Michał WOYCIECHOWSKI

Institute of Systematic and Experimental Zoology, Polish Academy of Sciences,
Sławkowska 17, 31–016 Cracow, Poland

EXPERIMENTAL STUDIES OF THE EXPLOITATION AND OVERCROWDING OF A NATURAL POPULATION OF THE ROMAN SNAIL, *HELIX POMATIA* L.

ABSTRACT: Surveys of the Roman snails were carried out in the Ojców National Park, at three experimental sites. In a population that had been rejuvenated due to exploitation a reduction in fecundity was found; with an increased mobility of individuals this meant a lack of partners for mating. Food supplies and migrations are factors determining the density. An experimental increase in density caused by man accelerates the mobility and reduces the fecundity. Emigration was more often found among introduced individuals, differing in size from the native ones. On the basis of the annual shell increments it has been established that the growth of an individual usually continues for 4 years, often still after the attainment of sexual maturity, whereas the body size of individuals from local habitats varies as a result of selection.

KEY WORDS: Terrestrial snails, *Helix pomatia*, Ojców National Park, field experiments, population, exploitation, overcrowding, density regulation.

Contents

1. INTRODUCTION

In studies of the Roman snail (*Helix pomatia* L.) the populational approach seems to be justified by many reasons. Attention has more and more often been given to the economic importance of the species and the possibility to increase its exploitation. On the other hand, it is supposed that an irrational collection leads on to the extinction of the Roman snail in many regions of its natural occurrence (U r b a ń s k i 1963, D z i a b a-s z e w s k i 1975, S t ę p c z a k 1976). Apart from the economical aspects and the nature conservancy requirements, the Roman snail is a convenient object for ecological studies (Ł o m n i c k i 1971). The possibility of marking individuals with unique numbers, their low mobility and high density, and the possibility of determining their age (P o l l a r d 1973) are the main features due to which a Roman snail population is, as it were, a model, whereas the phenomena observed in it can be referred to many other animal populations. This model is the more valuable as it is made up of individuals occuring in a natural habitat.

Though there have been many studies concerning this species, the problems of its maturation rate and the determination of the age of young individuals remain unsolved. None of the papers has described the response of a natural population to its exploitation, or overcrowding. The authors discuss also the hypothesis of population regulation in the Roman snail (Ł o m n i c k i 1971, P o l l a r d 1975).

In the experiment described in this paper the density of Roman snails was reduced at one of the study sites, while their number at another site was increased. The results obtained for the experimental sites were subsequently referred to the situation seen in an unchanged control site. Differences in the response of the individuals to the experiment were accounted for by the observed individual variation, and the age structure of a population.

In the considerations here presented, individuals from the study sites are referred to as local populations. At the beginning, an assumption was made that these populations were collections of individuals without any interrelations, to be able then to check this assumption, or reveal relationships.

2. STUDY AREA AND METHOD

The investigations were carried out in the years 1974 and 1975, in the Ojców National Park, at three equal-sized sites designated as E, I and C. Site E was marked out on a rock ledge, about 2 m above the bottom of the Sąspowska Valley. The two other sites with a distance of about 40 m separating them, were located on the Panieńskie Skały, at a height of about 25 m above the bottom of the Prądnik Valley. The plots, square in shape and with a side length of 14 m, were overgrown mainly with a herbaceous vegetation, typical of southern slopes with a shallow, dry and stony soil (M e d w e c k a-K o r-n a ś and K o r n a ś 1973). On this ecotone habitat, partially shaded by trees and shrubs, the density of the snails was especially high. Site E was the only one bordering on a moist meadow.

The experiment in which the density of Roman snails at two experimental sites, E and I, was changed was carried out on June 26, 27, 1974. On site E, 125 individuals were found which were subsequently transferred to site I. On site I, the density of the snails

was additionally increased by introducing 92 individuals collected on the same days in areas at a considerable distance from the study sites. After being marked, the introduced snails at site I were distributed in close vicinity of the native individuals, two or three new individuals were added to each of them.

Surveys were carried out at each site once a week throughout the period of activity of the snails, from the 10th of May to the 14th of September, 1974, and from the 10th of April to the 25th of September, 1975. During the survey, the site and its immediate surroundings were carefully searched and each Roman snail with fully developed shell, and each of those whose shells were assumed to be in the third season of their growth, was marked with a unique number. Younger individuals which could not be marked with permanent numbers were only measured and the results were taken into account when presenting the seasonal growth in shell size of age classes. Snails with shell increments during the observation year were considered to be young (J), their age, established on the basis of annual shell increments, was designated with numbers 1 to 6 indicating in which consecutive shell-growth season a snail was. Individuals with completed shell growth were placed in the adult group (A) divided into two age classes on the basis of the colouration of the shell. Individuals whose shells had lost the periostracum, and were almost white, were included in the old adult class (Aa), whereas those whose shells had even partially retained the periostracum, and because of this were brown, were included in the young adult class (Aj). In 1975, among the adult individuals another age class could be distinguished (Ajj); it included snails whose shells had still grown in size a year before. In the given year, age class membership was constant.

For the marking of the snails the method applied by Ł o m n i c k i (1971) was used. In this method the sequence numbers are painted on the shells. The painting of several identical numbers on the shell, corrected if necessary, considerably increased the durability of the marking.

During each survey the unique numbers of individuals were written in the appropriate 1 m^2 plot on the map of a site. At the study sites, guidance was provided by marked poles driven into the ground and dividing the study sites into squares, 2 m in side length. For each snail found, the age class was determined and shell measurement was made. The adopted measure of shell size was the so-called height of shell, or distance between the apex and the farthest edge of the shell aperture.

Data from experimental and control areas were a base for the comparison of number of snails and its change affected by the experiment. Simultaneously, observations carried out beyond experimental areas gave possibility to gather more information on the behaviour, growth and mobility of individuals. In the paper, only these observations from control site (C) were used which concerned the reproduction activity of snails; the other were omitted in order to avoid additional problems connected with seasonal migration of local population.

Changes in population size, or proportions of the individual age classes were assessed by the chi-square test, applying Yates's correction in necessary (B l a l o c k 1977). Smaller samples were compared by Fisher's test. Student's t-test was used for comparing average shell sizes of different groups of individuals. The distance covered by the snails was estimated by calculating the distance between the centres of the 1 m^2 plots in which a particular individual was found in the consecutive surveys. The coordinates of these plots were also used for calculating the home ranges, assuming that all captures are equivalent.

The material collected in the years 1974, 1975 included 1599 Roman snails of which 1397 individuals were marked with unique numbers. During the two years, at all the sites 125 surveys were carried out during which 5860 captures of the particular individuals were made at sites E and I.

