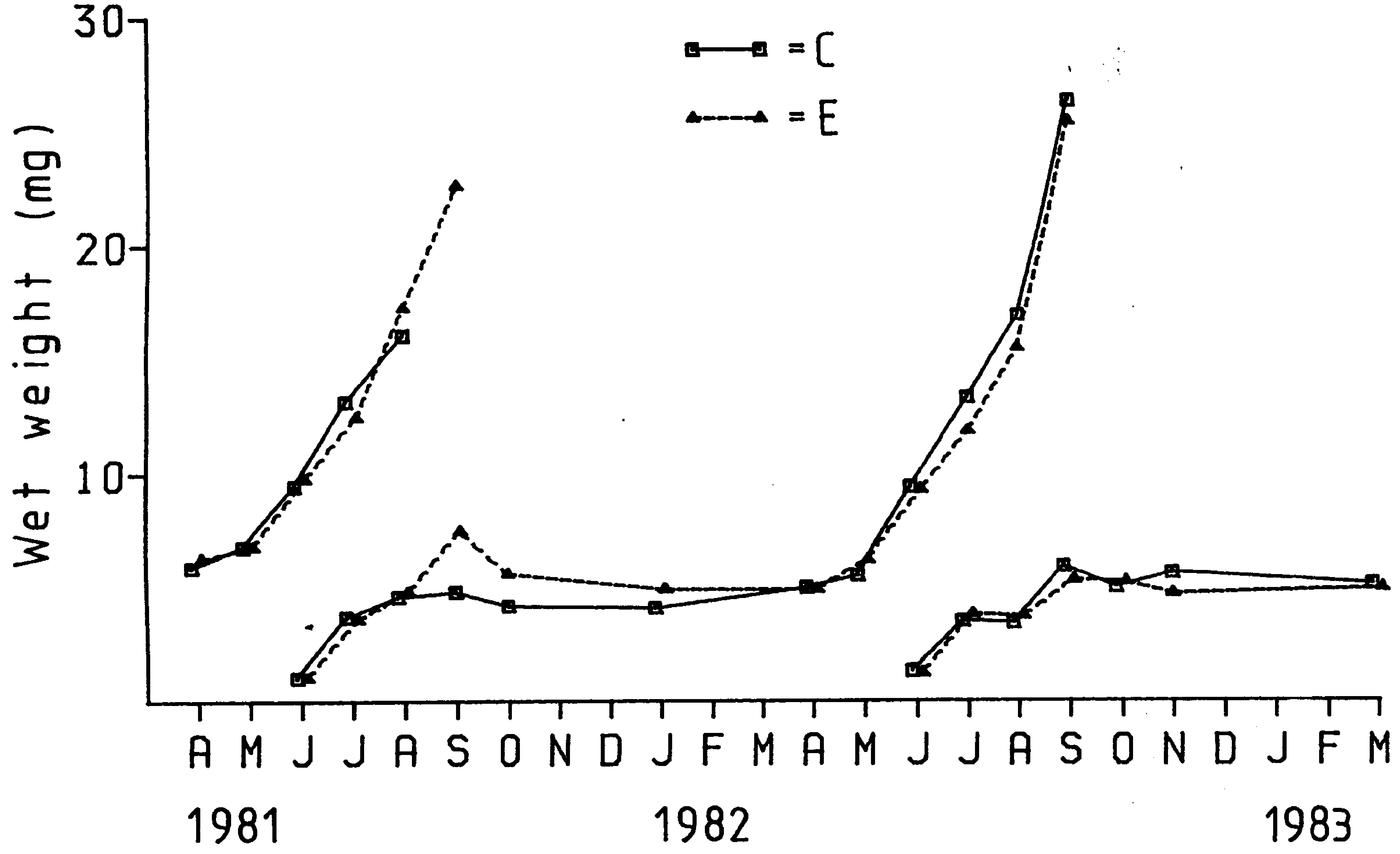
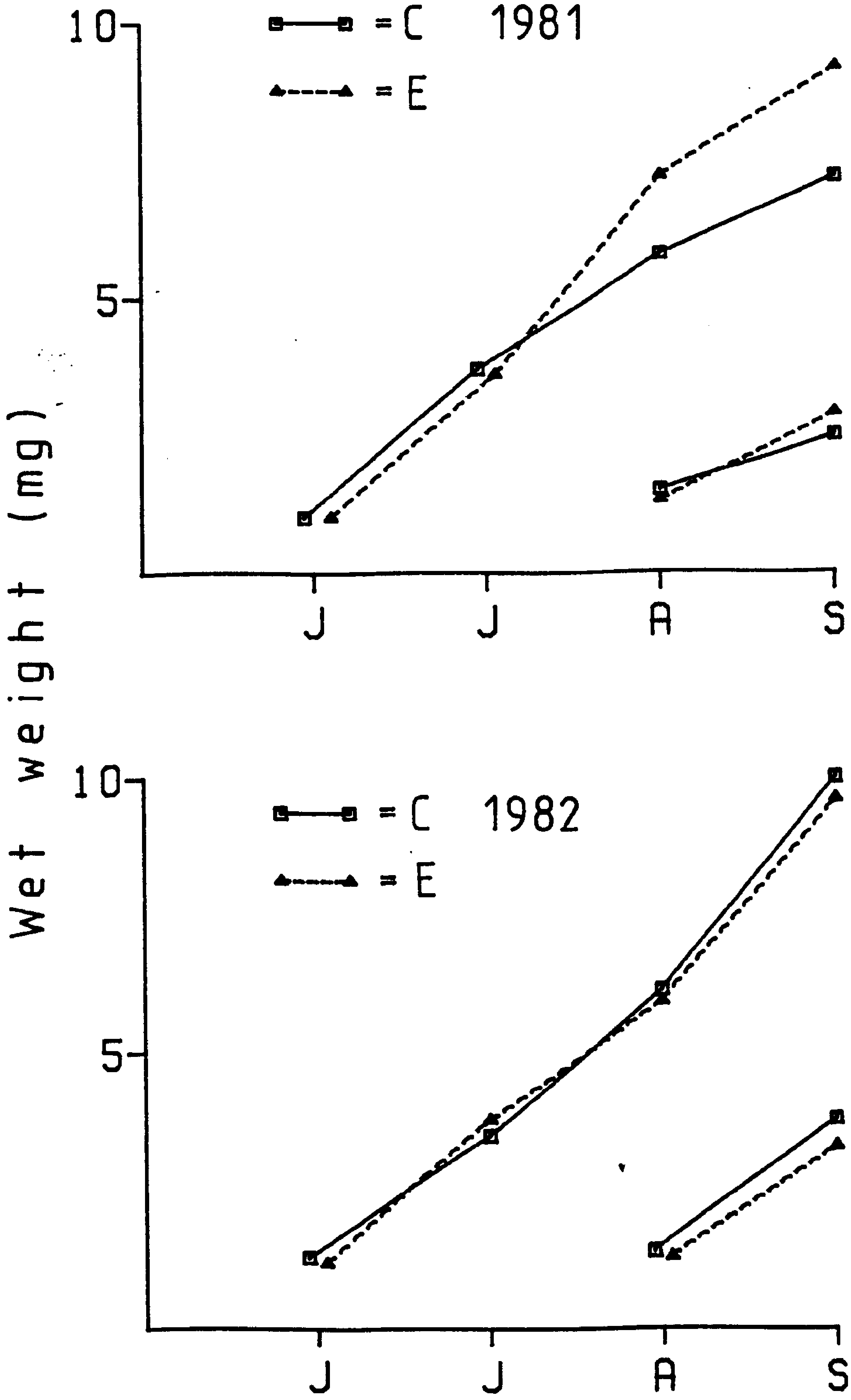


Figure 4.63. Helobdella stagnalis. Arithmetic mean individual weights for each cohort from combined stone and substratum sample data in control (C) and enclosed (E) sites (spring and summer broods of young combined).

Figure 4.64. Helobdella stagnalis. Arithmetic mean individual weights from combined stone and substratum sample data for the spring (June onwards) and summer (August onwards) broods of young in 1981 and 1982 for control (C) and enclosed (E) sites.



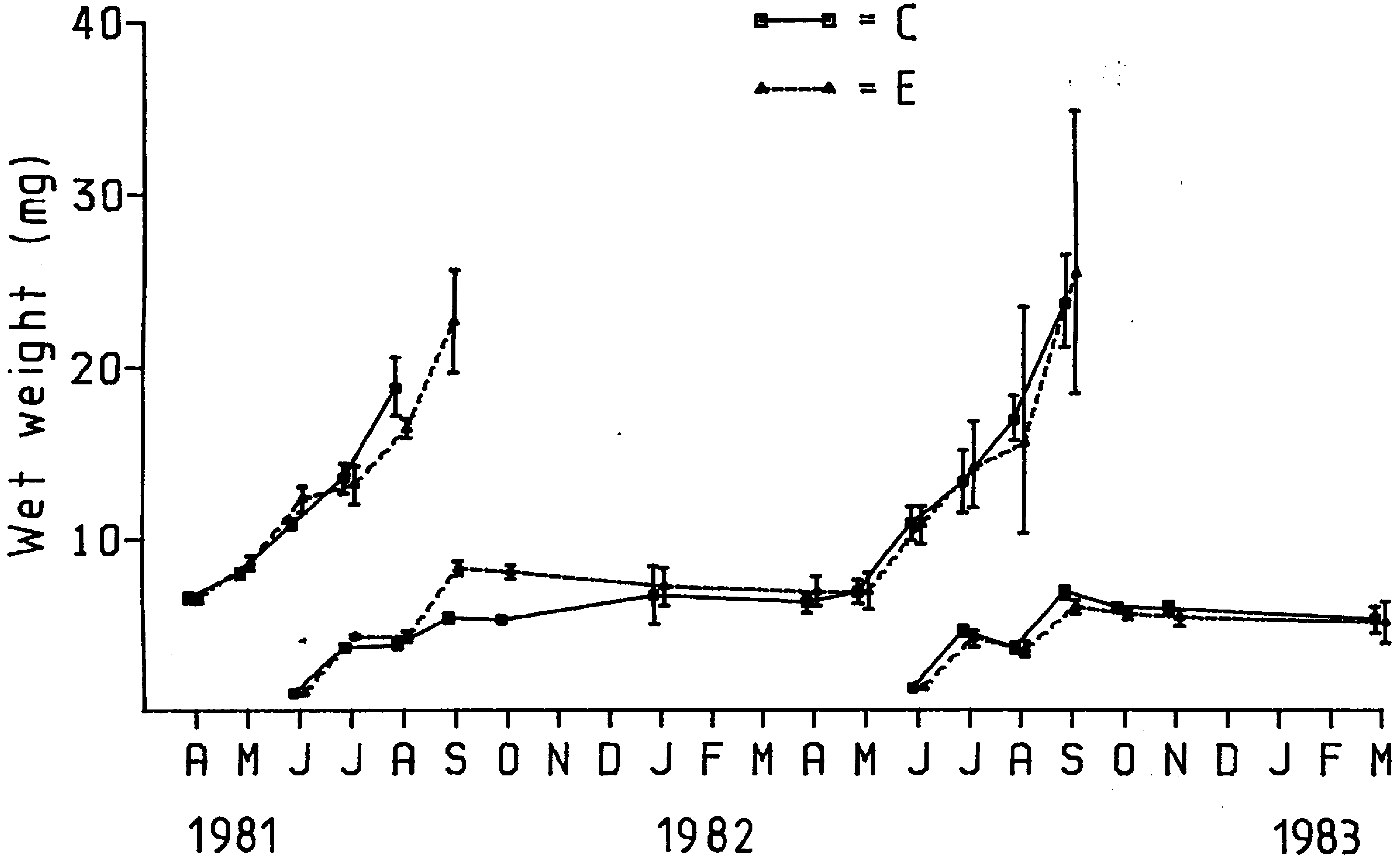


Figure 4.65. Helobdella stagnalis. Arithmetic mean individual samples ± 95% confidence limits for each cohort in stone samples from control (C) and enclosed (E) sites (spring and summer broods of young combined).

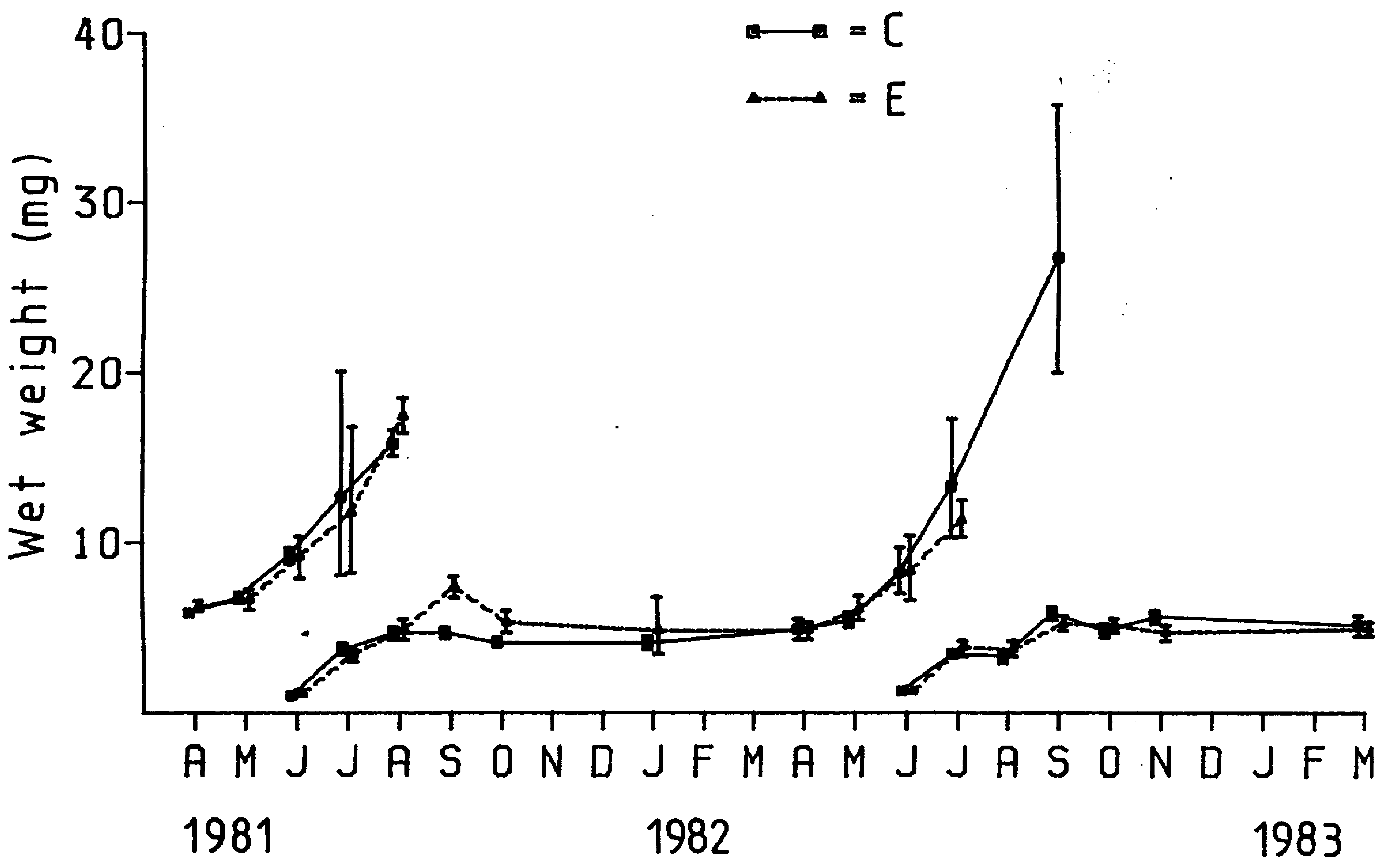


Figure 4.66. Helobdella stagnalis. Arithmetic mean individual weights ± 95% confidence limits for each cohort in substratum samples from control (C) and enclosed (E) sites (spring and summer broods of young combined).

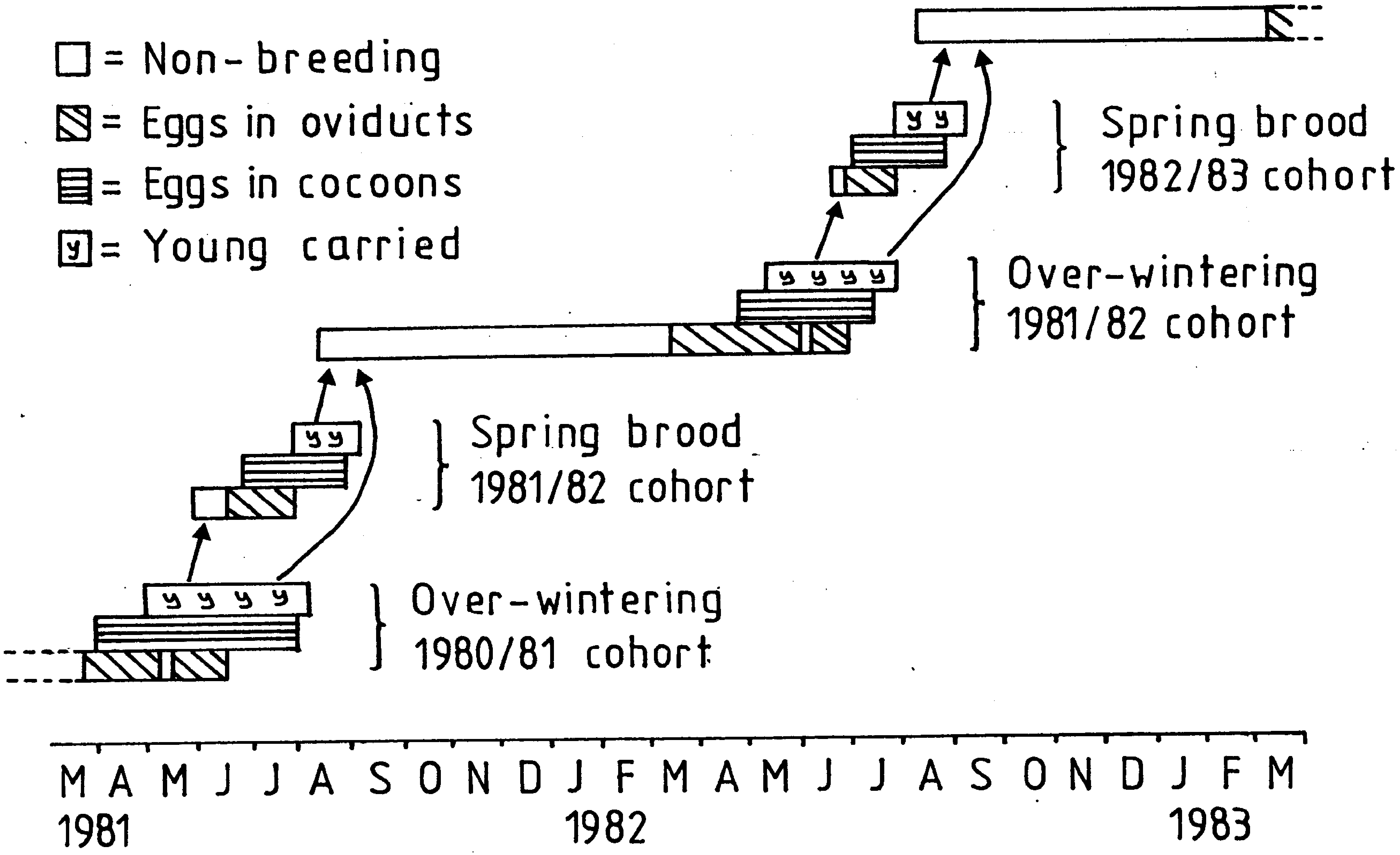


Figure 4.67. <u>Helobdella stagnalis</u>. A summary of the life-cycle in Crose Mere between April 1981 and March 1983.

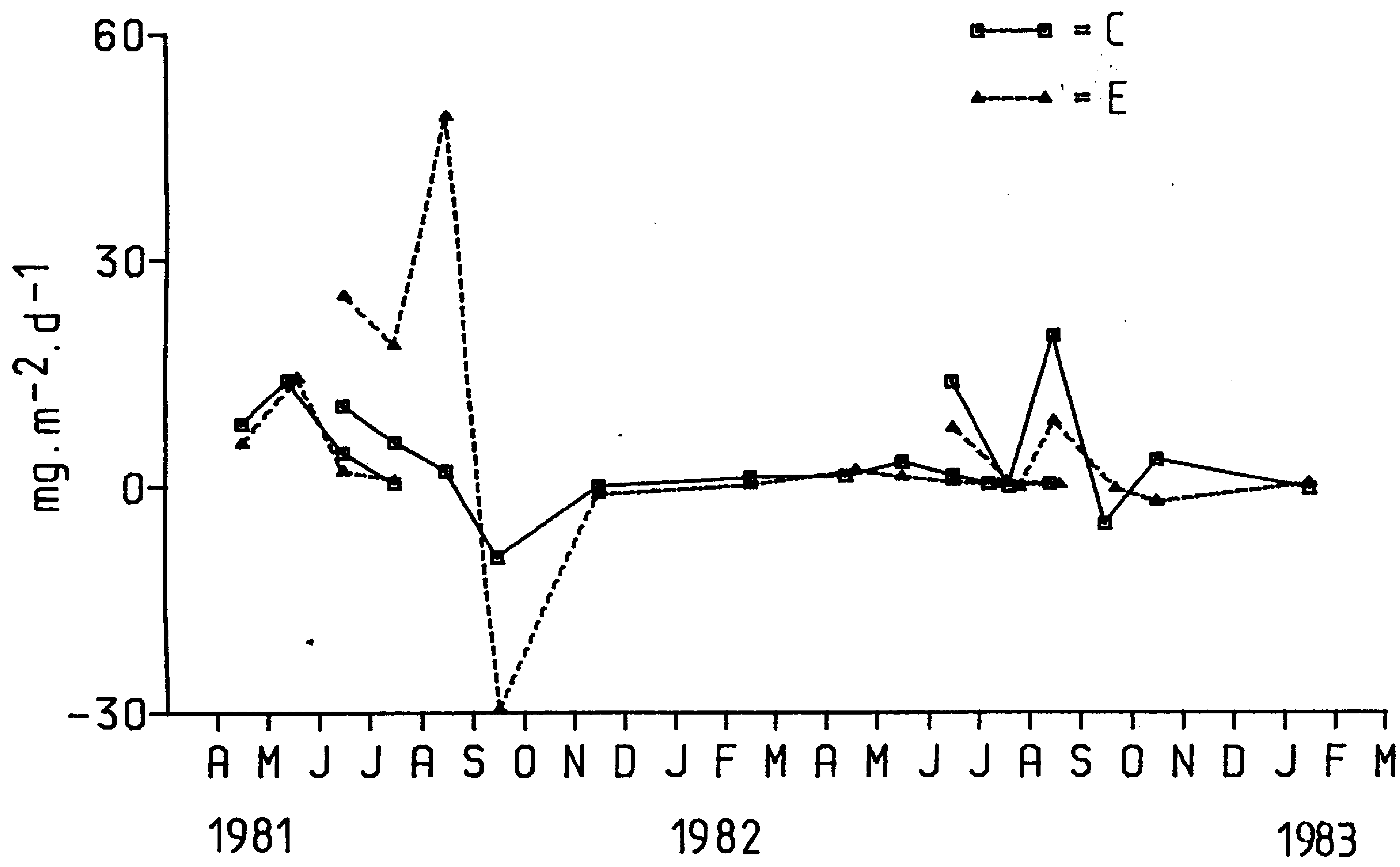


Figure 4.68. Helobdella stagnalis. The rate of biomass production for leeches of each cohort in Control (C) and enclosed (E) sites (spring and summer broods of young combined).

Figure 4.69. Helobdella stagnalis. The rate of biomass production for the spring (June onwards) and summer (August) broods of young in 1981 and 1982 for control (C) and enclosed (E) sites.

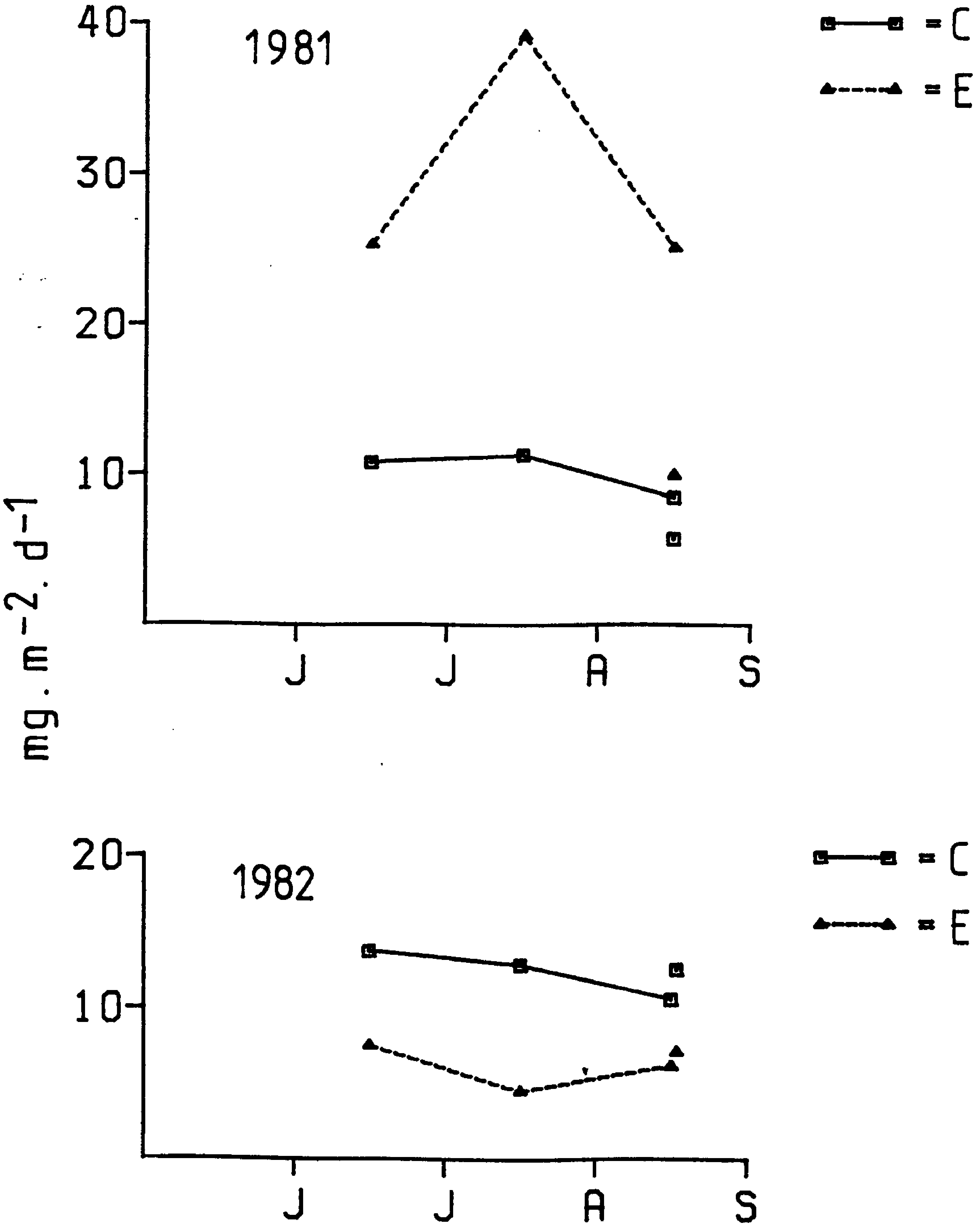


Figure 4.70. <u>Helobdella stagnalis</u>. The Allen curve for the 1981/82 cohort in control sites.

