ECOLOGICAL STUDIES OF ISOPODA AND DIPLOPODA IN DUNE GRASSLAND

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by

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ABSTRACT

Distribution, population dynamics, biomass and population production of macrodecomposers have been studied in order to clarify the role of four species in the processes of energy transfer in a dune grassland ecosystem. The species worked on were Armadillidium vulgare, Porcellio scaber, Philoscia muscorum (Isopoda) and Cylindroiulus latestriatus (Diplopoda). Population data were available for the species from 1968 to 1975.

Preliminary investigations indicated little difference in the diet of each species and in their interactions with predators, however there were significant differences in vertical and horizontal distribution.

The vertical distribution of each species changed with season, mainly in response to variations in temperature in winter and relative humidity in summer. Despite these movements there was a consistent difference in the mean depth of each species. The millipede showed a particularly marked difference from the woodlice because it was mainly a root layer inhabitant whereas they were most abundant in the litter layer.

Horizontal distribution studies indicated that P. muscorum predominated in the ~~mobile~~ stable dune while A. vulgare and P. scaber were more abundant towards the dune crest. The last two species showed evidence of migration between different areas of the dune system in early summer 1975.

Changes in abundance and aggregation were also observed. P. muscorum declined from a maximum density of 103.7 $0.1m^{-2}$ in August 1970 to zero in October 1974 whereas A. vulgare increased from a minimum of 1.7 $0.1m^{-2}$ in January 1969 to a maximum of 73.9 in September 1973. P. scaber and C. latestriatus exhibited smaller changes; maximum and minimum estimates were 27.1 and 0.9 $0.1\ m^{-2}$, and 16.0 and 1.9 $0.1m^{-2}$ respectively.

All species showed changes in aggregation during the course of the study. Aggregation increased in the woodlice in 1974 and 1975 and decreased in the millipede.

It is suggested that the changes in density and aggregation were related to changing conditions on the study site, particularly those caused by rabbit disturbance and sand accumulation.

There were seasonal density fluctuations also. Changes in size structure, the breeding biology and cohort dynamics of the *A. vulgare* and *P. scaber* populations were examined to obtain insight into the importance of natality, mortality and migration in determining these fluctuations. The density of each species peaked in late summer when brood release occurred and declined at other times due to continuous losses. Immigration caused spring and summer density increases and appeared to be the main determinant of breeding population size.

Population size structure, breeding biology and biomass of *C. latestriatus* was studied. The rate of development of *C. latestriatus* at Spurn is intermediate between that of populations to the North and South. It is suggested that the more northerly populations take longer to mature due to lower mean annual temperatures.

Comparison of biomass and population production for the three isopod species indicated large fluctuations in individual species but the total values were fairly steady with a maximum mean annual standing crop of 744 mg live weight $0.1m^{-2}$ during 1973/74 and a minimum of 295 during 1968/69. Maximum and minimum mean annual population production figures for the three isopods combined were 366.6 mg dry weight $0.1m^{-2}$ during 1971/72 and 147.4 during 1968/69.

Finally the results are discussed in relation to niche separation, life history strategies and the role of macrodecomposers in the dune grassland ecosystem.

ACKNOWLEDGEMENTS

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CONTENTS

CHAPTER ONE

1.1 INTRODUCTION

The activities of decomposers in the soil are among the most important life functions of natural ecosystems. Firstly they effect the release of nutrients which are locked up in dead plant and animal remains and secondly, in ecosystems where little of the net primary production is consumed by herbivores but instead falls to the earth as litter, they form the major supply of energy for predators and thus enhance the diversity of the ecosystem. Despite this it is surprising how little is known about the role of different species in these processes and how their activities contribute to the functioning of the system as a whole.

To gain this understanding it is essential to know how the different species populations partition the available resources. There is no detailed information of this kind for any sympatric group of macrodecomposers. At this level most functional studies have been upon single species populations.

The part played by any species in utilising the available resources, and thus its role in the ecosystem, depends on its abundance and size structure, the food material utilised, the rate of processing of that material, its contribution to other trophic levels and the changes of these in time and space. Information on the above parameters has been obtained for three species of woodlice - _Armadillidium vulgare_ (Latreille), _Porcellio scaber_ Latreille and _Philoscia muscorum_ (Scopoli) - and one species of millipede - _Cylindroiulus latestriatus_ (Curtis). On density and biomass figures these four appear to be the main macrodecomposers in the dune grassland ecosystem at Spurn (East Yorkshire).

Work on these species at Spurn has been in progress since 1968. Initial efforts were concerned with (1) identifying the predators feeding on the woodlice and estimating the predators consumption rates (Sunderland 1977), (2) the population dynamics of _P. muscorum_ (Sunderland, Hassall & Sutton 1976) and (3) clarifying certain aspects of the role of _P. muscorum_ (Hassall, 1976).

Sunderland (1977) found that at least 43 predatory species fed on woodlice at some time during the year causing between 11 and 56% of the juvenile mortality and about 15% of the spring mortality. The most abundant predators appeared to be polyphagous and showed no preference for any particular species. As a result the woodlice were consumed in proportion to their relative abundance. They would therefore form the base of a complex food web in which their relative importance (or role) was a simple function of their abundance.

The relative importance of each species in enhancing decomposition would also be directly related to their abundance if each one was consuming the same food material. Food preference tests and gut contents analysis have shown that P. muscorum finds a wide range of food types acceptable (Hassall 1976) and that the selection of plant material for consumption depends on its state of decay rather than the plant species. Similar rules appear to govern the diet and food preferences of a millipede (Kheirallah 1966). The lack of food specificity is a common feature of decomposers (Anderson 1974) and should lead to a very broad overlap in the food types eaten. This was tested by examining and comparing the gut contents of the woodlice and millipedes at Spurn.

The gut contents of animals collected from the study site in September 1975 were drawn through millipore filters and mounted in canada balsam following the procedure outlined in Hassall (1976). The percentage cover of each food type was then estimated by measuring the surface area of a random selection of fragments as seen through a binocular microscope. The results are given in table 1.1. The proportion of green monocot and green dicot material has been combined as it forms such a small part of the total gut contents. For comparative purposes table 1.1 also includes the results obtained by Hassall (1976) from a collection of P. muscorum in August 1973.

The same basic food source, namely dead dicot and monocot material, was used by all four species. The unidentifiable plant material was probably

Table 1.1 Percentage cover (± 1 S.E.) of different food items in the diet of woodlice and millipedes at Spurn. Males, females and juveniles combined. Data on P. muscorum (Aug. 1973) from Hassall (1976).

Data Collected	C.latestriatus	A.vulgare	P.scaber	P.muscorum	P.muscorum
	Sept. 1975	Sept.1975	Sept.1975	Sept.1975 (males only)	Aug. 1973
Food Item					
Dead dicot	43.4 ± 2.8	47.5 ± 2.2	51.4 ± 2.3	39.3 ± 3.3	60.5 ± 4.1
Dead monocot	29.1 ± 3.2	16.8 ± 2.2	12.9 ± 2.3	39.4 ± 3.1	21.5 ± 3.5
Unidentified dead plant	22.5 ± 1.6	21.2 ± 2.5	24.4 ± 1.6	14.0 ± 0.8	5.0 ± 0.8
Green plant	0.0	0.1 ± 0.1	6.9 ± 1.0	0.2 ± 0.1	0.5 ± 0.5
Animal	1.6 ± 0.6	7.5 ± 1.1	0.3 ± 0.3	2.4 ± 1.2	1.5 ± 1.1
Moss	0.0	0.1 ± 0.1	0.1 ± 0.1	0.0	0.0
Roots	0.2 ± 0.2	1.4 ± 0.6	0.9 ± 0.4	3.2 ± 1.3	4.5 ± 2.9
Fungi	2.4 ± 0.7	1.5 ± 0.5	2.4 ± 0.6	1.2 ± 0.5	2.5 ± 0.8
Sand	0.5 ± 0.2	3.9 ± 1.4	0.7 ± 0.2	0.3 ± 0.2	4.0 ± 1.6
Number of animals examined	28	30	30	5	5

also derived from monocotyledons or dicotyledons but was too finely fragmented to be clearly recognisable. There was a significant fall in the proportion of dicot material in the diet of *P. muscorum* between August 1973 and September 1975. This may be partly due to the fact that in this study only males of *P. muscorum* were examined whereas Hassall included females and juveniles too. More likely however it reflects a considerable reduction in the quantity and availability of dicot material on the study site resulting from the accumulation of wind blown sand between the two sample dates (see Chapters two and three).

The results in table 1.1. suggest that there is little difference in the diet of the macrodecomposers at Spurn but it is still possible that each is feeding on different species of monocots or dicots. The only data available to test this ~~was~~ were provided by the few plants such as *Hippophae rhamnoides* L., *Ononis repens* L. and *Rumex crispus* L., which produced clearly identifiable fragments. There was a large amount of variation in the occurrence of these plants in the gut of different individuals but none ~~were~~ was consumed to a significantly greater extent by any one of the macrodecomposer species studied. It does seem therefore that there is no distinct partitioning of the food resources. Consequently the role of each species in the process of degrading plant material should be, like their role in supporting predator populations, a simple function of their relative abundance.

Although there is now a considerable amount of information relating to the interactions of the animals with both their predators (Sunderland 1977) and food supply (Hassall 1976 and above) it is still not known how the four populations contrive to partition the resources in time and space. Once this aspect of their ecology has been studied it may be possible to assess, at least in a preliminary way, how the activities of each species contribute to the system as a whole. It is this problem which forms the contents of the present study.

The results of investigations into the spatial distribution of the woodlice and millipedes are presented and discussed in relation to niche separation, in chapters two and three. In chapter four variations in the density and aggregation between 1968 and 1975 are related to their habitat preferences and changes in the environment. The means by which varying levels of natality, mortality and migration of *A. vulgare* and *P. scaber* affect their density fluctuations are assessed in chapter five by an analysis of cohort dynamics (Sunderland et al. 1976 and Hassall 1976 give similar analyses for *P. muscorum*). Data on changes in the population's size structure from chapter five for *A. vulgare* and *P. scaber*, from Sunderland (1977) and Hassall (1976) for *P. muscorum*, and from chapter six for *C. latestriatus* are used to compute biomass standing crop and production values for each species from 1968 to 1975. These figures, which are given in chapter six for *C. latestriatus* and chapter seven for the isopods, are then used in chapter eight to evaluate the changing role of each species in the dune grassland at Spurn. This is then related to the spatial distribution of each species and the spatial and temporal heterogeneity of the dune grassland ecosystem.

CHAPTER TWO

HORIZONTAL DISTRIBUTION AND MICROHABITAT PREFERENCES

2.1 INTRODUCTION

It is generally considered that woodlice and millipedes are 'primary decomposers' and find a wide range of food types acceptable to them (Sutton 1972, Barlow 1957 and Wallwork 1970). As a result they show little food resource partitioning, as discussed in chapter one. It might be expected that sympatric species would restrict their diet so that each had a separate food niche (sensu Reynoldson & Davies 1970). However, MacArthur and Pianka (1966) suggest that this would not be so, instead animals living in a mosaic environment should specialise in the area in which they search for food.

If this hypothesis applies then spatial separation should be an important niche dimension in cohabiting macrodecomposers. Furthermore the factors determining their microdistribution should be other than the presence or abundance of a specific food material. The work presented here was undertaken to test this.

2.2 STUDY SITE

The main study site was an area of dune grassland 21 m. by 21 m. on the lee side of the main dune ridge at Spurn in East Yorkshire. It has been described in Sunderland, Hassall and Sutton (1976), while Davis, Hassall and Sutton (1977) have noted recent changes in the soil profile due to the accumulation of wind blown sand.

In addition to the four species of macrodecomposers, Armadillidium vulgare, Porcellio scaber, Philoscia muscorum and Cylindroiulus latestriatus, which are common on the site and are studied here, occasional specimens of Cylisticus convexus (De Geer), Oniscus asellus L. (Isopoda) and Polymicrodon polydesmoides (Leach) (Diplopoda) were encountered.

The topography of the site is shown in figure 2.1a together with contours indicating the depth distribution of the recently deposited sand (figure 2.1b).

Figure. 2.I Some features of the Spurn study site.

a. Topography. Contours indicate height in 0.5m intervals above high water mark on November 24 I976.

b. Depth distribution (cm) of sand which accumulated over the site during the winters of I973/74 and I974/75.

c-f. Distribution of selected plant species.

■ Greater than 25% cover.

▒ 5-25% cover.

░ Less than 5% but greater than I% cover.

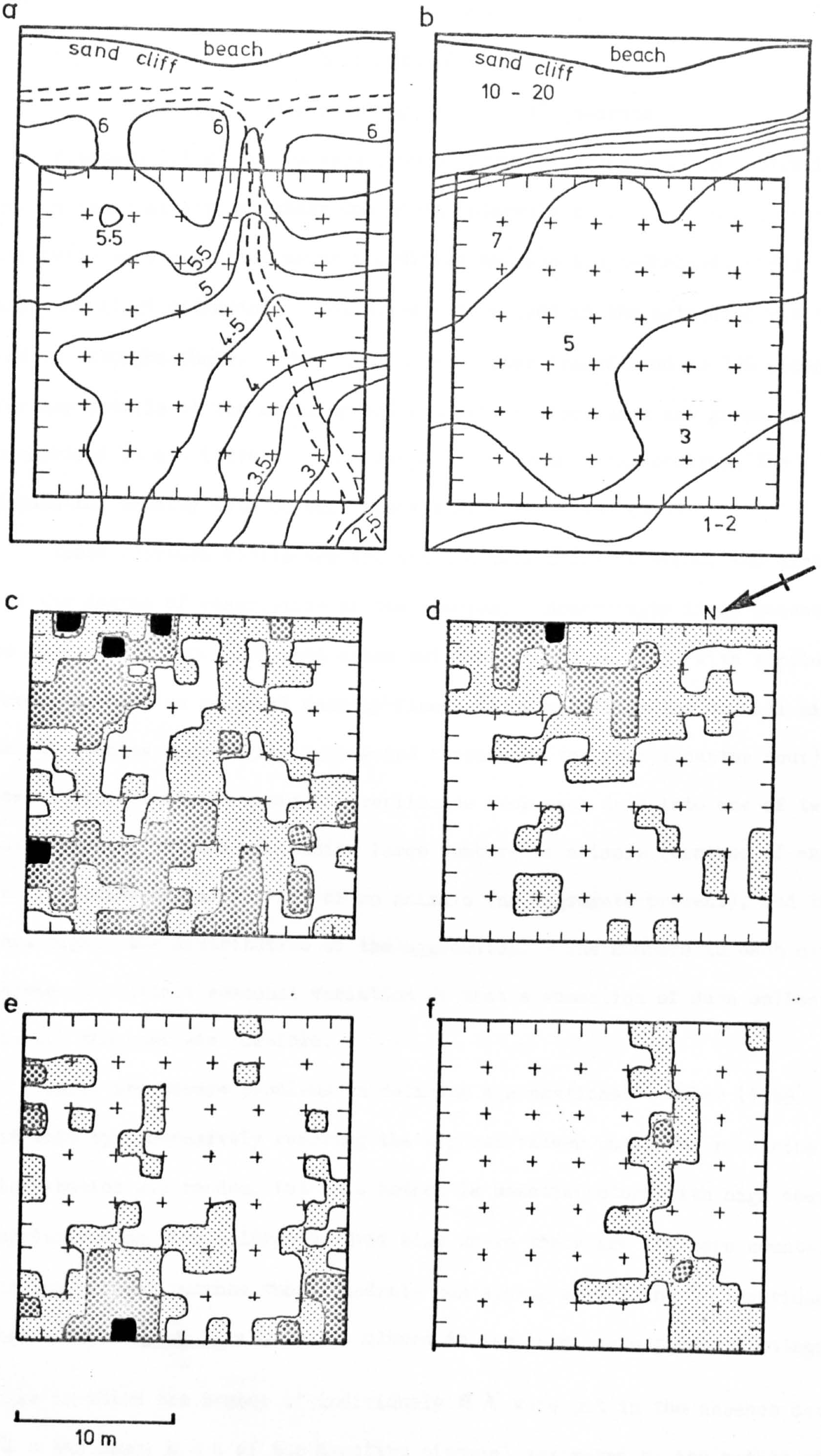
□ Absent to I% cover.

c. *Agropyron pungens*.

d. *Convolvulus arvensis*.

e. *Arrhenatherum elatius*.

f. *Carex arenaria*.


a
sand cliff
beach
6
6
6
5.5
5.5
5
4.5
4
3.5
3
2.5
b
sand cliff
beach
10 - 20
7
5
3
1-2
N
c
d
e
f
10 m

2.3 METHODS

(a) Horizontal distribution

Stratified random sampling with 0.1 m^2 quadrats

Fourteen 0.1 m^2 turves were removed from the study site on a stratified random basis at approximately one month intervals and the animals in each replicate were extracted using a modified Kempson-Lloyd-Ghelardi (1963) heat and light extractor. The preservative used in the extractor was tri-sodium orthophosphate. The animals were later transferred to 70% alcohol. Further details of the sampling and extracting procedures are given in Sunderland et al. (1976). This sampling programme also provided the population density data of each species given in later chapters.

These fourteen replicates are not adequate alone to assess the distribution and the degree of association of the species. Accordingly it is necessary to sum results from different dates but this is not possible with simple frequency data as seasonal density fluctuations will bias the overall picture. As all species were highly aggregated throughout the year (Chapter four) it seemed appropriate to group the replicates from each date into one of two categories, (1) those containing large numbers of animals (centres of aggregation) and (2) those containing few or no animals (no aggregate present), and then to investigate the distribution of the aggregates. The numbers in each category showed no distinct seasonal variation so that a summation of data collected through the year was possible.

There are severe problems in defining aggregations. Usher (1969) did this by successively removing the highest values until the remaining distribution was random, but this method is unsatisfactory with high density populations or with a large quadrat size where there are few zero counts. For the present purpose those quadrats containing more than λ individuals, where $\lambda = \frac{\bar{x}}{2k} \gamma$, were included in the 'aggregate present' category. Those in which the number of individuals $\leqslant \lambda$ were put in the absence category ($\bar{x}$ = the mean, k = k of the negative binomial estimated by the method of maximum likelihood (Bliss & Fisher 1953), and ψ is a function with a χ^2 distribution with 2 k degrees of freedom taken at the 0.5 probability level - see Southwood (1966)).

Contiguous quadrats

To investigate the possibility of microhabitat partitioning that might be undetected in 0.1 m^2 quadrats two series each of 64 0.006 m^2 contiguous quadrats were taken in October 1975. The animals were extracted by sieving after the samples had been dried.

The number of animals under stones

The distribution of animals in relation to different areas in the dune system was determined by counting the numbers of each species under stones.

Three main areas were recognised in relation to the dune succession, these were as follows.

1. The dune crest - which due to frequent sand movement is dominated by marram grass (*Ammophila arenaria* (L.) Link) and sea couch-grass (*Agropyron pungens* (Pers.)). There is very little litter on the surface and the soil profile is poorly developed.

2. The lee side of the dune - (including the main study site). Many additional grass and herb species become abundant, notably *Arrhenatherum elatius* (L.) J. and C. Presl., *Dactylus glomerata* L., *Poa pratensis* L. and *Festuca rubra* L. Furthermore the soil profile is better developed and some surface litter builds up between periods of sand accumulation.

3. A more stabilised area of dune - receiving little wind blown sand. The marram and sea couch grass are less vigorous and the other grasses begin to dominate. There is also a considerable increase in the amount of moss and surface litter. The soil profile is well developed.

A selection of flat stones was marked in each of the three areas, and the numbers of animals under each stone were counted at fortnightly intervals between March and November 1975.

(b) Plant distribution

The distribution of the plants was studied in July 1975 by visually assessing their abundance and cover in each of the 196 2.25 m^2 areas (fig. 2.1a) into which the study site was divided. The Domin scale was adopted for scoring the abundance of each species because it is easy to use and permits a fairly detailed assessment in a short time (Kershaw 1973). The entire site was surveyed in only a few days work.

2.4 RESULTS

(a) Horizontal distribution of animals

Stratified random sampling

The distribution of aggregates of each species on the study site between June 1973 and October 1974 (during which time a 0.1 m^2 quadrat was removed from almost every 1.5 m by 1.5 m block of the site) is shown in figure 2.2. An aggregate is shown to cover an entire block but in fact only 4.4% of a block was removed on any occasion.

Although at first sight no trends are obvious a close examination reveals an uneven distribution. Philoscia muscorum and Armadillidium vulgare have a greater proportion of aggregates in the north westerly half of the study site (i.e. lower end of the figure), Porcellio scaber and Cylindrouilus latestriatus have more on the north-easterly half (i.e. to left of the figure). An analysis of variance shows that these trends are significant but they do not necessarily indicate direct spatial separation. If isolation is resulting from animals specialising in the areas in which they search for food a negative association of aggregates would be expected. This can be tested using Cole's (1949) "Coefficient of interspecific association". The indices of association (tab. 2.1) based on the presence or absence of aggregates give no evidence of spatial isolation. The woodlice are positively associated. Only two of the six coefficients of interspecific association between the millipede and the three species of woodlice are positive, the remainder are not significant, indicating an independent distribution for this species. This suggests that there is very little interaction between them.

Table 2.1 The coefficients of interspecific association between the aggregates of *Porcellio scaber*, *Armadillidium vulgare*, *Philoscia muscorum* and *Cylindroiulus latestriatus* from monthly samples of 14 $0.1m^2$ quadrats. A 1974, B 1975. Significant associations are starred; * denotes $p<0.005$, ** denotes $p<0.001$, ns denotes not significant.

		A.v.	*P.m.*	*C.l.*
A	*P. scaber*	0.48**	0.35**	0.10ns
	A. vulgare		0.37*	0.14ns
	P. muscorum			-0.01ns
B	*P. scaber*	0.78**	0.91*	0.39*
	A. vulgare		0.91*	0.42*
	P. muscorum			0.42ns

Table 2.2 The coefficients of interspecific association between *Porcellio scaber*, *Armadillidium vulgare* and *Cylindroiulus latestriatus* in the second series of 64 $0.006m^2$ contiguous quadrats. Significant associations are starred; " denotes $p<0.01$, ns denotes not significant.

	A.v.	*C.l.*
P. scaber	0.55*	0.18ns
A. vulgare		0.13ns

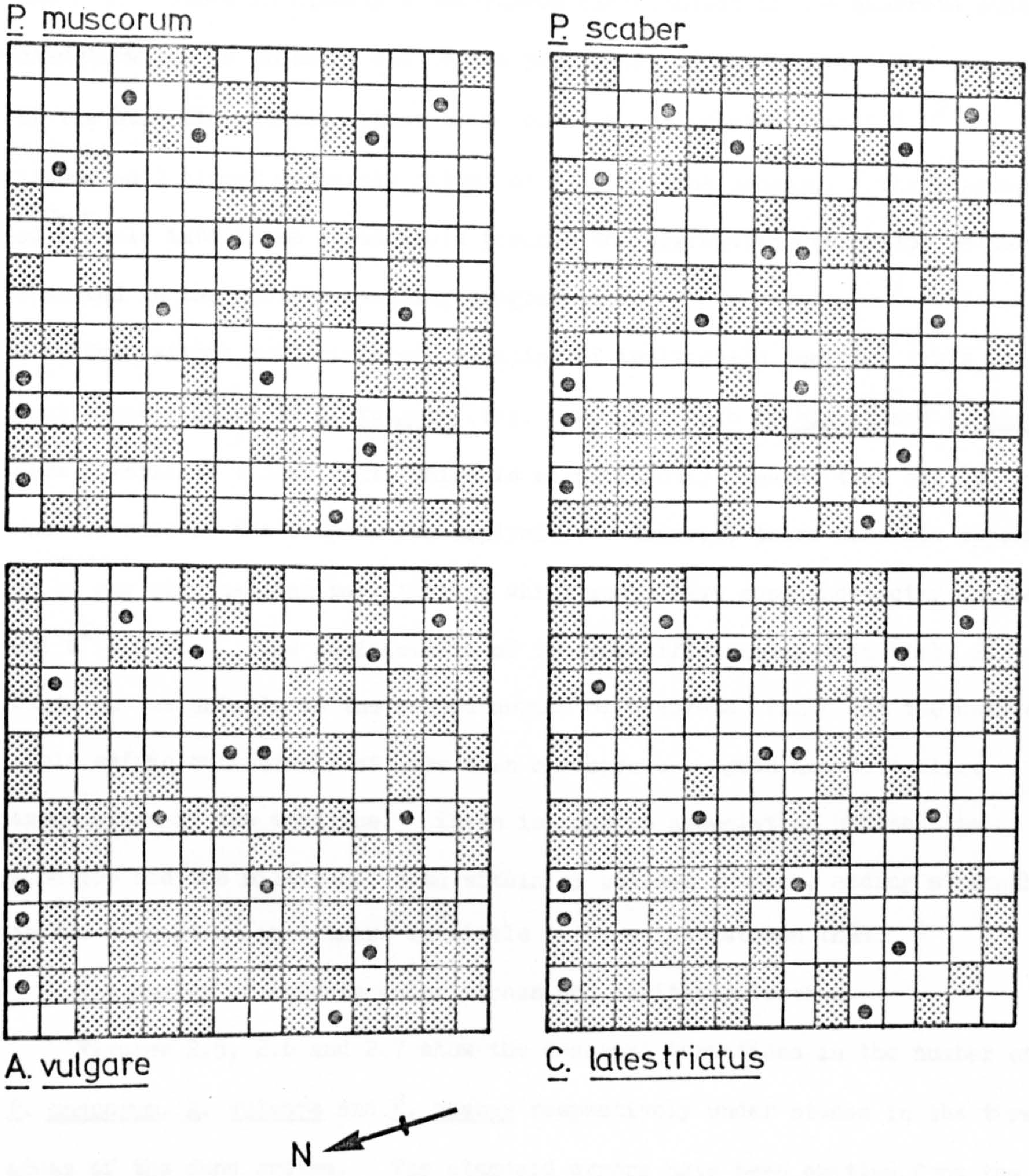
Figure. 2.2 The distribution of aggregates on the study site from June I973 to October I974.

☐ No aggregate.

▩ Aggregate present.

▨ Two samples taken. One containing an aggregate, the other not.

⊡ Block not sampled.


P. muscorum
P. scaber
A. vulgare
C. latestriatus
N

Contiguous quadrats

The numbers of A. vulgare, P. scaber, P. muscorum and C. latestriatus extracted from the two series of contiguous quadrats are shown in figures 2.3 and 2.4. There is clearly a non-random distribution of the quadrats containing animals which is probably due to the patchiness of the sites. The extent of the suitable patches appear to be equal to or greater than 0.1 m^2 and in series 2 almost certainly extend beyond the area sampled. The congregation of animals into these areas would produce the aggregated dispersion pattern observed in the monthly sampling programme.

Even within suitable areas clumping of individuals occurs. This is most clearly shown by A. vulgare (fig. 2.4), but both P. scaber and C. latestriatus have a variance : mean ratio which is significantly greater than one (P. muscorum was too rare in the samples for analysis). However, there does not appear to be any microhabitat partitioning which would have gone undetected in the 0.1 m^2 samples. The coefficients of interspecific association (tab. 2.2), based on the animals in the second series of quadrats, which was the only one to yield sufficient animals of more than one species, again indicate close association of the woodlice. There is also no association between the woodlice and the millipede, both within or between samples, adding strength to the suggestion that there is little interaction between them.

The number of animals under stones and habitat selection

Figures 2.5, 2.6 and 2.7 show the seasonal variations in the number of P. muscorum, A. vulgare and P. scaber respectively under stones in the three areas of the dune system. The standard errors have been omitted from the figures but are included in tables 2.3, 2.4 and 2.5. They are large due to the aggregation of the populations.

There is distinct habitat selection which differs between species and with season. P. muscorum increases in abundance towards the fixed dune area (fig. 2.5). P. scaber (fig. 2.7) and A. vulgare (fig. 2.6) show the reverse trend, increasing towards the crest of the dune. A two way analysis of variance on log (x + 1) transformed data shows these trends to be statistically

Table 2.3 The mean numbers of Philoscia muscorum (±1S.E.) per stone in three different areas, from March to November 1975.

	Dune crest	Lee side of dune	Fixed dune
14 Mar	0.00	0.18 ± 0.12	1.00 ± 0.55
31 Mar	0.18 ± 0.18	0.30 ± 0.21	0.44 ± 0.23
28 Apr	0.18 ± 0.12	0.09 ± 0.09	0.33 ± 0.16
20 May	0.36 ± 0.20	0.45 ± 0.21	1.56 ± 0.45
2 June	0.09 ± 0.09	0.36 ± 0.15	1.67 ± 0.45
15 June	0.00	0.18 ± 0.12	0.73 ± 0.36
30 June	0.00	0.00	1.27 ± 0.63
13 July	0.00	0.00	0.13 ± 0.09
27 July	0.00	0.00	0.07 ± 0.07
9 Aug	0.00	0.00	0.00
25 Aug	0.00	0.09 ± 0.09	0.00
7 Sept	0.00	0.00	0.13 ± 0.09
20 Sept	0.00	0.00	0.13 ± 0.09
5 Oct	0.00	0.00	0.60 ± 0.32
20 Oct	0.00	0.45 ± 0.21	0.33 ± 0.16
3 Nov	0.45 ± 0.31	0.36 ± 0.20	1.20 ± 0.69
18 Nov	0.45 ± 0.21	0.27 ± 0.19	0.13 ± 0.09

Table 2.4 The mean number of *Armadillidium vulgare* (±1S.E.) per stone in three different areas, from March to November 1975.

	Dune crest	Lee side of dune	Fixed dune
14 Mar	1.36 ± 1.07	1.00 ± 0.63	0.61 ± 0.39
31 Mar	5.27 ± 3.21	1.10 ± 0.67	0.94 ± 0.57
28 Apr	12.00 ± 2.25	8.18 ± 2.38	4.50 ± 0.92
20 May	11.00 ± 2.50	5.82 ± 1.07	2.94 ± 0.66
2 June	16.55 ± 4.99	7.45 ± 3.00	5.50 ± 1.71
15 June	12.18 ± 3.98	5.64 ± 1.57	4.80 ± 1.83
30 June	2.27 ± 1.06	0.18 ± 0.12	6.60 ± 2.54
13 July	5.00 ± 1.79	21.82 ± 6.55	6.47 ± 2.91
27 July	5.27 ± 2.85	1.82 ± 0.55	3.33 ± 1.30
9 Aug	0.27 ± 0.27	0.00	2.13 ± 1.73
25 Aug	2.91 ± 0.86	1.27 ± 0.52	1.47 ± 0.67
7 Sept	0. 45 ± 0.31	0.64 ± 0.28	3.47 ± 2.39
20 Sept	1.00 ± 0.36	2.36 ± 0.51	1.93 ± 0.64
5 Oct	1.91 ± 0.62	5.27 ± 2.28	1.80 ± 0.50
20 Oct	1.64 ± 0.89	3.73 ± 1.90	2.53 ± 0.91
3 Nov	0.82 ± 0.54	0.91 ± 0.31	0.67 ± 0.40
18 Nov	0.18 ± 0.18	0.09 ± 0.09	0.00

Table 2.5 The mean numbers of *Porcellio scaber* (±1S.E.) per stone in three different areas, from March to November 1975.

	Dune crest	Lee side of dune	Fixed dune
14 Mar	0.27 ± 0.14	0.36 ± 0.24	0.22 ± 0.17
31 Mar	0.82 ± 0.33	1.40 ± 0.69	0.44 ± 0.34
28 Apr	25.55 ± 8.40	6.82 ± 2.96	5.67 ± 2.64
20 May	23.73 ± 6.49	5.27 ± 2.40	4.89 ± 1.80
2 June	39.09 ± 13.63	2.91 ± 1.63	6.75 ± 3.55
15 June	37.00 ± 18.70	3.45 ± 2.39	2.27 ± 0.99
30 June	15.55 ± 13.57	0.09 ± 0.09	6.27 ± 3.11
13 July	9.45 ± 5.41	11.09 ± 4.73	7.00 ± 4.88
27 July	14 .27 ± 5.43	2.09 ± 1.10	0.40 ± 0.16
9 Aug	0.55 ± 0.45	0.00	0.33 ± 0.21
25 Aug	17.00 ± 4.34	2.09 ± 1.28	0.80 ± 0.55
7 Sept	13.36 ± 6.41	0.18 ± 0.12	1.60 ± 1.09
20 Sept	13.45 ± 5.23	5.09 ± 3.00	1.13 ± 0.41
5 Oct	26.00 ± 12.64	6.64 ± 2.96	1.07 ± 0.33
20 Oct	28.18 ± 12.19	6.27 ± 4.31	1.53 ± 0.83
3 Nov	24.45 ± 7.61	7.82 ± 6.30	0.27 ± 0.15
18 Nov	14.00 ± 4.30	0.64 ± 0.39	0.13 ± 0.09

Figure. 2.3 The numbers of *C. latestriatus* extracted from the first series of 64 0.006m^2 contiguous quadrats, taken in October 1975. *P. scaber*, *P. muscorum* and *A. vulgare* were represented only by one or two (*A. vulgare*) specimens. The location of these is indicated by the letters P.s., P.m. and A.v. respectively.

	3		1 A.v.				
3	6	4 A.v. P.s.		2			
2	3	1			1		1
	1		1	2	1	1	
			1	1	2	1 P.m.	
		2					
				1			
							1

Figure. 2.4 The numbers of animals extracted from the second series of 64 0.006m^2 contiguous quadrats, taken in October I975.

A. vulgare

	2	11	1	11	19	2	2
		11	3	1	5	9	6
6			1	12	1	10	2
2		1		6	4		
7	13					1	
3	19		1			1	
2				1			

P. scaber

	1				3	1	2
1		2	2	1	1	2	4
			1			2	
2	1		1		3		
3	1	1	1				
							1

C. latestriatus

4		3			4		1
		3	2		1	7	1
	2	3	2			5	
2		1	2	3	2		
1	4				1	3	
	2				1		1
2						1	1
1			1	1	3		

Figure. 2.5 The mean number of *Philoscia muscorum* per stone in three different areas of the dune system, from March to November 1975. (●——●) dune crest. (●---●)lee-side of dune. (●····●) stabilised dune.

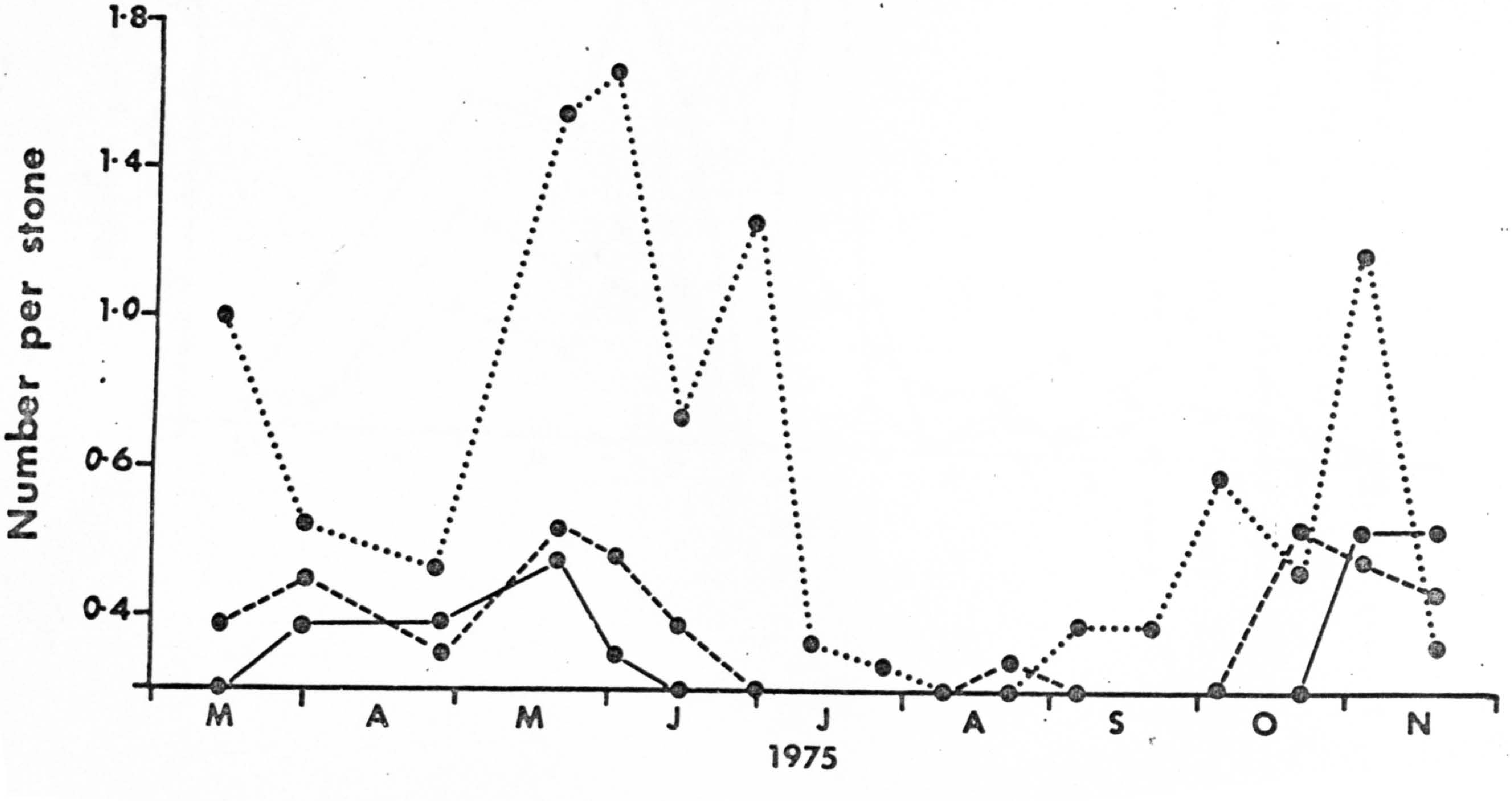
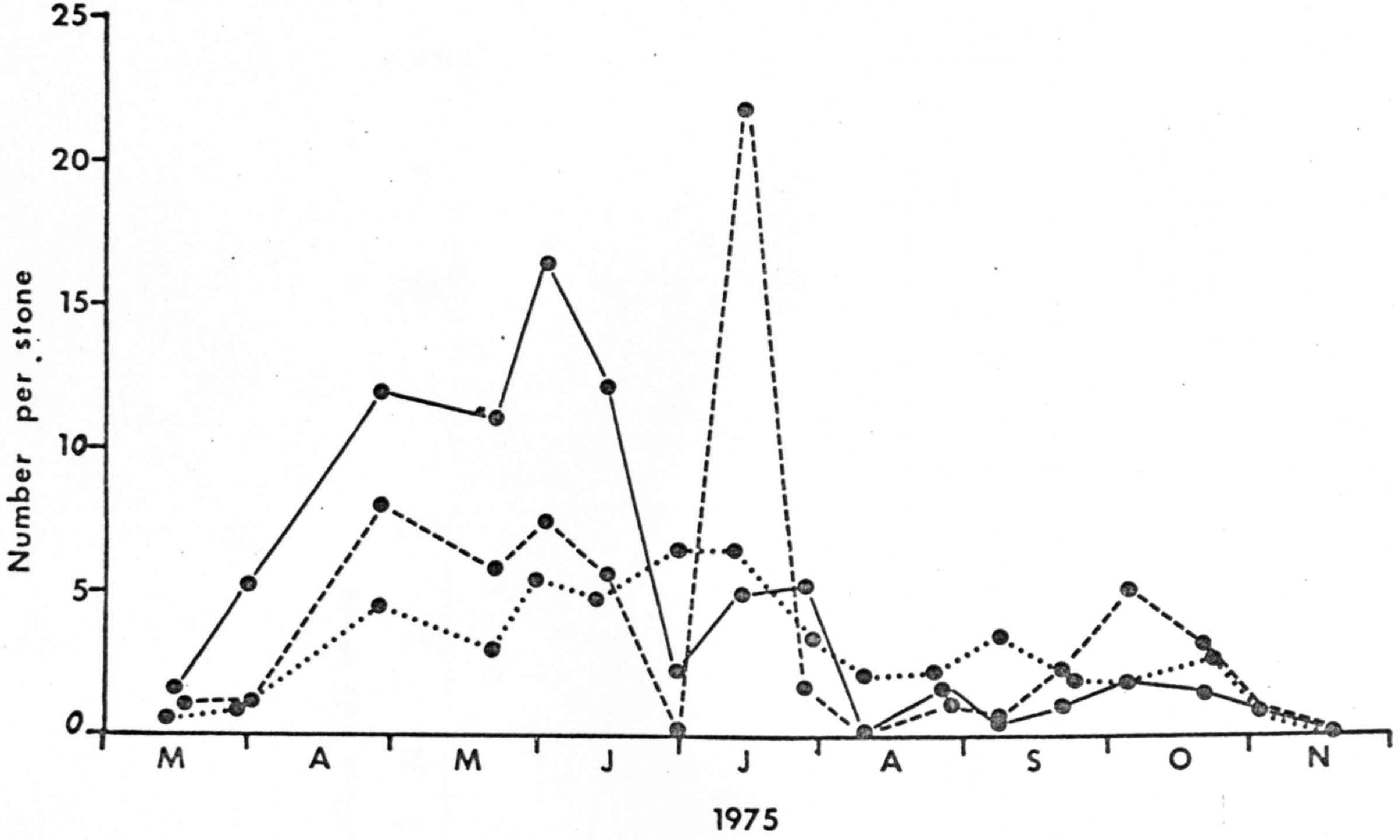
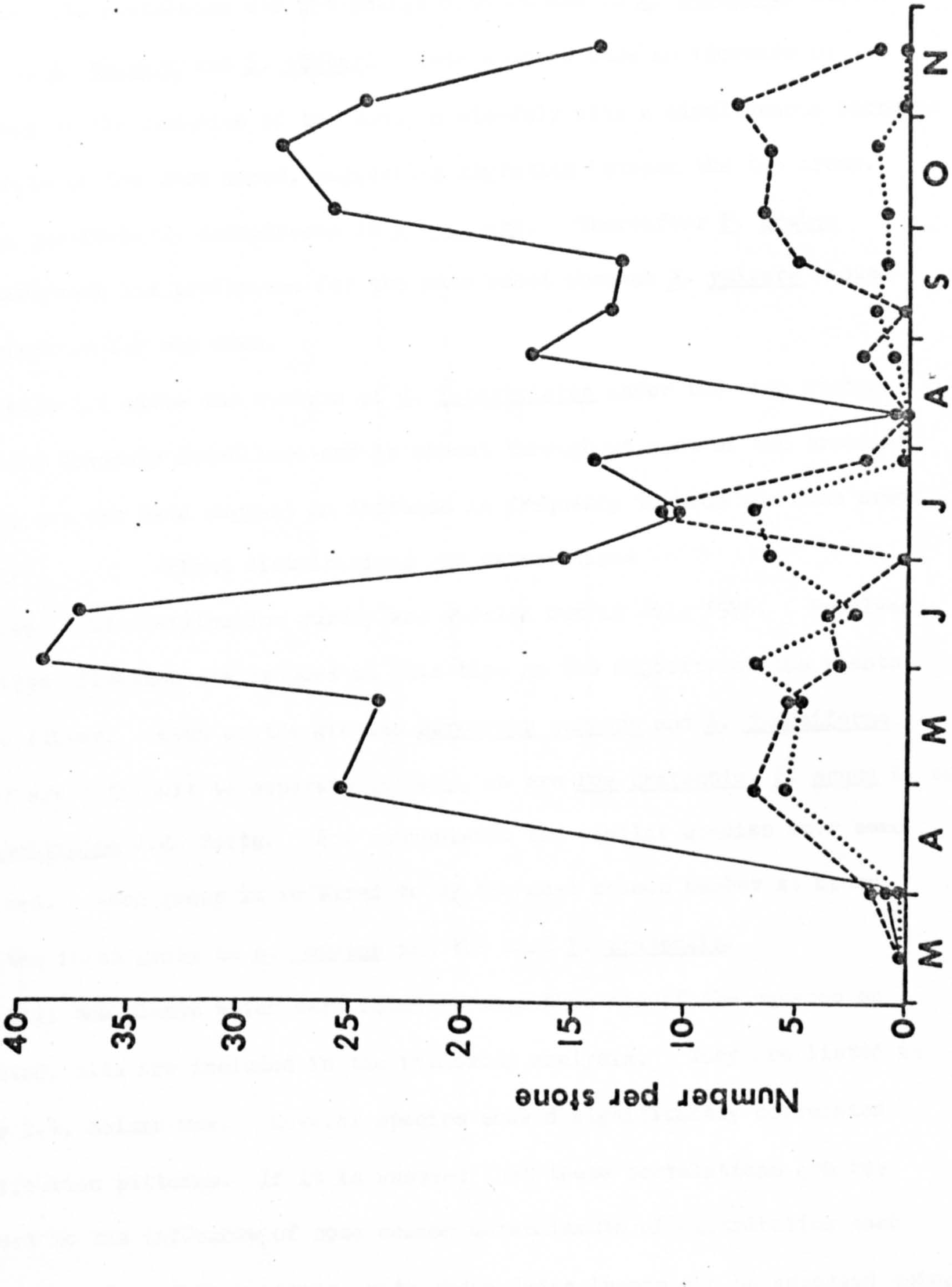

1·8
1·4
1·0
0·6
0·4
Number per stone
M
A
M
J
J
A
S
O
N
1975

Figure. 2.6 The mean number of *Armadillidium vulgare* per stone in three different areas of the dune system, from March to November 1975. (●——●) dune crest. (●---●) lee-side of dune. (●····●) stabilised dune.



25
20
15
10
5
0
Number per stone
M
A
M
J
J
A
S
O
N
1975

Figure. 2.7 The mean number of *Porcellio scaber* per stone in three different areas of the dune system, from March to November 1975. (●——●) dune crest. (●---●) lee-side of dune. (●····●) stabilised dune.


Number per stone
0
5
10
15
20
25
30
35
40
M
A
M
J
J
A
S
O
N
1975

significant. (F and p values for habitat selection of P. muscorum, P. scaber and A. vulgare respectively are: $F = 3.4$, $p < 0.001$; $F = 74.64$, $p < 0.001$; $F = 4.08$, $p < 0.025$).

The site preference did not change with season in P. muscorum, but it did so in A. vulgare and P. scaber. Both species show an increase in frequency on the lee-side of the dune in mid-July with a simultaneous decrease of animals on the dune crest, suggesting migration between the two areas. This is particularly conspicuous in A. vulgare. Thereafter P. scaber re-established its preference for the dune crest whereas A. vulgare showed no preference for any area.

Table 2.6 gives the numbers of C. latestriatus under the same stones. It is not commonly found here and is absent throughout most of the breeding season, but the data suggest an increase in frequency towards the dune crest.

(b) Plant distributions and associations

The plant distribution survey was carried out in July 1975. Problems with identification are reduced at this time as the majority of the plants are in flower. Even so the grasses Agropyron pungens and A. junceiforme (Love) are difficult to separate quickly, as are Poa pratensis, P. annua L. and P. subcaerulea J.E. Smith. For convenience the similar species have been combined. Each group is referred to by the most common member at Spurn, thus the first group is A. pungens and the last P. pratensis.