3. RESULTS

3.1. ACTIVITY AND POPULATION SIZE

In the two study years, 1974 and 1975, the Roman snails began their seasonal activity in the first half of April. In 1975, surveys were started before the snails had emerged from hibernation. It was established then that at site I the first individuals appeared on April 10, about 10 days earlier than at site E (Fig. 1), located closer to the bottom of a valley where more adverse weather conditions prevailed. In both study years the peak activity, as measured by the number of individuals captured, of the adult A group of snails occurred at site E during the first days of June, and at size I — in the second half of May. Individuals whose shell growth had not been completed (J), did not show periods of intensified activity (Fig. 1). The results discussed do not take into account the youngest snails which hatched in the current year of observation, or a year before, and had not been marked with unique numbers. These individuals occurred in large numbers in September when the activity of the older snails was already ending. This finding is confirmed by observations reported by other investigators (U r b a ń s k i 1963, Ł o m n i c k i 1971).

Figure 2 presents the number of Roman snails observed at the study sites in the year 1974 and 1975, divided into age classes. Marked in the Figure are also the numbers of snails captured prior to the experiment, to determine the changes caused by the latter. These data indicate that before the experiment at site E 1.7 times as many adult individuals, and 1.2 times as many young individuals were found as at site I. The percentage of adult snails in the total number of marked individuals before the experiment did not significantly differ between the two sites (E — 66.8%, I — 58.6%, χ^2 = 2.724, df = 1, $0.10 > P > 0.05$).

Though during the experiment care was taken to collect all snails from site E, the individuals collected represented 56.1% of the group A and 49.4% of group J snails found at this site before the day of exploitation (Fig. 2). During the same period of the following season, that is, between May 6 and June 24, 1975, the effects of the exploitation could only by seen in the adult group, because the number of individuals observed in this group represented 61.9%, and in the young group 93.5% of the numbers found before the exploitation. For reasons of mathematics, the changes observed at site E cannot be confirmed in a simple way by statistical tests. The results obtained were influenced not only by the ecological conditions changed due to the exploitation, but also — and primarily — by the exploitation itself. However, it may be presumed that as a result of the reduced density, there occurred a decrease in the pressure by the oldest age classes, due to which an ecological situation arose where the youngest of the age classes grew in numbers (Fig. 2).
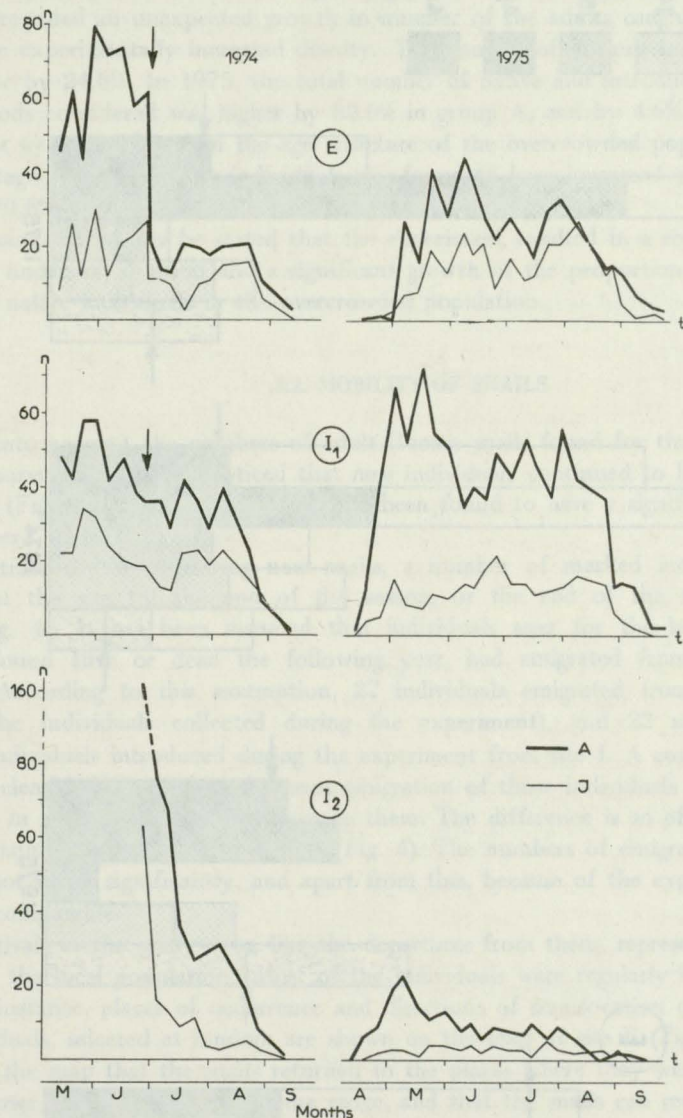
Fig. 1. Number (n) of young (J) and adult (A) individuals captured at sites E and I (I_1 — native individuals, I_2 — introduced individuals) in the successive surveys (t) in both study years
The arrow indicates the beginning of the experiment