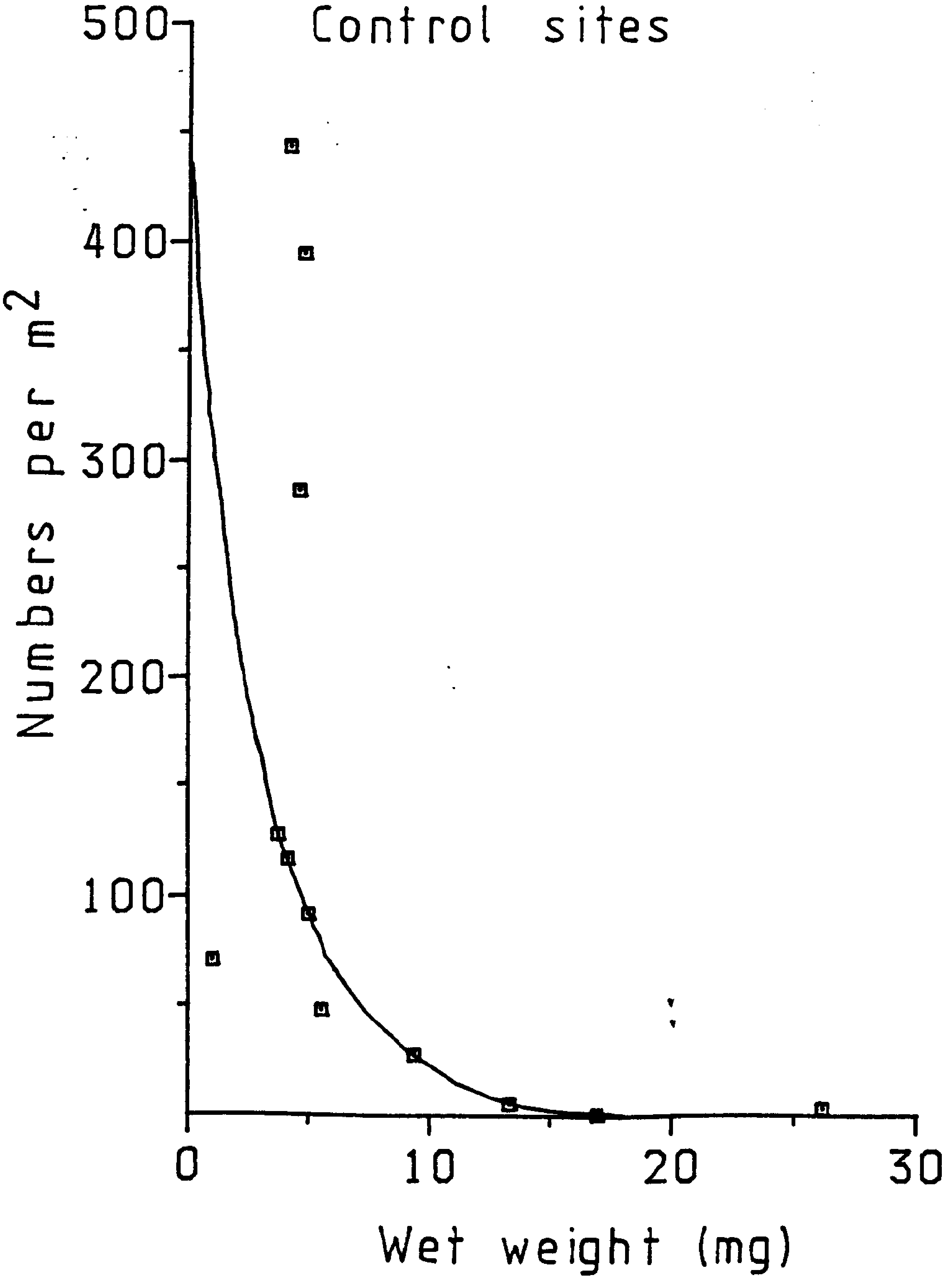


Figure 4.71. __Helobdella stagnalis.__ The Allen curve for the 1981/82 cohort in enclosed sites.

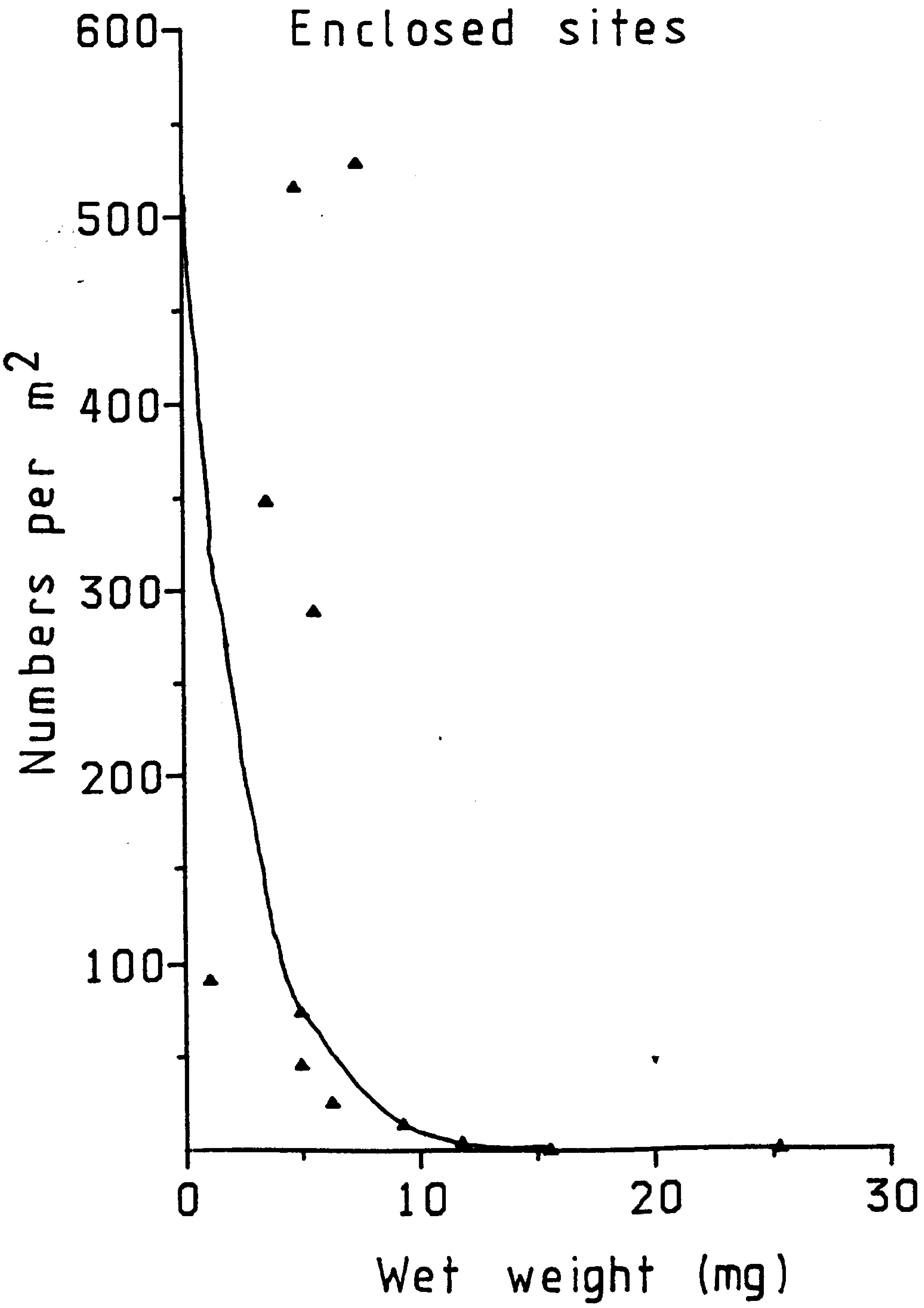


Table 4.15. *Helobdella stagnalis*. Mann-Whitney U tests comparing densities in stone (S) and substratum (G) samples between control and enclosed sites.

		U1	U2	N1	N2	Sig
1980/81 cohort						
1981						
April	S	57.5	102.5	20	8	-
	G	68	92	20	8	-
May	S	39	121	20	8	$p<0.05$
	G	25	15	10	4	-
June	S	70.5	89.5	20	8	-
	G	79.5	80.5	20	8	-
July	S	40.5	119.5	20	8	$p<0.05$
	G	14	26	10	4	-
August	S	34.5	125.5	20	8	$p<0.05$
	G	14	26	10	4	-
Spring brood 1981						
1981						
June	S	72.5	87.5	20	8	-
	G	75	85	20	8	-
July	S	54	106	20	8	-
	G	7	33	10	4	-
August	S	61.5	98.5	20	8	-
	G	18	22	10	4	-
September	S	24	56	10	8	-
	G	6	34	10	4	-
Summer brood 1981						
1981						
August	S	46.5	113.5	20	8	-
	G	10.5	29.5	10	4	-
September	S	45.5	34.5	10	8	-
	G	26.5	13.5	10	4	-

Continued

		U1	U2	N1	N2	Sig
Combined Spring and Summer broods **1981 (1981/82 cohort)**						
1981						
October	S	54.5	105.5	20	8	-
	G	24	8	8	4	-
1982						
January	S	53.5	106.5	20	8	-
	G	37	3	10	4	$p<0.05$
April	S	160	96	16	16	-
	G	30	26	7	8	-
May	S	161	95	16	16	-
	G	181	75	16	16	$p<0.05$
June	S	185.5	54.5	15	16	$p<0.05$
	G	162	94	16	16	-
July	S	181	75	16	16	$p<0.05$
	G	133.5	106.5	16	15	-
August	S	224	32	16	16	$p<0.05$
	G	-	-	-	-	-
September	S	161	95	16	16	-
	G	150	90	16	15	-
Spring brood 1982						
1982						
June	S	123.5	116.5	15	16	-
	G	129	127	16	16	-
July	S	220.5	35.5	16	16	$p<0.05$
	G	211	29	16	15	$p<0.05$
August	S	234.5	21.5	16	16	$p<0.05$
	G	135	121	16	16	-
September	S	186	70	16	16	$p<0.05$
	G	142.5	97.5	16	15	-
Summer brood 1982						
1982						
August	S	215	41	16	16	$p<0.05$
	G	162	94	16	16	-
September	S	168	88	16	16	-
	G	135.5	104.5	16	15	-

Continued

		U1	U2	N1	N2	Sig
Combined Spring and Summer broods 1982 (1982/83 cohort)						
1982						
October	S	166.5	89.5	16	16	-
	G	154.5	101.5	16	16	-
November	S	165.5	90.5	16	16	-
	G	153	103	16	16	-
1983						
March	S	149	107	16	16	-
	G	124	132	16	16	-

Table 4.16. ***Helobdella stagnalis.*** Mann-Whitney U tests comparing biomass in stone (S) and substratum (G) samples between control and enclosed sites.

		U1	U2	N1	N2	Sig
1980/81 cohort						
1981						
April	S	54.5	105.5	20	8	-
	G	64	96	20	8	-
May	S	32.5	127.5	20	8	$p<0.05$
	G	27	13	10	4	-
June	S	65	95	20	8	-
	G	84	76	20	8	-
July	S	43	117	20	8	-
	G	15	25	10	4	-
August	S	38	122	20	8	$p<0.05$
	G	14	26	10	4	-
Spring brood 1981						
1981						
June	S	72.5	87.5	20	8	-
	G	74.5	85.5	20	8	-
July	S	51	109	20	8	-
	G	9	31	10	4	-
August	S	54	106	20	8	-
	G	16.5	23.5	10	4	-
September	S	20	60	10	8	-
	G	2.5	37.5	10	4	$p<0.05$
Summer brood 1981						
1981						
August	S	51.5	108.5	20	8	-
	G	13.5	26.5	10	4	-
September	S	40.5	39.5	10	8	-
	G	24.5	15.5	10	4	-

Continued

		U1	U2	N1	N2	Sig
Combined Spring and Summer broods 1981 (1981/82 cohort)						
1981						
October	S	37	123	20	8	$p<0.05$
	G	20.5	11.5	8	4	-
1982						
January	S	61.5	98.5	20	8	-
	G	34	6	10	4	-
April	S	149.5	106.5	16	16	-
	G	28.5	27.5	7	8	-
May	S	157	99	16	16	-
	G	182.5	73.5	16	16	$p<0.05$
June	S	185.5	54.5	15	16	$p<0.05$
	G	156.5	99.5	16	16	-
July	S	170	86	16	16	-
	G	135	105	16	15	-
August	S	225.5	30.5	16	16	$p<0.05$
	G	-	-	-	-	-
September	S	153	103	16	16	-
	G	150	90	16	15	-
Spring brood 1982						
1982						
June	S	125	115	15	16	-
	G	132	124	16	16	-
July	S	228	28	16	16	$p<0.05$
	G	202.5	37.5	16	15	$p<0.05$
August	S	233	23	16	16	$p<0.05$
	G	147.5	108.5	16	16	-
September	S	190	66	16	16	$p<0.05$
	G	149.5	90.5	16	15	-
Summer brood 1982						
1982						
August	S	214	42	16	16	$p<0.05$
	G	163.5	92.5	16	16	-
September	S	169	87	16	16	-
	G	157	83	16	15	-

Continued

		U1	U2	N1	N2	Sig
Combined Spring and Summer broods 1982 (1981/82 cohort)						
1982						
October	S	167	89	16	16	-
	G	144	112	16	16	-
November	S	163	93	16	16	-
	G	182.5	73.5	16	16	$p<0.05$
1983						
March	S	150.5	105.5	16	16	-
	G	123.5	132.5	16	16	-

Table 4.17. *Helobdella stagnalis*. T and d tests comparing mean individual weights between stone and substratum samples for control (C) and enclosed (E) sites.

		F	(v1,v2)	Sig	Test	(d.f.)	Sig
1980/81 cohort							
1981							
April	C	1.042	(469, 613)	-	t=3.882	(1082)	p<0.001
	E	1.054	(335, 273)	-	t=1.345	(608)	-
May	C	1.605	(352, 279)	*	d=5.261	(631)	p<0.001
	E	2.566	(278, 48)	*	d=5.435	(98)	p<0.001
June	C	1.533	(597, 203)	*	d=5.792	(431)	p<0.001
	E	1.522	(196, 46)	*	d=4.459	(83)	p<0.001
July	C	1.344	(102, 3)	-	t=0.375	(105)	-
	E	3.352	(87, 3)	-	t=0.530	(90)	-
August	C	31.869	(22, 5)	*	d=3.191	(26)	p<0.005
	E	1.346	(35, 9)	-	t=1.618	(44)	-
Spring brood 1981							
1981							
June	C	4.457	(180,1148)	*	d=1.732	(193)	-
	E	Variance on stones = 0			d=1.773	(44)	-
July	C	1.075	(1052, 92)	-	t=0.000	(1114)	-
	E	1.552	(685, 103)	*	d=4.341	(156)	p<0.001
August	C	1.086	(202, 502)	-	t=1.506	(704)	-
	E	1.065	(291, 94)	-	t=3.076	(385)	p<0.005
September	C	1.411	(245, 162)	*	d=2.690	(384)	p<0.01
	E	1.305	(379, 112)	-	t=1.784	(491)	-
Summer brood 1981							
1981							
August	C	1.850	(73, 425)	*	d=6.727	(87)	p<0.001
	E	4.095	(57, 349)	*	d=3.883	(62)	p<0.001
September	C	1.282	(190, 179)	-	t=2.288	(369)	p<0.05
	E	1.593	(106, 43)	*	d=0.026	(100)	-

Continued

		F	(v1,v2)	Sig	Test	(d.f.)	Sig
Combined Spring and Summer broods 1981 (1981/82 cohort)							
1981							
October	C	1.490	(622,297)	*	d=6.859	(701)	p<0.001
	E	1.579	(342, 83)	*	d=7.364	(154)	p 0.001
1982							
January	C	7.005	(43,120)	*	d=2.928	(48)	p<0.01
	E	1.438	(44, 13)	-	t=2.262	(57)	p<0.05
April	C	1.539	(91, 54)	*	d=3.498	(133)	p<0.001
	E	2.454	(72, 71)	*	d=4.398	(123)	p<0.001
May	C	1.748	(61, 85)	*	d=3.513	(109)	p<0.001
	E	2.094	(44, 37)	*	d=1.252	(78)	p<0.05
June	C	2.579	(117, 28)	*	d=3.368	(68)	p<0.005
	E	3.330	(87, 13)	*	d=2.782	(29)	p<0.01
July	C	1.761	(31, 5)	-	t=0.024	(36)	-
	E	42.074	(17, 5)	*	d=1.666	(19)	-
August	C	No leeches in substratum					
	E	No leeches in substratum					
September	C	2.123	(4, 10)	-	t=1.084	(14)	-
	E	No leeches in substratum					
Spring brood 1982							
1982							
June	C	1.077	(204,202)	-	t=1.444	(406)	-
	E	1.232	(223,171)	-	t=0.461	(394)	-
July	C	1.745	(265,288)	*	d=6.194	(492)	p<0.001
	E	1.013	(116,113)	-	t=1.207	(229)	-
August	C	1.375	(239, 88)	-	t=2.461	(327)	p<0.05
	E	2.287	(90, 82)	*	d=3.445	(157)	p<0.001
September	C	1.685	(229, 99)	*	d=1.951	(241)	-
	E	1.277	(133, 77)	-	t=0.415	(210)	-
Summer brood 1982							
1982							
August	C	1.272	(124,341)	-	t=3.085	(465)	p<0.005
	E	1.070	(70,152)	-	t=0.431	(222)	-
September	C	1.124	(281,203)	-	t=0.335	(484)	-
	E	1.111	(222,171)	-	t=3.092	(393)	p<0.005

Continued

		F	(vl,v2)	Sig	Test	(d.f.)	Sig
Combined Spring and Summer broods <u>1982 (1982/83 cohort)</u>							
<u>1982</u>							
October	C	1.510	(609,195)	*	d=4.822	(400)	$p<0.001$
	E	1.431	(432,168)	*	d=1.735	(364)	-
November	C	1.046	(213,253)	-	t=1.260	(466)	-
	E	1.257	(214,190)	-	t=2.339	(404)	$p<0.05$
<u>1983</u>							
March	C	1.765	(126, 42)	*	d=0.347	(96)	-
	E	2.003	(30,129)	*	d=0.331	(37)	-

Table 4.18. *Helobdella stagnalis*. T and d tests comparing mean individual weights between control and enclosed sites for separate stone (S) and substratum (G) samples.

		F	(v1,v2)	Sig	Test	(d.f.)	Sig
1980/81 cohort							
1981							
April	S	1.090	(469, 335)	-	t=0.226	(804)	-
	G	1.103	(613, 273)	-	t=1.649	(886)	-
May	S	1.109	(278, 352)	-	t=2.522	(630)	p<0.05
	G	1.442	(279, 48)	-	t=0.283	(327)	-
June	S	1.685	(196, 597)	*	d=3.634	(277)	p<0.001
	G	1.698	(46, 203)	*	d=0.168	(59)	-
July	S	1.444	(87, 102)	*	d=0.599	(170)	-
	G	1.727	(3, 3)	-	t=0.422	(6)	-
August	S	5.921	(22, 35)	*	d=2.583	(27)	p<0.05
	G	3.999	(9, 5)	-	t=2.355	(14)	p<0.05
Spring brood 1981							
1981							
June	S	Variance enclosed sites = 0					-
	G	2.356	(44, 180)	*	d=0.987	(54)	-
July	S	1.415	(685,1052)	*	d=4.915	(1284)	p<0.001
	G	1.020	(92, 103)	-	t=1.329	(195)	-
August	S	1.468	(291, 502)	*	d=9.701	(502)	p<0.001
	G	1.268	(94, 202)	-	t=3.722	(296)	p<0.001
September	S	1.869	(379, 245)	*	d=7.982	(615)	p<0.001
	G	2.021	(112, 162)	*	d=5.740	(187)	p<0.001
Summer brood 1981							
1981							
August	S	2.612	(425, 349)	*	d=4.897	(722)	p<0.001
	G	1.180	(73, 57)	-	t=3.248	(130)	p<0.005
September	S	1.340	(190, 106)	-	t=4.401	(296)	p<0.001
	G	1.666	(179, 43)	*	d=2.332	(82)	p<0.05

Continued

		F	(v1,v2)	Sig	Test	(d.f.)	Sig
Combined Spring and Summer broods 1981 (1981/82 cohort)							
1981							
October	S	2.011	(342, 622)	*	d=12.548	(533)	$p<0.001$
	G	1.898	(83, 297)	*	d= 3.353	(109)	$p<0.005$
1982							
January	S	2.413	(43, 44)	*	d= 0.534	(73)	-
	G	2.019	(13, 120)	*	d= 0.801	(15)	-
April	S	1.799	(72, 91)	*	d= 1.321	(130)	-
	G	1.128	(71, 51)	-	t= 0.301	(125)	-
May	S	1.547	(44, 61)	-	t= 0.104	(105)	-
	G	1.291	(37, 85)	-	t= 1.707	(122)	-
June	S	1.171	(117, 87)	-	t= 0.175	(204)	-
	G	1.511	(28, 13)	-	t= 0.043	(41)	-
July	S	1.738	(17, 31)	-	t= 0.460	(48)	-
	G	13.749	(5, 5)	*	d= 1.235	(6)	-
August	S	18.935	(17, 1)	-	t= 0.647	(18)	-
	G	No leeches in substratum					
September	S	1.315	(3, 10)	-	t= 0.605	(13)	-
	G	No leeches in substratum					
Spring brood 1982							
1982							
June	S	1.020	(223, 202)	-	t= 0.317	(425)	-
	G	1.301	(204, 171)	*	d= 1.595	(374)	-
July	S	1.028	(265, 116)	-	t= 1.587	(381)	-
	G	1.675	(113, 288)	*	d= 1.352	(169)	-
August	S	1.216	(90, 239)	-	t= 0.991	(329)	-
	G	1.368	(88, 82)	-	t= 0.534	(170)	-
September	S	1.277	(229, 133)	-	t= 2.169	(362)	$p<0.05$
	G	1.033	(77, 99)	-	t= 0.669	(176)	-
Summer brood 1982							
1982							
August	S	1.038	(152, 341)	-	t= 0.318	(493)	-
	G	1.145	(124, 70)	-	t= 1.460	(194)	-
September	S	1.080	(281, 222)	-	t= 0.637	(503)	-
	G	1.067	(203, 171)	-	t= 3.340	(374)	$p<0.005$

Continued

		F	(v1,v2)	Sig	Test	(d.f.)	Sig
Combined Spring and Summer broods <u>1982 (1982/83 cohort)</u>							
<u>1982</u>							
October	S	1.111	(609, 432)	-	t= 1.838	(1041)	-
	G	1.053	(195, 168)	-	t= 1.141	(363)	-
November	S	1.174	(214, 253)	-	t= 1.900	(467)	-
	G	1.120	(213, 190)	-	t= 3.069	(403)	$p<0.005$
<u>1983</u>							
March	S	1.779	(30, 42)	*	d= 0.222	(53)	-
	G	1.988	(126, 129)	*	d= 0.555	(227)	-

Table 4.19. *Helobdella stagnalis*. Regression equations for arithmetic mean weight (mg) plotted against time (days) for data from control (C) and enclosed (E) sites.

Equation: $\ln Y = RX + \ln Q$ H_0: slope = 0

		R ± 95% C.I.	Q	t (d.f.)	Sig
1980/81 cohort					
April 1981 to August 1981	C	0.008 ± 0.002	1.712	11.551 (3)	$p<0.005$
	E	0.009 ± 0.002	1.716	12.091 (4)	$p<0.001$
1981/82 cohort					
June 1981 to September 1981	C	0.018 ± 0.031	0.356	2.454 (2)	$p>0.05$
	E	0.022 ± 0.021	0.267	4.635 (2)	$p<0.05$
September 1981 to April 1982	C	0.000 ± 0.003	1.475	0.477 (2)	$p>0.05$
	E	0.002 ± 0.004	1.879	1.972 (2)	$p>0.05$
April 1982 to September 1982	C	0.011 ± 0.002	1.523	18.304 (4)	$p<0.001$
	E	0.010 ± 0.002	1.557	17.189 (4)	$p<0.001$
June 1981 to September 1982	C	0.005 ± 0.002	0.781	5.402 (10)	$p<0.001$
	E	0.004 ± 0.002	0.953	4.420 (10)	$p<0.005$
1982/83 cohort					
June 1982 to September 1982	C	0.015 ± 0.017	0.434	3.713 (2)	$p>0.05$
	E	0.015 ± 0.022	0.456	2.899 (2)	$p>0.05$
September 1982 to March 1983	C	-0.001 ± 0.003	1.722	0.895 (2)	$p>0.05$
	E	0.000 ± 0.002	1.640	0.991 (2)	$p>0.05$

Table 4.20. Helobdella stagnalis. The proportions of leeches breeding in stone (S) samples in 1981 and in stone (S) and substratum (G) samples and from combined stone and substratum sample data (T) in 1982 for leeches in control (C) and enclosed (E) sites.

Date		Eggs in Oviducts		Carrying Cocoons		Carrying Young		Total Breeding and Sample Size (N)			
		C	E	C	E	C	E	C	N	E	N
Overwintering 1980/81 cohort											
22nd April 1981	S	40.3%	28.9%	4.5%	15.8%	-	-	44.8%	67	44.7%	38
27th May 1981	S	-	-	1.2%	-	22.9%	35.0%	24.1%	81	35.0%	40
30th June 1981	S	10.5%	32.5%	15.1%	22.5%	16.3%	15.0%	41.9%	86	70.0%	40
30th July 1981	S	-	-	4.9%	16.7%	58.5%	41.7%	63.4%	41	58.4%	12
26th August 1981	S	-	-	-	-	40.0%	60.0%	40.0%	5	60.0%	5
Spring brood of the 1981/82 cohort											
30th July 1981	S	5.0%	11.8%	9.9%	26.5%	-	-	14.9%	141	38.3%	68
26th August 1981	S	-	-	-	1.3%	7.3%	5.3%	7.3%	178	6.6%	75
Overwintering 1981/82 cohort											
15th April 1982	S	19.0%	14.0%	-	-	-	-	19.0%	58	14.0%	43
	G	19.4%	30.8%	-	-	-	-	19.4%	31	30.8%	26
	T	19.4%	29.9%	-	-	-	-	19.4%	-	29.9%	-
12th May 1982	S	14.8%	10.3%	33.3%	28.2%	7.4%	17.9%	55.5%	54	56.4%	39
	G	6.4%	8.7%	23.4%	17.4%	6.4%	4.3%	36.2%	47	30.4%	23
	T	7.1%	8.9%	24.3%	18.6%	6.5%	5.8%	37.9%	-	33.3%	-
18th June 1982	S	8.3%	11.1%	14.5%	22.2%	16.0%	7.4%	38.6%	62	40.7%	54
	G	-	-	-	-	-	-	-	-	-	-
	T	3.6%	4.3%	6.2%	8.5%	6.9%	2.8%	16.7%	-	15.6%	-
21st July 1982	S	11.1%	-	-	-	61.1%	53.9%	72.2%	18	53.9%	13
	G	-	-	-	-	66.6%	71.4%	66.6%	3	71.4%	7
	T	2.4%	-	-	-	65.4%	68.6%	67.8%	-	68.6%	-

Continued

Date		Eggs in Oviducts		Carrying Cocoons		Carrying Young		Total Breeding and Sample Size (N)			
		C	E	C	E	C	E	C	N	E	N
Spring brood of the 1982/83 cohort											
	S	6.6%	8.8%	-	3.5%	9.8%	7.0%	16.4%	61	19.3%	57
21st July 1982	G	-	6.0%	2.8%	4.0%	4.2%	2.0%	7.0%	72	12.0%	50
	T	0.3%	6.1%	2.7%	4.0%	4.5%	2.2%	7.5%	-	12.3%	-
	S	-	-	-	-	5.0%	5.9%	5.0%	80	5.9%	68
18th August 1982	G	-	-	-	-	-	-	-	71	-	77
	T	-	-	-	-	0.8%	0.3%	0.8%	-	0.3%	-

Table 4.21 *Helobdella stagnalis*. The mean numbers of eggs in oviducts, eggs carried in cocoons and young carried for leeches collected from control (C) and enclosed (E) sites in 1981 and 1982.

