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"AN INVESTIGATION OF THE RELATIONSHIPS BETWEEN SNAILS AND VEGETATION AT BISHOP MIDDLEHAM QUARRY, Co. DURHAM."

A dissertation submitted by P. J. Casement, B. A. (Oxon) to the University of Durham, as part of the requirements for the Degree of Master of Science.

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I. INTRODUCTION.

I.1. General Considerations.

The interactions between plants and animals are of fundamental importance to man, since our food supply is based on either animals fed on plants, or plants protected from animals which would otherwise eat them. Much attention has been paid to mammals and birds which provide most of our animal food, and which in terms of continuing biomass are the most important grazers. Invertebrates, however, may frequently become very serious competitors to both man and his domestic animals, mainly due to their capacity for rapid reproduction. Because of their small size and effective concealment invertebrates are generally more difficult to study, and until recently not a great deal was known of the detailed feeding habits of small herbivores. Recent studies on a variety of species including crickets (Hansen and Ueckert, 1970), grasshoppers (Bernays and Chapman, 1970), Mirid bugs (McNeill, 1971), aphids (Dixon, 1966), slugs (Pallant, 1969 & 1972) and snails (Grime et al., 1968, 1969, & 1970) (Wolda et al., 1971) have gone some of the way towards remedying the situation.

Among invertebrates terrestial molluscs provide some of the best experimental animals, being of limited mobility and convenient size. The larger species are also fairly easy to study in the field, being conspicuous and slow moving, though their largely nocturnal habits present some problems. In some habitats, notably limestone areas and sand dunes, snails may be extremely numerous, and must clearly be of considerable importance in the ecosystem. Such a habitat is found on the Magnesian Limestone of Co. Durham, which has long been famous for its unusual flora. Many of the most interesting habitats

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are now under threat from quarrying operations, and any attempt to preserve the unique floral communities should be based on sound knowledge of as many aspects of the whole ecosystem as possible. The present study was undertaken in an attempt to gain a greater understanding of aspects of both a herbivore - plant interaction and the effects of invertebrate grazing on a Magnesian Limestone habitat.

I.2. Study Area.

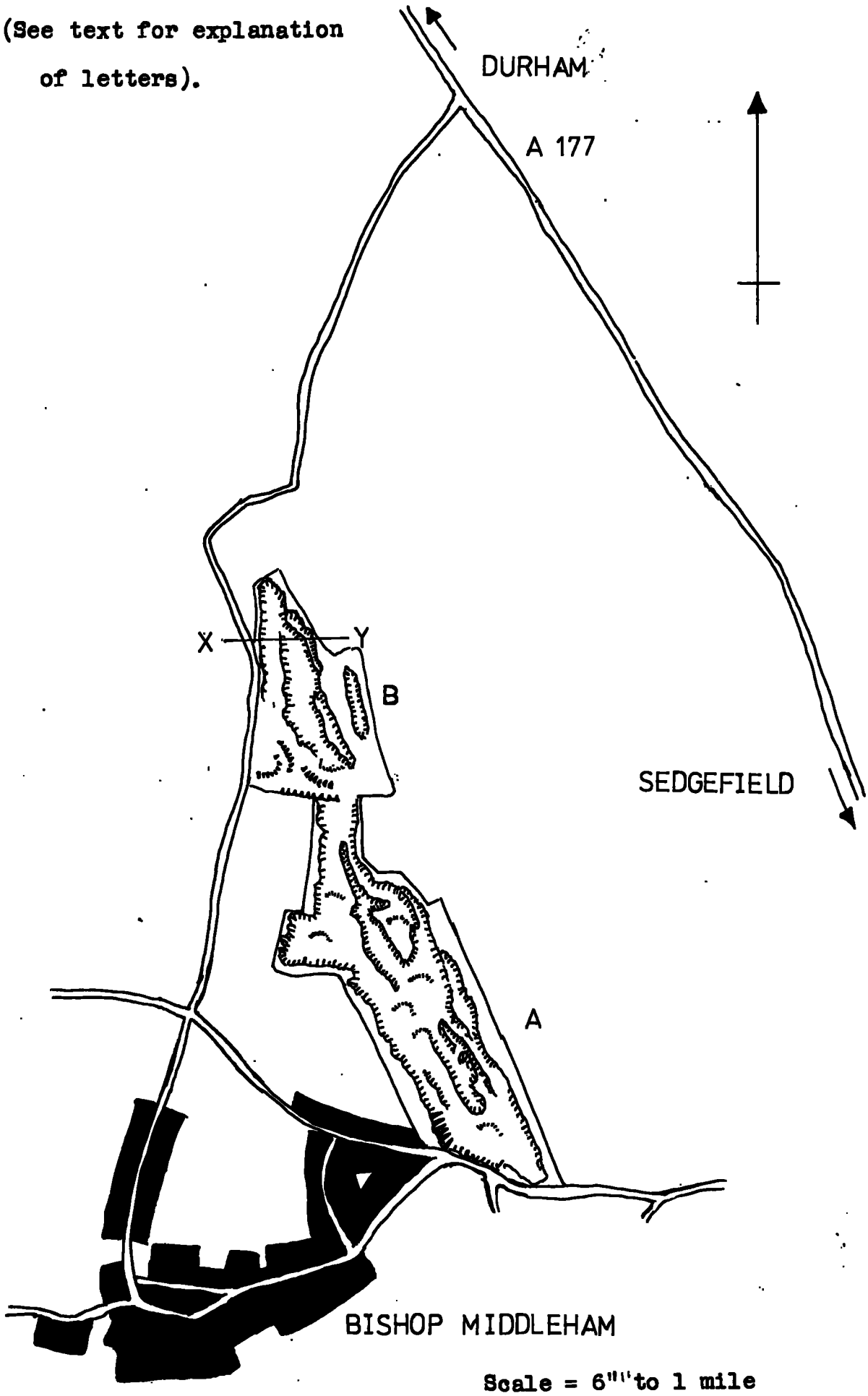
The study was carried out at Bishop Middleham quarry (Map Reference NZ 332327) situated between the villages of Coxhoe and Bishop Middleham in Co. Durham. (See Fig.1). The quarry, no longer worked, is a S.S.S.I. on account of its distinctive flora, and is divided into two main workings, a large southern area c.750m long (A on Fig.1), and a smaller northern part c.250m long (B on Fig.1). The latter area was used for this study because of its accessibility, large snail populations, more manageable size, and varied habitat. At the northern end of this working all the main vegetation types found within the quarry were in close proximity to each other, along with a variety of substrates. Most of the field work was confined to a transect running approximately East-West across this area. (See Fig.2).

I.3. Species Studied.

The molluscs found on the site were :-

Arion ater (L.)
Limax maximus (L.)
Agriolimax reticulatus Muller
Hygromia hispida (L.)

Fig.1. A map of the locality of the study site, showing its situation with respect to the village of Bishop Middleham. (See text for explanation of letters).



Scale = 6" to 1 mile

Fig. 2. Photograph showing the study area within the northern working of Bishop Middleham quarry.

T. T. = Top Terrace
M. T. = Mid Terrace
L. S. = Lower Slope
E. S. = Erosion Slope
N. S. = Nettle Slope

} See section II.1.

Numbers 1 - 8 indicate the sites at which mean temperature measurements were made. (See section II.6.)

Helicella itala (L.)
Cepaea nemoralis (L.)
Helix aspersa Muller.

Of these the four snail species were generally more common than the slugs, but only the last three were both common and widely distributed. Helicella itala however is rather small and inconspicuous during most of the year, reaching maturity in late summer and seldom living much longer than one year (Cook, 1970). Helix aspersa and Cepaea nemoralis, two of the commonest British snails, are undoubtedly the most important molluscs in this area, and their large size makes them ideal subjects for study in both the field and the laboratory. Therefore all the work was carried out on these two species alone.

H. aspersa (Fig. 3) is distributed fairly generally throughout Britain, and is our second largest snail, reaching a breadth of 30-35mm. It is found in a variety of habitats, in large numbers in gardens and stony places, and though not an obligate calcicole it prefers Calcium-rich environments. The snails have fixed resting places from which they forage for food, usually at night, or in wet weather. The normal life span is about two years, though individuals may live as long as ten years (Taylor, 1913) (Ellis, 1926). H. aspersa and its congener H. pomatia have been widely studied by physiologists, but surprisingly little work has been done on their ecology, though H. aspersa was among the species investigated by Mason (1970) in his study of woodland snails.

C. nemoralis (Fig. 4) is a smaller snail, the shell attaining about 20-22mm in breadth. It has a similar distribution to H. aspersa, living in woods, copses, hedges, sand dunes and also grassland, and like H. aspersa prefers limestone regions.

Fig. 3 Photograph of adult Helix aspersa. (Scale in cms.)

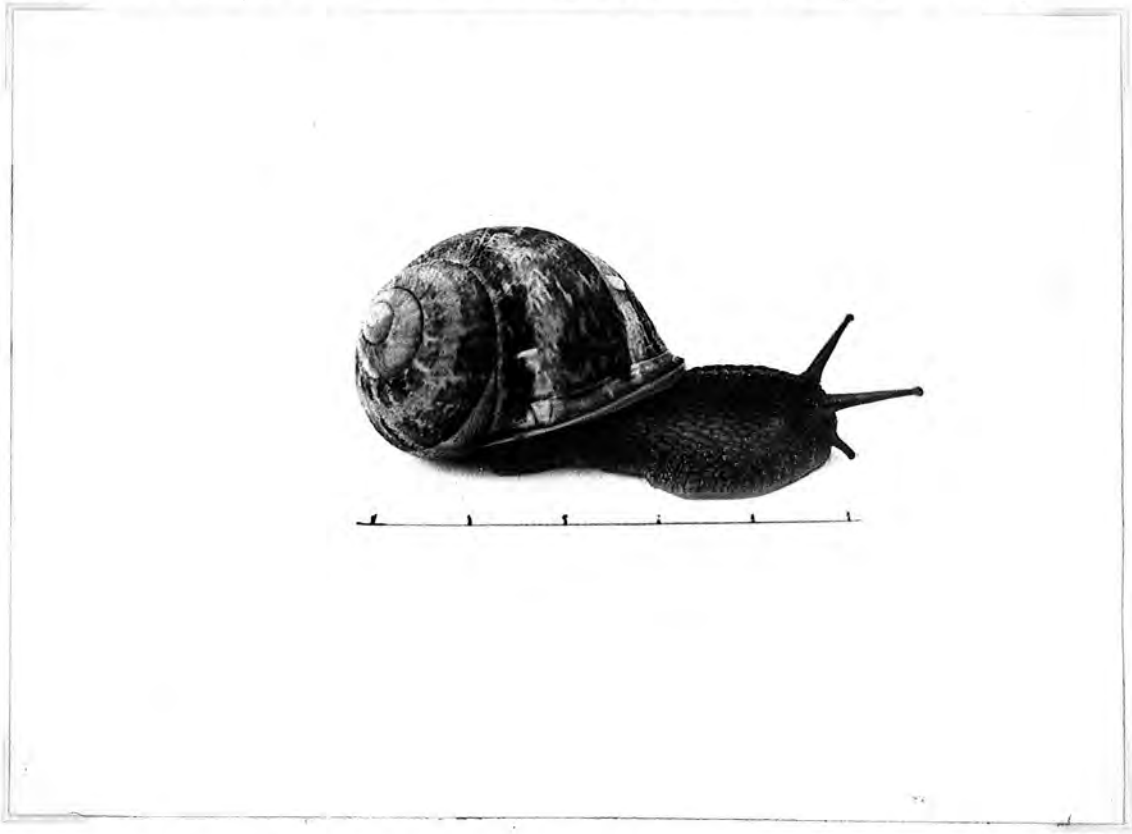
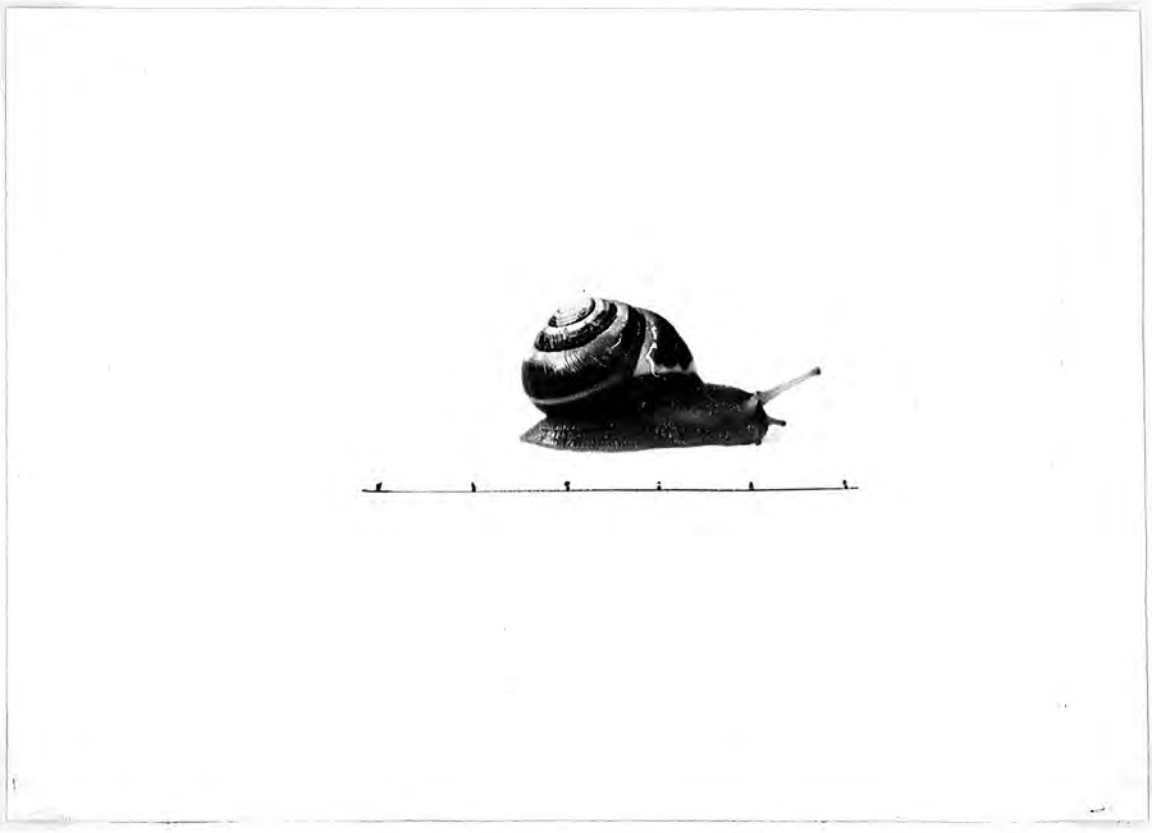


Fig. 4 Photograph of adult Cepaea nemoralis. (Scale in cms.)



It is almost identical in habits to the above species and also has a similar life span. This species has been extensively studied by geneticists since many populations show balanced polymorphisms in the banding pattern and ground colour of the shell, but little work has been done on other aspects of its ecology. Recently studies of feeding have been carried out by Grime et al. (1968, 1969, &1970) and Wolda et al. (1971). This investigation uses many of the techniques of these workers and can be regarded as an extension of the studies started by them.

I.4. Aims.

The aims of the study were to investigate the impact of the snails on the vegetation of the quarry, and hence the ecosystem in general, and to evaluate any effects of the vegetation on the density and distribution of the snail populations. Acheiving the first aim necessitated a detailed study of the feeding habits of the snails, including food selection in both the laboratory and the field, and calculation of assimilation and ingestion rates of typical foods. The second part of the study involved estimation of the size, structure, and distribution of snail populations across a spectrum of habitats, coupled with an analysis of certain aspects of the vegetation, such as standing crops and composition. In the course of the investigation it became clear that other environmental variables werealso affecting snail density and of these mean temperature and available shelter were also chosen for study.

II. METHODS

II.1. Snail Density and Distribution.

In order to study the density and distribution of snails within the quarry, two transects were laid out across the northern area so as to include the maximum diversity of habitat. The first (XY on Fig.1) was divided into four main areas: -

(a) Top terrace (T.T.), comprising a flat area of predominantly *Sesleria caerulea* grassland.

(b) Middle terrace (M.T. on Fig.2), consisting of a compacted former track, with a low cover of grasses and herbs.

(c) Lower slope (L.S. on Fig.2), made up of a scree of limestone rubble fairly well covered with vegetation.

(d) Erosion slope (E.S. on Fig.2), a sparsely vegatated steep slope of limestone dust, still undergoing considerable erosion.

The second transect (N.S. on Fig.2) covered a thickly vegetated slope on which the dominant plants were *Urtica dioica*, *Galium aparine*, and *Rubus*, with *Lamium album* also important in May and early June.

From the beginning of June until early August the numbers of snails within m^2-quadrats taken on alternate sides of the transect were counted at fortnightly intervals. Snails were found by thorough searching of the vegetation and other cover such as stones and crevices in the rock. To ensure that most of the snails present were found, counts were made soon after sunrise before the animals retreated into their daytime cover.

II.2. Snail population Structure and Life Cycles.

The breadth of each snail found in the distribution study was measured using Vernier calipers, and the population at each sampling occasion was then divided into size classes of mm intervals for H. aspersa and half mm intervals for C. nemoralis. For each size class the cumulative percentage of the population was calculated and this was then plotted against the size class on probability paper, following the method of Harding (1949). From these graphs the mean sizes of adult and juvenile snails at fortnightly intervals could be obtained, thus giving a picture of the rate of growth. In addition the proportions of adults and juveniles in the population at these intervals could also be worked out.

In order to find out more about the early life history of snails, several adults of each species found mating in the field were kept in the laboratory until they had laid their eggs. These were then timed until hatching, and the sizes of newly hatched juveniles measured.

II.3. Vegetation Analysis.

The vegetation of the transects was analysed in mid-August after the studies on snail distribution and population structure had been completed. The technique used was that of cropping all above ground vegetation in every third quadrat along the main transect, and every fifth on the nettle slope. In most cases, because of the quantity of material involved, only a 50cm x 50cm quadrat was cut, this square being situated more or less centrally within the m^2 in which the snails had

been sampled. The cut vegetation was then sorted into five categories ; (a) dead monocot, (b) live monocot, (c) dead dicot, (d) live dicot and (e) bryophyte, the dead material including senescent as well as fallen leaves. The sorted fractions were dryed at 80° C for 24hrs., or 48hrs in the case of large quantities. The resulting dry material was then weighed and the figures expressed in terms of dry wt./m^2 to give the standing crop for each of the five fractions.

II.4. Snail Feeding.

(a) Faecal Analysis.

Food preferences have been studied by means of identifying plant material in the faeces of a wide variety of herbivorous animals, including many mammals, crickets, grasshoppers, and molluscs. Almost every study has involved a different method of mounting and examining the faeces. Hansson (1970) reviewed several of the more widely used techniques and his recommend--ations have been followed in this investigation.

Snails were collected on several occasions during July and August from the immediate vicinity of the transects, though not necessarily from the quadrats sampled for snail density. In the laboratory they were individually isolated with filter paper for food, and left for 24hrs. Their faeces were then coll--ected, placed in a centrifuge tube with about 10mls of water and shaken vigourously for several minutes to separate the fragments. This acheived a more satisfactory separation than teasing on a slide as suggested by some authors. The staining and mounting technique used was that recommended by Hansson

(1970). The separated fragments were centrifuged, the water poured off, and the fragments stained with a few mls of Acid Haemalum for 10 minutes. After two washes with distilled water the fragments were left in alkaline alcohol for 1 minute to bring out the stain, and washed again. A representative sub-sample was then mounted on a microscope slide in Berlese's Gum Chloral, so as to give a uniform covering over the slide that could be easily scanned and counted.

It had been hoped that each plant fragment would be identifiable from epidermal characteristics, and so epidermal impressions of most of the plants found on and near the transects were made using cellulose acetate. These impressions were mounted in glycerine with a drop of Methylene Blue to increase the contrast, and photomicrographs at 100x were made. Figures 5 and 6 show a typical monocot and typical dicot respectively. Unfortunately it was found difficult to identify fragments of plant material in the snail faeces, since the epidermis was not often separated from the underlying layers of cells. It was however possible to distinguish between live and dead material, the former retaining traces of chlorophyll, and between monocot and dicot fragments, by the shapes of the cells. Bryophytes were easily identified since they pass through the snail gut almost unchanged. Therefore the numbers of fragments in each of the five categories, dead monocot, live monocot, dead dicot, live dicot and bryophyte were recorded when the slides of faecal material were examined at magnifications of 100x.