By introducing new Roman snails onto sites l in 1974, an increase in density was caused, in group A by 172.8%, and in group J by 95.4% of the number of individuals recorded for this site before the experiment (Fig. 2). As during a season the individuals constantly belonged to the particular age class, a possible effect of overcrowding on the age structure of the population could also be expected a year later. A comparison of the
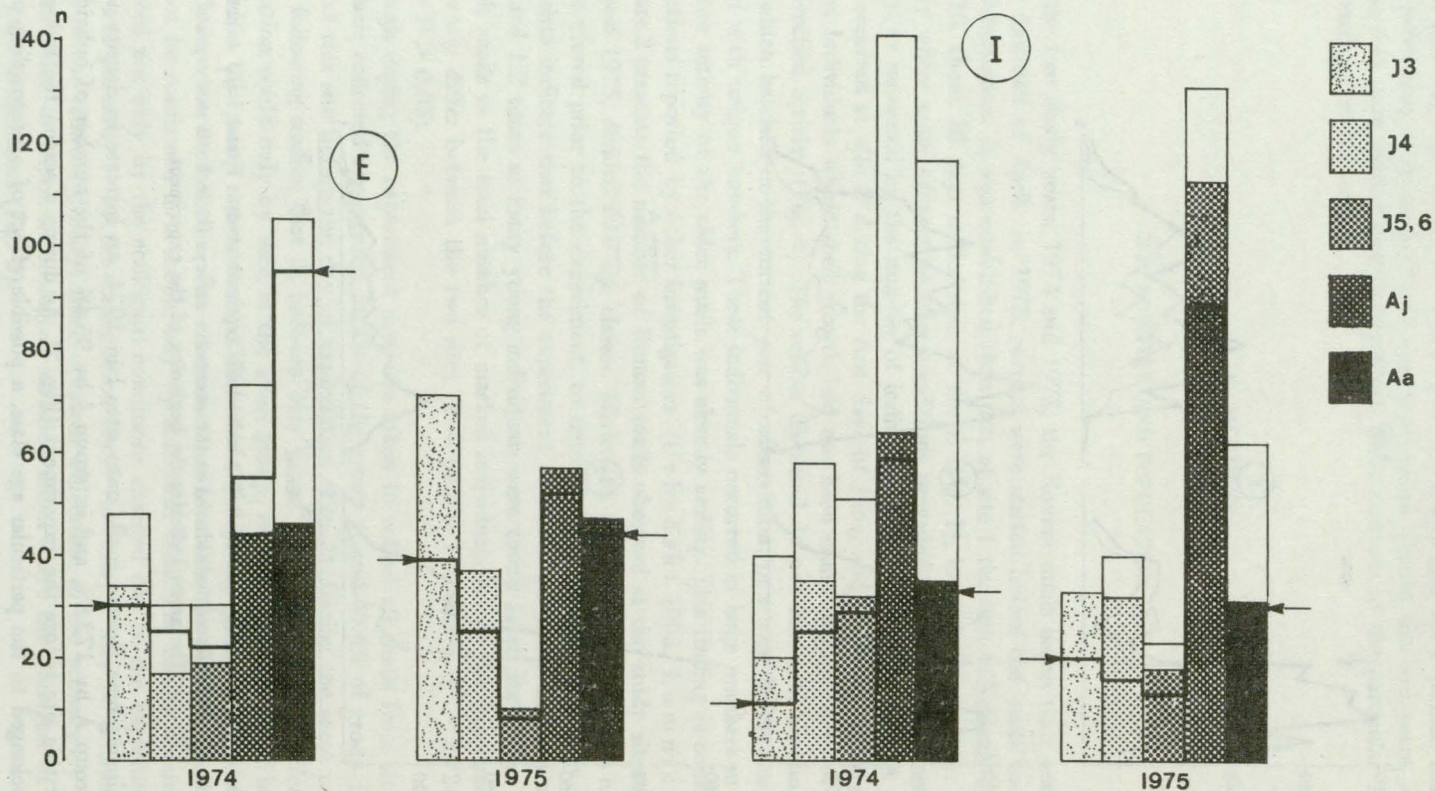
Fig. 2. Number (*n*) of individuals from the particular age classes, captured at sites E and I
The horizontal line pointed with arrows represents population size before the experiment in 1974, and in the respective period of 1975. Open columns represent the number of individuals captured at site E and of those introduced onto site I

number of individuals captured at site I before the experiment with the number of native individuals captured there in the corresponding period the following year (May 8 – June 26, 1975) revealed an unexpected growth in number of the adults caught, by 29.3%, in spite of the experimentally increased density. The number of juvenile individuals dropped at that time by 24.6%. In 1975, the total number of native and introduced individuals in the periods considered was higher by 82.6% in group A, and by 4.6% in group J (Fig. 2). Changes were also found in the age structure of the overcrowded population, because the percentage of adult native individuals was found to have increased significantly from 57.6% to 70.8% (χ^2 = 5.334, df = 1, $0.05 > P > 0.02$).

In summing up, it may be stated that the experiment resulted in a rejuvenation of the population under exploitation and a significant growth of the proportion of adult snails among the native individuals in the overcrowded population.

3.2. MOBILITY OF SNAILS

Taking into account the numbers of adult Roman snails found for the first time in the successive surveys, it may be noticed that new individuals continued to be found in the study sites (Fig. 3). The experiment has not been found to have a significant effect on their numbers.

By contrast to the appearing new snails, a number of marked individuals did not reappear at the site till the end of the season, or the end of the two years' observation (Fig. 4). It has been assumed that individuals seen for the last time in 1974 and not found alive or dead the following year, had emigrated from the local population. According to this assumption, 27 individuals emigrated from site E (leaving out the individuals collected during the experiment), and 22 native individuals and 120 individuals introduced during the experiment from site I. A comparison of these quantities clearly shows a more frequent emigration of those individuals which found themselves in new conditions, unknown to them. The difference is so obvious that it does not require statistical confirmation (Fig. 4). The numbers of emigrating native individuals do not differ significantly, and apart from this, because of the exploitation, they are not fully comparable.

New arrivals at the study sites, like the departures from them, represented a small proportion of the local population. Most of the individuals were regularly found at the study sites. For instance, places of occurrence and directions of translocation of a pair of mating individuals, selected at random are shown on the map of site E (Fig. 5). It can be seen from the map that the snails returned to the places where they were originally, from which follows that there exists a home range, and that the snails can recognize the area they occupy. Considering the size of the home ranges presented, estimated at about 60 m², and the known number of snails found at the site, a territory, an area defended against individuals of the same species, is out of question.

From the known coordinates of the plots in which snails were found throughout the season the geometric centres of the home ranges were calculated, and then the average distance was determined between the places of capture and these centres. The value obtained was adopted as the measure of the home range and mobility of the snails. Such calculations were made only for individuals observed while mating. In 1975, a significantly larger home range was found at both study sites (Table I), and the individuals introduced onto site I moved over areas almost of the same size as those over which the native indi-

viduals moved. The larger home ranges observed in 1975 at both study sites did not result from a larger number of surveys during that year, because the above measure of the range at site E amounted to 3.75 m already after sixteen surveys, and did not really change with the subsequent surveys. Its value after twenty-four surveys was 3.90 m. For site I this quantity increased very insignificantly from 4.18 m after sixteen surveys to 4.35 m after twenty-four surveys. The results represent yet another proof for the existence of home ranges in individuals of the local population.

