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Population dynamics of *Arianta arbustorum* and *Cepaea hortensis* in western Norway

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Natural population of *Arianta arbustorum* and *Cepaea hortensis* in western Norway were studied for two years (1975—1977) using quadrat sampling. A searching efficiency test was performed to obtain more realistic density estimates of juveniles. Most juveniles of both species take three years to become adult. The main egg laying period was June—August. The clutch size varied considerably. However, there were no differences between years. Mean clutch size was 48.1 (*A. arbustorum*) and 37.9 (*C. hortensis*). The clutch size of *A. arbustorum* decreased significantly during the period June—September 1975, but no such trend was found in 1976. Mean adult density of *A. arbustorum* declined from 4.9 to 0.8 m^{-2} between 1975 and 1977. Mean adult density of *C. hortensis* was 4.2 (1975), 4.3 (1976) and 3.3 (1977) m^{-2}. The size of juvenile cohorts varied. The 1975 cohort of *A. arbustorum* was three times as great as the 1976 cohort. In *C. hortensis* the 1975 cohort was half of the 1976 cohort. First year survival (October to October) of the 1975 cohort was 31 % (*C. hortensis*) and 15 % (*A. arbustorum*). Annual production due to growth and reproduction was: 14.4 (1975) and 12.2 (1976) kcal. m^{-2} for *A. arbustorum* 5.2 (1975) and 4.7 (1976) kcal. m^{-2} for *C. hortensis*.

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INTRODUCTION

The gastropods are among the most conspicuous invertebrate animals. In spite of this, relatively few population studies have been carried out for terrestrial gastropods. Mason (1970 a,b) studied several species of small litter dwelling snails, and Jensen (1975) has given an energy budget for *Arion ater* (L.). However, most attention has been drawn to the polymorphic helicid snail *Cepaea nemoralis* (L.), and its population ecology has been studied by several authors (e.g. Wolda 1963, 1972, Wolda & Kreulen 1973, Richardson 1975, Williamson 1976, Williamson et al. 1977, Oosterhoff 1977). The sibling species *Cepaea hortensis* (Müll.) has received attention because of its polymorphism (See Jones et al. 1977 for a review), and its life history is known from England (Williamson 1978). *Arianta arbustorum* (L.) has been much less studied, in spite of being common through most of Europe (Taylor 1914). It is a polymorphic helicid snail being dimorphic for colour (brown or yellow) and banding pattern (band present or absent). Apart from a study of growth, reproduction and hibernation in Southern Finland (Terhivuo 1978), little is known about the population ecology of the species.

This paper describes the results of a two year study on a polymorphic population of *C. hortensis* and a monomorphic (brown, banded) population of *A. arbustorum* in a rich herbaceous community in Western Norway. Details of the polymorphism of *C. hortensis* are published elsewhere (Andreassen 1978).

STUDY AREA

The field work was carried out at Lysandtræ (UTM 32VLM 047 785), Os, 30 km south of Bergen, Western Norway. Sampling was performed within an open area of 2000 m² situated on a slope facing west. The vegetation is dominated by *Filipendula ulmaria* (L.) Maxim. and grasses of the following species: *Phleum pratense* L., *Holcus lanatus* L., *H. mollis* L., *Deschampsia caespitosa* (L.) PB., and *Dactylis glomerata* L (Fig. 1). The area used to be grazed by sheep. Small stands of *Salix caprea* L. and *Prunus spinosa* L. suggest that the area is reverting to scrub and woodland. Other snails present included *Trichia hispida* (L.) and *Nesovitrea hammonis* (Strøm).

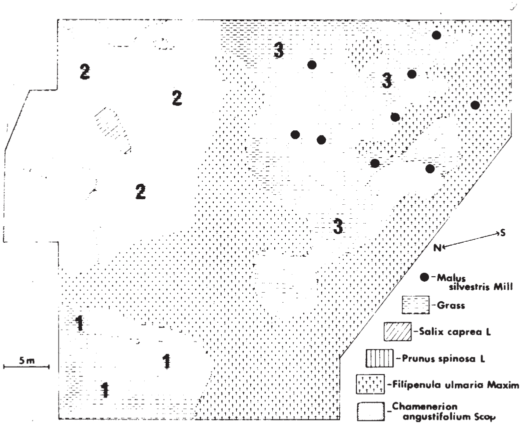

Fig. 1. Map of the vegetation at the sampling site, Os. Three different grass areas are distinguished: (1) dominated by *Deschampsia caespitosa;* (2) several species of grasses are abundant; (3) dominated by *Holcus mollis*.

METHODS

Estimates of population size were obtained by quadrat sampling between June 1975 and August 1977. No sampling was performed during winter. Samples were taken every third week (in 1977 only on two occasions). Twenty 0.25 m^2 quadrats were selected by random number co-ordinates. Snails and their eggs were collected by carefully removing the vegetation from each quadrat and sorting it thoroughly in the laboratory. The soil surface was also searched. Snails that had formed a shell lip were regarded as adults. The size of the snails was determined by measuring the maximum shell diameter with a vernier caliper to the nearest 0.1 mm. The smallest juveniles (less than 6 mm) were measured under a binocular microscope using a stage micrometer. The egg clutches were brought into the laboratory and put into test tubes with moistened moss. The tubes were kept in darkness at room temperature and the time to hatching and hatching success recorded. The efficiency of the quadrat sampling procedure was tested by releasing at random 14 small snails of *A. arbustorum* and 67 of *C. hortensis* (2.8—8.0 mm) in a 0,25m^2 quadrat in a locality where these snails were known not to occur. After allowing the animals to disperse in the vegetation for five minutes, the quadrat searching procedure was followed. The relation between mean shell diameter (D mm) in each size class and the proportion found (E%) was described by a regression equation: $E = 13.54D - 3.06$ ($r^2 = 0.974$) (Fig. 2). This equation was used to correct the figures on abundance for each mm size-class.