Only the plants which were found in more than ten of the squares on the study site are included in the following analysis. They are listed in table 2.7, column one. Several species showed significantly correlated distribution patterns. If it is assumed that these correlations are due in part to the influence of some common determinants of distribution then the association of each species with those determinants can be assessed using a 'common factor analysis' (Nie et al. 1975). Furthermore all the plants loading significantly on any single factor and with the same sign can be taken to form a positive association. Thus any factor can separate out three groups

Table 2.6 The mean numbers of Cylindroiulus latestriatus (±1S.E.) per stone in three different areas, from March to November 1975.

	Dune crest	Lee side of dune	Fixed dune
14 Mar	2.27 ± 0.91	0.36 ± 0.28	0.17 ± 0.09
31 Mar	1.36 ± 0.45	1.20 ± 0.57	0.39 ± 0.14
28 Apr	0.73 ± 0.35	0.73 ± 0.63	0.33 ± 0.18
20 May	0.64 ± 0.31	0.18 ± 0.12	0.22 ± 0.13
2 June	0.00	0.45 ± 0.31	0.00
15 June	0.00	0.00	0.00
30 June	0.00	0.00	0.00
13 July	0.00	0.09 ± 0.09	0.07 ± 0.07
27 July	0.00	0.00	0.00
9 Aug	0.00	0.00	0.00
25 Aug	0.00	0.00	0.00
7 Sept	0.09 ± 0.09	0.00	0.00
20 Sept	0.55 ± 0.31	0.36 ± 0.20	0.00
5 Oct	0.64 ± 0.20	0.18 ± 0.12	0.20 ± 0.14
20 Oct	1.64 ± 0.91	0.82 ± 0.58	0.27 ± 0.27
3 Nov	0.64 ± 0.28	1.00 ± 0.65	0.53 ± 0.31
18 Nov	0.45 ± 0.21	0.09 ± 0.09	0.13 ± 0.09

of plants. (1) Those plants forming an association due to a common positive loading on the factor, (2) an association due to a negative loading, and (3) those which are uninfluenced by that factor and therefore have a non-significant loading. The latter group can be further subdivided by extracting more factors. The first six factors accounted for 51.4% of the total variance, table 2.7.

Ammophila arenaria, the most conspicuous plant, was found in every 2.25 m^2 section of the study site. It was extracted as a major component of both factors one and two, which together accounted for approximately one quarter of the total variance. In factor one it has a positive loading in association with the grasses Arrhenatherum elatius, Dactylus glomerata and Poa pratensis. Convolvulus arvensis L. was the only plant with a significant negative loading on factor one. A. elatius and the other associated grasses are characteristic of semi-fixed to fixed dune conditions and occur more towards the north westerly end of the site (fig. 2.1e), whereas C. arvensis occurs in their absence in open sandy places towards the dune crest (fig. 2.1d). Ammophila arenaria and Agropyron pungens have a strong negative association with factor two. Both plants are common dune stabilising and building grasses. A. pungens can withstand high salt concentrations and is often present in the very early stages of dune succession (Salisbury 1952). It forms the densest grass tussocks towards the dune crest (fig. 2.1a). Plantago lanceolata L. loads positively on factor two as, to a lesser extent, do Galium verum L., Hypochoeris radicata L., Heracleum sphondylium L. and Taraxacum officinale Weber. Like C. arvensis the latter group are found in areas with only sparse grass cover. However, unlike C. arvensis they produce a dark compact turf.

Cerastium fontanum Baumgarten, Crepis capillaris (L.) and Diplotaxis muralis (L.) are associated with factor three. Factor four influences the distribution of Calystegia soldanella (L.), Cirsium arvense (L.) and Hippophae rhamnoides L. (which is present only as small developing plants as it is cut back annually), and factor six is loaded heavily on a single species, Ononis repens L.. Hypochoeris radicata loads positively not only on factor

Table 2.7 Factor matrix showing the relationships between each plant species
* donotes plants forming a positive association under one factor, and
‡ donotes plants forming a negative association.

Plant species	Factor one	Factor two	Factor three	Factor four	Factor five	Factor six
Ammophila arenaria	0.594*	-0.416‡	0.091	0.180	-0.015	-0.161
Agropyron pungens	0.184	-0.493‡	-0.039	0.195	0.130	-0.055
Arrhenatherum elatius	0.597*	-0.089	-0.009	-0.016	-0.141	0.221
Festuca rubra	-0.095	0.085	-0.198	-0.177	-0.611‡	0.188
Carex arenaria	-0.017	0.022	0.398	-0.318	0.652*	0.032
Dactylus glomerata	0.482*	0.215	0.287	0.016	0.050	-0.005
Poa pratensis	0.566*	-0.232	0.241	-0.133	-0.010	-0.195
Convolvulus arrensis	-0.608‡	-0.193	-0.056	0.094	-0.128	0.231
Galium verum	-0.018	0.394*	0.053	-0.016	0.110	0.010
Ononis repens	0.105	0.050	0.015	-0.086	-0.137	0.852*
Calystegia soldanella	-0.092	0.001	-0.002	0.508*	0.026	-0.084
Heracleum sphondylium	-0.011	0.332*	-0.281	-0.034	0.173	0.102
Plantago lanceolata	0.162	0.630*	0.095	0.073	-0.116	0.001
Cirsium arvense	-0.138	-0.213	-0.124	0.618*	0.038	0.110
Hippophae rhamnoides	0.164	0.019	0.115	0.471*	-0.084	-0.118
Cerastium fontanum	0.189	-0.034	0.496*	-0.014	0.064	-0.050
Taraxacum officinale	-0.010	0.365*	-0.039	-0.035	0.292	0.077
Hypochoeris radicata	-0.021	0.327*	-0.033	-0.067	0.417*	-0.019
Rosa spp	0.147	-0.022	-0.165	-0.130	-0.236	-0.175
Rubus spp	0.132	-0.091	0.040	0.083	-0.062	-0.200
Crepis capillaris	-0.060	0.154	0.464*	0.091	0.113	0.063
Diplotaxis muralis	0.055	-0.002	0.554*	-0.060	0.097	-0.011
Centauria nemoralis	0.329	0.032	-0.219	-0.025	0.002	0.102
Percentage of variance accounted for	12.5	11.2	8.8	7.0	6.2	5.7

two, but also on factor five in association with Carex arenaria L. which is common along trampled pathways through the dune (fig. 2.1 f). Festuca rubra loads negatively on factor five.

No biological significance is attached to the plant associations described above, nor indeed was any explanation searched for. The exercise was done to obtain the principle plant associations which could then be included in an analysis to find the factors influencing the animal distributions. A summary of the plant groupings obtained is shown in table 2.8. This table also includes one species of rose (Rosa spp - probably R. pimpinellifolia L.) which, though localised, was fairly abundant.

(c) Factors influencing the animals horizontal distribution

Relationship with plants on the study site.

The presence or absence of each plant group in each of the 196 squares of the study site was determined using the simple criteria laid out in table 2.8. For example, group IV would be present if three or more of the five species in that group were found together, and group V would be present if either Cerastium fontanum (the most abundant species in that group) plus one other were found within one square or if the cover value, on the Domin scale, of C. fontanum alone was equal to or greater than three. The presence of any relationships between the animal and plant distributions were then searched for by means of a series of two by two contingency tables in which the distribution of the animals' aggregations were cross-tabulated with the distribution of the plant associations. This method measures the departure from independence (i.e. no relationship) between the animal and plant association being tested (Southwood 1966). The statistical significance of such departures was determined using the chi-square (χ^2) test. The results are shown in table 2.9.

From table 2.9 it can be seen that the determinants of the millipede distribution were different from those influencing the woodlice, particularly A. vulgare and P. muscorum. This could be due to the distribution of specific food plants, to microclimatic conditions or to other factors.

Table 2.8 List of plant associations with notes on simple criteria used to determine the presence of those groups in any area of the study site. The figures in column two refer to the plants estimated cover value on the Domin scale.

	Plant Association	Conditions
I	*A. arenaria* *A. elatius* *D. glomerata* *P. pratensis*	Either/both *A. elatius* and *P. pratensis* have cover values ≥ 1 or/ all four species present together.
II	*A. arenaria* *A. pungens*	*A. pungens* must have a cover value ≥ 2
III	*C. arvensis*	The cover value ≥ 2
IV	*G. verum* *H. sphondylium* *I. officinalis* *H. radicata* *P. lanceolata*	Three species out of the five must be present together.
V	*C. fontanum* *C. capilaris* *D. muralis*	Either/ *C. fontanum* and one other must be present or/ *C. fontanum* must have a cover value ≥ 3
VI	*C. soldanella* *C. arvense* *H. rhamnoides*	Either/ *C. arvense* and one other must be present or/ *C. arvense* must have a cover value ≥ 2
VII	*C. arenaria* *H. radicata*	*C. arenaria* must be present
VIII	*F. rubra*	The cover value of *F. rubra* ≥ 4
IX	*O. repens*	The cover value of *O. repens* ≥ 3
X	*Rosa* spp.	*Rosa* must be present

Table 2.9 Relationships between macrodecomposer species and main plant associations which are significant at the 5% level or less. + denotes a positive relationship; - denotes a negative relationship. Roman numerals indicate same plant groups as in table 2.8.

Plant Association	*A. vulgare*	*P. scaber*	*P. muscorum*	*C.latestriatus*
I	+		+	+
II	-			
III				
IV				
V				
VI				
VII		-		-
VIII				
IX				
X				+

The most important part of the diet of the isopods and diplopod at Spurn was formed by dicotyledons (tab. 1.1). As none of the isopods showed a site preference due to the presence of dicots and the diplopod was positively associated with one dicot only it seems most unlikely that the distribution of food plants had an important effect on the microdistribution of these four species. Bernays and Chapman (1970) found a similar situation in grasshoppers.

2.5 DISCUSSION

Three important conclusions can be drawn from this study. Firstly the horizontal distribution of the millipede was uninfluenced by the presence or absence of woodlice suggesting that there was very little interaction between them. Secondly although the woodlice had a closely associated microdistribution pattern on the study site there was a marked difference in the habitat preference of *Philoscia muscorum* and the other two. Thus *P. muscorum* was most abundant in the stable dune area whereas *Armadillidium vulgare* and *Porcellio scaber* increased in abundance towards the dune crest. Thirdly the horizontal distribution of each species was probably not influenced by the distribution of food material.

These findings, plus the work on the vertical distribution (next chapter) provide evidence both for and against the hypothesis that spatial separation could be an important niche dimension in macrodecomposers because of specialisation in the areas in which they search for food.

The difference in habitat preference shown by *P. muscorum* from *A. vulgare* and *P. scaber* reflects their differential survival in these habitats. Evidence for this is provided in chapter four where the changing abundance of each species is related to variations in the environmental conditions on the site. Prior to 1973 the study site was approaching the 'dune heath' stage of development and *P. muscorum* was the dominant species in those conditions. However as a result of sand deposition in the successive winters of 1973/74 and 1974/75 there was a population crash in *P. muscorum*. At the same time

P. scaber and A. vulgare peak numbers rose 2½ and 3½ fold respectively.

The preference of P. muscorum for the more stable dune area and P. scaber and A. vulgare for the dune crest is unlikely to be related to different food requirements for two reasons. Firstly because it was shown in section 2.4c that the presence of the most important food plants were of little value in determining their microdistribution and secondly because many of the plant species are present in each area, although in different relative proportions. It is more likely that humidity tolerances play an important part, as is the case for the three species of diplopod studied by Barlow (1957). The dune crest becomes very dry at times due to the poor water retaining properties of clean sand. For this reason the plants there either have deeply penetrating roots (Ammophila arenaria, Agropyron pungens) or grow and flower in the spring (Convolvulus arvensis) before conditions become too unfavourable (Salisbury 1952).

The greater organic content and surface litter characteristic of the stable dune buffers the soil against severe water loss and helps to maintain a high humidity near the surface. Given these different properties of each site one could predict from the data presented by Edney (1954) that P. muscorum would be more abundant in the stable dune and the others would favour the drier conditions towards the crest. Furthermore if the crest became too dry for A. vulgare and P. scaber the observed migration onto the lee-side of the dune might be predicted. Similar observations on spatial separation in relation to varying microclimatic conditions in a seral ecosystem are reported for bog inhabiting pselaphid beetles (Reichle 1969).

However humidity preferences alone cannot provide the full answer for P. scaber is more abundant on the crest than A. vulgare and maintains this difference throughout the summer in contradiction of their humidity tolerances. Other factors such as the ease with which they can locate daytime refuges or their ability to right themselves once upturned may also be of importance.

P. scaber and P. muscorum are prominent members of the woodland isopod fauna in Britain and here too show spatial separation (Brereton 1957). The same author found A. vulgare to be present only in open fields and so was spatially isolated from the woodland species.

The evidence by which the distribution of the millipede can be judged is poor because it is rarely found under stones. However the data suggest that like P. scaber and A. vulgare it increases in abundance toward the dune crest.

From the above discussion it appears that there is little evidence of spatial separation between three of the species at Spurn. This could be resolved if there were microhabitat differences. The two sampling programmes (i.e. stratified random and contiguous, quadrats) should reveal this if it is present.

The data suggest that C. latestriatus interacts little with the woodlice. Thus its distribution on the study site is random with respect to them. The next chapter on vertical distribution indicates why this is probably so.

However Cole's Index of Interspecific Association shows that the woodlice aggregates occur together too often for them to be considered independent. They have a strong affinity for the same sites, even at a sample size of 0.006 m^2. It should be noted however that their distribution is associated not with the most frequently eaten food plants but with dense grassy areas (tab. 2.9) (in the case of P. muscorum and A. vulgare at least). Sutton (1966) similarly found the distribution of P. muscorum, Trichoniscus pygmaeus Sars and Glomeris marginata (Villers) to be very closely related to the grass distribution in limestone grassland near Oxford. It is possible that the grass matrix provides the most suitable physical conditions in which the animals can operate, but it may also maintain the best microclimatic conditions.

The vertical separation (next chapter) and independent microhabitat distribution of C. latestriatus and the horizontal separation of P. muscorum from A. vulgare and P. scaber fits well with the hypothesis of spatial separation. However it is difficult to reconcile with this the lack of any consistent separation of P. scaber and A. vulgare at Spurn and the high positive association of isopods in any one area (tabs: 2.1 & 2.2). There are three likely situations in which a high positive association could occur without invalidating the hypothesis:

(1) Migration. Movements of *P. scaber* and *A. vulgare* are indicated in the present study and are suspected in *P. muscorum* (Sunderland et al. 1976). Migration would enable each species to penetrate all areas of the dune and maintain a greater overlap in distribution than would otherwise be possible. Furthermore differences in migration pattern of *P. scaber* and *A. vulgare* just before the young are released produce a temporary and partial separation which may result in a reduced overlap of food search areas of the juveniles.

(2) Since the degree of association between the species was based on animals extracted from samples taken during the daytime the observed distribution may be related to daytime shelter sites. Area specialisation during feeding activity after dark is therefore not necessarily precluded.

(3) There could also be vertical separation. Studies on the vertical distribution of each species are reported in the next chapter.

CHAPTER THREE

VERTICAL DISTRIBUTION

3.1 INTRODUCTION

Many collemboles and acarines have been shown to occupy specific subhorizons in the soil profile (Davis 1963, Usher 1975, Curry 1971) but no studies have indicated this for Isopoda and Diplopoda. Furthermore the effect of the well documented vertical migrations of soil arthropods (Dowdy 1944, Biernaux & Baurant 1964, Bocock & Heath 1967, Usher 1975) on this implied vertical partitioning of the habitat has received little attention. Only Sutton (1966) and Anderson (1974) mention that the separation is likely to be reduced when the surface fauna is driven down by unfavourable microclimatic conditions.

There is a considerable amount of information concerning the effect of microclimatic conditions on the behavioural responses of woodlice & millipedes in the laboratory (Cloudsley-Thompson 1951; Perttunen 1953; Edney 1954; Peitsalmi 1974 and others). However, despite both Miller (1938) and Edney (1951) stressing the need for information on their effect on the distribution of isopods in the field, relatively few such studies have been made, as is apparent from the comments of Edney (1968) and Sutton (1972).

This chapter reports the results of studies on the vertical distribution of *Armadillidium vulgare*, *Porcellio scaber*, *Philoscia muscorum* (Isopoda) and *Cylindroiulus latestriatus* (Diplopda). The effects of temperature and relative humidity on the vertical distribution of these macrodecomposers are described and the observed spatial distribution is discussed in relation to niche separation.

3.2 METHODS

(a) Determination of vertical distribution

Four cores of turf each $0.05 m^2$ and 12-15 cm in depth were placed in fine mesh nylon bags and embedded in the ground on the study site. Two weeks were allowed for settling before twelve animals of each species were put into each bag. Two weeks later the turves were lifted and sectioned into five layers. Each section was placed in a separate polythene bag and taken to the laboratory where it was hand sorted within 12 hours of collection.

The five layers relate to the soil profile as follows:

1. Vegetation zone: the aerial vegetation above the surface of the sand (animals running over the surface were included in this fraction);
2. Litter zone: a 3-4 cm thick surface layer of recently accumulated sand with a small amount of freshly dead litter dispersed within it;
3. Root zone: a dark band of about 3 cm, composed of old decomposed litter (see Davis, Hassall & Sutton 1977) which is compressed and thoroughly bound up with plant roots;
4. Sub-root zone: 3 cm of lighter coloured soil containing a little humous and deeper roots;
5. Sand zone: the material between 9 cm and 12 cm below the surface consisting of sand and deeply penetrating roots.

The method worked well except in the dry conditions of July and August when, as the bags were lifted, loose sand from the surface layers and the animals in it became mixed with material from the deeper zones. In addition the mortality of the woodlice, particularly _P_. _muscorum_, was so great at that time that too few animals were recovered for satisfactory analysis. Due to these difficulties the July and August vertical distribution results have not been used in the analyses described below.

(b) Measurement of temperature

A Grant multichannel continuous temperature recorder was used to measure the temperature at the time of sampling and throughout the previous night at 0.5, 1.0, 1.5, 2.5, 3.0, 3.5, 6.0 and 8.0 cm below the soil surface and in the air 2 cm above soil level. In addition, the integrated mean temperature was measured using the sucrose inversion technique (Berthet 1960). Temperatures were recorded from 14 sites at 4 depths: 2 cm, 4 cm, 6 cm and 11 cm below the sand surface. After October 1974 measurements were made of the maximum and minimum temperatures in the litter layer during the two week periods between sampling dates.

(c) Measurement of relative humidity

The relative humidity of the air spaces in each layer of the soil profile was measured using cobalt thiocyanate papers positioned by means of a perspex holder (for details see Davis et al 1977). After two hours in the soil the holder was lifted and the colour of the papers compared with standards following the procedure of Solomon (1957). Two probes were used on each sampling date.

Saturation deficits were calculated from the relative humidity and daily temperature records, but as this did not improve interpretation of the results only the original humidity data are presented below.

3.3 RESULTS

(a) Vertical distribution

Data from replicates on each date were pooled and a grouped frequency analysis performed to calculate the mean depth of each species. The seasonal variation in the mean depth of the woodlice and millipedes in the soil are shown in figure 3.1. These data show that there are definite seasonal fluctuations in the vertical distribution of all four species and that they are consistently separated by differences in their mean depths.

They are nearest the surface in spring and Autumn and deeper in winter and summer. Cylindroiulus latestriatus is always the deepest, Philoscia muscorum and Porcellio scaber are always nearest the surface and Armadillidium vulgare is intermediate. A two way analysis of variance without replication (Sokal & Rohlf 1969) shows that the seasonal fluctuations and the difference in mean depth of each species are very significant ($F = 4.81$, $P < 0.001$ and $F = 60.22$, $P \ll 0.001$ respectively).

The mean depth of each species (± 2.S.E.) calculated using the 15 months data combined is shown in figure 3.2 along with the percentage of each species in each layer. From figure 3.2 it can be seen that although there are significant differences in the mean depth of each species major differences in the vertical distributions are apparent only between the woodlice on one hand and the millipede on the other. The former have a small spread about the mean and are mainly litter inhabitants; P. muscorum, P. scaber and A. vulgare

Figure. 3.I Seasonal changes in mean depth (± I SE) of *Philoscia muscorum* (○——○), *Porcellio scaber* (▲——▲), *Armadillidium vulgare* (●——●) and *Cylindroiulus latestriatus* (△——△).

Dashed lines indicate the period when the samples were too dry for adequate separation of the layers.

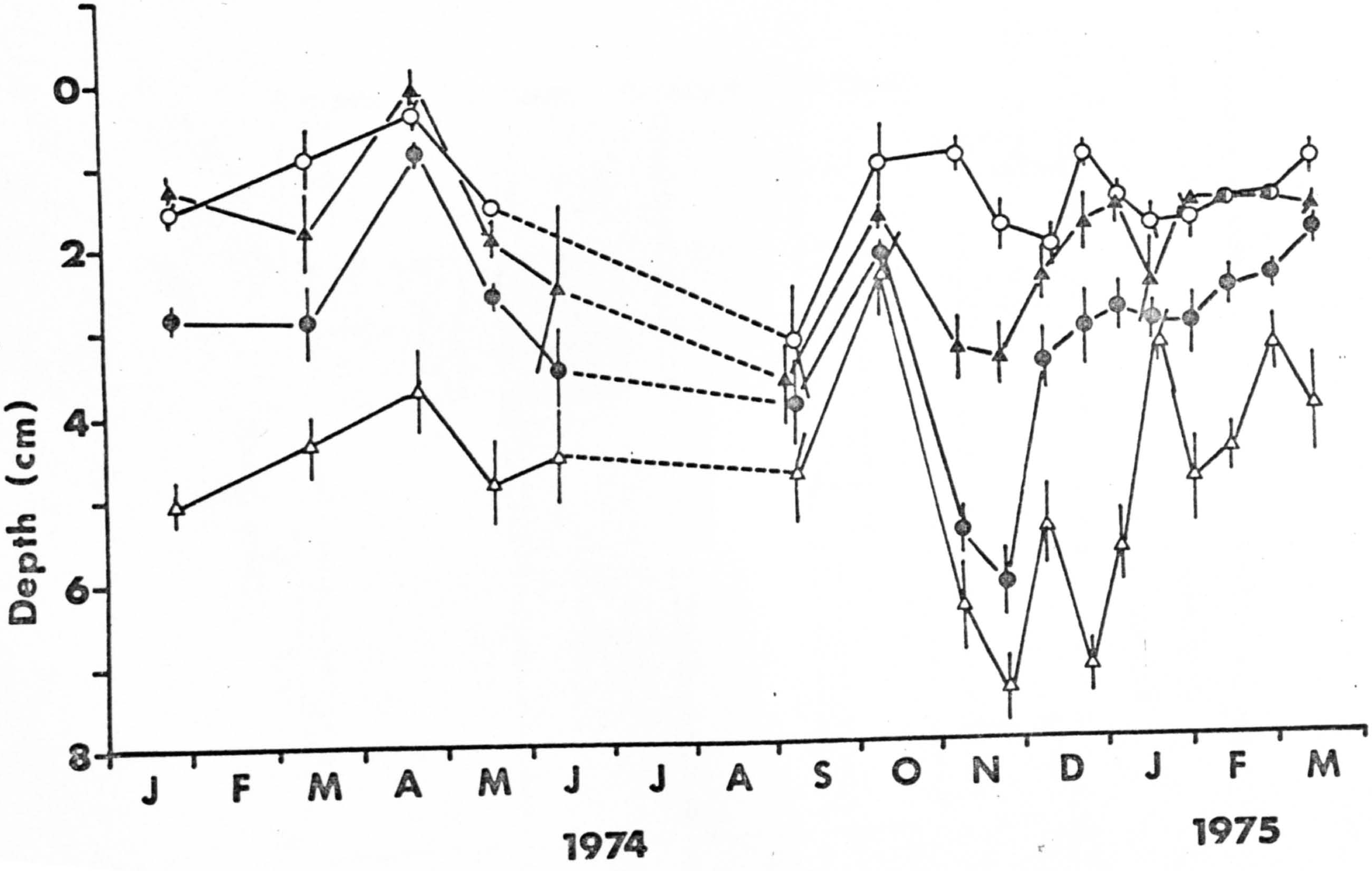
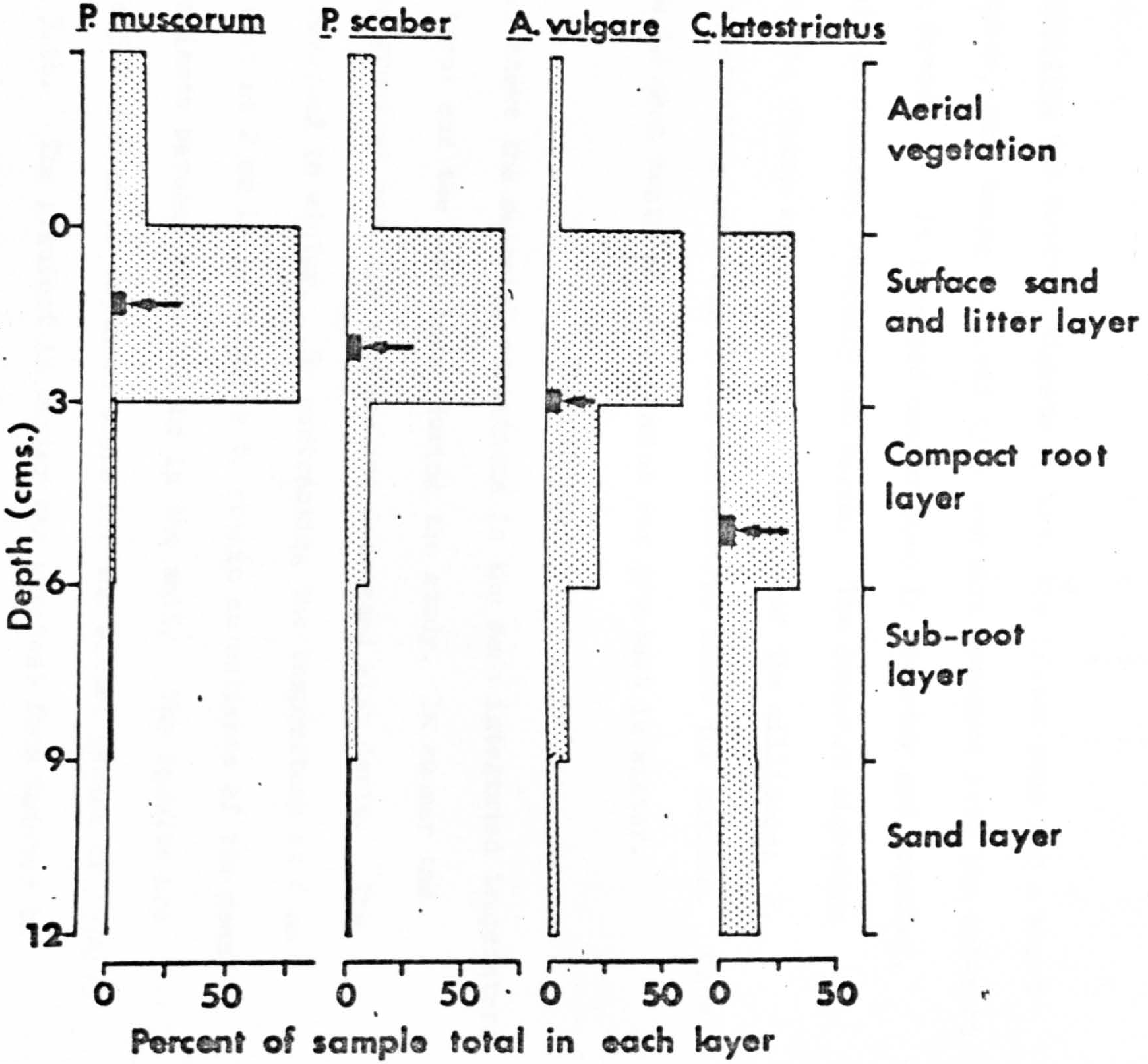

Depth (cm)
0
2
4
6
8
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1974
1975

Figure. 3.2 Percentageof the individuals extracted from each layer. ← indicates the mean depth. The solid black bars denote ± 2 SE. Sample sizes are; *Philoscia muscorum*- 42I, *Porcellio scaber*- 552, *Armadillidium vulgare*- I089, *Cylindroiulus latestriatus*- 783.


P. muscorum
P. scaber
A. vulgare
C. latestriatus
Depth (cms.)
0
3
6
9
12
Aerial vegetation
Surface sand and litter layer
Compact root layer
Sub-root layer
Sand layer
0
50
0
50
0
50
0
50
Percent of sample total in each layer

had 94%, 81% and 64% respectively of the populations above 3 cm. C. latestriatus was spread more evenly throughout the layers and was mainly a root layer inhabitant with only 33% above 3 cm.

In the summer the woodlice underwent a marked downward migration, but this was still not sufficient to completely avoid the effects of desiccation which caused particularly heavy mortality in P. muscorum. Nearly all the enclosed specimens of this species died during June and July. In contrast C. latestriatus moved relatively little during the summer when it was centred in the root zone.

C. latestriatus did however migrate up into the litter zone for a short period in October, this being followed by a downward movement into the sub-root zone early in November. It remained deeper down in November and December, moving up again in January, February and March. The downward migration of the woodlice in winter was not as great as that of the millipede; P. muscorum not penetrating more than a few centimetres below the surface. Thus the difference in mean depth of each species was greatest in winter.

(b) Temperature

Figure 3.3 shows the seasonal variations in the mean integrated temperature of the litter layer and the sand layer during the study. In summer the temperature was greatest near the surface and decreased with depth. The situation was reversed in winter. By subtracting the temperature at 4 cm and 6 cm from that at 2 cm it is possible to obtain an estimate of the mean temperature gradients between these depths in the soil. The results are shown in figure 3.4a and on an expanded scale for the winter period of 1974/75 only in figure 3.4b. The gradient in winter was greatest from October to December when the difference in temperature between the layers was significant at the 1% level.

When the animals descended in winter and returned to the surface in spring the mean integrated temperature was between 5^{o} and 10^{o}C. However, there is no correlation between the depth of any species and the temperature

Figure. 3.3 Mean integrated temperature (°C) at 2 cm (●——●) and at II cm (○——○) below the surface of the sand from January I974 to March I975. Temperature at 4 cm and 6 cm omitted for clarity.

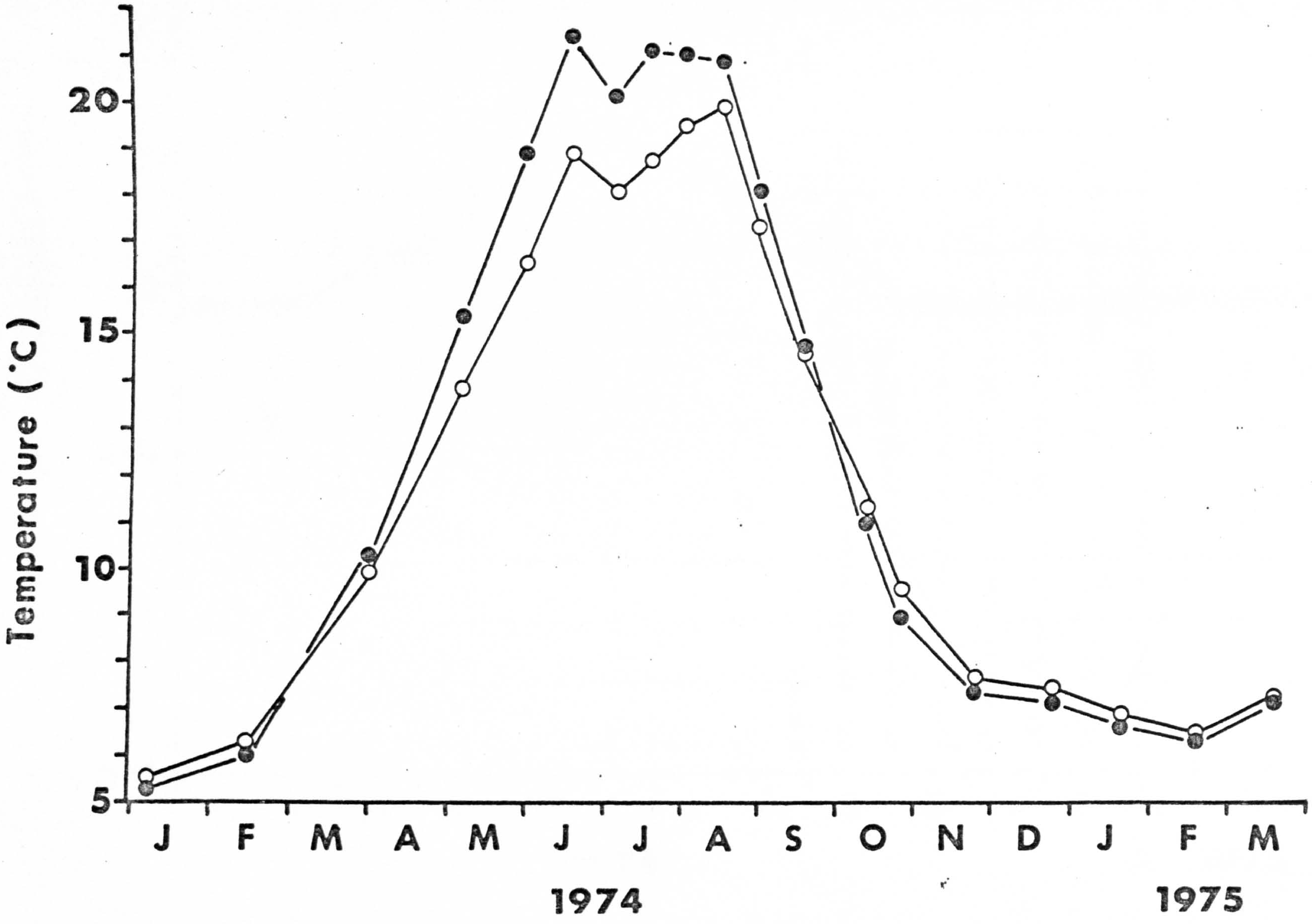
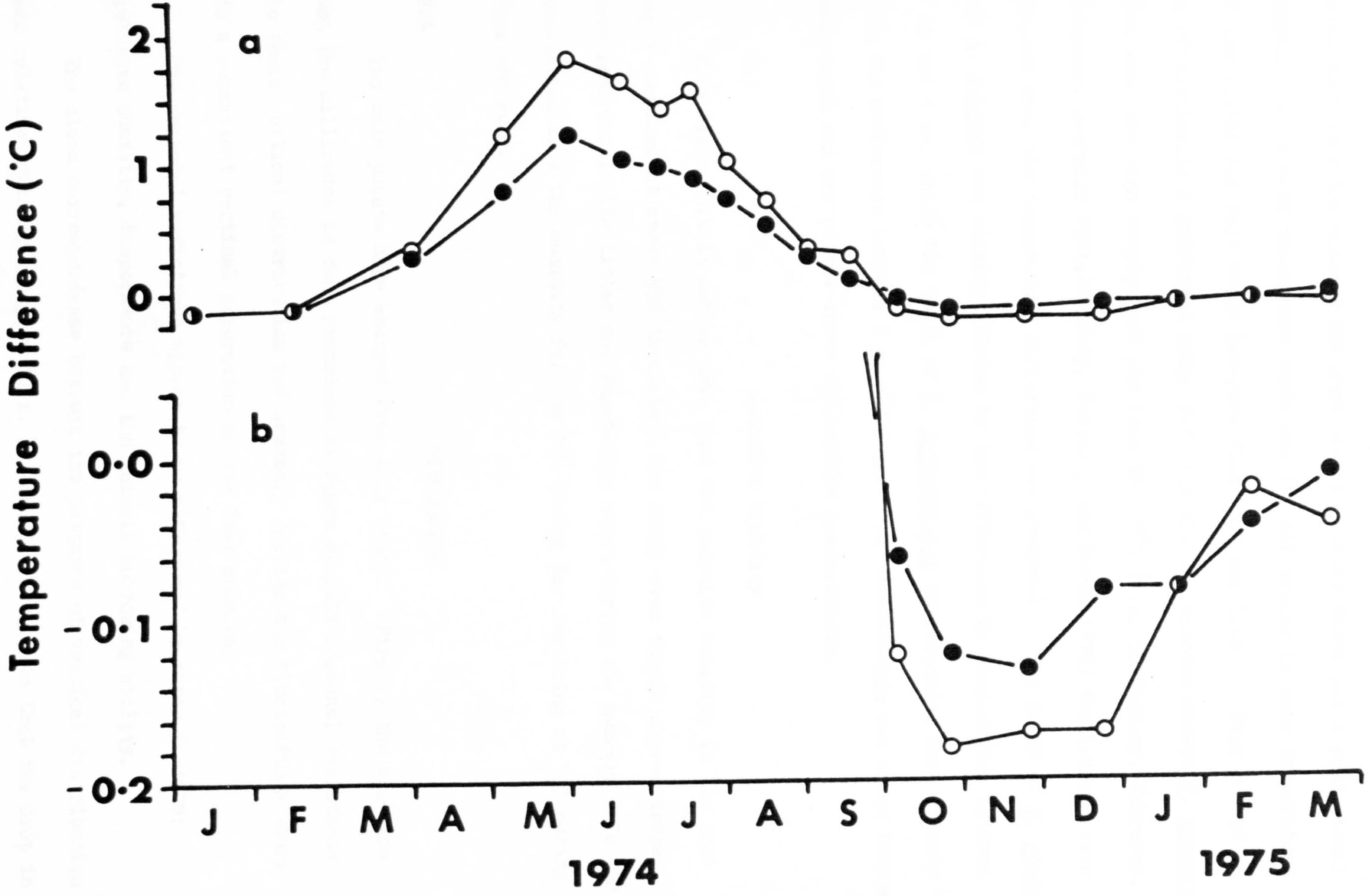

Temperature (°C)
20
15
10
5
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1974
1975

Figure. 3.4 Representation of mean temperature gradients within the soil. (●——●) mean temperature at 2 cm minus mean temperature at 4 cm. (○——○) mean temperature at 2 cm minus mean temperature at 6 cm.

a. January I974 to March I975.

b. Winter data I974/75 only, on expanded scale.


a
b
Temperature Difference (°C)
2
1
0
0·0
-0·1
-0·2
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1974
1975

at the time of sampling. Thus the animals were deeper in November 1974 than in February 1975 even though the latter was the colder month. It was noted that once the animals had gone down in winter there was a good visual correlation between their mean depth and the difference in mean temperature of the litter and root zones (compare figs. 3.1 and 3.4b). This proved to be statistically significant (fig. 3.5) for all the species except P. muscorum. Thus when the mean temperature was less than 8°C (i.e. in January, February, November, December 1974; January, February and March 1975) the animals were deepest when the temperature difference was greatest. The depth of P. scaber and A. vulgare was closely related to the difference in temperature between 2 cm and 4 cm, while the depth of C. latestriatus corresponded more closely with the difference between 2 cm and 6 cm. No relationship was found between mean depth and any of the other temperature measurements.

(c) Relative humidity

From figure 3.6 it can be seen that the relative humidity in the root layer remained at about 95% throughout the study even though marked drops were recorded in the litter and vegetation zones during the summer. In the vegetation zone the humidity fell to 40% during May remaining at 50% during June and July.

3.4 DISCUSSION

Two main points have emerged from this study. Firstly the woodlice and the millipedes in dune grassland at Spurn exhibit seasonal variations in their vertical distribution and secondly despite the fluctuations there is a consistent vertical separation of the four species.

The seasonal variations appear to be influenced by three factors; relative humidity, temperature and the animals burrowing ability.

The close correspondence between the patterns of vertical distribution and relative humidity (compare figs. 3.1 and 3.6) suggests that the drop in humidity in the litter layer causes the animals to take refuge deeper in the soil. This is similar to the summer migrations reported by Paris (1963)

Figure. 3.5 Relationship between mean depth and temperature gradient when mean temperature was less than 8°C.

a. Depth of *Armadillidium vulgare* plotted against temperature at 2 cm minus temperature at 4 cm. $r=-0.8I$, $p<0.0I$.

b. Depth of *Cylindroiulus latestriatus* plotted against temperature at 2 cm minus temperature at 6 cm. $r=-0.82$, $p<0.0I$.

c. Depth of *Porcellio scaber* plotted against temperature at 2 cm minus temperature at 4 cm. $r=-0.7I$, $p<0.02$.

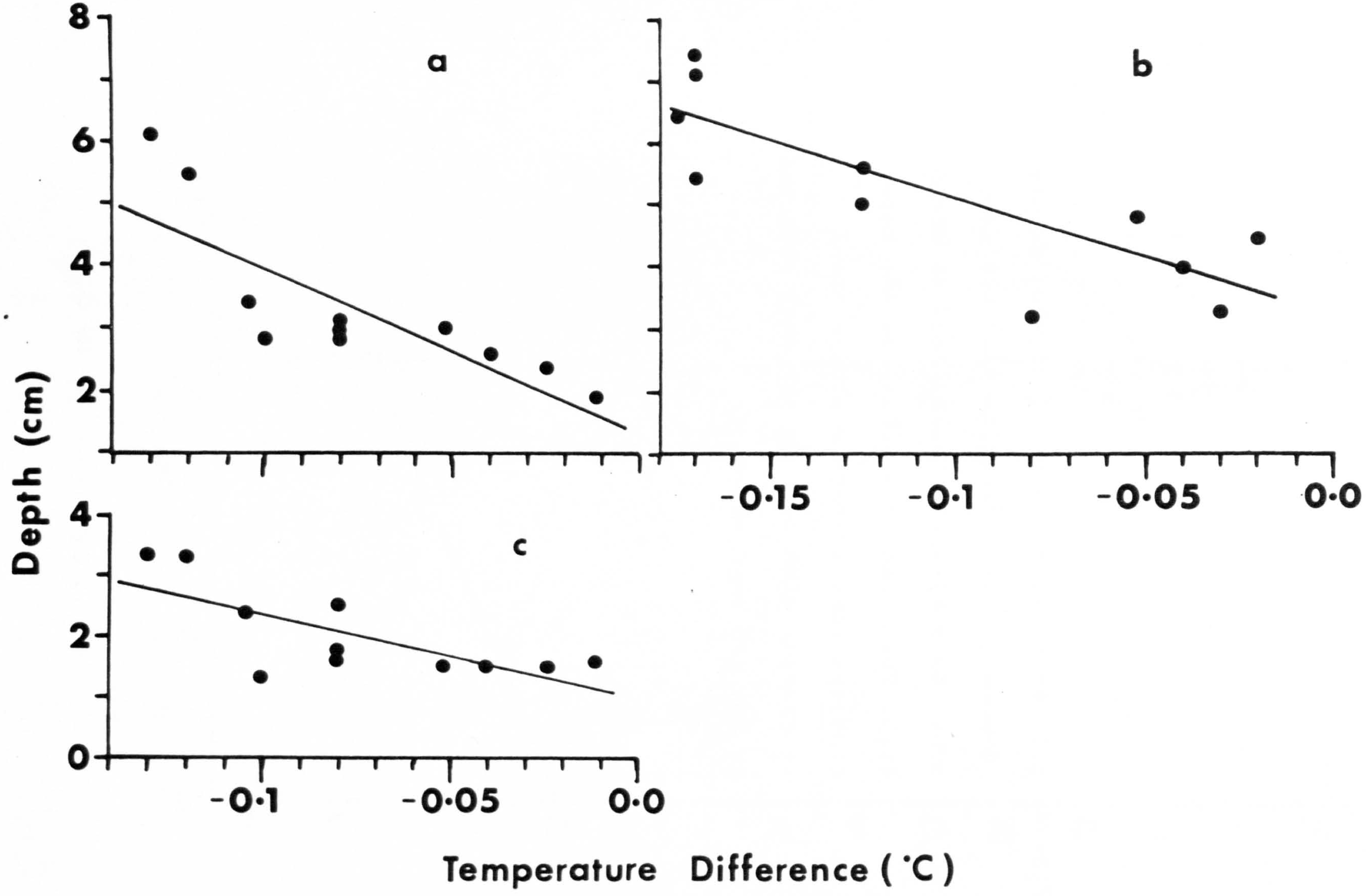
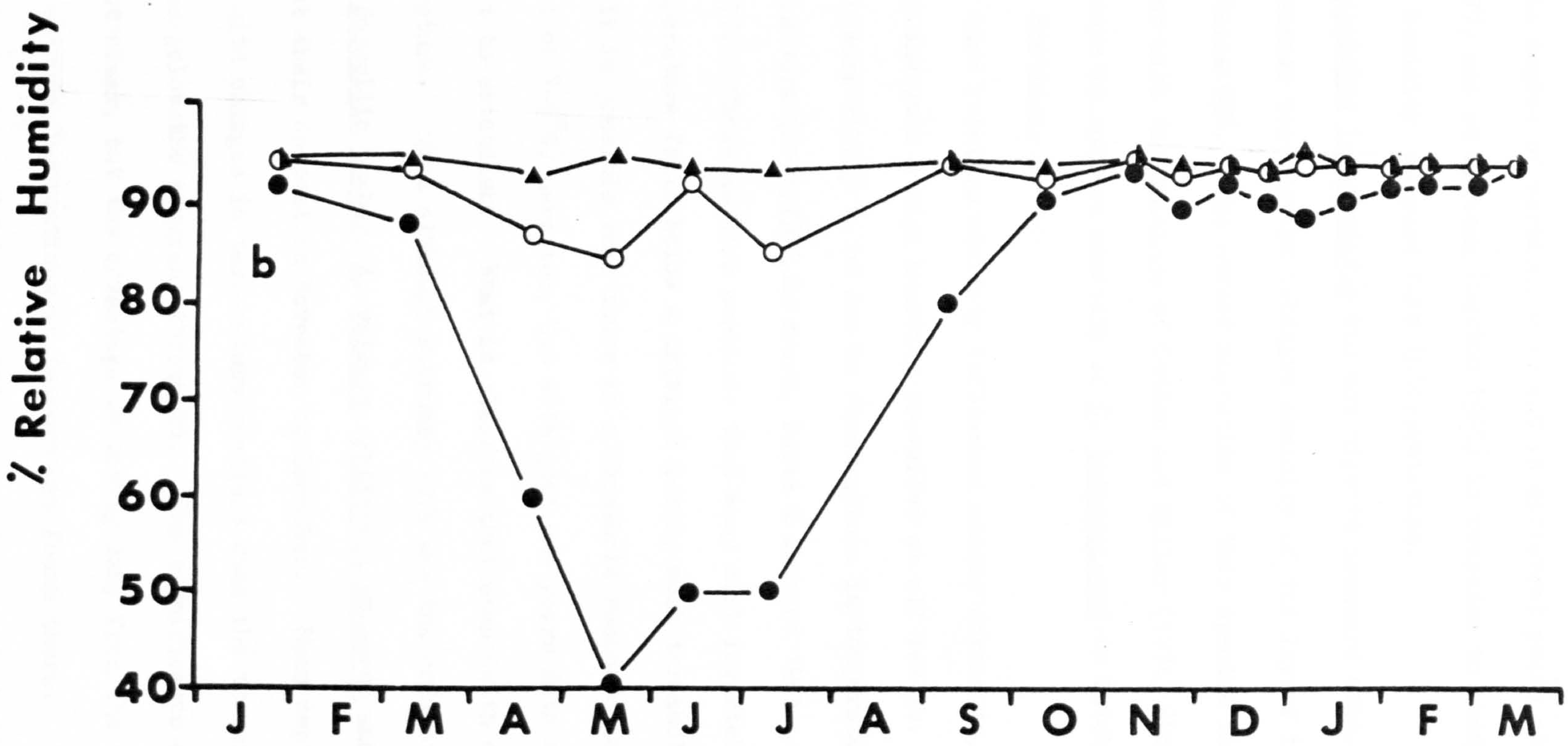

a
b
c
Depth (cm)
8
6
4
2
4
2
0
-0·15
-0·1
-0·05
0·0
-0·1
-0·05
0·0
Temperature Difference (˚C)

Figure. 3.6 Relative humidity of vegetation zone (●——●), litter zone (○——○) and root zone (▲——▲) from January I974 to March I975. The relative humidity of the sub-root and sand zones was always equal to or greater than that in the root zone and so has not been shown.