Knowing the places in which mating was observed, and the location of the remainder of the captures, it was possible to determine the effect of mating on the mobility of snails. Mating was found to take place usually at a shorter distance from the centre of a home range than the average distance of the remainder of places of sojourn. These results were not confirmed only by the findings obtained in 1975 at the exploited site E (Table II).
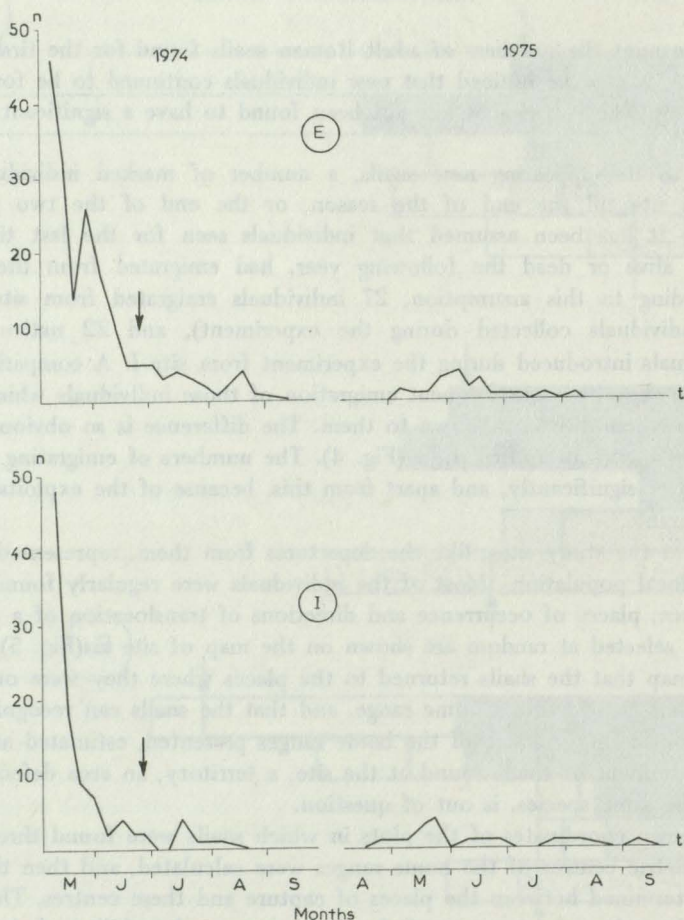

Fig. 3. Number (n) of Roman snails captured for the first time at sites E and I in successive surveys (t) in both study years
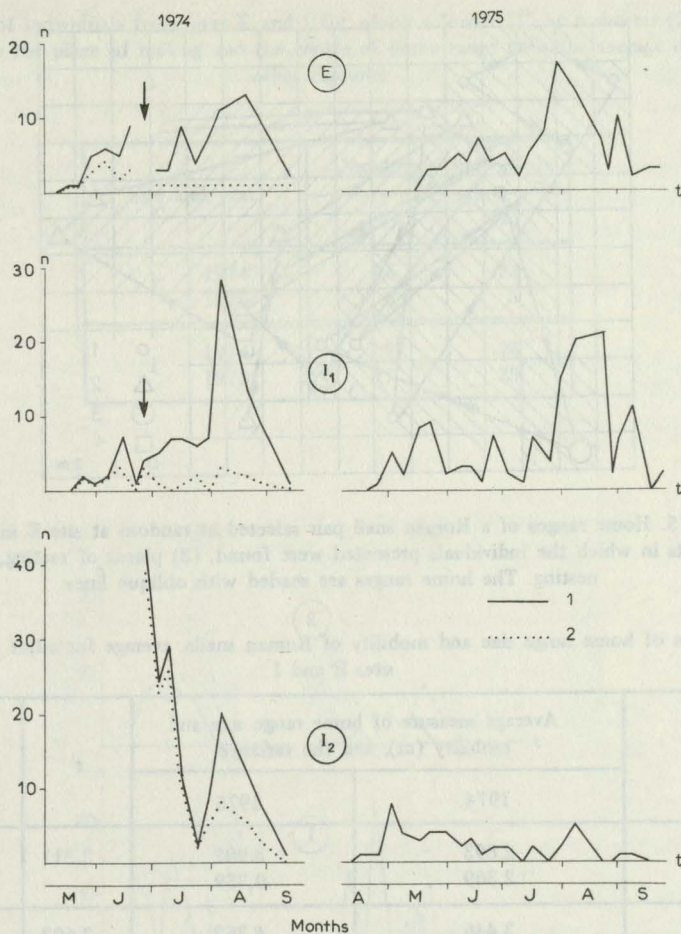
Fig. 4. Number (n) of individuals seen for the last time in the given study year (1), and of individuals regarded as emigrants (2) in the successive surveys (t) at sites E and I in both study years
I_1 — native individuals, I_2 — introduced individuals

3.3. MATING AND EGG-LAYING

Mating was observed at the study sites beginning from the first half of May. The largest number of mating individuals was seen towards the end of this month. A high mating activity was sometimes observed to continue until the middle of June. In July, only a few individuals mated, and the last mating pair was found on the 1st of August, 1975, at site I (Fig. 6). After mating the snails began to prepare egg cavities and lay eggs in them. At the study sites, the egg-laying began in the first half of June. The largest numbers of egg-laying individuals were observed between the 13th and 21st of June, whereas the last egg-laying snails were observed on July 26 (Fig. 6). Not in every egg-cavities did the snails lay eggs, consequently, the number of real clutches was much smaller than the number of excavated holes.
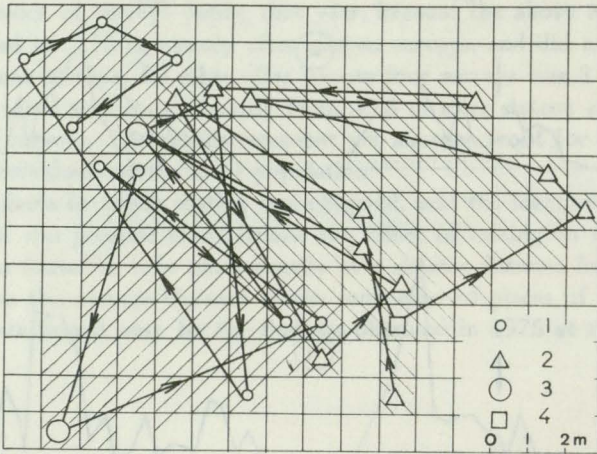
Fig. 5. Home ranges of a Roman snail pair selected at random at site E in 1975
(1) and (2) plots in which the individuals presented were found, (3) places of mating, (4) places of
nesting. The home ranges are shaded with oblique lines

Table I. Measure of home range size and mobility of Roman snails, average for adult individuals from
sites E and I

Site	Average measure of home range size and mobility (m), and the variance		t	df	P
	1974	1975			
E*	2.893 2.369	3.902 0.359	2.211	25	0.05—0.02
I Native individuals	3.446 1.282	4.352 1.672	3.603	91	0.001
I Introduced individuals	—	4.457 0.200	—	—	—

*Only individuals which were not taken during exploitation.