		$\bar{x} \pm$ 95% C.I.		
Eggs in oviducts (per breeding leech)				
22nd April 1981	C	20.9 ± 3.2	(n=21)	Over-wintering 1980/81 cohort
	E	26.7 ± 4.7	(n=10)	
30th July 1981	C	10.4	(n= 5)	Spring brood of the 1981/82 cohort
	E	17.5	(n= 2)	
15th April 1982	C	20.8 ± 2.5	(n=17)	Over-wintering 1981/82 cohort
	E	22.6 ± 4.5	(n=14)	
12th May 1982	C	14.8 ± 3.7	(n=11)	
	E	15.7	(n= 6)	
18th June 1982	C	18.5	(n= 6)	
	E	19.8	(n= 6)	
21st July 1982	C	12.3	(n= 4)	Spring brood of the 1982/83 cohort
	E	13.0	(n= 8)	
Eggs in cocoons (per breeding leech)				
22nd April 1981	C	26.7	(n= 3)	Over-wintering 1980/81 cohort
	E	22.6	(n= 6)	
30th June 1981	C	19.0 ± 4.4	(n=13)	
	E	19.2	(n= 9)	
30th July 1981	C	9.1 ± 1.8	(n=15)	Spring brood of the 1981/82 cohort
	E	9.3 ± 2.8	(n=17)	
12th May 1982	C	13.8 ± 2.5	(n=29)	Over-wintering 1981/82 cohort
	E	13.6 ± 4.1	(n=16)	
18th June 1982	C	17.9	(n= 9)	
	E	16.1 ± 4.8	(n=12)	
21st July 1982	C	13.0	(n= 1)	Spring brood of the 1982/83 cohort
	E	11.8	(n= 5)	

Continued

Young carried (per breeding leech)		$\bar{x} \pm$ 95% C.I.		
27th May 1981	C	9.1 ± 3.0	(n=24)	Over-wintering 1980/81 cohort
	E	10.5 ± 3.4	(n=14)	
30th June 1981	C	5.9 ± 2.5	(n=14)	
	E	2.7	(n= 6)	
30th July 1981	C	9.5 ± 2.1	(n=24)	
	E	7.2	(n= 5)	
26th August 1982	C	5.2 ± 2.9	(n=11)	Spring brood of the 1981/82 cohort
	E	10.4	(n= 8)	
12th May 1982	C	7.6	(n= 7)	Over-wintering 1981/82 cohort
	E	10.4	(n= 8)	
18th June 1982	C	14.2 ± 6.7	(n=10)	
	E	15.0	(n= 4)	
21st July 1982	C	7.0 ± 3.1	(n=13)	
	E	7.5 ± 5.1	(n=12)	
21st July 1982	C	4.4	(n= 9)	Spring brood of the 1982/83 cohort
	E	7.2	(n= 5)	
18th August 1982	C	7.7	(n= 3)	
	E	10.0	(n= 4)	

Table 4.22. *Helobdella stagnalis*. Mortality data for the 1980/81, 1981/82, 1982/83 cohorts from control (C) and enclosed (E) sites.

	1980/81 cohort		1981/82 cohort		1982/83 cohort	
	C	E	C	E	C	E
1. Estimated number of young entering cohort (.m^{-2})	-	-	5911.7	11470.2	1737.0	1460.6
2. Density of leeches in September of first year (.m^{-2})	-	-	394.5	528.2	254.0	195.0
3. Density of leeches in April of first year (.m^{-2})	342.6	410.5	91.8	73.7	94.1	89.2 (March 1983)
4. Density of leeches in August of second year (.m^{-2})	6.1	27.6	0.9	0.1	-	-
Mortality between points 1-2 above	-	-	93.3%	95.4%	85.4%	86.7%
Mortality between points 1-3 above	-	-	98.5%	99.4%	94.6%	93.9%
Mortality between points 1-4 above	-	-	100.0%	100.0%	-	-
Mortality between points 3-4 above	98.2%	93.3%	99.0%	99.9%	-	-

4.3.4. Other invertebrates

For those animals which were sampled frequently and in some abundance, values for density and biomass from combined stone and substratum sample data, and comparing control and enclosed sites are presented in this chapter. The means and confidence limits for density and biomass in separate stone and substratum samples, and the results of Mann-Whitney U tests, comparing density and biomass between control and enclosed sites are given in Appendix B.

Table 4.23 presents a list of the less commonly occuring invertebrates recorded in samples. The leech Theromyzon tessulatum O.F. Müller, though of common occurrence, is also included in this table. No further analysis of these limited data is made.

4.3.4.1 Oligochaeta

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.72 and 4.73 respectively.

Density

In April 1981, the density of oligochaetes was 151.9 m^{-2} in control sites and 251.7 m^{-2} in enclosed sites. The density rose to maximum levels of 4223.2 m^{-2} in control sites and 5158.5 m^{-2} in enclosed sites in September 1981 and then declined over winter. In 1982, a rise and then a decline in density occurred between January and June before a further rise to a maximum density of 4245.2 m^{-2} in control sites and 3297.3 m^{-2} in enclosed sites in November 1982. Density then declined between November 1982 and March 1983.

Biomass

In April 1981, the mean biomass was 0.3 $g.m^{-2}$ in control sites and 0.5 $g.m^{-2}$ in enclosed sites and reached a maximum of 7.0 $g.m^{-2}$ in August in control sites and 7.8 $g.m^{-2}$ in October in enclosed sites. Biomass declined over the winter, but sharply increased in control sites between January and April 1982 and went on to reach peaks of 5.3 $g.m^{-2}$ in April in control sites and 4.6 $g.m^{-2}$ in May in enclosed sites. Biomass then declined to a low of 1.0 $g.m^{-2}$ in control sites and 1.7 $g.m^{-2}$ in enclosed sites in June before rising again to a new peak of 7.2 $g.m^{-2}$ in control sites and 8.4 $g.m^{-2}$ in enclosed sites in November 1982.

There were no significant differences in either density or biomass between control and enclosed sites.

4.3.4.2 Chironomidae

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.74 and 4.75 respectively.

Density

In April 1981, the density of chironomids was 668.0 m^{-2} in control sites and 573.7 m^{-2} in enclosed sites. It had risen to 3855.8 m^{-2} in control sites and 4913.7 m^{-2} in enclosed sites by June, but then declined in both control and enclosed sites before rising to a new peak of 6983.7 m^{-2} in control sites and 3280.4 m^{-2} in enclosed sites in September. The density then remained more or less constant over the winter, but reached a low of 828.5 m^{-2} in control sites in July 1982 and of 567.5 m^{-2} in enclosed sites in August. A sharp increase occurred between August and September and maximum densities of 4235.2m^{-2}

in control sites and 3231.1 m^{-2} in enclosed sites were reached in October 1982. Large numbers of small chironomids were found in the samples of June, July and August in both 1981 and 1982 and in both control and enclosed sites.

Biomass

In April 1981, the biomass of chironomids was 7.4 $g.m^{-2}$ in control sites and 7.2 $g.m^{-2}$ in enclosed sites. A dip in biomass occurred between June and August and then a sharp rise to peak levels of 36.7 $g.m^{-2}$ in control sites and 28.1 $g.m^{-2}$ in enclosed sites in September 1981. The biomass then declined, but remained more or less constant over the winter months, before a more rapid decline to minimum levels of 1.8 $g.m^{-2}$ in July 1982 in control sites and of 1.6 $g.m^{-2}$ in August in enclosed sites. A sharp increase in biomass then occurred to reach maximum levels of 25.9 $g.m^{-2}$ in September in enclosed sites and of 28.4 $g.m^{-2}$ in October in control sites. The biomass then declined to the last sample in March 1983.

The density and biomass were significantly higher in control sites for stone samples in September and October 1981 and in April, August, September, October and November 1982. Density only, was higher in control sites in the stone samples of July 1981 and in the substratum samples of July, September and October 1981 and May 1982.

4.3.4.3 Asellus spp.

Both Asellus aquaticus L. and Asellus meridianus Racovitza were found in samples. However, A. aquaticus was always dominant in terms of numbers and biomass.

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.76 and 4.77 respectively.

Density

In April 1981, the density was 24.5 m^{-2} in control sites and 16.6 m^{-2} in enclosed sites. The trend was then more or less upwards and reached peaks of 666.3 m^{-2} in enclosed sites in August and 341.6 m^{-2} in control sites in September, before a drop in October and then a further increase to 455.6 m^{-2} in control sites and 623.5 m^{-2} in enclosed sites in January 1982. The density then decreased, reaching minimum levels of 69.1 m^{-2} in enclosed sites in April and 58.3 m^{-2} in control sites in May. The density then rose again to reach maximum levels of 938.8 m^{-2} in enclosed sites in September and 996.1 m^{-2} in control sites in November. The density then declined to the last sample in March 1983. Large numbers of small individuals were present in June, July, August and September in 1981 and 1982 in both control and enclosed sites.

Biomass

In April 1981, the biomass was 0.2 $g.m^{-2}$ in control sites and 0.1 $g.m^{-2}$ in enclosed sites. It then rose to a peak of 1.8 $g.m^{-2}$ in control sites and 4.1 $g.m^{-2}$ in enclosed sites in September, before a drop in October and then a further increase to 5.2 $g.m^{-2}$ in control sites and 5.0 $g.m^{-2}$ in enclosed sites in January 1982. The biomass then decreased to a minimum of 0.6 $g.m^{-2}$ in enclosed sites in April and of 0.6 $g.m^{-2}$ in control sites in May. It then rose again to reach maximum levels of 8.6 $g.m^{-2}$ in control sites and 7.8 $g.m^{-2}$ in enclosed sites in October and, thereafter, declined until the last sample.

The density and biomass were significantly higher in enclosed sites in the stone samples of May, July, August and September 1981 and January, April, May, June and July 1982 and in the substratum samples of June and August 1981. Density only was higher in enclosed sites in the stone samples of October 1981 and biomass only was significantly higher in enclosed sites in the substratum samples of May 1982.

4.3.4.4 Gammarus spp.

Both Gammarus pulex Schell and Gammarus lacustris Sars were found in samples. However, G. pulex was always dominant in terms of numbers and biomass.

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.78 and 4.79 respectively.

Density

In April 1981, the density was 245.1 m^{-2} in control sites and 60.2 m^{-2} in enclosed sites. A sharp dip occured in May and then the density rose again in June before yet another drop in July when the density reached 23.6 m^{-2} in control sites and 0.7 m^{-2} in enclosed sites. No Gammarus spp were found in substratum samples from enclosed sites in this month. The density then rapidly rose to reach peak levels of 815.7 m^{-2} in control sites and 65.2 m^{-2} in enclosed sites in August. Over the winter there was a general decline in density levels, but they started to rise again in April 1982 in enclosed sites and May 1982 in control sites, and peaked at 295.7 m^{-2} in control sites in August and 90.4 m^{-2} in September in enclosed sites. The density then rapidly declined to a low in October, but had increased to 282.6 m^{-2} in control sites and 382.2 m^{-2} in enclosed sites by the last sample of March 1983. Small individuals were present in the samples of June, July and August in 1981 and 1982 for both control and enclosed sites.

Biomass

In April 1981, the mean biomass was 3.8 $g.m^{-2}$ in control sites and 0.5 $g.m^{-2}$ in enclosed sites. It decreased in May and then rose again in June before dropping to minimal levels of 0.1 $g.m^{-2}$ in control sites and 0.005 $g.m^{-2}$ in enclosed sites in July. A rapid increase then occurred to a peak of 3.8 $g.m^{-2}$ in control sites and 0.3 $g.m^{-2}$ in enclosed sites in September. The biomass then declined over the winter, but in May 1982 a rise occurred in enclosed sites, while biomass dropped in control sites. The biomass then rose in control sites and dropped in enclosed sites before a general rise to peaks of 1.5 $g.m^{-2}$ in August in control sites and 0.7 $g.m^{-2}$ in enclosed sites. The biomass dropped in October but then there was a general rise to maximum levels of 4.4 $g.m^{-2}$ in control sites and 8.1 $g.m^{-2}$ in enclosed sites in March 1983.

The density and biomass were significantly higher in control sites in the stone sample of July and August 1981, and in the substratum samples of April 1981. Density, alone, was higher in control sites in the substratum samples of September 1981, and biomass, alone, was higher in the substratum samples of October 1981 and the stone samples of October 1982.

4.3.4.5 Potamopyrgus jenkinsi Smith

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.80 and 4.81 respectively.

Density

In April 1981, the density was 150.2 m^{-2} in control sites and 66.3 m^{-2} in enclosed sites. It then increased but fluctuated over the summer months. In control sites, maximum levels of 2275.7 m^{-2} occurred in September and in enclosed sites the maximum of 8060.5 m^{-2} occurred in July. The density declined over the winter and in control sites then rose between April and June 1982 before dropping to a low of 61.2 m^{-2} in September. In enclosed sites, density declined until May 1982, it then rose until August and then dropped again to a low of 77.1 m^{-2} in September. In both control and enclosed sites the density then rose until October, but declined again until the last sample in March 1983. Large numbers of small individuals were present in control and enclosed sites in the samples of May, June, July and August 1981 and in May, June and October 1982.

Biomass

In April 1981, the biomass was 0.5 $g.m^{-2}$ in control sites and 0.2 $g.m^{-2}$ in enclosed sites. It then increased but fluctuated over the summer months reaching maximum levels of 40.5 $g.m^{-2}$ in enclosed sites in July and 9.2 $g.m^{-2}$ in September in control sites. The biomass then declined and in control sites decreased until April 1982, when it again started to increase and reached a new peak of 3.3 $g.m^{-2}$ before declining to a low in September. In enclosed sites, the biomass decreased until May 1982 and then rose to a maximum of 5.5 $g.m^{-2}$ in August before dropping to a low in September. The biomass in both control and enclosed sites then rose until October, but declined again until the last sample.

The density and biomass were significantly higher in enclosed sites in the stone samples of May, July and August 1981 and July, August and September 1982, and in the substratum samples of May, July and September 1981. Biomass only was significantly higher in enclosed sites in the stone samples of June 1982.

4.3.4.6 *Bithynia tentaculata* L.

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.82 and 4.83 respectively.

Density

In April 1981, the density was 0.9 m^{-2} in control sites and 0.1 m^{-2} in enclosed sites and then rapidly rose to peaks of 33.6 m^{-2} in control sites and 22.7 m^{-2} in enclosed sites in July. In control sites it declined until January 1982 when no specimens were recorded in samples. In enclosed sites, the decrease was more rapid and none were found from August 1981. No further specimens were found until May 1982 when, in control sites, the density rose to a peak of 13.1 m^{-2}. In enclosed sites a peak of 11.7 m^{-2} was reached in July. In both control and enclosed sites, density decreased to a low In September 1982 before rising again. In control sites, the density then decreased to the sample of March 1983, while in enclosed sites it dropped between October and November, but had risen again by March 1983. Large numbers of small individuals were not recognised in samples.

Biomass

The biomass followed similar trends to the density data. In April 1981, the biomass was 0.004 $g.m^{-2}$ in control sites and 0.001 $g.m^{-2}$ in enclosed sites. It peaked at 2.1 $g.m^{-2}$ in control sites and 1.2 $g.m^{-2}$ in enclosed sites in August and then declined. In 1982, for control sites there were peaks of 0.138 $g.m.^{-2}$ in July and 0.051 $g.m^{-2}$ in October. In enclosed sites there were peaks of 0.669 $g.m^{-2}$ in July and 0.033 $g.m^{-2}$ in October.

There were no significant differences in either density or biomass between control and enclosed sites.

4.3.4.7 Valvata piscinalis Müller

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.84 and 4.85 respectively.

Density

In April 1981, the density in control sites was 2.0 m^{-2} but there were no specimens in enclosed sites. In May V.piscinalis was found in both control and enclosed sites and peaked at 40.4 m^{-2} in control sites in July and at 17.9 m^{-2} in enclosed sites in August. No specimens were found in either control or enclosed sites between September 1981 and April 1982. In May 1982 the density in control sites was 10.0 m^{-2}, with no specimens being found in enclosed sites. In June, V. piscinalis were found in both control and enclosed sites and were at peak densities of 24.6 m^{-2} in control sites and 7.6 m^{-2} in enclosed sites. The numbers then sharply dropped and remained at low levels until March 1983. Large numbers of small individuals were not recognised in samples.

Biomass

The biomass followed similar trends to the density data. In 1981, peak levels of 0.355 $g.m^{-2}$ in control sites and 0.138 $g.m^{-2}$ in enclosed sites occurred in July. In 1982 the maximum biomass of 0.225 $g.m^{-2}$ in control sites occurred in June, while in enclosed sites the maximum biomass was 0.065 $g.m^{-2}$ in July.

There were no significant differences in either density or biomass between control and enclosed sites.

4.3.4.8 Sialis lutaria L.

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.86 and 4.87 respectively.

Density

In 1981, S.lutaria first appeared in the samples of June in enclosed sites and July in control sites. Maximum levels of 3.6 m^{-2} in control sites and 22.7 m^{-2} in enclosed sites occurred in July,and then density rapidly declined. In September the density was 0.9 m^{-2} in control sites, but none were recorded in enclosed sites. No further specimens were found until June 1982 when a rapid rise occurred and peak levels of 16.5 m^{-2} in control sites and 51.5 m^{-2} in enclosed sites were reached in July. A decline to a low in October then followed and subsequently the density rose again in November before declining over the winter until the sample in March 1983. Large numbers of small specimens were not recognised in samples.

Biomass

Biomass followed similar trends to the density data. In 1981, a peak level of 0.007 $g.m^{-2}$ occurred in control sites in July. In enclosed sites the peak of 0.103 $g.m^{-2}$ occurred in August. In 1982, in control sites, there were peaks of 0.062 $g.m^{-2}$ in July and 94.1 $g.m^{-2}$ in November. In enclosed sites there were peaks of 0.589 $g.m^{-2}$ in July and 0.181 $g.m^{-2}$ in November.

The density and biomass were significantly higher in enclosed sites in the stone samples of July 1981 and the substratum samples of June 1981 and August 1982. Biomass alone was higher in enclosed sites in the substratum samples of July 1982.

4.3.4.9 Tinodes waeneri L.

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.88 and 4.89 respectively.

Density

In both 1981 and 1982 the density of T. waeneri in samples fluctuated wildly. In control sites there were peaks in April, July and September 1981 and in January, May, July and October 1982 and March 1983. The maximum density in 1981 was 15.7 m^{-2} in April, and in 1982 a maximum of 19.4 m^{-2} occurred in July. In 1981, for enclosed sites, the density peaked in May and then declined. No specimens were found between August 1981 and January 1982, and then peak levels occurred in May, July and October 1982 and March 1983. The maximum density in 1981 was 8.7 m^{-2} in May, and in 1982 the maximum density of 14.1 m^{-2} occurred in October. In March 1983 the density was 12.6 m^{-2} in control sites and 24.7 m^{-2} in enclosed sites. Large numbers of small individuals were not recognised in samples.

Biomass

The biomass data closely followed the trends observed in density, with peaks occurring in the same months. In 1981, the maximum biomass was 0.057 $g.m^{-2}$ in April in control sites and 0.041 $g.m^{-2}$ in May in enclosed sites. In 1982, the maximum biomass was 0.078 $g.m^{-2}$ in July in control sites and 0.038 $g.m^{-2}$ in October in enclosed sites. In March 1983, the biomass was 0.057 $g.m^{-2}$ in control sites and 0.091 $g.m^{-2}$ in enclosed sites.

There were no significant differences in either density or biomass between control and enclosed sites.

4.3.4.10 Leptocercidae

The data comparing total mean density and total mean biomass between control and enclosed sites are given in figures 4.90 and 4.91 respectively.

Density

In April 1981, the density was 5.3 m^{-2} in control sites and 0.2 m^{-2} in enclosed sites. In control sites the density then decreased and few specimens were present in the samples of July and August. In enclosed sites the density increased, peaked at 13.3 m^{-2} in June, and then decreased rapidly so that, again, few were present in July and August. In both control and enclosed sites, an increase in density now occurred and reached a maximum of 6.9 m^{-2} in control sites and 1.7 m^{-2} in enclosed sites in October before declining. In 1982, the density increased between June and July, then decreased, and subsequently rose to a peak of 30.7 m^{-2} in enclosed sites in September and 13.3 m^{-2} in control sites in October. By the last sample of March 1983, the densities were 2.0 m^{-2} in control sites and 4.0 m^{-2} in enclosed sites.

Biomass

The biomass data showed similar trends to the density data. In 1981, peak levels of 0.048 $g.m^{-2}$ in May and 0.006 $g.m^{-2}$ in October occurred in control sites, while in enclosed sites there were peaks of 0.156 $g.m^{-2}$ in June and 0.004 $g.m^{-2}$ in October. In 1982, in control sites, there were peaks of 0.11 $g.m^{-2}$ in April, 0.005 $g.m^{-2}$ in July and 0.055 $g.m^{-2}$ in October. In enclosed sites there were peaks of 0.015 $g.m^{-2}$ in July and 0.075 $g.m^{-2}$ in October. In March

1983 the biomass was 0.009 $g.m^{-2}$ in control sites and 0.023 $g.m^{-2}$ in enclosed sites.

The density was significantly higher in control in the stone samples of April and May 1981 and March 1983, and it was higher in enclosed sites in the substratum samples of June 1981 and the stone samples of September 1982. The biomass was significantly higher in control sites in the stone samples of May 1981, and it was higher in enclosed sites in the substratum samples of June 1981 and the stone samples of September and October 1982.

4.3.4.11 Dugesia polychroa Schmidt

The data comparing total mean density between control and enclosed sites are given in figure 4.92. No biomass data were collected for D. polychroa.

Density

D. polychroa showed no large-scale changes in density during the sampling period. In April 1981, the density was 10.6 m^{-2} in control sites and 8.4 m^{-2} in enclosed sites. In control sites, a peak of 15.9 m^{-2} occurred in August, while in enclosed sites, slight peaks occurred in June, August and October, with the maximum density of 16.5 m^{-2} occurring in October. In 1982, for control sites, a maximum level of 21.2 m^{-2} occurred in May while, in enclosed sites, the maximum was 17.4 m^{-2} in June. Thereafter, in both control and enclosed sites, the density declined and in March 1983 was 6.5 m^{-2} in control sites and 5.8 m^{-2} in enclosed sites.

There were no significant differences in density between control and enclosed sites.

4.3.4.12 *Polycelis tenuis* Ijima

The data comparing total mean density between control and enclosed sites are given in figure 4.93. No biomass data were collected for *P. tenuis*.

Density

In April 1981, the density was 26.4 m^{-2} in control sites and 25.2 m^{-2} in enclosed sites. The over-all trend was then downwards, reaching a nadir of 20.7 m^{-2} in control sites and 18.4 m^{-2} in enclosed sites in January 1982. The densities then rose to reach maximum levels of 40.9 m^{-2} in enclosed sites in May and 43.9 m^{-2} in control sites in June. The trend was then downwards and in March 1983, the density was 18.0 m^{-2} in control sites and 17.5 m^{-2} in enclosed sites.

There were no significant differences in density between control and enclosed sites.

4.3.4.13 *Polycelis nigra* Müller

The data comparing total mean density between control and enclosed sites are given in figure 4.94. No biomass data were collected for *P. nigra*.

Density

In April 1981, the density was 2.9 m^{-2} in control sites and 3.6 m^{-2} in enclosed sites. After dropping in enclosed sites, it then rose to a peak of 4.9 m^{-2} in control sites and 6.0 m^{-2} in enclosed sites in June.

The density then dropped until another rise from August, to reach peak levels of 4.4 m^{-2} in enclosed sites in September and 4.7 m^{-2} in control sites in October. In 1982, the density rose to a peak of 6.8 m^{-2} in control sites and 6.4 m^{-2} in enclosed sites in May and, thereafter, declined. By March 1983 the density was 1.4 m^{-2} in control sites and 1.1 m^{-2} in enclosed sites.

There were no significant differences in density between control and enclosed sites.

4.3.4.14 Dendrocoelum lacteum Müller

The data comparing total mean density between control and enclosed sites are given in figure 4.95. No biomass data were collected for D. lacteum.

Density

The density in April 1981, was 0.2 m^{-2} in both control and enclosed sites. It rose to a peak of 0.3 m^{-2} in control sites and 0.4 m^{-2} in enclosed sites in May and then decreased. The densities started rising again in October 1981 and there was a rapid rise between April and May 1982, when maximum levels of 1.3 m^{-2} in control sites and 1.2 m^{-2} in enclosed sites occurred. The density then dropped, and by March 1983 had reached 0.1 m^{-2} in control sites and 0.2 m^{-2} in enclosed sites.

There were no significant differences in density between control and enclosed sites.