% Relative Humidity
90
80
70
60
50
40
b
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M

for *Armadillidium vulgare* in a Californian grassland and Sutton (1968) for *Trichoniscus pusillus pusillus* (Brandt) in a calcareous grassland near Oxford. Changes in the degree of vertical movement in different years at Spurn (Davis et al. 1977) and at Wytham (Sutton 1968) in response to changes in rainfall (and hence humidity) support this interpretation.

In contrast *Cylindroiulus latestriatus* did not migrate downward even in the driest part of summer because the relative humidity of the layers it occupied did not fall below 95%. The upward migration of this species in the autumn is consistent with the findings of Cotton and Miller (1974) who observed a marked increase in surface activity of *C. latestriatus* in October in a dune grassland in Scotland.

It seems unlikely that relative humidity influenced winter movements, because at that time of the year a high humidity prevailed at all levels. Such movements are much more likely to be due to fluctuations in temperature as indicated in previous work (Dowdy 1944, Herrard, Bonte & Baurant 1963, and Bocock & Heath 1967). These authors conclude that many soil invertebrates move down when the temperature falls below a critical level, such thresholds ranging from 4-7°C. It is possible that there is a threshold response (at the rather higher level of 7-9°C) here too, but with just one years data at Spurn this is difficult to establish. What is clear is that mean depth did not follow mean temperature. Thus although February 1975 was the coldest month of that winter, *Porcellio scaber*, *A. vulgare*, *Philoscia muscorum* and *C. latestriatus* were at their deepest in November or December. Mean depth did however correlate with changes in temperature gradient when the temperature in the litter layer was below the apparent threshold. The significance of this correlation is not clear, but the advantage in moving away from the surface could be to avoid the extreme fluctuations in temperature found there. This might be particularly important early in the winter when the animals have not yet become acclimatized to low temperatures.

The only species not to show a significant correlation was P. muscorum which underwent the least vertical movement in this study. This was probably due to its inability to burrow. By analogy with the millipedes studied by Manton (1954, 1961) P. muscorum which has long legs and a light build is poorly adapted for burrowing and would therefore find it difficult to migrate downwards in the present conditions (although it did do so when a thick litter layer covered the surface (Davis et al 1977)). A. vulgare and C. latestriatus are both well adapted for burrowing and would have no such difficulty as is suggested by the substantial vertical migrations they show. P. scaber lies between P. muscorum and A. vulgare in burrowing ability and also in the degree of vertical movement.

There is other evidence to suggest that burrowing ability influences the extent of vertical migration. It can be predicted from laboratory studies on humidity optima and water loss rates (Edney 1954) that P. muscorum should, in the face of declining humidity, respond earlier and burrow deeper than other species. However this did not happen. In fact during the summer, P. muscorum did not burrow as deeply as A. vulgare and consequently suffered much heavier mortality having failed to reach sufficiently humid conditions. P. scaber was again intermediate with respect to both movement and mortality.

The varied potential for vertical movements of these four species may as explained above differentially affect their survival in unfavourable conditions. To this extent burrowing ability can be considered an important niche parameter. Vertical separation could lead to further niche separation in at least two ways. (1) The upper 3-4 cm of soil consists of a layer of freshly blown sand and recently dead plant material with some large air spaces and passages between the litter. The lightly coloured surface layer contrasts sharply with a very dark layer of compact well decayed litter and humus which merges into the root layer between 3 and 4 cm below the surface. Movement of animals through the lower layers can only be by burrowing as no large passages persist. Consequently the woodlice and millipedes occupy layers which present considerably different living conditions. (2) As the plant material progressively changes in quality through the soil profile due to differences in the degree of attack by microorganisms and leaching the vertical separation may result in the species utilising rather different food resources. This also occurs in certain oribatid mites (Anderson 1971). Moreover the decaying plant material in the root layer will be available almost exclusively to the millipede population.

The average degree of separation between C. latestriatus and A. vulgare (the deepest living woodlouse) measured by d/w (where d = difference in mean depth of the two species, and w = niche breadth or 1 standard deviation) equals 0.71, a value not inconsistent with that predicted for coexistence in such a system (May 1973). Sutton (1966) and Anderson (1974) suggest that the separation is likely to be reduced when the surface fauna is driven down by unfavourable conditions, but in fact the opposite occurred as the deeper living animals migrated furthest.

CHAPTER FOUR

DENSITY AND AGGREGATION

4.1 INTRODUCTION

The need for population studies of several years duration in order to gain a fuller understanding of the fluctuations in animal numbers has been stressed by Clark et al. (1967). This applies equally well to studies on the role of different species in promoting energy flow within an ecosystem. Firstly because such data are essential for estimating population energetics parameters (Phillipson 1963, 1967), and secondly because only through long term studies can any idea of the temporal changes in their role be gained. In addition such information permits an analysis of the way in which mortality, natality and migration determine the population density and helps to clarify the nature of the interactions of animals with their environment.

Chapter four presents the overall density changes of the four common macrodecomposers on the study site at Spurn and relates them to changes in the environment. Chapter five describes the dynamics of individual cohorts of the isopods *Porcellio scaber* and *Armadillidium vulgare*, and the diplopod *Cylindroiulus latestriatus* is treated in chapter six. Sunderland, Hassall and Sutton (1976) have already described the population dynamics of *Philoscia muscorum* at Spurn Head but where additional information is available or where useful comparisons can be made some of the data ~~is~~ are repeated here and in chapter five.

4.2 MATERIALS AND METHODS

(a) Study site

Sunderland, Hassall and Sutton (1976) have described the vegetation on the site as approaching the 'dune heath' stage of succession. However, as a result of rabbit overgrazing and disturbance in 1972 and 1973 and sand accumulation in the winters of 1973/74 and 1974/75 (fig. 4.1) succession has been reversed. *Ammophila arenaria* and *Agropyron pungens* which are characteristic of mobile conditions have been stimulated into rapid and vigorous growth

Figure. 4.I Log($\bar{x}$+I) of mean population densities per 0.Im^2, at quarterly intervals from I970 to I975.

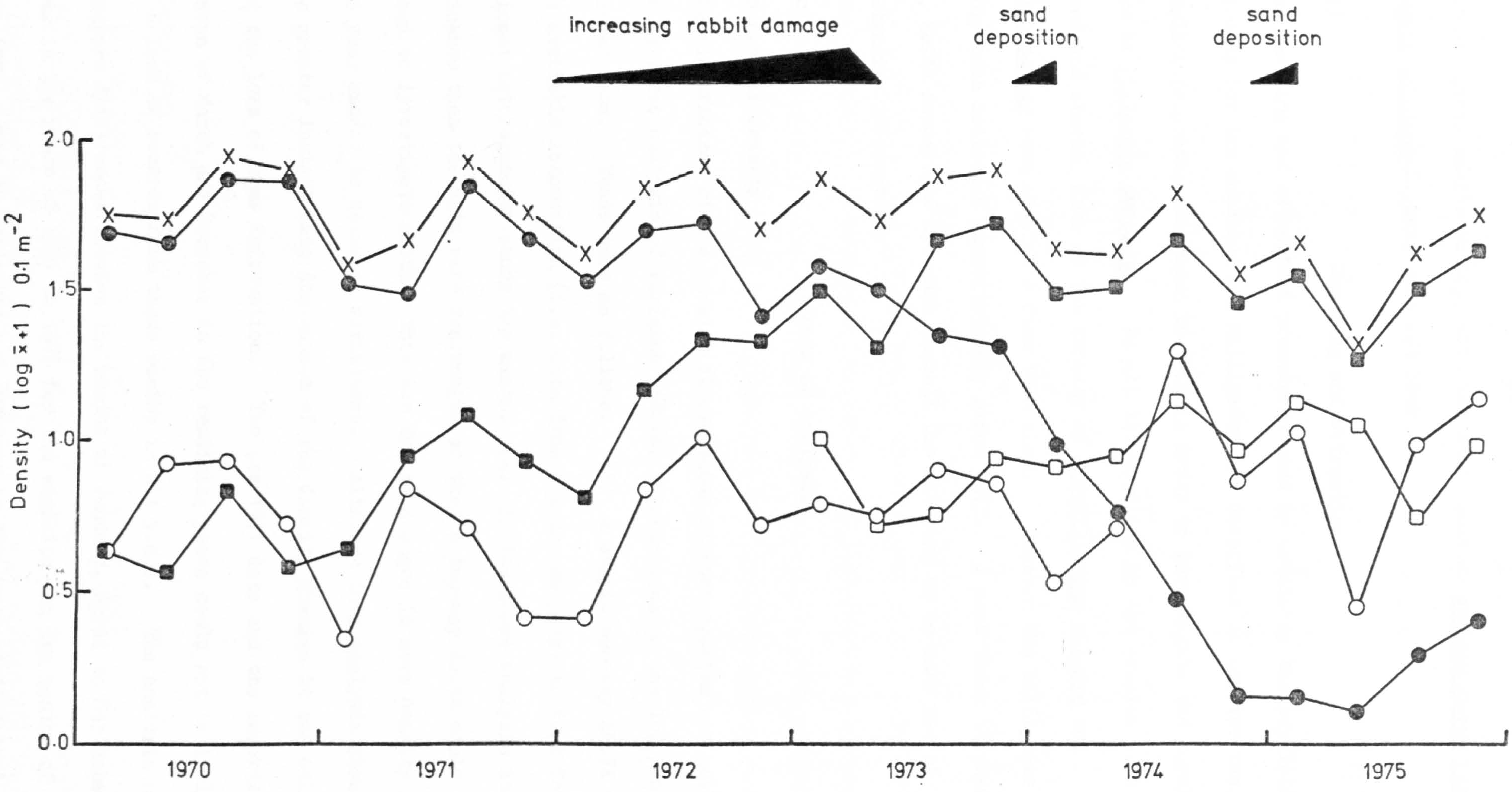
(■——■) *Armadillidium vulgare*.

(○——○) *Porcellio scaber*.

(●——●) *Philoscia muscorum*.

(□——□) *Cylindroiulus latestriatus*.

(X——X) Total woodlice.


increasing rabbit damage
sand deposition
sand deposition
Density (log x̄+1) 0·1 m^{-2}
2·0
1·5
1·0
0·5
0·0
1970
1971
1972
1973
1974
1975

while other plants unable to cope with the sand, such as *Arrhenatherum elatius* and *Senecia jacobaea* L. have been set back.

(b) Sampling and extraction

The sampling and extraction procedures used in obtaining the population density data for the woodlice and millipedes are described in chapter two. The sampling programme was begun in 1968 in order to investigate the population dynamics of *Philoscia muscorum*. As all the woodlice in the samples were collected and stored, data on the density of *Armadillidium vulgare* and *Porcellio scaber* were available from 1968 also. However the millipedes have only been collected quantitatively since 1973. I must thank Stephen Sutton, Keith Sunderland and Mark Hassall for allowing me to make use of this extensive information.

(c) Methods of analysis

Changes in density

The significance of the density fluctuations of each species was analysed in turn by three analysis of variance (ANOVA) calculations on the $\log_{10}(n + 1)$ transformed data. These were as follows. (1) A simple one-way ANOVA using all the available information (i.e. data from all the samples) to test for significant heterogeneity among the means. (2) If the above analysis indicated significance then the data were rearranged so that a two-way ANOVA could be performed to investigate whether this was due to changes in mean density from year to year and/or to seasonal variations. Although this analysis should provide greater insight into the causes of the density changes it can only be done at the loss of some information. The pre 1971 data and the records from the months of March and December in the remaining years could not be included due to a lack of records from these months in all years. The analysis could thus compare differences between the months of January, April to September and November in the years of 1971 to 1975 for the woodlice and the months of January, April, June to September and November in the years of 1973 to 1975 for the millipede. As no sample was taken in January 1971 and an extractor

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failure caused the loss of the July 1972 sample the mean and variance for these two dates had to be estimated. Also the sum of squares in April 1971 and May 1973 had to be corrected for a sample size of 14 (sample sizes on these dates were 13 and 10 respectively) in order that the analysis could be performed. (3) For the third analysis the transformed data from adjacent months were grouped to give six blocks, each representing a two month period. After performing a one-way ANOVA to test for seasonal variations, the means were compared using the Student-Newman-Keuls (SNK) procedure (Sokal & Rohlf 1969).

There are two ways in which adjacent months can be grouped in pairs. January may be combined with February, March with April, May with June and so on. Alternatively, December may be combined with January, February with March and April with May. Both combinations of the data were subjected to the ANOVA calculations. In every case one way of grouping gave a significant result and the other did not. Although there is probably a good explanation for this it indicates how the subjectivity involved in the blocking procedure can lead to radically different conclusions being drawn, depending on which blocks were chosen. Great care must be exercised when grouping data in this way.

The non-significant results were probably due to the month of peak abundance being adjacent to and combined with a month of very low abundance. This could happen as the animals should be least abundant just before recruitment resulted in the peak. If on the other hand these two months were not combined a significant result might be obtained. Only the combination which gave the significant result for each species is included in the results section below.

Aggregation

An initial indication of the animals dispersion patterns was obtained by examination of the variance : mean ratios of each species on each sampling date. In addition a plot of $\log_{10}$(mean) against $\log_{10}$(variance) for each species was performed. Taylor (1961, 1965) has shown that a linear relationship holds between these two variables fitting the linear regression equation $\log s^2 = a^1 + b \log \bar{x}$ (where s^2= variance and $\bar{x}$ = mean). The constant b (the gradient of the regression line) appears to be a true index of aggregation characteristic of a species while a^1 is largely a sampling factor. Two uses can be made of b. Firstly as a value of 1 indicates randomness and values greater than 1 over-dispersion, species dispersion patterns can be compared and secondly it indicates the appropriate variance stabilising transformation for the density data (Southwood 1966). The values obtained were near to 2. With such values Southwood suggests that a logarithmic transformation of density data be used before analysis. This was adopted when analysing the changes in density of each species. Neither of the above methods can be used to quantify changes in a species dispersion pattern. The first because it is so closely dependent on the mean and the second because it requires all the sampling data to compute a single value. 'k' of the negative binomial is ideally suited for this as the above restrictions do not apply. This was calculated by the method of maximum likelihood once the data had been tested for its fit to the negative binomial. k is inversely related to the degree of aggregation (or clumping); decreases in k indicate greater aggregation and the distribution approaches Poisson when $k > 8$ (Southwood 1966).

Changes in k were analysed by two ANOVA calculations similar to analyses 1 and 3 applied to the changes in population density.

4.3 RESULTS

(a) Changes in population density

The mean number of animals extracted from the 14 replicates making up each sample are given (± 2 S.E.) in table 4.1. The standard errors are large because the populations are highly aggregated. These data are summarised in figure 4.1 which shows the changes in numbers of each species and the total number of woodlice (as $\log_{10} (\bar{x} + 1)$, where $\bar{x}$ = the mean number per 0.1m^2) at three monthly intervals from 1970 to 1975 inclusive.

Table 4.1 Mean population densities of *A. vulgare*, *P. scaber* *P. muscorum* and *C. latestriatus* 0.1 m^{-2} (± 2 S.E.)

Sample date	Mean densities *Armadillidium*	 *Porcellio*	 *Philoscia*	 *Cylindroiulus*	 N*
1968					
17 Sept.	2.4 ± 2.8	2.2 ± 1.5	28.8 ± 12.3		10
1969					
8 Jan	1.7 ± 0.6	7.3 ± 8.0	57.5 ± 11.8		3
16 June	1.8 ± 1.7	-	24.4 ± 10.6		10
7 Aug	2.6 ± 2.4	-	49.4 ± 18.6		10
8 Sept.	6.1 ± 4.6	4.5 ± 2.0	73.4 ± 30.2		10
1970					
14 Jan	3.3 ± 3.6	3.3 ± 3.5	48.0 ± 26.7		3
27 May	2.6 ± 2.2	7.4 ± 5.1	43.6 ± 21.2		10
15 July	4.4 ± 4.4	5.4 ± 2.6	42.2 ± 15.9		10
19 Aug	7.0 ± 5.1	9.7 ± 12.2	103.7 ± 37.8		10
22 Oct	2.8 ± 1.3	5.9 ± 3.2	75.0 ± 29.8		20
11 Nov.	2.85 ± 1.9	2.6 ± 2.4	68.1 ± 27.8		20
1971					
28 Jan	3.4 ± 2.0	1.2 ± 0.7	32.0 ± 16.5		19
6 Apr.	4.1 ± 2.6	3.9 ± 2.8	35.4 ± 14.9		13
27 May	5.9 ± 3.7	4.3 ± 3.2	26.1 ± 6.1		14
25 June	13.3 ± 5.1	9.6 ± 6.5	27.6 ± 9.6		14
14 July	8.9 ± 3.1	4.1 ± 2.0	41.4 ± 20.6		14
28 July	9.7 ± 4.3	4.5 ± 2.9	68.1 ± 39.0		14
19 Aug	14.9 ± 6.9	3.8 ± 3.5	59.2 ± 22.7		14
15 Sept	10.3 ± 6.6	4.2 ± 3.0	102.2 ± 32.2		14
1 Nov	4.4 ± 1.4	1.6 ± 1.9	51.8 ± 22.4		14
9 Dec	10.5 ± 5.1	1.6 ± 1.2	40.2 ± 16.1		14
1972					
26 Jan	5.4 ± 2.9	0.9 ± 0.6	30.6 ± 17.3		14
28 Mar	5.6 ± 3.3	2.3 ± 1.7	35.6 ± 13.7		14
1 May	10.9 ± 7.9	2.3 ± 1.5	39.4 ± 10.6		14
26 May	10.4 ± 6.0	6.7 ± 3.9	72.2 ± 35.7		14
30 June	19.9 ± 7.0	8.9 ± 6.5	34.9 ± 6.5		14
26 Aug	16.6 ± 7.2	8.4 ± 6.5	60.0 ± 39.6		14
28 Sept	24.9 ± 17.5	9.9 ± 8.1	45.6 ± 20.4		14
28 Nov	20.3 ± 11.2	4.2 ± 4.2	25.0 ± 10.6		14
1973					
30 Jan	30.4 ± 8.3	5.1 ± 4.3	37.4 ± 27.8	9.0 ± 6.3	14
3 Apr	18.3 ± 6.7	3.3 ± 2.8	48.8 ± 33.7	2.0 ± 1.4	14
23 May	15.2 ± 10.9	3.9 ± 4.8	19.8 ± 9.8	5.5 ± 3.3	10
24 June	23.3 ± 6.6	6.1 ± 4.2	20.6 ± 14.9	5.6 ± 2.6	14
22 July	17.2 ± 5.5	5.1 ± 4.3	8.8 ± 5.3	1.9 ± 1.4	14
15 Aug	47.5 ± 20.5	7.5 ± 3.7	33.4 ± 21.8	4.1 ± 2.4	14
16 Sept	73.9 ± 30.7	8.0 ± 3.5	23.1 ± 9.1	8.0 ± 6.1	14
10 Nov	52.9 ± 22.3	6.2 ± 7.7	19.7 ± 14.4	7.8 ± 7.9	14

Table 4.1 contd.

1974					
25 Jan	30.1 ± 11.7	2.4 ± 2.6	8.8 ± 4.7	7.1 ± 4.5	14
21 Apr	25.9 ± 10.7	2.5 ± 1.5	8.6 ± 6.3	7.6 ± 4.0	14
7 May	43.9 ± 18.0	8.3 ± 5.4	4.3 ± 5.3	5.9 ± 3.5	14
2 June	24.9 ± 8.2	1.7 ± 1.5	1.7 ± 2.1	10.3 ± 4.9	14
21 July	41.2 ± 19.6	12.3 ± 16.3	0.2 ± 0.3	5.4 ± 2.6	14
8 Aug	42.8 ± 35.5	27.1 ± 43.8	4.8 ± 8.6	16.0 ± 10.1	14
8 Sept	54.0 ± 29.5	18.0 ± 24.7	1.0 ± 1.8	15.8 ± 7.7	14
10 Oct	20.9 ± 9.3	1.1 ± 1.0	0.0	8.1 ± 5.4	14
10 Nov	34.4 ± 17.6	11.8 ± 16.5	0.9 ± 1.0	8.4 ± 3.2	14
1975					
6 Jan	44.7 ± 41.7	13.6 ± 18.2	0.4 ± 0.5	10.5 ± 7.3	14
3 Mar	23.8 ± 22.7	6.0 ± 7.4	0.4 ± 0.4	14.0 ± 8.7	14
28 Apr.	24.7 ± 16.6	2.6 ± 1.5	0.5 ± 0.5	12.3 ± 5.7	14
27 May	10.9 ± 10.1	1.1 ± 0.8	0.0	8.0 ± 5.3	14
1 July	14.1 ± 13.0	1.6 ± 1.5	0.0	5.4 ± 2.6	14
29 July	39.1 ± 66.0	11.7 ± 14.8	0.71 ± 1.1	2.6 ± 1.2	14
26 Aug	37.4 ± 48.8	14.9 ± 23.5	1.3 ± 1.8	2.1 ± 1.3	14
29 Sept	31.3 ± 28.1	7.2 ± 6.9	1.6 ± 2.5	8.1 ± 2.7	14
18 Nov	41.3 ± 30.2	12.9 ± 9.7	1.5 ± 1.5	8.6 ± 2.9	14

* N = sample size

Significant heterogeneity among the sample means of each species (P. muscorum $F = 27.2$ $p < 0.001$, A. vulgare $F = 5.0$ $p < 0.001$, C. latestriatus $F = 3.1$ $p < 0.001$ and P. scaber $F = 1.8$ $p = 0.002$) was shown by the two-way ANOVA to be due to significant differences in the monthly and yearly means (tab. 4.2). Furthermore the changes in density from year to year were greater and therefore had higher F values than the seasonal variations. P. scaber proved to be the exception to this rule as only the seasonal variations were significant despite the fact that its peak 1974 density was more than 2½ times greater than in any of the previous years (tab. 4.1).

The long term changes can be summarised as follows. P. muscorum at a mean density of about 45-50 0.1 m^{-2} was initially between 5 and 10 times more abundant than A. vulgare and P. scaber and this difference was maintained until 1972. In late 1973 and 1974 there was a population crash in P. muscorum while P. scaber and A. vulgare peak numbers rose 2½ and 3½ fold respectively. The gradual increase in frequency of A. vulgare (which continued over approximately 20 months) occurred before the decline of P. muscorum whereas the peak P. scaber density was not observed until 1974. Although the density fluctuations of the individual woodlouse species populations were large the total numbers of woodlice on the site remained relatively constant throughout the study at about 55-60 0.1m^{-2} (Fig. 4.1). Regular seasonal variations were the main cause of change in the woodlice totals.

The three years of density data for C. latestriatus overlap the period of greatest fluctuations in the woodlice. During this time its density increased from an overall mean of 5.5 0.1m^{-2} in 1973 to 9.4 in 1974.

Analysis of the grouped data gave a significant difference between at least one pair of block means for each species (P. scaber $p < 0.001$, P. muscorum $p < 0.001$, A. vulgare $p < 0.01$ and C. latestriatus $p < 0.02$). The outcome of the SNK test on the P. muscorum data has been reported by Sunderland et al (1976). The only significant difference they found was between the August/September mean and the December/January mean. With an additional two years data the outcome of the analysis on P. muscorum was

Table 4.2 Results of two way analysis-of-variance testing for heterogeneity among the monthly and annual mean densities.

	Source of Variation					
Species	Year		Month		Interaction (year x month)	
	F	p	F	P	F	p
A. vulgare	23.10	$\ll 0.001$	1.86	> 0.05	1.61	< 0.05
P. scaber	0.96	> 0.05	2.60	$\hat{=} 0.06$	1.48	< 0.05
P. muscorum	194.48	$\ll 0.001$	3.22	< 0.01	2.30	< 0.001
C. latestriatus	12.24	< 0.001	3.66	< 0.01	2.28	< 0.025

Table 4.3 The constants b (± 1 S.E.) and a' of Taylors' power law (see text for details)

Species	b ± 1 S.E.	a'
A. vulgare	1.89 ± 0.12	0.20
P. scaber	2.26 ± 0.12	0.21
P. muscorum	1.45 ± 0.06	0.71
C. latestriatus	1.89 ± 0.18	0.14

unchanged. P. scaber gave the same result but the peak in A. vulgare occurred later. The October/November mean was significantly greater than the February/March mean. Sunderland et al (1976) attributed the summer peak to recruitment and the winter low to mortality in the absence of recruitment but large sampling errors and migration obscured the mortality trends. The same interpretation of the seasonal density changes can be applied to P. scaber and A. vulgare.

In C. latestriatus there was a gradual decline in density from the maximum in September/October to the minimum in July/August. This suggests that, unlike the woodlice where migration obscured the mortality trends (Sunderland et al. 1976 and chapter five), there was no migration affecting the diplopod population density at Spurn.

That other factors or events also influence the number of animals in a sample is suggested by the significant interaction between years and months (tab. 4.2). There is no direct indication of what these might be but likely causes will be discussed later.

(b) Aggregation

The variance : mean ratio showed significant overdispersion or contagion in at least 96% of the samples in all four species throughout the study. Consequently the constant (b) of Taylors (1961, 1965) power law estimated by the regression coefficient of $\log(\bar{x})$ on $\log(s^2)$ was significantly greater than unity in the four cases (tab. 4.3). P. scaber was the most highly aggregated species whereas P. muscorum was the least. A. vulgare and C. latestriatus with the same value were intermediate. Only the differences between C. latestriatus and P. scaber and A. vulgare were non-significant (Tab. 4.4).

None of the samples produced dispersion patterns which were significantly different from a negative binomial therefore estimates of k were made for each species in each sample. The ANOVA calculations revealed very significant changes in k for each species (P. muscorum $F = 42.0$ $p < 0.001$, A. vulgare $F. = 26.3$ $p < 0.001$, P. scaber $F = 13.0$ $p < 0.001$, C. latestriatus $F = 11.9$ $p < 0.001$). As this was not due to any regular (statistically significant)

Table 4.4 Interspecific comparison of the constant b of Taylors' power law (following the procedure in Bailey 1959). The numbers refer to the normal standard deviate (d). * denotes $p < 0.05$, ** denotes $p < 0.02$, *** denotes $P < 0.01$, ns denotes not significant.

	P. muscorum	*A. vulgare*	*C. latestriatus*	*P. scaber*
P. muscorum	-	3.31***	2.33**	6.13***
A. vulgare		-	0.00^{ns}	2.19*
C. latestriatus			-	1.72^{ns}
P. scaber				-

Table 4.5 Mean annual values of k of the negative binomial for each species from 1970 to 1975.

Year	*A. vulgare*	*P. scaber*	*P. muscorum*	*C. latestriatus*
1970	0.63	0.90	1.96	-
1971	1.95	0.67	1.96	-
1972	1.46	0.92	2.89	-
1973	2.32	0.71	0.98	0.84
1974	1.04	0.44	0.28	1.42
1975	0.38	0.21	0.21	1.72

seasonal effects mean yearly values were computed (tab. 4.5). In the woodlice k was generally highest or increasing in the first three or four years (1970-1973 inclusive), but then decreased sharply in the last two. This suggests that a common factor may have caused the late increases in aggregation. At the same time C. latestriatus showed a gradual rise in k.

(c) Joint changes in density and aggregation

Simultaneous density and aggregation changes are shown in figure 4.2 by a plot of the mean against k for each sample date with the points connected up in chronological order. The first sample date is arrowed in each figure. At first sight no trends are apparent above the large amount of variation. However, careful examination of figures 4.2a and 4.2b (A. vulgare and P. muscorum) reveals that the points form two non-overlapping fields. The first area (solid dots - solid lines) comes from the 1968 to 1972 samples. A. vulgare initially had a low density and low k but both parameters increased together. P. muscorum had a high density and high k. In the second group of points formed from the 1974 and 1975 samples (open circles - solid lines) both had low k values which in A. vulgare were accompanied by high density and in P. muscorum by low. The samples taken in 1973 (solid dots - broken line) appear to bridge these two fields and thus probably represent a transitional year.

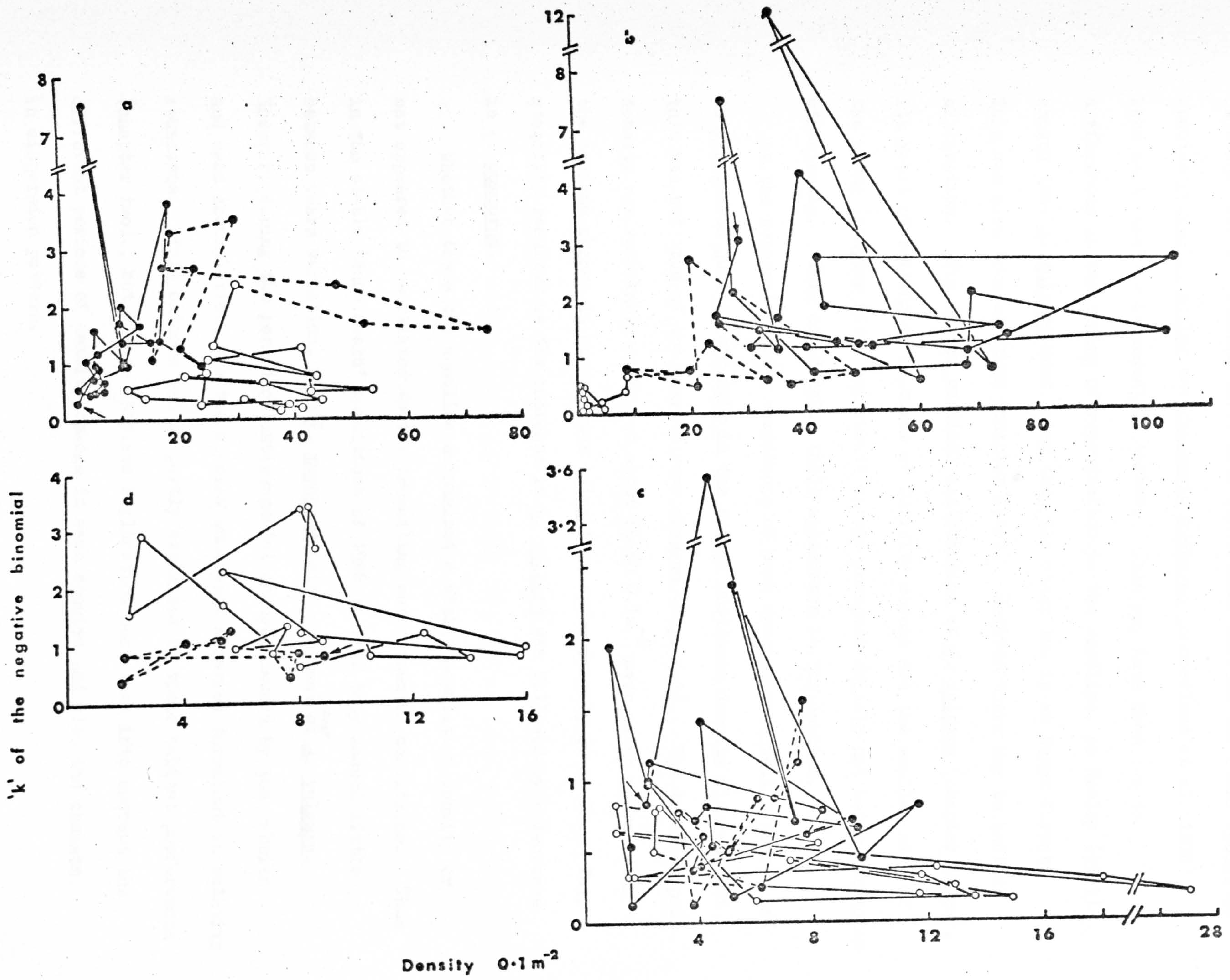
The density and degree of aggregation of P. scaber and C. latestriatus (figs. 4c & d) vary in a less regular apparently independent way.

4.4 DISCUSSION

The numbers of animals extracted from any sample have been shown to depend upon the sample date. Distinct seasonal and yearly changes in mean density were the cause of this.

For most of each year mortality caused the density to decline. However, each species had a peak in abundance, when, for a short time, recruitment exceeded mortality. This occurred in late summer or autumn, but there were differences between the species. In the case of Armadillidium vulgare peak

Figure. 4.2 Simultaneous changes in density and dispersion of a. Armadillidium vulgare, b. Philoscia muscorum, c. Porcellio scaber and d. Cylindroiulus latestriatus from September 1968 to November 1975. ← indicates first sample date in September 1968. (●——●) September 1968 to November 1972. (●----●) January 1973 to November 1973. (○——○) January 1974 to November 1975.


a
b
c
d
'k' of the negative binomial
Density 0·1 m⁻²
0
1
2
3
4
7
8
12
3·2
3·6
20
40
60
80
100
4
8
12
16
28

abundance was not reached until October/November whereas the other woodlouse species *Porcellio scaber* and *Philoscia muscorum* (Sunderland et al. 1976) were most numerous in August/September. This may have been due to differences in the timing of reproduction in the woodlice, as Heeley (1941) showed that *A. vulgare* bred later than the other two in an Essex forest. This was also true at Spurn (chapter five). However there may be another explanation. The deeper vertical distribution of *A. vulgare* (chapter three), its habit of rolling up in times of humidity stress and the smaller size of the young (chapter five) may result in the youngest animals not being extracted efficiently. This could delay their appearance in the samples.

As the seasonal density variations of each species were well synchronised they appeared just as strongly in the summed woodlouse density figures, but this was not true of the year to year changes (fig. 4.1). The total isopod density was remarkably stable at about 55-60 0.1m^{-2} over seven years, with the maximum change in any quarter being from approximately 20 to 68. This stability resulted as the increase in *A. vulgare* was followed by a decrease in *P. muscorum*.

Whether these two woodlice maintained a stable population density or not appeared to be related to the prevailing environmental conditions. Thus in the stable 'dune heath' conditions of 1968 to 1972 they showed little between years variation, with *P. muscorum* being dominant ~~of~~ over *A. vulgare*. However, during the period of environmental change, caused by the rabbits and sand accumulation, the two species underwent a marked turnabout in relative abundance. This outcome can be partly explained by their habitat preferences (chapter two)., but a more complete explanation must take into account the different periods of density change in each species and also the changes in dispersion pattern.

The density and dispersion of *A. vulgare* increased dramatically in 1972 and 1973 (fig. 4.2) in parallel with the incidence of overgrazing and damage by rabbits (fig. 4.2). This is in accord with its widespread occurrence in short open grassland (Sutton pers. comm.), Although *P. muscorum* showed evidence of being adversely affected at that time (fig. 4.2b shows that the fall in k and in density began in 1972) it was not until 1974 that its population crashed. The simultaneous increase in aggregation suggest that this may have been due to a reduction in the number of available shelter sites. The wind blown sand having covered them all up. A.vulgare and P. scaber becams more aggregated in 1974 and 1975 also (tab. 4.5) but this produced no obvious adverse affects on their population density. In fact P. scaber reached its maximum density in 1974 (tab. 4.1).

The only species to show a reduction in aggregation after the sand blow was C. latestriatus. An increase in density too suggests that the new conditions were particularly favourable to it. Reduced competition for the decaying litter which was previously on the surface and occupied by woodlice may account for the change. The observed vertical separation of C. latestriatus (chapter three) supports this conclusion.

The increasing or decreasing density of animals in some years and the stability in others, as described above, is sufficient to produce the significant interaction factor in the ANOVA calculations (tab. 4.2). Varying levels of recruitment, mortality and migration effect these changes. However, the analyses employed so far give no indication which may have had the major influence. This can only be obtained by an analysis of individual cohorts. The cohort dynamics of P. scaber and A. vulgare are described in chapter five and C. latestriatus is treated in chapter six.

CHAPTER FIVE

ISOPOD COHORT DYNAMICS

5.1 INTRODUCTION

In chapter four the density and aggregation of the most abundant macrodecomposers in the dune grassland at Spurn were examined. Variations from year to year and with season were recognised and described for all four species. Some explanation for the observed changes in relative abundance over the seven years for which data are available was put forward but no idea of the relative importance of changes in natality, mortality and migration in effecting those fluctuations could be gained by the simple analyses employed. In this chapter these changes are analysed at the cohort level. Furthermore, knowledge of the dynamics of individual cohorts is required in order to estimate production at the population level.

This chapter deals with Porcellio scaber and Armadillidium vulgare; Cylindroiülus latestriatus is treated in chapter six and the analysis of Philoscia muscorum is given by Sunderland et al (1976) and Hassall (1976).

5.2 METHODS

(a) Size and sex determination

Weight could not be used as an indicator of size as animals extracted from the monthly samples (i.e. KLG samples) were preserved initially in sodium orthophosphate and then in 70% alcohol. This treatment causes a variable amount of weight loss. Instead measurement of the width of the head capsule was employed. Sutton (1968) gives this as the best indicator of size and has used it on P. muscorum at Spurn (Sunderland et al 1976). This is preferred to body length as it is a single rigid structure which is not subject to variation caused by contraction and bending of the body at death. Head width measurements were taken using a microscope fitted with a micrometer eyepiece (1 micrometer unit (m.u.) = 0.056 mm) and refer to the greatest width in the horizontal plane of the animal, viewed dorsally.

The sexes at birth are indistinguishable by external characteristics, but males soon develop increasingly conspicuous external genitalia (Sutton 1972). As juveniles and females look alike, except when the latter are pregnant, all non-males are grouped together as females in the initial size frequency analysis.

5.3 RESULTS

(a) Size frequency analysis, sex ratios and growth.

Size frequency analysis

Changes in the size structure of the *Armadillidium vulgare* and *Porcellio scaber* populations between January 1972 and November 1975 are expressed in figures 5.1 and 5.2 respectively by means of size frequency distributions. The number in each size class is shown as a percentage of the total number extracted on each date. Size frequency analysis showed that both species had overlapping generations. The *A. vulgare* population consisted of three cohorts with a fourth just distinguishable in autumn, whereas *P. scaber* had only two cohorts with a third also distinguishable in autumn. A cohort is defined as the members of a population born in a single breeding season. In both *P. scaber* and *A. vulgare* there is a single breeding season each year with the bulk of the new cohort appearing in July and August. It is easily recognised as its size distribution does not overlap that of the previous cohort. On successive dates growth of the immatures is indicated by an upward movement through the size classes. Cohorts remain distinct except when the animals become very large. Some overlap then occurs.

Sex ratios

Changes in the percentage frequency of males with age in an average cohort of *P. scaber* and *A. vulgare* are shown in figures 5.3a and 5.3b. The mean curves are based on the seven cohorts of *P. scaber* and eight of *A. vulgare* which were present for some time in the respective populations between January 1972 and November 1975. From figure 5.3b it can be seen

Figure. 5.I Size structure of <u>Armadillidium</u> <u>vulgare</u> population from January I972 to November I975. Size classes are given by head width in micrometer units (I m.u.= 0.056mm) and the number in each size class is shown as a percentage of the sample total. Alternate cohorts are indicated by alternate solid black and open areas in the kite diagrams.

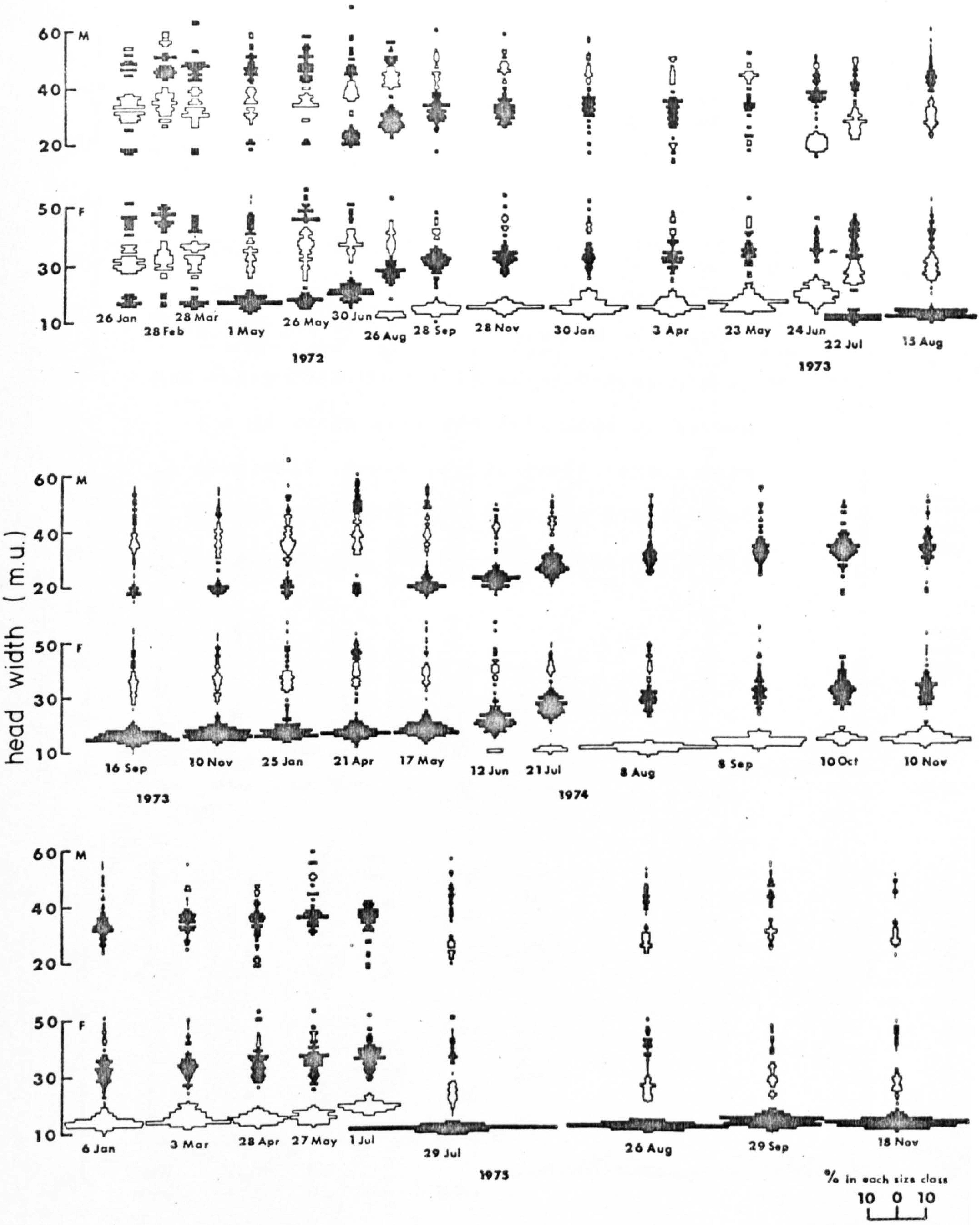

head width (m.u.)
60
40
20
M
50
30
10
F
26 Jan
28 Feb
28 Mar
1 May
26 May
30 Jun
26 Aug
28 Sep
28 Nov
30 Jan
3 Apr
23 May
24 Jun
22 Jul
15 Aug
1972
1973
16 Sep
10 Nov
25 Jan
21 Apr
17 May
12 Jun
21 Jul
8 Aug
8 Sep
10 Oct
10 Nov
1973
1974
6 Jan
3 Mar
28 Apr
27 May
1 Jul
29 Jul
26 Aug
29 Sep
18 Nov
1975
% in each size class
10 0 10

Figure. 5.2 Size structure of the Porcellio scaber population from January 1972 to November 1975. Size classes are given by head width in micrometer units (I m.u.=0.056mm) and the number in each size class is shown as a percentage of the sample total. Alternate cohorts are indicated by alternate solid black and open areas in the kite diagrams.