For the comparison of reproducing activity it was assumed that mating individuals and those seen laying eggs or preparing egg-cavities were taking part in the breeding. The frequency of reproductively active individuals was calculated from the number of Roman snails faund during catches made between the first and the last occurrence of reproductive activity during the season at the particular site.

Taking part in reproduction are individuals whose shells have not yet completed their growth in size. As regards their age, the youngest sexually active individuals were estimated to be in the fifth season of shell growth. For this reason, it is wrong to identify the completion of growth in the Roman snails with the attainment by them of the sexual maturity

Table II. Number of individuals from sites E and I for which a longer (1) or a shorter (2) distance was found between the place of mating and the centre of home range than the average distance of other captures

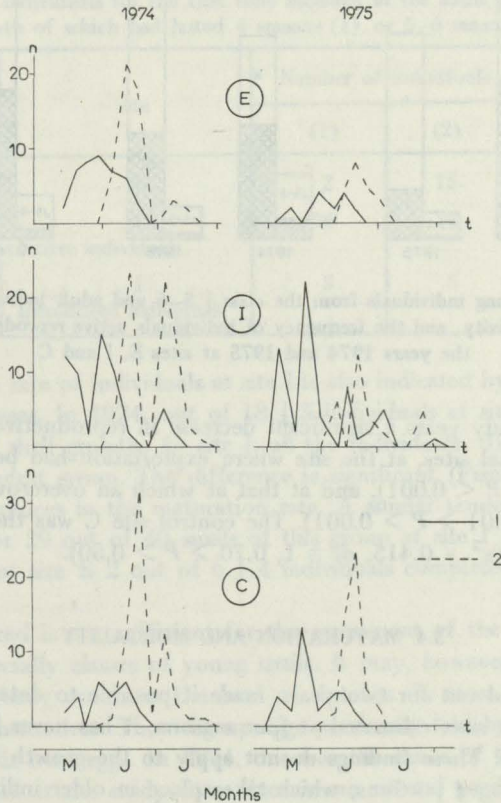| Site and year		Number of individuals	
		(1)	(2)
E	1974	14	24
	1975	8	5
I	1974	9	28
	1975	17	25

Fig. 6. Number of mating (1) and nesting (2) individuals in successive surveys (5) in both study years at sites E, I and C

(Urbański 1963, Łomnicki 1971, Dziabaszewski 1975). However, individuals of class J 5–6, in both years and at all sites, participated in reproduction less frequently than the adults (Fig. 7). Therefore in the comparison of the reproductive activity individuals whose shells were not fully developed were omitted, and since the two adult age classes, Aj and Aa, did not differ significantly in respect of their reproductive activity at any site in both years, they have been considered jointly (Fig. 7). The last observations do not confirm Künkel's (1916) and Dziabaszewski's (1975) suggestions that Roman snails lose their reproductive activity with age.
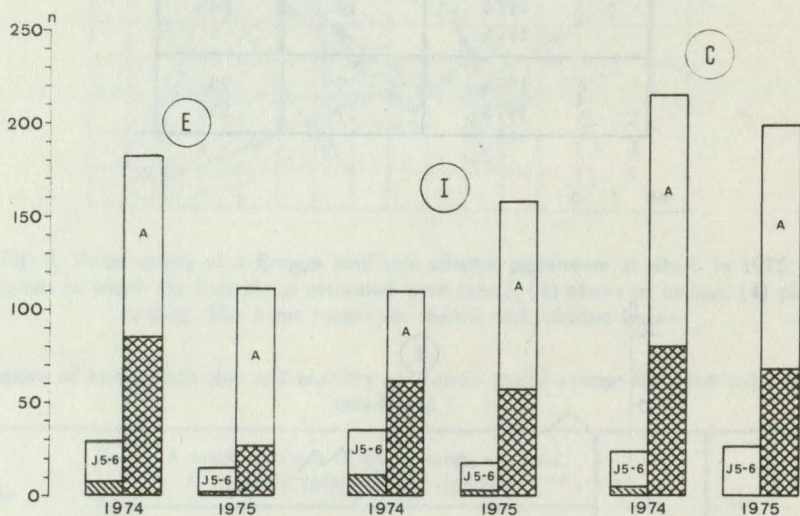

Fig. 7. Number (n) of young individuals from the class J 5–6 and adult individuals A, captured in the period of reproductive activity, and the frequency of individuals active reproductively (shaded field) in the years 1974 and 1975 at sites E, I and C

In the successive study years a significant decrease in reproductive activity was found at both the experimental sites, at the site where exploitation had been accomplished ($\chi^2 = 14.623$, $df = 1$, $P < 0.001$), and at that at which an overcrowding had been created ($\chi^2 = 9.882$, $df = 1$, $0.01 > P > 0.001$). The control site C was the only site where no differences was found ($\chi^2 = 0.415$, $df = 1$, $0.70 > P > 0.50$).

3.4. MATURATION AND MORTALITY

Investigations, carried out for two years, made it possible to determine the minimum time in shell growth in size, estimated at four seasons; it has never been found to last longer than six seasons. These findings do not apply to the growth in thickness of the shell, or repair of damaged portions, which takes place in older individuals.

Since, as has been proved so far, individuals in which shell growth has not yet been completed show a weaker reproductive activity than do adult Roman snails, it was assumed with a certain degree of simplification that an individual attains sexual maturity in the year in which its shell does not show any growth in size. On this basis the age of maturing could be determined in the second study year, taking into account the number of

annual increments. Among these individuals (Ajj) two groups were distinguished: individuals which had grown for four seasons, and those whose growth had lasted five or six seasons (Table III). In 1975, 11.8% of class Ajj individuals at site E were individuals which had grown for four seasons. Their percentage was significantly lower there among the native individuals at site I — 46.2% (χ^2 = 4.527, df = 1, $0.05 > P > 0.002$). Considerad jointly, 46.8% of the native and the introduced individuals of class Ajj at site I were found to have grown for four seasons. The percentage appears to be also high, significantly higher than at site E (χ^2 = 4.889, df = 1, $0.05 > P > 0.02$), indicating a higher maturation rate at the overcrowded site (Table III). To check if the above differences only appeared after the experiment, a comparison was made of the numbers recorded in 1974 in the age classes from which the adult individuals of the next year derived. As the frequency of the individuals of class J 4 and J 5—6 in 1974 did not significantly differ at either site, E or I, before (Fig. 2) (χ^2 = 0.063, df = 1, $0.90 > P > 0.80$) and after the experiment (χ^2 = 0.389, df = 1, $0.70 > P > 0.50$), it may be presumed that the change in density had significantly affected the maturation rate of the Roman snails.