Two cage experiments were carried out. (1) The growth of larger juveniles was investigated in 1976 by using five cages (50 x 50 x 60 cm) at the sampling site at Os (20 snails of each species in the cages). The snails were individually numbered with nail varnish. (2) Small juveniles were put into flowerpots half-filled with soil and mosses and fed on carrot and lettuce. Empty snail shells were used as a calcium source. The flowerpots were placed underneath a hedgerow near the Zoological Museum, Bergen. The snails were measured at irregular intervals.

Snails from the quadrat sampling in 1976 were collected to determine weight and energy content. They were killed by freezing, then thawed and the maximum diameter of the shell measured. Bodies were extracted, dried at 60°C for at least 36 hours and weighed. The tissue was ground, compressed into pellets and dried again before being weighed and burned in a modified Phillipson Microbomb Calorimeter (Phillipson 1964). The ash remains of the burned

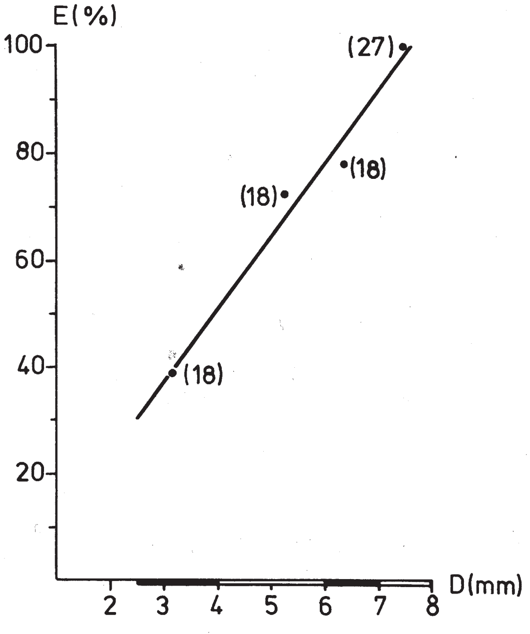

Fig. 2. Searching efficiency test. The proportion (E) of snails found by using the quadrat sampling procedure in relation to mean shell diameter (D) for each shelldiameter group. The regression line is drawn. Sample size in parenthesis.

sample were weighed and calorific content per ash free dry weight calculated. Eggs collected on 3 August 1977 were also burned in this instrument.

RESULTS

Life-cycle and growth

The snails were divided into 1 mm size-classes and the resulting size-frequency distributions are shown in Fig. 3. *(A. arbustorum)* and Fig. 4 *(C. hortensis).* On most sampling occasions three peaks can be recognized suggesting three years from hatching to lip formation (i.e. adult stage) for both species. Juveniles were allocated into cohorts by probability paper analysis (Harding 1949). However, in some cases the boundaries between cohorts were difficult to draw and the separation of cohorts was not always totally objective.

The cage experiments showed that growth rates varied considerably both between clutches (Table 1), individuals and with time of the year. However, the growth in shell diameter of individual *A. arbustorum* fits reasonably with changes in mean shell diameter of the cohorts (Fig. 5). At the start of the cage experiment in late May 1976, 50 snails of this species belonged to the 1974 cohort and 22 snails to the 1973 cohort. 2 individuals of the 1974 cohort and 17 individuals of the 1973 cohort formed a lip during summer 1976. No snails became adults after 17 July.

For unknown reasons *C. hortensis* almost stopped growing after three weeks in captivity and individual growth patterns could not be followed.

However, growth rates for both species were determined from changes in mean shell diameter of the cohorts. Shell growth started in May and continued until September. Around midsummer, the rate of increase in mean shell diameter peaked at 0.3—0.6 mm per wk. *(C.hortensis)* and 0.4—0.7 mm per wk. *(A. arbustorum).*