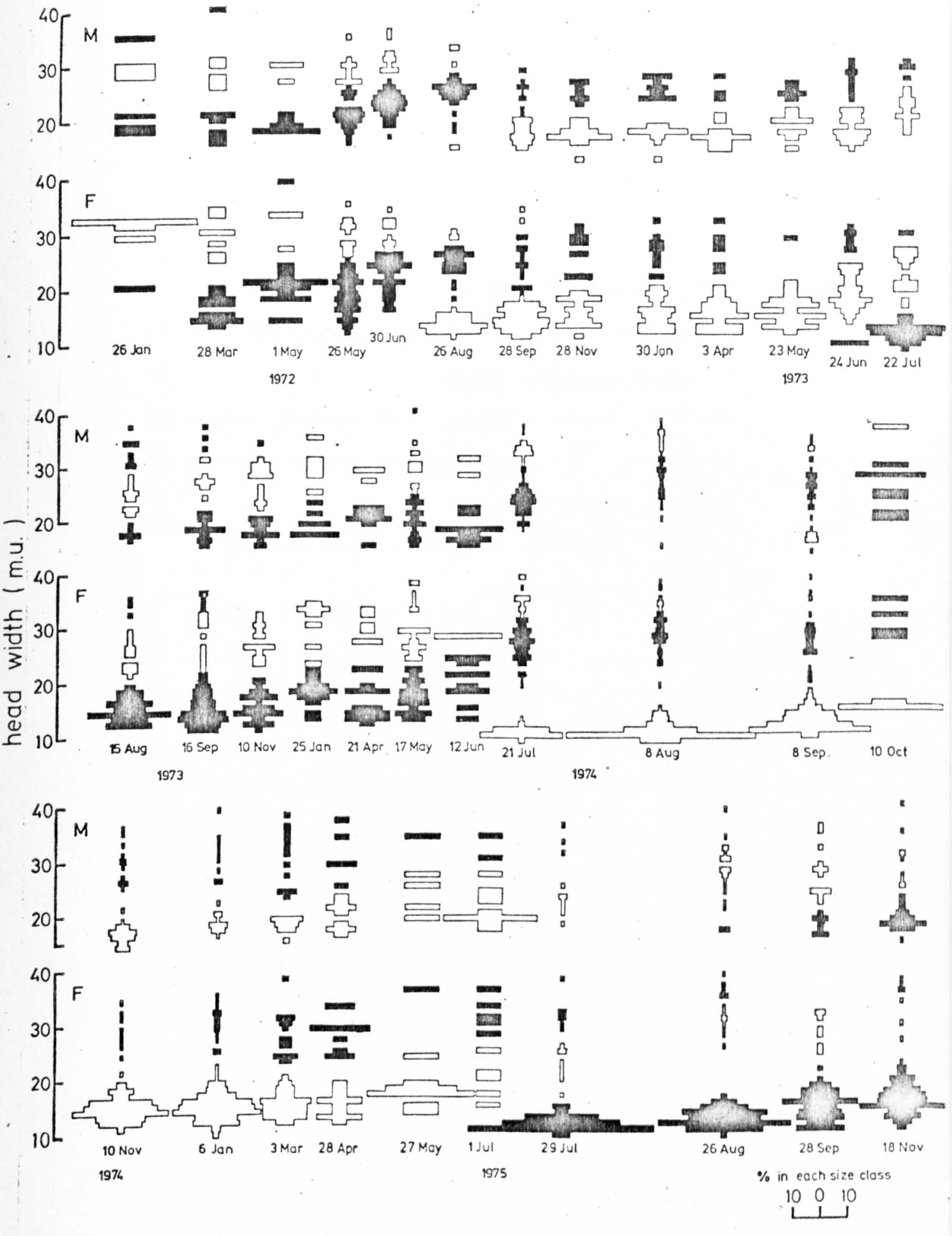
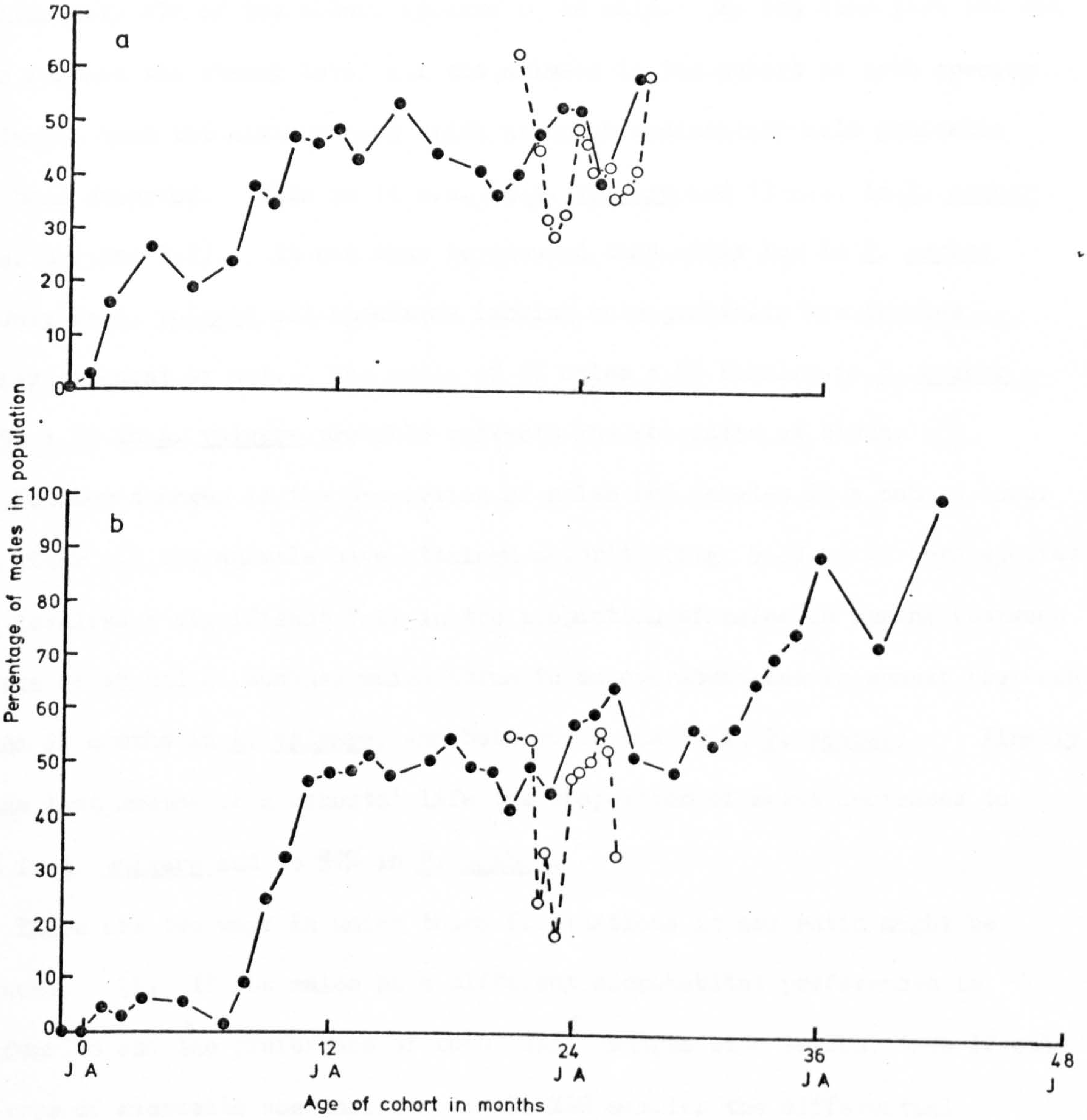

head width (m.u.)
M
F
40
30
20
10
26 Jan
28 Mar
1 May
26 May
30 Jun
26 Aug
28 Sep
28 Nov
30 Jan
3 Apr
23 May
24 Jun
22 Jul
1972
1973
15 Aug
16 Sep
10 Nov
25 Jan
21 Apr
17 May
12 Jun
21 Jul
8 Aug
8 Sep.
10 Oct
1973
1974
10 Nov
6 Jan
3 Mar
28 Apr
27 May
1 Jul
29 Jul
26 Aug
28 Sep
18 Nov
1974
1975
% in each size class
10 0 10

Figure. 5.3 Changes in sex ratio with age of an average cohort of a. *Porcellio scaber* and b. *Armadillidium vulgare*.

(●——●) Animals taken from monthly sampling programme. The points shown are the average of four years data.

(○----○) Animals collected from beneath stones in 1975 only.


a
b
Percentage of males in population
70
60
50
40
30
20
10
0
100
90
80
70
60
50
40
30
20
10
0
0
J A
12
J A
24
J A
36
J A
48
J
Age of cohort in months

that males of A. vulgare first appear in small proportions in September and October, and that they overwinter at this low level. In spring the proportion increases sharply and then plateaus when the sex ratio is 50 : 50. In contrast the proportional increase in P. scaber males (fig. 5.3a) is much greater in the first autumn so that 20-25% of the first year animals are male during winter. In addition the proportion of males continues to rise more steadily than in A. vulgare until a steady level is reached in late May. At this time approximately 47% of the cohort appears to be male. By the time that the sex ratio reaches the steady level all the animals in the cohort of both species are larger than the minimum head width at which rudimentary male genitalia have been observed. This is 14 m.u. in A. vulgare and 13 m.u. in P. scaber (figs. 5.1 and 5.2). It can thus be assumed that after May in P. scaber and July in A. vulgare all specimens lacking male genitalia are females whether pregnant or not. The ratio of 47 males : 53 females in P. scaber and 50 : 50 in A. vulgare probably reflects the sex ratio at birth.

Further changes in the proportion of males and females in a cohort occur even after all the animals have attained maturity (fig. 5.3). In both species this involves a significant fall in the proportion of males in spring (between the age of 18 and 21 months) which turns to an overabundance in summer (between 23 and 26 months in A. vulgare, and between 22 and 24 in P. scaber). Finally in the last months of a cohorts' life the proportion of males increases to 100% in A. vulgare and to 57% in P. scaber.

There are two ways in which these fluctuations in sex ratio might be produced. (1) If the males have different microhabitat preferences to the females and the preference of both sexes changes with season, then if only one type of microsite was included in the KLG samples the differential movements of males and females between their preferred sites could result in the observed variations in sex ratio. (2) Uneven changes in the mortality rate of the two sexes could also produce this effect. There is some evidence that both mechanisms are involved.

The sex ratio of adults was also determined from animals found under stones. Animals from this second microsite were collected at weekly intervals between May and November 1975. The results are shown in table 5.1 (data grouped into half monthly periods). There were fluctuations in the proportion of adult males found under stones but these did not always follow those in the KLG samples (figs. 5.3a and 5.3b). In early May when the proportion of males was low in the soil samples there was an excess of males under stones (fig. 5.3). Conversely in June and July when males increase in numbers in the soil they are proportionately less abundant under stones. This suggests a differential exchange of males and females between these two sites (soil and under stones). However later changes in the sex ratio of animals under stones followed the changes in the KLG samples more closely.

The differential exchange of males and females between different sites cannot account for the final increase in A. vulgare males, because this would require emigration of all the old females from the study site. If this occurred those females should be located in very large proportions somewhere else. No such build up of large females has ever been observed. It is more likely that it is caused by a very high mortality rate of the post reproductive females. Higher mortality in females than males has also been observed by Sunderland et al. (1976) in P. muscorum, by Hatchett (1947) in Cylisticus convexus and by Paris and Pitelka (1962) in A. vulgare in California.

Growth

As previously stated some males can be distinguished soon after the appearance of a cohort, but in the following analyses they are not treated separately until the first June after their birth in P. scaber and August in A. vulgare. By these times all the males should be recognisable. Treating all the young animals as juveniles in this way avoids errors in estimating the growth rates of the young due to maturation of the males. As an average figure is all that can thus be achieved it must be assumed that young of both sexes grow at the same rate. The following section will show that this is

Table 5.1 The percentage of males among adults collected from under stones.

Date 1975	*A. vulgare*	*P. scaber*
16-31 May	63.3	50-60*
1-15 June	45.3	53.7
16-30 June	32.3	23.7
1-15 July	29.0	32.5
16-31 July	32.8	18.0
1-15 Aug.	49.0	47.1
16-31 Aug.	45.8	48.2
1-15 Sept.	41.1	49.6
16-30 Sept.	42.0	56.0
1-15 Oct.	36.4	52.2
16-31 Oct.	38.2	33.3
1-15 Nov.	41.7	-
16-30 Nov.	59.3	-

* visual estimate only

\- not determined

probably not always true in A. vulgare, but it has little influence on the final interpretation.

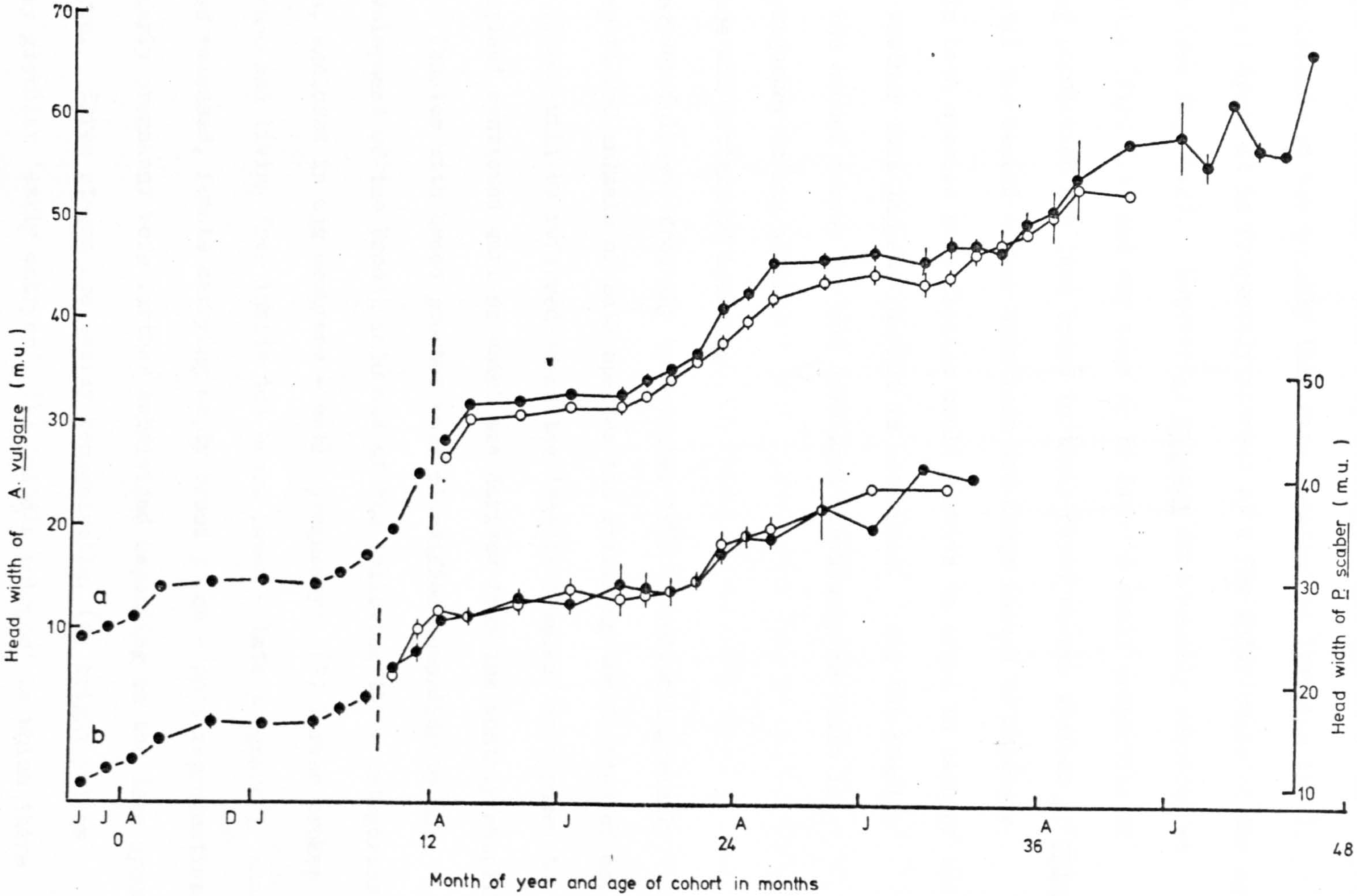
By tracing the increases in the size class distribution of each cohort (figs. 5.1 and 5.2) it can be seen that A. vulgare and P. scaber individuals continue growing throughout their life. But from these figures it is difficult to determine changes in growth rate from month to month. This is due to overlapping of the older cohorts as a result of increasing variation in size between older individuals. To clarify the growth patterns the mean head width of each group (i.e. juveniles, males and females) in each cohort was plotted against age of the cohort. As the pattern for the juveniles, males and females in each cohort was remarkably constant over the four years for which data are available average plots only (± 2 S.E.) are shown in figures 5.4a and 5.4b.

These figures show that growth in both P. scaber and A. vulgare is restricted almost entirely to the summer months. There is some growth during the first few months of a cohorts' life but the curves should actually be steeper. They are depressed by smaller animals being continually recruited to the population. However the figures do give a realistic guide to growth during the other summers. Growth of both species proceeds more rapidly in the first full summer than in the second, and in A. vulgare it continues at at an even slower rate for a third growing season. Mature males and females appear to grow at about the same speed but in A. vulgare the males are larger than the females at any given age. This suggests that either the males of A. vulgare are slightly larger at birth or they grow faster during the first 12 months. Unfortunately with no more information this problem cannot be resolved. The males also attain the greatest head width (maximum recorded was 67 m.u.) but this is partly a consequence of the males greater longevity.

Figure. 5.4 Change in mean head width (± 2 SE) with age of a cohort of a. *Armadillidium vulgare* and b. *Porcellio scaber*. The points shown are the average of four years data.

(●—●) Juveniles, before broken line, and males after it.

(○——○) Females.



Head width of A. vulgare (m.u.)
70
60
50
40
30
20
10
a
b
Head width of P. scaber (m.u.)
50
40
30
20
10
J J A D J A J A J A J
0 12 24 36 48
Month of year and age of cohort in months

(b) Breeding biology and natality

Introduction

P. scaber and A. vulgare breed in summer, but not until they have reached a minimum size of 23 m.u, and 31 m.u. respectively. The age at first reproduction depends on how quickly this size is attained (Merriam 1971). In P. scaber at Spurn it is frequently reached by a few individuals at the age of 10 months (see fig. 5.2). However A. vulgare more usually requires at least 13 months (fig. 5.1) and may take up to 24. A small proportion of the P. scaber population can thus breed in their first summer whereas A. vulgare must wait until the second summer when most are large enough to commence breeding. In both species some females could survive to breed in each of two seasons but whether this happens or not is not known. All the females breeding in the second season may not have bred previously as there is never 100% pregnancy in any cohort.

Incidence and pattern of breeding

Breeding was followed from May to November 1975 by collecting weekly samples of up to 250 animals of both species and examining the females of each age group. (These will be referred to as the 'weekly samples' as opposed to the 'KLG samples' mentioned earlier which are derived from the monthly sampling programme.) Females with brood pouches were classified according to the stage of development of the brood, into one of the following three categories. (1) embryos, enclosed in egg membrane - early pregnancy; (2) larvae broken out of egg membrane and living free inside the brood pouch - late pregnancy; and (3) juveniles released, female carrying empty brood pouch - post reproductives. Females in early pregnancy were further subdivided depending on the development of the embryos. Three stages are easily recognisable, (a) bright yellow and uniformly globular 'early embryos', (b) 'middle embryos' in which there are serially represented segments forming on the surface of the yolk, and (c) 'late embryos' with distinct larval woodlice enclosed within the embryonic membrane.

(i) Armadillidium vulgare

The percentage of two and three year old females which were pregnant in the weekly samples throughout 1975 is shown in figure 5.5a (solid dots) together (for comparison) with the percentage pregnancy of females in the KLG samples (open circles) over four years. The points from the two sources do not differ very much, except possibly in the very early stages of the breeding season. This may be due to a short period of high temperatures in KLG extractor. The single unimodal curve (fitted by eye) can be taken to describe the proportion of females breeding in any of the years at Spurn. There is a single period of breeding activity lasting from mid-May to mid-September.

The percentage of the pregnant females in each of the three developmental stages plus the proportion with early embryos is shown in figure 5.5b. The time from the first appearance of the post reproductive females on the 21st of July, to the 31st of August when all the females have empty brood pouches marks the period of brood release. Such a short interval (less than 45 days) shows a remarkable breeding synchrony. As only two out of many hundreds of females were found to be still carrying early embryos after 21st of July all females which are going to breed must be pregnant on that date. The peak of about 93% gravid females in mid-July thus represents the total proportion of two and three year old females which breed.

(ii) Porcellio scaber

The pattern of breeding in P. scaber is more complex than in A. vulgare as the first and second year females exhibit significant differences in the onset of reproduction and in the proportion breeding. For this reason the percentage pregnancy curves for the 1973 (two year old) and 1974 (one year old) cohort females in the weekly samples have been plotted separately (solid dots in figs. 5.6a and 5.6b). Changes in the percentage pregnancy of the females in the KLG samples are also plotted in figures 5.6a and 5.6b (open circles) for comparative purposes. However because of the small numbers of females in the KLG samples the breeding frequencies have been calculated on a half

Figure. 5.5 Pattern of breeding in A. vulgare females.

a. Percentage pregnancy of two and three year old females combined. Line fitted by eye. Solid dots are derived from weekly collections in I975. Open circles are derived from KLG samples.

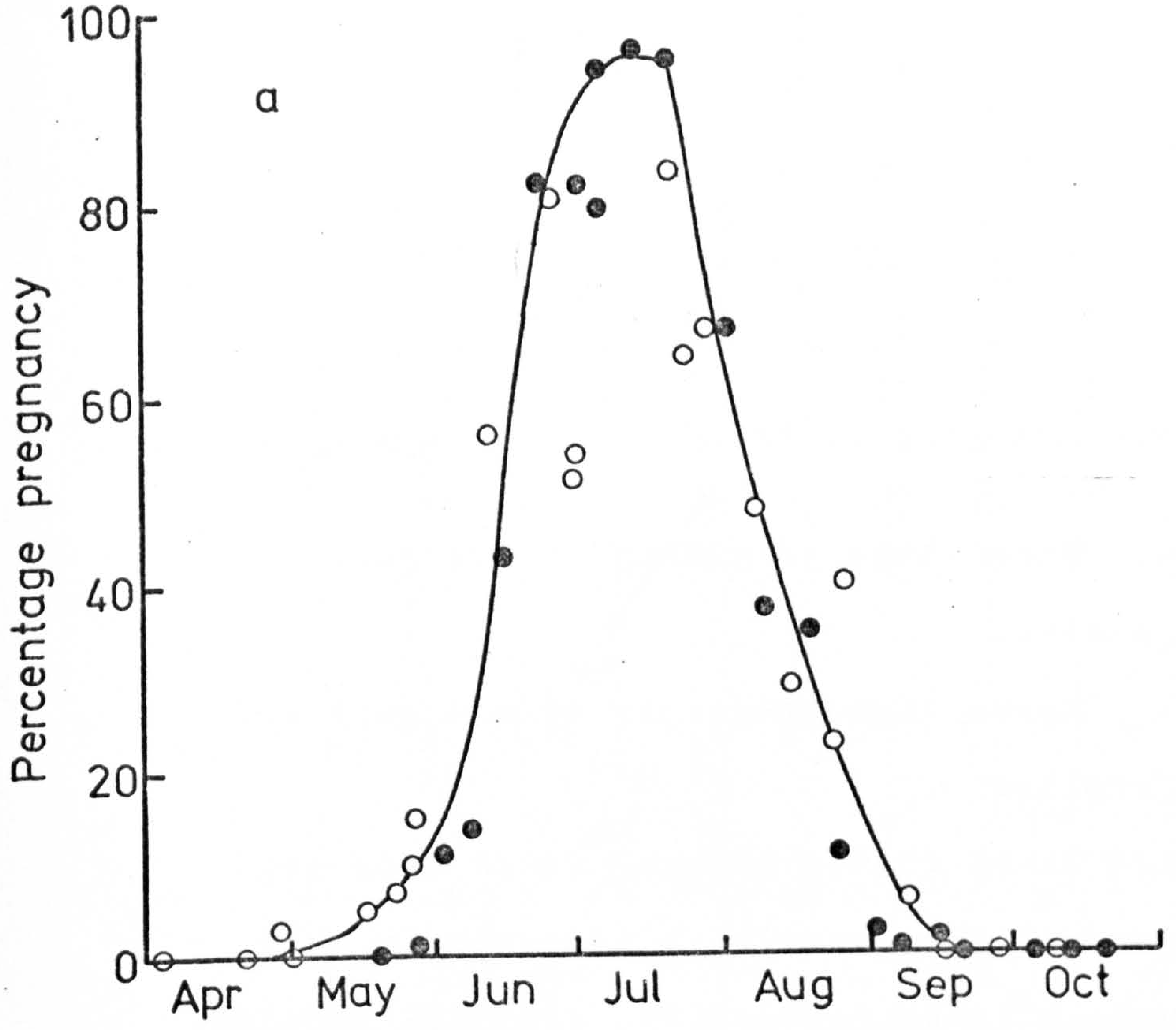
b. Percentage of pregnant females with embryos in each of the three stages of development throughout I975.

(●——●) Stage I, embryos.

(○——○) Stage 2, larvae.

(▲——▲) Stage 3, post reproductive females.

(△----△) Percentage of females with early embryos.


a
Percentage pregnancy
0
20
40
60
80
100
Apr
May
Jun
Jul
Aug
Sep
Oct

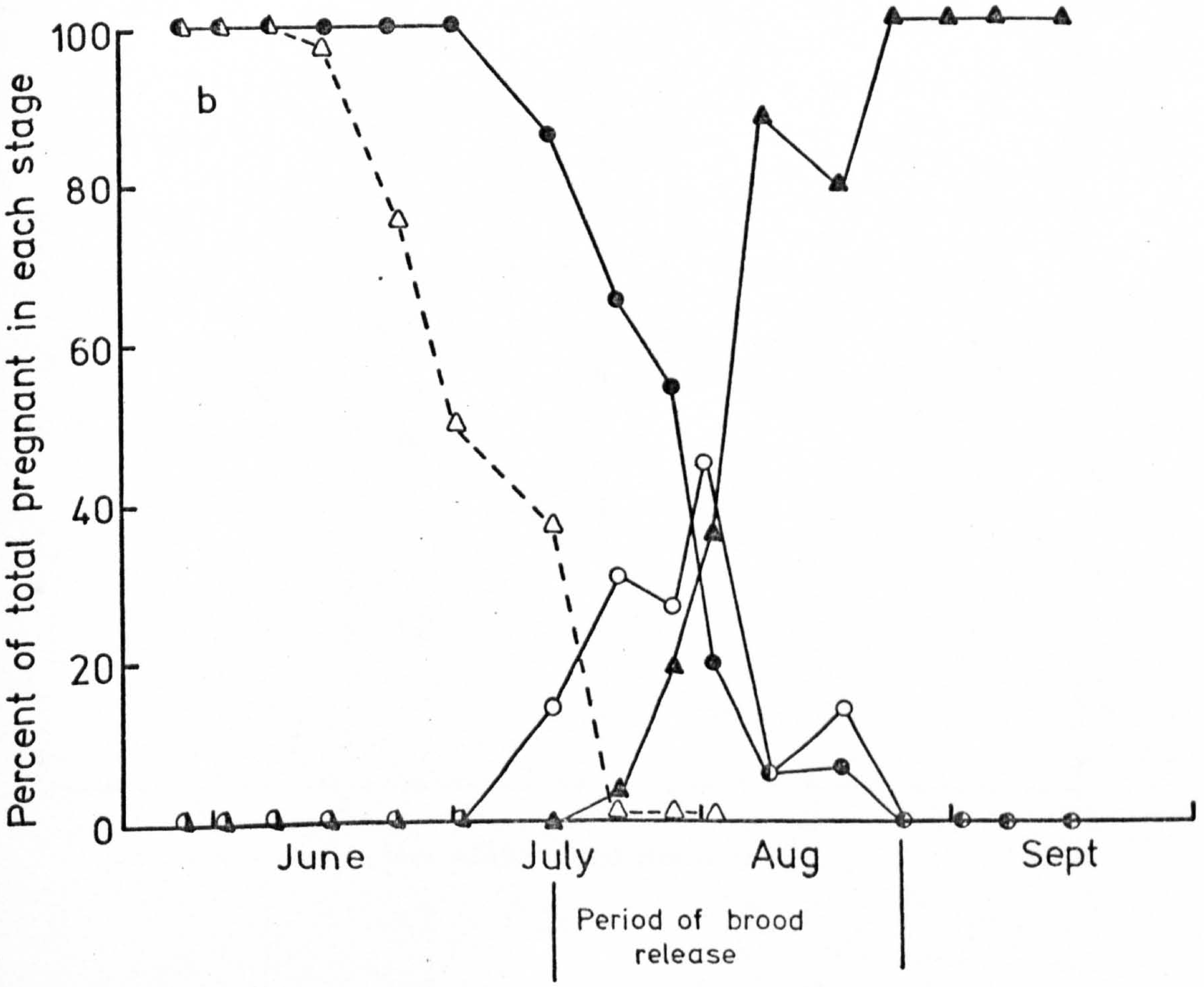

b
Percent of total pregnant in each stage
0
20
40
60
80
100
June
July
Aug
Sept
Period of brood release

Figure. 5.5 Pattern of breeding in A. vulgare females.

a. Percentage pregnancy of two and three year old females combined. Line fitted by eye. Solid dots are derived from weekly collections in 1975. Open circles are derived from KLG samples.

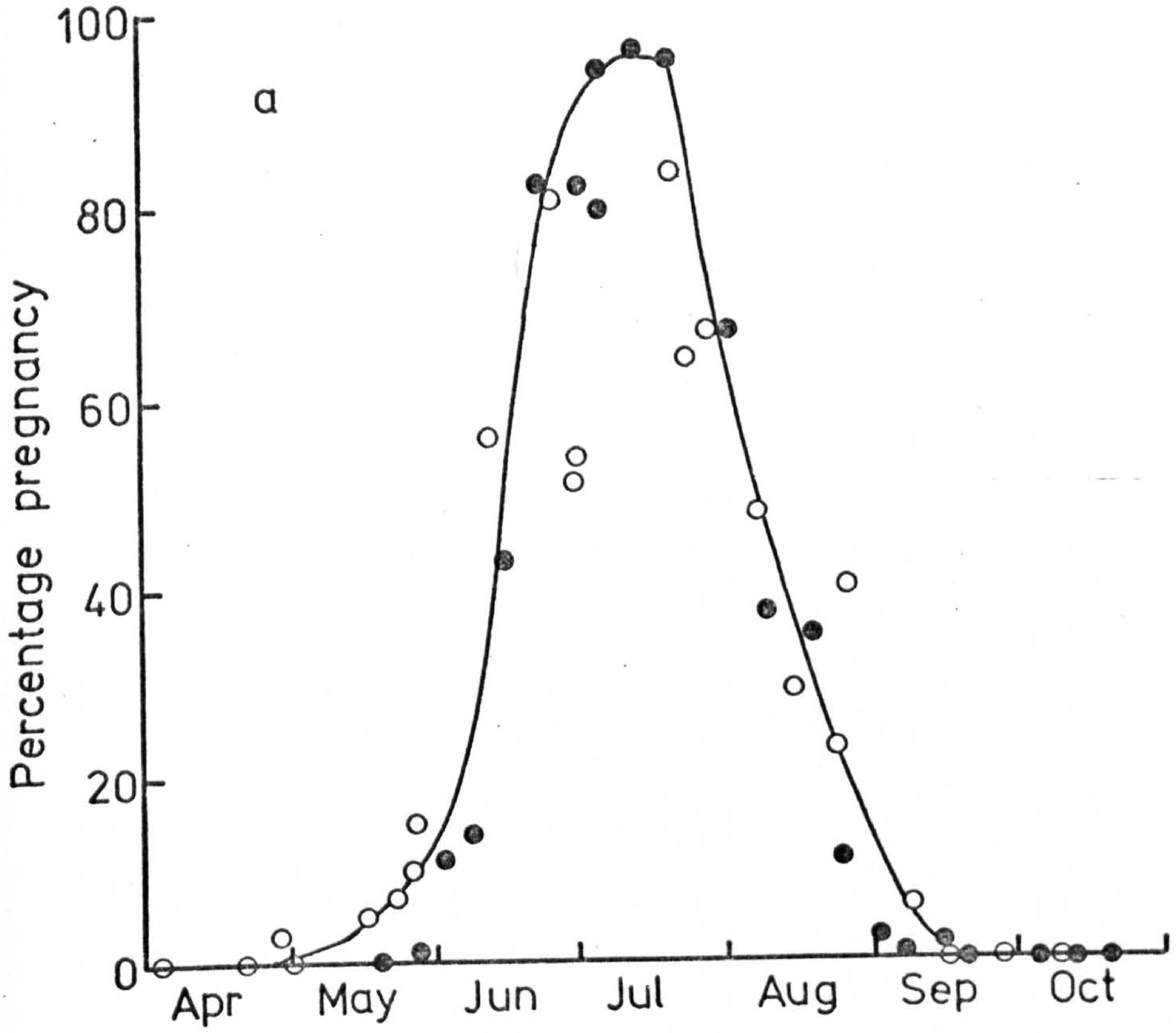
b. Percentage of pregnant females with embryos in each of the three stages of development throughout 1975.

(●——●) Stage I, embryos.

(○——○) Stage 2, larvae.

(▲——▲) Stage 3, post reproductive females.

(△----△) Percentage of females with early embryos.


a
Percentage pregnancy
0
20
40
60
80
100
Apr
May
Jun
Jul
Aug
Sep
Oct

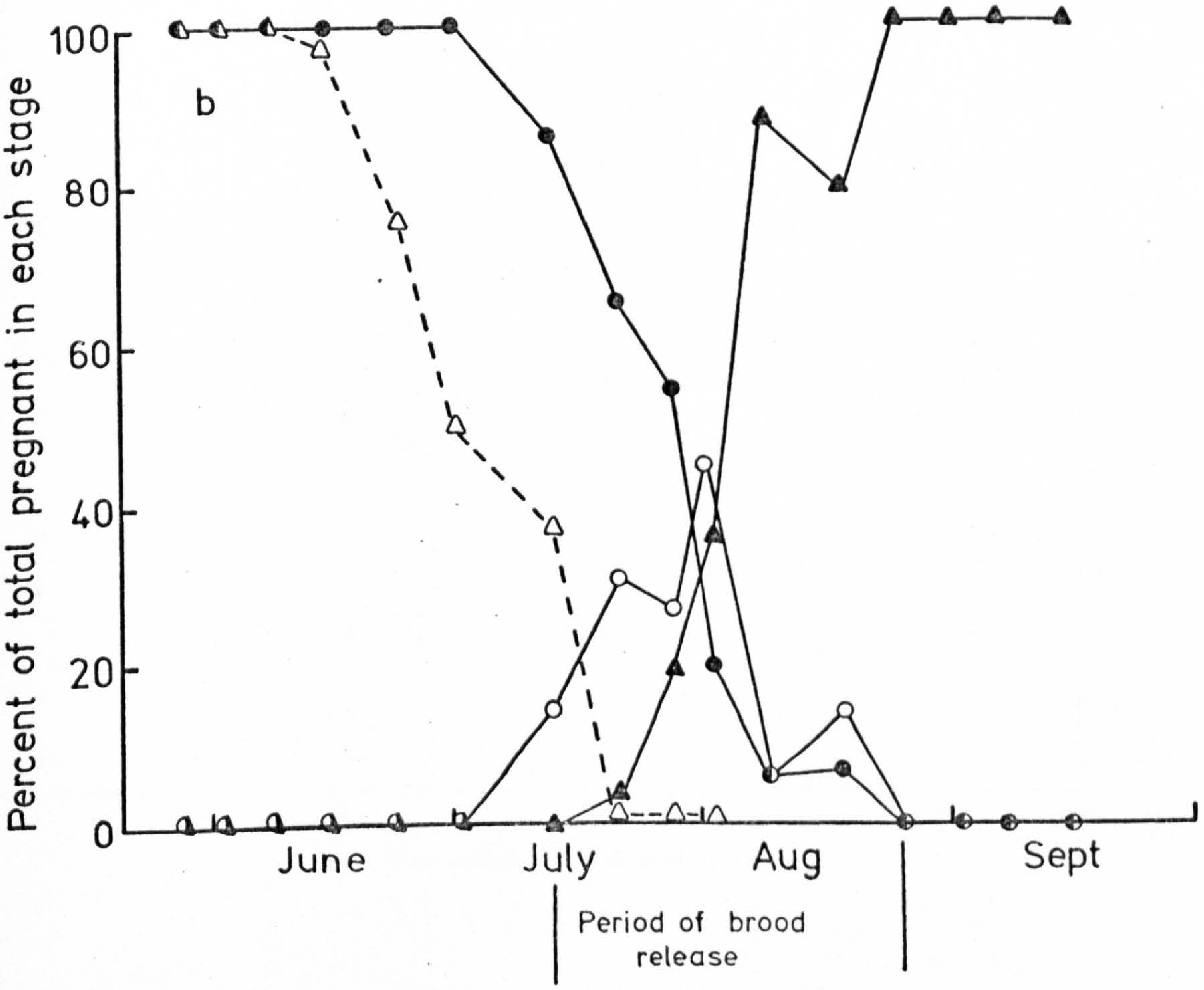
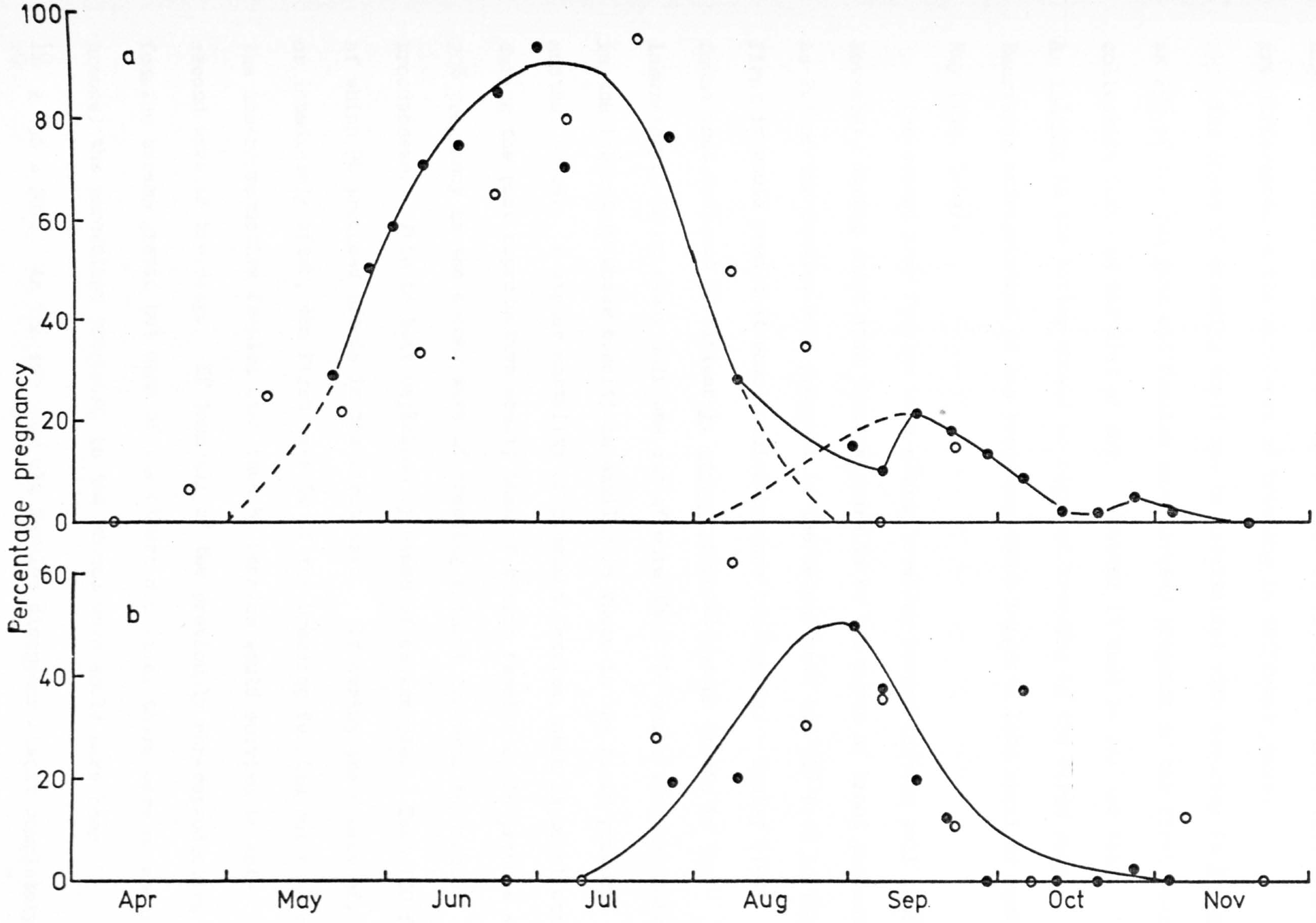

b
Percent of total pregnant in each stage
0
20
40
60
80
100
June
July
Aug
Sept
Period of brood release

Figure. 5.6 Pattern of breeding in P. scaber females.

a. Percentage pregnancy of two year old females.

b. Percentage pregnancy of one year old females.

All lines fitted by eye. Solid dots are derived from weekly collections in 1975. Open circles are derived from KLG samples.


a
b
Percentage pregnancy
100
80
60
40
20
0
60
40
20
0
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

monthly basis from the 1972 to 1975 data combined. These points are somewhat scattered and fit only poorly with the curves fitted by eye to the 1975 points. As was suggested with A. vulgare the differences may be due to the affect of high temperatures in the KLG extractor, but it is also possible that there are differences in the incidence of breeding in different years.

The onset of breeding could not be ascertained with accuracy in P. scaber as 29% of the two year old females were already pregnant in the first weekly collection taken on the 21st of May. However it must be earlier than A. vulgare as the latter showed no signs of breeding in the first sample. Backwards extrapolation of the pregnancy curve suggests late April or early May (fig. 5.6a).

The second year females have a long breeding season lasting well into November, during which time there appears to be two waves of brood production. As 20% of the females were pregnant in the second wave and 90% bred in the first it would seem that some females produce two broods. Heeley (1941) found that four out of fifteen P. scaber produced second broods in the laboratory. In my study only one out of more than 100 which were maintained in the laboratory under conditions similar to those in the field produced another brood. A higher mortality of pregnant females, such as might occur during the post reproductive moult, than of virgin females could produce a 20% pregnancy in the second wave of breeding without recourse to double broodedness. This is best explained by means of an example. Take 100 females of which 90 produced broods in the first wave. If during the course of, or immediately after, the first wave 50 of the breeding females but none of the non-reproductive females died then 50 females would survive to enter the second wave of breeding. If then all of the previously non-reproductive females became gravid but none of the others did (i.e. there were no second broods) the percentage pregnancy in the second wave would have been $\frac{10}{50} \times 100 = 20\%$. As the two year old females disappear almost completely from the samples after the breeding season there is probably a high mortality at this time. The above explanation may therefore be more likely than that requiring the production of two broods. However why 10% of the two year old females should delay breeding until so late is not known. It seems a hazardous process as late pregnancies tail on well into November when the animals are starting to migrate deeper to avoid sudden frosts or cold spells (chapter three). In addition the very late recruits may soon die as McQueen and Carnio (1974) and McQueen (1976) have shown that individuals of Porcellio spinicornis Say which are less than 5 mg live weight seldom survive the winter in Toronto, Canada.

In contrast the one year old females had a short breeding period which began in July and in which only about 50% became pregnant. Both the delay in onset of reproduction and the low breeding frequency, in comparison to the second year females, are probably a function of the need to reach a minimum size before breeding can commence (Merriam 1971).

The release of young into the population will also occur in two waves. The timing of this is indicated by the rapid decline in the percentage pregnancy curves (figs. 5.6a and 5.6b). The first way of young will be released mainly in late July (see also tab. 5.3) whereas the second wave will be released in September.

Fecundity and fertility

A number of pregnant P. scaber and A. vulgare females were dissected and counts made of the number of eggs removed from the brood pouches. In P. scaber the females were divided into those breeding in the first wave of brood production (early breeders) and those breeding in the second wave (late breeders). Early breeding females were defined as all those which were gravid up to June 30th plus those with larvae in July. To avoid overlap between the early and late breeders the latter were defined as the females carrying early embryos in August and all pregnant females thereafter. The late breeders included the single brood of the one year old females plus the two year old females which had either produced a second brood or had delayed the onset of reproduction. One hundred and forty A. vulgare females and 173 early and 84 late P. scaber females were dissected over size ranges of 32-59 m.u., 26-49 m.u. and 25-51 m.u. respectively.

In both species the number of eggs per brood increased with increasing size of the female. The regression equations giving the best fit to the relationships are:

$$y = 0.0138\, x^{2.3} - 25.9255 \qquad \text{(equation 6.1)}$$

$$y = 0.00011\, x^{3.5} - 2.6330 \qquad \text{(equation 6.2)}$$

$$y = 1.6196\, x - 31.3631 \qquad \text{(equation 6.3)}$$

where y = number of eggs in the brood,

and x = the female head width (m.u.)

Equations 6.1, 6.2 and 6.3 refer to the size/fecundity relationships for A. vulgare, P. scaber early breeders and P. scaber late breeders respectively. The correlation coefficient and level of significance, for equation 6.1 is $R = 0.945$ with 138 degrees of freedom (d.f.) $p < 0.001$, for equation 6.2 is $R = 0.945$ with 171 d.f. $p < 0.001$, and for equation 6.3 is $R = 0.875$ with 82 d.f. $p < 0.001$.

The relationship was curvilinear in both A. vulgare and P. scaber early breeders so that the equations accounting for most of the variance required the head width values to be raised to the power of 2.3 and 3.5 as shown. The number of eggs per brood for late breeding females of P. scaber was significantly less than in early breeders of the same size ($d = 10.4$, $p < 0.001$).

This appears to be the first time that a curvilinear relationship between size and fecundity has been found in the terrestrial isopods (Oniscoidea). Every other study has found a simple linear relationship (Brereton 1956 (in Al-Dabbagh 1976), Paris & Pitelka 1962, Sutton 1968, Saito 1969, McQueen & Carnio 1974, Sunderland et al. 1976, Al-Dabbagh 1976 and Lawlor 1977). Although the number of ova is usually linearly related to female size in isopods, Romanova (1974) gives a curvilinear relationship for the marine isopod Idotea baltica baltica (Pallas) from the Baltic sea.

Mortality within the brood pouch was estimated by counting the number of undeveloped eggs in brood pouches containing well developed larvae. The level of mortality was independent of female size, but in P. scaber it was approximately doubled in the late breeders. The values obtained were 2.69% from 37 A. vulgare females, 2.77% from 68 early breeding P. scaber and 5.66% from 21 late breeders. The different levels in P. scaber when evaluated using the Chi-squared test were found to be significant at the 0.1% level ($X^2 = 11.62$ with 1 d.f.).

Duration of pregnancy

The duration of pregnancy was determined by observations on females held captive in small plastic pots (6 cm deep and 5.5 cm diameter) in which the lid and floor had been replaced with fine nylon mesh. Small turf cores were fitted into the pots and the units were then placed in holes in the ground so that the lids were flush with the soil surface. Twenty such pots were set up in a small area on the study site and a further 18 were placed in an outside culture tank at Leeds to allow more frequent observation. Two easily distinguishable A. vulgare and two P. scaber females were introduced into each pot on the 2nd of May 1975 in the laboratory and on the 4th in the field. It was assumed that by this time mating would have already occurred and so no males were included. This was confirmed as most of the animals soon produced embryos. The field animals were examined at approximately weekly intervals whereas the laboratory ones were examined every two or three days at critical times. In this way moulting and the release of juveniles were frequently observed in the laboratory cultures, although in the field such events could only be estimated to the nearest three or four days. In such cases the timing of the event was assumed to have been half way between consecutive observations.

There were no significant differences between the duration of pregnancy estimates for the field and laboratory animals so the data from the two sources have been combined.

The brood development time (i.e. the time from the date of the first maternal moult when the brood pouch is formed to the day the brood is released) in A. vulgare was on average 49.6 days (tab. 5.2). Variation about this mean

Table 5.2 Duration of breeding stages in *Armadillidium vulgare* in 1975.

No	Size (m.u.)	Date of first maternal moult	Date of brood release	Brood development time (days)	Date of second maternal moult or of death*	Duration of post reproductive condition (days)
1	41.3	18 June	1 Aug.	44	10 Sept.*	-
2	49.7	4 July	15 Aug.	42	22 Sept.*	-
3	39.7	7 June	25 July	48	8 Sept.*	-
4	36.2	23 June	13 Aug.	51	25 Aug.	12
5	56.9	8 June	4 Aug.	57	8 Aug.*	-
6	40.8	6 July	9 Aug.	34	25 Aug.	16
7	37.7	7 June	27 July	50	1 Sept.*	-
8	50.6	7 June	27 July	50	2 Aug.*	-
9	53.4	7 June	27 July	50	2 Aug.*	
10	40.2	27 May	27 July	61	2 Aug.*	-
11	53.8	15 June	27 July	42	27 July*	-
12	-	27 May	21 July	55	21 July*	-
13	52.2	15 June	2 Aug.	55	9 Aug.*	-
14	41.7	2 June	21 July	56	21 July*	-
			Mean	49.6		Mean 14
			SE	1.9		
			N	14		

was independent of female size but related to the date of the first maternal moult. The brood development time decreased in animals becoming pregnant later in the season ($R = 0.65$ with 12 d.f. $p < 0.02$). Of the fourteen captive animals producing broods only two survived to the second maternal moult, when the costergites were lost, twelve and sixteen days later, The mean duration of pregnancy was therefore $49.6 + 14 = 63.6$ days. The duration of pregnancy is here defined as the time from the first maternal moult to the second maternal moult, This is the same as that used by Sunderland et al. (1976) for *Philoscia muscorum*. It includes the three stages recognised by Heeley (1941) which are 'embryonic' period, 'larval' period and the period between the liberation of the young and the second maternal moult. The 'embryonic' period plus the 'larval' period of Heeley is equivalent to the brood development time used above. Heeley (1941) gave a duration of pregnancy of 72 days for *A. vulgare* in the laboratory. This is fairly close, to the 63.6 days for *A. vulgare* at Spurn and Leeds, considering the number of factors which may affect it, including as seen here the date of the first maternal moult.