Table III. Number of individuals for the first time included in the adult group (Ajj) in 1975, the growth of which had lasted 4 seasons (1), or 5—6 seasons (2)

Site	Number of individuals	
	(1)	(2)
E	2	15
I	24	28
Native individuals		
I	5	5
Introduced individuals		

A faster maturation rate of individuals at site I is also indicated by the results of the comparison within age classes. In 1974, out of 18 J 5 individuals at site E 14 were found to be in the last year of shell growth. At site I, all the individuals, 31 in all, of this group were in 1975 in the adult group. The difference is significant (Fisher's test — P = 0.029) and results from differences in the maturation rate. A similar tendency was seen in the younger class, J 4. For 29 out of 40 snails of this group at site I 1974 was the last growth season, while at site E 2 out of 6 J 4 individuals completed growth (Fisher's test — P = 0.156).

The material gathered is not sufficient for the assessment of the mortality in the particular classes, especially classes of young snails. It may, however, be stated that a considerable reduction already occurs at the level of clutches. In most cases the cause of this is the Roman snails themselves. They dig up eggs previously laid by other individuals and replace them with their own eggs. In 1974, this was the cause of the destruction of 6 out of 10 clutches observed at the study sites. Because no natural predators of the Roman snail were observed there, it must be assumed that destruction of clutches by individuals of the same species was an important factor reducing the size of the local populations.

Among adult Roman snails the probability of death was significantly higher in the older class Aa, because out of the 194 individuals of this class 9 died during the two

years, while in class Aj only 2 dead individuals were found out of 249 snails observed
(x^2 = 6.091, df = 1, 0.02 > P > 0.01).

3.5. INDIVIDUAL BODY SIZE

To illustrate the age assessment method, based on annual shell increments, used for
young individuals, an example is given of shell size measurements in the age classes asses-
sed by this method at site E in successive surveys in 1975 (Fig. 8) . The adopted measure
of shell size was the height of a shell, that is, distance from the apex to the farthest edge
of the aperture. The curves represent the mean shell-size values for the particular age
classes in successive surveys. The results justify the choice of the age assessment method
for young snails, because the end size attained by a class in the season was the size at
which the growth of the next class began. The individuals of the youngest class (J 1)
measured in July were snails observed still in the egg cavities, so the mesurements repre-
sent the size of the individuals hatching from eggs. It is only the latter measurements of
the individuals of this class that derive from snails captured most often on herbaceous
vegetation. The first point separeted from the growth curve by the dashed line represents
the minimum shell size in the season, average for each class (Fig. 8). The growth of each
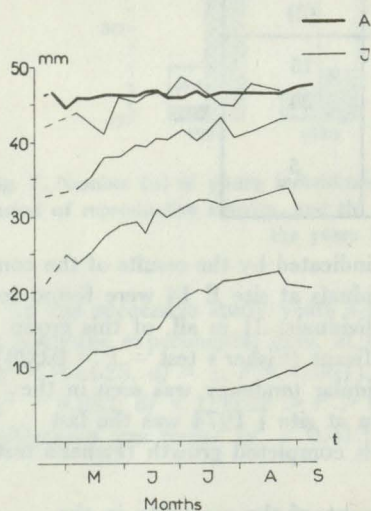young individual began in the season from this level.

Fig. 8. Mean shell height (in mm) in
five age classes of young individuals
(J) and adults (A), in successive sur-
veys (t) in 1975 at site E
For details see the text

In both study years, the shell height of the adult
snails captured at site E was significantly greater than
that of the native individuals from site I (1974:
t = 7.759, df = 1, P < 0.001, 1975: t = 6.249,
df = 278, P < 0.001, Table IV). Noteworthy seems
to be the fact that this difference was not seen in
the younger age classes, and no significant differences
in body size could be seen among the youngest adults
of class Ajj (Fig. 9). Differences could only be seen
– even increasing – at a later age of Aj and Aa.

The adult individuals introduced onto site I in
1974 were found to be significantly higher than the
native individuals from this site (t = 5.448, df = 263,
P < 0.001). This difference did not occur in the next
year (t = 1.901, df = 216, 0.10 > P > 0.05, Table
IV). Because the size of the native individuals from
site E did not show changes in either year, the lack
of difference between the shell height of the native
individuals and that of the introduced individuals
resulted from the fact that in 1975 the size of the
snails introduced onto site I the previous year was
smaller (Table IV). The change was caused by the
emigration of the larger introduced individuals from
the overcrowded habitat (Table V). By comparing the size of the individuals which had
been included in group A already in the first study year, a possible influence was elimina-
ted of the maturation rate on the shell height of the introduced individuals which remain-
ed on the new site until 1975. The division of the introduced adult individuals into two

Table IV. Mean shell height (and variance) of adult individuals of group A at sites E and I in both study years

Site	Mean shell height (mm) and the variance		t	df	P
	1974	1975			
E	46.529 5.294	46.178 5.060	1.311	305	0.20—0.10
I Native individusls	44.217 7.347	44.401 5.856	0.567	266	0.60—0.50
I Introduced individuals	45.962 5.980	45.107 5.391	2.279	213	0.05—0.01
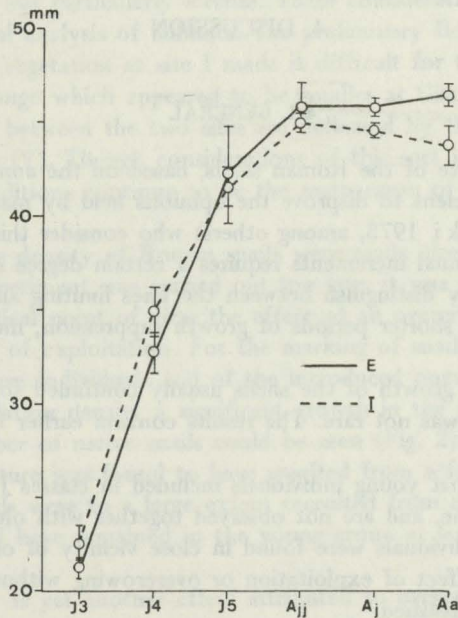
Fig. 9. The minimum, in a year, shell height (in mm), average for individuals from successive classes at sites E and I in 1975

age classes made it possible to state that as a result of an intensive emigration of larger Aj individuals, those individuals of this class that remained until 1975 were significantly smaller than the class Aa snails (Table V). The native Aa and Aj individuals did not significantly differ in shell size, at any of the study sites.