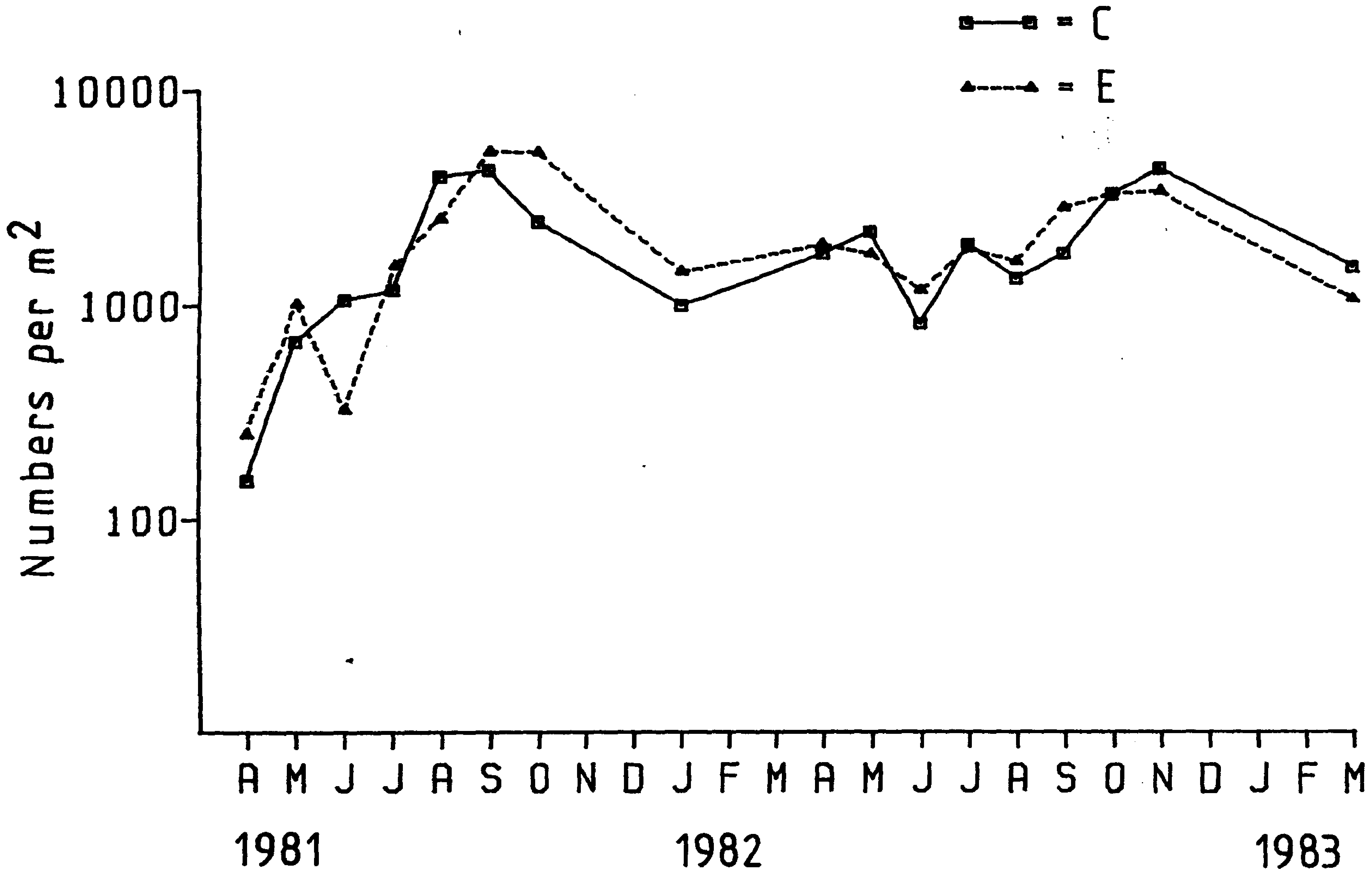


Figure 4.72. Oligochaetes. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

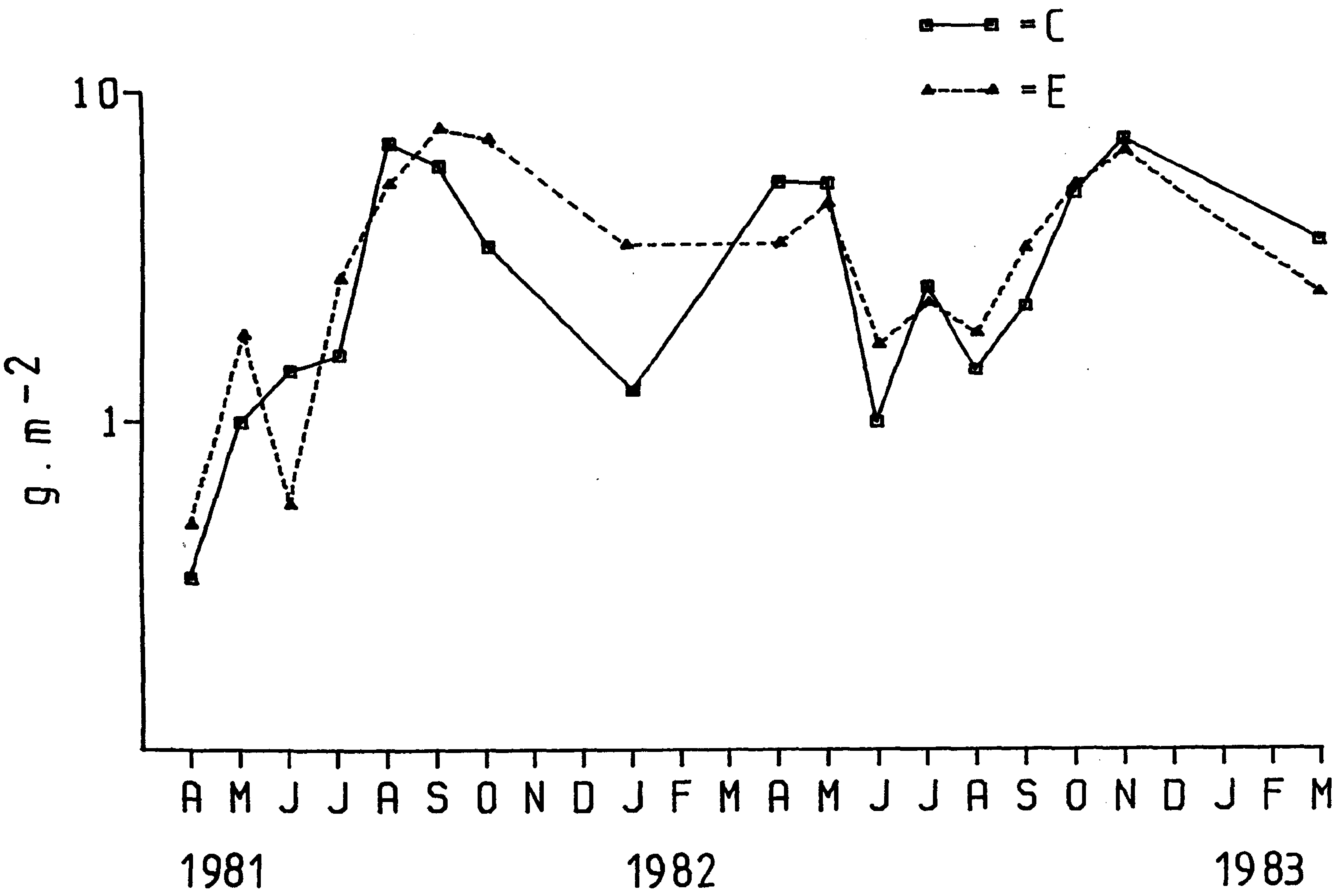


Figure 4.73. Oligochaetes. Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed (E) sites.

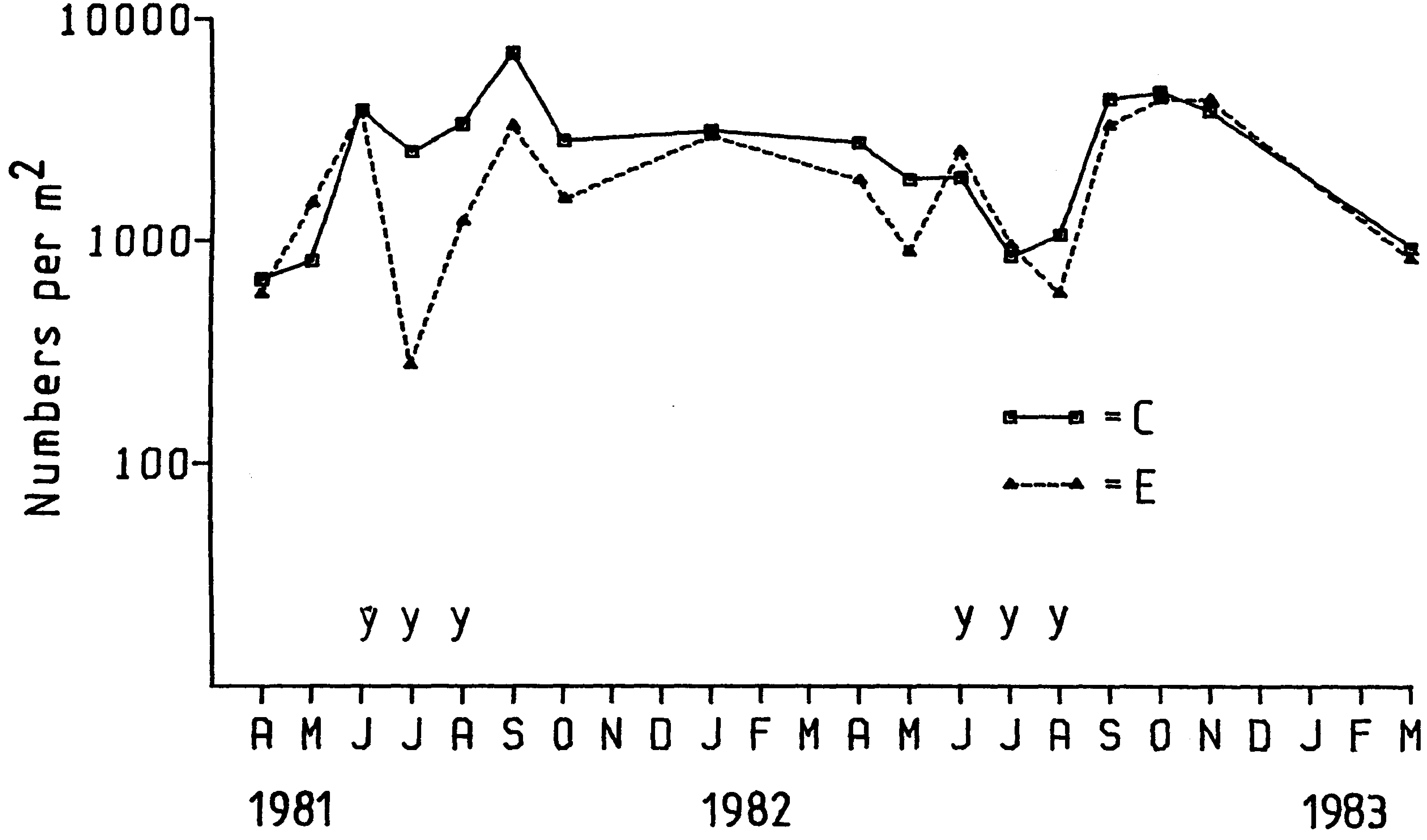


Figure 4.74. Chironomidae. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites and the months in which large numbers of small individuals (y) were present in samples.

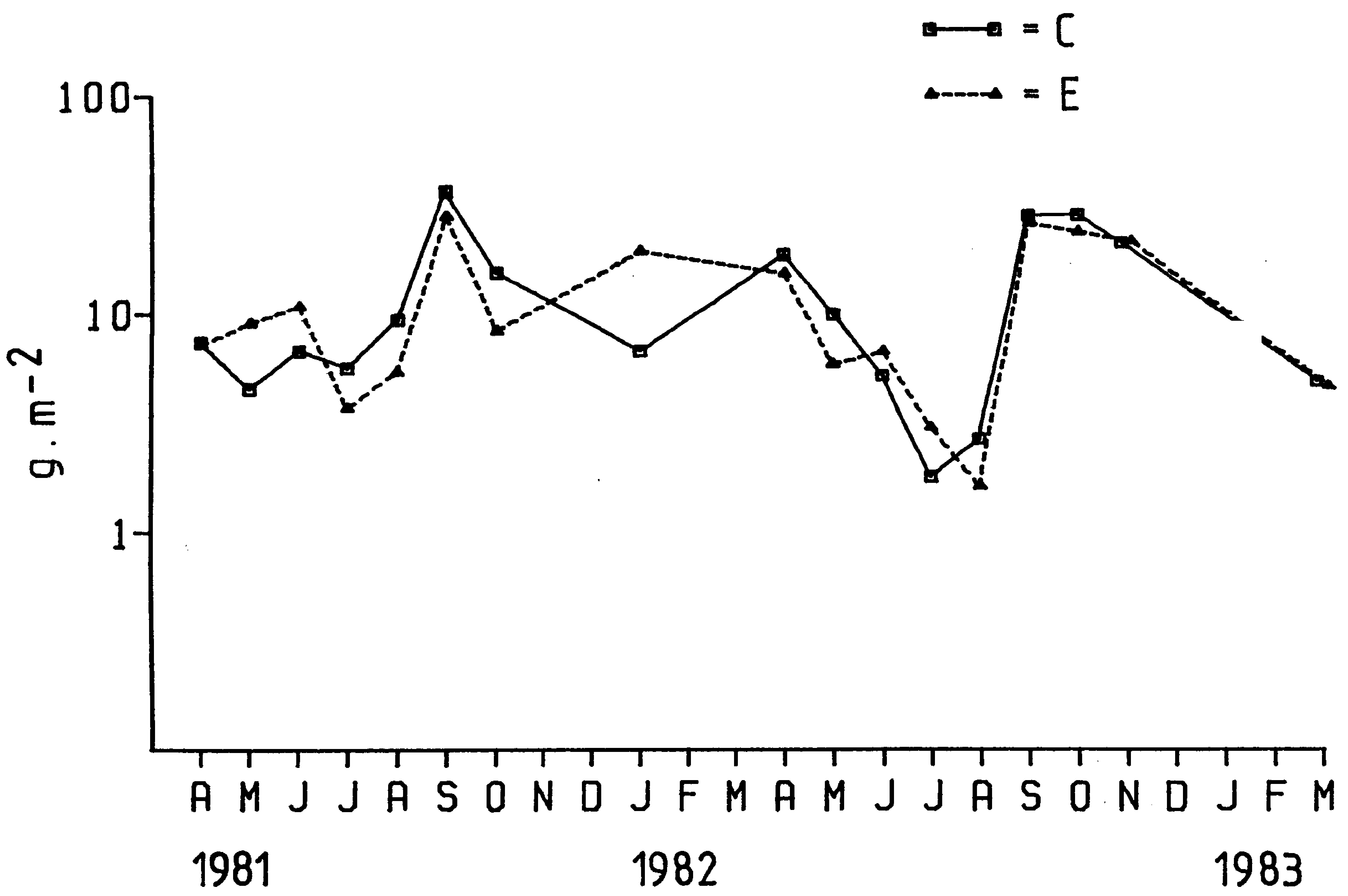


Figure 4.75. Chironomidae. Geometric mean biomass from combined stone and substratum sample data for control, (C) and enclosed (E) sites.

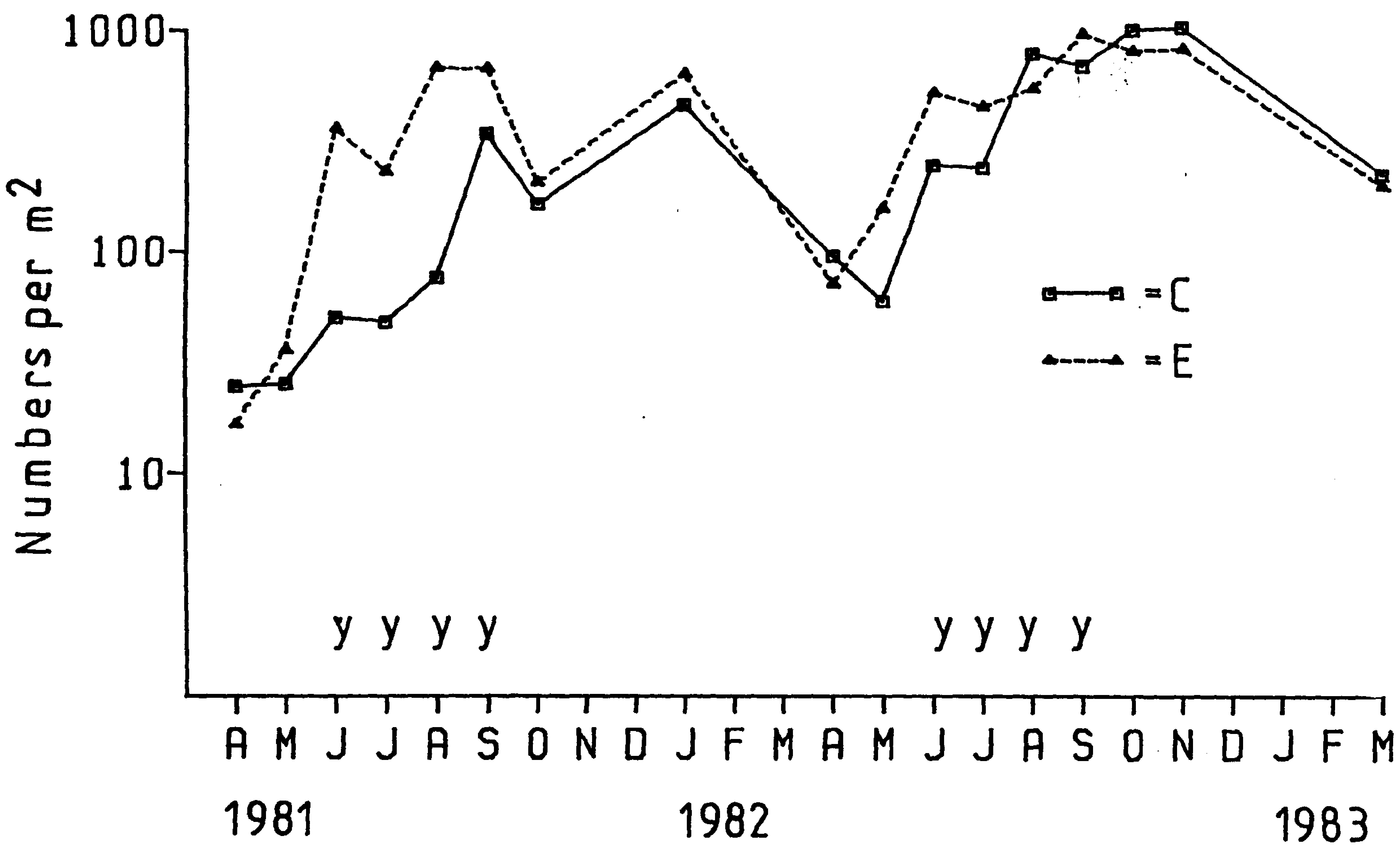


Figure 4.76. <u>Asellus spp</u>. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites and the months in which large numbers of small individuals (y) were present in samples.

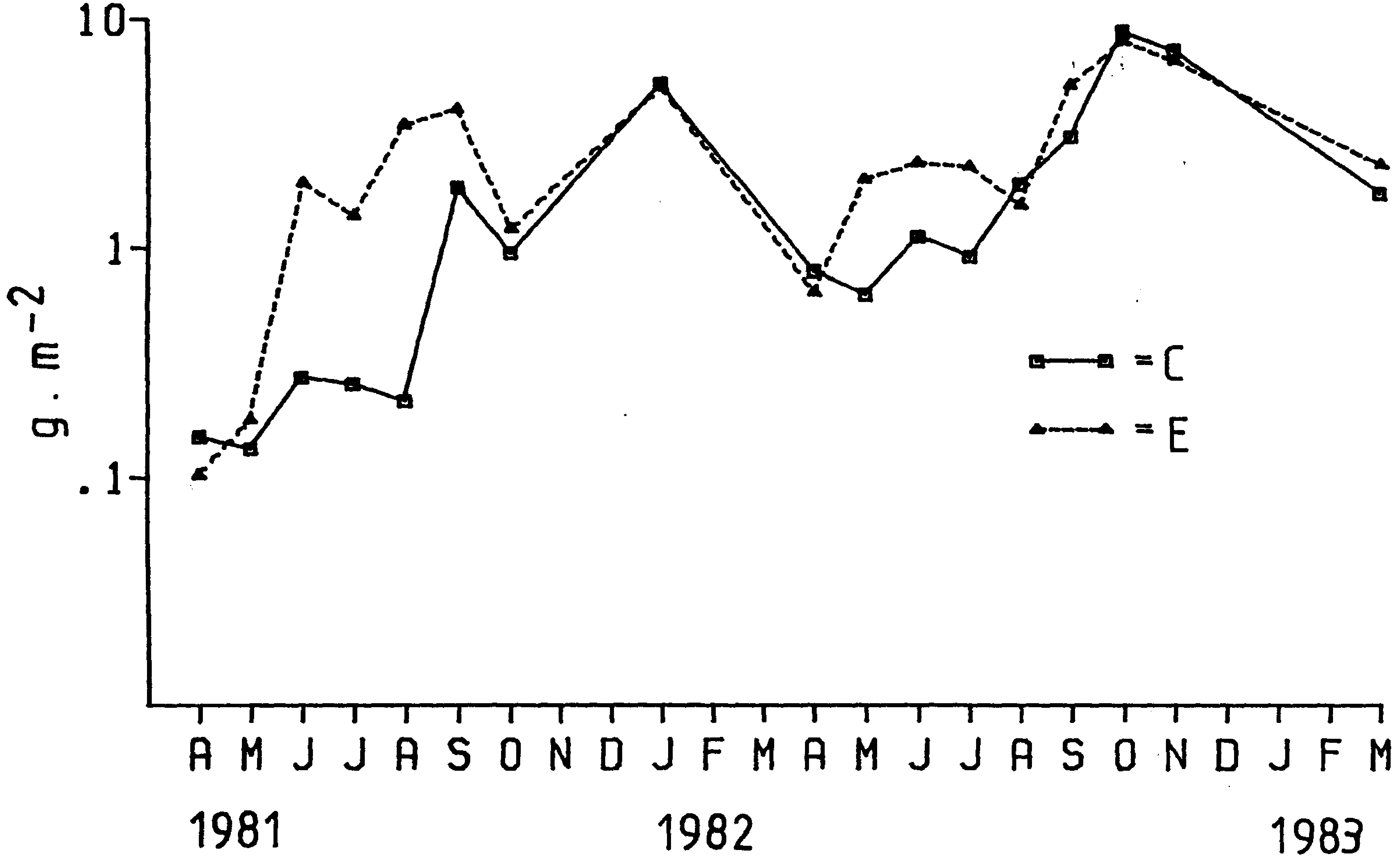


Figure 4.77. Asellus spp. Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed (E) sites.

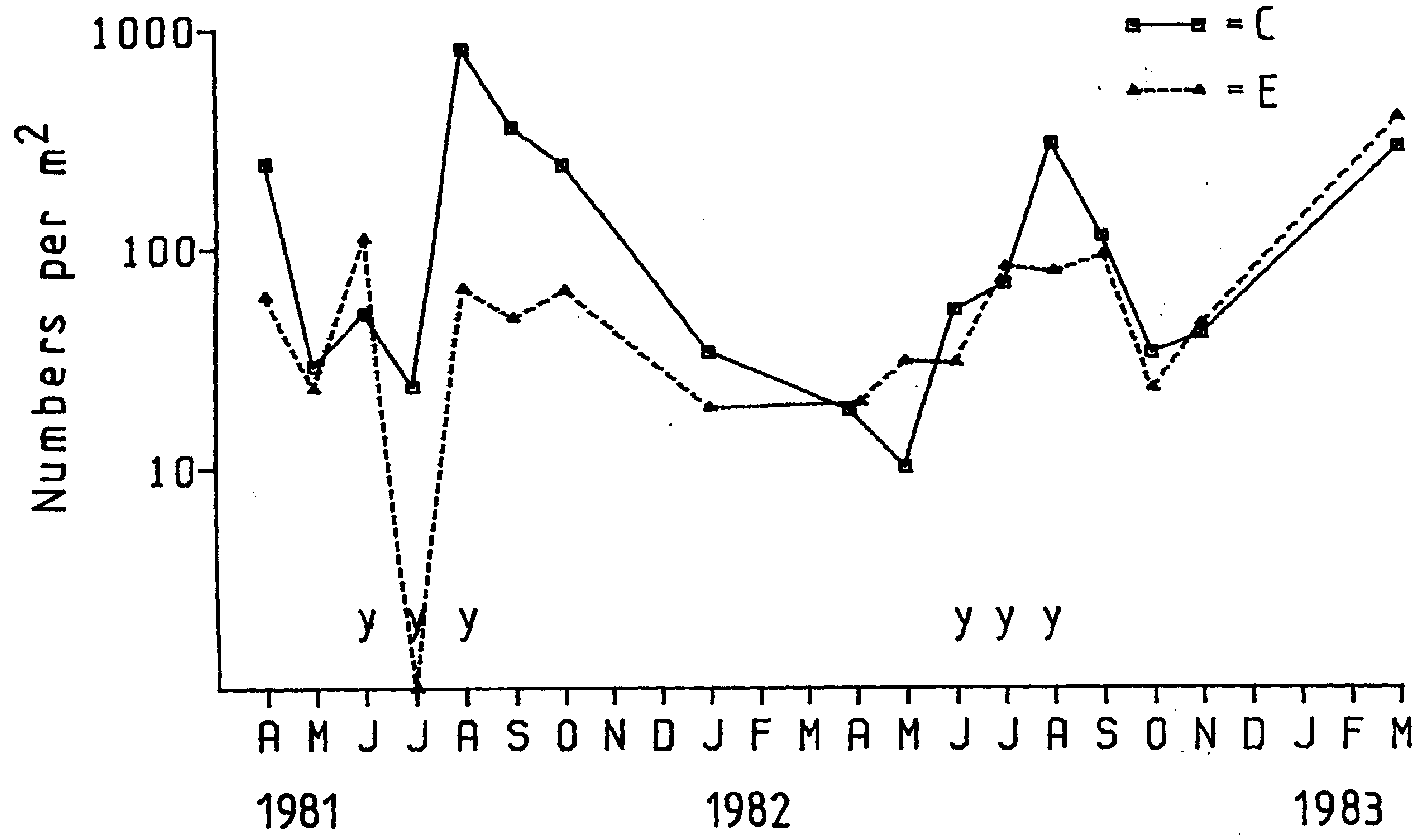


Figure 4.78. <u>Gammarus spp</u>. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites and the months in which large numbers of small individuals (y) were present in samples.

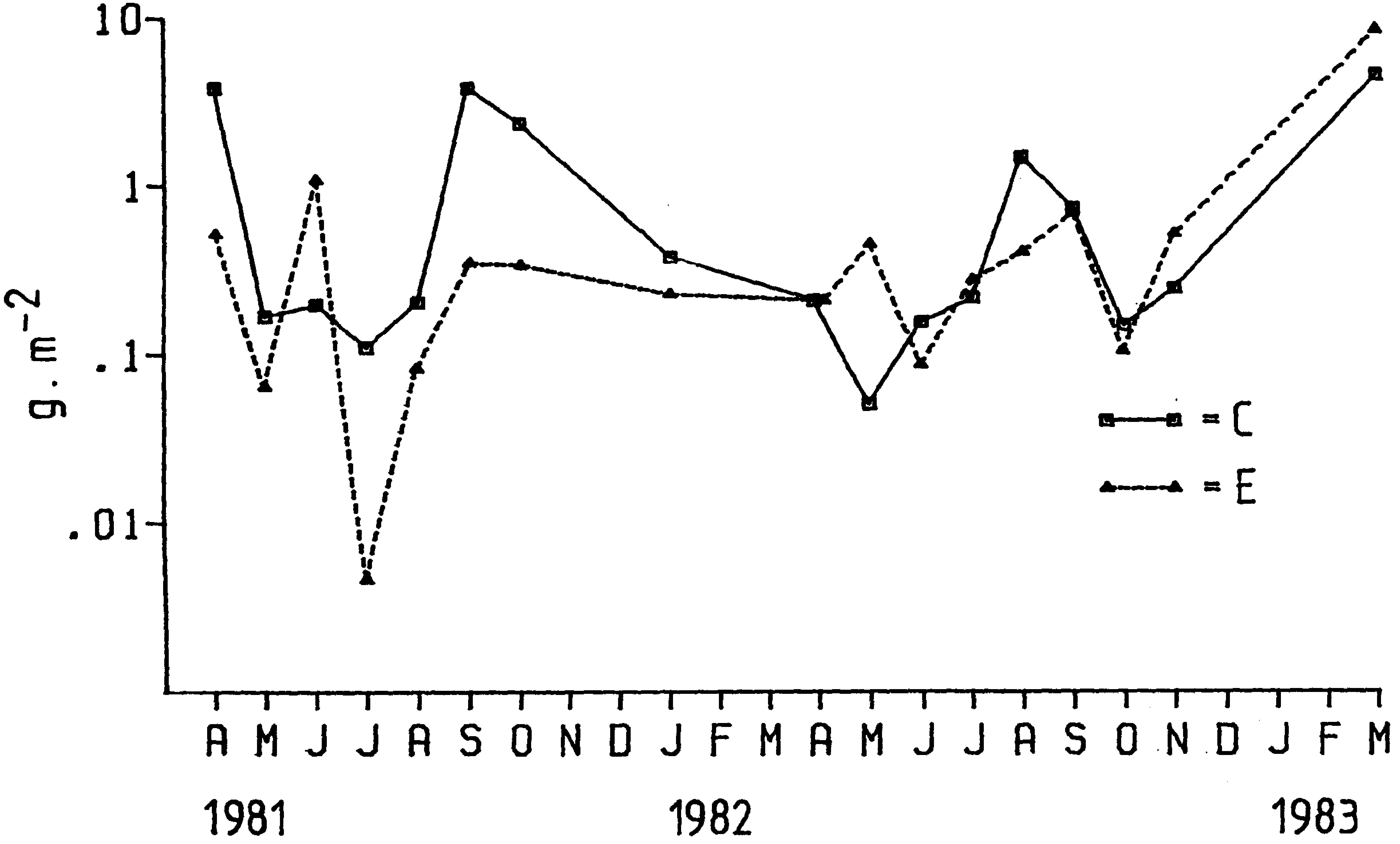


Figure 4.79. *Gammarus spp*. Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed (E) sites.