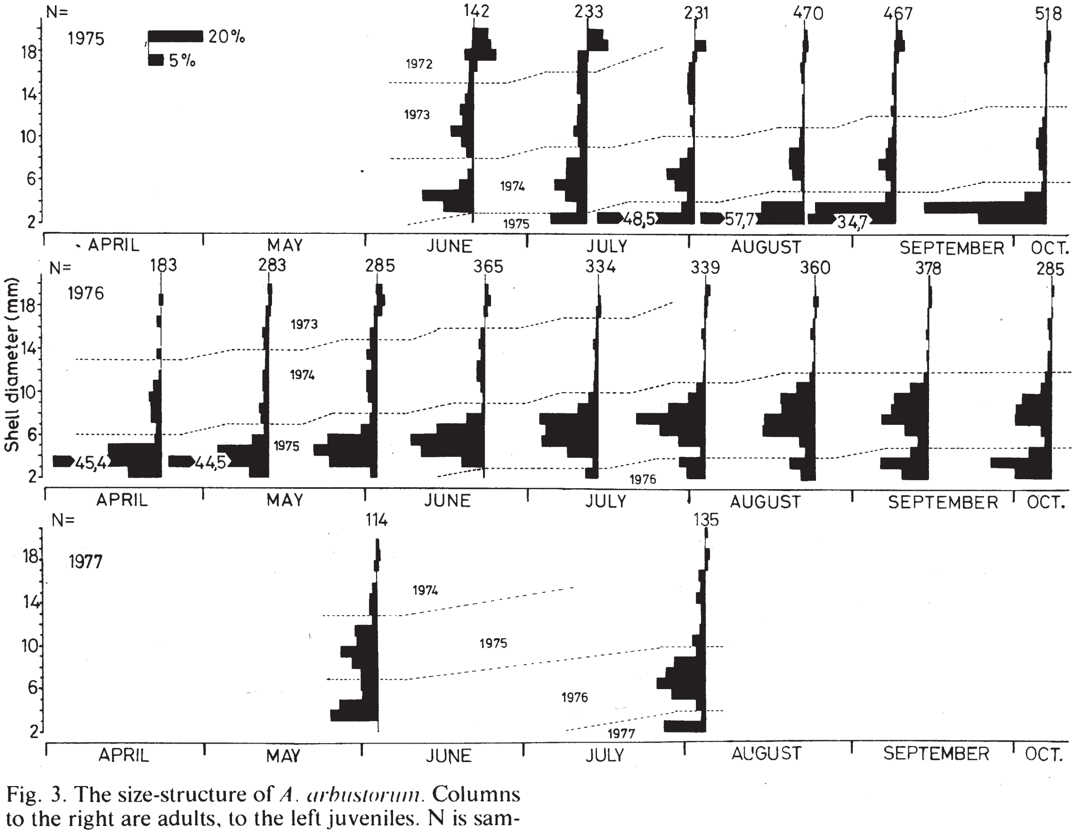

Fig. 3. The size-structure of *A. arbustorum*. Columns to the right are adults, to the left juveniles. N is sample size. The cohorts are indicated.

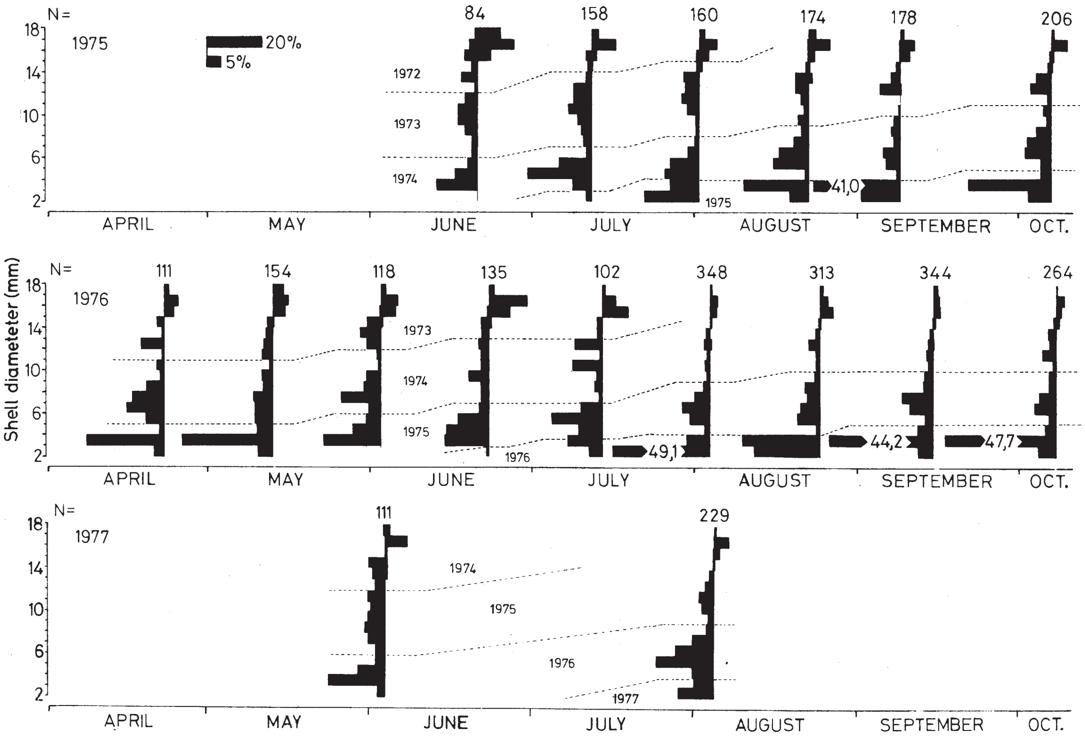

Fig. 4. The size-structure of *C. hortensis*. See Fig. 3 for explanation.

Clutch size

The eggs of *A. arbustorum* are off-white, soft and nearly spherical measuring 2.72 ± 0.12 x 2.86 ± 0.11 mm (minimum and maximum «diameter»; S.D.; n = 48) and are easily separated from eggs of *C. hortensis*: pure white, hard and oval measuring 2.36 ± 0.04 x 2.85 ± 0.13 mm (n = 18) (Fig. 6).

A. arbustorum eggs are laid in clusters at the roots of plants or in the moss. Laboratory studies at approximately 20°C showed that the eggs hatched in 20 days. A period of three weeks between each sampling ensured that few eggs were laid and hatched between sampling and that few eggs present on one sampling occasion remained as eggs on the next. Although oviposition seemed to occur throughout most of the season in both years, there was a definite peak in egg-laying in August and a smaller peak in June (Table 2). The production of eggs was three times as great in 1975 as in 1976. Clutch size varied con-

Table 1. Mean size (mm) ± S.D. of juvenile *A. arbustorum* hatched in 1976 and reared in flowerpots to 16 October 1976. Sample size in parentheses.

Date	Range of the 1976 cohort	Clutch hatched 15 June 1976	Clutch hatched 2 July 1976	Clutch hatched 6 July 1976
21 June 1976	2.0—2.9	2.8 ± 0.2 (20)		
6 July 1976	2.0—2.9		2.6 ± 0.1 (41)	2.6 ± 0.1 (28)
30 August 1976	2.0—3.9	3.8 ± 0.3 (12)	3.5 ± 0.2 (29)	5.2 ± 0.5 (17)
16 October 1976	2.0—4.9	4.4 ± 0.3 (5)	3.9 ± 0.6 (35)	5.8 ± 0.5 (21)