Table V. Mean shell height (and variance) of adult individuals of the particular age classes introduced
onto site I
Individuals which remained at the new site till 1975 (1), individuals which left the site in 1974 (2)

Age class	Mean shell height (mm) and the variance		t	df	P
	(1)	(2)			
Aj	44.440 6.875	46.115 4.941	2.919	75	0.01–0.001
Aa	46.067 3.931	46.481 6.686	0.757	80	0.50–0.40
Total A	45.327 5.835	46.298 5.791	2.417	157	0.02–0.01

4. DISCUSSION

4.1. GENERAL

Data on the growth rate of the Roman snails, based on the annual shell increments
(Fig. 8) seem to be sufficient to disprove the opinions held by many authors (C a d a r t
1955, D z i a b a s z e w s k i 1975, among others) who consider this method wrong. Hove-
ver, the assessment of annual increments requires a certain degree of experience, because
it is necessary to correctly distinguish between the lines limiting an annual increment and
those which arose during shorter periods of growth suppression, most often due to tempo-
rary droughts.

In the study area, the growth of the shells usually continued for 5 seasons, although
a difference of one year was not rare. The results confirm earlier findings reported by
P o l l a r d (1973).

It may be presumed that young individuals included in classes J 1 and J 2, occupy
a different ecological niche, and are not observed together with older ones (Ł o m n i c k i
1971). Only class J 3 individuals were found in close vicinity of older snails. For this
reason, searches for an effect of exploitation or overcrowing without taking into account
the youngest classes are justified.

4.2. EFFECT OF EXPLOITATION AND OVERCROWDING

The exploitation which caused a reduction mainly in the oldest age classes resulted
directly in a changed age structure and an evident rejuvenation of the local population.
But the youngest age classes of snails were seen on site E more often a year after the
exploitation (Fig. 2). It may, therefore, be supposed that the exploitation-caused changes
created favourable conditions for the growth in numbers of the snails of young age clas-
ses. Because of the insufficient number of obsrevations, it is impossible to state to what

extent this was due to immigration, decreased emigration, or a reduced mortality in the young age classes.

Comparisons of the numbers of native adult snails arriving at experimental sites E and I (Fig. 3), or leaving them (Fig. 4), did not indicate any significant density regulating role of migrations.

Mating propably occurs between chance partners (W o y c i e c h o w s k i and Ł o m n i- c k i 1977), as revealed by the analysis of the places where mating pairs were observed. Mating as a rule occurred closer to the centre of a home range than to the place of the remainder of captures (Table II). Thus there is no indication permitting one to believe that Roman snails tend to look for appropriate partners for reproduction, in order to ensure the distribution of genetic material, or greater heterozygosity of the offspring — advantages attributed to migrating individuals (L i d i c k e r 1962). A greater mobility (Table I), mating at the borderline of a home range (Table II), and a reduction in repro- ductive activity are the effects that could be interpreted as resulting from the lack of partners for reproduction and the necessity to look for them in a less dense population. This interpretation would be more justified had it not been for the fact that a year after exploitation the density of snails remained at a level recorded a year before at site I when the reproductive activity was particularly intense. These considerations should be supple- mented with an additional analysis of habitats. The preliminary findings permit the pre- sumption that the richer vegetation at site I made it difficult for the snails to move, as indicated by the home range which appeared to be smaller at this site (Table I). Differen- ces in habitat conditions between the two sites are indicated by the size of the shells of snails found there (Table IV). Though considerations of this sort may deserve the name of tautology, habitat conditions continue to be the main cause of the observable diversity of animals.

Trials at increasing the density of Roman snails were made already by Ł o m n i c k i (1964), but since the experiment was carried out too late, it was difficult to assess its effect. From a mathematical point of view the effect of an overcrowding is easier to assess than is the impact of exploitation. For the marking of snails made it possible to trace the fate of the native individuals and of the introduced ones separately. A year after the increase in the population density a significant growth in the percentage of adult indi- viduals in the total number of native snails could be seen (Fig. 2).

The changed age structure was found to have resulted from a faster rate of maturation. Newly matured individuals were to a large extent recruited from age classes which, under normal conditions, would have remained in the young group at least for another year (Table III).

A decreased fecundity is yet another effect attributed to overcrowding. Though it was found also a year after the exploitation, this was not related to the different study years, for at the control site the reproductive activity remained unchanged in both years (Fig.7).

4.3. DENSITY REGULATION

The state of equilibrium of a population is indicated by its stable level of numbers persisting for a number of generations (S l o b o d k i n 1964). The factors that regulate the size of a population are considered as self-regulating mechanisms acquired by group selec- tion, or individual selection. The appearance of any adaptations as a result of group selec-

tion may only occur in very specific conditions which are not very often encountered in nature (Ł o m n i c k i 1977). For this reason, it is difficult to recognize the principles assumed in the descriptions of the group selection, as well as the advantages gained by a species with a reduced adaptation of individuals, as phenomena occurring under normal conditions. Thus the social relations found in animals (W i l s o n 1975), the different spatial structure of individuals, or the tendency to emigrate (Ł o m n i c k i and S l o b o d-k i n 1966, Ż y r o m s k a-R u d z k a 1966) resulted from individual selection, whereas the altruistic behaviour could have arisen and been maintained only among closely related individuals (H a m i l t o n 1964). For this reason, it seems right to search for relations among the members of the snail population such that assure for them a greater chance to survive and produce offspring.

Observation of snails living at higher densities confirms the view held by Ł o m n i c k i (1971) who considers emigration to be a regulating factor. However, this only applies to newly introduced individuals whose chance to survive in a new, unknown habitat was the least (Fig. 4). For two basic reasons this group of individuals is regarded to be in a worse situation then that of the native individuals. Firstly, they found themselves in new sur-roundings, which no doubt reduces the chance to survive in the case of animals with a home range. Secondly, because of the lack of a phenotype adaptation to the environment. This supposition is suggested by the fact that individuals which had emigrated as the first ones differed much more by the height of their shells from the native individuals than did those which had stayed among them for a longer time (Table V). Variation of the form as a result of environmental conditions has already been described from another snail, *Cepaea nemoralis* (C a i n and S h e p p a r d 1950), and is easy to imagine. The authors concerned with the Roman snail also emphasize the variation of forms in relation to the habitat in which they were found (U r b a ń s k i 1963, S t ę p c z a k 1976), but they do not suggest that this is a direct effect of environmental conditions, or of selection. The following findings support the opinion that snail populations change due to the influence of selection. Young individuals (J), and the adult ones in the first year after reaching the adult size (Ajj) do not differ by shell height in either of the study sites, E or I. A vary-ing shell size was seen in the Aj class of adult snails, the greatest differences being found in the oldest class, Aa (Fig. 9). It may, therefore, be presumed that at site E individuals with higher shells survived for a longer time, and that was why more of them lived until old age. On the other hand, at site I individuals with a smaller body size had a better chance to survive, and this is the reason why their proportion in the older age classes grew. For the same reason, too, individuals with a smaller shell height, better adapted to the current conditions, were the only introduced snails that remained at this site (Table V).