Fig. 5 Photomicrograph of Cellulose acetate impression of lower surface of Carex flacca leaf (x 100).

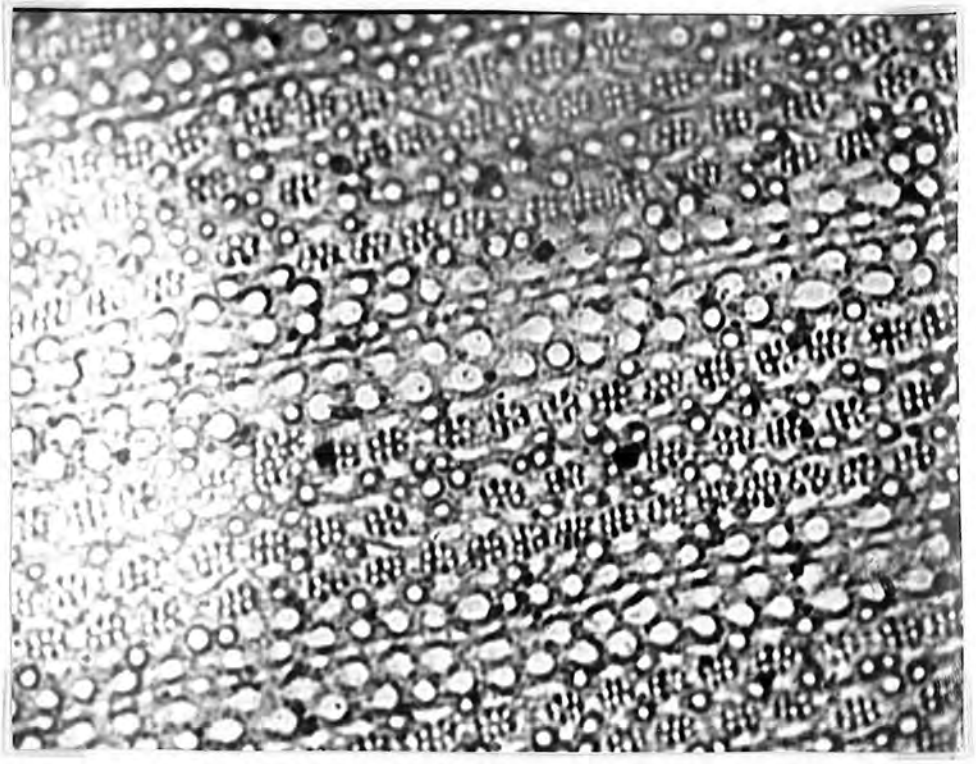
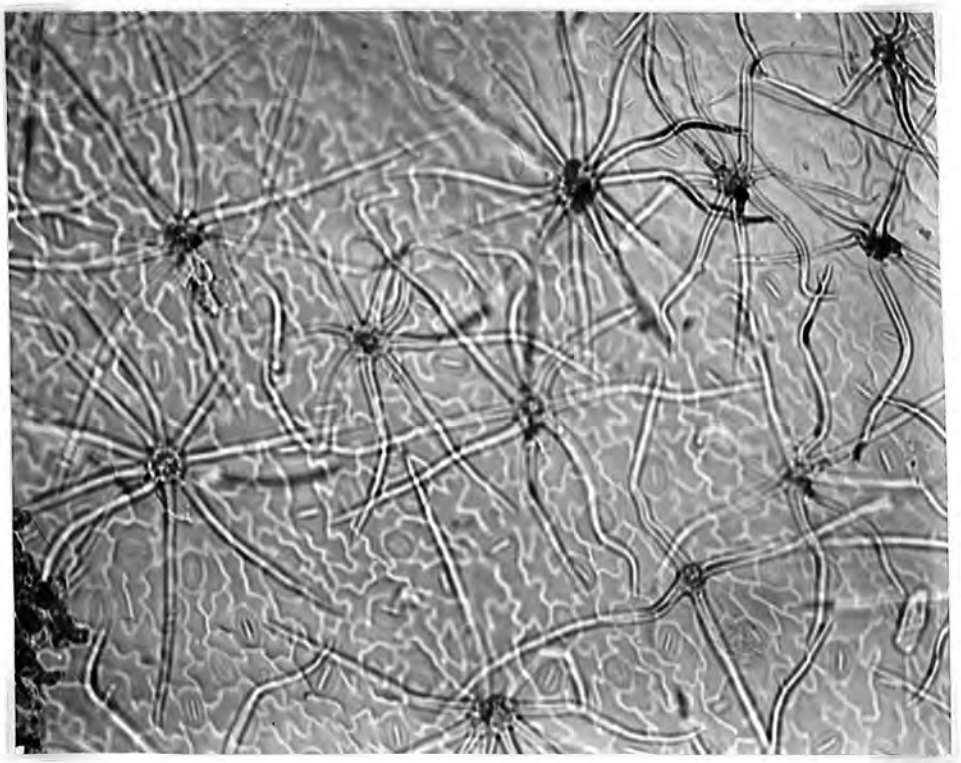


Fig. 6 Photomicrograph of Cellulose acetate impression of lower surface of Helianthemum chamaecistus leaf (x 100).



(b) Palatability Experiments.

The palatability of different plant species was tested by presenting individual snails with equal amounts of plant material and a reference material that they were known to eat readily, in this case filter paper. The technique is basically that of Grime et al. (1968), with several minor modifications. Individual snails were put into small plastic containers with equal amounts of plant material and filter paper against opposite walls. Dicots were presented as 20mm x 20mm squares for broad leaved species, 10mm x 40mm strips for narrower leaved species, and in the case of species with very small leaves, an appropriate number of whole leaves. Monocots were given as strips of whole blades, the length being chosen according to the width, so as to give a constant area. The pieces of filter paper were each presented in the same shape as the accompanying plant material. Both plant squares and filter paper were wetted so that the level of humidity in the containers was high enough for continuous snail activity. The experiments each lasted 24 hours, being carried out in a laboratory where temperatures ranged from about 14 C at night to about 19 C by day. The snails were then removed and the areas of paper and plant material eaten were measured using graph paper. Between experiments the snails were kept on filter paper rather than being starved for 24 hours as done by Grime et al. (1968). It was felt that these conditions, with varying daily temperatures were nearer to those experienced by snails in their natural habitat than conditions of constant temperature and intermittent starvation.

Each plant species was presented to 10 different snails and from the results a Palatability Index was calculated as :-

$$\text{Palatability Index (P.I.)} = \frac{\text{Area of plant eaten, mm}^2}{\text{Area of paper eaten, mm}^2}$$

The experiments were carried out for both H. aspersa and C. nemoralis first with live material from 41 species of plant and then with leaves from 33 of the same species. Dead material was obtained direct from the field in the case of monocots, and by drying live leaves for several days and then soaking them overnight with dicots.

(c) Feeding Observations.

Records were also made of all snails found feeding in the study area during the course of other field work. Wolda et al. (1971) and Grime and Blythe (1969) considered that if a snail was found resting on a plant it probably fed on that species, but their studies must have been carried out solely during the day when the snails were resting in shelter. In the present investigation feeding was only recorded if actually observed in an active snail. In general feeding snails have their foot and body extended, but remain stationary, and since they attack the edges of leaves, lifting the animal reveals any removed material. In each case the species of snail, the plant species and the condition of the leaf, live or dead/senescent was noted.

II. 5. Ingestion and Assimilation by Snails.

With the object of estimating the amount of plant material removed from the field during a given period by the snail population, measurements of ingestion and assimilation rates of the snails were made. In order to obtain a more realistic

measure of ingestion than a direct laboratory result, a figure was calculated using faeces production in the field and assimilation rates obtained in the laboratory.

The assimilation rates were measured using the method devised by Phillipson (1960) for Opilionids, and adapted by Mason (1970) for various species of woodland snail. Snails were collected in the field, isolated in plastic containers and fed on filter paper for two or three days, so that all traces of plant material had been eliminated from their guts, and their faeces were white. The filter paper was then removed and the snails given a known weight of plant food which had been kept at 100% humidity for several hours. After 24 hours the remaining plant material was taken out and weighed, being replaced by more filter paper, while all white faeces were also removed. When more white faeces appeared about 24 hours later all dark faeces, green or brown from live or dead food respectively, were removed, vacuum dried at 60 C for two days and weighed. Meanwhile, known fresh weights of the plant species used were also vacuum dried and reweighed to give a fresh weight : dry weight ratio. From this the dry weight of food eaten was calculated, and thence the percentage assimilation obtained from the formula :-

$$\% \text{ assimilation} = \frac{\text{Dry wt. food eaten} - \text{Dry wt. faeces produced}}{\text{Dry wt. food eaten}} \times 100$$

Faeces production in the field was measured by collecting snails and isolating them in the laboratory with filter paper to feed on. After 24 hours their dark faeces was removed, dried in a vacuum oven and weighed. 15 snails of each species were

investigated and a mean figure obtained. From this figure, using the laboratory estimates of assimilation rates a measure of the ingestion rates in the field could be obtained.

II.6. Mean Temperature Measurement.

Throughout the study period the mean temperatures at eight different points in the quarry were measured using the method of Berthet (1960), based on the rate of inversion of sucrose to glucose and fructose. Sucrose and buffer solutions were made up, mixed together and immediately divided into approx--imately 15ml portions in small screw top bottles, which were stored in a deep freeze until required in the field. These bottles were transported to and from the quarry in a vacuum flask containing solid CO_2, and were left out for seven days at a time, which gave figures close to the optimum amount of inversion. The degree of inversion is measured by the change in the angle of rotation of polarised light passed through the solution, indicated by a polarimeter. The mean temperature during the week could then be calculated using the following equations :-

(i) $T = \frac{5854}{Y - \log. x}$ where T = absolute temperature
Y = a constant, empirically determined.

and (ii) $x = \frac{1}{t} \log. \left(\frac{a_o - b}{a - b}\right)$ where t = time in field in days
a_o = initial rotation
a = final rotation
b = rotation at complete inversion.

Y was found by leaving three tubes for a week at constant temperatures of 5°, 10°, and 15° C, and then determining the rotation.

b was obtained by leaving several tubes at room temperature for a month and then measuring the rotation.

The experimental tubes were placed at eight different points in the quarry (see Fig.2),on or very close to the transect, and were concealed within the vegetation so that the temperature measured was close to that of the snails' micro--habitat.

II.7. Shelter for Snails.

Shelter is clearly one of the most important features of the environment as far as animals susceptible to desiccation and predation are concerned.However it is difficult to measure quantitatively,since snails use a variety of different features including vegetation,rocks,crevices and burrows,in which to conceal themselves.Any measurement must therefore be a subjective one,and so for this study a 0 - 5 scale was used,with 0 indicating no suitable shelter for snails,and 5 showing the maximum amount found on the transects.Each quadrat in the two transects was thus awarded a figure on this scale.

III. RESULTS

III.1. Snail Density and Distribution.

The numbers of snails found in each quadrat of the maim transect throughout the study period are shown in Figures 7 and 8 for H.aspersa and C.nemoralis respectively.Figures 9 and 10 show the results for the two species on the nettle slope transect.It is clear that there are considerable differences in distribution between the two species,and that neither is distributed randomly along the transects.C. nemoralis is most abundant in two areas of the main transect : on the top terrace (quadrats 1 - 13) and on the lower slope (quadrats 29 - 40).On the nettle slope (quadrats A1 - A33) this species is distributed fairly evenly with rarely more than two or three snails /m^2,while on the middle terrace (quadrats 14 - 28) and the erosion slope (quadrats 46 - 73) it is almost completely absent.H.aspersa on the other hand is found in small numbers throughout the main transect,with a slight peak on the lower slope,while on the nettle slope this species is very abundant,particularly on the lower and central parts.

The mean densities for each area of the transects is shown in Table 1.

Table 1.Mean numbers of C.nemoralis,Haspersa and total snails per m^2,June - August,for different areas of the study site.

Area	C.nemoralis	H.aspersa	Total
Top terrace	2.32	0.4	2.72
Middle terrace	0.08	0.2	0.28
Lower slope	0.75	0.57	1.32
Erosion slope	0.05	0.22	0.27
Nettle slope	0.9	2.9	3.8

Fig.7 Numbers of H. aspersa found / m^2 quadrat on main transect, June - August, 1974.

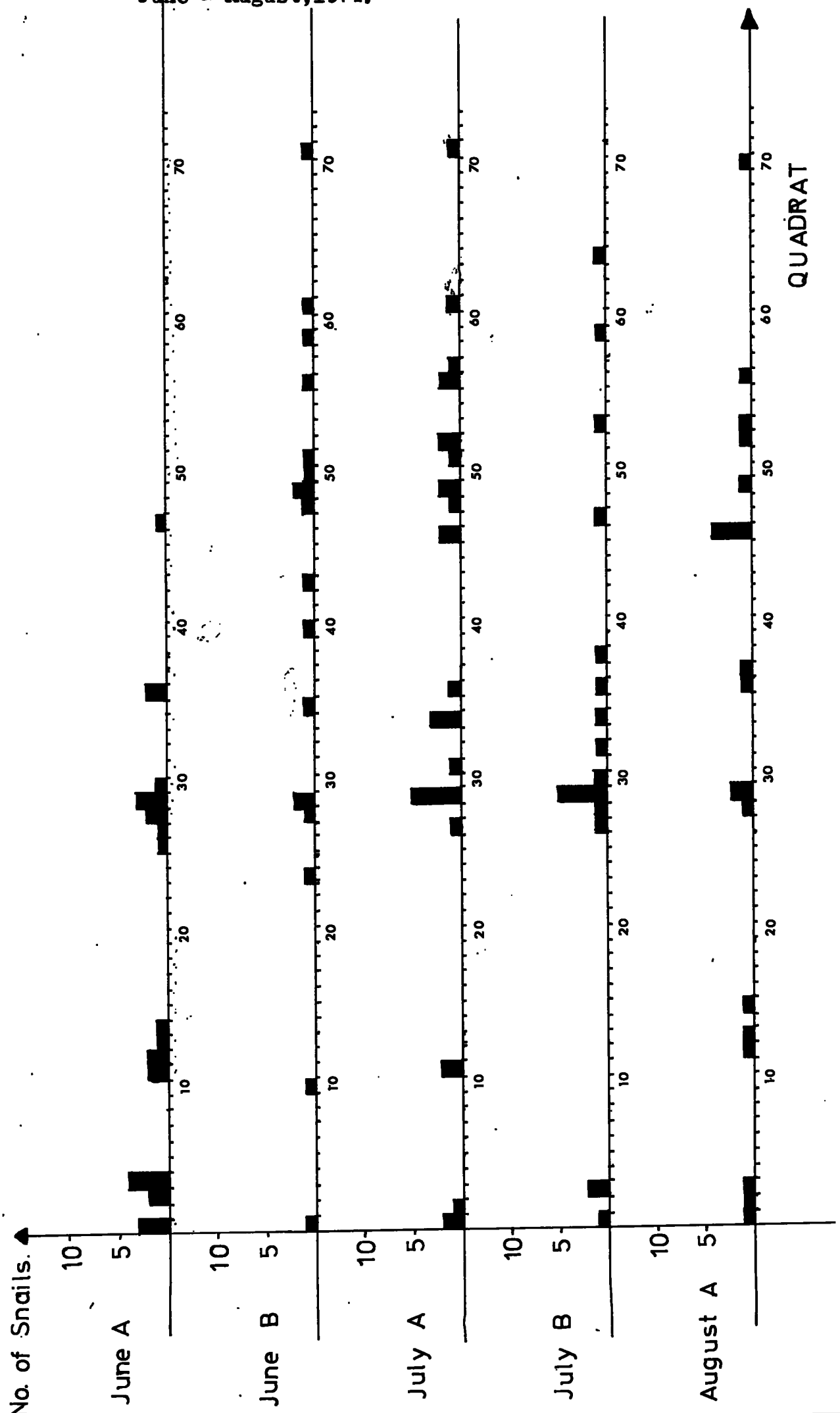


Fig. 8. Numbers of C. nemoralis found / m² quadrat on main transect June - August, 1974.

Fig. 9. Numbers of H. aspersa found / m^2 quadrat on nettle slope, June - August, 1974.