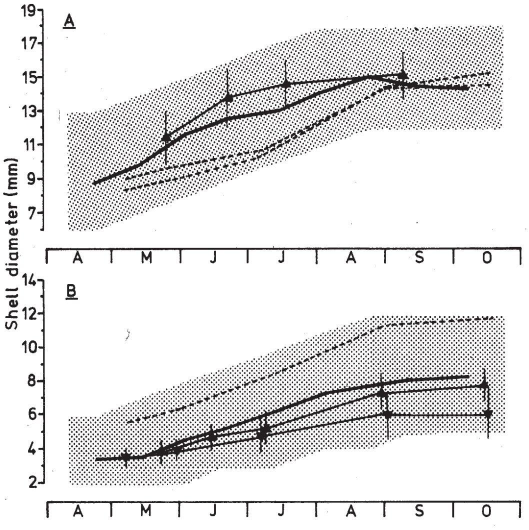

Fig. 5. Growth of *A. arbustorum* in 1976. Shaded area is the range and thick, unbroken line the mean size of *(A)* the 1974 cohort and *(B)* the 1975 cohort. Triangles are mean size (± S.D.) of snails belonging to *(A)* the 1974 cohort and reared in field cages, and *(B)* the 1975 cohort and reared in two different flowerpots. Stippled lines show the shell diameter of individual snails reared in flowerpots and hatched *(A)* in late May 1975 and *(B)* 30 June 1975.

Table 2. Number of clutches, eggs, and mean clutch-size of *A. arbustorum* from the quadrat sampling.

	Number of clutches per m^2	Number of eggs per m^2	Mean clutch size ± S.D.	Sample size
12 May* 1975	1.6	41.6	26.0 ± 12.7	2
20 June	1.6	111.2	69.5 ± 26.5	8
11 July	0.4	21.2	53.0 ± 1.4	2
1 August	2.6	158.9	61.1 ± 31.9	13
21 August	6.2	261.6	42.6 ± 18.1	27
8 September	1.2	44.8	37.3 ± 26.9	6
6 October	0.0			
Total 1975	13.6	639.3	49.7 ± 25.7	58
22 April 1976	0.0			
12 May	0.0			
2 June	0.2	5.6	28.0	1
22 June	1.4	48.2	34.4 ± 19.5	7
13 July	0.2	16.4	82.0	1
3 August	1.8	95.2	52.9 ± 12.2	9
23 August	0.6	20.0	33.3 ± 5.1	3
14 September	0.2	7.2	36.0	1
7 October	0.0			
Total 1976	4.4	192.6	43.8 ± 18.2	22
3 June 1977	0.0			
4 August	1.0	48.2	48.2 ± 10.8	5

* Based on twenty 25 x 25 cm, quadrats.

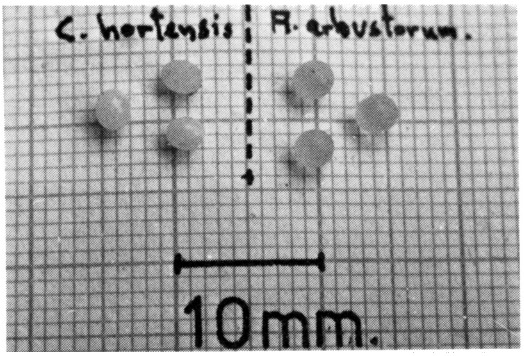

Fig. 6. Eggs of *A. arbustorum* and *C. hortensis*.

siderably ranging from 16 to 114. A cluster of 110 eggs was found on 21 August 1975, but in the laboratory some of the eggs hatched on 23 August and the rest on 3 September suggesting that the cluster consisted of two clutches. This was also observed in two other cases and may explain some of the very large clutches. Mean clutch size was larger in 1975 than in 1976 although the difference was not significant ($t = 0.98$, $P > 0.5$). Mean clutch size for all years was 48.1. In 1975 a decline in mean clutch size from June to September was observed (Table 2) and analysis of variance showed that the differences were significant ($F = 3.09$, $P < 0.05$, $df = 4{,}51$). There was a tendency for a similar decline from July to September in 1976, but the sample sizes are too small for statistical analysis. The data suggest that both early and late clutches tend to be relatively small. The overall hatching success in the laboratory was 65.9% ($n = 1388$) and 69.4% ($n = 873$) in 1975 and 1976 respectively. But the variation between clutches was great ranging from 0% to 100% hatching success.

Egg clutches of *C. hortensis* (1 in 1975, 5 in 1976 and 7 in 1977) were found between June and August. Hatching time seemed to be c. 3 wks: a freshly laid clutch took this time to hatch in the laboratory at 20°C. Comparison with juvenile densities suggest that only a minor proportion of egg clutches were found, probably because most were buried in the soil. The range of clutch size was 21—63 eggs, with a mean of 37.9 ± 12.7 (S.D.; $n = 13$).

Dispersion, abundance and mortality

A. arbustorum. The population is aggregated and the index of dispersion (variance to mean ratio, Southwood 1966) differed significantly ($P < 0.01$) from unity for juveniles on all sampling occasions. Larger juveniles (shell diameter ≥ 6 mm) also had an aggregated dispersion pattern ($P < 0.01$). The aggregation of the adults was significant ($P < 0.05$) on all occasions in 1975 except 21 August. In 1976 however, a significantly aggregated dispersion was found only on 2 June and 13 July ($P < 0.05$).