The brood development time in *P. scaber* early breeders was as in *A. vulgare* unrelated to female size though related to the date of the first maternal moult (tab. 5.3) ($R = - 0.93$ with 24 d.f. $p < 0.001$). The mean of twenty six observations was 53.9 days. A slightly higher proportion than in *A. vulgare* survived to complete the second maternal moult (seven out of twenty six) giving a mean post reproductive period of 16 days. The duration of pregnancy in the early breeders was therefore $53.9 + 16 = 69.9$ days.

Unfortunately the duration of pregnancy of the late breeders (both the two year and one year old females) was not determined due to high mortality in the observation chambers. Instead this value was estimated from the data given in Heeley (1941). The animals with first broods studied by Heeley showed a similar relationship between the duration of the brood development time and the date of the first maternal moult. The same trend continued into the second brood giving an even shorter developmental period.

Table 5.3 Duration of breeding stages in *Porcellio scaber* in 1975

No	Size (m.u.)	Date of first maternal moult	Date of brood release	Brood development time (days)	Date of second maternal moult or of death*	Duration of post reproductive condition (days)
1	33.8	22 May	18 July	57	25 July*	-
2	39.9	22 May	21 July	60	27 July*	-
3	28.0	22 May	21 July	60	4 Aug.	14
4	34.8	19 May	16 July	58	4 Aug.	19
5	38.4	14 May	14 July	61	21 July*	-
6	29.2	2 July	8 Aug.	36	11 Aug.*	-
7	30.4	19 May	12 July	54	14 July*	-
8	48.7	14 May	14 July	61	23 July*	-
9	27.9	7 July	15 Aug.	38	18 Sept.*	-
10	27.3	14 May	14 July	61	16 July*	-
11	41.2	31 May	14 July	44	14 July*	-
12	38.0	22 May	16 July	55	4 Aug.*	-
13	33.2	19 May	16 July	58	1 Aug.	16
14	40.0	26 May	21 July	56	18 Aug*	-
15	32.2	31 May	21 July	51	4 Aug.	14
16	33.7	23 June	4 Aug.	42	27 Aug.*	-
17	29.9	2 June	27 July	55	9 Aug.*	-
18	40.7	27 May	21 July	54	21 July*	-
19	33.1	20 May	21 July	66	27 July*	-
20	41.5	27 May	21 July	54	9 Aug.	20
21	29.6	15 June	27 July	43	9 Aug.	16
22	41.7	20 May	21 July	66	21 July*	-
23	39.6	7 June	21 July	49	9 Aug.	13
24	-	27 May	21 July	54	21 July*	-
25	31.2	6 July	18 Aug.	42	18 Aug.*	-
26	35.0	20 May	21 July	66	21 July*	-
			Mean	53.9	Mean	16.0
			SE	1.7	SE	1.0
			N	26	N	7

However the post reproductive period increased in duration so that the total duration of pregnancy in the second broods was not much shorter than in the first. In fact it was 65 days. This figure was taken for the duration of pregnancy in the late breeding females.

Natality

Natality is most easily estimated if it can be assumed that the females which are going to breed are all pregnant together for some time before any young are released. A census of the number of females and the proportion pregnant at that time will then yield the total number of females breeding in that season. It has been shown earlier that this applies to A. vulgare with its exceptionally high degree of breeding synchrony, but not to P. scaber. For this reason different methods of estimating natality are applied to the two isopod populations.

(i) Armadillidium vulgare

Maximum natality (R) in each year has been estimated from the following formula:

$$R = \bar{N} \times f \times F$$

where f = the maximum frequency of gravid females in the population (fig. 5.5a),

F = the mean fecundity of those pregnant females,

and $\bar{N}$ = the mean density of two and three year old females during the period of brood release, 13th July to 25th August (fig. 5.5b).

Maximum natality was then corrected for 2.69% brood pouch mortality to give a final estimate of natality (R').

The above method of calculation was based on the assumptions that (a) mortality of pregnant and non-pregnant females prior to the release of the broods was the same, (b) 50% of the pregnant females that die successfully release their young and (c) mortality prior to brood release is independent of female size.
It is possible that neither (a) nor (b) hold true but in the absence of data to the contrary they are the only acceptable assumptions (Petrusewicz &

Macfadyen 1970). In any case, given the synchronous nature of breeding errors are likely to be small. The section on cohort densities and mortality suggests that assumption (c) is probably quite reasonable.

The density of the females was obtained from the monthly sampling programme as was the size structure of the pregnant females. F was derived from the above and a knowledge of the size/fecundity relationship (equation 6.1). F was not the litter size of a female of mean head width, but the mean litter size of all females in each head width category. With a curvilinear relationship this gives the most accurate estimate. The density of females in 1971 was taken from the monthly sampling programme, but no size structure data was available for them. The mean litter size in 1971 has been calculated using the size structure data of the pregnant animals collected in the weekly samples in 1975 as the mean head width of those females lay midway between those in the other years.

The natality estimates for A. vulgare in each year from 1971 to 1975 are shown in table 5.4.

(ii) Porcellio scaber

Natality in P. scaber was estimated by following the procedure described in Sunderland et al. (1976). In doing this the number of embryos $0.1m^{-2}$ (egg standing crop) was calculated at ten day intervals throughout the breeding season. These values when plotted as in figure 5.7a gave a curve which enclosed an area equal to the total number of embryo days. The total number of embryo days divided by the mean duration of pregnancy and corrected for brood pouch mortality gave an estimate of natality. Separate calculations were made for each of the two waves of breeding in the two year old females and also for the single brood in the one year olds. The natality of each of these groups was then summed to obtain the total natality.

The only modifications made to the procedure outlined in Sunderland et al. (1976) were as follows. (1) The mean number of embryos per female (i.e. mean litter size) was estimated as the mean of the number of eggs produced by each female rather than the number of eggs for a female of mean head width as the

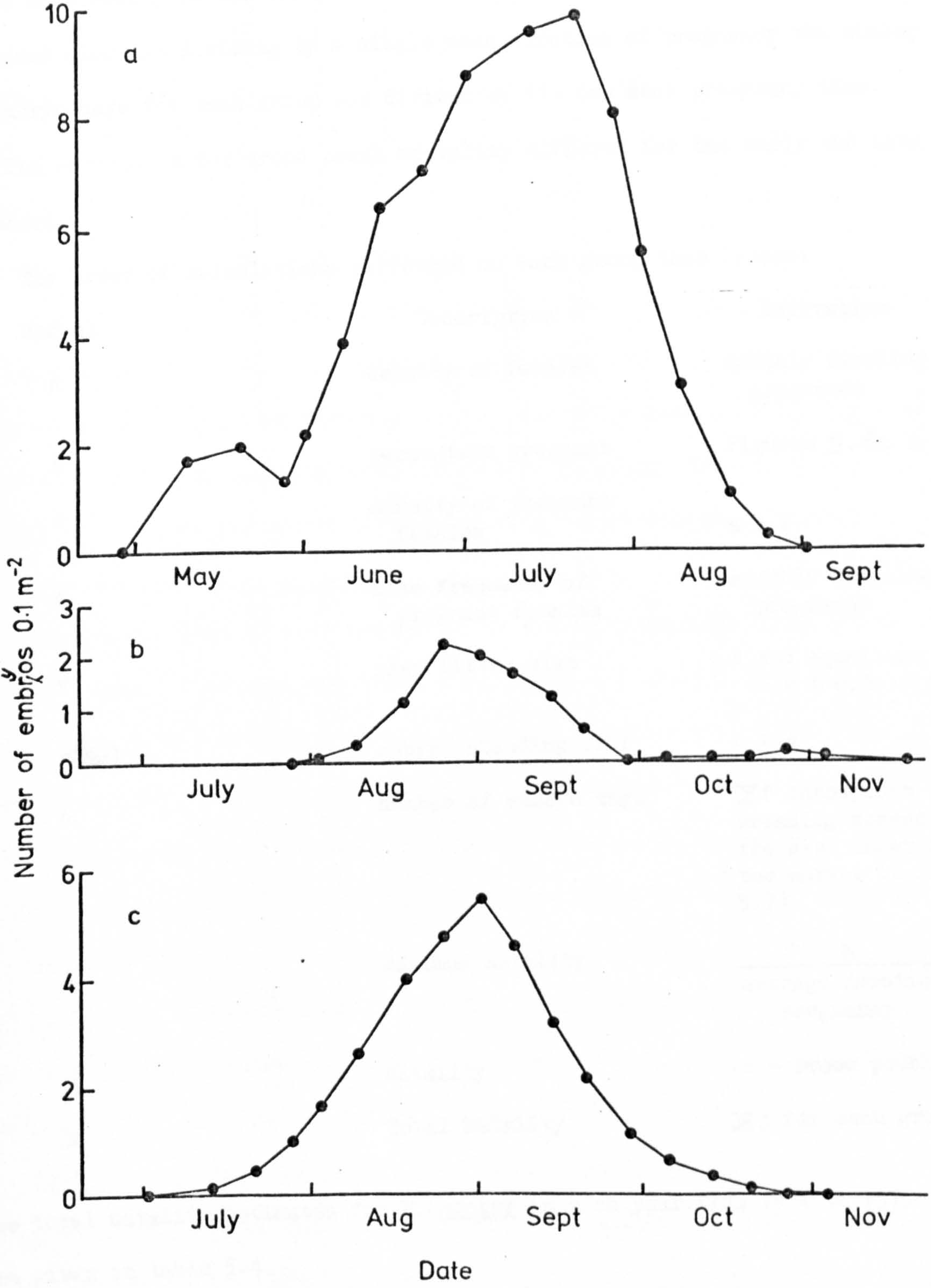
Table 5.4 Natality, juvenile mortality and overall loss rate in *A. vulgare* and *P. scaber*

Cohort	Natality (No. of juveniles $0.1\ m^{-2}$)	Juvenile mortality (No. of animals dying in first two months as a percentage of natality)	Overall loss rate (regression coeff x1000 for the regression of cohort density on age)
A. vulgare			
1971	87.3	80.0†	1.13
1972	119.4	94.0	1.06
1973	113.9	56.5	1.26
1974	88.7	70.1*	1.17
1975	106.7	78.4	-
P. scaber			
1971	15.9	76.7†	1.10
1972	35.0	80.0	0.77
1973	14.0	63.6	1.28
1974	33.7	63.5*	1.79
1975	12.1	51.2	-

† Juvenile mortality estimated assuming constant mortality rate in first seven months.

* Anomolous trough in 1974 cohort juveniles of both species in October sample by-passed by connecting September and November sample means (see figs. 5.10 and 5.11). If this is not done estimates of mortality are 85.0 in *A. vulgare* and 86.7 in *P. scaber*.

Figure. 5.7 Porcellio scaber embryo standing crop (number of embryos per 0.Im^2) during the I975 breeding season. a. First brood of the two year old females. b. Second brood of the two year old females. c. One year old females.


a
b
c
10
8
6
4
2
0
3
2
1
0
6
4
2
0
May
June
July
Aug
Sept
July
Aug
Sept
Oct
Nov
July
Aug
Sept
Oct
Nov
Number of embryos 0.1 m^{-2}
Date

latter is inprecise due to the curvilinear relationship between size and fecundity. (2) Instead of summing the number of embryo days for the two waves of breeding in the two year old females and for the single brood in the one year olds and dividing by a single mean duration of pregnancy the number of embryo days for each group was divided by its own mean pregnancy time. (3) The correction for brood pouch mortality differed for the early and late breeders.

The order of calculations performed on each group thus became:

Symbol	Description	Derivation
a	density of females	monthly sampling programme
b	percentage pregnant	Figures 5.6a & 5.6b
c	density of pregnant females	a x b
d	size frequency of pregnant females	monthly sampling programme
e	mean litter size	d and equations 6.2 & 6.3
f(&g)	embryo standing crop	c x e
h	number of embryo days	Σf throughout breeding season (i.e. the area under one of the curves in figure 5.7)
i	maximum natality	$\frac{h}{\text{average duration of pregnancy}}$
j	Natality	i ÷ brood pouch mortalit
k	Total Natality	Σj for each group.

The total natality estimates for P. scaber in each year from 1971 to 1975 are given in table 5.4.

It should be noted that there are three errors in table 4 in Sunderland et al (1976). The references to figures 8, 9 & 10 should be to figures 7, 8 & 9 respectively.

(c) Cohort density changes, migration and mortality

Changes in cohort density

Cohort density estimates were obtained by counting the number of individuals belonging to each cohort (as indicated by the size frequency analysis) in each of the fourteen replicates of a sample. From these data which are given in table 5.5 (± 1 S.E.) average survivorship curves for A. vulgare and P. scaber were computed on a monthly basis and are displayed in figures 5.8a and 5.9a respectively.

Peak numbers occurred during the period of brood release in P. scaber and immediately after it in A. vulgare. These recruitment peaks were not as great as mean estimated natality of 22.1 and 103.2 (taken from table 5.4), because of very high juvenile mortality and in P. scaber because of asynchronous breeding. The maximum observed duration of a cohort was three years in P. scaber and four in A. vulgare.

When recruitment is over the number in a cohort declines at an approximately constant rate. Thus when the numbers surviving are plotted on a logarithmic scale (figs. 5.8b & 5.9b) the sample points lie close to a straight line. To summarise the decline in numbers by fitting a regression line is useful because regression coefficients of different cohorts can be compared to see if there are statistically significant differences in the overall mortality rate of those cohorts. However to describe the mortality of woodlice throughout their life by a single regression equation is an oversimplification and will hide many events of interest. These will be seen merely as sampling variance adding to the scatter of the points. Thus the sudden fall in density of A. vulgare between the age of 35 and 38 months and of P. scaber between 23 and 27 months may be viewed with little significance. In fact this is due to differences in the mortality rate with season and also to different survivorship curves for the males and females.

Average survivorship curves for the males and females are depicted in figures 5.8c and 5.9c. They show that mortality is least in winter and spring and greatest in summer and autumn during or just after breeding

Table 5.5 Mean density of cohorts 0.1 m^{-2} (± 1 SE)

Sample date	Mean density *A. vulgare*	 *P. scaber*
	1968 Cohort	
26 Jan 1972	0.1 ± 0.1	
28 Feb	0.4 ± 0.2	
28 Mar.	0.1 ± 0.1	
1 May	0.1 ± 0.1	
26 May	0.2 ± 0.2	
30 June	0.1 ± 0.1	
26 Aug.	0.0	
	1969 Cohort	
26 Jan. 1972	1.1 ± 0.4	0.1 ± 0.1
28 Feb	2.8 ± 1.5	0.0
28 Mar	1.6 ± 0.6	0.1 ± 0.1
1 May	3.1 ± 0.8	0.1 ± 0.1
26 May	4.3 ± 1.4	0.0
30 June	2.9 ± 0.6	
26 Aug	1.5 ± 0.4	
28 Sept	0.1 ± 0.1	
28 Nov	0.1 ± 0.1	
30 Jan 1973	0.1 ± 0.1	
3 Apr.	0.0	
	1970 Cohort	
26 Jan 1972	3.1 ± 1.2	0.6 ± 0.3
28 Feb.	3.4 ± 0.9	0.1 ± 0.1
28 Mar	2.9 ± 0.8	0.9 ± 0.4
1 May	3.4 ± 0.7	0.4 ± 0.1
26 May	4.5 ± 1.4	1.9 ± 0.9
30 June	5.6 ± 1.3	1.8 ± 0.9
26 Aug.	4.6 ± 1.3	0.4 ± 0.3
28 Sept	3.1 ± 0.7	0.1 ± 0.1
28 Nov	2.9 ± 0.6	0.0
30 Jan 1973	2.9 ± 0.7	
3 Apr.	1.9 ± 0.6	
23 May	1.9 ± 0.4	
24 June	0.9 ± 0.4	
22 July	0.4 ± 0.2	
15 Aug.	0.1 ± 0.1	
16 Sept.	0.1 ± 0.1	
10 Nov.	0.0	
25 Jan 1974	0.1 ± 0.1	
21 Apr.	0.0	

Sample date	Mean density *A. vulgare*	 *P. scaber*
	1971 Cohort	
26 Jan 1972	0.9 ± 0.5	0.3 ± 0.2
28 Feb	0.3 ± 0.2	0.0
28 Mar	0.9 ± 0.7	1.3 ± 0.8
1 May	4.3 ± 3.5	1.8 ± 0.8
26 May	2.3 ± 1.0	5.4 ± 1.7
30 June	10.1 ± 2.4	6.6 ± 2.4
26 Aug	8.5 ± 2.6	4.3 ± 2.8
28 Sept	13.4 ± 4.3	2.1 ± 0.7
28 Nov.	10.6 ± 2.5	1.3 ± 0.6
30 Jan 1973	9.4 ± 1.5	1.8 ± 0.8
3 Apr.	7.6 ± 1.0	0.6 ± 0.2
23 May	4.0 ± 1.3	0.6 ± 0.6
24 June	6.3 ± 1.5	1.1 ± 0.5
22 July	4.9 ± 1.1	0.4 ± 0.2
15 Aug	9.2 ± 2.2	0.8 ± 0.5
16 Sept	6.1 ± 1.2	0.6 ± 0.3
10 Nov	4.1 ± 1.0	0.1 ± 0.1
25 Jan 1974	2.4 ± 0.9	0.1 ± 0.1
21 Apr.	5.5 ± 2.4	0.0
17 May	2.3 ± 1.7	0.1 ± 0.1
12 June	0.1 ± 0.1	0.0
21 July	0.0	
	1972 Cohort	
26 Aug 1972	1.7 ± 0.8	3.1 ± 1.0
28 Sept	7.4 ± 4.7	7.1 ± 3.2
28 Nov	6.3 ± 2.8	2.9 ± 1.7
30 Jan 1973	17.6 ± 2.6	3.2 ± 1.6
3 Apr.	8.7 ± 3.2	2.6 ± 1.4
23 May	9.1 ± 4.5	3.2 ± 2.0
24 June	16.0 ± 2.8	4.6 ± 1.8
22 July	7.5 ± 1.0	2.2 ± 0.7
15 Aug	15.6 ± 3.6	1.9 ± 0.8
16 Sept	14.2 ± 3.0	1.6 ± 0.4
10 Nov	11.3 ±2.1	2.4 ± 1.2
25 Jan 1974	10.3 ±2.2	0.9 ± 0.3
21 Apr	6.7 ± 1.5	0.6 ± 0.4
17 May	6.9 ± 2.5	2.9 ± 0.9
12 June	4.4 ± 1.7	0.4 ± 0.2
21 July	5.7 ± 2.1	2.1 ± 1.6
8 Aug	3.4 ± 1.3	1.9 ± 1.6
8 Sept	2.2 ± 0.8	0.6 ± 0.3

Table 5.5 (continued)

Sample Date	Mean Density	
	A. vulgare	*P. scaber*
1972 Cohort (cont'd.)		
10 Oct	0.9 ± 0.3	0.1 ± 0.1
10 Nov	1.1 ± 0.4	0.0
6 Jan 1975	2.1 ± 0.9	0.1 ± 0.1
3 Mar	1.3 ± 0.6	0.0
28 Apr	1.6 ± 0.6	
27 May	1.1 ± 0.6	
1 July	0.1 ± 0.1	
29 July	0.5 ± 0.4	
26 Aug	0.3 ± 0.2	
28 Sept	0.1 ± 0.1	
18 Nov	0.0	
1973 Cohort		
24 June 1973		0.4 ± 0.4
22 July	4.4 ± 1.8	2.4 ± 1.8
15 Aug	22.4 ± 5.6	4.7 ± 1.8
16 Sept	53.4 ± 12.5	5.6 ± 1.6
10 Nov	36.9 ± 9.9	3.7 ± 2.9
25 Jan 1974	17.4 ± 4.1	1.4 ± 1.2
21 Apr	13.3 ± 3.6	1.9 ± 0.7
17 May	34.1 ± 7.4	5.3 ± 1.9
12 June	19.5 ± 3.5	1.4 ± 0.7
21 July	30.5 ± 6.7	6.6 ± 5.3
8 Aug	16.4 ± 5.3	6.9 ± 5.0
8 Sept	20.2 ± 5.7	4.0 ± 2.4
10 Oct	15.1 ± 4.0	0.8 ± 0.5
10 Nov	15.1 ± 3.8	1.4 ± 0.5
6 Jan 1975	19.6 ± 8.9	1.9 ± 0.7
3 Mar	9.5 ± 3.2	2.1 ± 1.2
28 Apr	11.4 ± 2.3	1.1 ± 0.3
27 May	6.0 ± 2.2	0.1 ± 0.1
1 July	8.5 ± 3.7	0.5 ± 0.3
29 July	5.1 ± 3.0	0.7 ± 0.3
26 Aug	5.2 ± 3.7	0.5 ± 0.4
28 Sept	3.1 ± 1.6	0.0
18 Nov	2.3 ± 1.3	0.4 ± 0.2

Sample Date	Mean Density	
	A. vulgare	*P. scaber*
1974 Cohort		
12 June 1974	0.7 ± 0.7	
21 July	4.4 ± 2.5	3.5 ± 2.1
8 Aug	22.9 ± 13.5	18.3±16.4
8 Sept	31.4 ± 9.7	13.4 ±10.5
10 Oct	4.9 ± 1.5	0.3 ± 0.1
10 Nov	18.0 ± 5.7	10.4 ± 8.6
6 Jan 1975	23.5 ±11.5	11.6 ± 8.7
3 Mar	13.0 ± 7.8	3.9 ± 2.8
28 Apr	11.8 ± 6.6	1.5 ± 0.6
27 May	3.9 ± 2.5	0.9 ± 0.4
1 July	5.6 ± 3.8	1.1 ± 0.6
29 July	6.1 ± 3.4	1.1 ± 0.6
26 Aug	7.4 ± 2.8	1.9 ± 1.3
28 Sept	5.1 ± 1.8	1.6 ± 0.5
18 Nov	6.7 ± 2.7	0.8 ± 0.5
1975 Cohort		
29 July 1975	24.4 ± 23.9	6.7 ± 6.4
26 Aug	24.6 ± 19.0	12.4 ±10.3
28 Sept	22.9 ± 11.9	5.6 ± 3.1
18 Nov	32.3 ± 12.1	11.8 ± 4.6

Figure. 5.8 Mean survivorship curves for _Armadillidium vulgare_.

a. Changes in mean cohort density (arithmetic scale) with age of cohort in months.

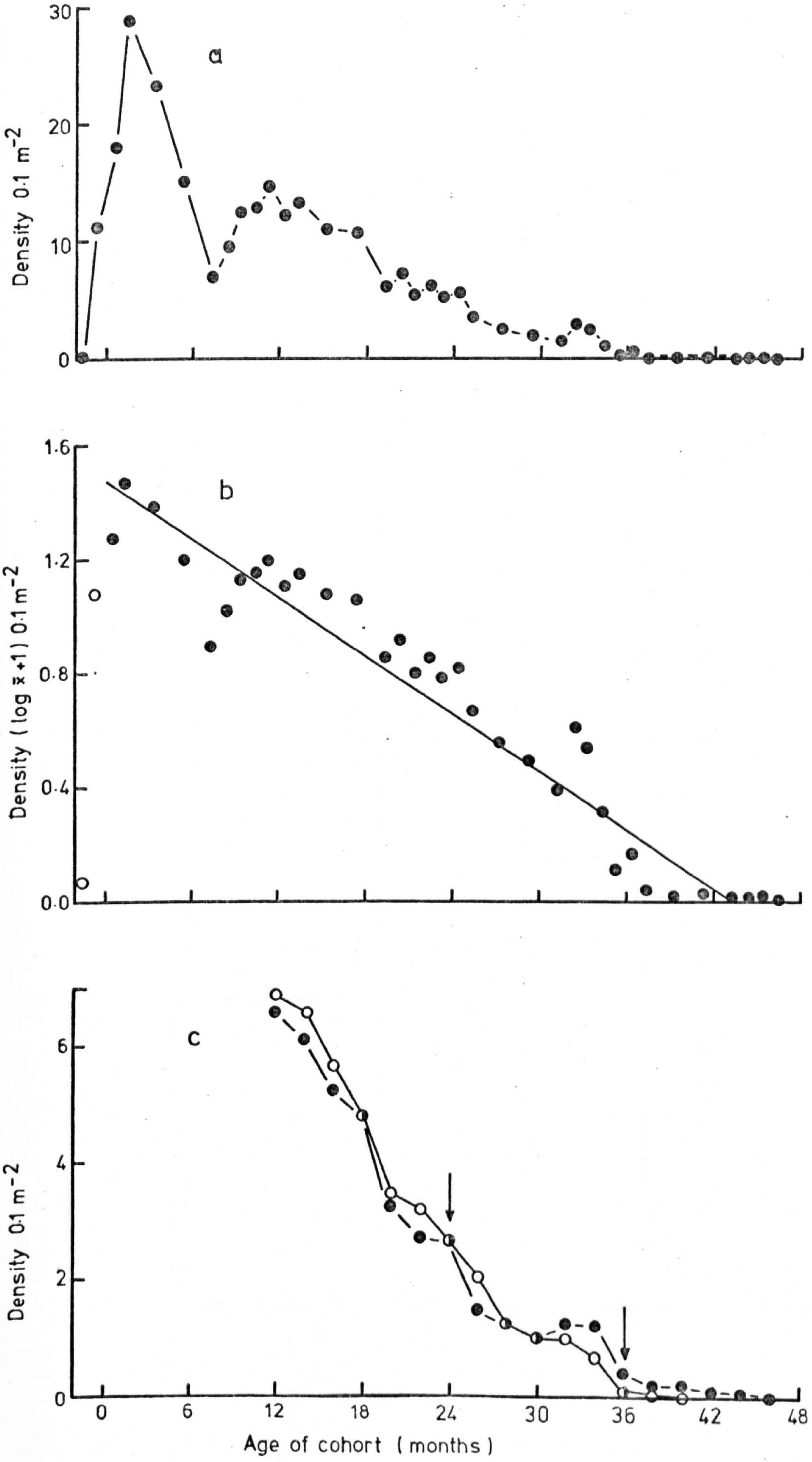
b. Changes in mean cohort density (logarithmic scale) with age of cohort in months. Open circles denote points not used to derive fitted regression line because of recruitment.

c. Changes in mean density of males and females (arithmetic scale) in a cohort with age of cohort in months.

(●—●) Males.

(○—○) Females.

← Denotes approximate date of peak period of brood release, ie I August.



a
30
20
10
0
Density 0·1 m^{-2}
b
1·6
1·2
0·8
0·4
0·0
Density (log x̄ +1) 0·1 m^{-2}
c
6
4
2
0
Density 0·1 m^{-2}
0
6
12
18
24
30
36
42
48
Age of cohort (months)

Figure. 5.9 Mean survivorship curves for *Porcellio scaber*.

a. Changes in mean cohort density (arithmetic scale) with age of cohort in months.

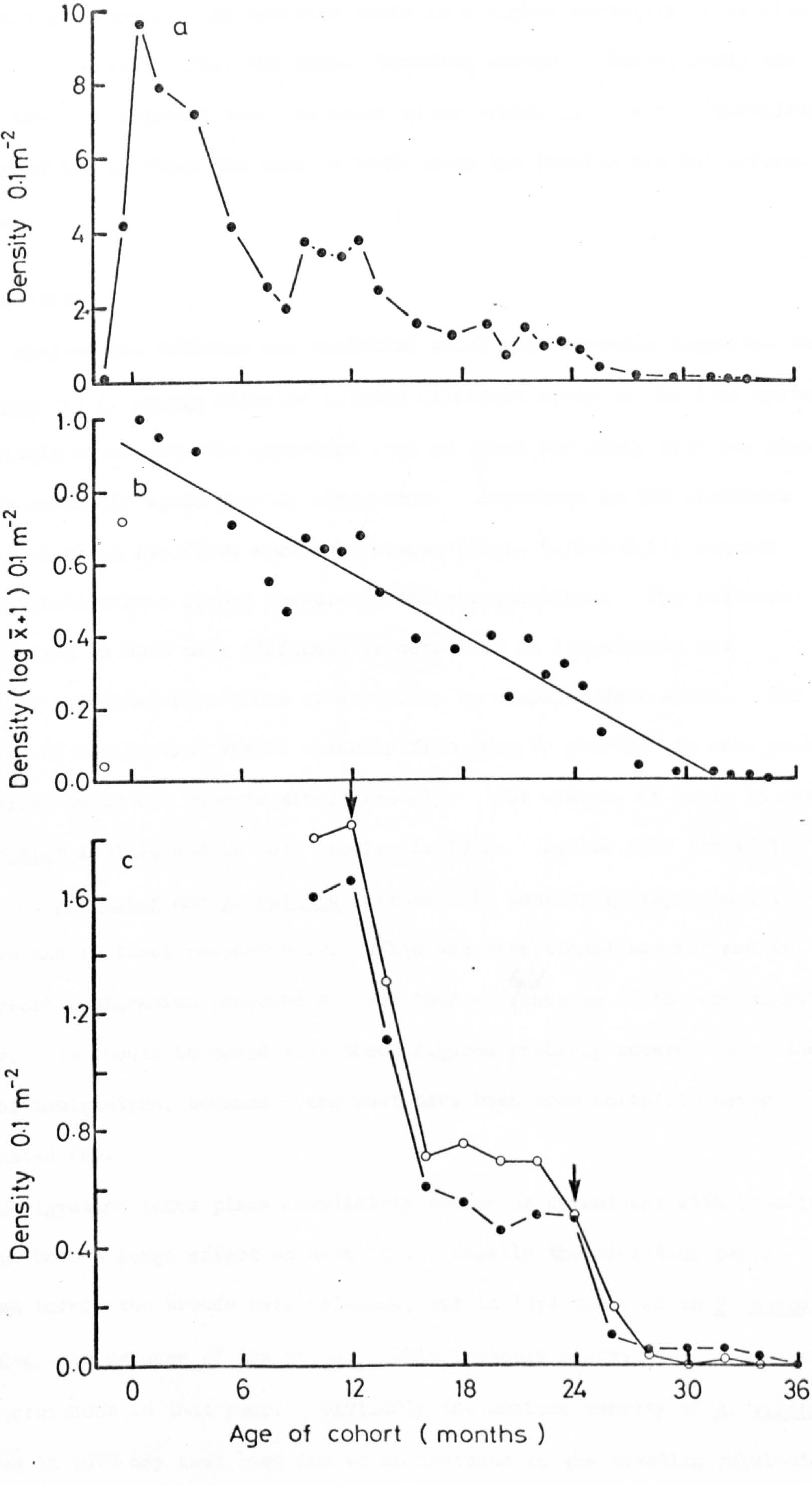
b. Changes in mean cohort density (logarithmic scale) with age of cohort in months. Open circles denote points not used to derive fitted regression line because of recruitment.

c. Changes in mean density of males and females (arithmetic scale) in a cohort with age of cohort in months.

(●——●) Males.

(○——○) Females.

← Denotes approximate date of peak period of brood release, ie I August.


a
Density 0·1 m⁻²
0
2
4
6
8
10
b
Density (log x̄+1) 0·1 m⁻²
0.0
0.2
0.4
0.6
0.8
1.0
c
Density 0·1 m⁻²
0.0
0.4
0.8
1.2
1.6
0
6
12
18
24
30
36
Age of cohort (months)

(indicated by arrows). In addition there is a higher mortality of females during or immediately after the second breeding season. Consequently the females are less abundant than the males after breeding. As the 'mortality rate thereafter is about the same in both sexes the females die out before the males.

Migration

In chapter two evidence was presented which very strongly suggested that *A. vulgare* and *P. scaber* migrated between different areas in the dune system. Many animals moved onto the grassland area on which the study site was placed and then moved off again shortly afterwards. Increases in the abundance of each cohort in its first spring or summer (figs. 5.10 & 5.11) suggest that immigration is a common feature in these populations. The presence of emigration is much more difficult to establish as its affects are not easily separated from those of mortality by sampling data alone. The intensity of immigration varied markedly from year to year and in some years was noticeable in all cohorts simultaneously. For example it could be seen in *P. scaber* in 1974 and in both species in 1972. During 1972 the 1971 cohorts of *P. scaber* and *A. vulgare* increased in density by approximately 22 times and 15 times respectively. This was exceptional however and in other years immigration produced no more than 4-5 fold changes on the pre-migration density. It should be noted that these figures probably underestimate the level of immigration, because there must have been some mortality being compensated for.

As migration takes place immediately before or coincident with breeding it could have a large effect on natality. Usually the migration peaks appeared before the broods were released, but in 1974 the peak in *P. scaber* coincided with release of the young. This probably contributed to the very high recruitment in that year. Similarly the maximum density of *A. vulgare* recorded in 1973 may have been due to an increase in the breeding population as a result of immigration in 1972.

Figure. 5.10 Mean density per $0.1m^2$ of eight cohorts of *Armadillidium vulgare* from January 1972 to November 1975. Successive cohorts indicated by alternation of continuous and broken lines.

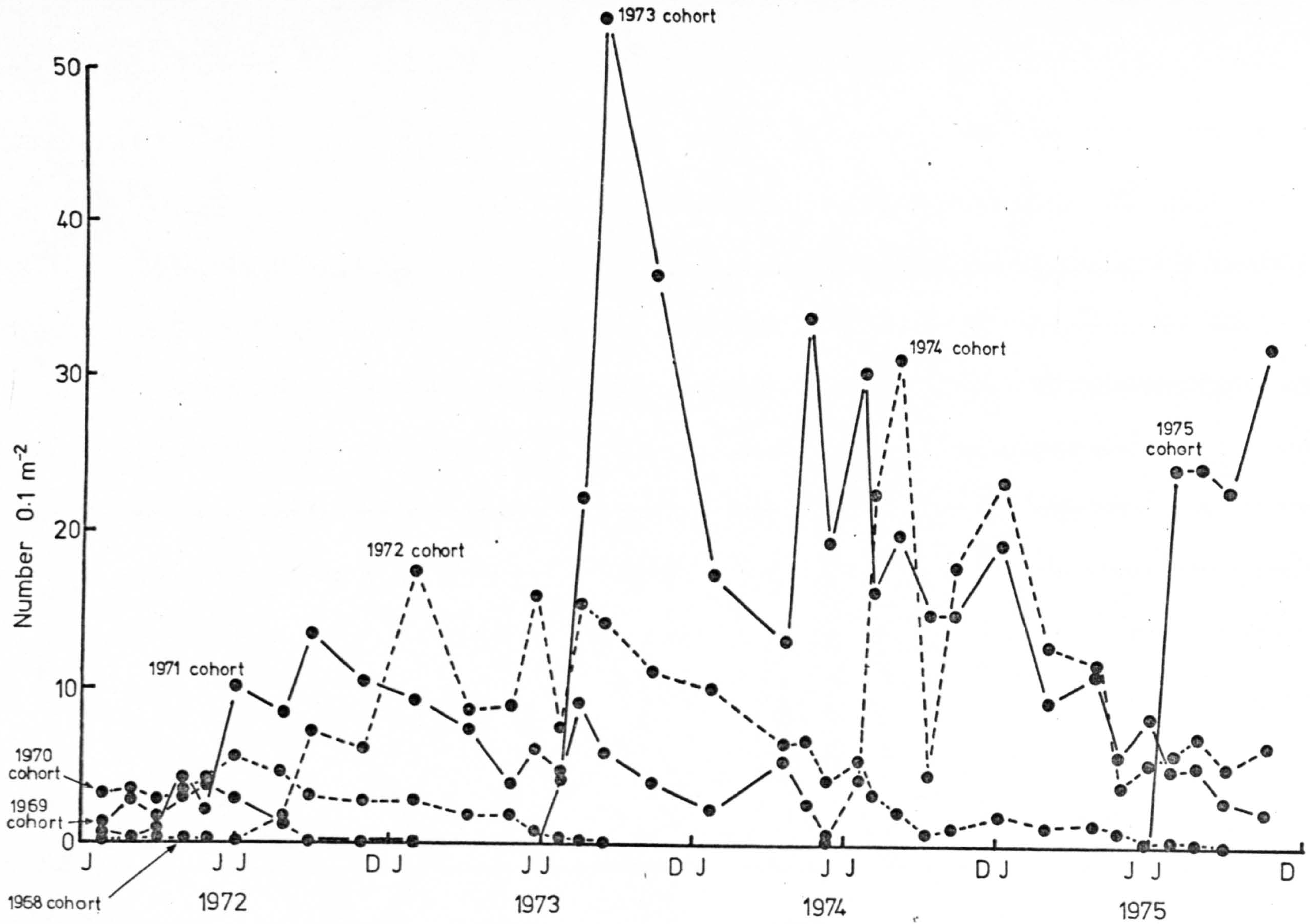
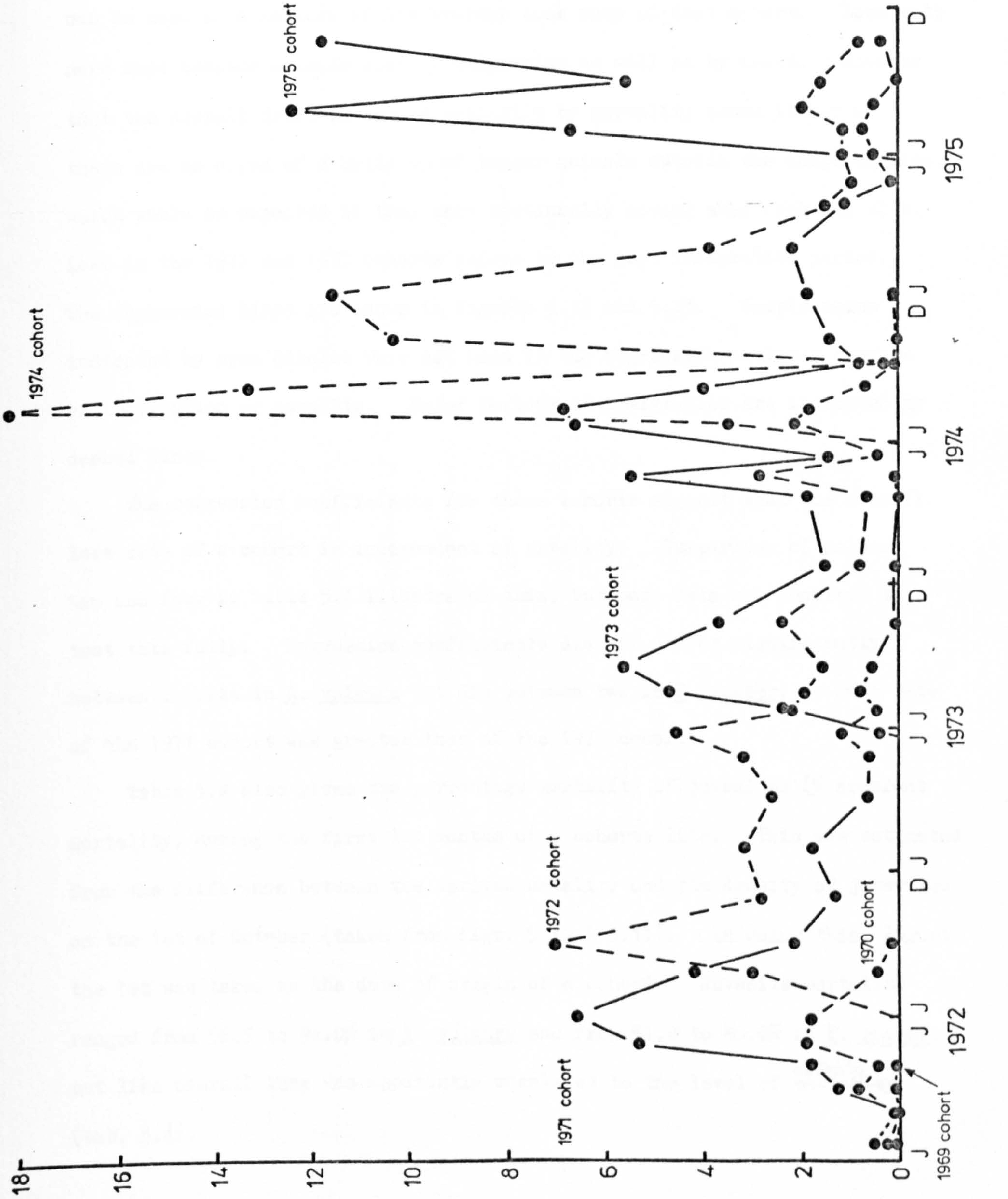

1973 cohort
1974 cohort
1975 cohort
1972 cohort
1971 cohort
1970 cohort
1969 cohort
1958 cohort
Number 0.1 m⁻²
50
40
30
20
10
0
J
J J
D J
J J
D J
J J
D J
J J
D
1972
1973
1974
1975

Figure. 5.II Mean density per 0.Im^2 of seven cohorts of *Porcellio scaber* from January I972 to November I975. Successive cohorts indicated by alternation of continuous and broken lines.


Number 0.1 m⁻²
0
2
4
6
8
10
12
14
16
18
J
J J
D J
J J
D J
J J
D J
J J
D
1972
1973
1974
1975
1969 cohort
1970 cohort
1971 cohort
1972 cohort
1973 cohort
1974 cohort
1975 cohort

Loss rate and juvenile mortality

As the survivorship curves approximately follow a pattern of exponential decline the regression coefficient describing the relationship between the logarithm of the mean density and the age of a cohort in days can be used as a measure of the average loss rate of that cohort. Loss rate here must include animals lost by emigration as well as by death. However that the overall trend is caused primarily by mortality seems likely as there are no signs of a build up of larger animals outside the sampling area, which would be expected if they were continually moving away from the site. Loss in the 1971 and 1973 cohorts refers to the post immigration period. The regression lines are shown in figures 5.12 and 5.13. Sample means indicated by open circles were not used in the regression analyses because of immigration or natality. Major periods of immigration are indicated by dashed lines.

The regression coefficients for these cohorts suggest that the overall loss rate of a cohort is independent of natality. Comparison of columns two and four in table 5.4 illustrates this, but more data are required to test this fully. Regression coefficients did not differ significantly between cohorts in A. vulgare but did between two in P. scaber. Loss rate of the 1971 cohort was greater than of the 1972 cohort.

Table 5.4 also gives the percentage mortality of juveniles (% apparent mortality) during the first two months of a cohorts life. This was estimated from the difference between the derived natality and the density of juveniles on the 1st of October (taken from figs. 5.10 & 5.11). In doing this, August the 1st was taken as the date of origin of a cohort. Juvenile mortality ranged from 56.5 to 94.0% in A. vulgare and from 51.2 to 80.0% in P. scaber, but like overall loss was apparently unrelated to the level of ~~mortality~~ natality (tab. 5.4).

Figure. 5.I2 Changes in separate Armadillidium vulgare cohort densities (logarithmic scale) with age of cohort in days. Open circles denote points not used to derive fitted regression lines because of recruitment or immigration.

a. I97I cohort.

b. I972 cohort.

c. I973 cohort.

d. I974 cohort.

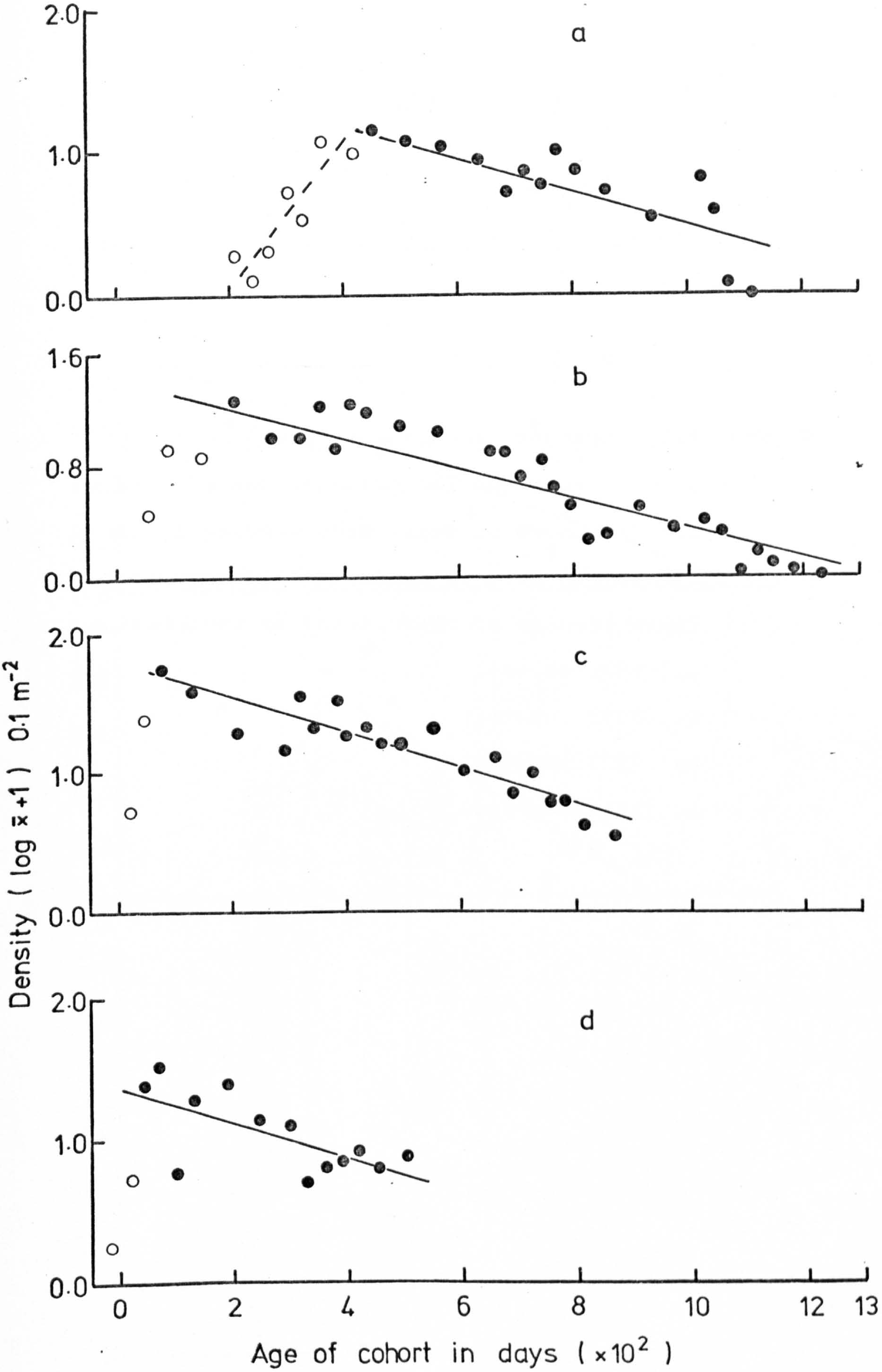
a
b
c
d
2.0
1.0
0.0
1.6
0.8
0.0
2.0
1.0
0.0
2.0
1.0
0.0
Density (log x̄ +1) 0.1 m^{-2}
0
2
4
6
8
10
12
13
Age of cohort in days (×10^2)

Figure. 5.I3 Changes in separate Porcellio scaber cohort densities (logarithmic scale) with age of cohort in days. Open circles denote points not used to derive fitted regression lines because of recruitment or immigration.

a. I97I cohort.

b. I972 cohort.

c. I973 cohort.

d. I974 cohort.


a
b
c
d
1.0
0.8
0.6
0.4
0.2
0.0
1.4
1.2
Density (log x̄+1) 0.1 m^{-2}
0
2
4
6
8
10
Age of cohort in days (×10^2)

The role of natality, mortality and migration in the cohort dynamics of isopod species

The identification of key factors causing population change adds considerably to the understanding of the population dynamics of a species. Morris (1963) and Varley and Gradwell (1960) have shown how to identify key factors or at least how to determine the contribution of each age interval to variation in total generation survival, and hence to changes in population trend, from a series of life tables. Although only three full cohorts of *A. vulgare* and four of *P. scaber* are available here the data have been analysed by these methods, because so much insight can be gained from them. However with such a limited amount of data the conclusions drawn must be considered extremely tentative and certainly require further verification.