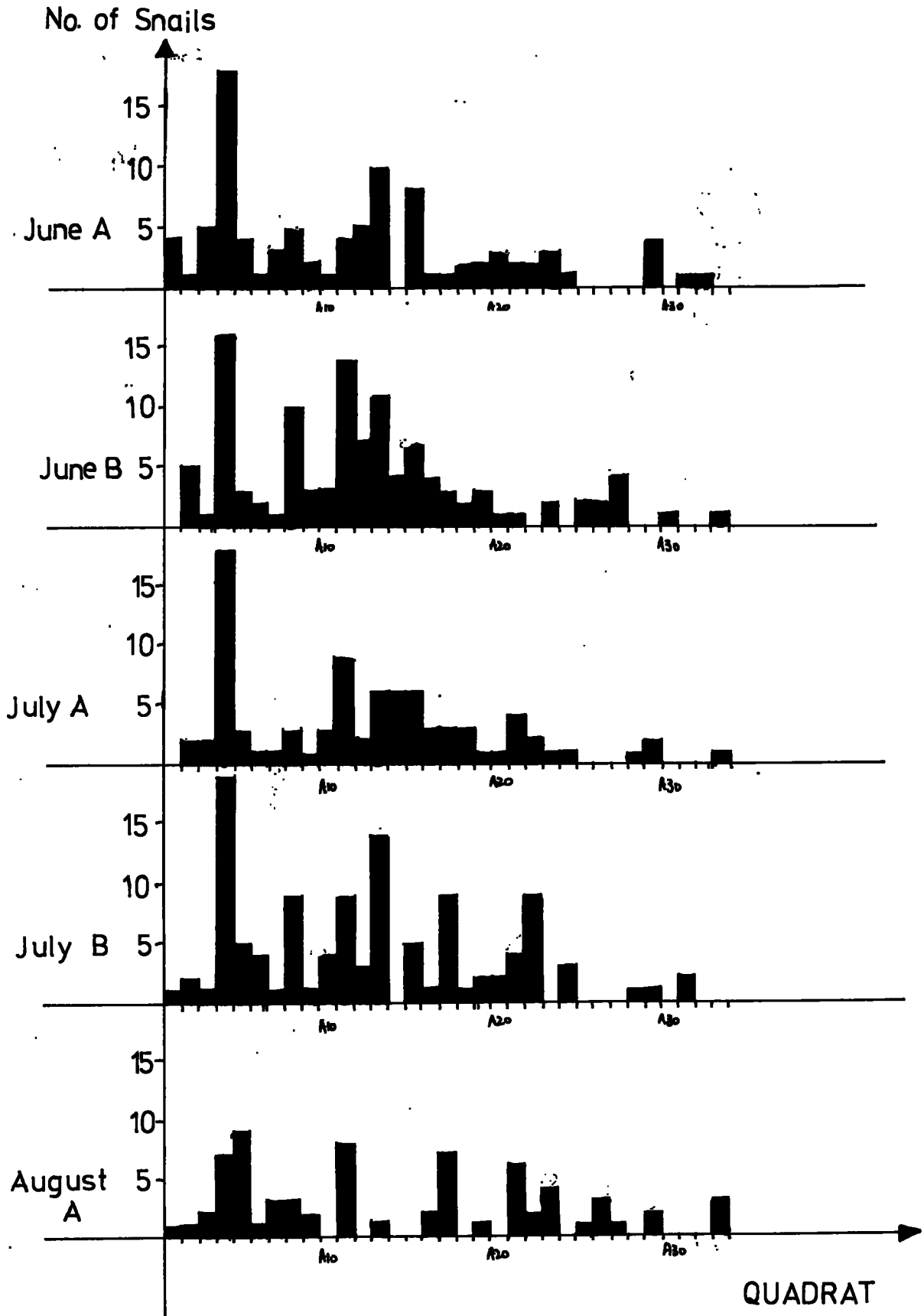
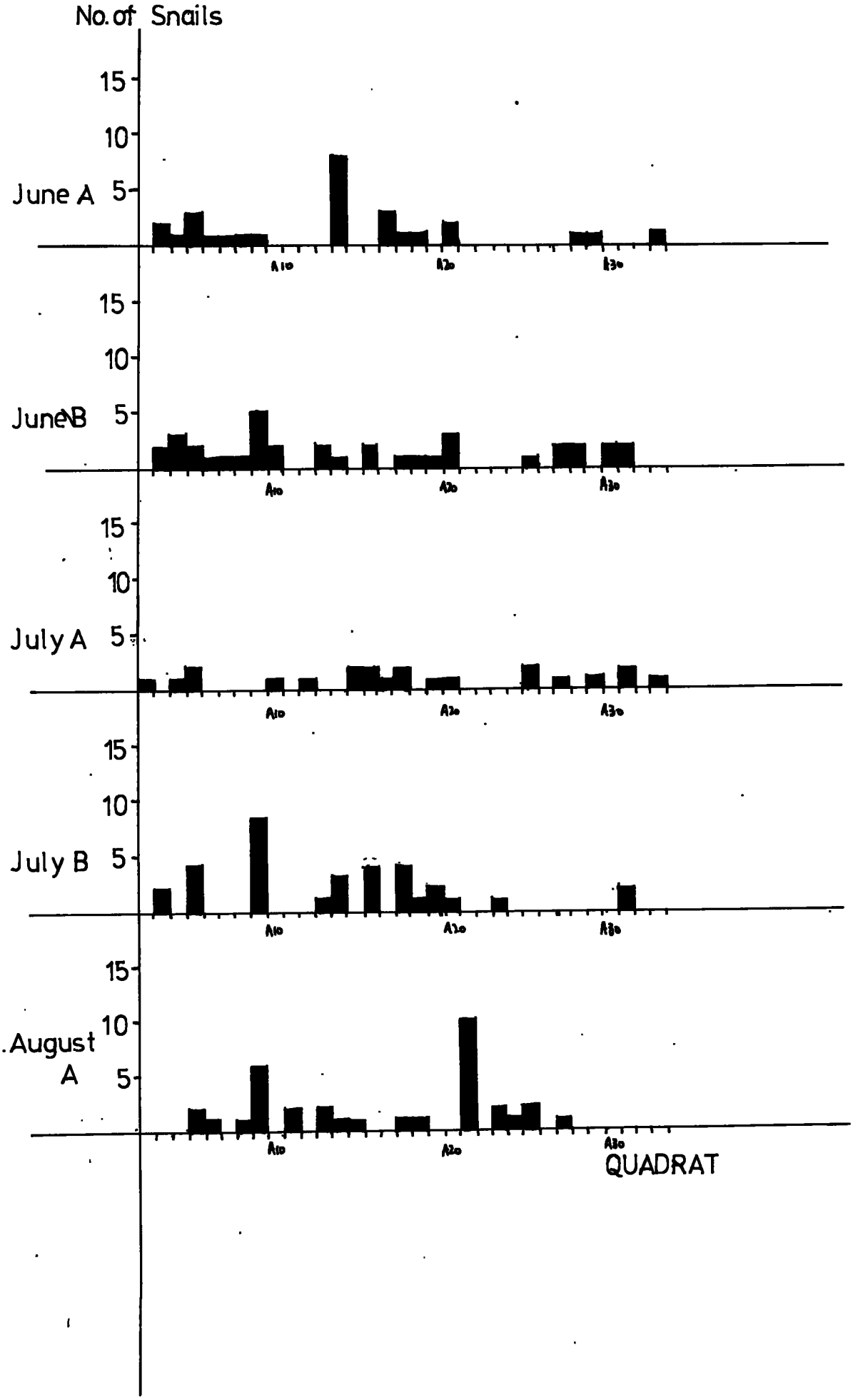


Fig.10. Numbers of C.nemoralis found / m^2 quadrat on nettle slope June - August,1974.



Thus the highest density of snails is on the well vegetated nettle slope, while the lowest densities are on the very sparsely vegetated middle terrace and erosion slope. Seasonal changes in density appear to be very small, with a slight reduction in numbers found in August.

A summary of the data in Figures 7 to 10 is given in Tables 2 (a) and (b), which show the mean number of snails per quadrat for the two species both separately and combined, on the main transect and the nettle slope respectively.

III.2. Snail Population Structure and Life cycles.

(a) Helix aspersa.

A typical plot of size class against cumulative frequency (Fig.11) shows that the population of H. aspersa was clearly divided into two sub-populations, which can be regarded as adults and juveniles, though the former contained a few sub-adult individuals. The numbers and relative proportions of these two groups throughout the sampling period are shown in Table 3.

Table 3. The numbers and percentages of juvenile and adult snails in the population of H. aspersa collected at fortnightly intervals within the study area, June-August, 1974.

Date	Juveniles Nos.	%	Adults Nos.	%	Total Nos.
June A (4th-6th)	47	38	76	62	123
June B (18th-20th)	64	48.5	68	51.5	132
July A (2nd-4th)	51	45	63	55	114
July B (16th-18th)	45	34	88	66	133
August A (1st-3rd)	20	22	70	78	90

Table 2. Mean no. of snails/ m^2 quadrat, June-August.

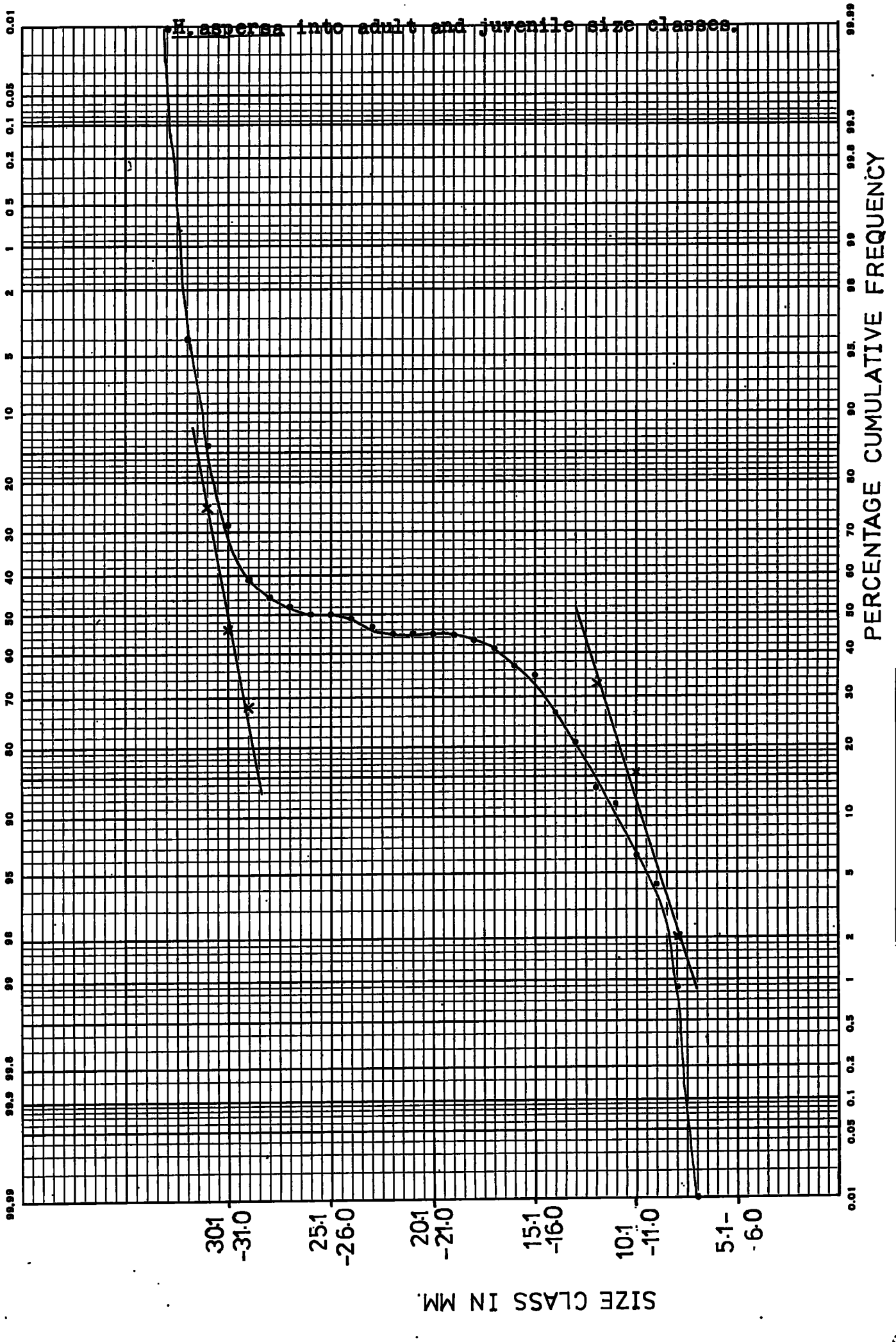
(a) Main Transect.

Quadrat	Cepaea	Helix	Total	Quadrat	Cepaea	Helix	Total
1	6.2	1.6	7.8	38	0.2	0.2	0.4
2	4.4	0.4	4.8	39	0.2	0	0.2
3	4.8	1.0	5.8	40	0	0.2	0.2
4	2.8	0.8	3.6	41	0.2	0	0.2
5	0.2	0	0.2	42	0	0	0
6	0.8	0	0.8	43	0	0.2	0.2
7	1.6	0	1.6	44	0	0	0
8	0.4	0	0.4	45	0	0	0
9	1.6	0	1.6	46	0.2	1.2	1.4
10	0.4	0.2	0.6	47	0	0.4	0.4
11	4.4	0.8	5.2	48	0	1.0	1.0
12	2.6	0.6	3.2	49	0	0.4	0.4
13	0.4	0.4	0.8	50	0.6	0.2	0.8
14	0.2	0.2	0.4	51	0	0.4	0.4
15	0	0.2	0.2	52	0.2	0.6	0.8
16	0	0	0	53	0	0.4	0.4
17	0	0	0	54	0	0	0
18	0	0	0	55	0	0	0
19	0	0	0	56	0.2	0.8	1.0
20	0	0	0	57	0.2	0.2	0.4
21	0	0	0	58	0	0	0
22	0	0	0	59	0	0.4	0.4
23	0	0	0	60	0	0	0
24	0	0.2	0.2	61	0	0.4	0.4
25	0	0	0	62	0	0	0
26	0	0.2	0.2	63	0	0	0
27	0	0.6	0.6	64	0	0.2	0.2
28	0.6	1.0	1.6	65	0	0	0
29	0.8	3.4	4.2	66	0	0	0
30	0.8	0.4	1.2	67	0	0	0
31	1.2	0.2	1.4	68	0	0	0
32	1.8	0.2	2.0	69	0	0	0
33	1.8	0	1.8	70	0	0.2	0.2
34	1.2	0.8	2.0	71	0	0.2	0.2
35	0.2	0.2	0.4	72	0	0	0
36	0.2	1.0	1.2	73	0	0	0
37	0.6	0.2	0.8				

Table 2. (b). Nettle slope.

Quadrat	C. nemoralis	H. aspersa	Total
A1	0.2	1.2	1.4
A2	1.2	2.4	3.6
A3	1.0	2.2	3.2
A4	2.6	15.6	18.2
A5	0.6	4.8	5.4
A6	0.4	1.8	3.2
A7	0.6	1.8	2.4
A8	4.0	6.0	10.0
A9	0.6	1.8	2.4
A10	0.4	2.2	2.6
A11	0.2	8.8	9.0
A12	1.0	3,4	4.4
A13	1.6	8.4	10.0
A14	0.6	2.0	2.6
A15	1.6	5.2	6.8
A16	0.8	2.2	3.0
A17	1.8	4.6	6.4
A18	0.8	1.6	2.4
A19	0.8	1.8	2.6
A20	1.4	1.4	2.8
A21	2.0	3.4	5.4
A22	0	3.0	3.0
A23	0.6	2.0	2.6
A24	0.2	1.0	1.2
A25	1.0	0.6	1.6
A26	0	1.0	1.0
A27	0.8	1.0	1.8
A28	0.6	0.4	1.0
A29	0.4	1.8	2.2
A30	0.4	0.2	0.6
A31	1.2	0.6	1.8
A32	0	0.2	0.2
A33	0.4	1.0	1.4

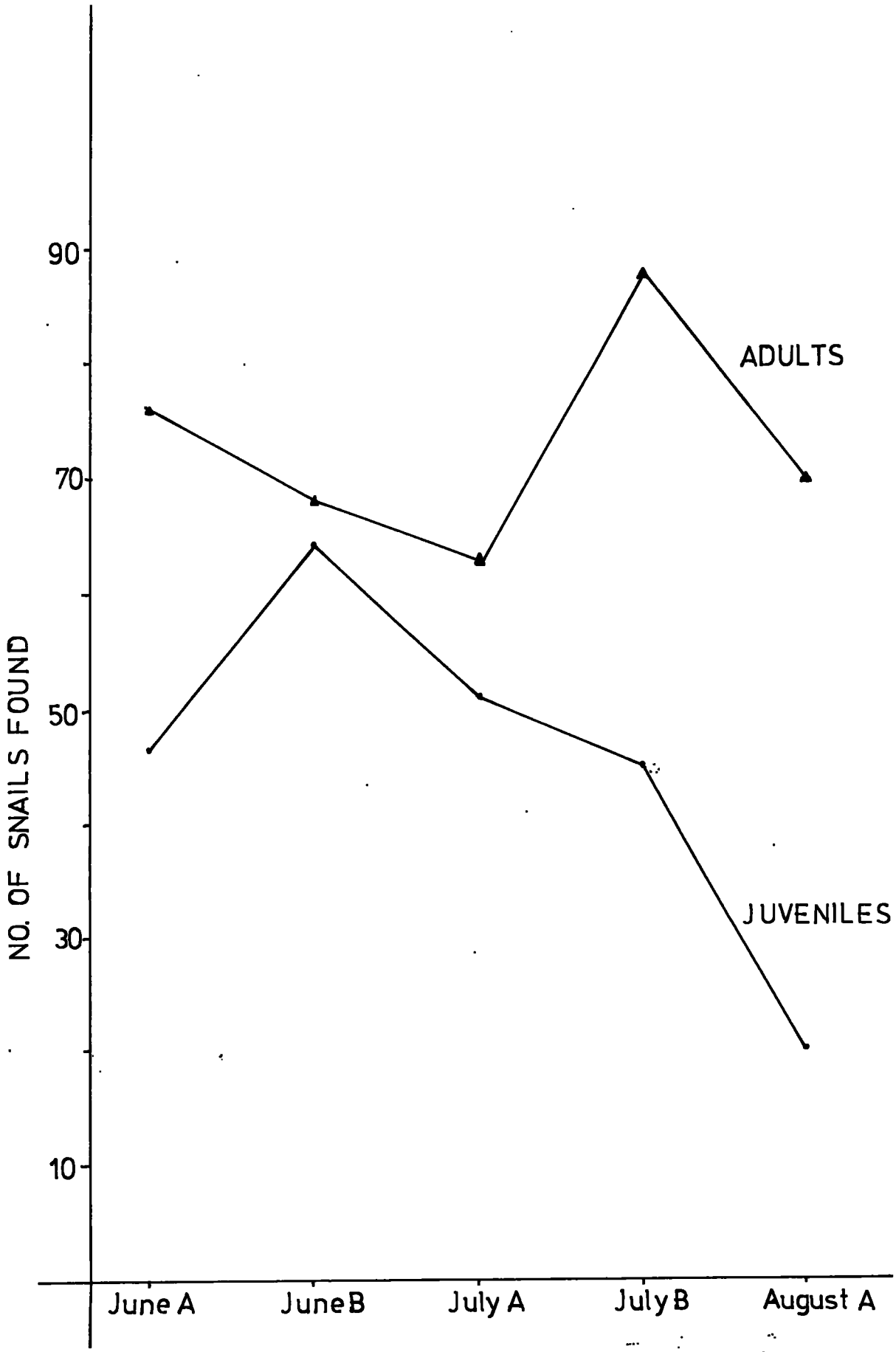
Fig.11. Plot of size class in mm against cumulative % frequency for July A,1974 to show division of population of H.aspersa into adult and juvenile size classes.



It is clear that these figures do not give an accurate picture of the structure of the population, since in each case the number of adults exceeds the number of juveniles, whereas in a population where adults live only one or two years and fecundity is high, a large preponderance of juveniles would be expected during and immediately after the breeding season. this discrepancy is due to the small size of the youngest snails which makes them more difficult to find than the larger adults, particularly in dense vegetation. However it is likely that the trend shown in the figures with the number of juveniles decreasing through the summer (Fig.12) is a true reflection of the life cycle of the species. This could be due to either predation of the small, thin shelled juveniles, or the fact that juveniles are growing into the adult size group. It will be shown below that predation is probably more important than growth in bringing about this reduction of numbers.

From the series of plots like Figure 11, together with laboratory breeding results and field observations it was possible to build up a picture of the snail's life cycle. Mating occurs mainly in spring and summer and about thirty eggs are laid in a hole in the ground excavated by the foot, approximately three weeks later. Hatching occurs after about twenty five days in the laboratory, though under the cooler conditions in the field the incubation time would be nearer to thirty days. Newly hatched snails are 4 to 4.5 mm in breadth and in the laboratory at least tend to remain aggregated close to their hatching place for some time. This could render them very open to predation.

Fig. 12. The total numbers of adult and juvenile H. aspersa found within the study area at fortnightly intervals, June - August.

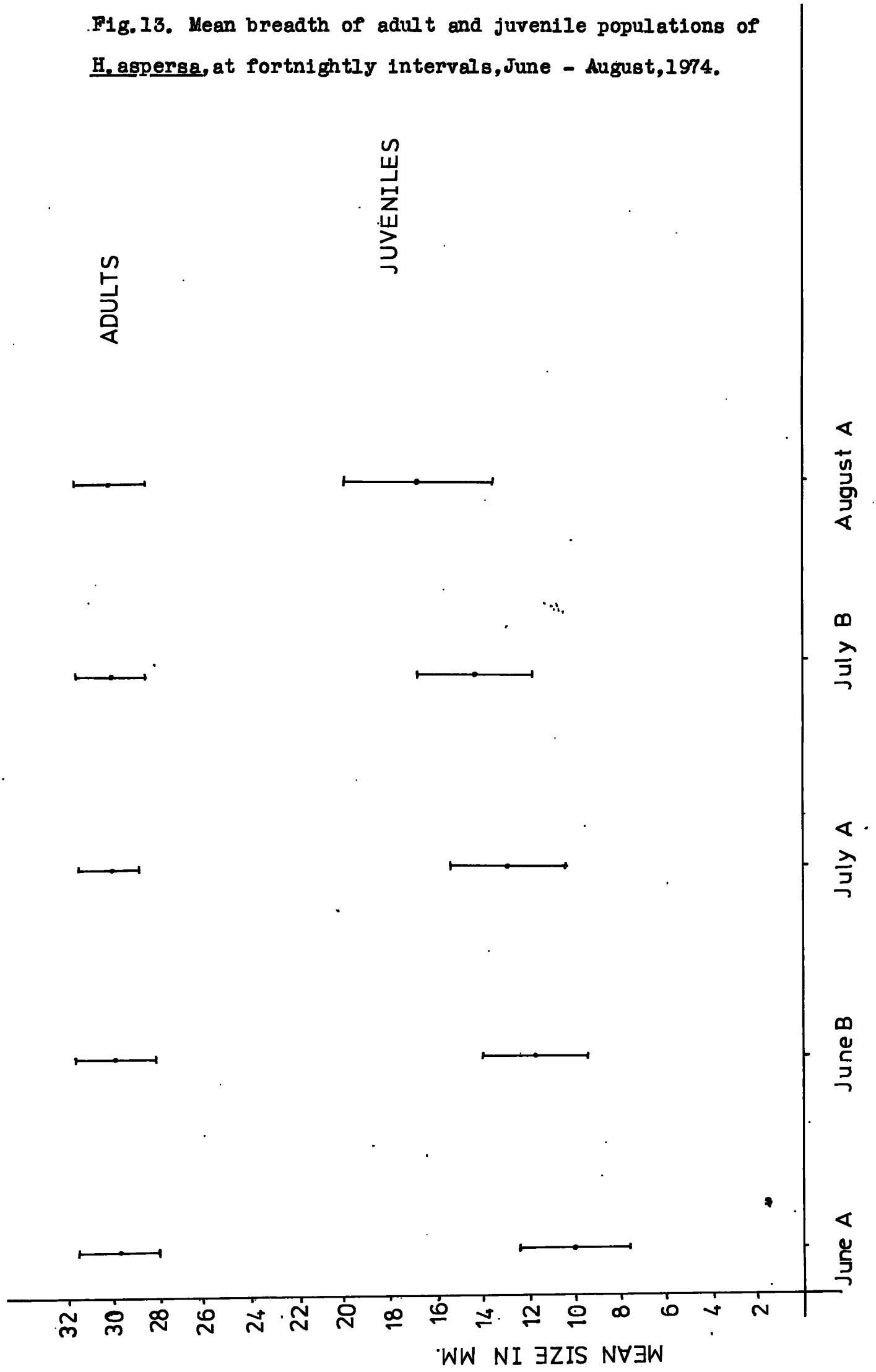


A picture of growth was obtained from the cumulative frequency plots, by finding the mean breadths of the adult and juvenile sub-populations using the method of Harding (1949). The results of mean sizes with standard deviations were plotted against time (Fig. 13) and show a steady increase in the size of the juveniles through the summer, with the changes in each case being significant (t = 4.18, 2.64, 2.74, and 3.1 respectively for the four intervals). In contrast there was no significant change in the mean size of the adult population.