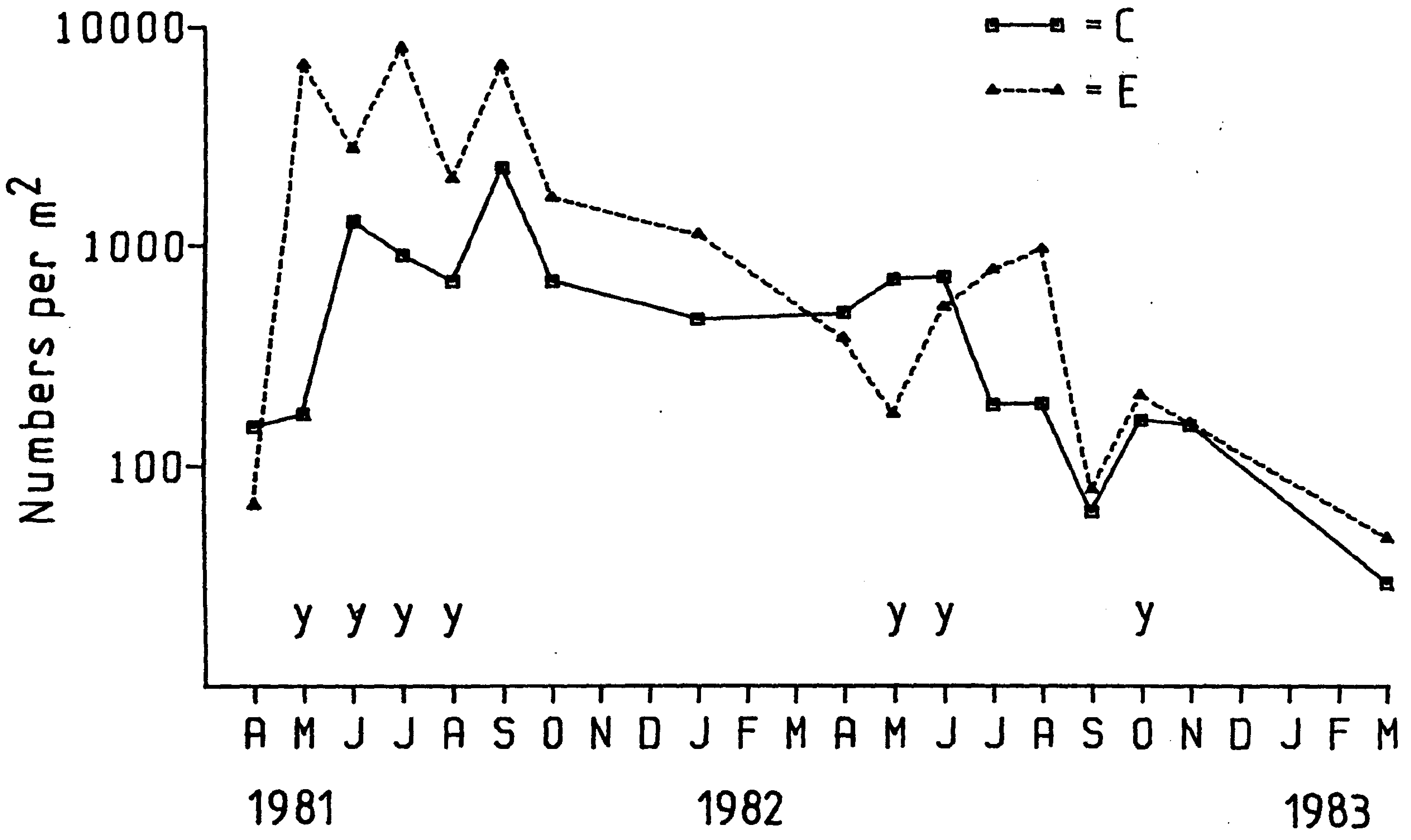


Figure 4.80. Potamopyrgus jenkinsi. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites and the months in which large numbers of small individuals (y) were present in samples.

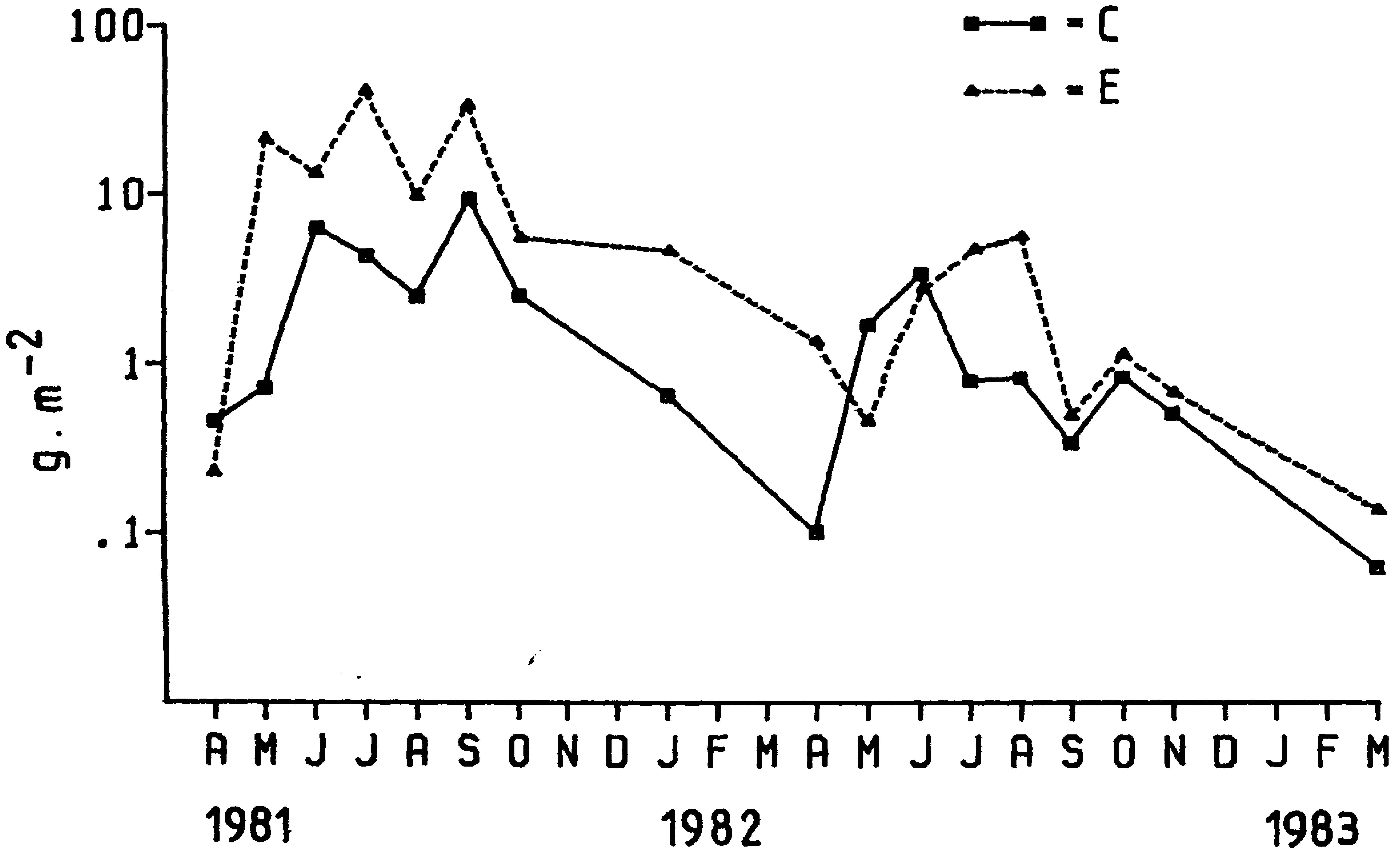


Figure 4.81. *Potamopyrgus jenkinsi*. Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed (E) sites.

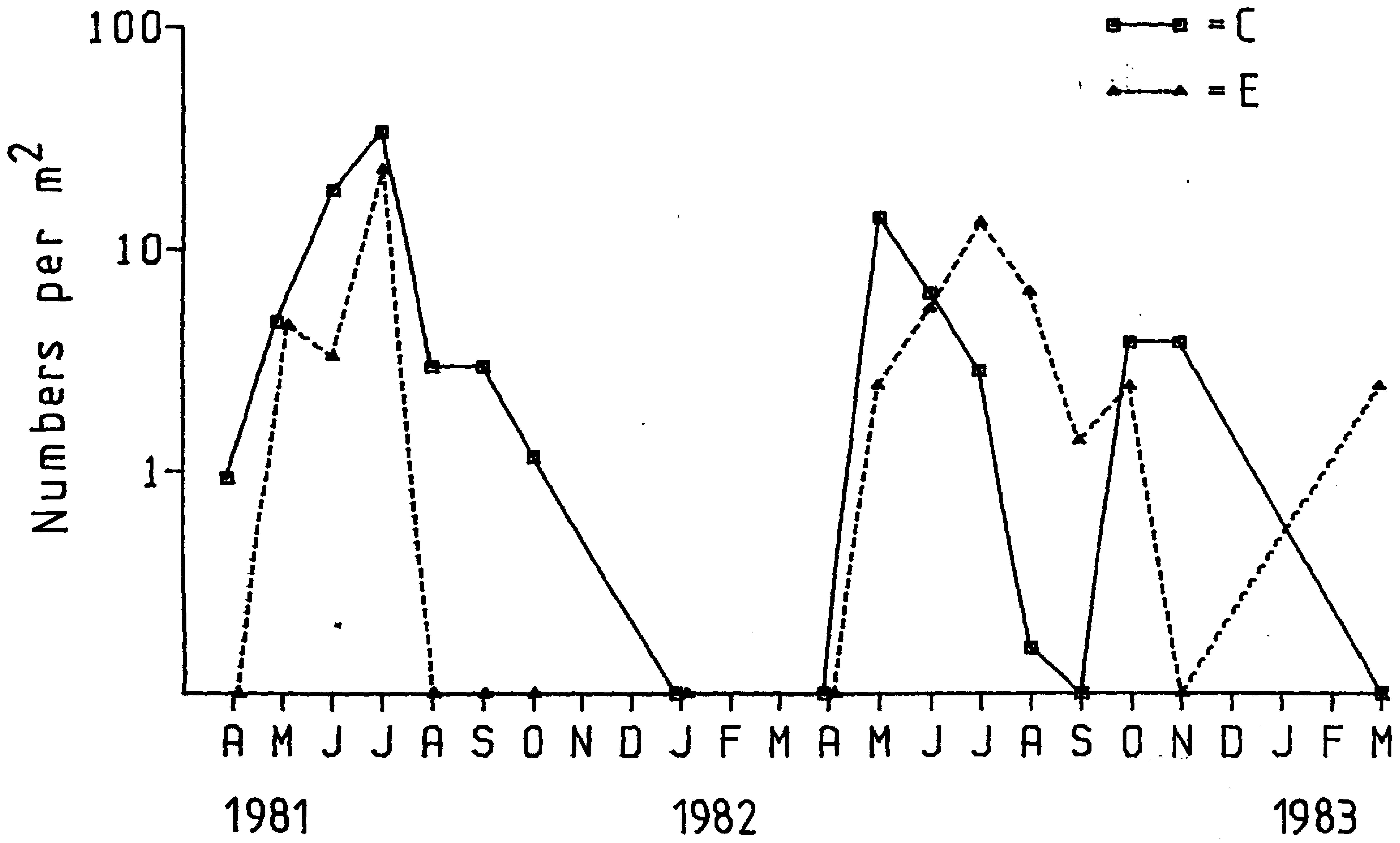


Figure 4.82. Bithynia tentaculata. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

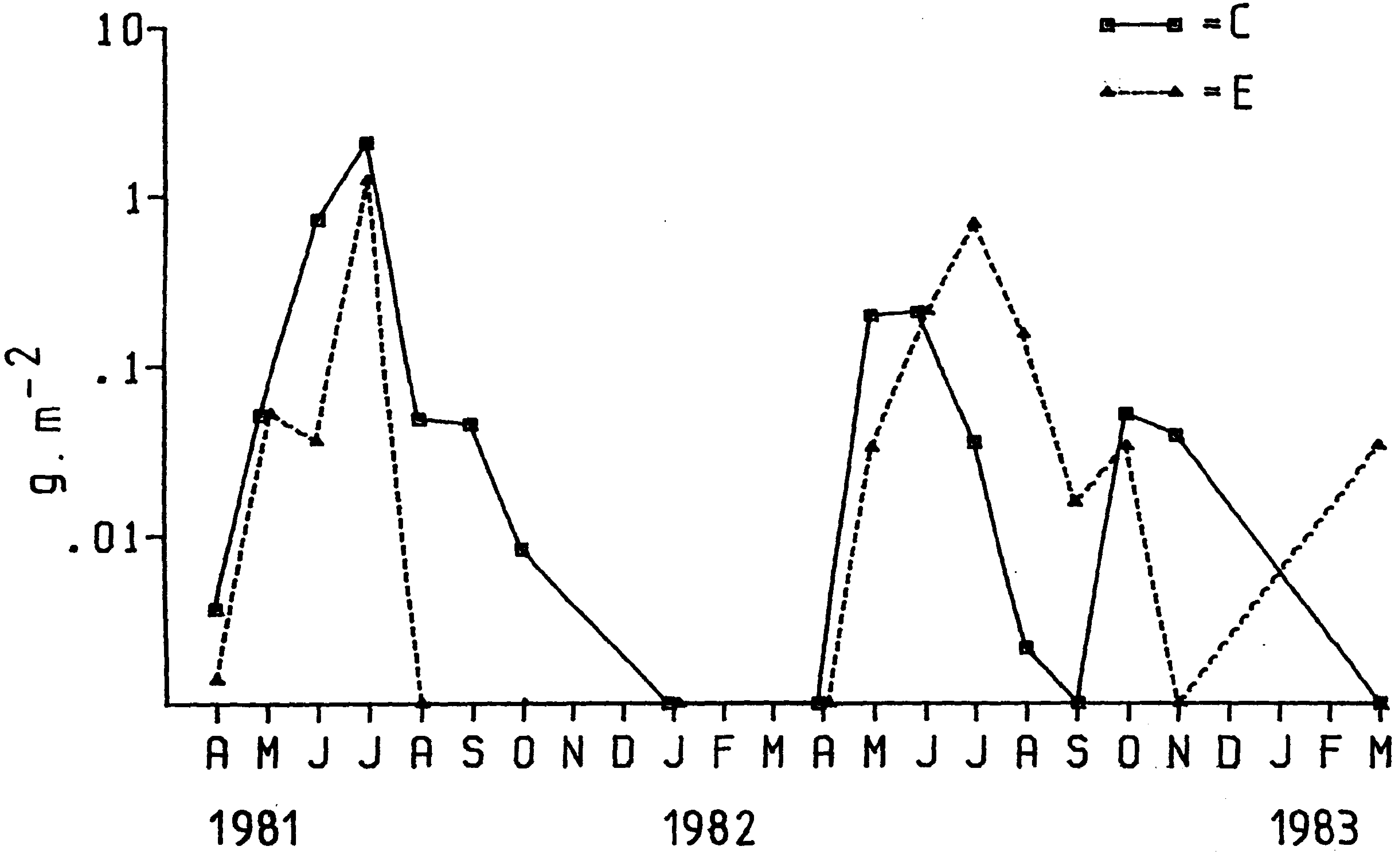


Figure 4.83. Bithynia tentaculata. Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed (E) sites.

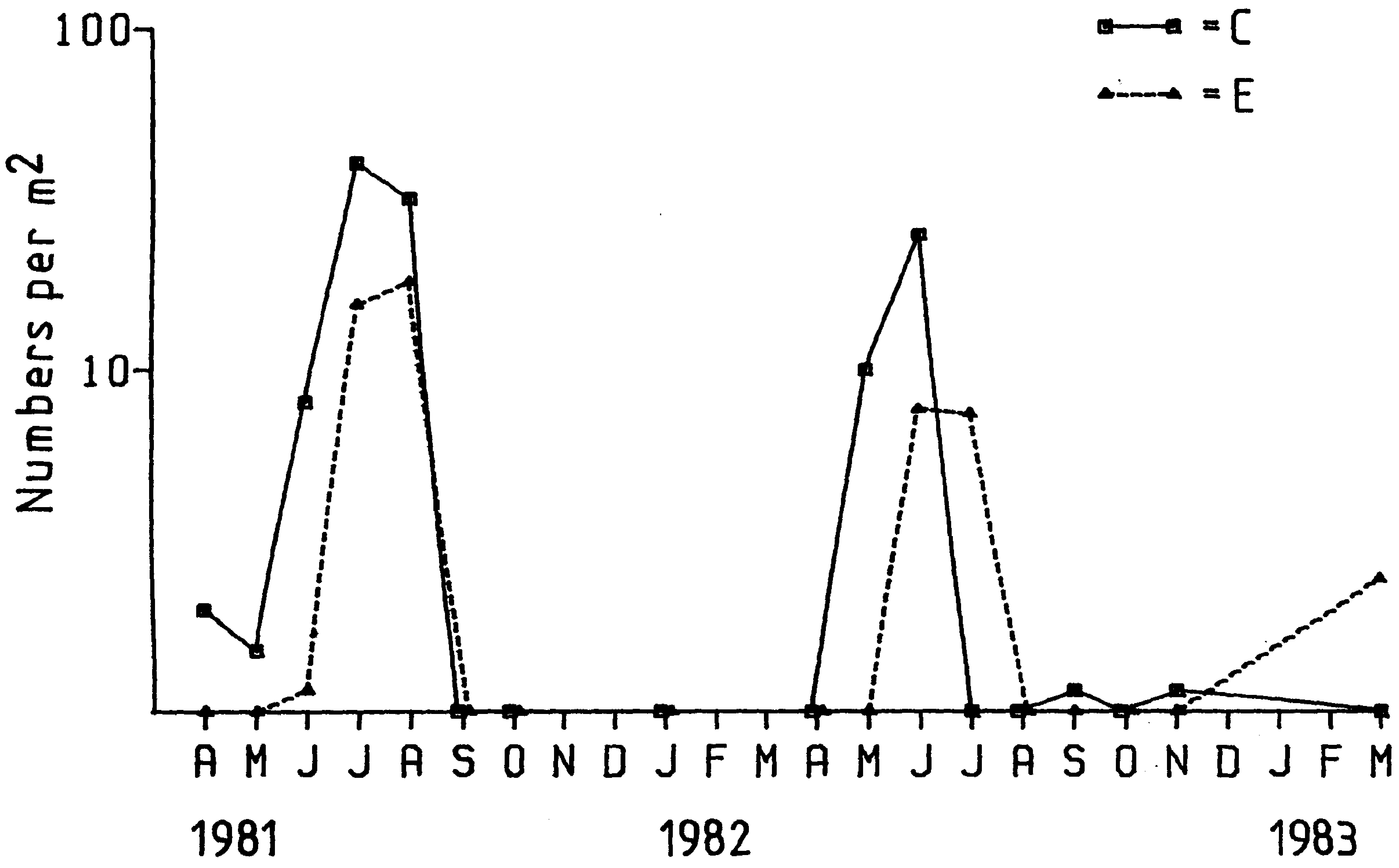


Figure 4.84. Valvata piscinalis. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

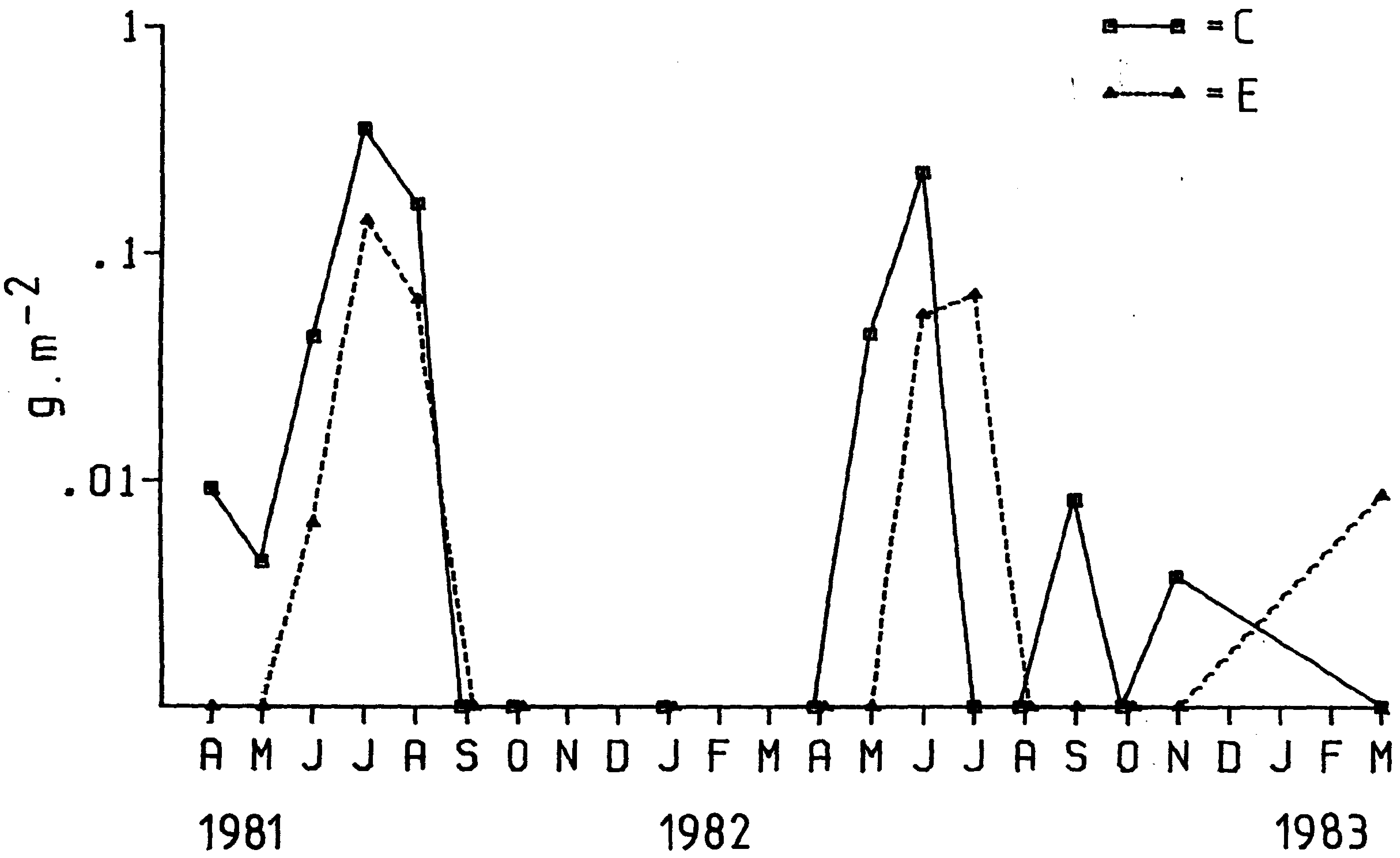


Figure 4.85. Valvata piscinalis. Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed(E) sites.

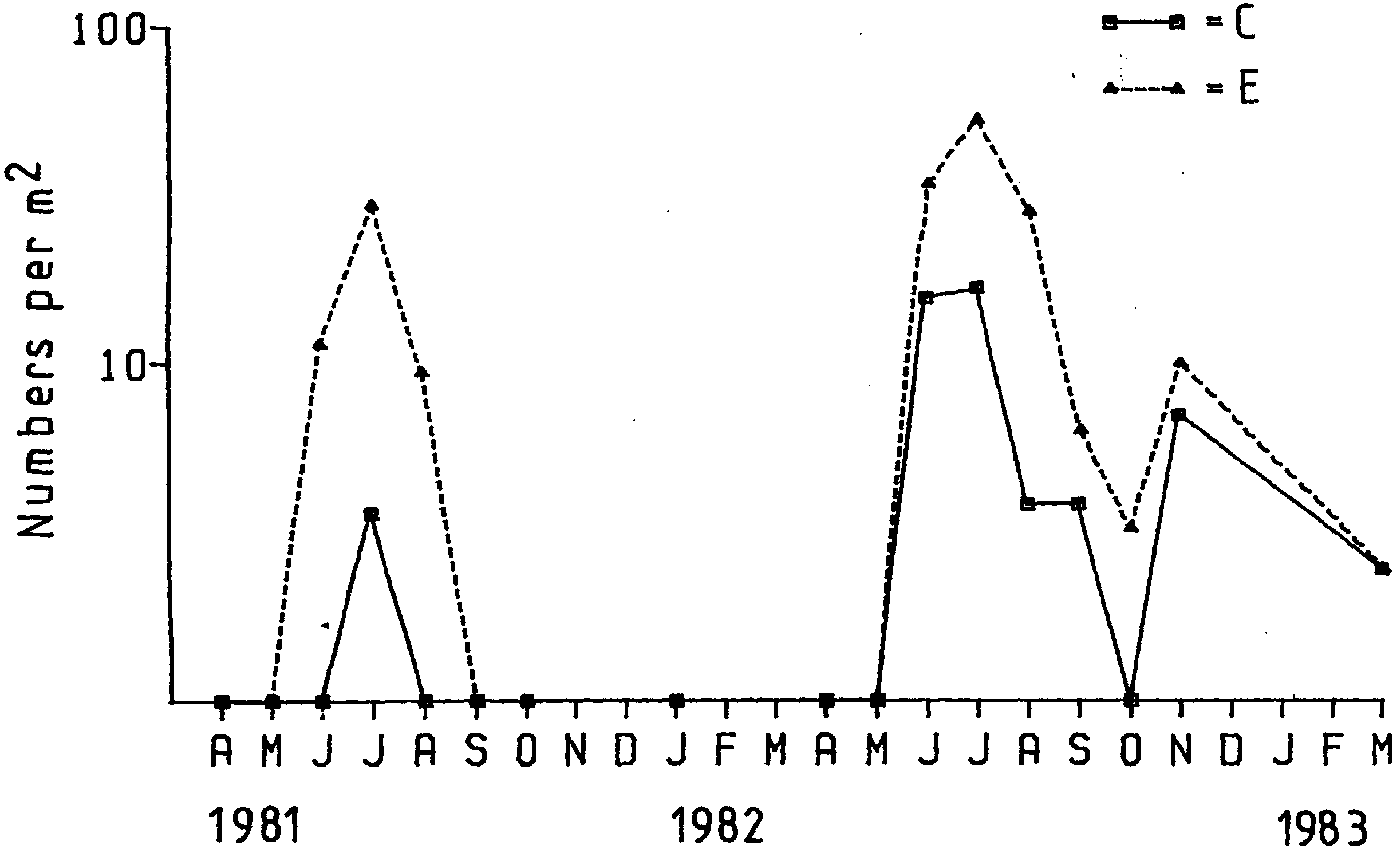


Figure 4.86. Sialis lutaria. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

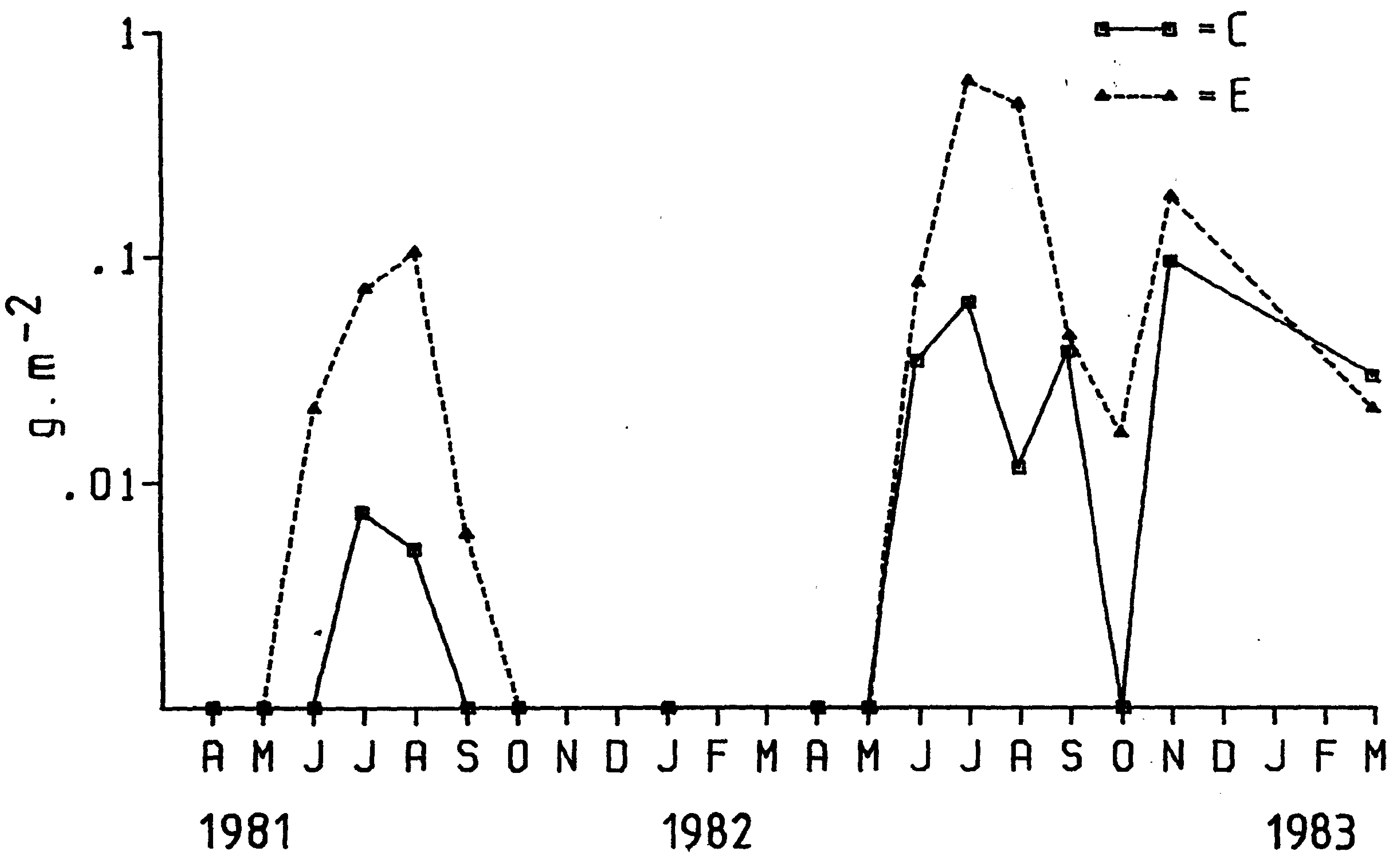


Figure 4.87. *Sialis lutaria.* Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed (E) sites.