The modification of Varley and Gradwell's graphical correlation method given by Southwood (1966) has been used. Natality estimates given in table 5.4 were combined with the cohort density data (figs. 5.10 & 5.11) to produce life tables (tabs. 5.6 and 5.7) in which attention has been focussed on age intervals of specific interest. For example in the first two months of life (August 1st to October 1st) when there are heavy juvenile losses (k_0) and in the spring and summer (k_2 and k_3) periods when migration usually occurs.

Initially changes in the number of animals reaching the first breeding season (P_R) were compared with the densities of eggs (P_E) giving rise to them and to the total mortality (Kappa - K) over the intervening period (figs. 5.14~~a~~ & 5.15~~a~~). In both species changes in P_R appeared to be influenced by changes in K only, unlike the situation with *Philoscia muscorum* where variation in natality was equally important (Hassall 1976).

By dividing K into the various seasonal (time specific) components it was shown for *P. scaber* that it was the variation in spring and summer losses (k_2 & k_3) (or gains if immigration was involved) which formed the most important part of K and paralleled the changes in log P_R equally well. Similarly k_2 and k_5 made up an important component of K in *A. vulgare*, but juvenile mortality (k_0) also appeared to be important in determining overall

Table 5.6 *Armadillidium vulgare* life tables

	1971 cohort			1972 cohort			1973 cohort		
Date and Age of Cohort (x) in months	Density $0.1m^{-2}$	log	k values	Density $0.1m^{-2}$	log	k values	Density $0.1m^{-2}$	log	k values
1st August (0) NATALITY (PE)	87.3	1.94		119.4	2.08		113.9	2.06	
Juvenile mortality k_o			0.07			1.22			0.37
1st October (2)	17.4‡	1.24		7.2	0.86		49.5	1.69	
Overwintering loss k_1			1.76			-0.26			0.50
1st March (7)	0.3	-0.52		13.3	1.12		15.6	1.19	
Spring effects k_2 (migration & mortality)			-1.52			-0.03			-0.20
1st July (11)	10.0	1.00		14.2	1.15		24.5	1.39	
Summer losses k_3			-0.12			0.02			0.17
1st October (14)	13.3	1.12		13.5	1.13		16.7	1.22	
Winter losses k_4			0.19			0.19			0.21
1st March (19)	8.5	0.93		8.7	0.94		10.2	1.01	
Spring effects k_5 (migration & mortality)			0.17			0.26			0.08
1st July (23) ADULTS REPRODUCING (PR)	5.8	0.76		4.8	0.68		8.5	0.93	
	Kappa = 1.18			K = 1.40			K = 1.13		

‡ estimated value based on constant loss rate between age 0 and age 7 months

Table 5.7 <u>Porcellio scaber</u> life tables

Date and Age of Cohort (x) in months	1971 cohort			1972 cohort			1973 cohort			1974 cohort		
	Density 0.1m^{-2}	log Density	k value	Density 0.1m^{-2}	log Density	k value	Density 0.1m^{-2}	log Density	k value	Density 0.1m^{-2}	log Density	k value
1st August (0) NATALITY (PE)	15.9	1.20		35.0	1.54		14.0	1.15		33.7	1.53	
Juvenile mortality k_0			0.63			0.69			0.44			0.44
1st October (2)	3.7‡	0.57		7.0	0.85		5.1	0.71		12.3*	1.09	
Overwintering k_1 losses			1.57			0.39			0.51			0.47
1st March (7)	0.1	-1.00		2.9	0.46		1.6	0.20		4.2	0.62	
Spring effects k_2 (mortality & migration)			-1.74			-0.08			-0.34			0.62
1st June (10)	5.5	0.74		3.5	0.54		3.5	0.54		1.0	0.00	
Summer effects k_3 (mortality & migration)			0.14			0.28			-0.13			-0.28
1st Sept. (13) ADULTS REPRODUCING (PR)	4.0	0.60		1.8	0.26		4.7	0.67		1.9	0.28	
	Kappa = 0.60			K = 1.28			K = 0.48			K = 1.25		

‡ estimated value based on constant loss rate between age 0 and age 7 months

* anomolous trough in 1974 cohort juveniles in October 1974 sample by passed by connecting September and November sample means (see fig. 5.11). If this is not done estimate of density is 4.5 0.1 m^{-2}

Figure. 5.I4 Graphical investigation of the roles of natality (P_E) and mortality, both overall (K) and during specific time intervals (k's), in determining the size of the resulting breeding population (P_R) of Porcellio scaber.

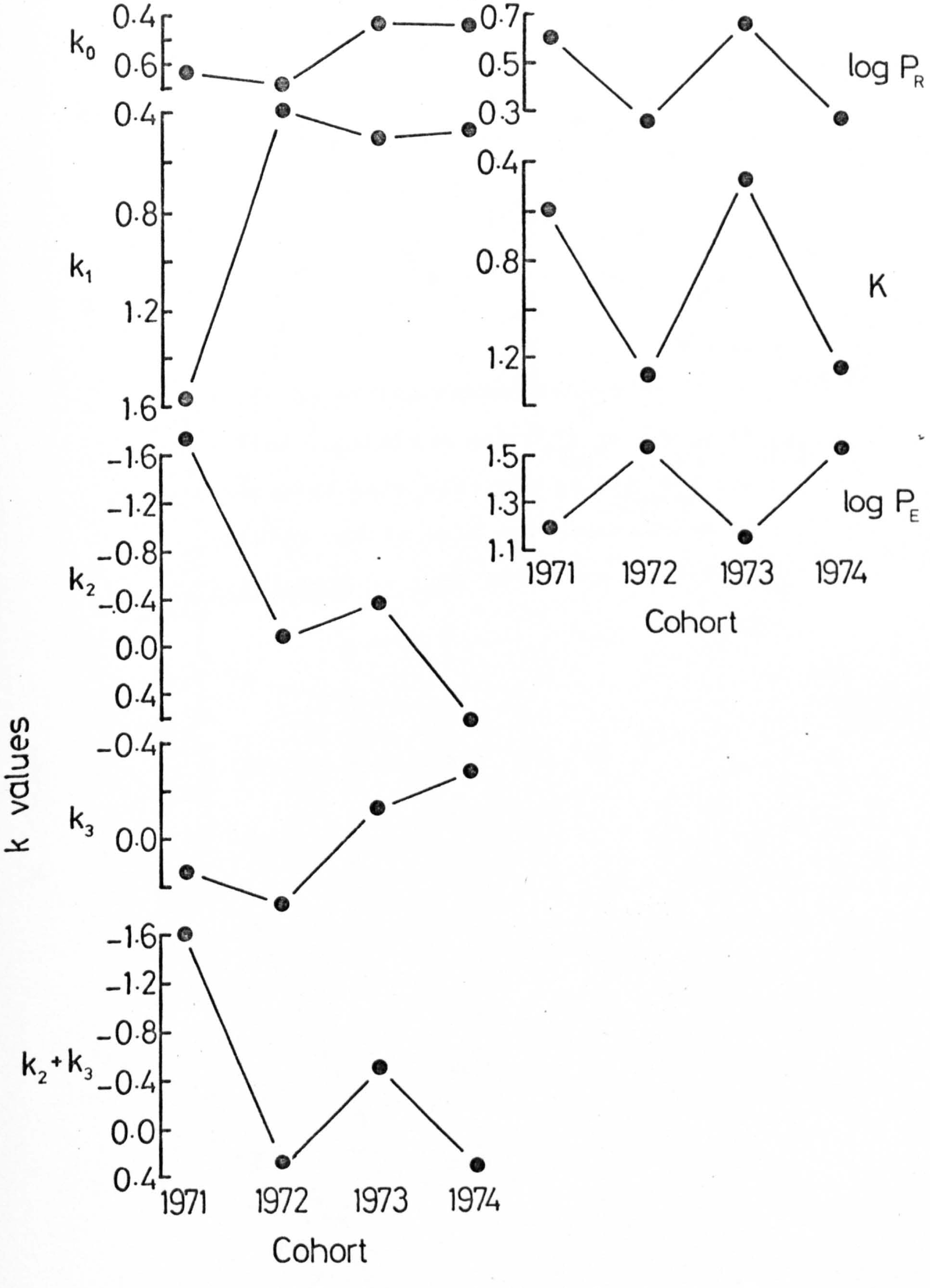
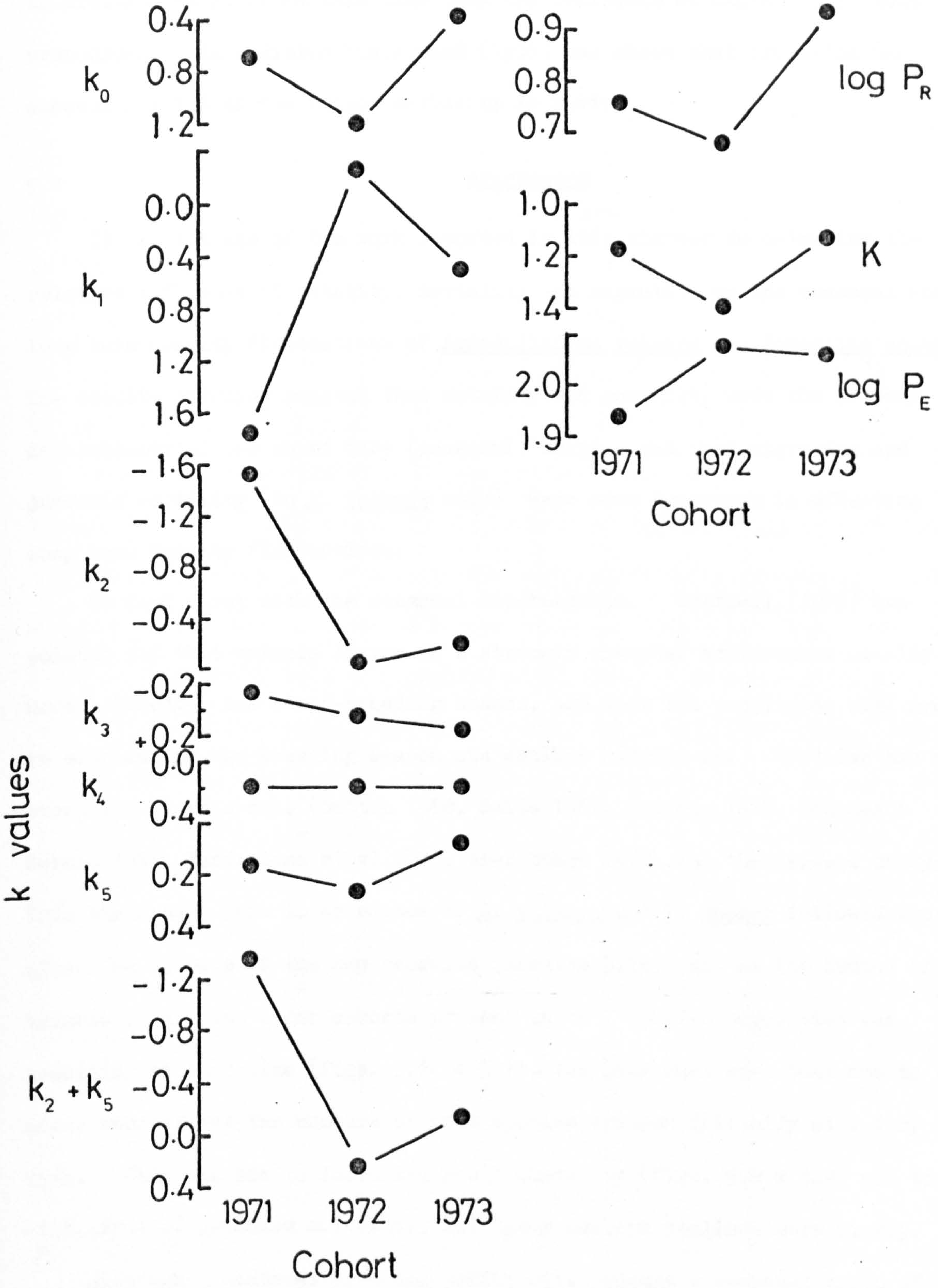

k values
k0
0.4
0.6
k1
0.4
0.8
1.2
1.6
k2
-1.6
-1.2
-0.8
-0.4
0.0
0.4
k3
-0.4
0.0
k2+k3
-1.6
-1.2
-0.8
-0.4
0.0
0.4
1971
1972
1973
1974
Cohort
log P_R
0.7
0.5
0.3
K
0.4
0.8
1.2
log P_E
1.5
1.3
1.1
1971
1972
1973
1974
Cohort

Figure. 5.I5 Graphical investigation of the roles of natality (P_E) and mortality, both overall (K) and during specific time intervals (k's), in determining the size of the resulting breeding population (P_R) of *Armadillidium vulgare*.


k values
k_0
0.4
0.8
1.2
k_1
0.0
0.4
0.8
1.2
1.6
k_2
-1.6
-1.2
-0.8
-0.4
k_3
-0.2
+0.2
k_4
0.0
0.4
k_5
0.2
0.4
$k_2 + k_5$
-1.2
-0.8
-0.4
0.0
0.4
1971
1972
1973
Cohort
log P_R
0.9
0.8
0.7
K
1.0
1.2
1.4
log P_E
2.0
1.9
1971
1972
1973
Cohort

density of breeding females.

The spring and/or summer effect in both species is particularly interesting as it is at this time that the influence of migration is most pronounced. In addition Sunderland (1977) has shown that predation can account for 15% of the isopod mortality in spring.

5.4 DISCUSSION

It was the aim of the work reported in this chapter to determine the relative influence of natality, mortality and migration on the seasonal and long term density fluctuations of Armadillidium vulgare and Porcellio scaber. The results obtained suggest that natality and mortality were the primary determinants of the short term (seasonal) changes and that migration and juvenile mortality (in A. vulgare only) were more important in affecting long term density fluctuations.

To deal first with the seasonal fluctuations. Fretwell (1972) has pointed out that animals living in a strongly seasonal environment usually have a breeding and a non-breeding season, and that the population will grow in size during the breeding season and decline outside it. Woodlice are no exception to this rule (Sutton 1968, Saito 1969, Standen 1973, McQueen & Carnio 1974, Sunderland et al 1976, Al-Dabbagh 1977, and the present study). Thus the annual peak in abundance of A. vulgare and P. scaber followed shortly after the release of the new recruits (section 5.3b), and as the number of animals in all the other cohorts present in each species population was declining at that time (figs. 5.10 & 5.11) the peak must have been due to births. After recruitment the numbers of both species dropped initially at a very high rate. This was due to increased adult mortality (figs. 5.8 & 5.9) and to a high level of juvenile mortality, but later numbers declined more slowly.

Although a seasonal breeding period will produce a seasonal cycle of abundance, a seasonal peak in abundance of animals at one site does not necessarily indicate natality. Migration could have the same effect. This point is spectacularly demonstrated by movements of large game in Tanzania where big herds move in to and out of certain areas as their annual migrations take them in search of food (in Emmel 1976). There is some evidence which suggests that this also occurs in isopods. Paris & Pitelka (1962) found the greatest density of A. vulgare in California in winter or spring despite the fact that most of the young were released in late spring or summer. The authors concluded that this was due to animals descending out of sampling depth in the dry summer months and moving up again with the winter rains. If, in this study, the seasonal density fluctuations were caused entirely by natality and mortality the last sample date before the young were released should have contained the least number of animals. This was the case with Cylindroiulus latestriatus (chapter four) but with P. scaber and A. vulgare the lowest densities were usually recorded in winter or early spring. Sunderland et al (1976) found the winter mean of Philoscia muscorum at Spurn to be the lowest also. Changes in the vertical distribution cannot account for this as the woodlice did not burrow below sampling depth, which was 10-12 cm (chapter three and Sunderland et al 1976). In section 5.3 and chapter two evidence was put forward strongly suggesting that lateral migration was responsible. However as the occurrence of this migration was more variable than recruitment in its timing, duration and intensity and as the magnitude of the increase in numbers was less (except in 1972 - tab. 4.1) its effect on the seasonal abundance was not as conspicuous as that of natality.

Turning now to the long term density changes migration would appear to have a more important role. Evidence for this was provided by the 'k' factor analysis and by examination of the cohort density curves (figs. 5.10 & 5.11). For example the most pronounced episode of immigration occurred in 1972. During that year the 1971 cohort of P. scaber increased from a density of 0.3 $0.1m^{-2}$ in January to 6.6 $0.1m^{-2}$ in June and the 1971 cohort of A. vulgare increased from 0.9 $0.1m^{-2}$ in January to 13.4 $0.1m^{-2}$ in September (tab. 5.5). In P. scaber this was followed by a large fall in density, possibly due to emigration, but in A. vulgare the population density continued to rise during the winter by immigration of animals belonging to the 1972 cohort. Consequently the density of *A. vulgare* on the study site had increased markedly by the end of 1973.

According to Sutton (1972) lateral migration is not a common feature of isopods, although vertical migration is (Paris 1963, Sutton 1968, Standon 1973 and Davis et al 1977). However lateral-migration over short distances has been noted by Stachurski (1968). Populations of *Ligidium hypnorum* (Cuvier) studied by Stachurski in a Polish swamp moved in and out of the wetter areas according to season. Furthermore Paris (1963) has shown that *A. vulgare* in California can cover a distance of 13 m in 12 hours during normal foraging for food and shelter sites and Brereton (1957) found that *P. scaber* climbed trees in Oxford during summer.

Migrations of *L. hypnorum* in Poland occurred in response to a seasonal availability of food in areas which were flooded in the winter (Stachurski 1968). However in this study the migrations provided a mechanism by which the woodlice populations were able to keep pace with changes in the location of suitably humid microsites (Southwood 1962). Thus animals would move from the dune crest to the lee side of the dune as the crest dried out in spring (chapter two).

In *A. vulgare* migration did not act alone in affecting the long term density fluctuations. The 'k' factor analysis suggested that juvenile mortality was also important. High juvenile mortality is a typical feature of isopod populations. Studies undertaken so far give values of 80% and 67-77% in two populations of *A. vulgare* (Al-Dabbagh 1976), 57-81% in *P. muscorum* (Sunderland et al 1976) and 80% in *Trichoniscus pusillus* (Sutton 1968). These are very similar to the figures of 57-94% in *A. vulgare* and 51-80% in *P. scaber* observed in this study. Brereton (in Al-Dabbagh 1976) suspected that juvenile mortality resulting from cannibalism by the adults was density dependent and regulated populations of *P. scaber* in the laboratory and perhaps also in the field. Juvenile mortality, from unknown causes, may play a similar role in *T. pusillus* in limestone grassland near Oxford as Sutton (1968) reports that it appeared to compensate for the disrupting effects of a drought. Changes in the juvenile mortality of P. muscorum also appeared to contribute to the numerical stability of a population near Oxford (Sutton 1968). In this study the number of young extracted from the KLG samples bore little relation to the estimated natality. Comparing the 1972 and 1973 recruits natality was 119.4 and 113.9 $0.1m^{-2}$ respectively (tab. 5.4), yet the density of young on 1 October following recruitment was 7.2 and 49.5 $0.1m^{-2}$ (fig. 5.10). Thus a reduction in natality turned to a large increase in abundance. This indicates that juvenile mortality was much lower in 1973 than in the previous year. The large contribution made by the 1973 recruits to the rising abundance of A. vulgare during that year (chapter four and fig. 5.10) was therefore due to a marked improvement in juvenile survival.

The high level of juvenile mortality found in woodlice may be augmented by cannibalism as was indicated by Brereton (see above) in P. scaber and by Paris (1963) in A. vulgare. Some reduction in cannibalism may be achieved if the males and females are segregated during brood release. This does occur in the common shrew, Sorex araneus L., where males, if they come in contact with the young, will attack and kill them (Crowcroft 1957). Although no results have been interpreted in this way with woodlice there is some evidence from changes in sex ratios that segregation of the sexes may occur during breeding. Much of the variation in sex ratio of isopods reported in the literature can be accounted for by difficulties in identifying small males and by a higher post reproductive mortality of females (Paris & Pitelka 1962). However not all of the variation can be explained in this way. Thus Paris & Pitelka (1962) found a very significant excess of A. vulgare females in soil samples taken in April 1959 which gradually turned to an excess of males in early September and then evened out at approximately 50 : 50. Hatchett (1947) observed similar variations in the sex ratio of Cylisticus convexus in Michigan. The sex ratio of Porcellio spinicornis collected from under boards in Canada clearly showed a bimodal fluctuation which coincided with two periods of brood production (McQueen 1976). The latter result closely resembles the variations in sex ratio found in P. scaber and A. vulgare under stones at Spurn.

McQueen gave no explanation for his observations, nor could Paris & Pitelka or Hatchett. However in the present study inversely related changes in the sex ratio of animals under stones occurred in the soil samples strongly suggesting that males and females were partly segregated, at that time. This may be related to breeding as in both P. spinocornis and P. scaber there were two waves of brood production and two periods during which the females predominated under stones or boards. In A. vulgare there was only one brood and females predominated under stones at that time. The additional variation in sex ratios therefore appears to stem from differences in the microdistribution of the two sexes.

The population consequences of sex segregation in isopods have not been fully assessed. It does however provide a warning to be heeded when attempting to determine the sex ratio of any woodlouse species from a single sample. Great care must be taken to obtain a representative number of replicates from all the sites that males and females may occupy.

CHAPTER SIX

THE BIOLOGY AND BIOMASS OF CYLINDROIULUS LATESTRIATUS (CURTIS)

6.1 INTRODUCTION

The methods used for studying Diplopoda and Isopoda are so different, due to their contrasting biologies, that it is convenient to separate the analysis of the population data for the two groups. In this chapter the size structure of the *Cylindroiulus latestriatus* population at Spurn is described and used to compute biomass estimates for the species.

Despite the fact that millipedes can attain their highest biomass in grassland (Macfadyen 1963b) most of the ecological work on them has been done on the more diverse woodland fauna. *C. latestriatus* is one of the few species which has been studied in both grassland (Cotton & Miller 1974 and Deshmukh 1974) and woodland sites (Blower & Gabbutt 1964).

The earliest detailed study of *C. latestriatus* was by Blower & Gabbutt (1964). From the data they obtained on this species, in a Devon oak wood, it was concluded that mature females (stadia VII to XIII) release eggs singly or in small groups at a rate of no more than three per month into the soil from March to July. From each egg hatches a pupoid still enclosed within a membrane. The blind and immobile first stadium which emerges from the pupoid develops at the next moult a single ocellus on each side of its head. This coincides with the onset of activity and feeding. They found that most animals reach either stadium IV or V by the first winter and, progress to stadium VII or VIII by the second winter. Oviposition occurs for the first time at the age of 24 months. The females continue to moult once a year (in autumn) and a few may reach stadium XIII which suggests a seven or eight year life span. On the other hand once the males reach maturity, which they may do at either stadium VII, VIII or IX, they stop moulting. The males are distinguishable at stadium V, but at least two more moults are required before full maturity is reached.

At Tentsmuir (Fife, Scotland) *C. latestriatus* takes 2.5 years to reach stadia VII and VIII (Deshmukh 1974); one year longer than in Devon. This difference probably results from a direct relationship between growth and temperature.

6.2 MATERIALS AND METHODS

(a) Determination of Density

The density of Cylindroiulus latestriatus at Spurn was determined along with the woodlice by taking 14 0.1 m^2 soil samples at approximately monthly intervals. The animals were driven from the soil samples using a modified KLG extractor (chapter two). The sampling and extraction procedure was designed specifically for woodlice and may not have been as efficient in determining millipede numbers. Even so it was thought best not to alter the methods lest it upset the extraction efficiency for the woodlice.

(b) Determination of stadia

The stadium of each millipede was determined using the ocular field method (Vachon in Blower 1970). This relies on the addition of a single row of ocelli to each of the two ocular fields at each moult. Stadium I has no ocelli. At the moult to stadium II one ocellus appears and at the next moult two more are added to form a second row. A row of ocelli is added at each subsequent moult each with one more ocellus than the previous row. The stadium number is determined by counting the number of ocelli rows and adding one.

Although Blower had difficulty in distinguishing the rows in C. latestriatus, and hence turned to an analysis of body length for characterisation of the stadia (Blower & Gabbutt 1964), this technique has been used by Cotton & Miller (1974) and Deshmukh (1974). Cotton & Miller (1974) in assessing the ocular field method concluded that a few of the larger individuals, e.g. stadia XI and upwards, may be misplaced but as animals of this size are very rare the errors involved would be small. In addition when Blower (1970) compared the two methods with data from Ophyiulus pilosus it was found that the method of plotting lengths on probability paper as used by Blower & Gabbutt (1964) was inadequate for certain stadia. In this study, because many of the longer millipedes were broken during sorting of the extracted material and others often died in an irregularly twisted fashion so that they could not be measured accurately the use of body length would have seriously reduced the amount of data for analysis. The ocular field method was chosen, as it would yield the maximum amount of information from the sample data.

The sexing of iulid millipedes is easy as the two pairs of legs on the seventh diplosegment of the males are reduced and modified to form gonopods. The development of gonopods in immature males of C. latestriatus always coincides with stadium V (Blower & Gabbutt 1964) thus in all stadia from V upwards all non-males must be females. Mature males possess in addition a pair of hook-like modified first pair of legs.

(c) Length, live weight and biomass determination

Specimens collected at Spurn in April 1976 were used to obtain information about the weight to size relationships. Following weighing the animals were killed using ether vapour so that they died relaxed and could be laid out flat on a piece of mm graph paper. The length was then measured from the most anterior part of the head (excluding the antennae) to the most posterior tip of the anal-valves. Finally the stadium number of each specimen was determined using the ocular field method.

The biomass standing crop (B) (mg live weight 0.1 m^{-2}) on each sample date was estimated as follows:

$$B = \left(\sum_{i=5}^{i=11} f_i . x_i + \sum_{j=2}^{j=9} f_j . x_j \right) /N$$

where i = female stadium number

j = juvenile or male stadium number

f_i = frequency of stadium i in the sample

x_i = mean live weight of stadium i

N = number of 0.1 m^2 replicates in the sample

The area beneath the curve obtained by plotting the changes in biomass with time was used as a direct estimate of the mean biomass ($\bar{B}$) as recommended by Petrusewicz & Macfadyen (1970).

6.3 RESULTS

(a) Stadial frequency distribution and phenology

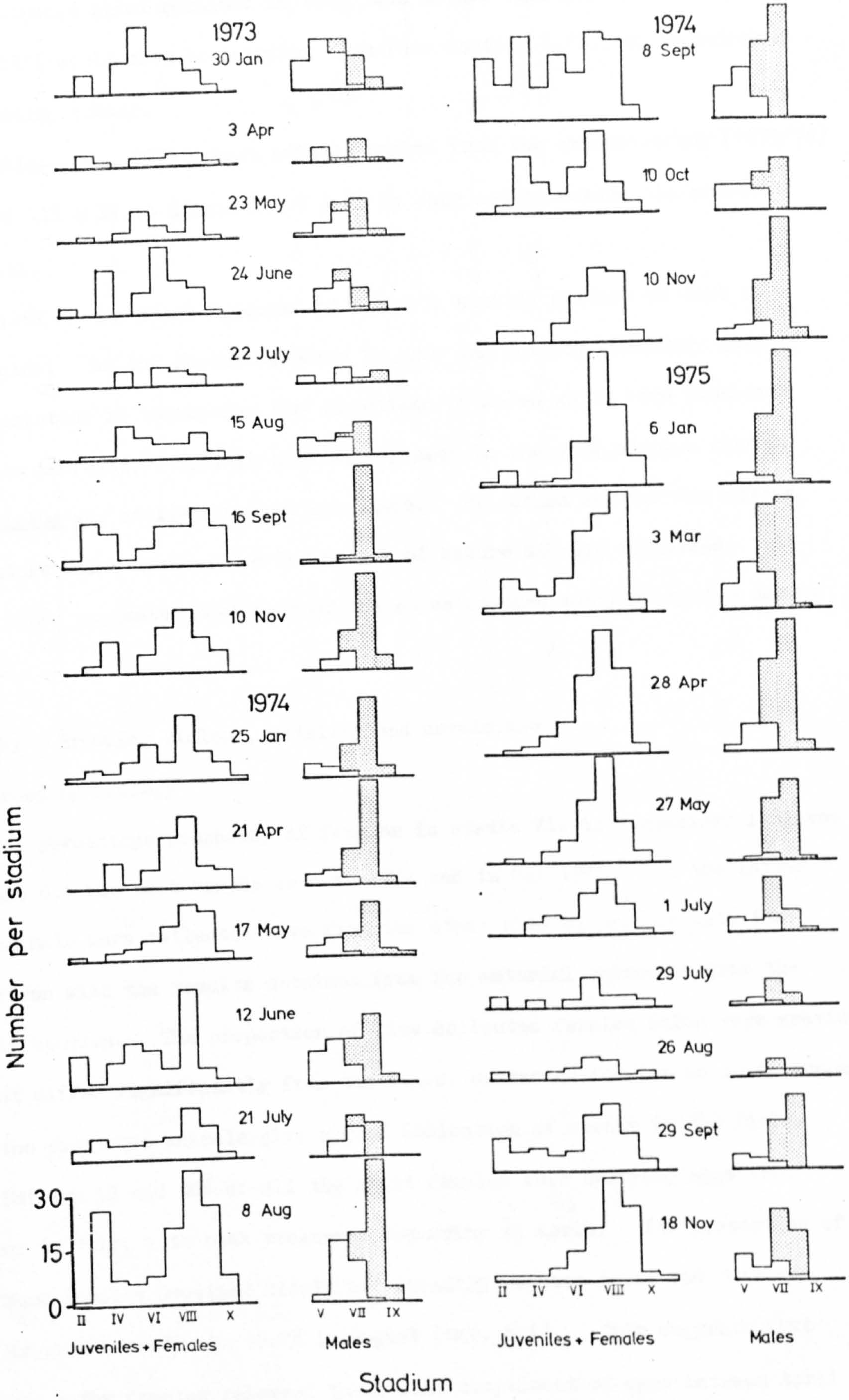
Changes in the number of juveniles (stadia II to IV), males and females in each stadium on successive sampling occasions are shown in figure 6.1.

Juveniles were very poorly represented in the samples and as a result it is not easy to determine from this information alone exactly when they were recruited to the population or to follow their development up through the stadia. The situation is made more difficult by the affects of sampling variance on the size structure and the small number of life history stages. Possible reasons for the lack of juveniles are discussed later (section 6.4). The following description of the phenology of <u>Cylindroiulus latestriatus</u> at Spurn must therefore be considered extremely tentative.

Although a few specimens of stadium II were present for most of the year they were more frequent between June and September and never occurred in April. Recruitment thus appears to occur in summer. In 1974 there were no animals in stadia II or III in April. The single specimen in stadium II in May would probably be the very earliest of recruits. By June of that year the number of animals in stadium II had increased. This was followed by a peak in stadium III in August and in IV in September and October. Growth appeared to stop at that time with the animals remaining in either stadium III, IV or V until the following March. The pattern of growth in the first six months of life was repeated each year. Thus in both 1972/73 and 1973/74 the first year animals overwintered as stadia III & IV.

In January and April 1973 the overwintering juveniles were mainly in stadium III. With the recommencement of growth in spring the number of animals in stadium III declined as the number in IV increased, reaching a peak in June. This was followed by an increase in stadium V in July and in stadia V & VI by August. The number of animals in stadium V subsequently fell away to zero by November. As the number of animals in stadium VII increased from August to September and the number in VIII then increased by November when growth would probably have stopped it is suggested that

Figure. 6.I Size frequency distribution of <u>Cylindroiulus latestriatus</u>. Stippled areas denote mature males.


1973
30 Jan
3 Apr
23 May
24 June
22 July
15 Aug
16 Sept
10 Nov
1974
25 Jan
21 Apr
17 May
12 June
21 July
8 Aug
1974
8 Sept
10 Oct
10 Nov
1975
6 Jan
3 Mar
28 Apr
27 May
1 July
29 July
26 Aug
29 Sept
18 Nov
Number per stadium
30
15
0
II
IV
VI
VIII
X
V
VII
IX
Juveniles + Females
Males
Stadium

the 1972 cohort females were mainly in stadia VII and VIII by their second winter although a few remained in VI. The mature individuals in stadia VII and VIII would then be carrying eggs (see section 6.3b), to be released the following summer.

Similarly the 1973 cohort animals passed from the overwintering (1973/74) stadia of III & IV to stadia IV, V & VI by June and by autumn had reached adult size.

Growth of the males appeared to follow a similar pattern to that of the females. As the juveniles began to grow and develop secondary sexual characteristics in the spring the proportion of males which were immature tended to increase. This is most easily seen in the 1974 samples when C. latestriatus was at its greatest abundance. By autumn however the number of immature males declined as the number of mature animals increased. It is therefore suggested that most of the males reached maturity by the second winter.

(b) Breeding biology, natality and development

Breeding biology

The percentage pregnancy of females in stadia VII to X combined is given in table 6.1 for each sample date in 1974 and in May 1975. On the latter date animals were collected live from the study site to provide data for comparison with the results obtained from the material extracted from the monthly samples. The proportion of live collected females which were gravid did not differ significantly from the K.L.G. extracted females so it is assumed that the extracted animals give a good indication of events in the field.

Between 62 and 96% of all the adult females were carrying eggs from October to July, with peak pregnancy occurring in April. The proportion of ovigerous females declined slowly but steadily between April and July and then dropped markedly to 10.7% in August (tab. 6.1). This suggests that although a few females released their full compliment of eggs between April and July the majority did not discharge the last eggs until late July or early

Table 6.1 Percentage pregnancy of all females, in stadia VII to X combined, in monthly samples.

Date	Percentage pregnancy	Number of animals examined
1974		
25 Jan.	66.7	12
29 Mar.	76.9	26
21 April	95.5	22
17 May	87.5	24
12 June	75.0	20
21 July	62.5	16
8 Aug.	10.7	28
8 Sept.	9.1	11
10 Oct.	66.7	9
10 Nov.	80.0	5
1975		
7 May	84.2	19
	Total	192

Table 6.2 Percentage pregnancy of animals in each stadium.

Stadium	Percentage pregnancy	Number of females examined
VII	68.0	25
VIII	88.1	67
IX	91.1	45
X	75.0	12

August. The initial decline was mainly due to females in stadium VII. Thus, in April, seven out of eight females examined were pregnant, in May only 2 out of 4 were pregnant and in June only 1 in 5 was found to be pregnant. As none of the 16 stadium VII females examined from July to October were found with eggs, it is suggested that they released their eggs in April, May and June, about 2 months before the females in stadia VIII, IX and X.

Table 6.2 gives the percentage pregnancy of females in each stadium. These estimates are based on the data from samples taken between September and June (i.e. excluding the July and August samples when the females were not carrying eggs) for stadia VIII, IX and X, and between September and April for stadium VII. The proportion of gravid females changes from 68.0% in stadium VII to 91.1% in stadium IX. Not all stadium VII females would be mature (Blower & Gabbutt 1964) and this might also apply to a few stadium VIII, but stadia IX and X were expected to show 100% pregnancy. The low percentage pregnancy in October suggests that the values in table 6.2 may underestimate the true figures, because a few animals do not produce their eggs until November or December.

The number of eggs produced by the females in each stadium is given in table 6.3 Egg production was very variable, ranging from 1 to 27, but much of the variation was accounted for by changes in the size of the females. Thus the mean value increased from 6.6 per female in stadium VII to 20.2 per stadium X female.

Table 6.3 Number of eggs per pregnant female

Stadium	Mean number of eggs (± 1 S E)	Number of pregnant females examined
VII	6.6 ± 0.9	16
VIII	10.2 ± 0.8	49
IX	13.9 ± 1.6	22
X	20.2 ± 2.0	6

Natality

The information obtained on numbers in each size class (fig. 6.1), percentage pregnancy (tab. 6.2) and fertility (tab. 6.3) is sufficient to make a reasonable estimate of natality (N) in the *C. latestriatus* population at Spurn. Natality (0.1 m^{-2}) was calculated as follows:

$$N = \sum_{i=7}^{i=10} \bar{N}_i \times p_i \times \bar{L}_i$$

where i = stadium number

$\bar{N}_i$ = mean density 0.1 m^{-2} of females in stadium i, in the May, June and July samples

p_i = the proportion of stadium i females which become pregnant.

$\bar{L}_i$ = the mean fertility of stadium i females

The natality estimates for 1973, 1974 and 1975 are given in table 6.4.

Table 6.4 Natality and juvenile mortality

Year	1973	1974	1975
Natality (numbers 0.1 m^{-2})	13.1	23.9	22.0
Juvenile Mortality (% Apparent mortality)	87.5	85.1	93.5

Development

Attempts to breed *C. latestriatus* in small containers both in the laboratory and in the field were generally unsuccessful. Copulation was frequently observed but only 1 female kept in the laboratory (at 20°C and 18 hours daylength) produced eggs. This specimen was collected from the study site in early May 1976. It was maintained in a small plastic pot (58 mm diameter and 65 mm deep) with plaster-of-paris in the base and with a mixture of monocot and dicot litter for a food supply.

Between collection and 25 May 1976 it laid at least 23 eggs. A few may have escaped detection as they were not enclosed in any nest but scattered in ones and twos among the litter. Unfortunately as the specimen was not initially under close observation (it was accidentally enclosed with

Philoscia muscorum during work on that species - Wilkins pers comm.) the duration of the egg and pupoid stages were not determined accurately. By 27 May 1976 all but three of the eggs had hatched and the juveniles had progressed as far as stadium I (11 of the 23) or stadium II (9). Only one of the remaining eggs hatched from which the pupoid stage was estimated to be less than seven days.

By 1 June all the animals were in stadium II, but four of them were in a pre-moult condition. These four plus two others reached stadium III by 8 June. Thus stadium II is also short-lived, lasting for about 10-14 days. A month later when the animals were next examined they were all in stadium III. Stadium III is therefore the first stage to remain in the population for any length of time. Six months after the eggs had been laid four animals were in stadium VI and one was in stadium V.

At this rate of development animals emerging from eggs laid in May would overwinter mainly in stadium VI. However oviposition by this female was considerably earlier than the average, possibly due to disturbance and laboratory conditions. With lower mean temperatures in the field it seems most unlikely that stadium VI would be reached by animals overwintering for the first time at Spurn.

(c) Juvenile mortality

The difference between the estimated natality (tab. 6.4) and the density of juveniles (stadia II, III, IV) in September (the time of peak abundance in each year - fig. 6.1) provides a rough estimate of the level of mortality in the first two months of life. Juvenile mortality expressed as a percentage of initial density (i.e. the natality estimates) in 1973, 1974 and 1975 is given in table 6.4. These estimates suggest a very high level of mortality ranging from 85.1 to 93.5%.

(d) Relationship between stadium number, length and live weight.

The mean live weight (mg) of each stadium and of each sex determined from the 47 animals is given in table 6.5.

Table 6.5 Mean live weight (mg) of different stadia.

* indicates values estimated from relationship between length and weight.

Stadium	Juveniles	Males	Females
I	0.32 n = 2	-	-
II	0.54 n = 2	-	-
III	0.79 n = 2	-	-
IV	1.40*	-	-
V	-	1.9*	1.9 n = 1
VI	-	4.14 n = 6	4.2 n = 1
VII	-	6.28 n = 7	7.04 n = 3
VIII	-	7.91 n = 3	10.75 n = 9
IX	-	9.9*	16.72 n = 9
X	-	11.8*	20.80 n = 2
XI	-	-	25.0*

Among those 47 there were no specimens of stadia IV or XI, and no males in stadia V, IX and X. The mean live weight of those stages was determined instead from the relationships between stadium number and length (fig. 6.2) and between length and live weight, (fig. 6.3).

There was no significant difference between the mean length of males and females in the same stadium so the data for the two sexes ~~was~~ were combined to produce figure 6.2. However the females were heavier than the males(tab. 6.5 and fig. 6.3) and the data for the two had to be kept separate when estimating the stadial weights. The mean length of each unrepresented stadium as determined from figure 6.2 was used to estimate the mean live weight of the stadium by interpolation from figure 6.3. The values obtained in this way are marked with an asterisk in table 6.5.

(e) Biomass

Biomass estimates for each sample date made from the combined information on the number of animals in each stadium (fig. 6.1) and the mean live weight of those stadia (tab. 6.5) are given in table 6.6. From those figures the mean biomass ($\bar{B}$) between 1 August 1973 and 1 August 1974 was estimated to be 58.6 mg live weight 0.1 m^{-2} and in the following year to be 89.1 mg 0.1 m^{-2}. The mean annual biomass was therefore 73.9 mg 0.1 m^{-2} or approximately 0.7 g m^{-2}.

6.4 DISCUSSION

If the difference in age at first reproduction observed in Cylindroiulus latestriatus in Devon and in Fife was due to the effects of temperature on growth rate, as suggested in the introduction, then it should be possible to speed up the development of millipedes by rearing them in warmer conditions. In fact the development in laboratory reared animals was about 1.5 to 2 times faster than in the field. Thus in six months the majority of the laboratory animals reached stadium VI whereas most of the field animals only reached stadium IV. As the laboratory cultures in the present study were kept at 20°C and the mean temperature in the litter layer at Spurn during the six months immediately after recruitment in 1974 was 13°C it seems likely that

Table 6.6 Biomass standing crop (B) mg live weight 0.1 m^{-2}

Date	B	Date	B	Date	B
1973		1974		1975	
30 Jan.	47.6	25 Jan.	59.2	6 Jan.	104.6
3 April	15.0	21 April	63.2	3 Mar.	116.1
23 May	43.3	17 May	52.0	28 April	112.0
24 June	39.8	12 June	60.9	27 May	72.5
22 July	14.5	21 July	41.6	1 July	42.5
15 Aug.	29.2	8 Aug.	127.8	29 July	19.4
16 Sept.	72.3	8 Sept.	99.6	26 Aug.	15.9
10 Nov.	67.6	10 Oct.	57.5	29 Sept.	59.6
		10 Nov	80.0	18 Nov.	77.9

Figure. 6.2 Mean length (mm) of animals belonging to each stadium (± 2 SE).

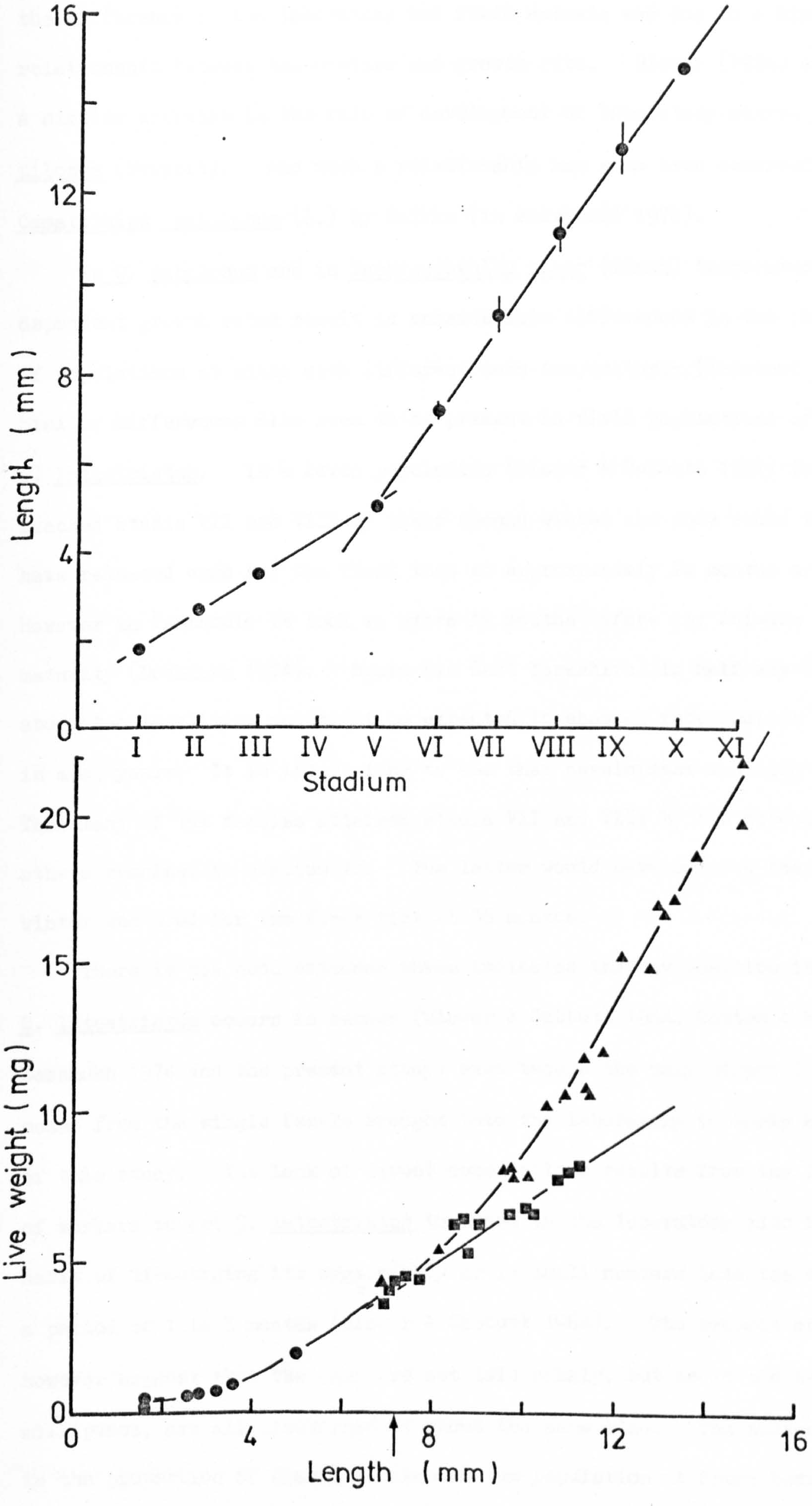
Figure. 6.3 Relationship between length (mm) and live weight (mg). Lines fitted by eye.

● Juveniles.

■ Males.

▲ Females.

← Indicates mean length of stadium VI.


16
12
8
4
0
Length (mm)
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
Stadium
20
15
10
5
0
Live weight (mg)
0
4
8
12
16
Length (mm)

the difference in the laboratory and field animals was due to a direct relationship between temperature and growth rate. Blower (1974) observed a similar increase in the rate of development of laboratory reared Ophyiulus pilosus (Newport). And such a relationship has also been observed in Ommatoiulus sabulosum (L.) by Halkka (in Fairhurst 1974).

In O. sabulosum and in Tachypodoiulus niger (Leach) temperature dependent growth rates result in considerable differences in the phenology of populations at sites with different mean temperatures (Fairhust 1974). Similar differences also seem to be present in field populations of C. latestriatus. In a Devon population (Blower & Gabbutt 1964) females reached stadia VII and VIII by their second winter and some would therefore have released eggs for the first time at approximately 24 months of age. However in Tentsmuir it took an extra 12 months before any animals attained maturity (Deshmukh 1974). Spurn (in East Yorkshire) is half way between the above two localities and might be expected to show an intermediate temperature in most years. It is interesting to see that development was also intermediate. Thus many of the females attained stadia VII and VIII by the second winter while others remained in stadium VI. The latter would have matured the following winter and bred for the first time at 36 months.