The division of the population into the two well separated groups indicates that recruitment occurs almost entirely at one time. However, the size of the largest juveniles in early June and the field growth rate estimates from increase in mean size suggest that these individuals could not have hatched this year, but must have been the product of an autumn laying in 1973. Thus it seems probable that reproduction in H. aspersa is not confined to spring and early summer, as suggested earlier, but also occurs in autumn. Since the snails hibernate throughout the winter (Taylor, 1913 : Ellis, 1926), the two periods of reproduction cannot be separated by the examination of the size class distribution of a sample.

The estimated growth rates indicate that this species does not attain maturity until its second summer, and it is likely that the estimate of life span of 2 years given by Taylor (1913) and Ellis (1926) is too short. Mortality must be mainly due to predation, though some adult snails were found dead for no apparent reason, with desiccated bodies within their shells. Juveniles will certainly be much more susceptible to predation than adults due to their smaller size and thinner shells,

Fig.13. Mean breadth of adult and juvenile populations of H. aspersa, at fortnightly intervals, June - August, 1974.



which will enable a wider variety of predators to attack them. Juvenile mortality due to badgers, small mammals, birds, frogs and toads, and the larvae of carabid beetles is probably the main factor behind the drop in numbers of juveniles found during the summer. Adult H. aspersa are only attacked commonly by Song Thrushes, badgers and brown rats, though only evidence for the first was found at Bishop Middleham. There is a peak in Song thrush predation on snails during June, July and August, (Goodhart, 1958), (Davies and Snow, 1965), (Cameron, 1969), and this could account for the smaller numbers of adult snails found in August.

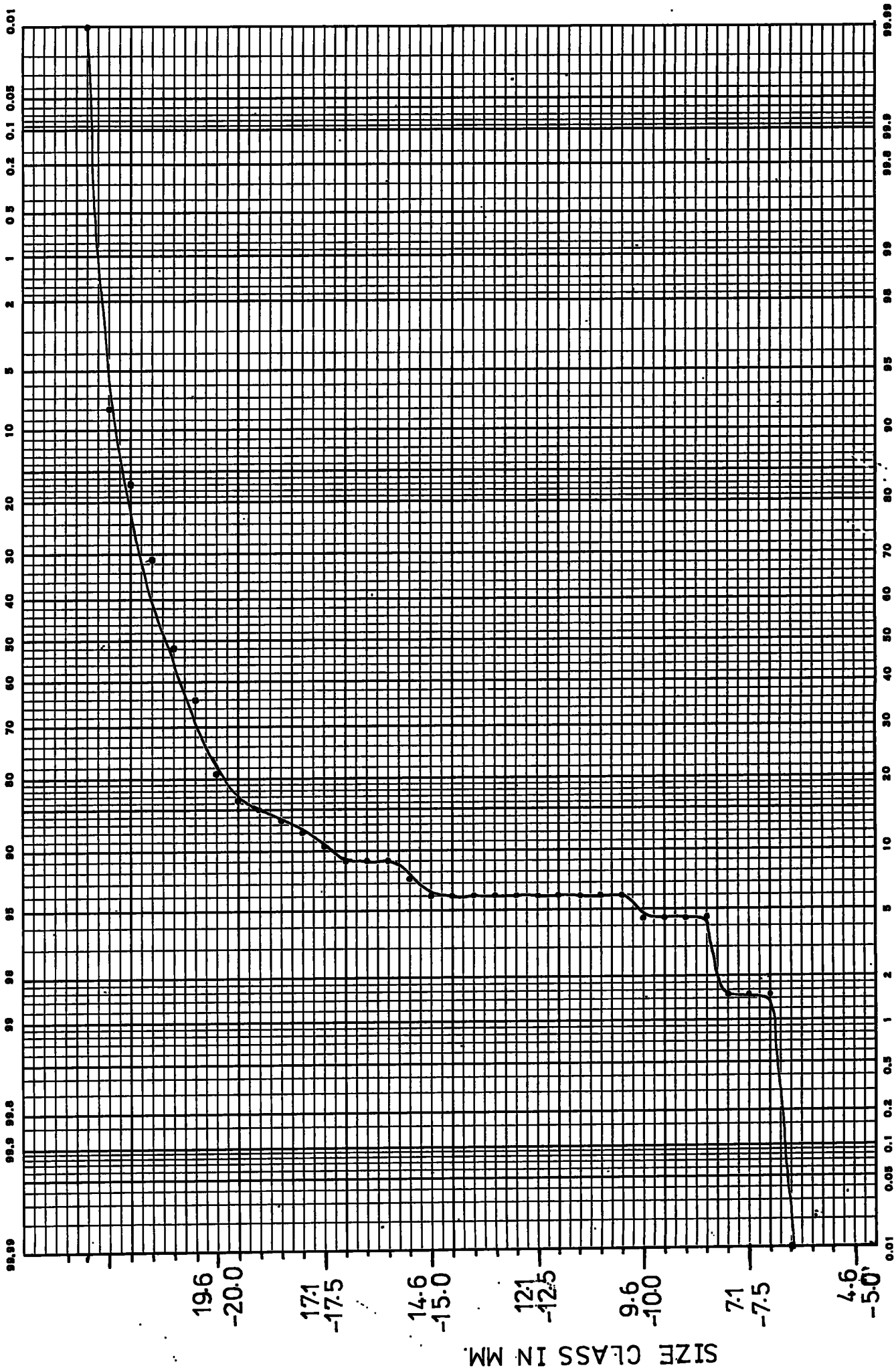
(b) C. nemoralis.

Figure 14 shows the plot of size class against percentage cumulative frequency for C. nemoralis in early August. This is typical of all the five plots obtained, and in each case it is impossible to confidently divide the population into sub-populations corresponding to different age classes. It is however possible to divide the snails into adults (18.5mm or more in breadth) and sub-adults which are smaller than this. (See Table 4) Adults are characterised by the presence of a black lip round the edge of the shell, which is absent in juveniles.

Table 4. The numbers and percentages of sub-adult and adult snails in the population of C. nemoralis collected at fort-nightly intervals within the study area, June-August, 1974.

Date	Sub-adults		Adults		Total
	Nos.	%	Nos.	%	Nos.
June A	25	37	43	63	68
June B	21	24	66	76	87
July A	12	17	58	83	70
July B	13	17	62	83	75
August A	9	14	57	86	66

Fig.14.Plot of size class in mm against cumulative percentage for August 1974,for C.nemoralis.



The proportion of sub-adults again drops dramatically through the summer due probably to a combination of predation and sub-adults growing to join the adult size class. Also the proportion of sub-adults is very much lower than expected, and much lower than the figures obtained for H. aspersa, as a result of the smaller size of this species, which makes young snails even more difficult to locate. Thus the confused appearance of the cumulative frequency plot could be due to the low numbers of sub-adults found on each sampling occasion. However it could also be due to recruitment taking place throughout the summer rather than on one or two discrete occasions as found with H. aspersa.

The life cycle of C. nemoralis is very similar to that of H. aspersa though the incubation period is rather shorter, at about twenty five days, and it is probable that young hatching early in spring may breed the following autumn. The time taken for development may be assessed by breaks in the banding pattern, caused by cessation of growth during hibernation. Most adult C. nemoralis found showed two such breaks, but some were found with only one. Thus a life span of $2\frac{1}{2}$ to 3 years is probable.

III. 3. Vegetation Analysis.

The standing crops, divided into the five categories, Bryophyte, live dicot, dead dicot, live monocot, and dead monocot, are shown in Figures 15 and 16 for the main transect and the nettle slope respectively. Many of the changes in the vegetation along the transects can be seen from these Figures and can

Fig.15. Standing crop in g.dry wt./ m^2 quadrat on the main transect, August, 1974.

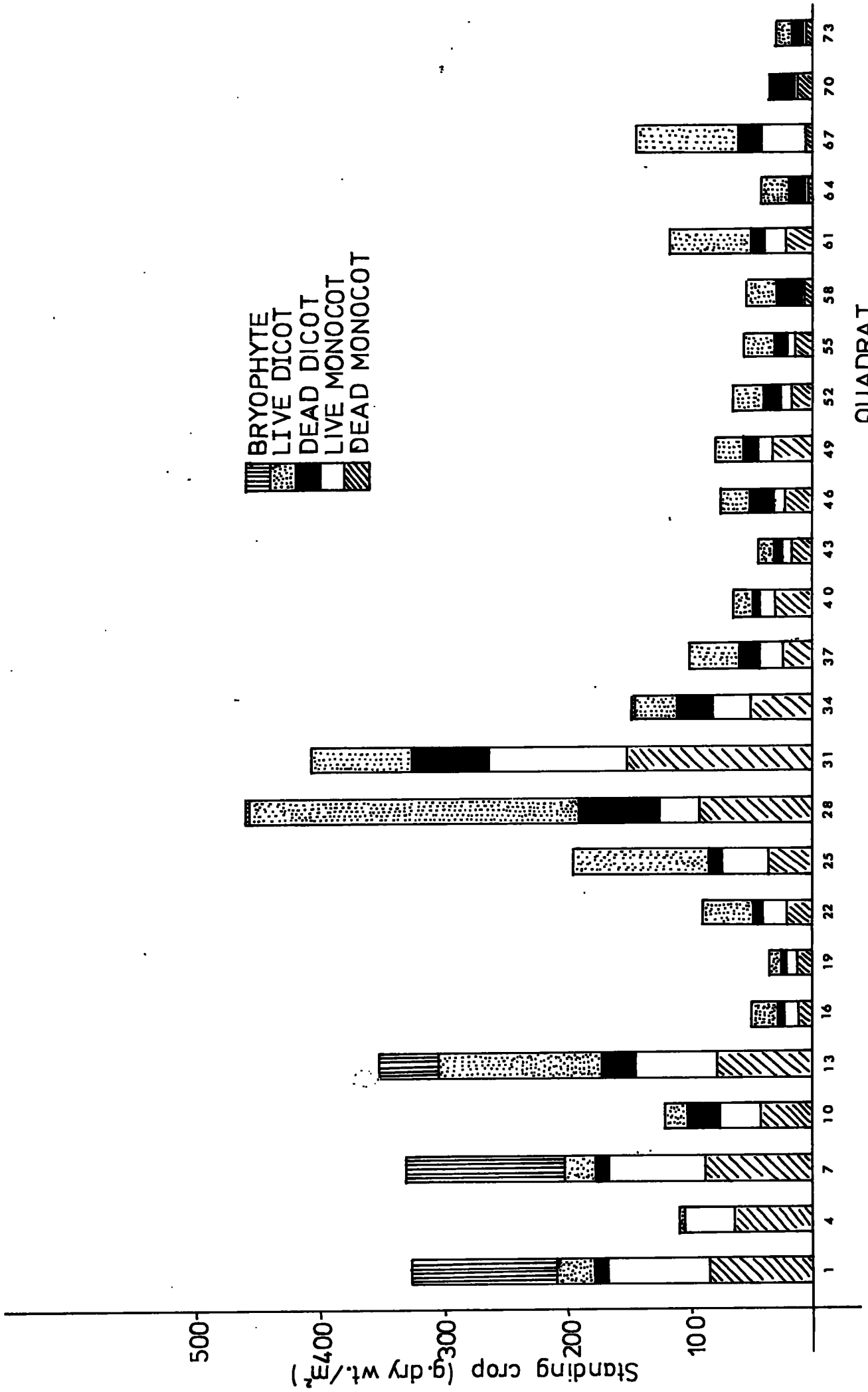
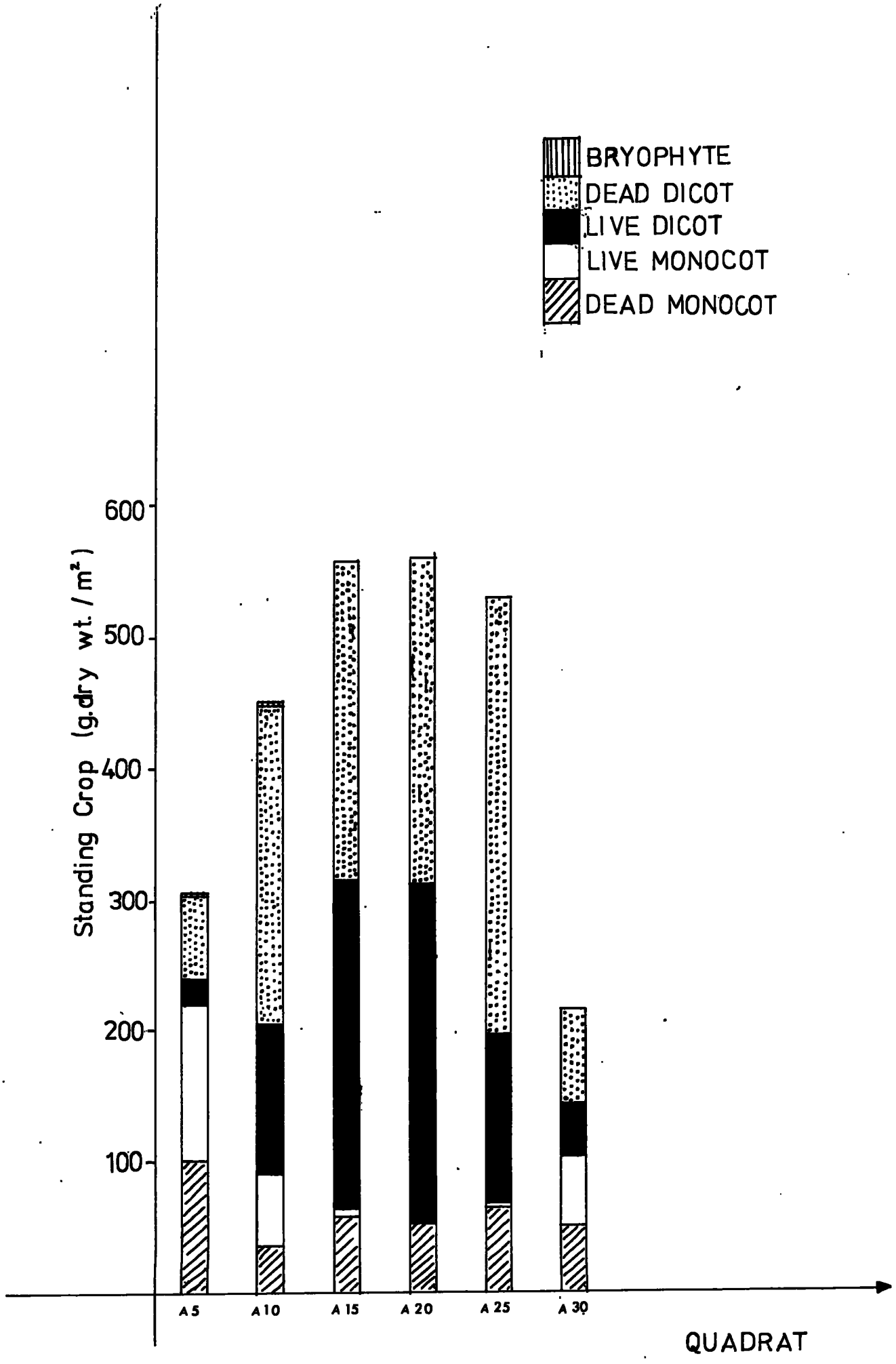


Fig.16. Standing crop in g.dry wt./ m^2 quadrat on the nettle slope, August 1974.



best be described by considering each of the five principal areas in turn: -

(i) Top terrace (quadrats 1 - 13). Total standing crop is high, made up mostly of Sesleria caerulea underlain by a carpet of moss.

(ii) Middle terrace (quadrats 16 - 28). Typified by a lower standing crop, with almost equal amounts of dicots and monocots and no bryophytes. The higher standing crops in quadrats 25 and 28 are due to high densities of Ononis repens and Leontodon hispidus respectively, which grow well on the less compacted soil at the edge of the terrace.

(iii) Lower slope (quadrats 29 - 40). The standing crop decreases gradually down the slope as the substrate becomes increasingly unstable. Monocots and dicots occur in almost equal quantities.

(iv) Erosion slope (Quadrats 43 - 73). The unstable substrate results in a low standing crop, composed of scattered, fairly large plants, with considerable areas of bare ground between them. Monocots are more common near the bottom of the slope, but the proportion of dicots increases towards the top.

(v) Nettle slope (quadrats A1 - A33). The central part of this area is fairly uniformly vegetated, dominated by dicots, mainly Urtica dioica, Galium aparine, and Rubus, with a steady but low dead monocot component. At the bottom of the slope Monocots are more conspicuous, dominated by Helictotrichon pubescens. The very top of the transect shows a similar vegetation to the middle of the lower slope.

Table 5 shows the mean standing crops for each of these areas divided into the five categories of vegetation.

Table 5. Mean standing crops in g.dry wt./m^2 for different areas of the study site, August 1974.

Area	Dead monocot	Live monocot	Dead dicot	Live dicot	Bryophyte
Top terrace	79.02	68.21	5.43	20.99	81.39
Mid terrace	34.45	22.67	17.24	91.65	0.35
Lower slope	68.43	45.00	27.22	43.60	0.63
Erosion slope	13.42	9.32	13.20	31.43	0
Nettle slope	52.57	30.58	129.30	188.13	0.61

III.4. Snail Feeding.

(a) Faecal Analysis.

Table 6. shows the numbers of fragments of the five recog-nisable categories of plant material found in the faeces of different snails at different sites within the quarry. Each figure is the total from ten snails.

Table 6. Numbers of fragments of different categories of vegetation recognised in the faeces of ten adult snails on different areas of study site, July and August, 1974.

Area	Snail species	No. of fragments D.M.	L.M.	D.D.	L.D.	Br.	Total
Top terrace	C.nemoralis	559	0	238	0	280	1077
Mid terrace	H.aspersa	388	0	497	191	157	1233
Lower slope	H.aspersa	379	0	843	62	382	1666
	C.nemoralis	982	0	524	67	101	1674
Nettle slope	H.aspersa	177	0	920	110	17	1224
	C.nemoralis	66	0	1032	37	6	1141

It should be pointed out that there are various possible sources of error in these figures, some of which have been listed by Hansson (1970). Firstly all identification is subjective, and related to this is a gradual improvement in

the ability to recognise items, which may be at different rates for different categories of fragment. Probably the greatest source of error occurs due to the fact that snails break down different plant materials in different ways. Thus live dicot material may emerge as an amorphous mass of very fine particles, among which only hairs are recognisable. Monocots on the other hand tend to be less fragmented and often quite considerable lengths of grass blade may be voided. Finally bryophyte is passed out virtually unaltered, and so may be over-represented in the totals in Table 7. In spite of these provisos it is probable that the figures obtained do bear a fairly close relation to the relative amounts eaten by the snails.