Mean adult density decreased from 4.9 individuals per m^2 in 1975 to 1.6 in 1976; the difference being significant ($d = 3.82$, $p < 0.05$) (Fig. 7a). This decrease corresponds to a 67% reduction in population size per year. The actual adult mortality was probably larger because of recruitment of adults in early summer 1976 (Fig. 7a). Adult density decreased further (to 0.8 m^{-2}) in 1977. The density of juveniles was high and the 1975 cohort amounted to nearly 200 individuals per m^2 in October 1975 (Fig. 7b). The survival of first year juveniles was approximately 10% (starting at the egg stage; Table 3). Of the animals belonging to the 1975 cohort, another

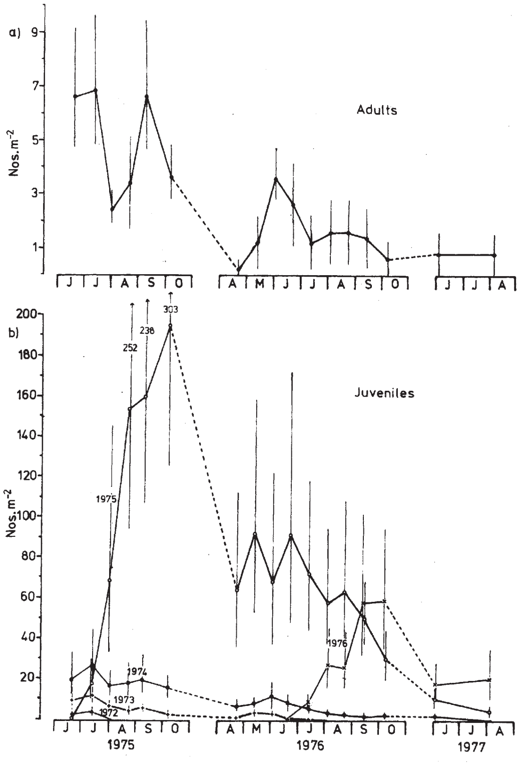

Fig. 7. A. arbustorum. Number m^{-2} ± 95% confidence limits of adults and juveniles (divided in cohorts and corrected for estimated searching efficiency).

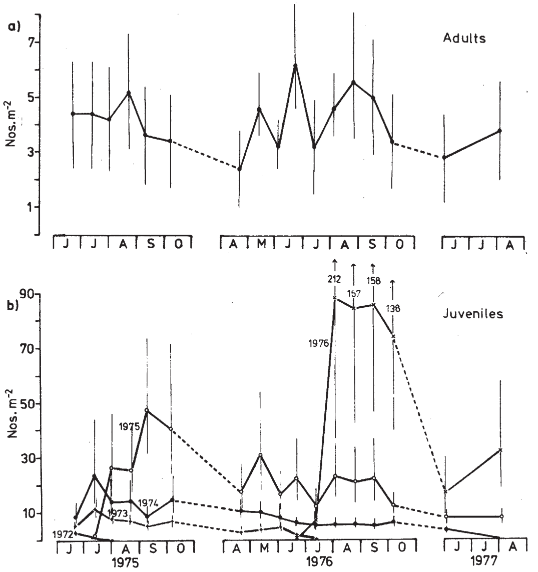

Fig. 8. *C. hortensis.* Number m^{-2} (± 95% confidence limits) of adults and juveniles (divided in cohorts and corrected for estimated searching efficiency).

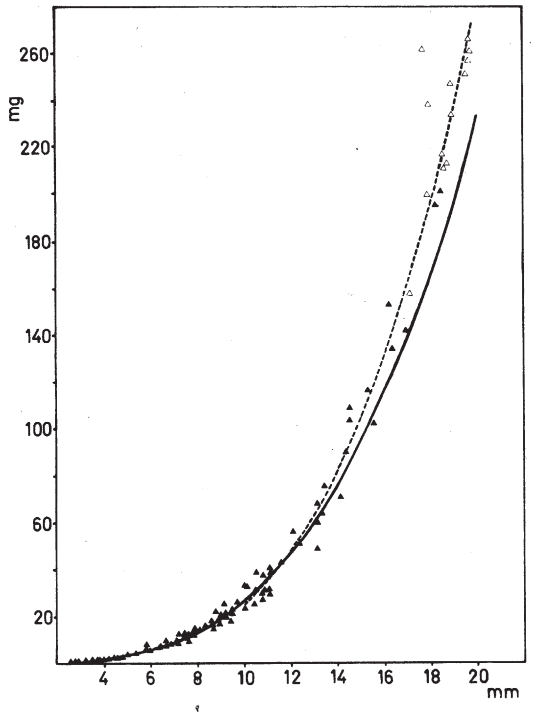

Fig. 9. Relationship between ash free dry tissue weight (W) and maximum shell diameter (D) in *A. arbustorum.* All data (solid line): $\log W = 3.101 \log D - 1.668$ ($r^2 = 0.992$, $n = 107$). Above 10 mm (dashed line): $\log W = 3.474 \log D - 2.066$ ($r^2 = 0.974$, $n = 46$). Below 10 mm (not plottet): $\log W = 3.001 \log D - 1.565$ ($r^2 = 0.988$, $n = 61$). Open triangles are adults, black juveniles.

87.8 m^{-2} indicating a higher production of juveniles in 1976. Unfortunately the number of eggs laid is not known. It is therefore impossible to make survival tables starting at the egg stage. However, the survival of the 1975 cohort from October 1975 (the snails being approximately two months old) to October 1976 was 31%. Overall weekly survival rate was better during winter (0.991 and 0.973) than during summer (0.967 and 0.962) (Table 4).

Biomass and production

The relation between maximum shell diameter and mg. ash free dry tissue weight is shown in Fig. 9 *(A. arbustorum)* and Fig. 10 *(C. hortensis).* No changes with time of year were found, and all data were combined. To obtain a better fit to the data on *A. arbustorum,* separate regressions were calculated from the log-transformed data above and below 10.0 mm.

No significant seasonal trends in the energy content of the snails were found (Analysis of variance; $F = 0.75$, $P > 0.05$, df = 4,55 and $F = 1.47$, $P > 0.05$, df = 5,64 for *C. hortensis* and *A. arbustorum* respectively). The energy content of adult and juvenile *C. hortensis* differ significantly ($t = 2.16$, $P < 0.05$) from each other (Table 5). No such difference was found for *A. arbustorum.* The eggs have a very low energy content.