There is now good evidence which indicates that oviposition in C. latestriatus occurs in summer (Blower & Gabbutt 1964, Cotton & Miller 1974, Deshmukh 1974 and the present study) even though the only direct information comes from the single female brought into the laboratory in early May 1976 of this study. The lack of direct observations results from the inability of workers to get C. latestriatus to breed in the laboratory plus its suspected habit of discharging its eggs singly or in small numbers into the soil over a period of 1 to 5 months (Blower & Gabbutt 1964). The present observations however suggest that the eggs are not laid singly, but as in the nest building millipedes, are all discharged at about the same time. The sudden decline in the proportion of gravid females in the population at Spurn between July and August and the oviposition rate of the female which produced eggs in the laboratory, both support this suggestion. The latter female produced more than twice the number of eggs expected from the data obtained by Blower & Gabbutt (1964). It was however close to the average number of 20.2 eggs produced by stadium X females at Spurn (tab. 6.3).

From the information on the number of eggs produced by C. latestriatus at Spurn it was possible to estimate the annual recruitment to the population (tab. 6.4). The estimate of 23.9 0.1 m^{-2} for 1974 is similar to the value of 24.8 0.1m^{-2} given by Deshmukh (1974) for C. latestriatus in Tentsmuir, 1971. However the resulting peak density of juveniles appearing in the samples was very different at the two sites (3.6 compared to 14.0 respectively). This suggests that the apparent juvenile mortality at Spurn (90%) was approximately double that in Tentsmuir (44%).

The significance of this difference is difficult to determine as errors affecting the reliability of the mortality estimates are complex and not easy to quantify. Errors in estimating are (1) the female and juvenile densities arising from their aggregated dispersion pattern, (2) the true stadial frequency distribution of the population and (3) the fertility and percentage pregnancy of the females. These are likely to influence both estimates equally. However the different sampling and extraction techniques employed in these two studies may well be largely responsible for the differences observed due to different extraction efficiencies of the juveniles. Deshmukh (1974) sampled more deeply and extracted the millipedes by sieving. This contrasts with the dynamic method of extraction employed here, which may not be efficient in driving the juveniles out of the soil.

The estimates of juvenile mortality for C. latestriatus at Spurn seem very high for an animal which produces so few eggs. Ophyiulus pilosus which produces about 75 eggs per female (Blower & Miller 1974) and Iulus scandinavius which produces about 149 (Blower 1970) both have a lower juvenile mortality (53% and 83% respectively). The value of 44% for C. latestriatus derived from Deshmukhs' data is, therefore, probably a better estimate than the one derived from the Spurn data.

Fortunately the small size of stadia II, III & IV means that they make only a small contribution to the total biomass of the population. The estimated mean annual biomass of 73.9 mg 0.1 m^{-2} live weight is therefore considered to be short of the true biomass value by only a small amount.

CHAPTER SEVEN

BIOMASS, GROWTH RATES AND POPULATION PRODUCTION OF ARMADILLIDIUM VULGARE AND PORCELLIO SCABER

In temperate grasslands the decomposer trophic groups are usually far more important than the herbivores. This situation arises as most grasses are well protected from primary consumers and so produce large amounts of litter (Petrusewicz and MacFadyen 1970). The decomposers in grassland must therefore serve as the major suppliers of chemical energy for predators.

An initial guide to the relative importance of different species in the process of making the energy trapped in plant material available to predators can be obtained from a comparison of the biomass of each. However large interspecific variations in metabolism, growth and turnover rates may seriously affect the usefulness of biomass. This problem is overcome if population production is used (Odum 1959).

With this point in mind changes in the biomass, growth rates and productivity of Porcellio scaber, Armadillidium vulgare and Philoscia muscorum at Spurn from 1968 to 1975 are examined.

7.2 MATERIALS AND METHODS

Details of the methods of sampling extraction and measuring the macrodecomposer populations at Spurn Head in order to obtain their density and size structure have been given in earlier chapters. To make biomass and production estimates utilising that data it was necessary to relate the head width measurements to the live and dry weight of the animals.

Animals collected from around the study site in the summer of 1976 were used to obtain size/weight relationships for Porcellio scaber and Armadillidium vulgare. Each specimen was first weighed alive and the width of the head capsule was then measured. Finally they were dried for 24 hours under vacuum at 60°C and weighed again. To obtain developing embryos for live and dry weight determination females carrying broods were induced to abort by enclosing them in an atmosphere of carbon dioxide. Young animals were weighed shortly after release from the brood pouch of females kept in the laboratory. The relationship between head width and live weight of Philoscia muscorum, the weight of embryos and newly released young are given in Hassall (1976).

Biomass standing crop of the three species of isopod on each sample date was estimated from the density and size structure data as follows. First, the mean live weight of animals in each size class was derived from the size/weight relationship. The products of the mean live weight and the number of animals for each size class were then summed to give the total weight of animals in the sample. This divided by the number of replicates gave the biomass in mg live weight per 0.1 m^2. The presence of breeding females in summer made the calculation of biomass standing crop at that time a little more complicated. All the females were treated as if they were non-pregnant and included in the analysis described above. The weight of the embryos was estimated separately as the product of the embryo number standing crop (determined in chapter five for estimating natality) and the mean live weight of the embryos. This figure was then added to the biomass of the adults. Mean annual biomass ($\bar{B}$) was estimated from the area under the graph produced by plotting the changes in biomass standing crop with time as recommended by Petrusewicz and MacFadyen (1970).

Growth was studied by following changes in the mean dry weight of the juveniles, males and females of each species with age. This was possible as separate generations were easily distinguishable in the samples on the basis of size (see chapter five). The total weight of males in a given cohort in a sample was estimated as for total biomass by summing the products of dry weight and numbers for each head width category. The mean dry weight was then obtained by dividing the total weight by the number of males in that cohort. The same procedure was followed in calculating the mean dry weight of the juveniles and females.

Population production due to growth (Pg) was estimated using the graphical method developed by Allen (in Petrusewicz & Macfadyen 1970) as it is easy to apply and permits one to partition the production into specific time intervals (Petrusewicz and Macfadyen 1970). This method was used by Hassall (1976) for P. muscorum at Spurn and by Al-Dabbagh (1976) for two populations of A. vulgare on heathland in East Anglia. Consecutive estimates of the density and mean size of the animals in a cohort are plotted and connected to yield a size/density curve. The area beneath the curve is a direct estimate of the production due to growth by that cohort.

Al-Dabbagh (1976) when calculating the production of A. vulgare combined the juveniles, males and females thus producing a single size/density curve for each cohort, but Hassall (1976) constructed separate curves for each group (i.e. juveniles, males & females). He further divided the females into slow and fast growing individuals as these had different mortality rates (Sunderland, Hassall & Sutton 1976). In the present study where the males and females had been adequately sorted (all samples from 1972 to 1975) separate curves were produced. This was considered the most accurate method as differences in the size/weight relationship of males and females and in their mean size at any given age combined with seasonal variations in the sex ratio of the population (chapter five) caused distortion of the curve when they were assessed together. However inadequate separation of the sexes of A. vulgare in the pre-1972 samples meant that size/density curves for the cohort subgroups combined had to be used for analysis of that data.

Production due to reproduction (Pr) was calculated separately from that of growth as follows:

$$Pr = Vr . Wr$$

where, Vr = the number of young born into the population, and Wr = their mean dry weight at birth (Petrusewicz & Macfadyen 1970).

7.3 RESULTS

(a) Relationships between head width, live weight and dry weight

The live and dry weights of 86 immatures, males and non-pregnant females of Armadillidium vulgare and of 64 Porcellio scaber, ranging in head width from 8-58 mm and 9-41 mu. respectively, increased directly with increasing head width. The nature of the relationships between head width and live and dry weights was curvilinear in both species. By taking the cube root of the weights straight line relationships were obtained (fig. 7.1) to which simple linear regression analysis could be applied.

Figure. 7.I Relationship between head width (m.u.) and cube root of dry weight (mg).

a. *Armadillidium vulgare*.

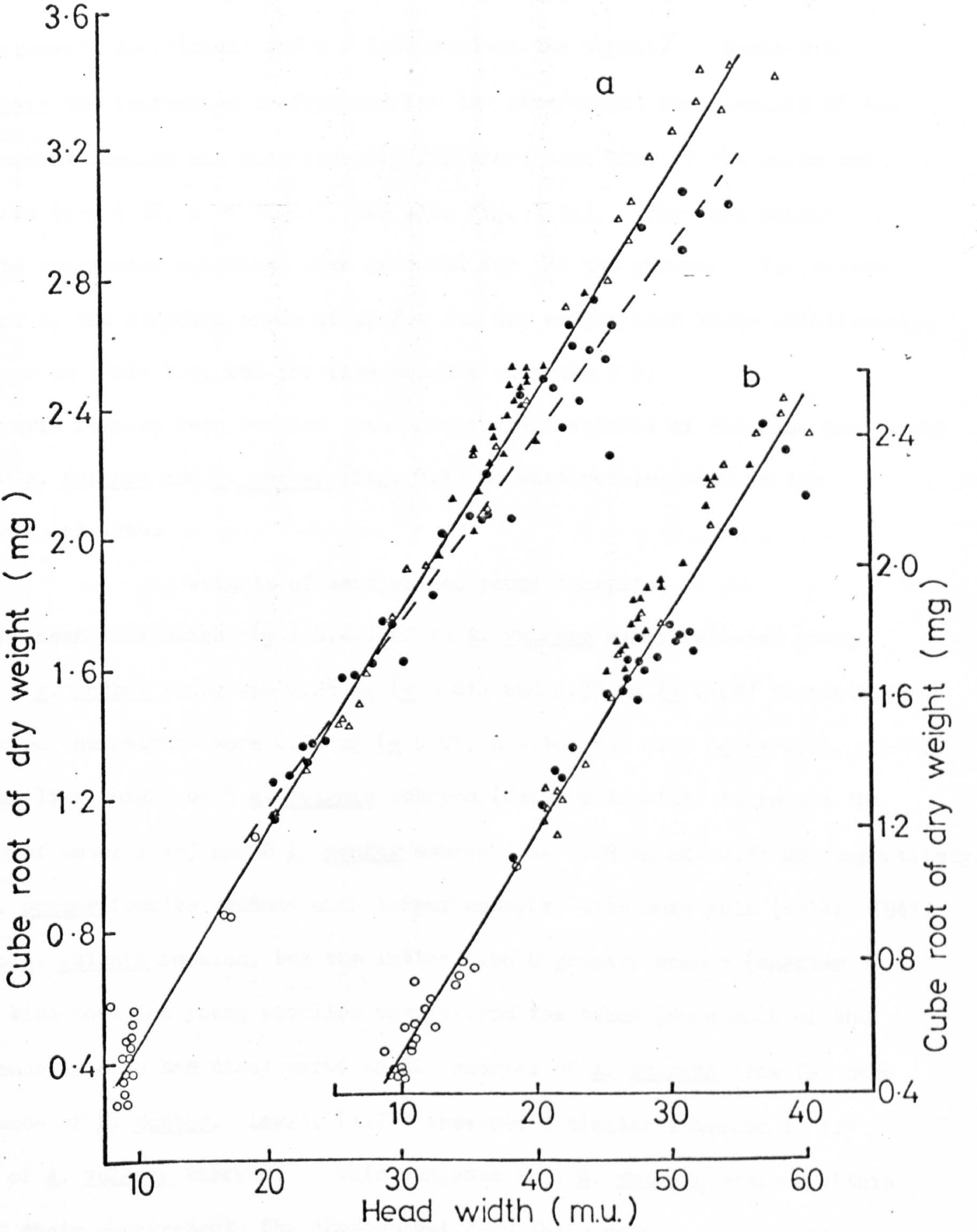
b. *Porcellio scaber*.

● Non-pregnant females.

▲ Pregnant females.

○ Juveniles.

△ Males.


a
b
Cube root of dry weight (mg)
3·6
3·2
2·8
2·4
2·0
1·6
1·2
0·8
0·4
10
20
30
40
50
60
Head width (m.u.)
2·4
2·0
1·6
1·2
0·8
0·4
10
20
30
40
Cube root of dry weight (mg)

In P. scaber there was no significant difference between the size/weight relationships of non-pregnant females and of males and immatures. All the data were therefore combined and one regression equation, of the form $y = mx + c$, was derived for the live weight/headwidth relationship and one for the dry weight relationship. (y = cube root of weight (mg), x = head width (m.u.), m = regression coefficient and c = intercept on the y axis). However in A. vulgare the regression coefficient for the size/weight relationship of the non-pregnant females was significantly different from that of the males and immatures ($d = 4.72$, $p < 0.001$) (see also fig. 7.1a). For that reason separate regression equations were produced for the two groups. The values of m and c, the standard error of m, for the dry weight/head width relationships are given in table 7.1, and for live weights in table 7.2.

Gravid females were heavier than non-pregnant animals of the same head width in both A. vulgare and P. scaber (fig. 7.1) so were not included in the regression analyses.

Weights of embryos and young recruits

The mean live weight (± 1 S.E.) of 19 A. vulgare newly released young and of 9 P. scaber young was 0.25 mg (± 0.01) and 0.33 mg (± 0.02) respectively. When dried the weights were 0.08 mg (± 0.01, n = 18) and 0.12 mg (± 0.01, n = 12). The mean live weight of 5 A. vulgare embryos (weighed together to reduce the effects of water loss) and 8 P. scaber embryos was 0.09 mg and 0.31 mg respectively.

P. scaber females produce much larger embryos, with more yolk (Heeley 1941) than do A. vulgare females, but the latter have a greater number (chapter 4). By the time that the young woodlice emerge from the brood pouch much of the difference in size has disappeared as the embryos of A. vulgare grow far more than those of P. scaber. Lawlor (1977) observed a similar increase in dry weight of A. vulgare embryos. This suggests that A. vulgare embryos obtain more of their requirements for development from their mother. That the cotyledons in A. vulgare are greatly enlarged would support this idea. They form pockets within the brood pouch in which the embryos sit thus reducing diffusional distances to a minimum. In P. scaber these structures are only

Table 7.1 Relationship between head width and dry weight. All regression equations take the form y = mx + c where y = cube root of dry weight. x = head width, m = regression coefficient and c = intercept on y axis.

	c	m	Standard error of m	sample size
P. scaber				
males, females & juveniles	-0.1463	0.0666	0.0012	63
A. vulgare				
males, & juveniles	-0.2108	0.0664	0.0008	47
females	0.0553	0.0563	0.0018	38

Table 7.2 Relationship between head width and live weight. All regression equations take the form y = mx + c where y = cube root of live weight, x = the head width, m = regression coefficient and c = intercept on y axis.

	c	m	Standard error of m	Sample size
P. scaber				
males, females & juveniles	-0.2890	0.1023	0.0009	64
A. vulgare				
males & juveniles	-0.2526	0.0942	0.0006	48
females	-0.3142	0.0958	0.0012	38

simple finger-like processes which hang in the marsupium.

(b) Biomass

The biomass standing crop (mg live weight 0.1 m^{-2}) of P. muscorum, P. scaber and A. vulgare in each sample date from 17 September 1968 to 18 November 1975 is given in table 7.3. These figures were used to estimate the mean annual biomass from 1st August of 1 year to 1st August of the next for each species in each of the seven years of study. The results are given in table 7.4 along with the mean annual density and mean live weight of the animals in the same time intervals.

There were large fluctuations in the mean annual density of P. muscorum and A. vulgare which were not fully mirrored by changes in the mean annual biomass as the latter was also influenced by variations in the mean live weight of each species (table 7.4). Thus in A. vulgare the variation in biomass was only half of that in numbers as at minimum density the mean live weight of the animals was approximately double the figure at maximum density.

In contrast comparative stability in total biomass (table 7.4) resulted from counter changes in A. vulgare and P. muscorum. This is clearly seen in figure 7.2 in which the raw biomass data (table 7.3) is averaged over three-monthly periods. Although so much less variable the total biomass did increase between September 1968 and late 1970 as P. muscorum increased and fell in 1974 and 1975 closely following the decline of A. vulgare.

The mean annual biomass of P. scaber was remarkably steady (table 7.1) but seasonal variations were evident (figure 7.2 and table 7.3). Biomass increased in the spring, peaked in late summer and declined over winter. Seasonal trends were also present in the biomass figures for A. vulgare and P. muscorum but were partially obscured by pronounced annual variations. They can be seen by taking monthly averages from the years with most complete data i.e. 1970-1975 (figure 7.3). All three species attain a peak biomass in the warmer months of the year, but the individual patterns of change are very different.

Table 7.3

Biomass Standing Crop

mg live weight 0.1 m^{-2}

Date	*A. vulgare*	*P. scaber*	*P. muscorum*	TOTAL
1968				
17 Sept.	74.69	28.75	159.11	263.55
1969				
8 Jan.	53.67	42.68	264.59	360.94
16 June	49.91	50.73	158.58	259.22
7 Aug.	77.45	64.79	277.18	419.42
8 Sept.	137.20	21.81	332.01	491.02
1970				
14 Jan.	65.91	8.36	256.54	330.81
27 May	130.24	57.26	374.41	561.91
15 July	113.06	69.07	426.00	608.13
19 Aug.	94.04	111.21	430.48	635.73
22 Oct.	136.93	101.61	486.37	724.91
11 Nov.	116.47	66.69	502.32	685.48
1971				
28 Jan.			220.79	
6 Apr.			272.18	
27 May	174.66	43.87	307.39	525.92
25 June	279.03	140.28	351.77	771.08
14 July			510.10	
28 July	346.02	13.83	366.95	726.80
19 Aug.			185.69	
15 Sept.	216.88	28.35	376.68	621.91
1 Nov.			305.15	
9 Dec.	234.68	26.29	283.20	544.17
1972				
26 Jan.	158.94	16.89	240.62	416.45
28 Mar.	182.35	25.57	320.71	528.63
1 May	322.06	22.39	428.11	772.56
26 May	418.17	72.98	769.74	1260.89
30 June	531.00	111.55	449.84	1092.39
26 Aug.	466.88	69.16	169.35	705.39
28 Sept.	452.87	46.33	190.93	690.13
28 Nov.	441.61	24.57	120.02	586.20
1973				
30 Jan.	440.61	34.32	169.77	644.70
3 Apr.	294.35	16.58	242.42	553.35
23 May	239.51	18.91	125.07	383.49
24 June	358.46	46.49	170.51	575.46
22 July	326.86	32.10	88.31	447.27
15 Aug.	809.46	56.59	100.31	966.36
16 Sept.	896.78	63.79	138.66	1099.23
10 Nov.	694.52	50.96	78.96	824.44

Table 7.3 (continued)

	A. vulgare	P. scaber	P. muscorum	TOTAL
1974				
25 Jan.	557.70	26.77	58.92	643.39
21 Apr.	702.04	20.15	65.45	787.64
17 May	570.44	88.12	41.31	699.87
12 June	308.10	15.68	14.42	338.20
21 July	612.49	155.38	1.14	769.01
8 Aug.	440.57	202.51	4.87	647.95
8 Sept.	559.65	99.81	2.47	661.93
10 Oct.	370.59	17.66	0.00	388.25
10 Nov.	415.24	51.47	7.18	473.89
1975				
6 Jan.	573.93	70.23	4.40	648.56
3 Mar.	326.24	52.90	3.14	382.28
28 Apr.	389.63	27.23	4.61	421.47
27 May	257.43	10.72	0. 00	268.15
1 July	282.68	23.12	0.00	305.80
29 July	309.06	37.08	1.47	347.61
26 Aug.	333.60	75.34	2.66	411.60
29 Sept.	268.83	41.15	4.62	314.60
18 Nov.	239.58	69.84	12.30	321.72

Table 7.4 Mean density, biomass and size

Year	*P. scaber*	*P. muscorum*	*A. vulgare*	Total
1 Aug-1 Aug.				
		density (numbers 0.1 m^{-2})		
1968/9	4.93	42.10	1.81	49.84
1969/70	5.09	52.73	3.75	61.57
1970/71	4.77	48.81	5.80	59.38
1971/72	3.38	48.28	9.74	51.66
1972/73	5.53	32.31	21.39	59.13
1973/74	5.33	12.35	41.10	58.78
1974/75	8.73	0.66	30.57	39.96
Magnitude of change	x2.6	x79.9	x22.7	x1.5
		biomass (mg live weight 0.1 m^{-2})		
1968/69	39.50	194.60	60.47	294.57
1969/70	32.52	297.57	101.86	431.95
1970/71	72.49	348.41	158.54	579.44
1971/72	35.64	336.06	268.19	639.89
1972/73	31.37	162.27	377.45	571.09
1973/74	50.60	63.36	630.11	744.07
1974/75	56.80	3.65	391.72	452.17
Magnitude of change	x2.3	x81.5	x10.4	x 2.5
		Mean Live weight (mg)		
1968/69	8.01	4.52	33.41	
1969/70	6.39	5.64	27.16	
1970/71	15.20	7.14	27.33	
1971/72	10.54	6.96	27.53	
1972/73	5.67	5.04	17.65	
1973/74	9.49	5.13	15.33	
1974/75	6.51	5.53	12.81	

Figure. 7.2 Summary of isopod biomass data averaged on a three monthly basis.

(●——●) Total.

(○——○) Philoscia muscorum.

(□——□) Armadillidium vulgare.

(△——△) Porcellio scaber.

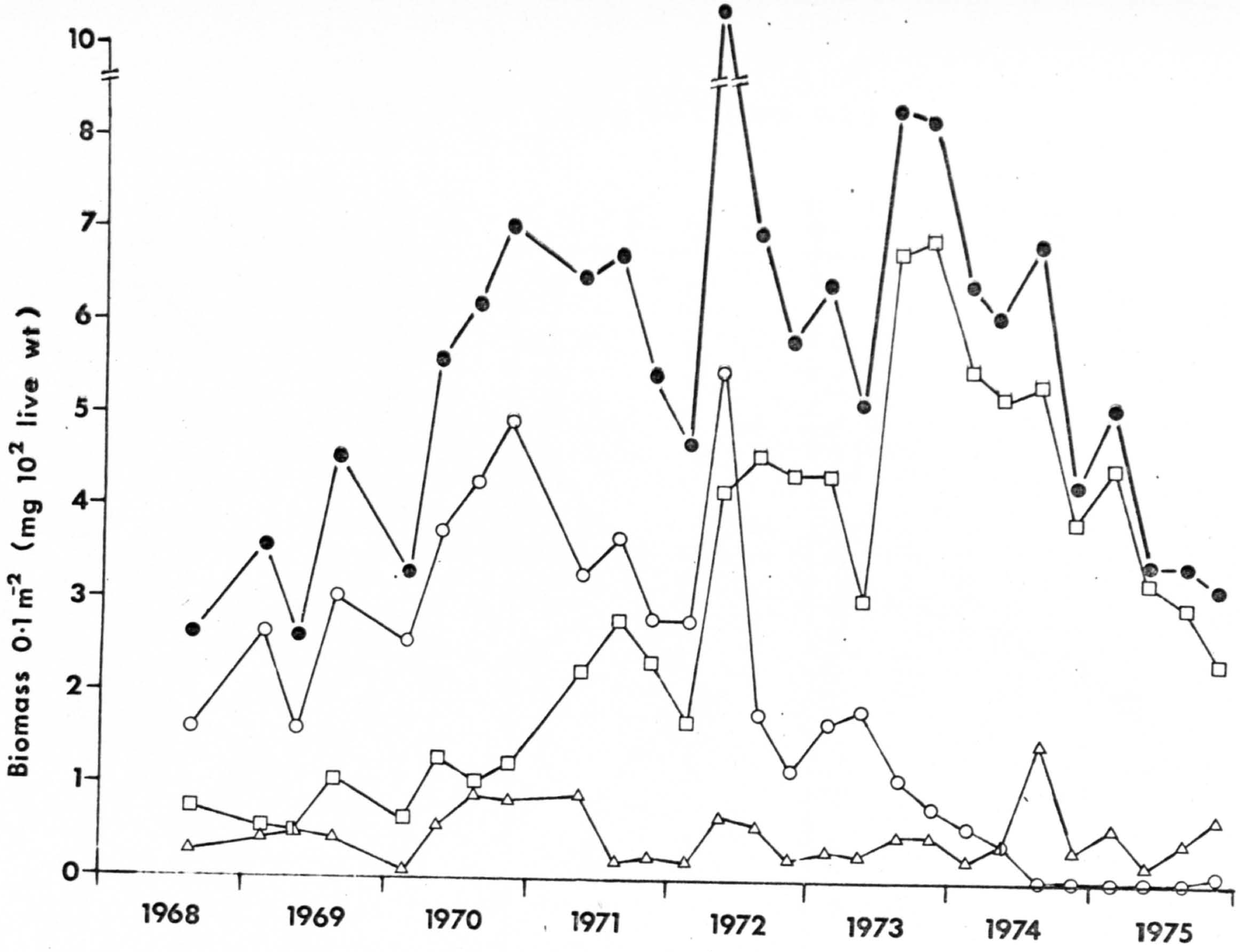
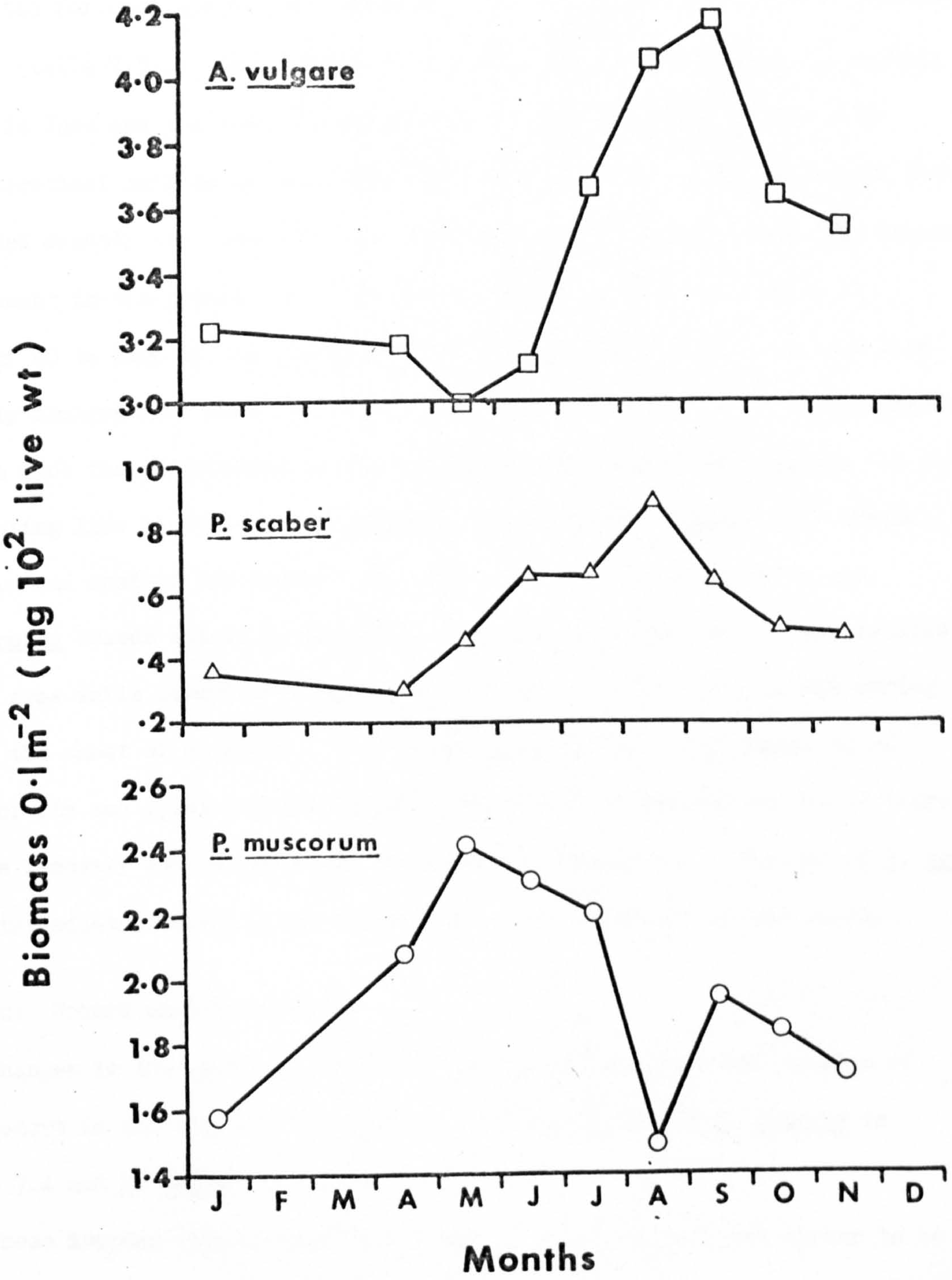

Biomass 0·1 m^{-2} (mg 10^2 live wt)
0
1
2
3
4
5
6
7
8
10
1968
1969
1970
1971
1972
1973
1974
1975

Figure. 7.3 Seasonal variations in biomass.


A. vulgare
P. scaber
P. muscorum
Biomass 0·1m^{-2} (mg 10^2 live wt)
4·2
4·0
3·8
3·6
3·4
3·2
3·0
1·0
·8
·6
·4
·2
2·6
2·4
2·2
2·0
1·8
1·6
1·4
J F M A M J J A S O N D
Months

Increase in biomass occurs when the gains due to growth of body tissues or of embryos exceeds the losses due to mortality (assuming no net migration) and it is of interest to discover which of these two processes has the major effect. The live weight of embryos on each sample date in 1973 has been calculated for each species and expressed as a percentage of the total biomass of each (table 7.5). The highest percentage observed was 8.35% in P. scaber on the 24 June and the theoretical maximum is less than 10% for all three. The theoretical maximum is the value that would be obtained if the sample date coincided exactly with the date on which the maximum number of breeding females was present in the population. As the increases in biomass were in the order of 40 to 200% of the pre-summer estimates, growth of body tissues (and possibly immigration) must have made the largest contribution to that increase.

In fact the differences in the seasonal variations of biomass are due to contrasting life histories. A. vulgare reaches maturity only at 22 months at Spurn and most of the biomass increase is due to growth of juveniles. P. muscorum breeds mainly in the first year (at 10 months) and as the females do not grow while carrying young growth exceeds mortality only in the spring before the onset of breeding. On release of the young heavy mortality of new recruits and spent females causes a rapid fall in biomass but later there is some recovery due to growth of the surviving juveniles. Females of P. scaber are intermediate, breeding equally in both their first and second years.

(c) Cohort growth patterns

Changes in the mean dry weight of the juveniles, males and females of each cohort in the samples from 1972 to 1975 are shown for A. vulgare in figure 7.4 and P. scaber in figure 7.5.

These isopods grew continually throughout life and did not appear to be restricted by any upper size limit. However growth varied with season being greater in summer than winter.

Although the absolute increment in size did not diminish with age the growth rate per mg of body tissue did. This can be seen if the summer

Table 7.5

Embryo biomass standing crop (mg live weight $0.1m^{-2}$) and % of total biomass accounted for by embryos in 1973.

	P. muscorum		*P. scaber*		*A. vulgare*	
Date 1973	Embryo biomass	% total biomass	Embryo biomass	% total biomass	Embryo biomass	% total biomass
23 May	0.40	0.32	0.50	2.64	0.46	0.19
24 June	6.00	3.52	3.88	8.35	7.02	1.96
22 July	5.20	5.89	1.42	4.42	9.99	3.06
15 August	1.40	1.40	2.29	4.05	3.00	0.37
16 September	0.40	0.29	1.92	3.01	0.03	0.00
Estimated max. biomass at peak of breeding		9%		9%		3%

Figure. 7.4 *Armadillidium vulgare* growth curves expressed as the increase in mean dry weight (± 2 SE) with time. Each cohort is labelled by its year of origin.

a. Females (non-pregnant females only).

b. Males.

c. Juveniles, ie unsexed animals with a head width of less than 20 m.u.

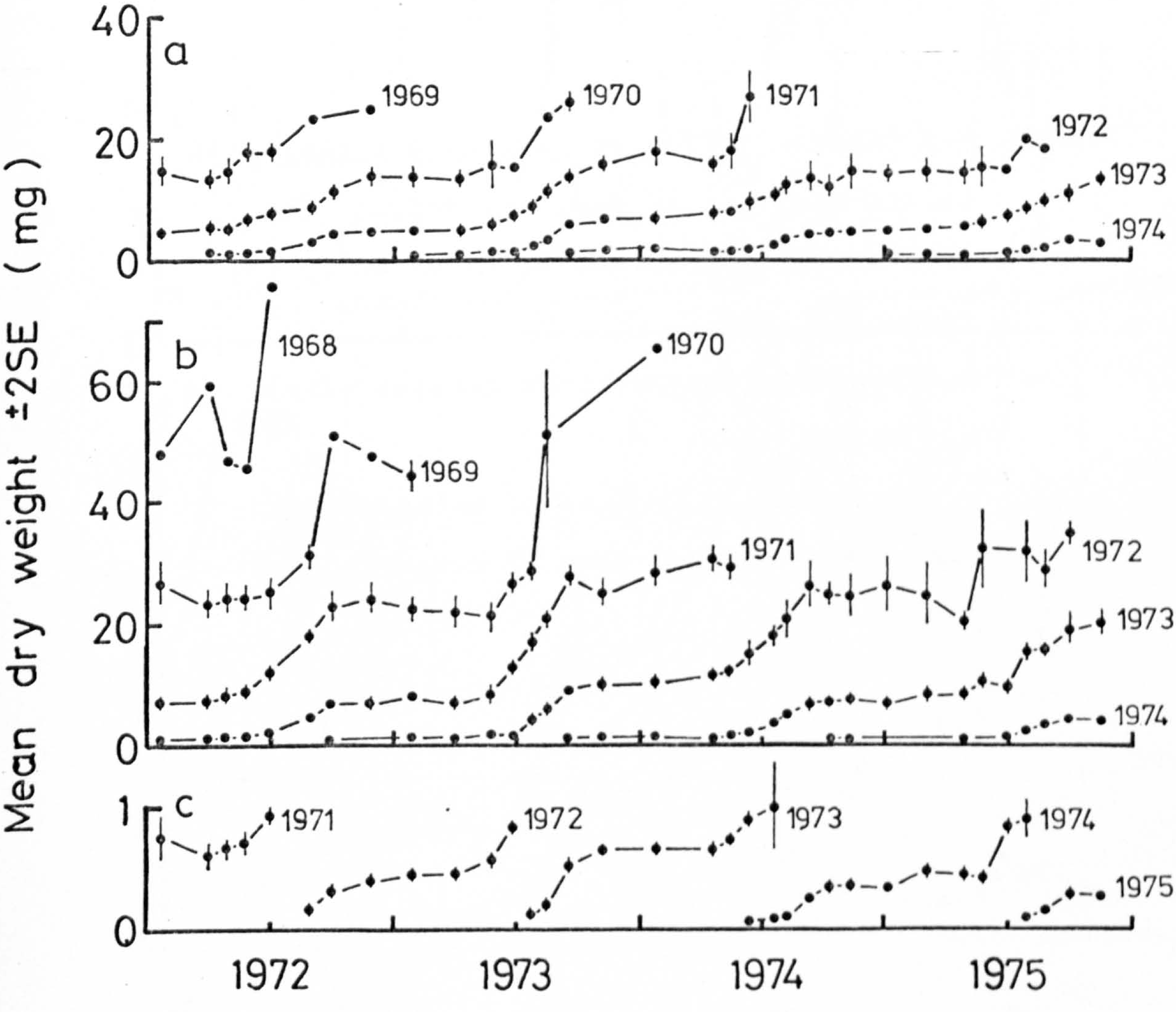
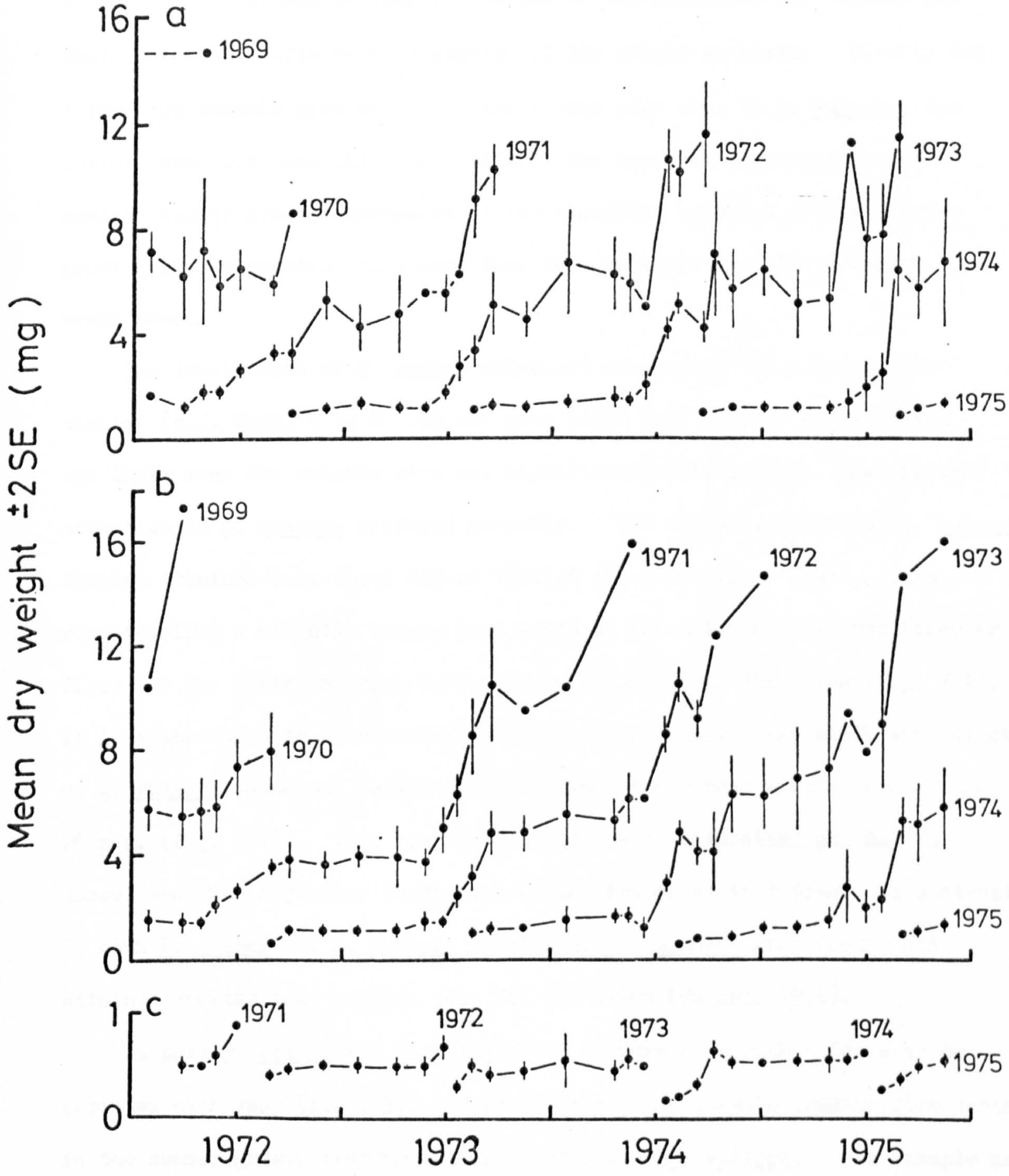

Mean dry weight ±2SE (mg)
40
20
0
a
1969
1970
1971
1972
1973
1974
60
40
20
0
b
1968
1969
1970
1971
1972
1973
1974
1
0
c
1971
1972
1973
1974
1975
1972
1973
1974
1975

Figure. 7.5 Growth curves of <u>Porcellio</u> <u>scaber</u> expressed as the increase in mean dry weight (± 2 SE) with time. Each cohort is labelled by its year of origin.

a. Females (non-pregnant females only).

b. Males.

c. Juveniles, ie unsexed animals with a head width of less than I7 m.u.


a
b
c
Mean dry weight ±2SE (mg)
16
12
8
4
0
1969
1970
1971
1972
1973
1974
1975
1
0
1972
1973
1974
1975

growth increments of the males and females in each cohort present during each summer are compared (table 7.6). The summer growth increment was defined as the increase in mean dry weight between April 1st and November 1st as a percentage of the size on April 1st of that year. For the juveniles it was the difference in mean dry weight of the overwintering animals and their weight at birth as a percentage of the weight at birth. Clearly the 1 year old animals grew more than the 2 year olds and, in A. vulgare, the latter grew more than the 3 year olds. The apparent contradiction of smaller summer growth increments of the immatures resulted from a shorter growing season starting only once they were released from the females' brood pouch.

The growth rate of P. scaber males and females of the same age was similar (c.f. figs. 7.5a & 7.5b and also table 7.6) so that at any given age their mean dry weights were not significantly different. However the situation in A. vulgare differed markedly. The dry body weight of A. vulgare females attained only about 60% of that of the males (fig. 7.4). This resulted from a slightly larger head width of the males at all ages (chapter five) and the different size to weight relationship of the sexes (fig. 7.1). It is interesting to note that the relationship between head width and weight of A. vulgare males and females diverged when their head widths were at about 26 m.u. (fig. 7.1). This roughly coincides with maturation and may be associated with a greater energy demand on females at that time. In contrast to both P. scaber and A. vulgare females of P. muscorum grew faster and attained greater body weights than did the males (Hassall 1976).

In both P. scaber and A. vulgare the pattern of growth appears to be repeated each year (figs. 7.4 & 7.5) but table 7.6 reveals considerable variation in the summer growth increments, particularly in A. vulgare. For example in 1973 growth in all groups of A. vulgare averaged almost double that in 1975. That this difference is statistically significant can be seen by comparing the overwintering mean dry weights of animals of the same age following those years (fig. 7.4). It might be expected from the apparent influence of

Table 7.6

Summer growth increments of cohort subgroups, rainfall (mm) and mean integrated temperature from April to September in each year from 1972-1975.

A. vulgare

Year	Immatures	Males			Females			Rainfall	Temperature
		1 year	2 year	3 year	1 year	2 year	3 year		
1972	180	680	333	212	385	255	187	199	14.7
1973	260	1000	364	261	700	314	191	347	15.3
1974	140	700	223	-	278	175	-	237	18.0
1975	120	420	244	128	300	229	128	197	17.4

P. scaber

Year	Immatures	Males			Females		
		1 year	2 year	3 year	1 year	2 year	3 year
1972	152	271	146	-	338	134	-
1973	152	436	256	-	450	215	-
1974	159	388	239	-	400	164	-
1975	167	400	218	-	542	215	-

temperature on growth that the summer of 1973 had been hotter than 1974 and 1975. In fact this was not true. The mean integrated temperature from April to September in 1975 was more than 2°C above that in 1973 (tab. 7.6). Davis, Hassall & Sutton (1977) have shown that 1974 was much drier than 1973. Table 7.6 shows that 1975 was drier still. In addition an accumulation of 2-4 cm of wind blown sand blanketed the study area in the last two years. This combination of dry summers and surface sand appears to have had a greater influence on the growth of A. vulgare than the ambient summer temperature. Deleterious effects of these conditions on quality and accessibility of food may account for the unexpected results as Cromack (1967) and Merriam (1971) have shown that food quality is very important for the survival, growth and reproduction of A. vulgare in Texas. Hatchett (1947) also found the summer growth of an isopod to be related to rainfall instead of temperature.

Summer growth in P. scaber appeared to be independent of both temperature and rainfall, but data from more than four years will be needed to test this fully.

(d) Population production

Size-density curves were constructed for the juveniles, males and females of all the P. scaber and A. vulgare cohorts found in the samples from 1968 to 1975. The 1972 cohort curves are shown in figures 7.6 and 7.7 to illustrate their construction.

The first point of the curves for immatures (figs. 7.6a and 7.7a) was derived from the natality estimates (chapter five) and their mean dry weight on release from the brood pouch. The last point for the immatures came from the size and density figures for the females in the first sample in which there were no longer any juveniles belonging to that cohort. If, as in A. vulgare this was always the August 1st sample taken in the year following the cohort's appearance then production of the immatures was measured up to August 1st only. The remainder was attributed to the females. The size of the animals on August 1st (indicated by the arrow in figure 7.7a) was

Figure. 7.6 Porcellio scaber size/density curves of a. juveniles, b. males and c. females belonging to the 1972 cohort. Size is expressed as mean dry weight of individuals. Arrows indicate size on 1 August in each year.