The most striking feature of the results is the complete absence of live monocots in the diets of the snails, and the relatively small proportions of live dicots eaten. Dead material with some bryophyte makes virtually the whole diet of both species.

To investigate any difference in type of material eaten between the two species Chi-squared tests were carried out for the lower slope and the nettle slope data where both species were collected. The result in both cases showed a significant difference (Chi-squared = 505.12 and 95.93 for lower slope and nettle slope respectively, $p \doteq 0.001$), and on both areas the most important terms were the dead monocot and the dead dicot. On the lower slope C. nemoralis is clearly taking much more monocot material than H. aspersa, which eats more dicot. On the nettle slope this result is reversed, but

this could be due to all ten C. nemoralis individuals being collected evenly down the whole slope whereas half the H. aspersa individuals were collected near the bottom of the transect, where monocots comprise the main component of the vegetation. These five snails provided 141 out of 177 observations of dead monocot material. When the collections were made it was intended to double the sample size, but lack of time prevented faecal analysis of more snails.

Fragments of a variety of plant species were also recognised in the snail faeces, though not regularly or frequently enough to permit quantitative treatment. (See Table 7). On the nettle slope considerable numbers of insect fragments were also found in the faeces of both species. Most of these appeared to be from aphids, and were probably eaten with leaf material rather than separately.

Table 7. Species of plant recognised in the faeces of C. nemoralis and H. aspersa. (*** = frequent, ** = occasional, * = single observ--ations) July and August, 1974.

Plant species	C. nemoralis	H. aspersa
Sesleria caerulea	***	**
Briza media	**	**
Carex flacca	*	-
Helianthemum chamaecistus	**	**
Lotus corniculatus	**	**
Trifolium medium	*	*
Poterium sanguisorba	*	-
Galium aparine	*	*
Centaurea scabiosa	*	-
Tussilago farfara	*	**
Hieracium vulgatum	-	*
Urtica dioica	*	-

(b) Palatability Experiments.

The results of this set of experiments, carried out between June and August, are presented in Tables 8 and 9, for H. aspersa and C. nemoralis respectively. Unfortunately, because of the variability found in many of the replicates, with Palatability Indices ranging from zero to infinity in some instances, the values for the Index for each plant species comprise combined data for all ten replicates in each case. However, it is felt that these indices are still a meaningful guide to the palatability of the different plant species, since the most highly variable results were always due to snails that ate little or nothing during the experiment. Consequently it was not possible to carry out statistical tests on the individual indices, but only on the whole sequence.

The results for C. nemoralis with live plant material agree closely with those of Grime et. al. (1968), as well as the observations of Gain (1891), showing that relatively few dicot species and no monocot species offered to them are palatable when alive. The only exceptions are some Compositae, such as Hieracium vulgatum, Taraxacum officinale and Sonchus asper, and also Ononis repens and Urtica dioica. It is clear however that dead plants are very much more palatable, the Palatability Indices for dead material being higher than those for live food almost without exception. Even a small quantity of three dead monocot species was taken.

H. aspersa, on the other hand, seem to find most dicot material offered to them fairly palatable, with the notable exception of the family Rosaceae, while the Compositae are again favoured foods. Monocots were again left untouched.

Differences in the palatability of the tested species between C. nemoralis and H. aspersa were investigated using the Wilcoxon

Table 8. Palatability Indices (P.I.) for H.aspersa fed on 41 species of live plant and 33 spp. of dead plant, June - August 1974.

	Live			Dead		
Plant species	Plant eaten mm	Paper eaten mm	P.I.	Plant eaten mm	Paper eaten mm	P.I.
Reseda luteola	3596	3935	0.91	2000	2994	0.67
Helianthemum chamaecistus	33	1858	0.02	137	2360	0.06
Silene vulgaris	1487	3962	0.38	889	3437	0.26
Ononis reptens	2403	2260	1.06	1400	2162	0.65
Trifolium medium	3969	3812	1.04	3585	3893	0.92
Anthyllis vulneraria	0	3942	0			
Lotus corniculatus	1230	3399	0.36	3550	3536	1.00
Poterium sanguisorba	0	2235	0	694	3015	0.23
Potentilla reptans	2050	4000	0.51	1045	3025	0.35
Fragaria vesca	0	3219	0			
Rubus sp.	0	2814	0	2	3112	0
Geum urbanum	435	3979	0.11			
Rosa sp.	0	3895	0			
Chamaenerion angustifolium	0	3946	0	1717	3859	0.44
Heracleum sphondyleum	1319	3528	0.37	3968	3774	1.05
Sambucus nigra	2154	2995	0.72	2482	3327	0.75
Galium aparine	730	1615	0.45	1591	3200	0.49
Achillea millefolia	2720	4000	0.68	1221	1891	0.94
Chrysanthemum leucanthemum	2758	3499	0.79			
Tussilago farfara	1360	3014	0.45	4000	3587	1.12
Senecio jacobaea	14	3800	0	1518	3919	0.39
Centaurea nigra	3882	3600	1.08	2477	3274	0.76
C. scabiosa	1446	2788	0.52	1792	3600	0.50
Hieracium vulgatum	3200	3044	1.05	4000	3398	1.18
H.pilosella	2076	4000	0.52			
Leontodon hispidus	4000	3940	1.02	3399	3600	0.94
Taraxacum officinale	3600	2202	1.13	3200	2242	1.42
Sonchus asper	4000	3912	1.02	4000	3266	1.22
Primula veris	0	1200	0	13	3823	0
Thymus drucei	1410	3889	0.36			
Stachys sylvatica	618	4000	0.15	3120	3651	0.85
Lamium album	4000	4000	1.00	4000	3889	1.03
Plantago media	2779	3293	0.84	4000	3767	1.06
P.lanceolata	679	3145	0.22	3038	3867	0.79
Urtica dioica	2719	3492	0.78	4000	3814	1.05
Carex flacca	0	1429	0	0	1800	0
Helictotrichon pubescens	0	3857	0	249	3682	0.07
Sesleria caerulea	0	2474	0	0	2000	0
Dactylis glomerata	0	3124	0	160	1605	0.1
Briza media	0	2000	0	0	2000	0
Festuca ovina	0	1785	0			

Table 9. Palatability Indices (P.I.) for C.nemoralis fed on 41 spp.of live plant and 33 spp.of dead plant,June - August 1974.

Plant species	LIVE			DEAD		
	Plant eaten mm	Paper eaten mm	P.I.	Plant eaten mm	Paper eaten mm	P.I.
Reseda luteola	174	3973	0.04	257	1379	0.19
Helianthemum chamaecistus	58	3491	0.02	89	2440	0.04
Silene vulgaris	19	3837	0	14	2578	0
Ononis reptens	2055	3378	0.61	20	3000	0.02
Trifolium medium	44	3786	0.01	1932	3886	0.50
Anthyllis vulneraria	0	4000	0			
Lotus corniculatus	17	3373	0	3660	2524	1.43
Poterium sanguisorba	0	3066	0	0	2700	0
Potentilla reptans	109	3920	0.03	1615	2879	0.56
Fragaria vesca	0	3652	0			
Rubus sp.	0	3671	0	0	2395	0
Geum urbanum	0	4000	0			
Rosa sp.	0	3293	0			
Chamaenerion angustifolium	0	3875	0	1405	2886	0.49
Heracleum sphondyleum	2	2629	0	3582	3007	1.19
Sambucus nigra	260	2488	0:1	2039	1309	1.56
Galium aparine	94	2207	0.04	255	2935	0.09
Achillea millefolium	152	3825	0.04	1221	1891	0.65
Chrysanthemum leucanthemum	434	4000	0.11			
Tussilago farfara	54	3324	0.02	428	3775	0.11
Senecio jacobaea	10	3903	0	392	1869	0.21
Centaurea nigra	103	4000	0.03	164	3367	0.05
C. scabiosa	158	3679	0.04	897	3344	0.27
Hieracium vulgatum	3236	3170	1.02	2749	2583	1.06
H.pilosella	87	3550	0.02			
Leontodon hispidus	3229	3612	0.89	1527	2596	0.59
Taraxacum officinale	3600	2202	1.63	3262	2961	1.10
Sonchus asper	3774	3646	1.04	3205	3270	0.98
Primula veris	0	3420	0	0	3293	0
Thymus drucei	0	3836	0			
Stachys sylvatica	0	3938	0	495	2093	0.24
Lamium album	94	3508	0.03	2513	3951	0.64
Plantago media	6	3488	0	2492	2681	0.93
P.lanceolata	0	2857	0	1413	2514	0.56
Urtica dioica	2070	3469	0.60	3458	1652	2.09
Carex flacca	0	2000	0	0	1800	0
Helictotrichon pubescens	0	3658	0	142	2756	0.05
Sesleria caerulea	0	4000	0	0	1950	0
Dactylis glomerata	0	4000	0	17	1729	0.01
Briza media	0	1655	0	90	1800	0.05
Festuca ovina	0	1760	0			

Signed rank Test (Campbell,1967). This gave a figure for the test statistic 'z' of 4.96, which is significant at the 0.05 level, showing that there is a considerable difference in the foods that are acceptable to the two snail species.

(c) Feeding Observations.

The number of times that snails were observed feeding on a variety of plants in the field is recorded in Table 10 for H. aspersa and Table 11 for C. nemoralis. Because the relative abundances of the different plant species were an important factor in the number of observations made of feeding snails, these results cannot be compared with those from the palatability experiments. However it is clear that these results are consist--ent with those obtained from laboratory work, which emphasises the usefulness of the experimental approach.

Comparisons between the feeding habits of the two snail species can be made on these data in terms of proportions of live and dead material taken (Table 12) and of monocot and dicot taken (Table 13).

Table 12. The number of observations of C. nemoralis and H. aspersa feeding on live and dead material.

Snail species	Dead	Live	Total
C. nemoralis	26	13	39
H. aspersa	50	33	83
	$X^2 = 0.467$	$p => 0.05$	

Table 10. The number of observations of H. aspersa feeding on different plant species in the field, June - August, 1974.

Plant species	Condition	No. of observations
Urtica dioica	Dead	16
Galium aparine	Dead	9
Urtica dioica	Live	5
Tussilago farfara	Dead	5
Taraxacum officinale	Dead	4
Hieracium vulgatum	Live	4
Galium aparine	Live	3
Lamium album	Dead	2
Lamium album	Live	2
Tussilago farfara	Live	2
Centaurea scabiosa	Dead	2
" "	Live	2
Silene vulgaris	Live	2
Plantago lanceolata	Live	2
Trifolium medium	Live	2
Heracleum sphondylium	Live	2
Poterium sanguisorba	Dead	2
Rubus sp.	Dead	2
Sesleria caerulea	Dead	2
Cirsium vulgare	Live	2
Centaurea nigra	Dead	1
" "	Live	1
Hieracium vulgatum	Dead	1
Lotus corniculatus	Dead	1
Silene vulgaris	Dead	1
Plantago lanceolata	Dead	1
Thymus drucei	Flowers	1
Heracleum sphondylium	Dead	1
Leontodon hispidus	Live	1
Stellaria media	Live	1
Ulex europaeus	Flowers	1
Total no. of observations =		83

Table 11 . The number of observations of C. nemoralis feeding on different plant species in the field, June - August, 1974

Plant species	Condition	No. of observations
Sesleria caerulea	Dead	11
Hieracium vulgatum	Live	5
Taraxacum officinale	Dead	3
Tussilago farfara	Live	3
Galium sparine	Dead	3
Urtica dioica	Dead	2
Bryophyte spp.	-	2
Poterium Sanguisorba	Dead	2
Taraxacum officinale	Live	1
Cirsium vulgare	Live	1
" "	Dead	1
Urtica dioica	Live	1
Lamium album	Dead	1
Lotus corniculatus	Live	1
Thymus drucei	Flowers	1
Plantago lanceolata	Dead	1
Festuca ovina	Dead	1
Centaurea scabiosa	Dead	1
Total no. of observations		41

Table 13. The number of observations of C.nemoralis and H.aspersa feeding on monocot and dicot material.

Snail species	Monocot	Dicot	Total
C.nemoralis	12	27	39
H.aspersa	2	81	83
	$\chi^2 = 20.81$	$p=<0.001$	

Clearly there is no difference between C.nemoralis and H.aspersa in respect of the amounts of dead and live material taken,but there is a significant difference in the relative proportions of monocots and dicots in the diets of the two species,with C.nemoralis consuming much more monocot than H.aspersa.

III.5. Ingestion and assimilation by snails.

Considerable difficulty was experienced in persuading both H.aspersa and C.nemoralis to feed,even when presented with apparently highly palatable foods.A series of experiments in which the snails were kept in small glass jars failed completely.Plastic containers were then tried,and the experi--ments using these yielded results for two species of live plant,out of four tried for adult H.aspersa,and one species of dead plant ,out of three tried for adult C.nemoralis.In each case ten replicates were set up,though not all the individuals responded by eating.The figures obtained are shown in Tables 14 to 16.

Table 14 Assimilation rates for H. aspersa fed on live Tussilago farfara. (Adult specimens, August 1974)

Fresh wt. of food eaten (g)	Dry wt. of * food eaten (g)	Dry wt. of faeces produced (g).	% assimilation
0.6380	0.0759	0.0393	48.26
0.5186	0.0627	0.0092	85.33
0.9010	0.1089	0.0290	73.39
0.3582	0.0433	0.0129	70.22
0.5940	0.0718	0.0292	59.35
0.7258	0.0878	0.0280	68.10
		MEAN =	67.44±12.63

*Using conversion figure, dry wt. : fresh wt. of 0.1209, mean of 10 conversions.

Table 15 Assimilation rates for H. aspersa fed on live Sonchus asper. (Adult specimens, August 1974)

Fresh wt. of food eaten (g)	Dry wt. of * food eaten (g)	Dry wt. of faeces produced (g).	% assimilation
1.4484	0.1593	0.0306	80.79
1.2981	0.1427	0.0257	81.99
1.3164	0.1448	0.0263	81.83
0.7989	0.0878	0.0186	78.81
1.0113	0.1112	0.0175	84.26
0.6853	0.0764	0.0113	85.20
0.8367	0.0920	0.0107	88.36
1.3850	0.1523	0.0625	58.96
0.5959	0.0655	0.0269	58.93
0.6963	0.0765	0.0305	60.13
		MEAN =	73.93±11.74

*Usingconversion figure, dry wt. : fresh wt. of 0.1101, mean of 10 conversions.

Table 16. Assimilation rates for C. nemoralis fed on dead Sonchus asper. (Adult specimens, August 1974)

Fresh wt. of food eaten (g)	Dry wt. of * food eaten (g)	Dry wt. of faeces produced (g).	% assimilation
0.4203	0.0383	0.0121	68.4
0.3223	0.0294	0.0045	84.7
0.4733	0.0432	0.0071	83.6
0.1077	0.0098	0.0045	54.1
0.7615	0.0695	0.0306	56.0
0.0873	0.0079	0.0047	40.5
0.6200	0.0566	0.0070	87.6
0.3459	0.0315	0.0051	83.8
		MEAN =	69.8±17.8

*Using conversion figure, dry wt. : fresh wt. of 0.0913, mean of 10 conversions.

The mean percentage assimilation is approximately 70% for both H. aspersa and C. nemoralis, which agrees well with Mason's figure of 66% for Haspersa at 15 C, obtained by the same method. However, compared with other mollusc values, such as 53% for H. aspersa measured by an ash-ratio method (Mason, 1970) and 57% for Littorina littorea (Grahame, 1973), this figure seems rather high. The difference could be due to some plant material remaining in the gut after most of it has passed out as faeces. Certainly the transition from green to white faeces due to plants and filter paper respectively was not very sharp, and small amounts of green tended to appear in white faeces. The other possible source of error lies in changes in weight due to evaporation or uptake of water from fresh material. In spite of these reservations it is clear that these snails show a high rate of assimilation compared to most invertebrates.

The amount of faeces produced in 24 hours by snails collected from the study area is shown in Table 17.

Table 17. Amount of faeces produced per day (g. dry wt.) by individual adult H. aspersa and C. nemoralis.

Snail species	No. of replicates	Mean wt. faeces produced g. dry wt./day ± S. D.
H. aspersa	16	0.0652 ± 0.025
C. nemoralis	14	0.0155 ± 0.0103

From these figures, using an assimilation rate of 70%, mean figures for ingestion rates can be calculated (Table 18).

Table 18. Ingestion rates (g. dry wt./day)for individual adult H. aspersa and C. nemoralis.

Snail species	Ingestion rate, g. dry wt,/day.
H. aspersa	0.217
C. nemoralis	0.051

III.6. Mean temperature measurement.

The mean temperatures for the eight sample sites through the duration of the study period are shown in Figure 17. The results from tubes 1,2,4,7, and 8 for June A are missing due to the plastic tubes that were used on this occasion forcing their caps off. The remainder of the results were obtained using screw top glass jars.

Apart from site 1 in the second half of June, the temperature profiles are fairly consistent, showing a peak at site 3, with lower temperatures on either side, on the main transect. Temp--eratures on the nettle slope (sites 7 and 8) were generally rather lower.

III.7. Shelter.

The results of the analysis of available shelter are shown in Figure 18. Clearly the nettle slope provides more shelter than the main transect, mainly due to the denser vegetation, but also due to a considerable number of small rocks underlying the plants. On the main transect most shelter is available on

Fig.17. Mean temperatures measured by the sucrose inversion method at 8 different sites on study area, June - August, 1974.