In 1975 adults of *A. arbustorum* constituted 53% of the biomass (Fig. 11a). In 1976, however, 71% of the standing crop was due to the juveniles because of the abundant 1975 cohort and the decrease in the adult population. In late summer and autumn the 1975 cohort alone accounted for more than 50% of the standing crop. The mean values of the biomass were: 11.3 (1975), 6.9 (1976) and 3.5 (1977) kcal.m^{-2}. The adults of *C. hortensis* constituted approximately half of the biomass in all years (Fig. 11b): 50% (1975), 54% (1976) and 43% (1977). Annual mean values of the standing crop were relatively constant: 5.6 (1975), 5.3 (1976) and 5.1 (1977) kcal.m^{-2}. For both species, eggs and newly hatched juveniles, although numerically abundant, contributed little to total standing

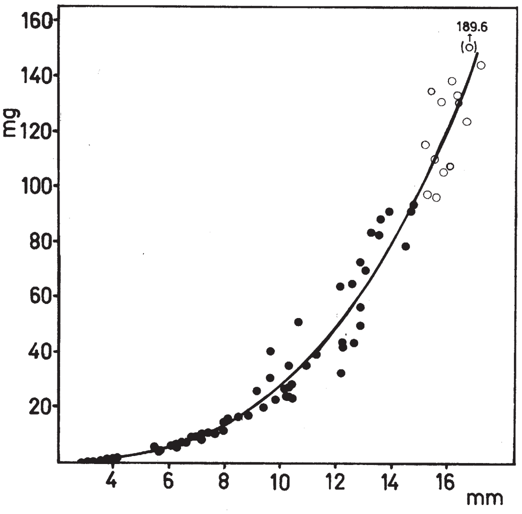

Fig. 10. Relationship between ash free dry tissue weight (W) and maximum shell diameter (D) in *C. hortensis* (all data): logW = 3.115 logD — 1.663 (r^2 = 0.988, n = 90). Open circles are adults, black juveniles.

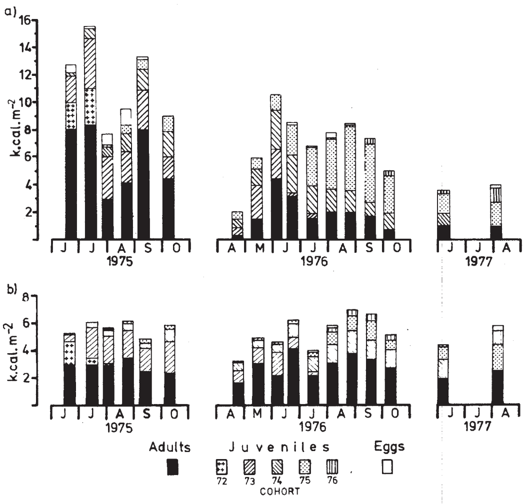

Fig. 11. Population standing crop (kcal.m.$^{-2}$) of (a) *A. arbustorum*, (b) *C. hortensis*).

crop. However, the contribution by *C. hortensis* eggs is almost certainly underestimated.

The production due to growth was calculated using Allen's (1951) graphical method (Table 6). The production of juveniles becoming adults can be approximately estimated by making the following assumptions: (1) The 1972 cohort matured in the period May—August 1975, the 1973 cohort one year later. (2) Weekly survival rate was 0.96 for both species during the period the snails matured (mean value from Table 4). The latter is a reasonable assumption because data on *C. nemoralis* suggested that the process of becoming adult is not a particularly hazardous stage of life (Williamson et al. 1977).

Table 5. Calorific values of adults, juveniles, and eggs of *A. arbustorum* and *C. hortensis*.

	Kcal/g.ash free dry tissue weight ± S.E.	Sample size
A. arbustorum		
Adults	5.27 ± 0.05	13
Juveniles	5.25 ± 0.03	57
Eggs	3.80 ± 0.05	8
C. hortensis		
Adults	5.31 ± 0.03	14
Juveniles	5.21 ± 0.02	46
Eggs	3.55 ± 0.01	10

Production due to reproduction was calculated as egg biomass. However, the number of *C. hortensis* eggs laid is not known; by assuming 50% hatching success (mean value for *C. nemoralis* (Wolda 1963, Wolda & Kreulen 1973)) an approximate production of eggs can be estimated from maximum density of newly hatched juveniles («youngest» cohort). Mucus production is not considered. As 30% of the production (valid for both species) in 1976 can be attributed to the period prior to 22 June, total production in 1975 was probably close to 14.40 *(A. arbustorum)* and 5.25 *(C. hortensis)* kcal.m^{-2}.

DISCUSSION

This study has shown that in Western Norway *A. arbustorum* and *C. hortensis* generally take three years from hatching to lip formation, i.e. to become adult. Grime & Blyth (1969) studied *A. arbustorum* in a north-facing slope at the Winnats Pass in Derbyshire, England. Their Fig. 1 suggests three years to lip formation. The same conclusion is drawn for *A. arbustorum* in Southern Finland (Terhivuo 1978), and for *C.*

Table 6. The production (kcal.m^{-2}) of *A. arbustorum* and *C. hortensis* in 1975 and 1976. Estimates based on Allen's (1951) graphical method and on biomass of eggs.

	1975		1976	
	20 June—6 October		12 May—7 October	
	A. arbustorum kcal.m^{-2}	*C. hortensis* kcal.m^{-2}	*A. arbustorum* kcal.m^{-2}	*C. hortensis* kcal.m^{-2}
1972 cohort	0.73	0.38		
1973 cohort	3.43	1.86	1.33	0.92
1974 cohort	1.92	0.77	3.43	1.53
1975 cohort	1.08	0.13	6.14	1.02
1976 cohort			0.35	0.24
Eggs	2.91	0.53	0.94	0.98
Total	10.06	3.67	12.19	4.68

nemoralis and *C. hortensis* in England (Williamson 1976, 1978). However, other studies have shown that *C. nemoralis* takes only two years to become adult in Holland (Wolda 1970) and perhaps in S. England (Cain & Currey 1968, Richardson 1972).