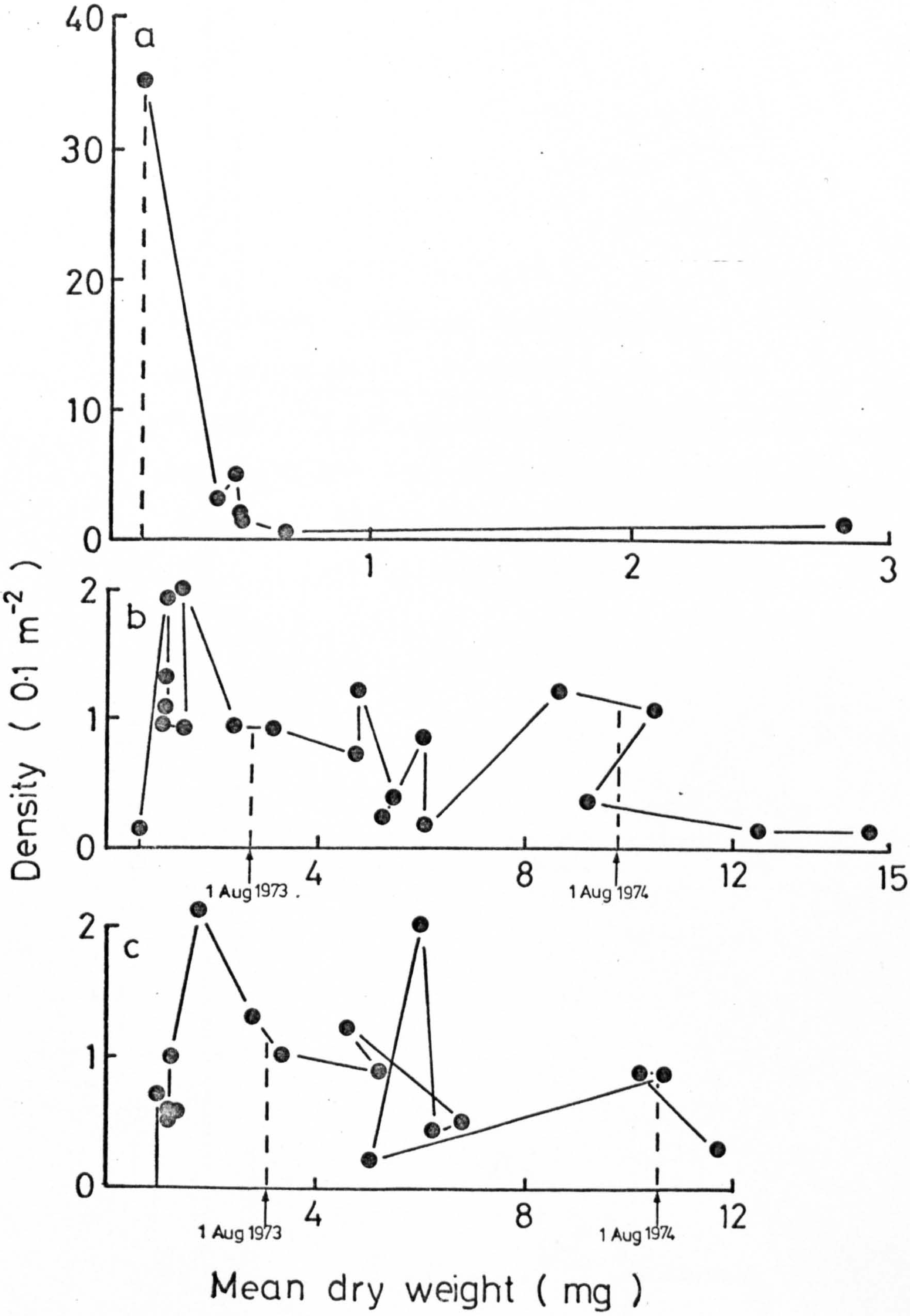
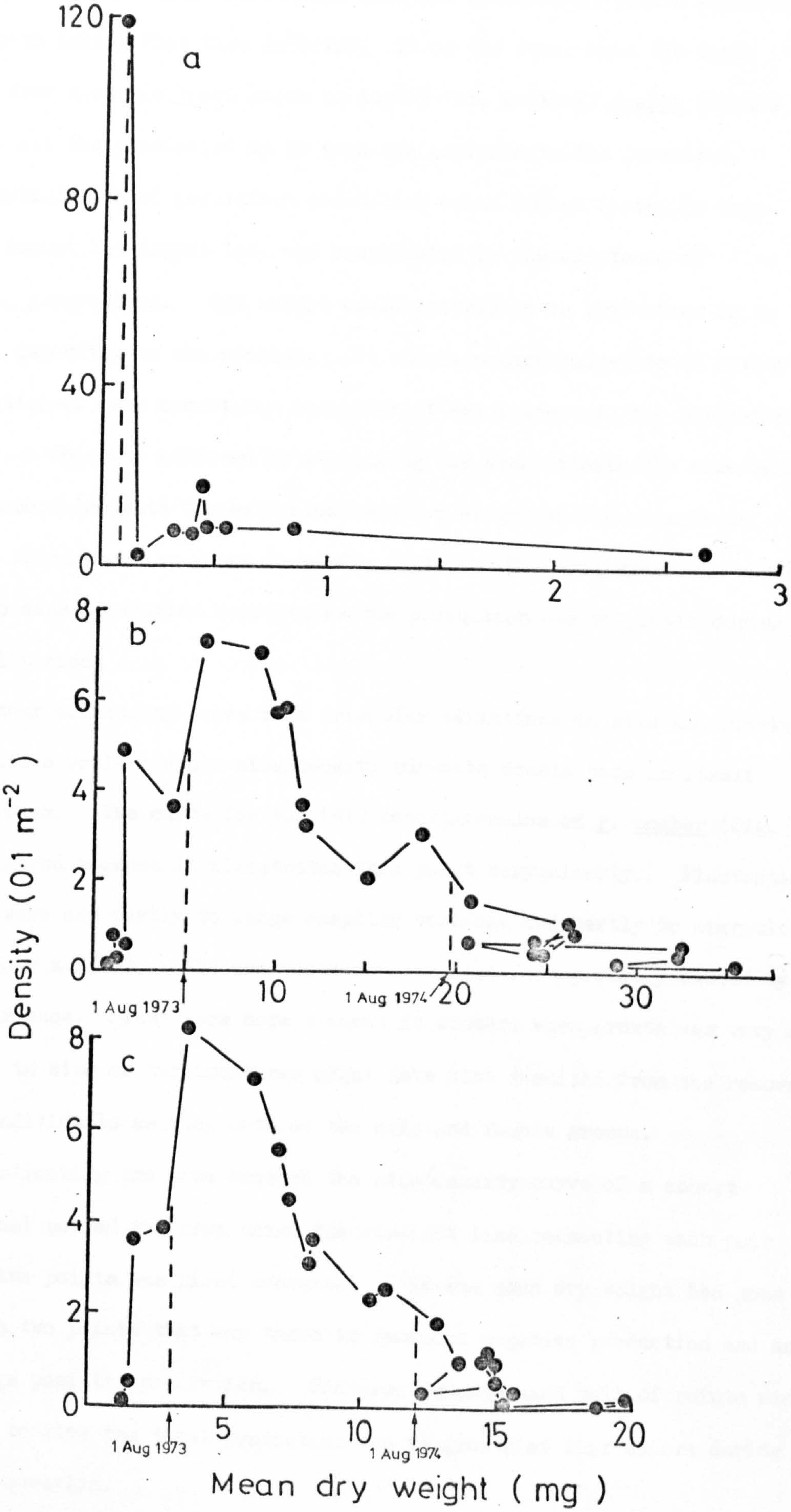
40
30
20
10
0
a
1
2
3
Density (0·1 m^{-2})
2
1
0
b
4
8
12
15
1 Aug 1973
1 Aug 1974
2
1
0
c
4
8
12
1 Aug 1973
1 Aug 1974
Mean dry weight (mg)

Figure. 7.7 Armadillidium vulgare size/density curves of a. juveniles, b. males and c. females belonging to the 1972 cohort. Size is expressed as mean dry weight of individuals. Arrows indicate size on 1 August in each year.


a
120
80
40
0
1
2
3
b
8
6
4
2
0
10
20
30
1 Aug 1973
1 Aug 1974
c
8
6
4
2
0
5
10
15
20
1 Aug 1973
1 Aug 1974
Density (0·1 m^{-2})
Mean dry weight (mg)

estimated by interpolation between the last and second last points assuming linear growth during that time interval. If on the other hand the last point was from a sample taken prior to August 1st, as in P. scaber (figure 7.6a) then all the production up to then was assigned to the juveniles.

The calculation of population production on an annual basis, in this case from August 1st-August 1st, was complicated by the existence of overlapping generations. Any cohort could contribute to production in up to 4 years depending on the species. It was necessary therefore to estimate the production of each cohort for each year it was present in the population separately. This was achieved by sectioning the area beneath the size/density curve in accordance with the estimated mean dry weight of the animals on August 1st in consecutive years (e.g. fig. 7.7c). The area under the curve between two size boundaries constitutes the production due to growth during that annual period.

A further difficulty arose from irregular variations in size and density which sometimes would cause a size/density curve to double back on itself and loop around. The curve for the 1972 cohort females of P. scaber (fig. 7.6c) is figured because it illustrates this point very clearly. Fluctuations in density were due partly to large sampling variance and partly to migration (chapters four & five). The decreases in mean size were probably caused by sampling variance. They were more evident in winter. when growth was very slow. A reduction in size of the immatures might have also resulted from the removal of larger individuals as they entered the male and female groups.

When estimating the area beneath the size/density curve of a cohort for any annual period the area under the straight line connecting each pair of consecutive points was first measured. If the mean dry weight had gone down between two points that was taken to indicate negative production and an upward change positive production. The area beneath each pair of points was then summed to give the total production due to growth of that cohort during the year in question.

The estimates of production due to growth (Pg) derived from the cohort subgroup size/density curves and the production due to reproduction (Pr) of P. scaber, A. vulgare and P. muscorum are given in tables 7.7, 7.8 and 7.9 respectively. The values of Pg in A. vulgare run from 1972/73 to 1974/75 only, because the subgroups in the pre-1972 samples were not analysed separately due to inadequate identification of the sexes. The first five values for P. muscorum are taken from Hassall (1976), but are converted to dry weights from the calorific values given by Hassall. The last two values have been calculated from density and size structure data obtained during the course of the present study, but which are unpublished.

To make a comparative study of the changes in production of each species during the seven years for which data are available it was necessary to compute total production figures (i.e. Pg + Pr) for A. vulgare between 1968/69 and 1971/72. This was done by calculating the production due to growth from size/density curves constructed from data for the juveniles, males and females combined. To check that the values obtained using the combined subgroup data were the same as those derived when the subgroups were analysed separately both methods were applied to the 1972/73 to 1974/75 data. Total production estimates obtained from the combined data are indicated by P' in table 7.10 and from the separated subgroup data by P. P' was on average 5.4% greater than P in the last three years (tab. 7.10). Hence to obtain total production figures for A. vulgare from 1968/69 to 1971/72 which were comparable with the totalled subgroup estimates for the later years, and also with P. scaber and P. muscorum, the P' values were multiplied by a correction factor of 0.9446. These results are also given in table 7.10.

The total annual production of each species in each year from 1968 to 1975 at Spurn is summarised in table 7.11.

The mean annual production by all three isopod populations combined was 256.9 mg dry weight 0.1 m^{-2} yr^{-1}. A. vulgare, produced 119.2 mg 0.1 m^{-2} yr^{-1} (46.4% of the total), P. muscorum produced 112.5 mg 0.1 m^{-2} yr^{-1} (43.8%) and P. scaber produced the remaining 25.1 mg 0.1 m^{-2} yr^{-1} (9.8%).

Table 7.7

Production estimates for <u>P. scaber</u> in mg dry wt 0.1 m^{-2}

Cohort and Sub group		1968/69	1969/70	1970/71	1971/72	1972/73	1973/74	1974/75
	I	-						
1966	M	1.41						
	F	0.42						
	I	-						
1967	M	1.19	-0.16					
	F	1.74	-0.10					
	I	5.14						
1968	M	0.65	3.09	0.70				
	F	1.67	5.03	1.11				
	I		4.48					
1969	M		4.49	6.55	0.58			
	F		5.54	13.38	0.77			
	I			7.20				
1970	M			-0.85	3.02	0.10		
	F			0.62	1.23	0.40		
	I				5.66			
1971	M				3.92	2.94	1.74	
	F				4.49	2.89	0.61	
	I					7.96		
1972	M					2.51	5.67	1.01
	F					3.02	4.55	0.59
	I						10.18	
1973	M						6.43	3.36
	F						7.69	2.38
	I							6.09
1974	M							1.47
	F							0.91
Total Production due to growth		12.22	22.37	28.71	19.67	19.82	36.87	15.81
Production due to reproduction		2.00	5.40	1.87	4.12	1.64	3.97	1.42
Total annual population production Pg + Pr		14.22	27.77	30.58	23.79	21.46	40.84	17.23

Table 7.8 Estimates of population production for *A. vulgare* in mg dry wt. 0.1m^{-2}

Cohort and Sub Group		1972/73	1973/74	1974/75
1969	I			
	M	18.44		
	F	0.83		
1970	I			
	M	26.31	4.05	
	F	8.01	0.41	
1971	I			
	M	51.28	41.65	
	F	26.45	27.45	
1972	I	17.38		
	M	14.59	63.78	11.92
	F	6.02	44.15	3.84
1973	I		27.50	
	M		39.48	52.85
	F		16.03	38.22
1974	I			10.75
	M			1.70
	F			0.92
Total production due to growth Pg		169.31	264.50	120.20
Production due to reproduction Pr		7.97	6.21	7.47
Total annual Pop' production Pg + Pr		177.28	270.71	127.67

Production due to reproduction from 1968/69 - 1971/72

	1968/69	1969/70	1970/71	1971/72
Pr	1.37	1.51	6.11	8.36

Table 7.9 Population production of P. muscorum (mg dry weight 0.1 m^{-2})

Year 1 Aug - 1 Aug	Pg	Pr	Pg + Pr
1968/69	86.9	11.8	98.7
1969/70	111.6	12.3	123.9
1970/71	164.2	31.1	195.3
1971/72	213.7	15.6	229.3
1972/73	82.4	5.2	87.6
1973/74	50.1	0.2	50.3
1974/75	2.6	0.1	2.7

Table 7.10 A. vulgare population production estimates based on combined subgroup data (P') and separated subgroup data (P). (mg dry weight 0.1 m^{-2}).

Year 1 Aug - 1 Aug	P'	P
1968/69	36.49	34.47*
1969/70	34.64	32.72*
1970/71	82.49	77.92*
1971/72	120.15	113.49*
1972/73	188.72	177.28
1973/74	294.16	270.71
1974/75	131.05	127.67

* denote values obtained by mutiplying P' with a correction factor of 0.9446.

Table 7.11 Total population production of each species (mg dry weight 0.1 m^{-2})

Year 1 Aug - 1 Aug	*P. muscorum*	*P. scaber*	*A. vulgare*	Total
1968/69	98.7	14.2	34.5	147.4
1969/70	123.9	27.8	32.7	184.4
1970/71	195.3	30.6	77.9	303.8
1971/72	229.3	23.8	113.5	366.6
1972/73	87.6	21.5	177.3	286.4
1973/74	50.3	40.8	270.7	361.8
1974/75	2.7	17.2	127.7	147.6
Magnitude of change	x 84.9	x 2.9	x 7.8	x 2.5

Total production, like total biomass, did not vary much during the seven year study. It was maintained by large counter changes in the production of *A. vulgare* and *P. muscorum* (table 7.11). Thus the percentage of the total produced by these two species was far from constant. For instance in 1968/69 the production by *P. muscorum* was 67.0% of the total but by 1974/75 its share had fallen to 1.8%. Variations in the production of *A. vulgare* made up most of the difference as *P. scaber* remained at the low but steady level of about 10%.

7.4 DISCUSSION

When assessing the importance of different species in the role of supporting predator populations production is the best index (Odum 1959) for it permits comparison between taxonomically unrelated groups from different sites and from different times. The isopod production estimates given here indicate that *A. vulgare* was on average slightly more important than *P. muscorum* - even though the latter had the greater production in 4 out of the 7 years (table 7.11) - and that *P. scaber* was the least important species.

Few other studies on macrodecomposers have been sufficiently detailed to enable the assessment of population production. Since they detail only biomass or numbers it is worthwhile discussing which of these two indices most closely simulates the interspecific differences in productivity and hence might be used for comparing the ecological importance of macrodecomposers at different sites.

The mean density of woodlice during this study was 55.7 0.1 m^{-2} (derived from table 7.4) and the mean biomass was 530.5 mg live weight 0.1 m^{-2} (also derived from table 7.4). *P. muscorum* was the most abundant species contributing 61.0% to the total number of woodlice on the site, *A. vulgare* was second with 29.3% and *P. scaber* was third with 9.7%. Judging by density the rank order of *A. vulgare* and *P. muscorum* would have been reversed from that based on production. In contrast *A. vulgare* had the greatest mean biomass (53.5% of the total). It was followed by P. muscorum (37.9%) and then by *P. scaber*

(8.6%), giving the species the same order of importance as production. In addition variations in the biomass of A. vulgare and P. muscorum simulated the changes in production more closely than density (c.f. tabs 7.4 and 7.11). The differences were caused mainly by the environmentally induced variations in individual growth rates shown in table 7.6.

From the above it is clear that the biomass of animals would form a firmer basis for comparing species at different sites than density. However it is limited by its inability to incorporate variations in growth and metabolic rates.For this reason comparisons using biomass are most useful where metabolic rates are similar as between millipedes and woodlice (see Phillipson 1967, Newell, Weiser & Pye 1974 and many others). Such a comparison is attempted in table 7.12. There appear to be no published studies which give estimates of biomass changes from year to year at one site. Until such information is available comparisons must be restricted to differences between sites.

Both isopods and diplopods have higher biomass values in grassland than woodland (table 7.12). This is partly due to the fact that the only data available for grasslands refer to base rich sites, in which both groups are particularly common. The isopod figures are much more consistent than those for diplopods and it is of interest that Macfadyen's early estimates have proved so accurate.

Table 7.12 Total biomass estimates of isopods and diplopods at different sites.

	Grassland		Deciduous Woodland	
	Total biomass ($gm\ m^{-2}$ live wt)	Source	Total biomass ($gm\ m^{-2}$ live wt)	Source
Isopoda	8.1*	Paris & Pitelka (1962)	0.5	Dunger (1958)
	5	Macfadyen (1968)	0.2	Macfadyen (1963 b) (mean of 4 sites)
	2.1	Sutton (1972)	0.1	Gere (1962)
	4.7	Al-Dabbagh (1976)	0.2	White (1968)
	6.6	--- " -- (")	4.0***	Saito (1969)
	5.3	present study	0.7	Stachurski (1972)
			0.1	Standen (1973)
Diplopoda	12.5	Macfadyen (1963 b)	3.0	Dunger (1958)
	0.7	present study	2.3	Gere (1962)
	12.5	Sutton (unpublished)**	3.7	Macfadyen (1963) (mean of 4 sites)
			0.1	Kitazawa (1967)
			1.2	Blower (1970)
			1.7	Blower & Miller (1974)
			0.3	Dowdy & Blem (1975)

* Density figures given by author, multiplied by a representative mean live weight of species at Spurn Head.

** 1964 Wytham Woods, Berks.

*** Water content assumed to be 70%

CHAPTER EIGHT

8.1 DISCUSSION

In this study an attempt has been made to clarify the role of four species of macrodecomposer in the transfer of energy from dead plant material to higher trophic levels. Within this general field attention has been focused on niche separation, population dynamics and population production. In the discussion that follows each of these aspects will be considered in turn, and their relevance to the overall aim of the work made clear.

Considering first niche separation. The coexistence of four species with apparently very similar niches conflicts with the 'one species - one niche' concept derived from the competitive exclusion principle. If this principle holds some form of resource partitioning between the species must be expected, yet the examination of their food resource utilization and predators (chapter one) gave no indication of any differences. In fact there is little evidence of resource partitioning in the decomposer trophic group as a whole (Anderson 1974). However there is now a view that the spatial heterogeneity of the soil provides a mosaic of conditions (Anderson 1973) to which the various elements of the fauna can specialise so that each has a separate food search area and thereby coexist. The work of Brereton (1957), Reichle (1969), Anderson (1977) and Friend and Richardson (1977) provide evidence to support this view, as does the present work. For example in chapters two and three it was shown that Cylindroiulus latestriatus was spatially separated from the woodlice because it lived deeper in the soil profile, and that the three woodlice were separated from each other by horizontal differences in distribution. Philoscia muscorum predominated in the stable dune whereas Porcellio scaber and Armadillidium vulgare predominated in more mobile conditions.

Although the last two species showed only small differences in distribution there was evidence which suggested that seasonal differences in migration patterns could have resulted in a partial separation of juveniles.

This means of achieving coexistence through small scale spatial separation which may be due to separate food search areas has been widely observed in other groups of animals. In *Drosophila* (Shorrocks 1975), in lizards (Schoener 1968), in field mice (Crowell & Pimm 1976) and in many closely related species of birds. MacArthur (1958) showed that American warblers of the genus *Dendroica*, which eat the same caterpillars from the same trees forage in such specialised ways in different parts of the trees that each ensures it has a private part of the resource. Reed warblers (*Acrocephalus scirpaceous* (Hermann)) and sedge warblers (*A. schoenobaenus* (L.)) in Britain show distinctly separate food search areas. The sedge warbler feeds mainly near the ground in *Phragmites communis* Trin. marshes whereas the reed warbler feeds in willow beds (*Salix sp.*)(Catchpole 1973). In addition to the above examples Lack (1944) has shown that closely related pairs of British passerines more frequently effect niche separation through habitat differences than by any other means.

By effecting niche separation through spatial differences and not through dietary specialisation or interactions with predators the macrodecomposers at Spurn could be considered to have an equal role in the transfer of energy from dead organic material to higher trophic levels. However their roles will differ because at any one site the biomass and hence quantity of energy transferred by each species will be different. Furthermore each one will be of greatest importance in a different region of the dune system. *P. muscorum* was the main species in the litter layer of the stable areas of dune while *A. vulgare* and *P. scaber* were more important in unstable areas. C. latestriatus was the most important macrodecomposer at depths greater than 3-4 cm below the sand's surface. The study of niche separation has therefore been of relevance in clarifying the role of the macrodecomposers at Spurn, because it has indicated how each species makes its major contribution to energy transfer and decomposition in different microhabitats. Through this they will effect a more even pattern of energy flow over the dune grassland ecosystem than if there was just a single species, or if they all had identical distributions.

Associated with the observed spatial separation is likely to be a contrast in the reproductive, mortality and migratory patterns or evolved strategies of each species. This is to be expected as their life history features should be best adapted to the prevailing conditions, and associated selection pressures, of the stage in the dune succession in which they predominate. In the early successional stages r-selection should operate while in later stages there should be a shift to K-selection (MacArthur & Wilson 1967, Odum 1969). A. vulgare, P. scaber and C. latestriatus, which are well adapted to early stages in dune succession, might therefore be expected to possess more r-type life history features than P. muscorum, because the latter occupies the later stages of succession. This is tested below by comparing aspects of their biology with the features expected in r- and K-selected species (Pianka 1970). The data (tab. 8.1) are taken from chapters four, five and six, for A. vulgare, P. scaber and C. latestriatus, and from Sunderland et al (1976) for P. muscorum.

There are no hard and fast rules for ordering species along the r-K continuum using the attributes given in table 8.1. In trying to come to some objective decision each species was ranked from 1-4 on each attribute. A species was ranked 1

Table 8.1 Life history features of *Armadillidium vulgare* (*A.v.*), *Porcellio scaber* (*P.s.*), *Philoscia muscorum* (*P.m.*) and *Cylindroiulus latestriatus* (*C.l.*) at Spurn. Ranking of species along the r-K continuum by each attribute shown in parentheses.

* Errors involved in making these estimates are too large and the interspecific overlap too great for useful comparison to be made.

** Estimates are probably too large. See chapter six.

† Refers to number of broods (or waves of breeding) in a year and the number of years in which animals of a single cohort may breed. It is not always possible to say that because animals in one cohort breed in more than one year that any individual breeds in more than one year. For example, females of *Philoscia muscorum* may breed at the age of one year or two years but no females breed at both one and two years of age. All those that breed at two years of age do not breed at one year and all those breeding after one year die before reaching a second year (Sunderland et al 1976).

†† Fecundity is the number of ova produced by a single female in one brood.

††† Refers to potential for increased fecundity by rapid and sustained growth (as under very favourable conditions) and is estimated from the head width/fecundity relationship in woodlice and stadium/fecundity relationship in the millipede.

Attribute	<u>P.s.</u>	<u>A.v.</u>	<u>P.m.</u>	<u>C.l.</u>
Survivorship* curve	---- all approximately type three of Slobodkin ----			
% juvenile* mortality	51-88	57-94	57-81	85-94**
Longevity (years)	3 (2)	4 (3)	2 (1)	5 (4)
Population stability	very good (3.5)	good (1.5)	good (1.5)	very good (3.5)
<u>Reproductive features</u>				
Breeding† frequency	2/2 (2.5)	1/2 (2.5)	2/2 (2.5)	1/3 (2.5)
Age at 1st reproduction (years)	1 (1.5)	2 (3.5)	1 (1.5)	2 (3.5)
Fecundity††	5-100 (2)	8-156 (1)	5-31 (3)	1-27 (4)
Size/fecundity††† relationship	intermediate (2)	steep (1)	shallow (3.5)	shallow (3.5)
Size of recruits	intermediate (3)	small (1.5)	large (4)	small (1.5)
Complexity of life cycle	simple (2)	simple (2)	complex (4)	simple (2)
Ranking total	18.5	16.0	21.0	24.5

if it appeared to be the most r-selected for that attribute up to 4 if it appeared to be the most K-selected. The ranking on any one attribute was made independently of that on the others. The sum of the scores has been used to indicate the relative positions of each species along the r-K continuum with the most r-selected having the lowest total and the most K-selected the highest.

If just the sums of the rankings are examined (tab. 8.1) then the expectation that P. muscorum would show more K-selected characteristics than A. vulgare and P. scaber seems to be borne out, as it has the highest total of the three. However this conclusion may be spurious because the species rank differently on different attributes. For example judging by longevity (maximum length of life) A. vulgare would appear least r-selected, because it lives longest; but it has the highest fecundity and by this attribute appears most r-selected. Unfortunately this conflict cannot be resolved at present, because it is difficult to assess the relative importance of the attributes chosen. However support for the conclusion that P. muscorum is the more K-selected woodlouse can be drawn from life history studies on these species reported by other workers. Data relevant to the present discussion which have been extracted from those studies are shown in table 8.2 (results from the present study are included also). Firstly, P. scaber and A. vulgare have been studied in Japan (Saito 1969) and in North America (Hatchett 1947, Paris & Pitelka 1962) and have been disseminated around the world by man (Sutton 1972). As they are believed to have originated in Europe (Van Name - in Hatchett 1947) their widespread distribution is indicative of a good colonizing ability, a feature which would be expected for r-selected species (MacArthur & Wilson 1967). In contrast, P. muscorum is a poor colonizer and has not established itself outside Europe. Secondly, there is a greater variation in the life history features of P. scaber and A. vulgare than of P. muscorum (tab. 8.2) suggesting that they can adapt more readily to new environments, a feature essential for colonizing species. Although the difference may stem partly from the greater variety of habitats in which P. scaber and A. vulgare have been studied it is unlikely to account for all the differences for two reasons, (a) because no two population studies on A. vulgare or P. scaber give life history features as similar to one another as the two on P. muscorum and (b) because two populations of A. vulgare less than 15 Km apart in the English Brecklands studied by Al-Dabbagh (1976) were as different as those studied in America and Japan. Thus the animals in one population were iteroparous, had a maximum longevity of 3.5 years and an apparent juvenile mortality of 81% while in the other they were semelparous, rarely lived to three years and had a juvenile mortality of 65-77%. Finally, a comparison of the life cycle of P. muscorum with that of A. vulgare and P. scaber suggests that the first is more K-selected because it is more complex (Odum 1971). This greater complexity in P. muscorum is attributed to cohort splitting (Sunderland et al 1976) which is absent in the other two. Furthermore it was suggested by Sunderland et al (1976) that cohort splitting may contribute to stability whereas Lawlor (1977) suggests that the type of reproductive strategy exhibited by A. vulgare would appear to augment the population fluctuations observed in the species by Paris & Pitelka (1962). Thus the initial conclusion that A. vulgare and P. scaber are more r-selected than P. muscorum seems to be justified.

In contrast C. latestriatus appears to have the most K-selected characteristics (tab. 8.1) and yet also has a horizontal distribution similar to that of the r-selected A. vulgare and P. scaber (chapter

Table 8.2 Life history features of isopods. Numbers in brackets refer to authors cited below.

1	Present study
2	Al-Dabbagh 1976
3	Hatchett 1947
4	Heeley 1941
5	Paris & Pitelka 1962
6	Saito 1969
7	Sunderland, Hassall & Sutton 1976
8	Sutton 1968

*	number of broods per year / number of years in which animals of one cohort may breed
**	Weeting Heath
/	Lakenheath Warren
?	not determined

Attribute	Armadillidium vulgare	Porcellio scaber	Philoscia muscorum
Age at 1st reproduction (years)	1 (5) 2 (1,2,4,6)	1 (1) 2 (6)	1 (7,8)
Breeding* frequency	1/1 (2**) 1/2 (1,2†,6) 2/2 (3,5)	2/2 (1) 3/? (3) ?/1 (6)	1/2 (8) 2/2 (7)
Longevity (years)	3 (2**,6) 3.5 (2†) 4 (1,5)	2 (6) 3 (1)	2 (7,8)
Fecundity	5-62 (3) 8-156 (1) 10-37 (6) 12-125 (5) 15-95 (2)	5-100 (1) 6-22 (6) 6-42 (3)	5-30 (8) 5-31 (7)
% juvenile mortality	57-94 (1) 65-77 (2**) 81 (2†) approx. 80 (5)	51-88 (1)	57-81 (7) approx. 50 (8)

two). The resolution of this paradox may lie in the vertical distribution of the millipede for it lives much deeper down than the woodlice (chapter three) where it will experience a more stable microclimate and also a more constant food supply as the food will be less frequently made inaccessible by desiccation or periodic cold spells. This may result in a greater degree of K-selection and the production of life history characteristics in the millipede similar to species which occupy the later successional stages where the conditions are more stable. However although *C. latestriatus* is K-selected in comparison to the woodlice it seems to be r-selected as compared to other cylindroiulid millipedes (Blower & Gabbutt 1964). Like *A. vulgare* and *P. scaber* it is a good colonizer. It also matures one stadium and one year earlier than the closely related *C. punctatus* which gives it a greater potential for rapid population increase during colonizing episodes (Blower & Gabbutt 1964). Thus *C. latestriatus* like the woodlice has a life history strategy suited to its distribution in the dune succession.

Detailed consideration of life history strategies in relation to distribution and environmental stability has been undertaken because it clarifies the factors determining changes in relative abundance and therefore role of the species within the dune grassland ecosystem. For instance it provides insight into the population shifts which occurred on the study site during the period of investigation. *P. muscorum*, the more K-selected woodlouse, predominated when conditions were stable (1968 - 1972) and litter accumulated on the surface over a number of years, but in the semi-mobile conditions brought about through disturbance by rabbits and moving sand the more r-selected *A. vulgare* and *P. scaber* were able to maintain the larger populations. The population dynamics studies (chapters four, five and six) were further relevant to the present work because they yielded the density and size structure data necessary for the computation of population biomass and production.

Although there were marked changes in relative abundance, biomass and productivity of the individual species overall figures were markedly constant. The maximum, minimum and mean isopod production were 3.7, 1.5 and 2.6 g dry weight m^{-2} yr^{-1} respectively for the seven years considered. This stability seems remarkable in face of the habitat variation observed and suggests that strong homeostatic mechanisms were operating at the macrodecomposer trophic level.

This finding is of considerable interest in the context of community stability. Ricklefs (1973) states that 'the stability of a community depends on the stability of its component populations'. Although Ricklefs' statement was directed towards the stability of numbers it implies that the stability of energy flow through the whole community and within the different trophic levels is also dependent on the stability of individual species. The present study suggests that energy flow can be maintained in a second way; that is by compensatory changes in the contribution by the constituent species. This principle has hitherto been overlooked possibly because workers have always restricted their consideration of stability to numbers of individuals or numbers of species. For instance the five aspects of stability considered worthy of study by Krebs (1972) all refer to density or species composition. It is probably this bias which has led Ricklefs (1973) to question the biological significance of stability. It can be argued however that stability of energy flow is of fundamental importance to ecosystems and should be of great interest to ecologists.

Unfortunately there appears to be no other long term studies of energy flow in any group of decomposers with which these findings can be compared. This is despite Phillipson (1966) pointing out the importance of such studies for a clearer understanding of the energy relations of ecosystems.

Future work may reveal functional differences in decomposition or in energy transfer for isopods and diplopods but at Spurn the varying populations served to enhance the stability of the biological system. This was achieved as they provided alternative pathways through which resources were channelled in the conditions that varied in time and space.

REFERENCES

Al-Dabbagh, K.Y. (1976). Population dynamics and bioenergetics of the terrestrial isopod *Armadillidium vulgare* (Latreille) in grassland ecosystems. Ph.D. Thesis, University of Leicester.

Anderson, J.M. (1971). Observations on the vertical distribution of Oribatei (Acarina) in two woodland soils. *IV Colloquium Pedobiologiae, C.R. 4ème Coll. Int. Zool. Sol.* (Ed. by Anon.) pp. 257-272. Inst. Nat. Récherche Agron., Paris.

Anderson, J.M. (1973). Stand structure and litter fall of a coppiced beech (*Fagus Sylvatica*) and sweet chestnut (*Castanea sativa*) woodland. *Oikos* *24*, 128-135.

Anderson, J.M. (1974). The enigma of soil species diversity. *Proc. 5th Int. Cong. Soil Zool.*, Prague 1973.

Anderson, J.M. (1977). Soil animal species diversity and soil habitat structure. *Soil Organisms as Components of Ecosystems. Proc. VI International Soil Zoology Colloquium*. (Ed. by U. Lohm & T. Persson) Ecol. Bull. (Stockholm) *25*.

Bailey, N.T.J. (1959). *Statistical Methods in Biology*. The English University Press Ltd.

Barlow, C.A. (1957). A factorial analysis of distribution in three species of diplopods. *Tijdschr. Ent*. *100*, 349-426.

Bernays, E.A. & Chapman, R.F. (1970). Food selection by *Chorthippus parallelus* (Zetterstedt)(Orthoptera : Acrididae) in the field. *J. Anim. Ecol*. *39*, 383-394.

Berthet, P. (1960). La mesure écologique de la température par détermination de la vitesse d'inversion du saccharose. *Vegetatio* *9*, 197-207.

Biernaux, J. & Baurant, R. (1964). Au sujet de la présence de *Blaniulus guttulatus* Bosc. et d' *Archiboreoiulus pallidus* Br.-Bk. (Myriapodes , Diplopodes) dans les couches superieures du sol, au moment des semis de betteraves. Meded. LandbHoogesch. OpzoekStns. Gent 29, 1063-1070.

Bliss, C.I. & Fisher, R.A. (1953). Fitting the negative binomial distribution to biological data. Biometrics 9, 176-200.

Blower, J.G. (1970). The millipedes of a Cheshire wood. J. Zool. Lond. 160, 455-496.

Blower, J.G. (1974). Food consumption and growth in a laboratory population of Ophyiulus pilosus (Newport). Symp. zool. Soc. Lond. 32, 527-551.

Blower, J.G. & Miller, P.F. (1974). The life cycle and ecology of Ophyiulus pilosus (Newport) in Britain. Symp. zool. Soc. Lond. 32, 503-525.

Blower, J.G. & Gabbutt, P.D. (1964). Studies on the millipedes of a Devon oak wood. Proc. zool. Soc. Lond. 143, 143-176.

Bocock, K.L. & Heath, J. (1967). Feeding activity of the millipede Glomeris marginata (Villers) in relation to its vertical distribution in the soil. (Progress in Soil Biology). Proc. Int. Soc. Soil Sci. commission III, Dynamics of soil communities , Braunschweig-Volkenrode.

Brereton, J. le G. (1957). The distribution of woodland isopods. Oikos 8, 85-106.

Catchpole, C.K. (1973). Conditions of coexistence in sympatric breeding populations of Acrocephalus warblers. J. Anim. Ecol. 42, 623-635.

Clark, L.R., Geier, P.W., Hughes, R.D. & Morris, R.F. (1967). The Ecology of Insect Populations in Theory and in Practice. Methuen & Co. Ltd., London.

Cloudsley-Thompson, J.L. (1951). On the responses to environmental stimuli, and the sensory physiology of millipedes (Diplopoda). Proc. zool. Soc. Lond. 121, 253-277.

Cole, L.C. (1949). The measurement of interspecific association. Ecology 30, 411-424.

Cotton, M.J. & Miller, P.F. (1974). A population of Cylindroiulus latestriatus (Curtis) on sand dunes. Symp. zool. Soc. Lond. 32, 589-602.

Cromack, K. (1967). Some consequences of food quality for Armadillidium vulgare populations (Isopoda : Oniscoidea). M.A. Thesis, University of Texas, U.S.A.

Crowcroft, P. (1957). The Life of the Shrew. Max Reinhardt, London.

Crowell, K.L. & Pimm, S.L. (1976). Competition and niche shifts of mice introduced onto small islands. Oikos 27, 251-258.

Curry, J.P. (1971). Seasonal,and vertical distribution of the arthropod fauna of an old grassland soil. Scient. Proc. R. Dubl. Soc. Series B. 3. 49-71.

Davis, B.N.K. (1963). A study of microarthropod communities in mineral soils near Corby, Northants. J. Anim.Ecol. 32, 49-71.

Davis, R.C., Hassall, M. & Sutton, S.L. (1977). The vertical distribution of isopods and diplopods in a dune grassland. Pedobiologia 17, 320-329.

Deshmukh, I.K. (1974). Primary production and leaf litter breakdown of Ammophila arenaria in a sand dune succession. Ph.D. Thesis, University of Dundee.

Dowdy, W.W. (1944). The influence of temperature on vertical migration of invertebrates inhabiting different soil types. Ecology 25, 449-460.

Dowdy, W.W. & Blem, C.R. (1975). Energetics of the diplopod Autures evides. Am. Midl. Nat. 93, 459-563.

Dunger, W. (1958). Über die Zersetzung der Laubstreu durch die Boden-Makrofauna in Auenwald. Zool. Jb. (Syst.) 86, 139-180.

Edney, E.B. (1951). The evaporation of water from woodlice and the millipede Glomeris. J. Exp. Biol. 28, 91-115.

Edney, E.B. (1954). Woodlice and the land habitat.Biol. Rev. 29, 185-219.

Edney, E.B. (1968). Transition from water to land in isopod crustaceans. Am. Zool. 8, 309-326.

Emmel, T.C. (1976). Population Biology. Harper & Row, Publishers, New York & London.

Fairhurst, C. (1974). The adaptive significance of variations in the life cycles of schizophylline millipedes. Symp. zool. Soc. Lond. 32, 575-587.

Fretwell, S.D. (1972). Populations in a Seasonal Environment. Princeton University Press, Princeton, New Jersey.

Friend, J.A. & Richardson, A.M.M. (1977). Niche partition in two Tasmanian amphipod species. Soil Organisms as Components of Ecosystems, VI International Soil Zoology Colloquium. (Ed. by U. Lohm & T. Persson) Ecol. Bull. (Stockholm) 25.

Gadgil, M. & Bossert, W.H. (1970). Life historical consequences of natural selection. Am. Nat. 104, 1-24.

Gere, G. (1962). Nährungsverbrauch der Diplopoden und Isopoden in Freilanduntersuchungen. Acta. zool. hung. 8, 385-415.

Hassall, M. (1976). Studies on the biology of Philoscia muscorum (Crustacea : Isopoda) with particular reference to its role in a dune grassland ecosystem. Ph.D. Thesis, University of Leeds.

Hatchett, S.P. (1947). Biology of the Isopoda of Michigan. Ecol. Monogr. 17, 47-79.

Heeley,W. (1941). Observations on the life histories of some terrestrial isopods. Proc. zool. Soc. Lond. 111, 79-149.

Kempson, D., Lloyd, M. & Ghelardi, R. (1963). A new extractor for woodland litter. Pedobiologia 3, 1-21.

Kershaw, K.A. (1973). Quantitative and Dynamic Plant Ecology. Edward Arnold, London.

Kheirallah, A.M. (1966). Studies on the feeding behaviour of the millipede Iulus scandinavius (Latzel 1884). Ph.D. Thesis, University of Manchester.

Kitazawa, Y. (1967). Community metabolism of soil invertebrates in forest ecosystems in Japan. Secondary Productivity of Terrestrial Ecosystems. (Ed. by K. Petrusewicz) pp. 649-661. Warsaw.

Krebs, C.J. (1972). Ecology. Harper & Row, Publishers, London & New York.

Lack, D. (1944). Ecological aspects of species formation in passerine birds. Ibis 86, 260-286.

Lawlor, L.R. (1977). Parental investment and offspring fitness in the terrestrial isopod Armadillidium vulgare (Latr.) (Crustacea : Oniscoidea). Evolution 31, 775-785.

MacArthur, R.H. (1958). Population ecology of some warblers of northeastern coniferous forests. Ecology 39, 599-619.

MacArthur, R.H. & Pianka, E.R. (1966). On optimal use of a patchy environment. Am. Nat. 100, 603-609.

MacArthur, R.H. & Wilson, E.O. (1967). Theory of Island Biogeography. Princeton University Press, Princeton, U.S.A.

Macfadyen, A. (1963a). Animal Ecology : Aims and Methods. Second edition. Pitman, London.

Macfadyen, A. (1963b). The contribution of the microfauna to total soil metabolism. Soil Organisms (Ed. by J. Doeksen & J. Van Der Drift) pp. 3-17. North Holland Publishing Co., Amsterdam.

Macfadyen, A. (1968). The animal habitat of soil bacteria. The

Ecology of Soil Bacteria. (Ed. by T.R.G. Gray & D. Parkinson) pp. 66-76. Liverpool University Press.

Manton, S.M. (1954). Part 4 : the structure, habits and evolution of the diplopoda. J. Linn. Soc. (Zool.). 42, 299-368.

Manton, S.M. (1961). Part 7 : Functional requirements and body design in Colobognatha (Diplopoda), together with a comparative account of diplopod burrowing techniques, trunk musculature and segmentation. J. Linn. Soc. (Zool.) 44, 383-461.

May, R.M. (1973). Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, U.S.A.

McQueen, D.J. (1976). Porcellio spinicornis Say (Isopoda) demography. II. A comparison between field and laboratory data. Can. J. Zool. 54, 825-842.

McQueen, D.J. & Carnio, J.S. (1974). A laboratory study of the effects of some climatic factors on the demography of the terrestrial isopod Porcellio spinicornis Say. Can. J. Zool. 52, 599-611.

Merriam, H.G. (1971). Sensitivity of terrestrial isopod populations (Armadillidium) to food quality differences. Can. J. Zool. 49, 667-674.

Miller, M.A. (1938). Comparitive ecological studies on terrestrial isopod Crustacea of the San Francisco Bay region. Univ. Calif. Publs Zool. 43, 113-142.

Morris, R.F. (1963). Predictive population equations based on key factors. Mem. entomol. Soc. Can. 32, 16-21.

Newell, R.C., Weiser, W. & Pye, V.I. (1974). Factors affecting oxygen consumption in the woodlouse Porcellio scaber Latr. Oecologia 16, 31-51.

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. & Bent, D.H. (1975). Statistical Package for the Social Sciances. McGraw-Hill Book Company, New York.

Odum, E.P. (1959). Fundamentals of Ecology : Second Edition. W. B. Saunders Company, Philadelphia and London.

Odum, E.P. (1969). The strategy of ecosystem development. Science, N.Y. 164, 262-269.

Odum, E.P. (1971). Fundamentals of Ecology : Third Edition. W.B. Saunders Company, Philadelphia and London.

Paris, O.H. (1963). The ecology of Armadillidium vulgare (Isopoda : Oniscoidea) in California grassland : Food, enemies and weather. Ecol. Monogr. 33, 1-22.

Paris, O.H. & Pitelka, F.A. (1962). Population characteristics of the terrestrial isopod Armadillidium vulgare in California grassland. Ecology 43, 229-248.

Peitsalmi, M. (1974). Vertical orientation and aggregations of Proteroiulus fuscus (Am. Stein) (Diplopoda : Blaniulidae). Symp. zool. Soc. Lond. 32, 471-484.

Perttunen, V. (1953). Reactions of diplopods to the relative humidity of the air. Investigations on Orthomorpha gracilis, Iulus terrestris and Schizophyllum sabulosum. Ann. Soc. Zool. Fenn. Vanamo 16, 1-67.

Petrusewicz, K. & Macfadyen, A. (1970). Productivity of Terrestrial Animals, Principles and Methods. Blackwell Scientific Publications, Oxford and Edinburgh.

Phillipson, J. (1963). The use of respiratory data in estimating annual respiratory metabolism with particular reference to Leiobunum rotundum (Latr.) (Phalangiidae). Oikos 14, 212-223.

Phillipson, J. (1966). Ecological Energetics. Edward Arnold (Publishers Ltd.).

Phillipson, J. (1967). Studies on the bioenergetics of woodland Diplopoda. Secondary Productivity of Terrestrial Ecosystems (Ed. by K. Petrusewicz).

Pianka, E.R. (1970). On r- and K- selection. Am. Nat. 104, 592-597.

Pierrard, G., Bonte, E. & Baurant, R. (1963). Observations sur l' hibernation de Blaniulus guttulatus Bosc. (Myriapode - Diplopode - Blaniulidae). Bull. Inst. agron. Stns Rech. Gembloux 31, 127-141.

Reichle, D.E. (1969). Distribution and abundance of bog-inhabiting pselaphid beetles. Illinois State Academy of Science 62, 233-264.

Reynoldson, T.B. & Davies, R.W. (1970). Food niche and coexistence in lake-dwelling triclads. J. Anim. Ecol. 39, 599-617.

Ricklefs, R.E. (1973). Ecology Nelson.

Romanova, Z.A. (1974). Length-weight ratios and fecundity in Idotea baltica baltica (Pallas) from the Baltic Sea. Hydrobiological Journal 10, 59-62.

Saito, S. (1969). Energetics of isopod populations in a forest of central Japan. Res. Popul. Ecol. 11, 229-258.

Salisbury, Sir E.J. (1952). Downs and Dunes. G. Bell & Sons Ltd., London.

Schoener, T.W. (1968). The Anolis lizards of Bimini : resource partitioning in a complex fauna. Ecology 49, 704-726.

Shorrocks, B. (1975). The distribution and abundance of woodland species of British Drosophila (Diptera : Drosophilidae). J. Anim. Ecol. 44, 851-864.

Sokal, R.R. & Rohlf, F.J. (1969). Biometry. W.H. Freeman & Co., San Francisco.

Solomon, M.E. (1957). Estimation of humidity with cobalt thiocyanate papers and permanent colour standards. Bull. ent. Res. 48, 489-506.

Southwood, T.R.E. (1962). Migration of terrestrial arthropods in relation to habitat. Biol. Rev. 37, 171-214.

Southwood, T.R.E. (1966). Ecological Methods. Chapman & Hall, London.

Stachurski, A. (1968). Emigration, mortality rates and the food shelter conditions of Ligidium hypnorum L. (Isopoda). Ekol. pol. Ser. A. 16, 445-459.

Stachurski, A. (1972). Population density, biomass and maximum natality rate and food conditions in Ligidium hypnorum L. (Isopoda). Ekol.pol. Ser. A. 20, 185-197.

Standen, V. (1973). The life cycle and annual production of Trichoniscus pusillus pusillus (Crustacea : Isopoda) in a Cheshire wood. Pedobiologia 13, 273-291.

Sunderland, K.D. (1977). The population dynamics of Philoscia muscorum (Crustacea : Oniscoidea) in a dune grassland ecosystem with a serological study of mortality due to predation. Ph. D. Thesis, University of Leeds.

Sunderland, K.D., Hassall, M. & Sutton, S.L. (1976). The population dynamics of Philoscia muscorum (Crustacea : Oniscoidea) in a dune grassland ecosystem. J. Anim. Ecol. 45, 487-506.

Sutton, S.L. (1966). The ecology of isopod populations in grassland. D. Phil. Thesis, University of Oxford.

Sutton, S.L. (1970). Predation on woodlice, an investigation using the precipitin test. Entomologia exp. appl. 13, 279-285.

Sutton, S.L. (1968). The population dynamics of Trichoniscus pusillus and Philoscia muscorum (Crustacea : Oniscoidea) in limestone grassland. J. Anim. Ecol. 37, 425-444.

Sutton, S.L. (1972). Woodlice. Ginn & Company Ltd., London.

Taylor, L.R. (1961). Aggregation, variance and the mean. Nature, Lond. 189, 732-735.

Taylor, L.R. (1965). A natural law for the spatial disposition of insects. Proc. 12th Int. Cong. Ent. London. pp. 396-397.

Taylor, L.R. & Taylor, R.A.J. (1977). Aggregation, migration and population mechanics. Nature, Lond. 265, 415-421.

Usher, M.B. (1969). Some properties of the aggregations of soil arthropods : Collembola. J. Anim. Ecol. 38, 607-622.

Usher, M.B. (1975). Seasonal and vertical distribution of a population of soil arthropods : Cryptostigmata. Pedbiologia 15, 364-374.

Varley, G.C. & Gradwell, G.R. (1960). Key factors in population studies. J. Anim. Ecol. 29, 399-401.

Wallwork, J.A. (1970). Ecology of Soil Animals. McGraw-Hill, London.

White, J.J. (1968). Bioenergetics of the woodlouse Tracheoniscus rathkei Brandt in relation to litter decomposition in a deciduous forest. Ecology 49, 694-704.

Williams, C.K. & Main, A.B. (1976). Ecology of Australian chats(Epthianura Gould) : Seasonal movements, metabolism and evaporative water loss. Aust. J. Zool. 24, 397-416.