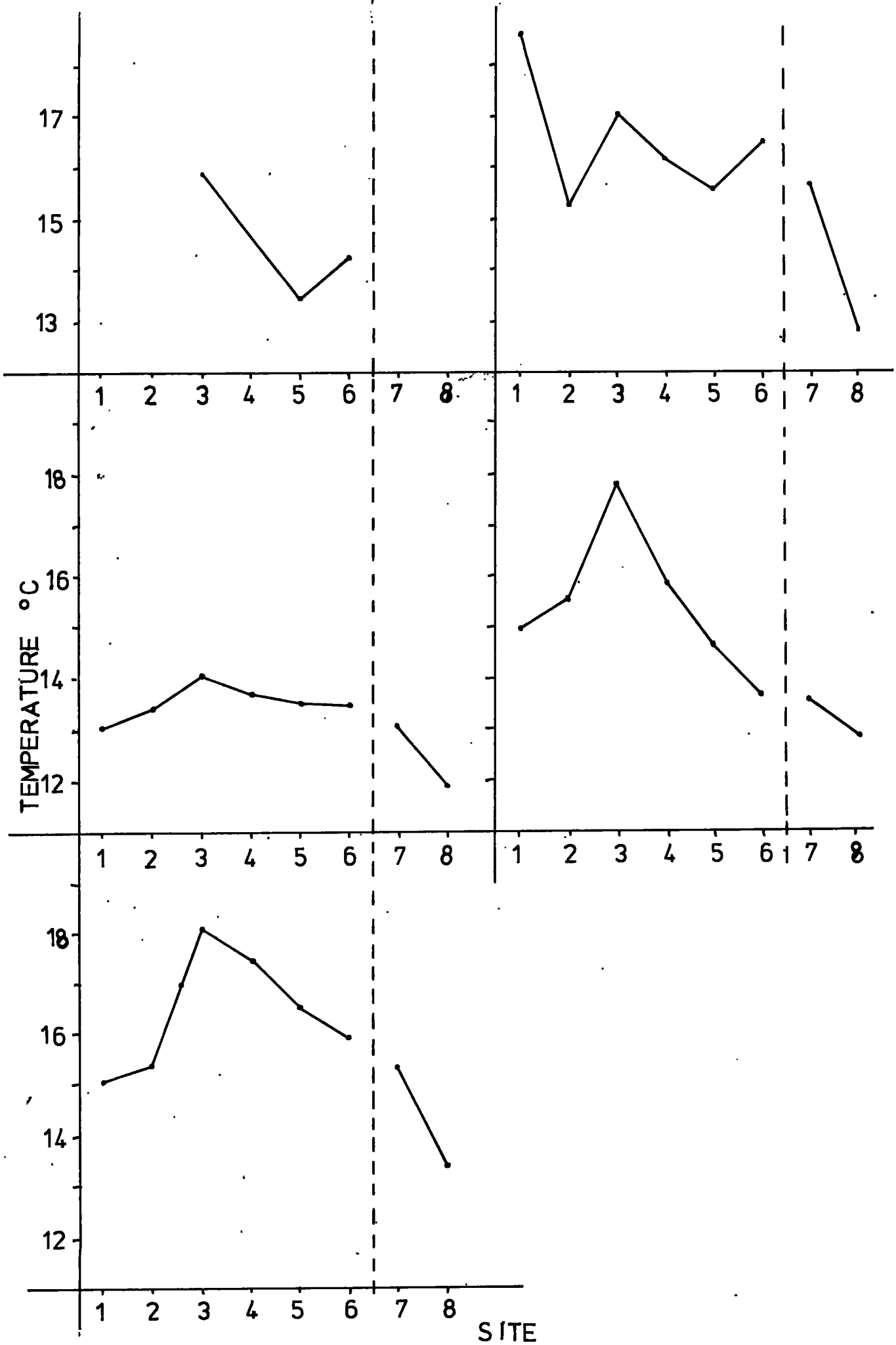
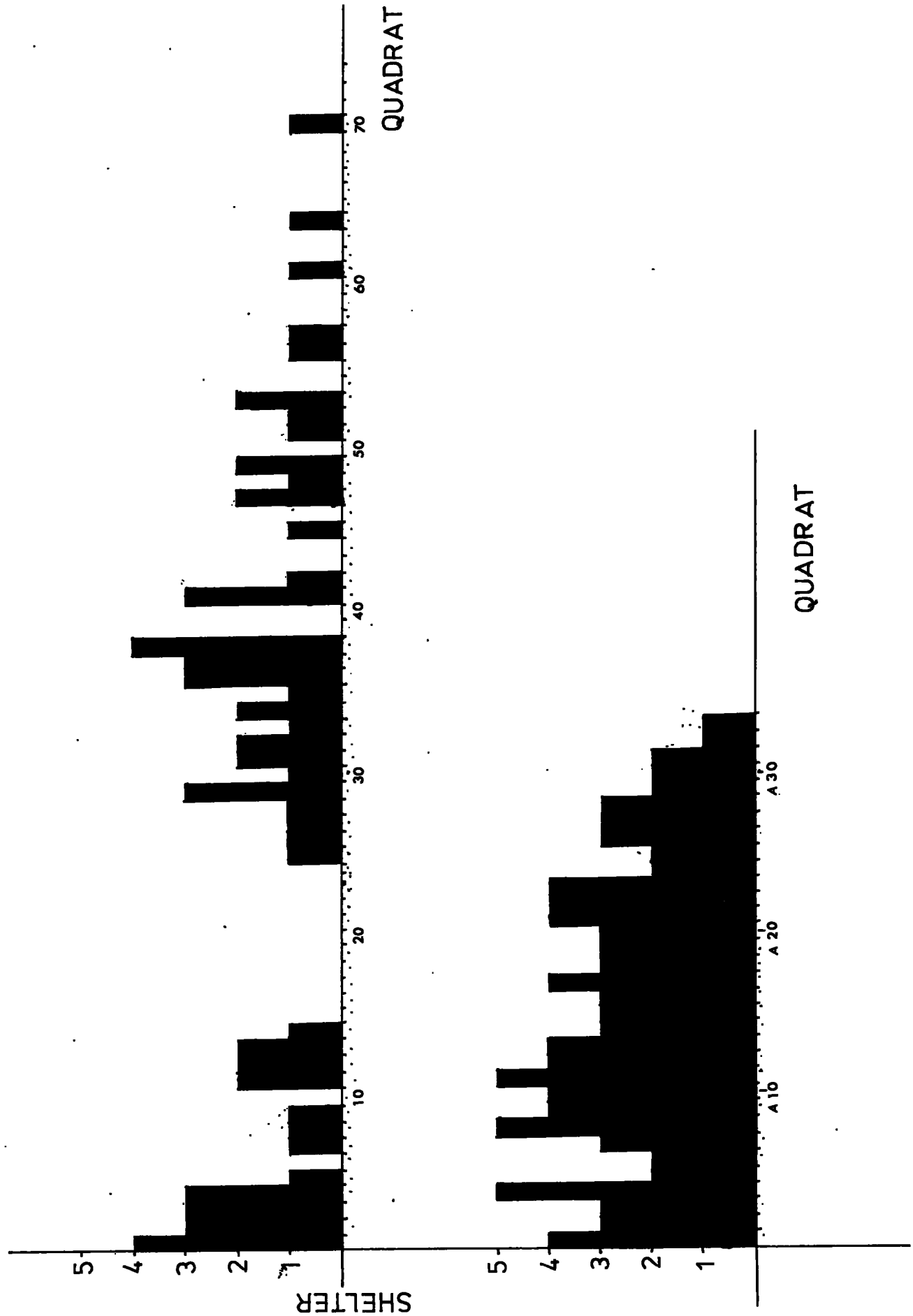


Fig.18. Available shelter for each quadrat assessed on a 1 - 5 scale, August 1974.



the top terrace, due to thick grass and large boulders, and on the lower slope, due to the rubble scree. Scattered large plants on the middle terrace and the erosion slope provide the lower levels of shelter available on these areas.

IV. DISCUSSION.

IV.1. Snail Density and Distribution.

In an early discussion of the factors affecting snail distribution, Boycott (1934) states "there is, in short, no evidence that the abundance of Mollusca is, under any ordinary circumstances, conditioned by the quantity of food available (which is always in excess)." This contention is echoed by Wolda et al. (1971), in their study of C. nemoralis, though they point out that food quality may be an important but unknown factor, the nutritional requirements of the species being largely unknown. Grime and Blythe (1969) and Grime, Blythe and Thornton (1970) on the other hand, considered that numbers of C. nemoralis are related to available diet, again stressing the possible role of food quality.

The present study represents an attempt to investigate in more detail how vegetation and snail density are related, by dividing the vegetation into components which might be important to the snails. The five basic components described in sections II and III, dead monocot, live monocot, dead dicot, live dicot and bryophyte, can also be combined to give total monocot, total dicot, total dead material, total live material and total standing crop. Correlations were attempted between the figures obtained for all these components and the density of snails, expressed as the mean number of snails per m^2 quadrat over the five sampling occasions. The correlation coefficients obtained are shown in Table 19.

It can be seen from these results that not only are some of the components of the vegetation important factors influencing

Table 19. Coefficients for correlations between densities of C. nemoralis, H. aspersa and total snails and standing crops of components of the vegetation.

Component	C. nemoralis		H. aspersa		Total	
	r	r^2	r	r^2	r	r^2
Total dead	0.329	0.108	0.670**	0.449	0.644**	0.414
Total live	0.226	0.051	0.603**	0.363	0.571*	0.326
Monocot	0.596**	0.355	0.219	0.048	0.486*	0.236
Dicot	0.087	-	0.640**	0.410	0.485*	0.235
Total	0.382	0.146	0.578**	0.334	0.668**	0.446
Dead dicot	-	-	0.639**	0.409	-	-
Dead monocot	0.534*	0.285	-	-	-	-

* = p 0.01 ** = p 0.001

Table 20. Coefficients for the correlations between H. aspersa, C. nemoralis, and total snails and indices of shelter.

	Shelter	
	r	r^2
H. aspersa	0.660**	0.436
C. nemoralis	0.512*	0.262
Total	0.733**	0.537

* = p 0.01 ** = p 0.001.

snail density,but that the two snail species are affected by different components.

C.nemoralis is evidently most influenced by the amount of monocot available,with 35% of the variation in numbers being due to changes in the amount of monocot.(See Figures 19a and 19b).In contrast,dead material,live material,dicot material and total standing crop appear to have little effect on this species.

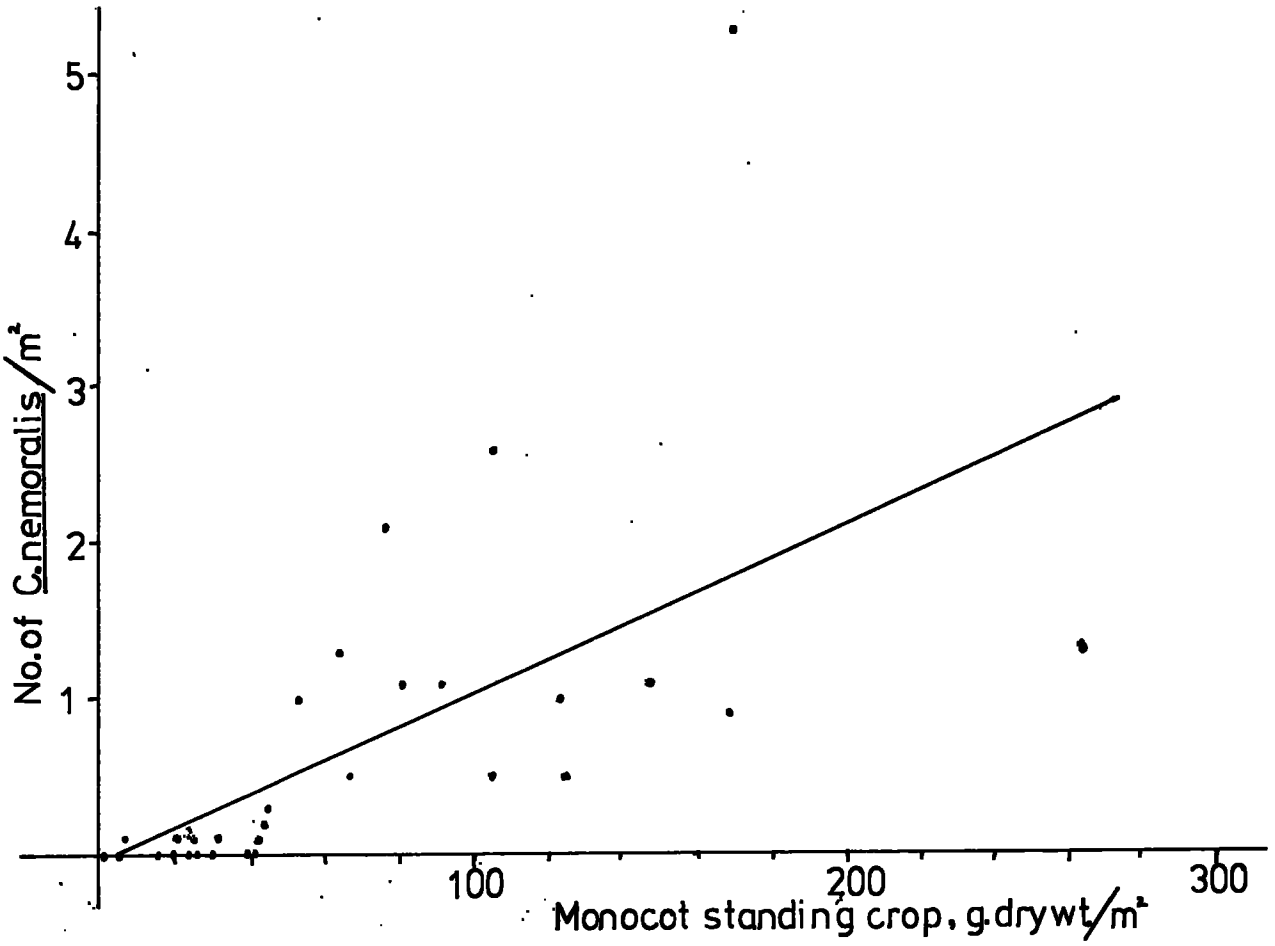
H.aspersa, on the other hand,is clearly affected by the total standing crop,which accounts for 33.5% of the variation in density,but more important are the amounts of dead material and of both dead and total dicot present,explaining 44.9% , 40.9% and 41% of the variation respectively. (See Figures 20a and b,and 21a and b).

When the numbers of the two species are combined,the strongest correlations are found with the total standing crop and dead standing crop. (See Figures 22a and 22b).This strong correlation of total snail density with total standing crop,combined with those for C.nemoralis with amount of monocot,and H.aspersa with dicot quantity,suggest that these two species of large snail are to some extent dividing the available food resources between them,thereby avoiding competition.This difference is also reflected in the diets of the two species which are discussed below.

Grime and his co-workers (1969 & 1970) while considering the importance of food quality to C.nemoralis suggested that "phosphorus,either through a deficiency in the diet,or by reducing the contribution of palatable species to the vegetation is a limiting factor on snail numbers." Their study site at

Fig.19. Mean number of C.nemoralis/m^2 correlated with :-

(a) Total monocot standing crop, g. dry wt./m^2 (August)



(b) Dead monocot standing crop, g. dry wt./m^2 (August).

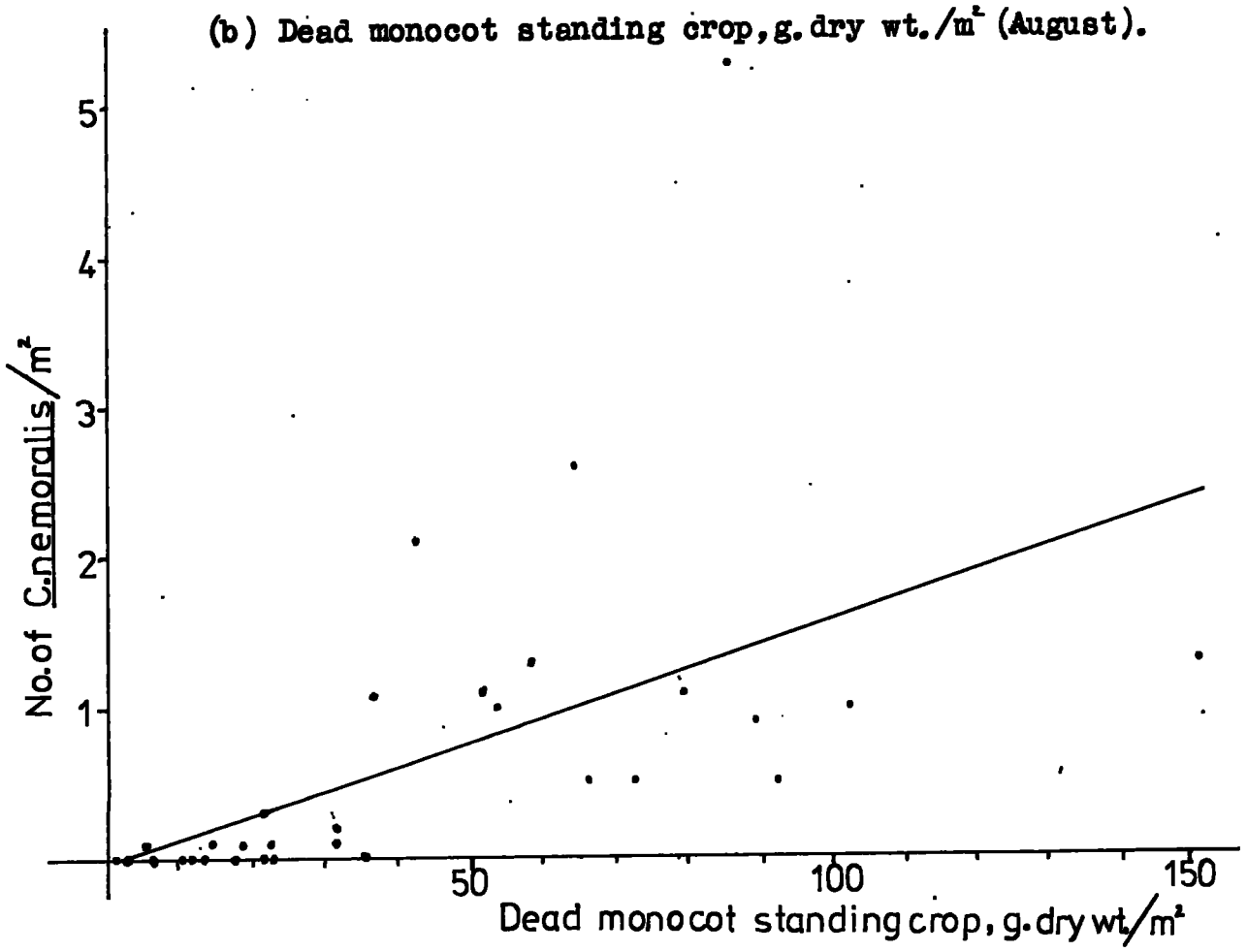
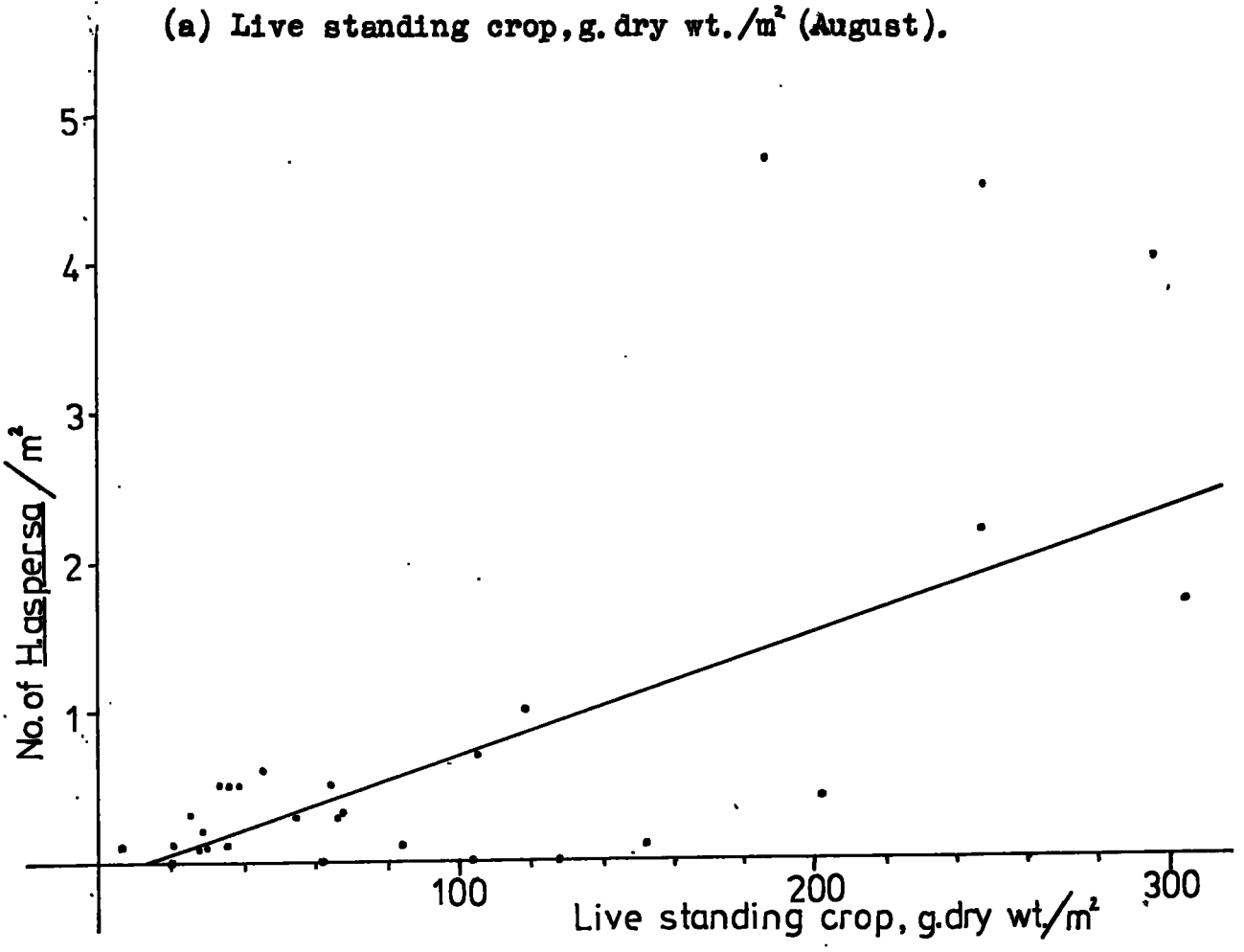


Fig. 20. Mean number of H. aspersa /m², June - August, 1974, correlated with :-

(a) Live standing crop, g. dry wt./m² (August).