A faster maturation rate recorded for the overcrowded population is another reason against the factors self-regulating the population size. In a rapidly changed situation, impossible to foresee, an earlier maturity makes it possible to produce offspring at an earlier time. An adaptation of this type may have evolved by way of individual selection, and is more likely to occur in animals without parental care, though a similar phenomenon has also been observed by P e t r u s e w i c z (1957) in mice cultures.

The lower fecundity that could be seen after the increase in population density did not result from an altruistic behaviour of the individuals. Its causes should be looked for outside the relations interlinking the members of a local population. The possibility that an overcrowding may have a significant effect on the behaviour of individuals is indicated by the mobility which appears to be increased under these conditions (Table I). This, in

turn, may be evoked by a deteriorated quality of the available food. The problem of food quality deterioration due to the pressure by herbivores has been pointed by M a y (1975), in the summing-up of the results from studies of slugs. A significant limitation of reproduction due to insufficient food supplies was observed in snails by E i s e n b e r g (1966). W y n n e-E d w a r d s (1977) has found that a shoratge of highest quality food may become a number limiting factor.

In the Roman snail population under study, the mutal destruction of egg-laying that occurs frequently in this species could be considered as the only sign of density self-regulation. When the number of suitable places for nesting is limited, attempts at holding egg cavity lead on to the nest destruction previously prepared by other individuals. This type of self-regulation is possible, and its model, based on the observation of a marine turtle population, has been presented by B u s t a r d (1969). In the Roman snail population nest destruction dependent on population size is not observed. So this density-dependent mechanism is possible only if there is not enough space suitable for nesting. This is then a limitation by resources, and not due to selection.

Roman snails under observation usually moved over a small area, because they found there suitable places for wintering and nesting. E d e l s t o m (1969) and P o l l a r d (1975) describe individuals making seasonal movement from hibernating areas to suitable sites for egg laying. Individuals of the control site belonged to such migrating population. A current situation makes it necessary for the individuals to adopt the appropriate strategy. As has been stated by C o h e n (1967), such a variety of behaviour can be encountered when the chance to survive of migrating and sedentary individuals cannot be foreseen and changes from year to year. A tendency to migrate may also be caused by the fact that places suitable for wintering, like the conditions ensuring a successful hatching, are not good for adult individuals. Also during the maturation of the snails their habitat preference varies.

All the above factors, along with the uneven distribution of resources, make the Roman snails increase their mobility, with a previous konwledge of the areal. With the assumption that the maturation time varies considerably, the behaviour of an individual, if not fixed by generations through selection, is fortuitous, but individuals which more fully use the available resources have a better chance to survive.

5. SUMMARY

Investigations were carried out in 1974 and 1975 in the Ojców National Park, at three experimental sites, each of 196 m^2 in area. In June, 1974, an experiment was carried out in which the density of Roman snails was reduced at one of the study sites (E), and increased at another (I). Where possible, the results of the experiment were compared with those from the control site (C).

Weekly surveys (Fig. 1), combined with marking and measuring of the snails found, made it possible to assess the age of young individuals (J), on the basis of annual shell increments. Shell growth was found to continue usually for 5 seasons, but this period may be longer or shorter by one year. The growth often continues after the attainment of sexual maturity (Fig. 7). Three age classes were distinguished among the adult individuals: Ajj, Aj and Aa. Differences in shell height in older classes of individuals of local populations (Table IV), strengthened with age (Fig. 9), are attributed to selection which eliminates less fit individuals (Table V).

As a result of exploitation at site E, the rejuvenated population with a reduced density showed a weaker reproductive activity (Fig. 7) and an intensified mobility (Table I), which may be attributed to lack of partners for mating.

The overcrowding at site I caused an intensified emigration of the introduced individuals, less adapted to the new conditions (Fig. 4), and accelerated maturation (Table III), which resulted in an increase in the percentage of adult individuals (Fig. 2). The increased mobility (Table I) and reduced reproductive activity (Fig. 7) were considered to have resulted from a deteriorated quality of the available food. Food supplies and emigration of less fit individuals seem to regulate the size of a population.

6. POLISH SUMMARY

Badania prowadzono w latach 1974 i 1975 na terenie Ojcowskiego Parku Narodowego, na 3 doświadczalnych powierzchniach, 196 m^2 każda. Przeprowadzony w czerwcu 1974 r. eksperyment polegał na zmniejszeniu zagęszczenia winniczków na jednej z badanych powierzchni (E), przy jednoczesnym zwiększeniu ich zagęszczenia na innej (I), Wyniki eksperymentu w miarę możności porównywano z uzyskanymi na powierzchni kontrolnej (C).

Cotygodniowe połowy (rys. 1) połączone ze znakowaniem i pomiarem odnajdowanych winniczków dały możność oceny wieku młodych osobników (J), dokonywanej na podstawie rocznych przyrostów skorupy. Stwierdzono, że wzrost skorupy trwa zwykle 5 sezonów, z możliwością rocznego przesunięcia tego okresu. Wzrost trwa często dłużej niż osiągnięcie dojrzałości płciowej (rys. 7). Wśród dorosłych osobników wyróżniono 3 klasy wieku: Ajj, Aj i Aa. Różnice wysokości skorup starszych klas dojrzałych osobników z lokalnych populacji (tab. IV), pogłębiające się z wiekiem (rys. 9), tłumaczy działanie doboru eliminującego gorzej dostosowane osobniki (tab. V).

W wyniku przeprowadzonej na powierzchni E eksploatacji odmłodzona populacja przy zmniejszonym zagęszczeniu przejawiała osłabioną aktywność rozrodczą (rys. 7) i zwiększoną ruchliwość (tab. I), co można tłumaczyć brakiem partnerów do kopulacji.

Przegęszczenie na powierzchni I wywołało wzmożoną emigrację niedostosowanych do nowych warunków wprowadzonych osobników (rys. 4), przyspieszyło dojrzewanie (tab. III), co doprowadziło do wzrostu udziału dojrzałych osobników (rys. 2). Zwiększoną ruchliwość (tab. I) i osłabioną aktywność rozrodczą (rys. 7) uznano za wynik pogorszenia się jakości dostępnego pokarmu. Zasoby pokarmu i migracje gorzej dostosowanych osobników wydają się regulować liczebność populacji.

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