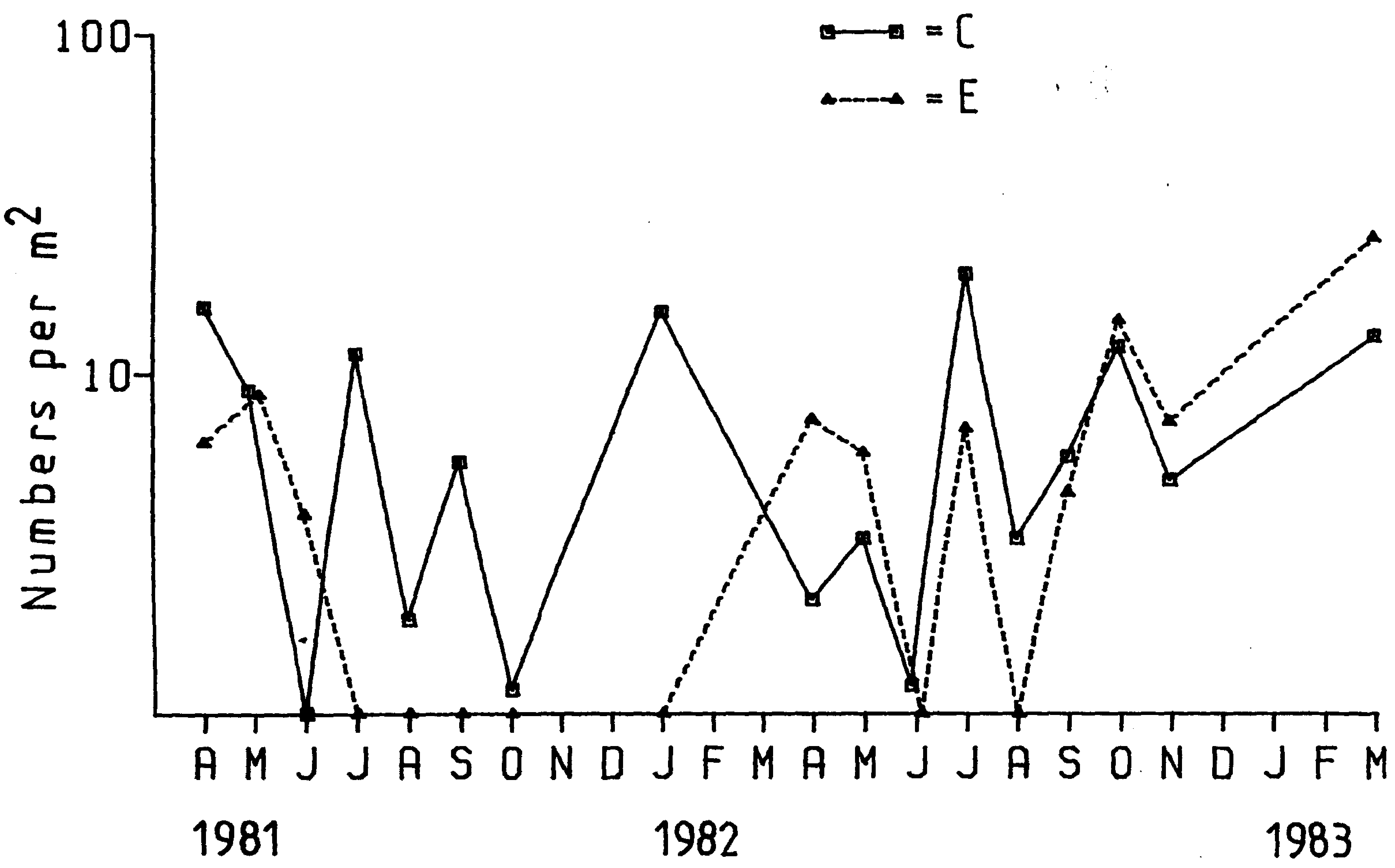


Figure 4.88. Tinodes waeneri. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

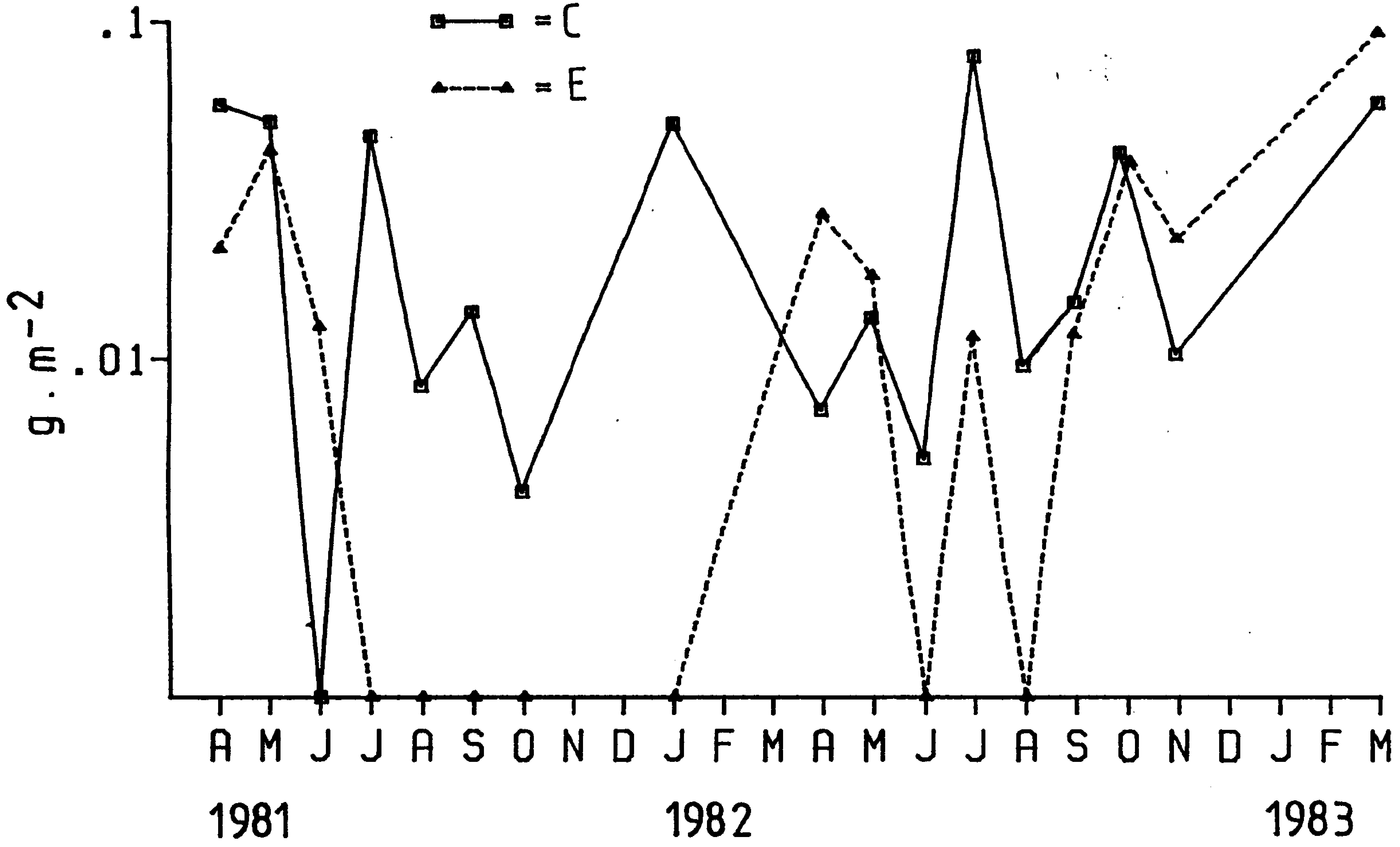


Figure 4.89. Tinodes waeneri. Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed (E) sites.

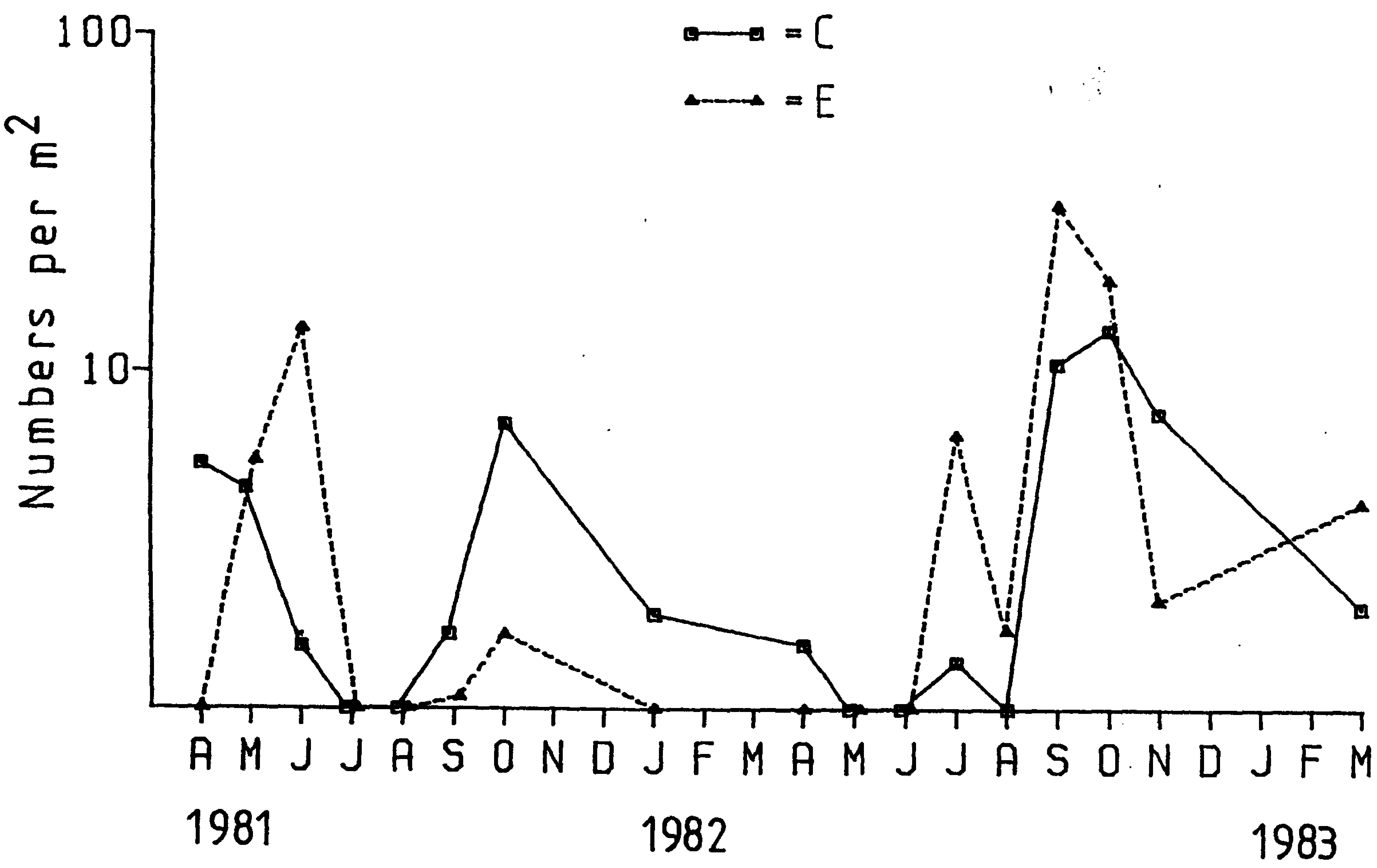


Figure 4.90. Leptocercidae. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

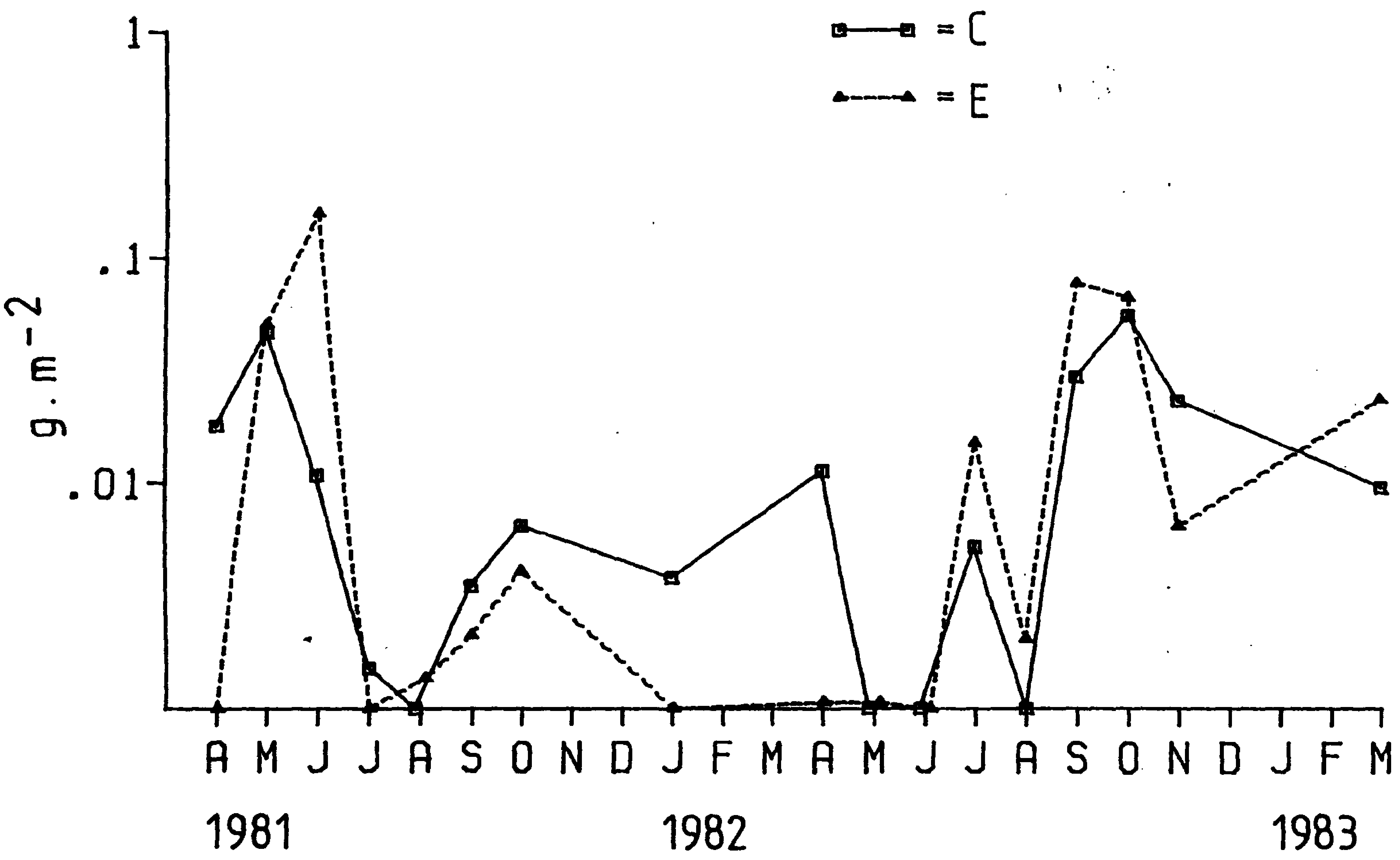


Figure 4.91. Leptocercidae. Geometric mean biomass from combined stone and substratum sample data for control (C) and enclosed (E) sites.

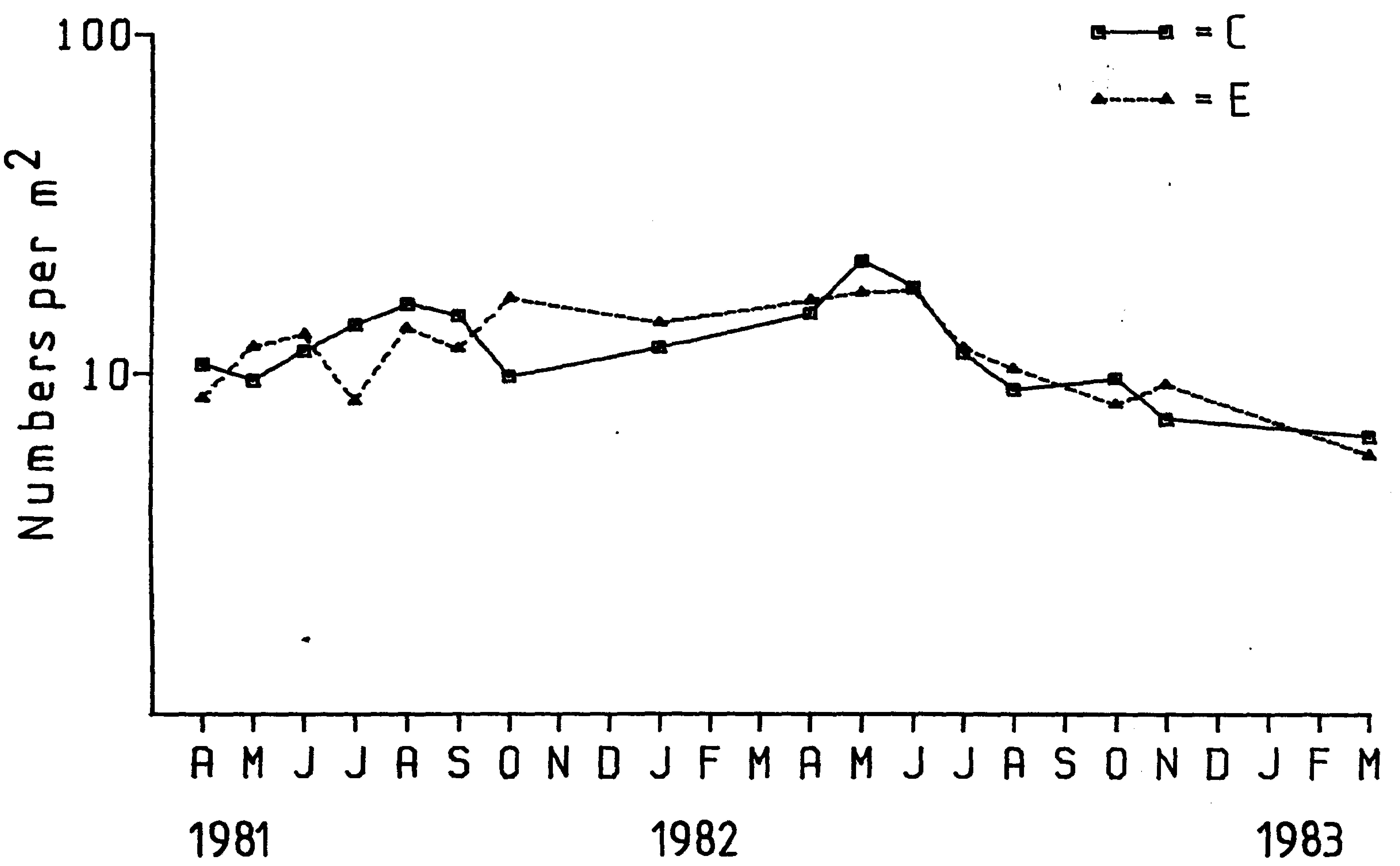


Figure 4.92. Dugesia polychroa. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

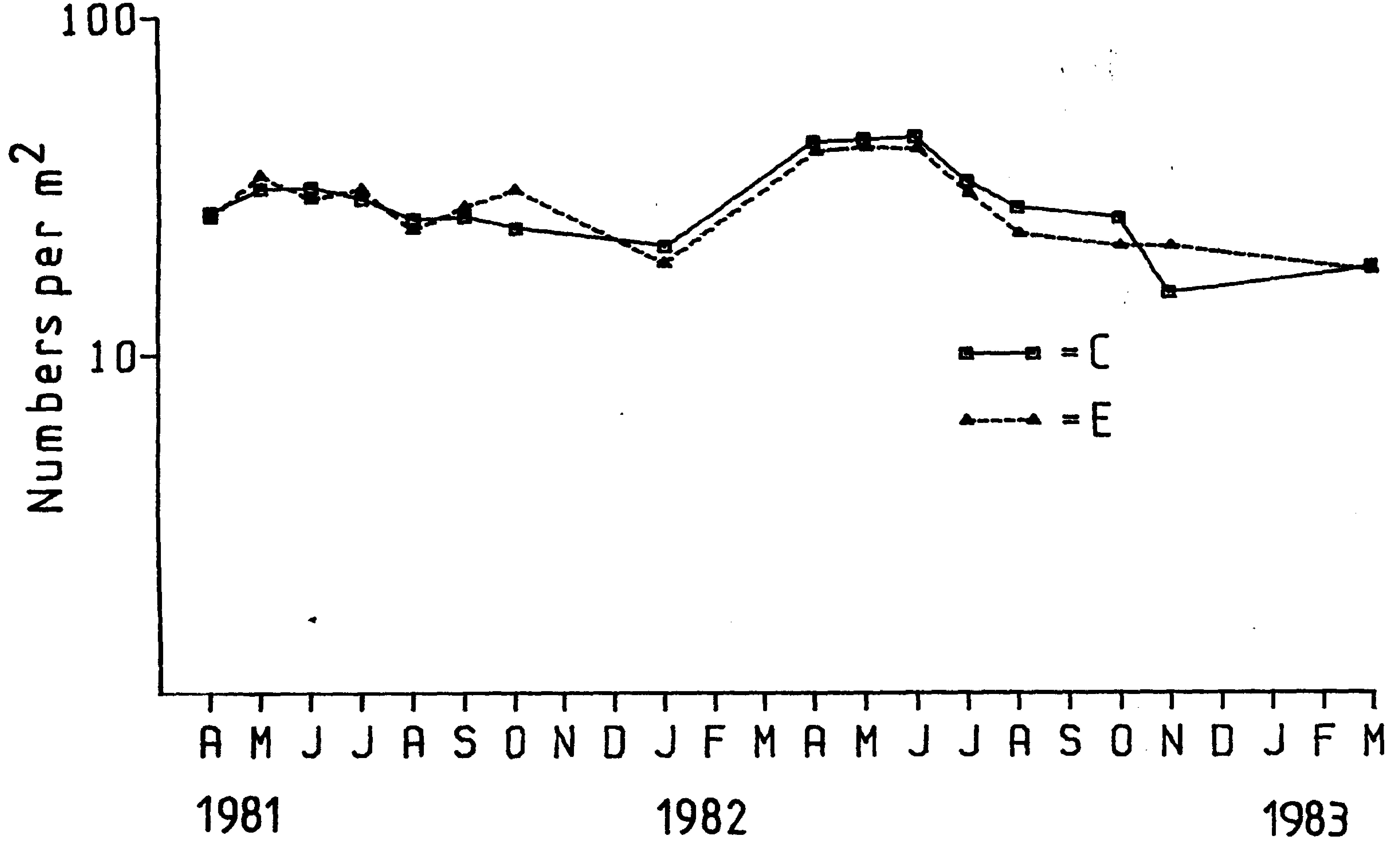


Figure 4.93. Polycelis tenuis. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

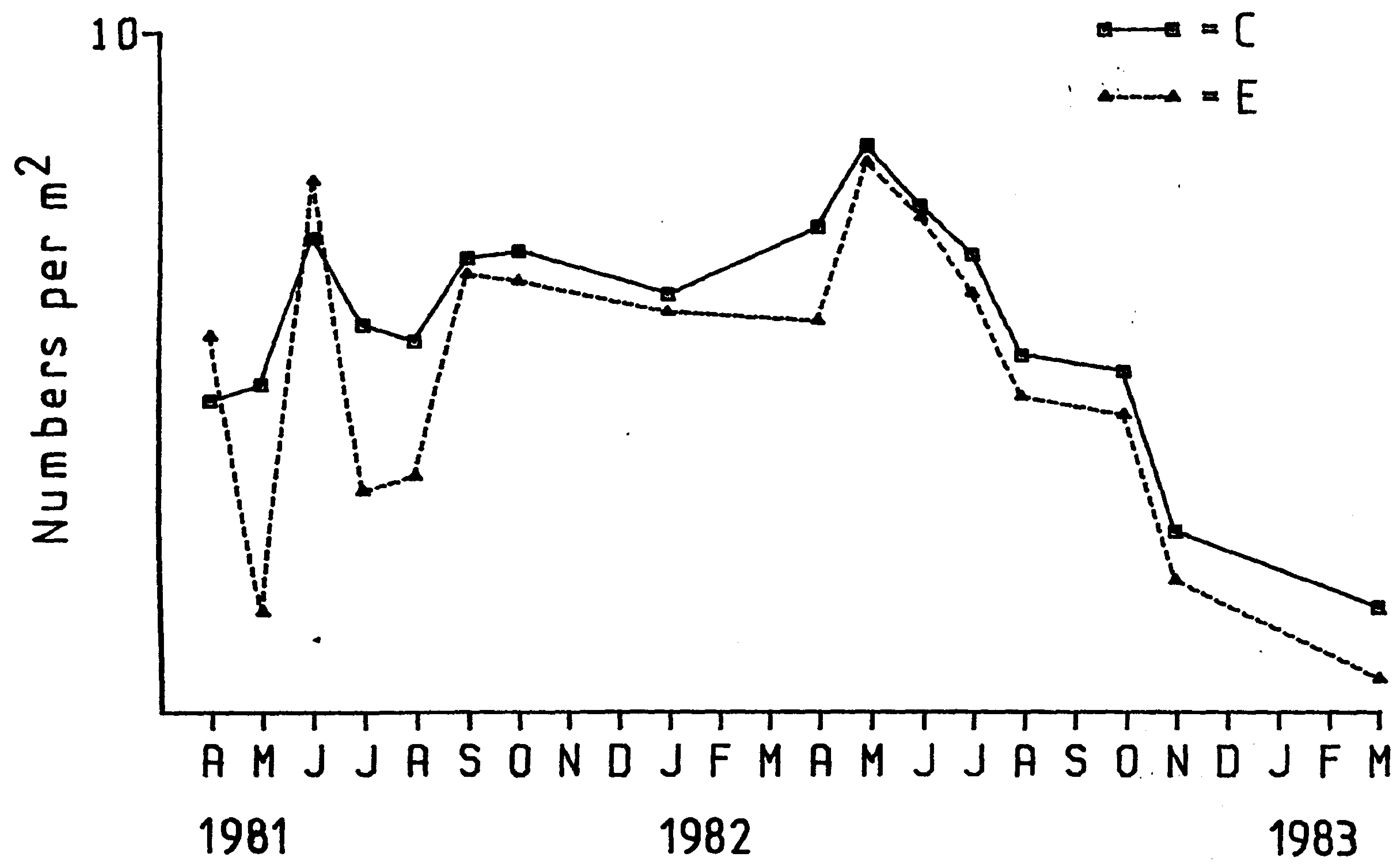


Figure 4.94. Polycelis nigra. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

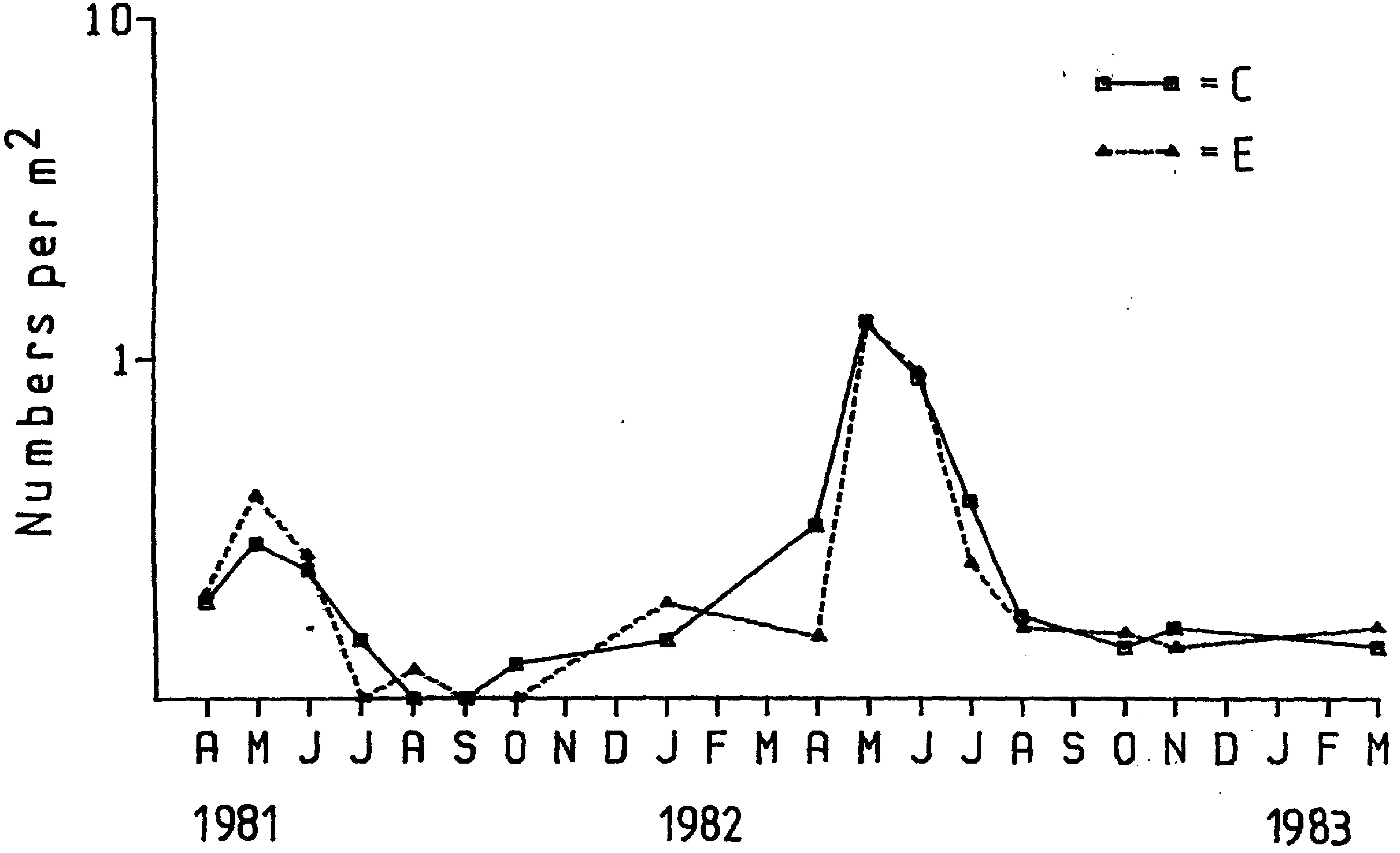


Figure 4.95. Dendrocoelum lacteum. Geometric mean density from combined stone and substratum sample data for control (C) and enclosed (E) sites.