In captivity *C. hortensis* showed hardly any increase in shell diameter after late June. Richardson (1972) had the same experience with juvenile *C. nemoralis* kept in field cages in late summer. Thus, field cage experiments do not seem to be an applicable method for growth studies of *Cepaea*.

The aggregation found for *A. arbustorum* and *C. hortensis* could not be closely correlated with the type of vegetation. Even in areas with a relatively uniform plant cover, great variation in density exists. But in the north-eastern part of the study site (grass 2 in Fig. 1) few snails were found. This area is dominated by several species of grasses and a dense layer of the moss *Rhytidiadelphus squarrosus* Warnst. Compared to the rest of the study site the area appeared to be rather dry. Low humidity may account for the sparse population. In a small plot of *Chamenerion angustifolium* Scop. (Fig. 1) the density was 60% and 19% higher than average for *A. arbustorum* and *C. hortensis*, respectively. The aggregation of adult *C. hortensis* and *A. arbustorum* in 1976 coincided with the period prior to egg laying suggesting that mating behaviour was responsible. Limited dispersal by newly hatched snails was not the only factor responsible for the aggregation of juveniles because larger juveniles also were aggregated.

Density estimates of adult *A. arbustorum* (0.6—6.8 m^{-2}) and *C. hortensis* (2.4—6.2 m^{-2}) in this study are slightly higher than values reported for the extensively studied *C. nemoralis* viz. 0.3—1.0 m^{-2} and 0.9—5.0 m^{-2} for grassland (Cain & Currey 1968, Williamson et al. 1977), 1.9—2.8 m^{-2} for sand dunes (Richardson 1975) and 3.5 m^{-2} for dyke bank (Goodhart 1962). Williamson (1978) estimated adult population density of *C. hortensis* to 8.3 m^{-2} in a roadside verge in N.E. England. At Flesland, near Bergen, the density of *A. arbustorum* increased from 11.3 m^{-2} in June 1976 to 17.3 m^{-2} in June 1977 in a 90 m^2 plot of *Urtica dioica* L. and *Filipendula ulmaria* (mark-recapture; unpublished data). However, Grime & Blyth (1969) have pointed out that *A. arbustorum* is abundant in tall vegetation dominated by *U. dioica* and *Mercurialis perennis* L. and *C. nemoralis* is found at high densities (5.4—11.8 m^{-2}) in patches of nettles (Cain & Currey 1968). The high densities of helicid snails in stands of *U. dioica* are probably a result of food selection by the snails (Grime & Blyth 1969, Grime et al. 1970).

The reduction in mean adult density of *A. arbustorum* during the study period suggests an annual survival lower than 33% (1975—76) and 50% (1976—77). Annual survival values for *A. arbustorum* do not seem to be available in the literature, but at Flesland 81.4% of adult *A. arbustorum* survived from 12 June 1976 to 10 June 1977 (unpublished data). Adult survival has been estimated several times for *C. nemoralis*: 33% (recalculated after Richardson 1975), 50% (Schnetter 1951, Goodhart 1962, Wolda 1972), 70—75% (Cain & Currey 1968, Williamson et al. 1977). Compared to these values the survival of *A. arbustorum* at Os seems poor. The reason for the decrease in adult density of this species is not known. Sampling has probably not affected density because the vegetation has been removed from only 4% of the study site. Further, the *C. hortensis* population did not show any tendency to decrease during the same period. A high proportion of the mortality of adult *C. nemoralis* has been attributed to predation by thrushes (Cain & Currey 1968, Wolda 1972). There is no evidence of thrush predation at Os although both Redwing, *Turdus iliacus* L. and Blackbird, *T. merula* L. occur. The few broken shells that were found showed signs of rodent predation (Morris 1954). In both years adult density of *A. arbustorum* and *C. hortensis* declined in autumn, probably because recruitment has ended. Much of the reduction in density of adult *A. arbustorum* seems to have occurred between autumn 1975 and spring 1976 (Fig. 7a). Terhivuo (1978) estimated winter mortality for *A. arbustorum* to 3.3% among the adults. Population studies of *C. nemoralis* (Cain & Currey 1968) indicate that even in hard winters the mortality of adult snails from October to April was low and resistence experiments with the same species have used temperatures of −8°C to produce mortality (Lamotte 1959). This evidence suggests that normal extremes of cold do not cause heavy adult mortality during hibernation.

The searching efficiency test has an important effect on density estimates for small juveniles. Unfortunately, separate regression lines could not be drawn for *C. hortensis* and *A. arbustorum* because the sample size of the latter was too small. Difference in recovery could be expected due to difference in shell colour and/or behaviour. Behaviour will probably not seriously effect the result because only a five minute dispersion period was chosen prior to sampling (to prevent the animals from crawling out of the quadrat). Colour is certainly of minor importance compared to size. Therefore a single regression line, applied to both species, is considered justifiable. The searching efficiency test will not cope with buried, inactive snails. However, I have never found summer aestivating snails buried in the soil during the study period.

The production of eggs and juveniles of *A. arbustorum* was more than three times as great in 1975 than in 1976. The ratio of total egg number per m^2 to mean adult number per m^2 was 130.5 and 120.4 in 1975 and 1976 respectively. The 1975 ratio is probably an underestimate because of the lack of sampling from mid-May to mid-June. But few clutches seem to be laid in this period and the error is probably small. The reduction in adult density therefore accounts for most of the difference in total egg production.

The production of *C. hortensis* juveniles was nearly twice as great in 1976 as in 1975 although mean annual adult density was similar these years. Variation in the production of juvenile *C. nemoralis* has been shown by Wolda & Kreulen (1973) and Williamson et al. (1977).