(b) Dead standing crop, g. dry wt./m² (August).

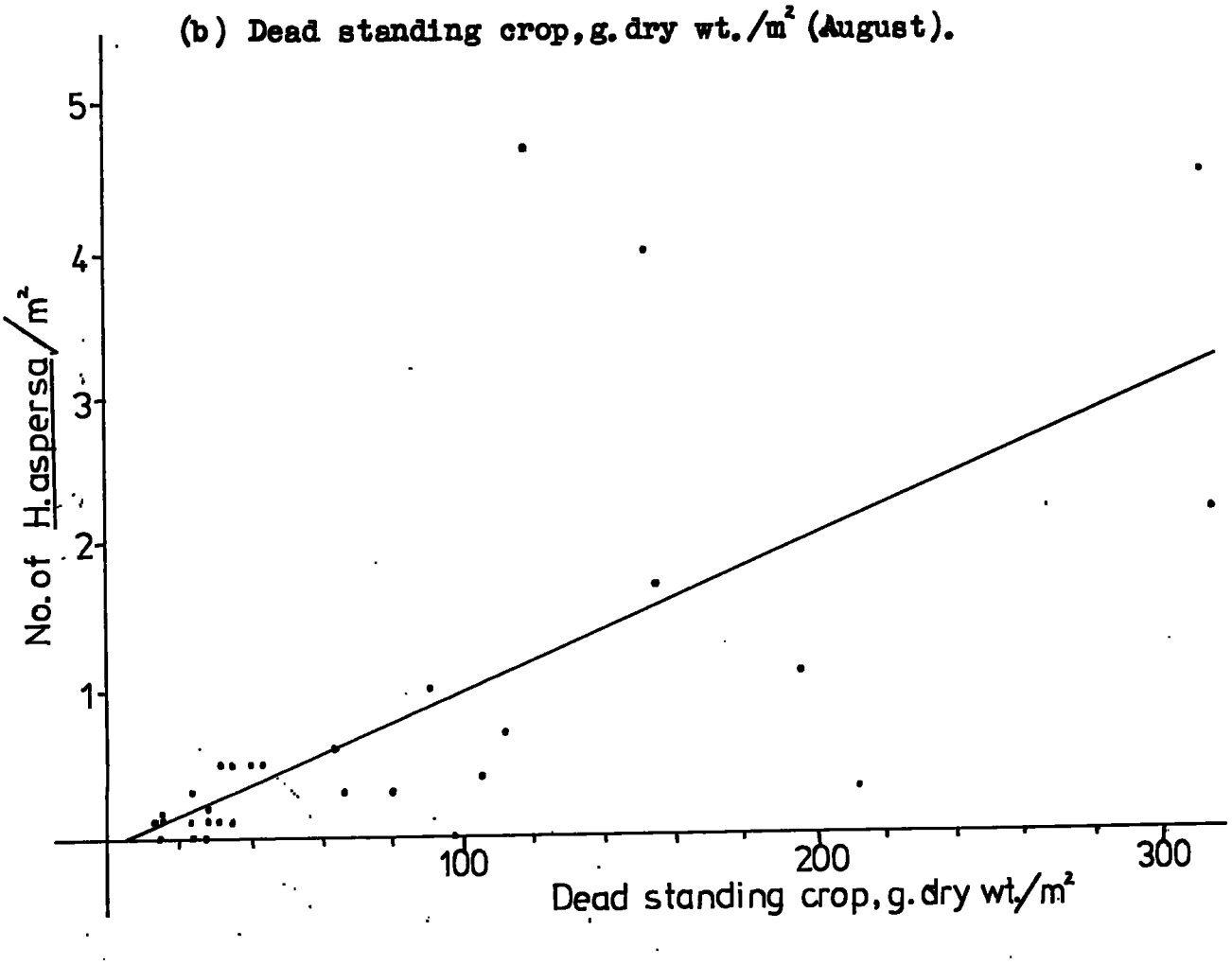
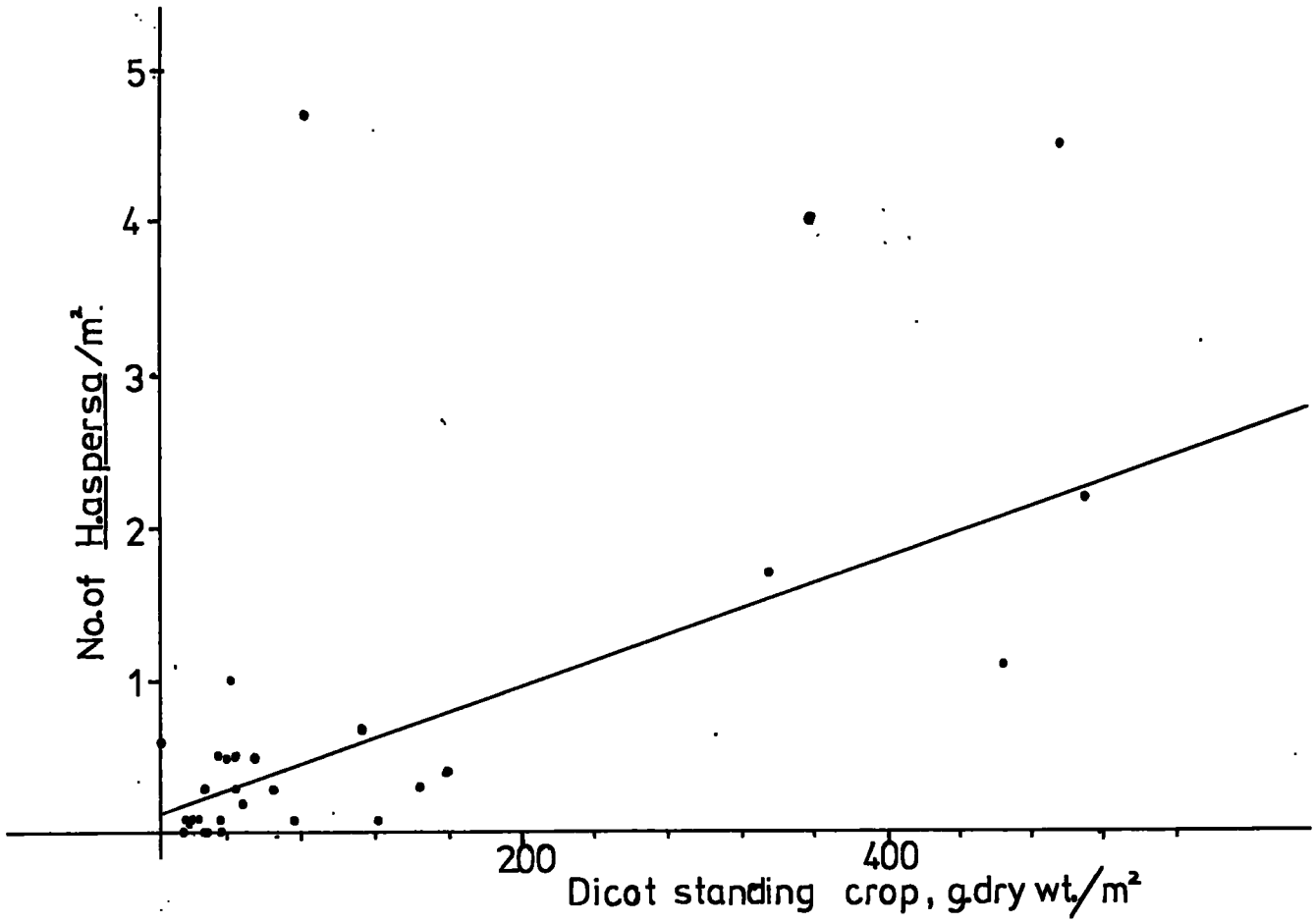


Fig. 21. Mean no. of H. aspersa/m², June - August, correlated with :-

(a) Total dicot standing crop, g. dry wt./m² (August).



(b) Dead dicot standing crop, g. dry wt./m² (August).

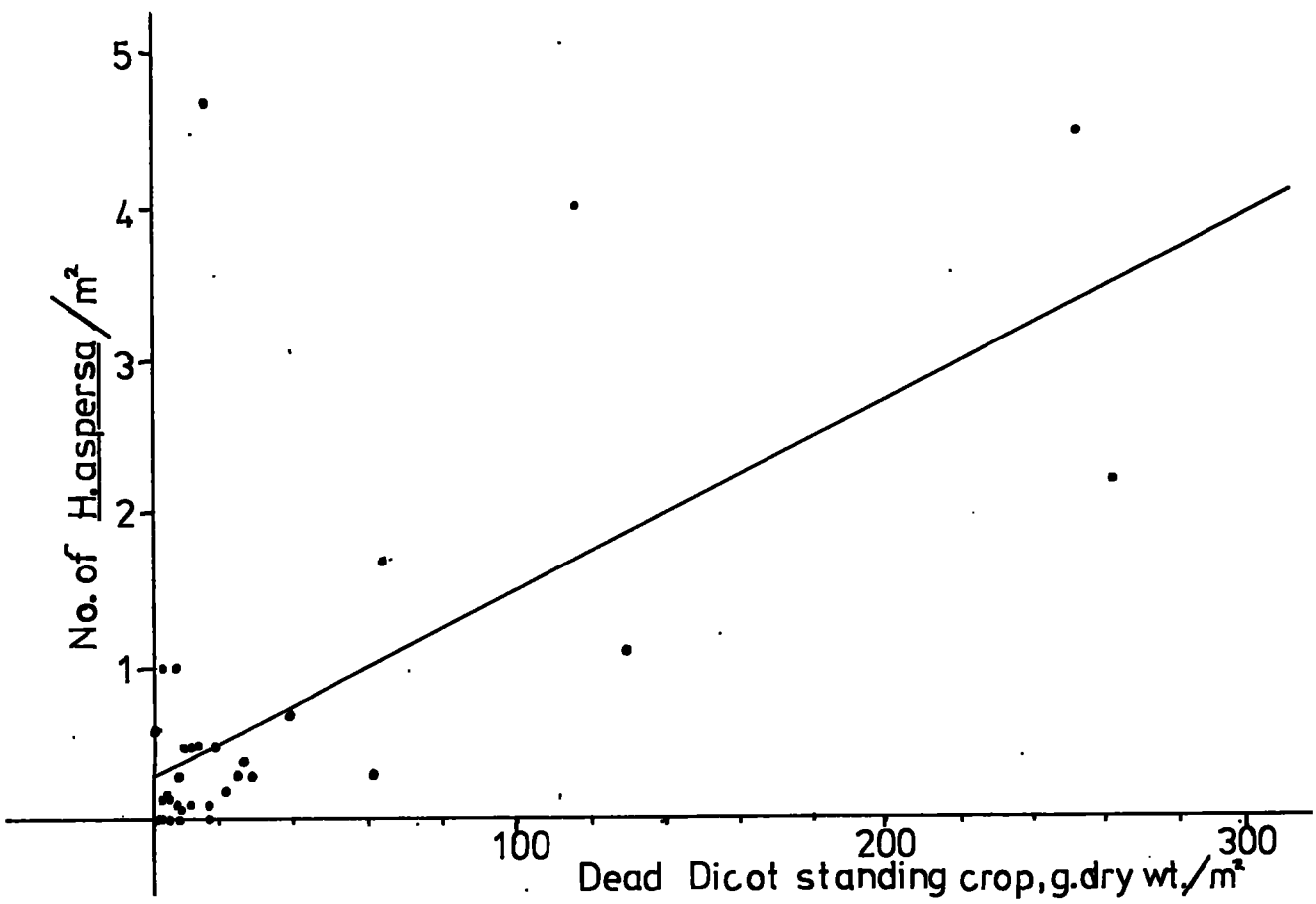
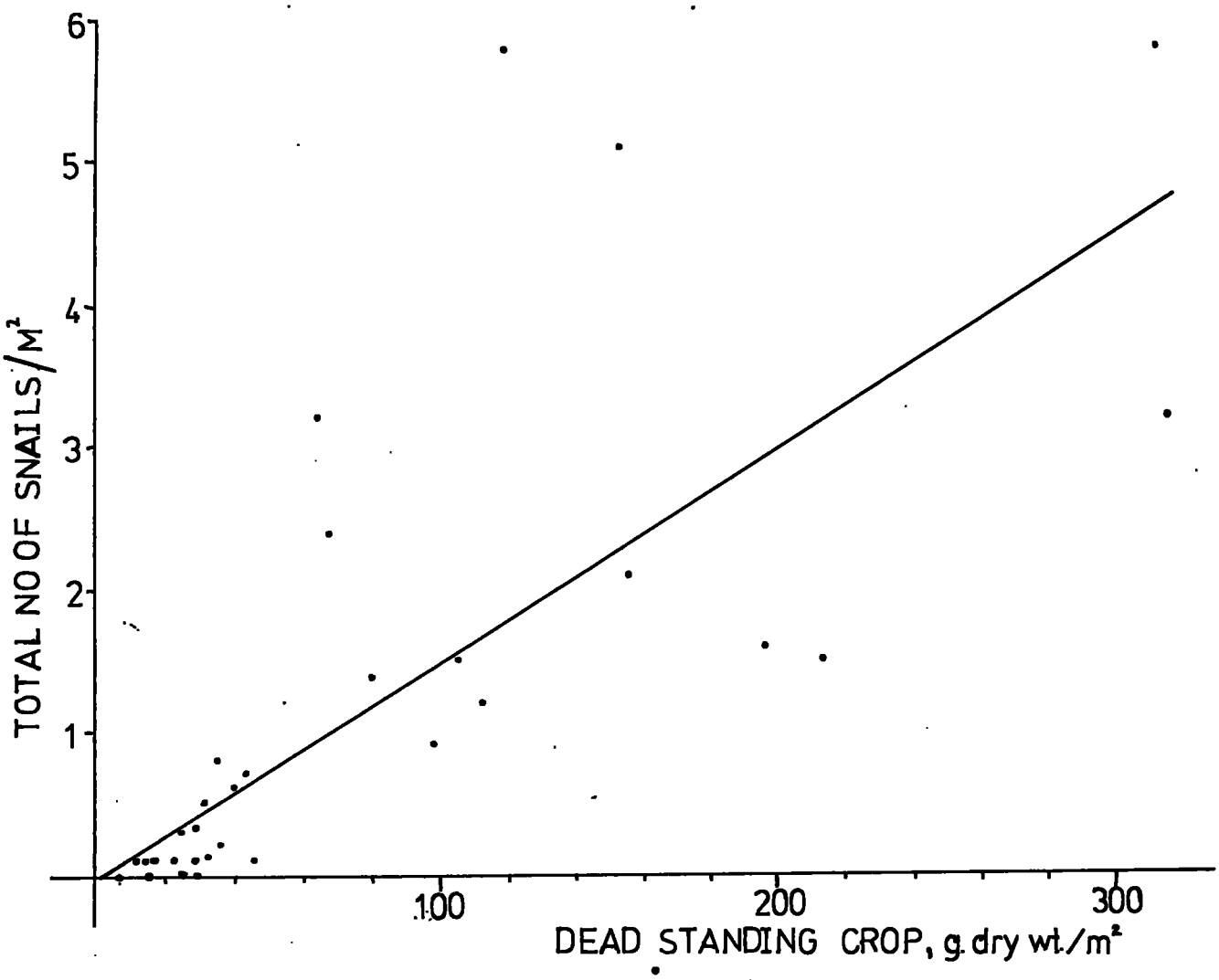
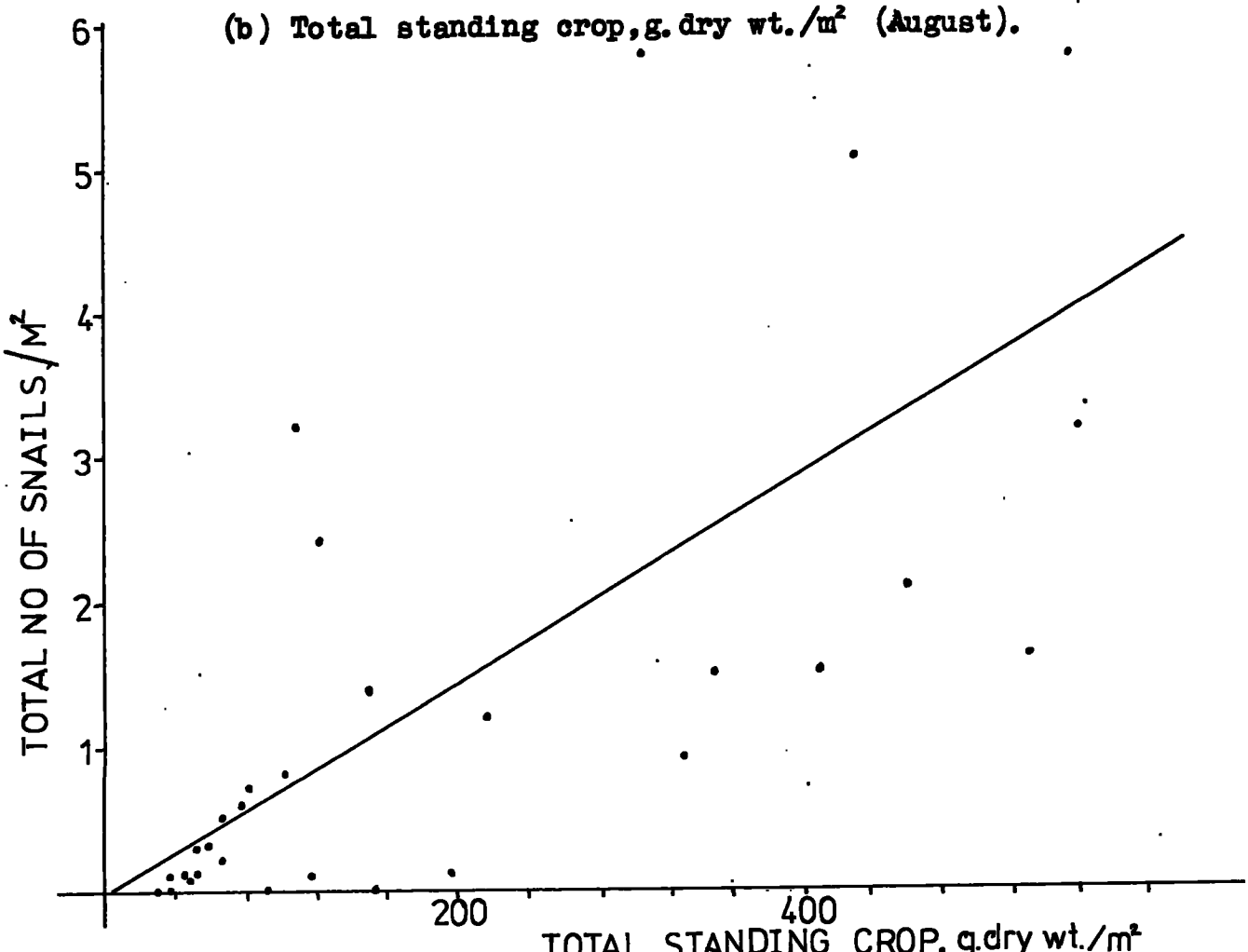


Fig. 22. Mean total no. of snails /m², June - August correlated with :-

(a) Dead standing crop, g. dry wt./m² (August).



(b) Total standing crop, g. dry wt./m² (August).



Winnats Pass, Derbyshire comprised two slopes facing north and south respectively. C. nemoralis was confined, apparently by its preference for relatively high temperatures to the south facing slope, where it occurred at low densities. Another snail species, Arianta arbustorum was found only on the other side of the pass, reaching much higher densities than C. nemoralis, particularly in stands of Urtica dioica, a plant associated with high phosphate levels (Pigott and Taylor, 1964). In contrast the soils of the south facing slope were known to be deficient in phosphorus. Therefore it was concluded that the numbers of C. nemoralis might be limited by the availability of phosphorus, while its distribution was defined by its temperature requirements.