Table 4.23. The occurrence of the rarer groups recorded in samples from control (C) and enclosed (E) sites (+ = < 10; ++ = > 10 individuals present).

		1981							1982									1983
		Apr	May	June	July	Aug	Sep	Oct	Jan	Apr	May	June	July	Aug	Sep	Oct	Nov	Mar
Phylum Nematoda	C	++	+	+	+	+				+	++		+	+	+		+	
	E	+	+	+	++					+	++	+	+	+		+		+
Phylum Mollusca Class: Gastropoda Sub-class: Pulmonata																		
Acroloxus lacustris (L.)	C	+																
	E														+			
Lymnaea peregra (Müll.)	C	+	+	+		+	+	+	+	+		+					+	
	E										+	+	+	+	+	+		+
Lymnaea stagnalis (L.)	C														+			
	E																	
Physa fontinalis (L.)	C			+		+										+	+	
	E													+	+	+		+
Planorbis spp.	C		+	+	+	+	+	+			+	+	+	+	+	+	+	
	E		+			+		+			+	+	+	+	++	+	+	+
Class: Lamellibranchia																		
Pisidium spp.	C	++	++	++	+		++	+	++	++	++	+	+	++	+	+	+	
	E	+	++	++					++	++	++		+	++	+	+	+	+
Sphaerium spp.	C		+	++	+	+	+	+	+	+	+	+	+	++	+			
	E	+	+	++	++		+	+	+	+			+		+	+		

Continued

		1 9 8 1							1 9 8 2									1983
		Apr	May	June	July	Aug	Sep	Oct	Jan	Apr	May	June	July	Aug	Sep	Oct	Nov	Mar
Phylum Annelida Class: Hirudinea																		
<u>Haemopsis sanguisuga</u> (L.)	C	+	+								+							+
	E	+							+	+	+							+
<u>Glossiphonia heteroclita</u> (L.)	C	+	+	++	+	+	+	+		+	+	+	+	+	+	+		
	E	+	+	+	+	+	+			+		+	+	+	+	+		+
<u>Hemiclepsis marginata</u> (Müll.)	C			+		+	+				+							
	E								+		+	+						
<u>Theromyzon tessulatum</u> (Müll.)	C	++	++	++	++	++	++	++	++	+	+	++	++	++	++	++	++	+
	E	+	+	+	+	++	++	++	++	+	+	++	++	++	++	++	++	++
Phylum Arthropoda Class: Insecta Order: Ephemeroptera																		
<u>Caenis horaria</u> (L.)	C	++	++	+													+	
	E		+	+													+	
Order: Hemiptera Family: Nepidae																		
<u>Nepa cinerea</u> (L.)	C																	
	E												+					
Order: Trichoptera Family: Limnephilidae																		
Spp. indetermined	C	+	+	+		+		+	+	+			+		+		+	+
	E						+								+	+	+	+
Family: Goeridae																		
<u>Goera pilosa</u> (Faber)	C	++	+				+	+	+	+			+		+	+	+	+
	E		+							+						+		

Continued

		1981							1982										1983
		Apr	May	June	July	Aug	Sep	Oct	Jan	Apr	May	June	July	Aug	Sep	Oct	Nov	Mar
Family: Polycentropidae																		
<u>Polycentropus flavomaculatus</u> (Pict.)	C																	+
	E												+			+	+	+
Order: Coleoptera Family: Haliplidae																		
<u>Haliplus sp</u>. (adult)	C				+	+	+					+						
	E						+	+			+	+						
<u>Haliplus sp</u>. (larvae)	C	+							+					+	+	+	+	
	E						+											
Family: Dytiscidae																		
Spp. indetermined (adult)	C		+	+	+	+	+	+						+	+		+	+
	E			+				+									+	+
Spp. indetermined (larvae)	C			+	++							+						
	E			+														
Family: Elmidae																		
<u>Oulimnius sp</u>	C			+													+	
	E																	
Order: Diptera Family: Ceratopogonidae	C	+	+	+			+		+	+	+							+
	E	+	+	+					+		+	+						
Family: Ptychopteridae	C																	
	E																+	

Continued

		1981							1982									1983
		Apr	May	June	July	Aug	Sep	Oct	Jan	Apr	May	June	July	Aug	Sep	Oct	Nov	Mar
Family: Psychodidae	C																	
	E	+																
Family: Tipulidae	C			+		+			+		+							
	E										+				+			+
Phylum Chelicerata Class: Arachnida Order: Hydracarina	C				++													
	E				+													

4.3.5 Physico-chemical data

4.3.5.1 Water analysis

The data obtained from the environmental multi-probe (see section 4.2.2), and comparing control and enclosed sites are given in table 4.24.

In 1981, only three measurements of temperature and conductivity were made using the multiprobe. The maximum temperature difference between control and enclosed sites was just 0.4°C. The conductivity ranged from 35.2 x 10^{-5} ohms^{-1} to 39.0 x 10^{-5} ohms^{-1} and the maximum difference between control and enclosed sites just 0.8 x 10^{-5} ohms^{-1} in both April and May. In 1982, the maximum temperature difference between control and enclosed sites was 1.0°C in July. Mean conductivity ranged between 25.1 x 10^{-5} ohms^{-1} to 40.0 x 10^{-5} ohms^{-1} in control sites and between 26.6 x 10^{-5} ohms^{-1} to 39.8 x 10^{-5} ohms^{-1} in enclosed sites. The maximum difference between control and enclosed sites was 1.5 x 10^{-5} ohms^{-1} in both April and July, and in these cases, the conductivity was higher in enclosed sites. The pH ranged between 7.9 - 9.0 in control sites and between 8.0 - 8.9 in enclosed sites and the maximum difference between them was 0.2 in July. The concentration of dissolved oxygen ranged between 11.0 - 14.8 ppm in control sites and between 9.0 - 17.4 ppm in enclosed sites. The maximum difference between control and enclosed sites was just 2.6 ppm in April.

4.3.5.2 Particle-size analysis

The results of particle-size analyses for substratum samples taken from each bay in 1983 are given in figure 4.96. The size-frequency distribution of the larger stones overlying the substratum, sampled from each bay in 1983, are given in figure 4.97.

In the substratum samples, the particle-size distribution is clearly bimodal, with peaks in the pebble and fine sand ranges of the Wentworth scale. Although there is some variation between the bays, there is little over-all difference between control and enclosed sites. For the larger stones, the modal value for stone bottom surface area was in the range 60 - 99 cm^2 for all bays except by 7, which had a higher frequency of larger stones.

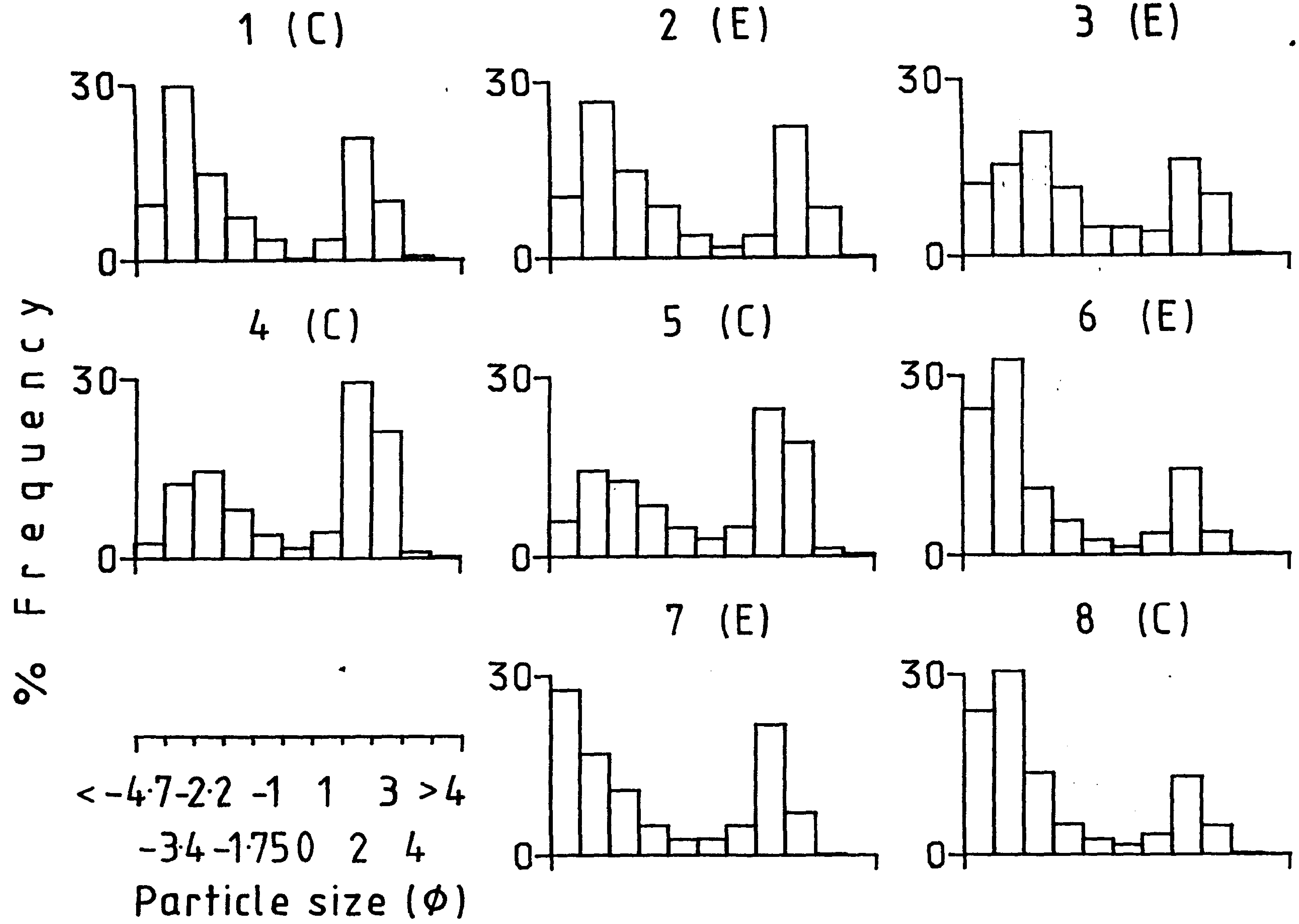


Figure 4.96. The particle-size distribution in substratum samples taken from each bay in 1983. Control (C) and enclosed (E) sites.

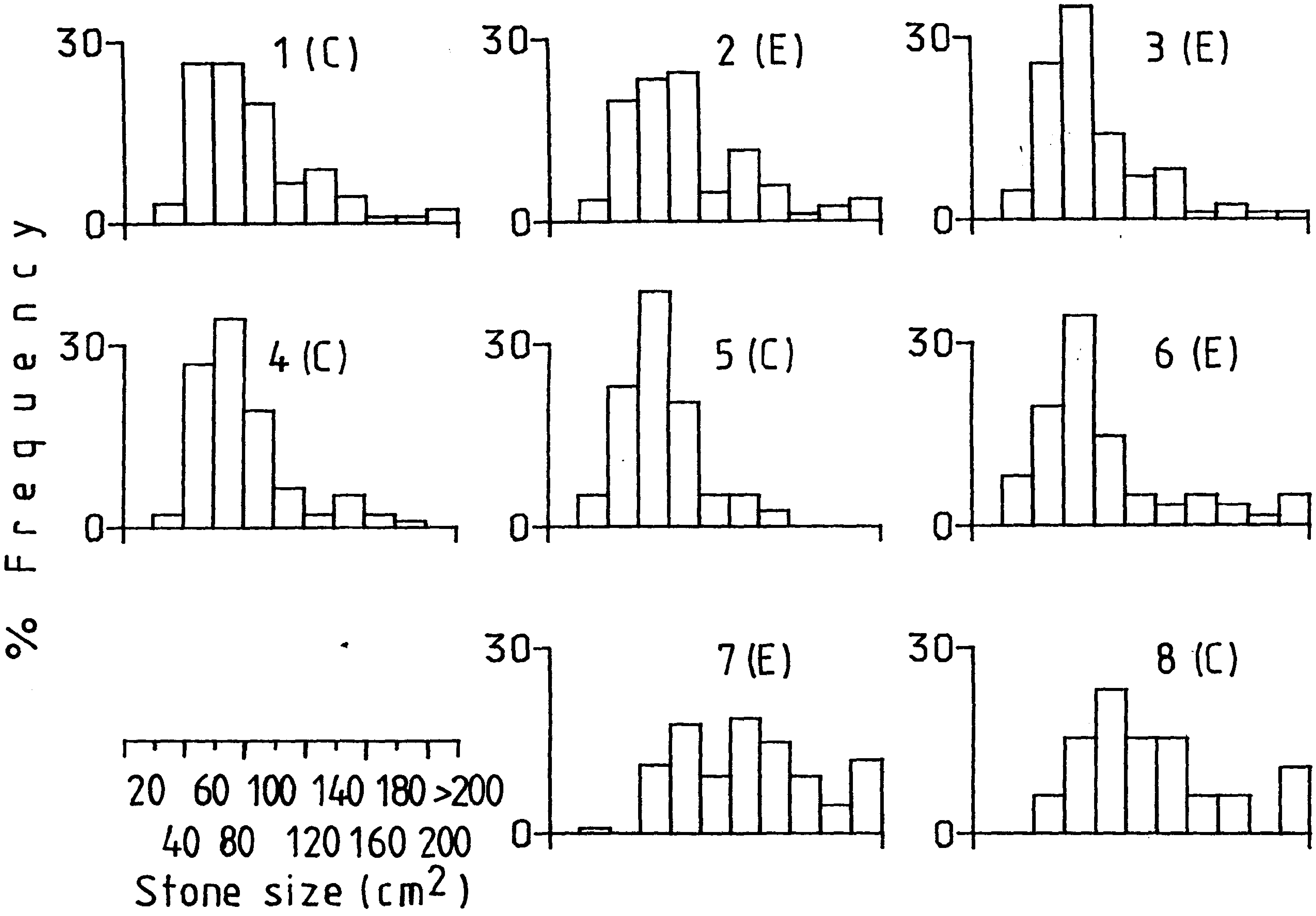


Figure 4.97. The range of stone sizes present in each bay from data collected in 1983. Control (C) and enclosed (E) sites.

Table 4.24. Physico-chemical data for water samples from Crose Mere in control (C) and enclosed (E) sites.

		Temp (^oC)	Conductivity ($ohms^{-1}. 10^{-5}$)	pH	Dissolved oxygen (ppm)
1981					
8th April	C	9.9	35.2	-	-
	E	9.8	36.0	-	-
28th April	C	8.5	36.0	-	-
	E	8.5	36.0	-	-
10th May	C	11.4	38.2	-	-
	E	11.8	39.0	-	-
1982					
22nd April	C	15.3	28.8	7.9	14.8
	E	15.1	30.3	8.0	17.4
2nd June	C	19.8	34.8	-	-
	E	19.4	35.3	-	-
24th June	C	15.9	33.5	9.0	11.0
	E	15.6	32.8	8.9	9.0
28th July	C	19.5	25.1	8.6	13.1
	E	18.5	26.6	8.8	11.6
23rd September	C	15.0	40.0	8.4	-
	E	14.6	39.8	8.4	-

4.4 Discussion

In this section, the basic ecological information for each leech species is discussed first, followed by a discussion of the effects of the enclosures on that species. The effects of the enclosures on the other invertebrate groups present and the physico-chemical data are then reviewed. Finally, general conclusions are made. The significance of these results are further discussed in the final chapter.

Erpobdella octoculata

Data on the life cycle of E. octoculata in Crose Mere during this study are similar to the results presented in Young & Ironmonger (1982a) for leeches from the same lake, with the species exhibiting an annual life cycle.

In other studies, Mann (1953b),in a study on Foundry Brook, Berkshire, found that the species lived for two years and bred in each year before dying. Elliott (1973a), working on Wilfin Brook, Cumbria, also found a two-year life cycle, but in this case the leeches only bred once and then died. Aston & Brown (1975), working on the River Trent, found a two-year life cycle in unpolluted areas and an annual life cycle in polluted areas. Dall (1979b), working on Lake Esrom, Denmark, found that the leeches had an annual life cycle with 85% - 95% of the year-class breeding after one year. Murphy & Learner (1982), working on the River Ely, South Wales, also found an annual life cycle. Young & Ironmonger (1982a), found that 91% - 95% of the leeches were breeding after one year and that 81% of the leeches died soon after breeding.

In the present study, very few leeches survived into their second year and, for the 1980/81 cohort, a maximum of between 91.4%-99.9% of the leeches were found breeding after one year. For the 1981/82 cohort, the breeding estimates were between 81.8% - 94.5%.

Leeches of the 1980/81 cohort started breeding at the end of May 1981 when the water temperature had reached 15°C. In 1982, breeding started in mid-June, when the temperature had reached 18.5°C. Young & Ironmonger (1982a) found that breeding in Crose Mere started when water temperatures approximated 11°C.

The mean number of cocoons produced by each breeding leech ranged from 7.3 - 14.3. This is higher than the estimates of 7.6 - 8.0 cocoons/leech by Elliott (1973a) and of 4.1 - 7.7 cocoons/leech by Dall (1979b), but less than the estimates of 15.6 cocoons/leech by Murphy & Learner (1982) and the field estimates of 33.4-126.8 cocoons/leech given in Young & Ironmonger (1982a). Young & Ironmonger (1982b), gave estimates of between 10.4 - 14.0 cocoons/leech for field-collected leeches at different temperatures in the laboratory. The reason for the estimates being much lower than those of Young & Ironmonger (1982a) probably lies in the fact that they only sampled the leech populations on the stones and did not take into account the large number of breeding leeches in the substratum. About 22% of the cocoons in the present study were found to be damaged or infertile and this compares with 25% from Young & Ironmonger's (1982a) data.

The mean number of young/fertile cocoon, at 5.4 - 5.5, was the same as estimates from Young & Ironmonger (1982a), higher than the 3.8 - 4.2 young/cocoon estimated by Elliott (1973a) and 3.4 - 3.5 young/cocoon estimated by Dall (1979b), but lower than the laboratory results of Murphy & Learner (1982) who presented an estimate of 9.4 leeches/cocoon.

The young leeches were first recorded in July in both years and the density of each cohort continued to rise until August or September.

The density then declined and, as there is little evidence for migration of the leeches into deeper waters in Crose Mere, it was assumed that this was due to mortality. The mortality rate after hatching was thought to be extremely high with between 86% and 97% of the leeches dying between hatching and October of their first year. For the 1981/83 cohort, the mortality rate was then constant between October 1981 and July 1982, but there was a high mortality rate again after breeding in July and August. No leeches of this cohort were present in September. The estimated mortality between hatching and sexual maturity was estimated at about 99%. Dall (1979b), found a mortality rate of 85% in the first two months of the life cycle, and Murphy & Learner (1982) estimated that the mortality between hatching and sexual maturity was some 98.6%.

Three periods of growth were apparent in the life cycle. A period of rapid growth from July until October, a period of slow growth from October to April, and a period of high growth from April to July leading to sexual maturity. However, regression equations did not give a significant fit to these individual growth-periods, but did when applied to the whole life-span. Dall (1979b) and Murphy & Learner (1982) also found these three phases of growth for their annual populations and Aston & Brown (1975) noted low or negative growth over the winter months. The reason for the low growth over winter would seem to be connected with low food searching activity rather than a lack of available food (Elliott,1973b).

The production estimates obtained in this study should be interpreted with care. The instantaneous growth-rate method (Ricker, 1946) is suitable for cohort-reproducing species without prolonged recruitment and it assumes that the mortality rate is constant between the sampling intervals. This was not strictly true for the data collected. Recruitment into the population spanned some three months (July to September) and the mortality rate was rapidly changing in the first few months of the life cycle. An attempt was made to incorporate the production contributed by the large numbers of young estimated to have entered the population but which died before they could be sampled. If the mortality rate of these leeches was constant between sampling intervals and their growth rate was the same as for the leeches actually recorded, then the production estimates, over the life-span of the cohort, were more than doubled when these leeches were incorporated. In using the Allen Curve method (Allen, 1951) for estimating production, the prolonged recruitment meant that the maximum densities did not coincide with the minimum mean weights and this, together with periods of negative growth, made the position of the line drawn, arbitrary. Again, if the young, estimated to have entered the cohorts, were incorporated into the curve, the production estimates were greatly increased.

Of the other workers who have given estimates of the production by E. octoculata, only Elliott (1973a) incorporated estimates of the young produced into his data. He did this on an Allen curve. However, the shape of the curve drawn meant that the young contributed little to the over-all production figures. To compare the current data with other workers,therefore, it is perhaps best to use the data based on leeches that were actually recorded. In any case, the most probable hypothesis is that most of the young do die shortly after hatching and add little to the production estimates. If not, then they should have been found in greater numbers by sampling.

However, there is a further problem in comparing the production estimates obtained in this study with those of the other workers. This lies in the variety of ways in which the population parameters of density, biomass and mean weight have been expressed. In the present study, geometric mean biomass and arithmetic mean weight were used in the instantaneous growth-rate method and geometric mean density was plotted against arithmetic mean weight for the Allen curve. Elliott (1973a) used just the arithmetic means for both calculations and Dall (1979c) also used arithmetic means in his estimates. Murphy & Learner (1982) used the arithmetic mean biomass and the geometric mean weight when using the instantaneous growth-rate method.

Using geometric means in either axis of the Allen curve will tend to lower the production estimates because they are lower than the respective arithmetic means and their use, therefore, will decrease the area under the curve. In the instantaneous growth-rate method, using geometric mean biomass will lower the estimates,but using geometric mean weights can work in either direction. For example, if the mean biomass was 2.0 $g.m^{-2}$ and the arithmetic mean weights were 5.0 mg and 20.0 mg at times t_o and t_1 respectively, then the production in this interval would have been

$$2.0 \times (\text{Ln } 20 - \text{Ln } 5) = 2.8 \text{ g.m}^{-2}$$

However, if the geometric means were to lower the weight estimates over this time to, say, 3.5 mg and 16.0 mg at t_o and t_1 then the production would have been

$$2.0 \times (\ln 16.0 - \text{Ln } 3.5) = 3.0 \text{ g.m}^{-2}$$

i.e. the production estimate has risen despite the mean weight having been lowered. This occurs because it is the rate of growth, rather than the growth increment which is used in the calculation. Thus the use of geometric mean weights may have the opposite effects in the instantaneous growth-rate method and the Allen curve.

This problem can only be resolved by accepting that the population parameters presented by other workers, and in this study, are the best descriptions of the particular populations studied, but to bear in mind the effects of using different methods of calculation when comparing the estimates. It would not have made any sense to use the arithmetic mean biomass or density in this present study, when the data was obviously not normally distributed.

The production estimates from other workers are presented in the following table

Annual Production $(g \cdot m^{-2})$	Mean Annual Biomass $(g \cdot m^{-2})$	$\frac{P}{B}$	Author
2.04	0.58	3.52	Mann (1971)
11.63	7.82 - 20.96	1.38 - 1.60	Elliott (1973a)
17.97	3.60	5.0	Dall (1979b)
29.4	5.6	5.3	Murphy & Learner (1982)
2.7 - 3.1	1.1 - 1.6	2.5 - 2.0	This study (from instantaneous growth-rate)
3.5 - 3.6	1.1 - 1.6	3.4 - 2.3	This study (from Allen curve)

From the data presented above, it seems that the annual production and mean annual biomass in Crose Mere is considerably lower than the other studies excepting that of Mann (1971) for the River Thames. It would be expected that the turnover rate will be higher for populations completing their life cycle in one year rather than in two (Waters, 1977) and this seems to be the case. However, the turnover rate in Crose Mere is considerably lower than the estimates presented for the annual populations studied by Dall (1797b) and Murphy & Learner (1982).

In the 1981/82 cohort in Crose Mere, negative production occurred between October 1981 and January 1982, coinciding with the period of negative growth. Negative production also occurred at the end of the cohort. Murphy & Learner (1982) also noted negative production at the end of the cohort, and the probable reason for this is the high rate of mortality of post-reproductive leeches.

A particularly interesting result from the current study was the demonstration of differences in the populations inhabiting stones and the underlying substratum. In all samples, the majority of the population, in terms of both numbers and biomass, were to be found in the substratum (the area of which was far greater than the available area of stone-bottom surface area). However, for each cohort, the proportion of leeches on the stones increased to a maximum during the breeding season. The density of leeches per unit area of stone-bottom, at this time, was usually higher than per unit area of substratum and thus there seemed to be some preference for being on the larger stones. However, the scarcity of such stones precluded most leeches from achieving this end.