Wolda & Kreulen (1973) compared an increasing and a decreasing experimental population of *C. nemoralis* and found that egg production, egg survival and juvenile survival were better in the former than in the latter. They estimated 26.8% and 1.1% survival for the first year (starting at the egg stage) for the increasing and the decreasing population respectively. In this study the first year survival of *A. arbustorum* was intermediate (10%) to that found by Wolda & Kreulen. After two years 6.1% and 3.0% had survived in the increasing and decreasing population respectively, compared to 0.7% for the 1975 cohort in this study. The survival of *A. arbustorum* for the first two years is therefore more similar to the declining population of *C. nemoralis*. In addition *A. arbustorum* takes one year more than *C. nemoralis* (in Holland) to mature and it is therefore likely that few juveniles of the abundant 1975 cohort will reach adulthood. Juvenile survival seems to be a key factor for year class success. Wolda & Kreulen (1973) and Williamson et al. (1977) claimed that survival of juveniles in their first year is of critical importance in determining year class success. This study has shown that survival the second year may be equally important.

The mortality factors are not known. Wolda (1963) and Cain & Currey (1968) observed the snail, *Oxychilus cellarius* (Müll.), eating eggs of *C. nemoralis*. *O. cellarius* is present at Os but its significance as an egg predator is not known. In two clutches of *A. arbustorum* found at Os on 1 August 1975 and 3 August 1976 no eggs hatched because they were inhabited by unidentified *Diptera* larvae. Wolda & Kreulen (1973) suggested that drought as well as predation by shrews, toads and frogs are the major factors affecting juvenile survival. Some beetles eat small juveniles (Cain & Currey 1968, Pollard 1975). Richardson (1972) found that the most significant predator on juveniles was probably the shrew, *Sorex araneus* L. *Apodemus sylvaticus* L. and *S. araneus* fed radily on young *Helix pomatia* L. in the laboratory (Pollard 1975). Shrews are present at Os and may eat juveniles, but direct evidence is missing. Juveniles seemed to survive better during winter than during summer (Table 6), suggesting the existence of an important mortality factor operating in summer. It may be beetles, frogs or toads which are hibernating during winter, or it may be drought.

Cameron (1970) found adult *C. hortensis* to be more drought resistant than *A. arbustorum*. Unfortunately no data is available for juveniles. However, in daytime sampling juvenile *A. arbustorum* seems to be more frequent on the ground and less frequent in the vegetation than *C. hortensis*, and this could be a response to the vertical humidity gradient. On the ground, *A. arbustorum* would be more susceptible to predation by frogs, toads and beetles and this might partially account for the greater mortality observed for juveniles of this species. However, more work has to be done to confirm these ideas.

A decrease in clutch size during the breeding season is often observed in animal populations, particularly in birds (Lack 1966) but the phenomenon also occurs in experimental populations of *C. nemoralis* (Wolda 1963, Wolda & Kreulen 1973). This survey has shown the same trend in a natural population of *A. arbustorum*. For birds the decreasing clutch size is often attributed to food shortage (Lack 1966). In *C. nemoralis*, however, a change in the quality of the food has been suggested as the factor responsible (Wolda & Kreulen 1973). It has been established that food quality affects clutch size in *Lymnaea stagnalis* (L.) and *L. elodes* Say (Steen 1967, Eisenberg 1970). In contrast to *C. nemoralis*, early clutches of *A. arbustorum* tend to be rather small. The quality of food may be inadequate after winter or the snails may be in poor condition after the hibernation. It is difficult to imagine that the amount of food available for the snails may cause the variation in clutch size.

The energy content of eggs for both species was very low. Richardson (1972) also found a relatively low energy value for *C. nemoralis* eggs (c. 4 kcal./g. ash free dry weight). He suggests that this could be an underestimate due to incomplete combustion. In a recently published paper on calorimetry of *Helix pomatia*, Sisula & Virtanen (1977) found that the ash content determined by oxygen-bomb combustion was underestimated by one-third as compared to that determined by muffle furnace incineration. Further, the ash content was significantly affected by prestorage homogenization and storage time. Thus expressing results in terms of ash free dry weights may not necessarily improve the comparability of data.

Mucus production constitutes an appreciable proportion of yearly total production in gastropods: 36% for *Ancylus fluviatilis* Müll. (Otto 1976) and 31—49% in *C. nemoralis* (Richardson 1975, Williamson 1975). This part has been neglected in this study and only production due to growth and reproduction is considered. Annual production has been estimated for *C. nemoralis* in England (3.80—4.18 kcal.m^{-2} (Richardson 1975) and 3.33—4.51 kcal.m^{-2} (Williamson 1975)) and for *Arion ater* in Denmark (2.85 kcal.m^{-2} (Jensen 1975)). The production estimates of *C. hortensis* (5.25 and 4.68 kcal.m^{-2}) are slightly larger and the production of *A. arbustorum* (14.40 and 12.10 kcal-m^{-2}) considerably larger than the estimates for *C. nemoralis* and *A. ater*. The differences are primarily due to juvenile density. The juvenile density of *C. nemoralis* is estimated to be 9.2—22.4 m^{-2} (Table 6, Williamson et al. 1977) and approximately 6—23 m^{-2} (Fig. 1b, Richardson 1975), considerably lower than that estimated for *C. hortensis* (16.7—116.7 m^{-2}) and *A. arbustorum* (103.5—212.8 m^{-2}). However, the values can not be directly compared because the densities in this study are corrected for estimated searching efficiency. Nevertheless, uncorrected juvenile densities are also high; 12.4—65.0 m^{-2} *(C. hortensis)* and 55.4—100.0 m^{-2} *(A. arbustorum)*.

This study has shown that *A. arbustorum* produced more offspring and suffered heavier mortality than *C. hortensis*. However, both species have a high potential fecundity and this makes extinction unlikely. A single successful year class may raise adult density considerably.

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