Evidence from the present study however suggests that at Bishop Middleham the level of phosphorus cannot be critical for C. nemoralis. This species is found at highest densities on Sesleria caerulea grassland, while on the south facing slope covered in Urtica dioica, which indicates a high level of phos-phorus, it does not reach particularly high numbers. H. aspersa on the other hand shows a distribution pattern that agrees well with the hypothesis that high phosphate levels are necessary to support a large population of snails, peak numbers being found on the nettle covered slope.

Vegetation, however, not only provides food for snails, but also acts as a source of shelter, and it is probable that both roles are involved in the correlations found above. Boycott (1934) stresses the importance of sources of shelter when considering requirements of the habitat, but this factor is not discussed by Grime et al. (1969 & 1970) nor by Wolda et al. (1971). Therefore the indices of shelter for each quadrat (see section III.7) were correlated with the density of snails, the results being

given in Table 20 and Figure 23.

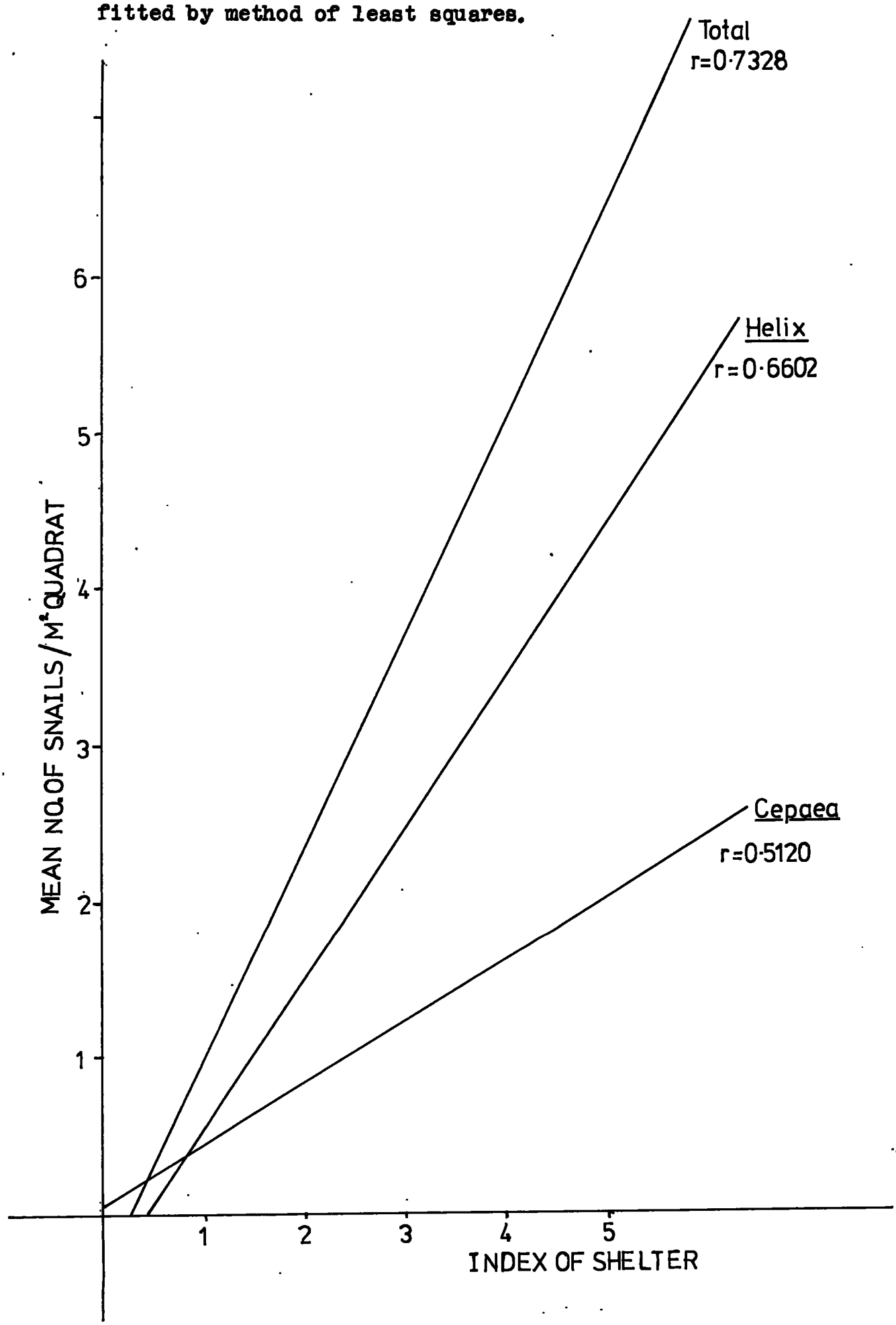
Clearly shelter represents an extremely important influence on total snail density, explaining 53.7% of the variation, and also has a strong effect on both species individually. Thus it can be concluded that while the availability of shelter is probably the most important single factor influencing snail density, the food supply also plays a significant role.

The distribution patterns of the snails in terms of presence and absence from different areas of the quarry is also of some interest. Both species are absent from much of the middle terrace and this is undoubtedly due to the almost complete lack of cover in this area, coupled with very low standing crops. C. nemoralis is also completely absent from the upper part of the erosion slope, where H. aspersa is found in small numbers. Shelter is unlikely to be the cause of this difference in distribution, since it should affect both species almost identically, as they use very similar types of resting place, either thick vegetation, or cracks and crevices in rocks or the ground. If anything C. nemoralis, by virtue of its smaller size should be able to find shelter more easily than H. aspersa.

Food supply could contribute towards the difference between the species, since monocots, with which C. nemoralis is associated, are almost absent from this area, where most of the vegetation is composed of large individual dicot plants, separated from each other by considerable distances of bare ground. This spacing of the plants could also be of some relevance, with the smaller C. nemoralis having difficulty in foraging from plant to plant to find enough food before returning to shelter.

Temperature is certainly an important factor influencing local snail distribution, as shown at Winnats Pass by Grime and

Fig. 23. Mean no. of H. aspersa, C. nemoralis, and total snails/m^2, June - August, correlated with index of shelter. Regression line fitted by method of least squares.



Blythe (1970), where C. nemoralis is confined to the south facing slope. In the present study however the mean temperatures measured in III.6. above do not seem to be related to snail distribution in any simple way. The mean temperatures on the west facing erosion slope, for instance (sites 5 and 6, Fig.16) lie roughly between those at site 1 and site 3, on the top terrace and lower slope respectively, where high numbers of C. nemoralis are found. These figures are mean temperatures and it is possible that the diurnal range of temperature is more important to the snails. This would probably be greatest on the erosion slope where the minimal vegetation cover will provide very little insulation. The presence of H. aspersa on this area could be due to its larger size giving it greater control of its internal temperature than C. nemoralis, thereby surviving the wide variations in external temperature. Certainly H. aspersa can remain active for some days at 35° C. (Russel-Hunter, 1964), and was never observed aestivating during the present study, while C. nemoralis were found in this state on several occasions. The same considerations may also apply to humidity.

Thus it seems likely that local distribution of snails is influenced by factors other than distribution of food and shelter, and that these factors, such as temperature and humidity, exert their influence on different species with different effects.

IV.2. Snail Feeding.

That C. nemoralis selects strongly for certain components of the vegetation is suggested by the data of both Grime and Blythe

(1969) and Wolda et al. (1971), but in neither case could the authors show selections by means of statistical tests. This is due to the difficulty of measuring food taken by snails and the food available to them in the same or comparable units. The same problem was encountered in the present investigation where the food taken was measured as the number of fragments found in the faeces and the food available as the dry weight of plant material per square metre. It is clear however from Table 21, which compares the percentages of the five components of the vegetation in the faeces with those for four areas in Bishop Middleham quarry, that some selection is taking place. In each case a Selection Index (S.I.) has been calculated as

$$S.I. = \frac{\% \text{ present in the vegetation}}{\% \text{ present in the faeces}}$$ so that a S.I. of 1.0 indicates that the snails feed more or less at random from the available food, a S.I. of < 1.0 indicates selection for a component, and a S.I. of > 1.0 shows selection against it. It is assumed that the five components of the vegetation were identified in the faeces with equal ease.

The most striking conclusion to be drawn from this table is the selection against live material and against live monocots in particular. No fragments of live monocot were ever observed in the faeces of any snail, so that all S.I.'s equal infinity, while this component comprises between 7.6%, for the nettle slope, and 26.7%, for the top terrace, of the total vegetation. This result is supported by the Palatability Indices of zero for all species of live monocots found experimentally with both species of snail, and by the field feeding observations, in which no snail was found eating live monocot tissues. This result is of interest when compared with the feeding of the

Table 21. Comparison of percentages of components of vegetation in the field and in snail faeces for different areas of the study site, by means of Selection Indices (S.I.).

Area of transect	Snail species		D.M.	L.M.	D.D.	L.D.	Br
Top terrace	C. nemoralis	Vegetation	31.0	26.7	2.1	8.2	31.9
		Faeces	51.9	0	22.1	0	26.0
		S.I.	0.6	∞	0.09	∞	1.22
Mid terrace	H. aspersa	Vegetation	20.7	13.6	10.4	55.1	0.2
		Faeces	31.5	0	40.3	15.5	12.7
		S.I.	0.65	∞	0.25	3.55	0.01
Lower slope	H. aspersa	Vegetation	35.3	25.0	15.1	24.2	0.3
		Faeces	22.7	0	50.6	3.7	22.9
		S.I.	1.56	∞	0.29	6.54	0.01
Lower slope	C. nemoralis	Vegetation	35.3	25.0	15.1	24.2	0.3
		Faeces	58.7	0	31.3	4.0	6.0
		S.I.	0.60	∞	0.48	6.05	0.05
Nettle slope	H. aspersa	Vegetation	13.1	7.6	46.9	32.2	0.1
		Faeces	14.5	0	72.5	9.0	1.4
		S.I.	0.90	∞	0.64	3.57	0.07
Nettle slope	C. nemoralis	Vegetation	13.1	7.6	46.9	32.2	0.1
		Faeces	5.8	0	90.4	3.2	0.5
		S.I.	2.25	∞	0.51	10.0	0.2

D.M. =Dead monocot
L.M. = live monocot
D.D. = dead dicot
L.D. = live dicot
Br = Bryophyte

slug Agriolimax reticulatus on grassland where it feeds almost exclusively on live monocots,particularly Holcus lanatus (Pallant,1972).It would seem that slugs and snails are widely separated in their feeding preferences,and willnot compete,at least for food.

Live dicots are taken by both species of snail in small amounts,but generally more frequently by H.aspersa than by C.nemoralis,but in all cases the proportion in the diet is less than that in the vegetation,with S.I.'s ranging from 3.55 to infinity.The difference between the two species in this respect is supported by the results of the palatability experiments which show that live material is almost invariably more palatable to H.aspersa than to C.nemoralis.

Dead material on the other hand is clearly selected for by both species,particularly dead dicot,with S.I.'s all smaller than one.Dead monocot is selected against on two areas of the quarry,the lower slope,by H.aspersa,and the nettle slope by C.nemoralis.It is possible that H.aspersa also selects against dead monocot on the whole of the nettle slope.The observed S.I. may be biased by the fact that 50% of the sample was collected from the lower,monocot dominated part of the slope, as discussed in III.4(a) above.Clearly dead monocot material is eaten when it is the dominant component of the vegetation, but when plentiful dead dicot is available this is strongly preferred.

Finally,of considerable interest is the selection for bryo--phytes shown in every case,except the top terrace,where this component is found in abundance.On both the middle terrace and the lower slope there were areas of bryophyte several

metres outside the collecting area round the transects, and it is probable that the snails make foraging trips to eat this evidently palatable food. These figures may be inflated, due to the over-representation of bryophyte in the faecal fragments, since it passes through the gut almost undamaged. In contrast, much of the angiosperm material is broken into minute fragments which are often unrecognisable. (See section III.4(a)).

Thus the faecal analysis, together with the observations of feeding in the field and the Palatability Indices, show that snails generally select against live plant material, particularly monocots, and select for dead material, particularly dicots, also eating a good deal of bryophyte. The feeding observations support a trend seen in the faecal analysis, with C. nemoralis eating more monocot than H. aspersa which appears to prefer dicot material. This result agrees closely with the relationships found between snail densities and different components of the vegetation. The significant result from the feeding observations (see section III.4 (c)) could be the result of the distribution pattern rather than being the cause of it, since the feeding records were made at random throughout the site. Thus records for C. nemoralis will be more numerous where this species reaches high densities, such as the top terrace, where standing crop of monocot is also high. Nevertheless it does seem likely that the food preferences of the snails are a factor in determining their distribution patterns in the field.

With regard to feeding on individual plant species, the palat-ability experiments show several interesting results. Clearly the family Compositae are the most palatable taxonomic group of plants to both the snail species, all representatives on the

site being readily eaten both live and dead, except Senecio jacobaea. This species is extremely poisonous to vertebrates, containing six or more toxins (Forsyth, 1968) which must also affect snails in some way. Urtica dioica, Lamium album and the plantains (Plantago spp.) are also preferred foods, though C. nemoralis appears to eat them in quantity only when they are dead or senescent. The least palatable group of plants are the Rosaceae, of which only Potentilla reptans is eaten in any amount, but the reasons for this unpalatability remain unclear. The leaves and stems of the species involved are neither uniformly hairy nor glabrous, and Rubus for instance is frequent-ly used by both species of snail as a resting place. Many members of the family show high Tannin levels (Gibbs, 1974), but filter paper soaked in leaf extracts of Poterium and Rubus was found to be highly palatable to C. nemoralis (Grime et al., 1968), so that soluble tannins seem an unlikely deterrent. Feeding on live Lotus corniculatus was found, in contrast to Wolda et al. (1971), who observed only the flowers of this species being eaten, which they suggested was due to the cyanogenetic properties of the leaves. Jones (1962) however has shown selective eating of acyanogenetic plants by H. aspersa, and in the present study six replicates were eaten, while four were left untouched. Though no tests for cyanogenesis were carried out, it is possible that the snails were showing selective eating and thereby helping to maintain the polymorphism.

Using the ingestion rates calculated in section III.5., approximate figures for the amount of material eaten by the snail population during a year can be calculated. In doing so a number of assumptions were made about population structure,

ingestion rates of juvenile snails, and periods of snail activity. These were :-

(i) The population of C. nemoralis, found by searching, comprises 70% adults and 30% juveniles (see section III.2).

(ii) The population of H. aspersa, found by searching, comprises 60% adults and 40% juveniles (see section III.2).

(iii) Juvenile snails have an ingestion rate that is 50% of that of an adult snail.

(iv) Snails are active for 175 days per year, from about mid-April until late September.

All these assumptions, except (iii) are based on observations made during the course of the investigation.

The results for the different areas of the transect are shown in Table 22, expressed both in g. dry weight eaten per square metre per year, and as a percentage of the mean August standing crop. The top terrace, lower slope and erosion slope show very close figures of 11.66%, 12.89% and 10.69% respectively of the standing crop eaten per year, which represents an important contribution to energy turnover within the ecosystem. The figure for the middle terrace, 3.97% is very low, due to the small snail population, probably caused by the almost total lack of shelter. The figure of 19.58% of standing crop eaten per year for the nettle slope appears high by comparison with the other figures, but is more acceptable when the vegetation of this area is taken into account. Virtually all the plants on this slope are annuals (e.g. Urtica dioica, Galium aparine and Lamium album) with high rates of production relative to the standing crop, in contrast

Table 22. Amounts of plant material eaten by C. nemoralis and H. aspersa on different areas of Bishop Middleham quarry expressed in g. dry wt./ m / year.

Area	Top Terrace	Mid Terrace	Lower Slope	Erosion Slope	Nettle Slope
Mean no. of * C. nemoralis/m	1.97	0.06	0.64	0.04	0.77
Mean no. of ** H. aspersa/m	0.32	0.16	0.46	0.18	2.30
Amt. eaten by C. nemoralis *** g. dry. wt./yr.	17.59	0.53	5.72	0.36	6.88
Amt. eaten by H. aspersa *** g. dry wt./yr.	12.15	6.08	17.47	6.84	87.35
Total amt. eaten by snails g. dry wt./yr.	29.74	6.61	23.19	7.20	94.23
Mean August standing crop g. dry wt./m	255.04	166.36	179.88	67.37	481.29
% of mean standing crop eaten /year	11.66	3.97	12.89	10.69	19.58

* Corrected to all adults by assuming 70% of population is adult and 2 juveniles = 1 adult in terms of ingestion.

** Corrected to all adults by assuming that 60% of population is adult and 2 juveniles = 1 adult in terms of ingestion.

*** Assuming that snails are active for 175 days /year.

to the perrenial grasses such as Sesleria caerulea, which are more common on the other areas.

These figures give some indication of the importance of the snails in the ecosystem at Bishop Middleham, with consumptions of up to 20% of the August standing crop. However, it is evident from the feeding studies that on the whole H. aspersa and C. nemoralis are not acting as herbivores and grazing on the living tissues of the plants. On the other hand they are not strict detritivores either, since as Grime et al. (1969) and Wolda et al. (1971) point out and personal observations on feeding in the field confirm, most of their food is senescent material, often still attached to the plant. Thus the snails are removing vegetation at a point after it has ceased to be available to strict herbivores, and before it becomes available to strict detritivores. It is probable that such senescent material is more nutritive than dead material in the litter layer, where leaching will lead to loss of soluble substances. It may also be less toxic than live material due to poisonous substances breaking down as the leaf senesces.

Another point of interest in considering the role of snails in the community is the very high assimilation rates that they exhibit. Most detritivores in contrast show very low assimil-ation rates, as shown in Table 23. This means that these animals will be acting primarily as comminutors of dead material, break-ing up large quantities into finer particles, but turning relatively little into biomass. Snails on the other hand, with their high assimilation rates, must convert considerable amounts of senescent material into their own biomass, rather

Table 23. Assimilation rates for various species of detritivore compared with H. aspersa and C. nemoralis.

Species		% assimilation	Source
Armadillidium vulgare	(isopod)	21 - 29	Hubbell et al. (1965)
Oniscus asellus	(")	16.2	Hartenstein (1964)
Glomeris	(millipede)	6 - 10.5	Bocock (1963)
Dixidesmus sp.	(")	6.4	Reichle and Crossley (1965)
Parcoblatta sp.	(cockroach)	2.5	
Nemobius sp.	(cricket)	3.0	
Ceuthophilus sp.	(")	2.2	"
Helix aspersa	(mollusc)	70.0	
Cepaea nemoralis	(")	70	

than merely physically breaking it up.

Thus observations on the feeding behaviour of snails show that they are specialist feeders on senescent material, representing a trophic level between herbivores and detritivores. However, during the spring and summer, when the snails are active, this food source is relatively scarce, most plant material existing either as live tissues or as dead material within the litter layer. The high assimilation rates of H. aspersa and C. nemoralis may be the factor enabling them to utilise this nutritive but somewhat transitory food supply.

V. SUMMARY.

The aims of this study were to investigate the effects of the vegetation on the density and distribution of populations of the snails Helix aspersa and Cepaea nemoralis, and to evaluate the impact of the snails on the vegetation, at Bishop Middleham quarry Co. Durham.

This involved study of the following aspects of snail ecology: density and distribution of the populations along fixed transects within the quarry, population structure and life cycles, and feeding habits in both the laboratory and the field, including faecal analysis, palatability experiments and measurements of ingestion and assimilation rates. The vegetation was analysed by cropping quadrats on the transect, and sorting into dead monocot, live monocot, dead dicot, live dicot and bryophyte, to obtain measures of standing crop. Mean temperatures and available shelter were also investigated.

Snail density was found to be most influenced by available shelter, though the vegetation was also of considerable importance. Total snail density was correlated with total standing crop while H. aspersa showed correlation with the amount of dicot present and C. nemoralis with amount of monocot available. Temperature, humidity and size of snail were considered to be other factors influencing snail distribution patterns.

Snails were found to select against live material and in part-icular against live monocots, while selecting strongly for dead dicot and bryophyte. The quantity of dead monocot eaten appears to depend on the quantity available, with C. nemoralis consuming more of this component than H. aspersa. It was concluded that these snails feed mainly on senescent material, which their high assim-ilation rates (approx. 70%) enables them to exploit, taking about 10% of the August standing crop per year.

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