In addition, the mean weight of the leeches on the stones was higher in virtually all samples, and in several cases this was statistically significant. The differences were particularly marked during the breeding season, when the proportion of mature animals on stones was also greater than in the substratum. Again, this seems to indicate a preference for these leeches to be on the stones, and a possible reason for this may be that the habitat provides a less abrasive environment for both adults and cocoons than the underlying substratum.

The effects of the enclosures on the population of E. octoculata in Crose Mere seems to have been minimal. As most of the population was present in the substratum, it is differences between control and enclosed sites for this portion of the habitat that are important in looking for numerical changes in the populations. Differences between control and enclosed sites for leeches on the stones were not so important numerically, though they could have reflected differences in the predation pressure on the stones or perhaps behavioural responses.

In terms of density, the only significant difference between control and enclosed sites in the substratum was in the last sample taken in March 1983, when the density was higher in enclosed sites. On the stones there were significant differences, in favour of the control sites, in August 1981 for the 1980/81 cohort (when very few leeches of the cohort were still alive), January and June 1982 for the 1981/82 cohort, and August and September 1982 for the 1982/83 cohort. The sample of January 1982 was the only sample in which the density was significantly higher in enclosed sites. Biomass largely followed the same pattern as density, with the only significant differences in the substratum with higher values in control occurring in August 1981 for the 1980/81 cohort and in March 1983 for the 1983/83 cohort. There is no obvious reason why the density should have been higher on the stones in control sites at the times when it occurred. If fish or waterfowl predation was acting on the population then one might expect the opposite result with the density of leeches in control sites being reduced and the surviving leeches left seeking refuge in the substratum. Taken as a whole, the density and biomass data showed no large-scale enclosure effects.

The mean weight of leeches was significantly different between control and enclosed sites in the substratum in August 1981 for the 1980/81 cohort, when it was higher in control sites, and in January 1982 for the 1981/82 cohort and November 1982 for the 1982/83 cohort, when it was higher in enclosed sites. For all other samples there were no significant differences in the substratum. On the stones the mean weight was higher in control sites in July 1981 for the 1980/81 cohort and in October 1981 and June and July 1982 for the 1981/82 cohort. It was higher in enclosed sites for the samples of September 1981 and April 1982 for the 1981/82 cohort. The growth-rate of each cohort was also very similar for control and enclosed sites and for the 1981/82 cohort the growth-rate over the cohort was 0.008 ± 0.004 mg/day in control sites and 0.008 ± 0.003 mg/day in enclosed sites. Thus there also seemed to be little enclosure effect on either the growth rate or mean weight of E. octoculata, though there was more variability between stone than substratum samples.

The breeding data were also essentially similar for control and enclosed sites with between 94.5% - 99.9% in control sites and 81.8% - 91.4% in enclosed sites of the leeches breeding after one year. The mean number of eggs per fertile cocoon and young per fertile cocoon did not differ between control and enclosed sites, and neither did the proportion of infertile or damaged cocoons. However, bearing in mind that similar densities of adult leeches were present in respective habitats in control and experimental bays at the start of each breeding season, the number of cocoons produced by each breeding leech was found to be higher in control than in enclosed sites in the summer of 1981, with the density of cocoons being higher on the stones in June, July and August and in the substratum in September. This, coupled with the slightly higher proportion breeding, lead to a greater production of young in control sites in 1981. In 1982, there was no difference in the number of cocoons produced by each leech and the input of young into the population was similar. The mortality of the post-reproductive leeches was also the same in control and enclosed sites and, in both years, the post-reproductive leeches were all dead by September.

An interesting result of the different numbers of young entering the cohorts in control and enclosed sites in 1981 lies in the mortality of the leeches between hatching and October of their first year. In 1981, the input was estimated at 7177.5 m^{-2} in control sites and 1899.4 m^{-2} in enclosed sites, but by October the densities were similar at around 230 m^{-2}. The respective mortality rates were 97.2% and 86.3% In 1982, the input of young was the same in control and enclosed sites and the mortality rates did not differ.

It thus seems that the different mortality rates in 1981 were not an enclosure effect, but rather a consequence of differing initial densities.

The production estimates at 2.7 $g.m^{-2}$ in control sites and 3.1 $g.m^{-2}$ in enclosed sites were also essentially the same, though the turnover rate was higher in control sites (2.5 in control sites and 2.0 in enclosed sites).

To summarise, it seems that the enclosures had little effect upon either the density, biomass or growth of the leeches. Reproductive activity was essentially the same within and outside enclosures, though in 1981 output was greater, with more young being produced in the control sites. A higher rate of mortality in the first few months of the cohort in control sites in 1981 resulted in similar densities inside and outside the enclosures by October. In 1982, mortality rates inside enclosures and in the controls were similar, suggesting that the greater rate recorded in controls in 1981 was not due to enclosure effects.

Glossiphonia complanata

In the present study, G.complanata in Crose Mere was found to exhibit a two-year life-span with most leeches which survived to reach an adult size, dying within two years of birth. Only a few leeches possibly lived for three years. The life-cycle of the species was similar to that recorded by Young & Ironmonger (loc cit) from the same lake, though these workers referred to the life cycle as an annual, in view of the fact that the majority of surviving adult leeches in a cohort bred one year after birth and then died over the following few months.

Leeches of the 1980/82 and 1981/83 cohorts were breeding in the samples taken in April 1981 and April 1982 respectively, when the water temperature was in excess of 10°C. The breeding season then continued until the end of May. These results are in accordance with Young & Ironmonger (loc cit). Young (1983) has reported that the stimulus for egg production is a period of low temperature followed by rising and higher temperatures and that photoperiod is not a contributary factor.

Mann (1957a) found that eggs were laid in two broods, with an early brood in March/April produced by the two-year old leeches, and a later brood in May/June by the one-year old leeches. Furthermore, he found that of the early brood of leeches, all bred at one year of age while only 40% of the later brood bred at one year. The temperature ranged between 8.5°C - 15°C during the breeding period in his study. Bennike (1943) and Sapkarev (1967) found that the breeding season extended from May to July but did not notice the double breeding pattern described by Mann (1957a). Dall (1982) recognised two sub-species of G. complanata, name G. complanata typica (L.) and G. complanata concolor (Apathy) (Bennike 1943), in Lake Esrom and found that G. complanata concolor bred some two weeks in advance of G. complanata typica, with the breeding seasons extending from mid-May to mid-June and from late May to late June respectively. Leeches were found with eggs when the water temperature was in excess of 10°C. The sub-species of G. complanata were not recognised in the present study.

In the present study, the mean number of eggs produced by each breeding leech was estimated at between 23.3 - 26.8 (from data on eggs carried in cocoons). This compares with estimates of 40/leech by Bennike (1943), 33/leech by Mann (1957a), 84/leech by Wilkialis (1970), 29/leech by Dall (1982) and 23.1/leech by Young & Ironmonger (1982a).

In both 1981 and 1982, the young leeches first appeared in samples from May onwards and their density continued to rise until August or September. The reason for this continued rise was unclear, as breeding had finished by the end of May, but it may have been a consequence of the sampling method used. In employing trays to sample the underlying substratum, the method relies upon the animals colonising the trays from the surrounding substratum to obtain quantitative estimates. If the young leeches did not show strong dispersive behaviour until mid-summer, then this might explain the continued increase in density. Young & Ironmonger (1982a) also noted an increase in density on the stones in the autumn and suggested that this may have been connected with movement from the substratum onto the stones, but there was no evidence for this in the present study.

The mortality of leeches soon after release from the adults was thought to be extremely high with between 87.8% - 96.5% of the leeches dying by September of their first year. Of those animals present in September, only 3.4% - 4.9% were present a year later and only 1.3% - 1.8% were present during the breeding season at two years old. Mann (1957a)found a 97.4% mortality rate in the first six months of life, followed by lower mortality rates. Young & Ironmonger (1982a) suggested that 21% - 31% of the leeches survived into their second year.

Four phases of growth were observed in the life cycle. A period of rapid growth from after release from adults until September/ October, low or negative growth from October to April, rapid growth from May of the second year until the late autumn and then low growth again over the winter. Regression equations indicated that, during the periods of rapid growth, the growth rate was constant. Mann (1957) described similar periods of growth to those observed in the present study.

The problems associated with the production estimates for E. octoculata have been discussed above. For the G. complanata data, the additional problems caused by the continued rise in density of the young after breeding had stopped were resolved by assuming these leeches were present at the end of the breeding season. On this basis, the estimates of annual production ranged from 9.4 $g.m^{-2}$ - 14.9 $g.m^{-2}$ in 1981/82 and between 4.1 $g.m^{-2}$ - 3.8 $g.m^{-2}$ in 1982/83 and, from the annual biomass data, this led to turnover rates of between 3.2 - 5.1 in 1981 and 2.2 - 2.6 in 1982. These rates are within the range described for species with a predominantly one-year life-span (Waters 1977). The only data available for comparison come from Mann (1971) for leeches from the Rives Thames. His estimate of annual production, based on an Allen curve was 5.6 $g.m^{-2}$ over a mean annual biomass of 2.7 $g.m^{-2}$, giving a turnover rate of 2.1.

Again there were significant differences between the populations on the stones and in the substratum. In most samples the majority of the leeches in terms of both numbers and biomass were to be found in the substratum. However, there was a tendency for the two-year old leeches to be found on the stones at the end of their life span. In the majority of samples, the mean weight was higher in stone samples and this difference was statistically significant on several occasions. No reasons, other than those stated above for E. octoculata can be proposed for this phenomenom.

In common with the E. octoculata data, the effects of the enclosures on G. complanata seem to have been minimal. In terms of density, there were differences in May and August 1981 for the 1980/82 cohort when the density was higher in enclosed sites in the substratum, and in October 1981 and July and August 1982 for the 1981/83 cohort when the density was higher in the substratum in control sites. On the stones there were differences in April, May, June, July and

August 1981 for the 1980/82 cohort and October 1981 for the 1981/83 cohort when the densities were higher in enclosed sites. Biomass followed similar trends to density, but there were only significant differences between control and enclosed sites in the substratum in the samples of April, August and September 1981 for the 1980/82 cohort. Thus, in most samples, density and biomass did not differ significantly and in those samples,where there were differences, they were not consistantly higher in either control or enclosed sites.

The mean weight of the leeches was significantly higher in enclosed sites in the substratum samples of April, June and July for the 1980/82 cohort, in August, September and October 1981 and January 1982 for the 1981/83 cohort, and in July and October 1982 and March 1983 for the 1982/84 cohort. The same was true in the stone samples of April, June and July 1981 for the 1980/82 cohort, August, September and October 1981 and January and October 1982 for the 1981/83 cohort and in June, August, September, October and November 1982 and March 1983 for the 1982/84 cohort. The mean weight was higher in control sites only in the sample of July 1981 for the 1981/83 cohort.

However, where comparisons between the growth rate in control and enclosed sites could be made, the differences in the rates were not found to be significant. Possible reasons for the higher mean weights in enclosed sites are given later, but in most cases the weight difference was of the order of 1 or 2 mg and was statistically significant by virtue of the large number of observations comprising the estimates.

In 1981, 73.7% in control sites and 77.2% in enclosed sites of the leeches were thought to have bred. In 1982, the figures were 86.2% and 82.3% respectively. In 1981, data comparing fecundity between control and enclosed sites were not available, but in 1982 the mean number of eggs found in oviducts was 31.7 in control sites and 36.9 in enclosed sites and this difference was statistically significant. As a consequence of the significantly higher density in April 1981 in enclosed sites, the estimated recruitment into the population was over twice as high in enclosed sites than in control sites. However, the mortality between April and September at 87.8% in control sites and 96.5% in enclosed sites was higher in enclosed sites. In 1982, bearing in mind that density at the start of the breeding period was higher outside the enclosures, though not significantly so, but that fecundity was greater in enclosures, the recruitment into the population was roughly the same in control and enclosed sites, and the mortality by September, at 95.3% in control sites and 94.4% in enclosed sites, was essentially the same. There was certainly no evidence in these data for the enclosures reducing the mortality of the enclosed leeches, and the observed greater mortality in enclosures in 1981 may have been a response to higher densities of recruited animals.

The production estimates, with corrections made for the 'missing' young, were higher in enclosed sites in 1981, but slightly lower in enclosed sites in 1982. The turnover rates followed a similar pattern. For the estimates based on the leeches actually present in samples, the production was, again, higher in enclosed sites in 1981 but, in 1982 production, mean biomass and, therefore, turnover rates were identical in control and enclosed sites. Allen curve estimates for the 1981/83 cohort gave similar production estimates for control and enclosed sites. So, again, there is no apparent enclosure effect upon production and the observed differences are a consequence of differences in mean weight and density at particular stages of the study.

Thus, for G. complanta, the enclosures seem to have some effect on the mean weights of the leeches present and, on occasions, the density of leeches on the stones (in both instances the values being higher in enclosed sites). However, no large-scale differences in density or biomass other than could be explained through heterogeneity of the sampling sites have been demonstrated. Breeding behaviour was also essentially the same in control and enclosed sites.

Helobdella stagnalis

In the present study, H. stagnalis was found to exhibit a basically annual life-cycle, with some leeches breeding after only a few months, and no animals recognised as living for two years.

Various patterns of breeding have been described by other workers. Some have simply observed an extended breeding season (for example Bennike, 1943; Thut, 1969 and Wilkialis, 1970) while others have noted two peaks in breeding activity. Mann (1957b) working on Whiteknights Lake, England, found that the over-wintering adults produced a brood in spring and then died. Some 60% of this brood then bred in the summer and the over-wintering population was then composed of both broods. Learner & Potter (1974) described a similar breeding pattern for leeches from Eglwys Nunydd Reservoir, Wales, but only 33% of the spring brood bred in the summer. Davies & Reynoldson (1976), working on Marion Lake, Canada, also found a similar pattern, but in this case all of the spring brood bred. Tillman & Barnes (1973) suggested, for a population from Utah Lake, U.S.A., that the over-wintering population produced two broods of young and backed this up with histological evidence on gonad development. Davies & Reynoldson (1976), for a population in Newsome Pond, Canada, found a simpler life history with a single breeding season in which the new generation completely replaced the old generation and did not breed until one year of age.

Young & Ironmonger (1982a), working on Crose Mere, also found two breeding peaks, but were unable to define its cause. They suggested several possible reasons:

1. That the over-wintering adults bred once and then the offspring grew rapidly so that a proportion were breeding by mid-summer. This was supported by laboratory evidence (Young & Ironmonger 1982b) which, at the water temperatures of the lake during this study, suggested that the young could have reached breeding condition in the time available.

2. That the over-wintering adults could have produced two broods. This was the explanation proposed by Tillman & Barnes (1973), but Young & Ironmonger (1982b) found that only 4 out of 354 field-collected leeches managed to produce two broods.

3. That each brood takes a year to mature, and the two breeding peaks represent the spring and summer broods from the previous year reaching breeding condition. This is unlikely, for over a number of years, the discrete breeding peaks should have merged into a single prolonged reproductive period.

4. That some of the leeches copulated in the autumn and were ready to breed as soon as the water temperatures increased in spring. Again, this was regarded as unlikely because laboratory studies (Young & Ironmonger, 1982b) indicated that copulation and egg production could have occurred in the spring in plenty of time for the leeches to breed during the first peak.

In this study, the over-wintering adults were found to breed in two pulses. Leeches with eggs in their oviducts were found from mid-April to May, when the water temperature was in the range 10-12°C.. There was then a short break before the over-wintering generation were again found with eggs in their oviducts. In addition, between 7.5% - 38.3% of the spring brood were found to be breeding by July. Thus the two breeding peaks in Crose Mere were caused by the separate breeding of the over-wintering populations and the spring brood of young. However, the cause of the over-wintering population apparently breeding in two pulses was not clear and could be explained by one, or a combination of, the points 2 - 4 described above. This is similar to the pattern described by Young & Ironmonger (1982a) who found that breeding commenced at a water temperature of around 11°C.

The mean number of eggs produced by each breeding leech in this study was between 15.7 - 26.7 for the over-wintering population and between 10.4 - 17.5 for leeches of the spring brood. Estimates from other workers include those of 20/leech by Bennike (1943), 13.5 - 17.2/leech by Mann (1957b), 17.4/leech (spring breeders and 13.6/leech (summer breeders) by Tillman & Barnes (1973), 14.0/leech by Learner & Potter (1974) and 18/8 leech (spring breeders) and 22.9/leech (summer breeders) by Young & Ironmonger (1982a).

The density of the young, from combined spring and summer brood data, continued to rise until September in this study, and thereafter declined. From October onwards it was impossible to distinguish between spring and summer broods. By September of their first year between 85-95% of the young produced in total were found to have died. This figure had increased to between 94 - 99% by April of the following year and by August/September all leeches of the cohort were dead.

Few other estimates of mortality or population density have been presented in the literature, but the mean annual density in this study of between 166 - 336 leeches . m^{-2} compares with densities of 262 - 615 m^{-2} by Hilsenhoff (1967) for Lake Winnebago, 44 m^{-2} by Thut (1969) for Lake Washington, 343 - 1366 m^{-2} by Learner & Potter (1974) for a Welsh reservoir and 73 m^{-2} by Dall (1979c) for Lake Esrom.

Three phases of growth were noted in the populations from Crose Mere. Rapid growth after release from the parents until September, low growth over the winter until April and then rapid growth again until death. The growth rate was higher in the first phase of growth than in the second phase and over both period of growth,the growth rates were constant.

The annual production estimates, based on the actually recorded leeches, ranged between 0.8 $g.m^{-2}$ - 2.7 $g.m^{-2}$, with turnover rates of between 1.6 and 2.3. This compares with the estimates of 1.3 $g.m^{-2}$ by Mann (1971), for the River Thames (based on an Allen curve) and 2.3 - 8.9 $g.m^{-2}$ by Learner & Potter (1974) (using the method of Chapman, 1968). The turnover rates of 4.8 from Mann (1971) and of 3.0 from Learner & Potter (1974) were higher than in the present study.

In most samples, the majority of the leeches, in terms of both density and biomass, were in the substratum, though the proportion on the stones increased during the breeding season and reached over 50% in some months. In addition, the proportion of leeches breeding was also higher on the stones. Thus there was a clear preference for breeding on the larger stones and, as a consequence, the proportion of the young on the stones was initially high, though it rapidly decreased. In most samples, the mean weight of the leeches on the stones was also higher and this was statistically significant in many samples.

In terms of density, the numbers were significantly higher in control sites in the substratum samples of January and May 1982 for the 1981/82 cohort and in July 1982 for the spring brood of the 1982/83 cohort. There were no other significant differences in the substratum. On the stones, the density was significantly higher in enclosed sites in the samples of May, July and August 1981 for the 1980/81 cohort and higher in control sites in the samples of June, July and August 1982 for the 1981/82 cohort, July, August and September 1982 for the spring brood of the 1982/83 cohort and in August 1982 for the summer brood. Biomass followed similar trends to density,and in the substratum was significantly higher in control sites in the samples of May 1982 for the 1981/82 cohort and November 1982 for the 1982/83 cohort. It was higher in enclosed sites in September for the spring brood of the 1981/82 cohort. There were no other differences in the substratum. Thus, numerically there was little difference between control and enclosed sites, and any variation was greater on the stones. Where differences occurred, they were not consistantly biased towards enclosures or controls.

In the substratum, the mean weights were significantly higher in control sites in the samples of August 1981 for the summer brood of the 1981/82 cohort, in September 1982 for the summer brood of the 1982/83 cohort and in November 1982 for the over-wintering population. It was higher in the substratum in enclosed sites in the samples of August 1981 both for the 1980/81 cohort and the spring brood of the 1980/81 cohort, and in September 1981 for both the spring and summer broods of the 1981/82 cohort. Thus, in most samples there were few differences between control and enclosed sites for the population as a whole, and those differences that did occur did not show any consistant pattern. The growth rates did not differ between control and enclosed sites. However, there was some evidence for the spring and summer broods growing more quickly in August and September 1981 in enclosed sites.

In 1981, some 79.8% of the over-wintering population and 15% of the spring brood bred in control sites, while in enclosed sites the respective figures were 83.4% and 38.3%. In 1982, the figures were 80.0% and 7.5% in control sites and 79.1% and 12.3% in enclosed sites respectively. Thus, there were slightly more of the spring brood breeding in enclosed sites. In 1981, the mean number of eggs in oviducts was significantly higher in enclosed sites in April but the reverse was true of young carried in June. No such differences occurred in 1982. In 1981, the slightly higher proportion of the slightly higher proportion of the over-wintering population breeding, the resulting higher density in the spring brood, and the higher mean number of eggs in oviducts resulted in about double the input of young into enclosed sites than in control sites. By September of the first year, the mortality rates at 93.3% in control sites and 94.5% in enclosed sites were only slightly higher in enclosed sites, and the densities were still higher in the latter. By April of the following year, the mortality had increased to 98.5% and 99.4% respectively, and the densities were similar. In 1982, the input of young was slightly higher in control sites and the mortality rates were essentially the same. There was certainly no evidence for the enclosures affecting mortality.

The production estimates were slightly higher in enclosed sites in 1981/82, but the reverse was true in 1982. The turnover rates followed a similar pattern. This was caused by the higher densities of young in enclosed sites during the period of rapid growth in 1981, and the same in control sites in 1982.

In summary, the enclosures had little effect upon the H. stagnalis populations. The observed differences in density and biomass showed no bias to either control or enclosed sites. In respect of growth rate and breeding behaviour, there were also no consistent differences and, again, it seems that such variation as there was, was more likely to be caused by variation between the sampling station.

Other groups

There were no significant differences between control and experimental sites for either the density or biomass of oligochaetes, Bythnia tentaculata, Valvata piscinalis, Tinodes waeneri or any of the triclad species recorded. For the remaining groups, with the exception of the Leptocercidae where there was no consistent pattern with regard to abundance within and outside enclosures, there were differences in certain months and these were consistent within each group.

For the Chironomidae and Gammarus spp., those differences occurred when the density or biomass was higher in control sites. For the Chironomidae, these differences were more marked in the first year, but over most of the experimental period the densities and biomasses were similar in control and experimental sites. Thorp & Bergey (1981a) suggested that their enclosures may have restricted lateral recruitment of midge larvae, and this is a possible explanation for the observed differences. Another possibility is that Sialis were recorded from samples in the summer months at a greater abundance in the enclosures, and it is known that the larger instars include chironomids in their diet (Elliott, 1977b). Thus, it might be suggested that this predator may have contributed to the similar densities of midge larvae within the enclosures in 1981. However, this is most unlikely since, in 1982, when higher densities of Sialis were recorded, densities of chironomids within and outside enclosures were similar. For the Gammarus spp., the only consistent pattern was the density and biomass in control sites increased to far higher peaks in August of both years. In 1981, density was significantly higher in controls throughout the autumn. Thorp & Cothran (1982) also noted that amphipods were more abundant outside their enclosures but did not suggest any reasons for this.

For *Asellus spp.*, *Potamopyrgus jenkinsi* and *Sialis lutaria* (mentioned above), the values were higher in enclosed sites where significant differences in density or biomass occurred. For *Asellus spp.*, the densities were higher in enclosed sites from May to July in both years and extended through to the winter in the first year. For *P. jenkinsi*, the densities were higher in May 1981 to January 1982 in enclosed sites, but there was no consistent pattern in 1982/83. However, the densities were higher in enclosed sites between July and September 1982. For *S. lutaria*, the density was higher (though not always significantly so) in all samples in enclosed sites. However, the observed differences were not of a large magnitude.

These above observations could be consistent with reduced predation pressure in the enclosures. However, the data from fish diet analyses presented in Chapter 3, revealed that, of these groups, only *Asellus* regularly occurred in the diet of perch and roach. However,for *P. jenkinsi* an alternative explanation comes from dietary studies on waterfowl, which have revealed that this species may form a substantial proportion of the diets of Goldeneye (*Bucephala clangula*), Mallard (*Anas platyrynchos platyrynchos*) and Tufted Duck (*Aythya fuligula*) (from Olney, 1963 and 1967 and Olney & Mills, 1963), all species reported from Crose Mere during this study. For *S. lutaria*, the species may have been benefitting from reduced predation by vertebrate predators, e.g. fish (see Elliott, 1977b)or, perhaps, from improved conditions for egg laying by the adults. The enclosures would form an ideal site from which the adults might lay their eggs. The appearance of *Sialis* larvae in samples in June would be associated with the commencement of egg-laying by adults in May and partly to the migration of larger instars from deeper to shallow waters to emerge for pupation (see Elliott, 1977b). The absence of larvae from samples from September onwards in 1981 may have been due to the movement of growing animals to deeper waters. This is relevant to the enclosures, since the deepest waters within these were not sampled.

In summary, the enclosures did not have a great effect upon the invertebrate groups studied, and though there were differences between control and enclosed sites, these were rarely of a large magnitude. The exceptions to this were Gammarus spp., Asellus spp. and P. jenkinsi and the latter two showed far higher densities in enclosed sites in certain monthly samples.

Physico-chemical data

No major differences between control and enclosed sites were found during the present study for either temperature, conductivity, pH or dissolved oxygen. The large size of the enclosures used reduced to a minimum the effects that may occur in small enclosures, for example, where all the nutrients may be used up by organisms and the mesh-size of netting was sufficient to allow the exchange of water with the open lake. Fouling of the netting increased during each summer but, as the netting was replaced over the winter, it never became a major problem.

Though other workers have suggested the possible physico-chemical effects of enclosures, few have actually reported any measurements. However, Crowley et al (1983) reported no enclosure effects upon temperature or dissolved oxygen for their design (see section 4.1).

From the particle size analyses, though there were differences along the sampling shore, it was clear that the nature of habitats sampled were the same in control and enclosed sites.

General conclusions

The effects of the enclosures on the leech populations in Crose Mere appear to have been minimal. There also seems to have been little effect on most of the other macro-invertebrate species present. The only marked effect upon the leech populations was the higher mean weights of G. complanata and H. stagnalis in enclosed sites noted particularly in 1981, especially in the summer. E. octoculata did not exhibit this phenomenon. A possible explanation for the increased mean weight lies in the greater densities of P. jenkinsi and Asellus spp. present in the enclosures during this time. Dietary studies by Young & Ironmonger (1979) and Young (1980 & 1981 a,b) have shown that, for the Crose Mere populations, Asellus and Molluscs formed some 34% of the diet of H. stagnalis and 61% of the diet of G. complanata, while they formed only about 1% of the diet of E. octoculata. The greater availability of these prey organisms may well have led to the observed increase in weights, though they did not give rise to any major increased densities or reduced mortality rates in the leech populations from enclosed sites.

The results of previous predation field experiments, using enclosures, by other workers, were briefly discussed in section 4.1, and it would be true to say that few have demonstrated any effects of fish predation on the invertebrate populations as a whole. However, some have found effects on specific groups, and in particular on planktonic species (for example, Straskraba 1965, Meijering 1970, Kajak 1977, Lynch 1979, Fairchild 1982 and Hall et al 1970). However, Kajak (1977) and Hayne & Ball (1956) found that the standing crop of invertebrates increased in the absence of fish and, in the latter study, the rate of production was found to decrease when fish were present. In the present study, the planktonic species were not investigated and there was no general increase in biomass or changes in production of the benthic species.

Hall et al (1970) found that invertebrate predators and, in particular, the zygoptera, did well in the absence of fish. In Crose Mere, the numbers of invertebrate predators in the stony littoral were always low and, of those that were present, the Leptocarcidae and Tinodes waeneri showed no enclosure effect. S. lutaria did show positive enclosure effects and this may have been a result of predator release or, perhaps, a side-effect of the structure of the enclosures themselves.

Thus, for the leech population in Crose Mere, there was no evidence for predation by fish or waterfowl having a direct effect upon any of the population parameters studied. Some small-scale effects, however, were observed on some of the other macro-invertebrate species present. These results, together with further evidence from serological studies on the invertebrate predators from Crose Mere (and other lakes), fish diet studies from Crose Mere and evidence from a literature survey are further discussed in the final chapter.