POPULATION DYNAMICS OF *PHYSA ANATINA* LEA IN A NATURAL SPRING COMMUNITY

A Thesis

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by

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INTRODUCTION

Physa anatina Lea is a common and widespread snail in Kansas, occurring in a variety of permanent and temporary freshwater habitats. Its probable range extends from Nebraska south to central Texas, and it is known to occur east as far as Illinois and west to New Mexico and Colorado (Leonard, 1959; Brown, 1937).

Leonard (1959) stated that *P. anatina* is found in much the same types of habitats as *P. hawnii* Lea and that there is little difference in life cycles and habits of these two species. The reproductive period of *P. hawnii* usually begins during February and continues into the fall.

There is no previous record of the occurrence of *P. anatina* on Ross Natural History Reservation. Basch, Bainer, and Wilhm (1961) compiled an annotated list of the molluscan fauna of the Ross Natural History Reservation and did not mention collecting *P. anatina*. Although they reported *P. hawnii* to be the most common aquatic gastropod found during their study, only a single specimen was collected from the spring, the study habitat for my research. During the fall, 1973, numerous *Physa* were observed in the small pool at the head of the spring. Specimens were collected and identified as *P. anatina*. Dr. W. J. Clench, Harvard Museum of comparative Zoology, verified identification of the specimens.

Because of the small size of the habitat and the fact that no other species of gastropods were present, this spring presented an excellent opportunity to observe selected aspects of the population dynamics of *P. anatina*. In November, 1973, a study was initiated to record seasonal variations in population density, reproduction, and population structure of *P. anatina* inhabiting the pool area of the spring.

DESCRIPTION OF STUDY AREA

The Ross Natural History Reservation is operated by the Division of Biological Sciences of the Emporia Kansas State College. It is located approximately 8.4 km west of Americus and 22.4 km northwest of Emporia. The history, topography, and vegetation of the area have been described by Hartman (1960), Wilson (1963), and Basch, et al. (1961).

The study site, hereafter referred to as Ross spring, is located in the southeast corner of grid A39. It consists of an unshaded rectangular pool approximately 1.0 m x 3.5 m bordered by limestone rocks. The pool varies in depth from 8 cm near the spring outflow to 25 cm near the source. Outflow from the pool seeps down a northeast-facing slope, forming a marsh environment. The pool is matted with watercress (*Nasturtium officinale*), which sometimes fills the pool.

Water temperatures in the pool varied from 11 to 16 C during the study. Dissolved oxygen and methyl orange alkalinity also exhibited slight seasonal variations during the period of this study (Table I).

Table I. Seasonal average physicochemical characteristics of Ross Spring.

	Temperature C	Dissolved Oxygen ppm	M.O. Alkalinity ppm
Spring	11	5.3	413
Summer	16	4.1	348
Fall	15	6.1	367
Winter	11	6.6	*

* not obtained

METHODS AND MATERIALS

Physa anatina was found predominantly among the watercress plants, which necessitated the use of a special device to collect both snails and watercress. A metal cylinder 12.5 cm in diameter and 28.5 cm in height was used. The bottom of the cylinder had a sharp edge that would cut through the watercress mat. Watercress within the cylinder was then removed and placed in plastic bags, labelled, and returned to the laboratory. A small mesh strainer of approximately 0.08 mm mesh was passed through the water within the cylinder to collect loose plant materials and animals, which were added to the samples.

Field samples were collected periodically from November 1973 through September 1974. The pool was divided into fifteen 0.25 m^2 quadrats, using nylon twine. Quadrats were numbered and on each sampling date collections were made from two quadrats. The quadrats to be sampled were determined by drawing numbered cards. In general, field samples were collected at intervals of four weeks, with more frequent samples during spring (four day intervals) and summer (8 day intervals) to detect changes in population structure and reproduction. Each plastic bag was marked with the number of the quadrat sampled so that snails and egg masses could be returned to the same general location after the materials had been examined in the laboratory.

In the laboratory, samples were washed through soil sieves; the finest mesh used was 0.04 mm. The snails, egg masses, and watercress were separated. All snails in each sample were counted and examined with the aid of a binocular microscope. Using a vernier caliper, the maximum length of each shell was measured from the spire apex to the outer edge of the aperature. The greatest width of the aperature was also recorded. The product of the shell length and width was used as a size index.

Volume of watercress in each sample was measured by water displacement. After the watercress had been separated from the rest of the sample and washed, it was blotted dry. The plant material was then placed in a graduated cylinder that contained a known volume of water. The increase in volume in the cylinder was recorded as the volume of watercress.

Observation revealed the majority of the snail population occurred within the watercress mat, which occupied from approximately 30 % of the basin during the winter to 80 % during the summer. Since the watercress represented a substrate on which the snails lived and grazed, feeding on the aufwuchs growing on the plant surface, estimates of standing crops were related to the equivalent plant surface area in samples.

Plant surface area was estimated in the following manner. Volumes of five separate plant samples were measured and dry weights of each obtained. Another five samples were used to measure surface areas; dry weights of these samples were also recorded. The surface area of stems and roots was determined using the method of Harrod and Hall (1962). Several plant roots and five pieces of stems were placed on a glass plate and cut into small cylindrical lengths. The diameter and length of each piece was measured using an ocular micrometer in a binocular microscope. The areas of stems and roots were calculated using the formula, area= dh, where d is diameter and h is length. A compensating planimeter was used to measure areas of leaves. Leaf areas were doubled to include both sides. The areas for stems, roots, and leaves were then added to estimate the total surface area of each of the five samples of plant material.

The average volume in one milliliter per gram dry weight was then calculated and equated to the average surface area per gram dry weight. One milliliter of watercress averaged 0.06 g dry weight, and one gram dry weight contained 8946.2 cm^2 of surface area. Therefore, one milliliter of plant material was considered the equivalent of 536.8 cm^2 of surface area.

Population density per sampling date was then determined in the following fashion. The average number of snails per milliliter of watercress was multiplied by the area equivalent (1 ml watercress = 536.8 cm^2). The resulting values were then converted to average number of snails per meter.

A standard procedure was used for culturing snails in the laboratory. Snails were kept in glass containers filled with spring water. All laboratory cultures were maintained in a constant temperature room (15 C) which was equipped with a lighting system that produced a photoperiod that was similar to that occurring at the spring, changing with seasonal change. Watercress taken from the spring was used as the food for laboratory populations.

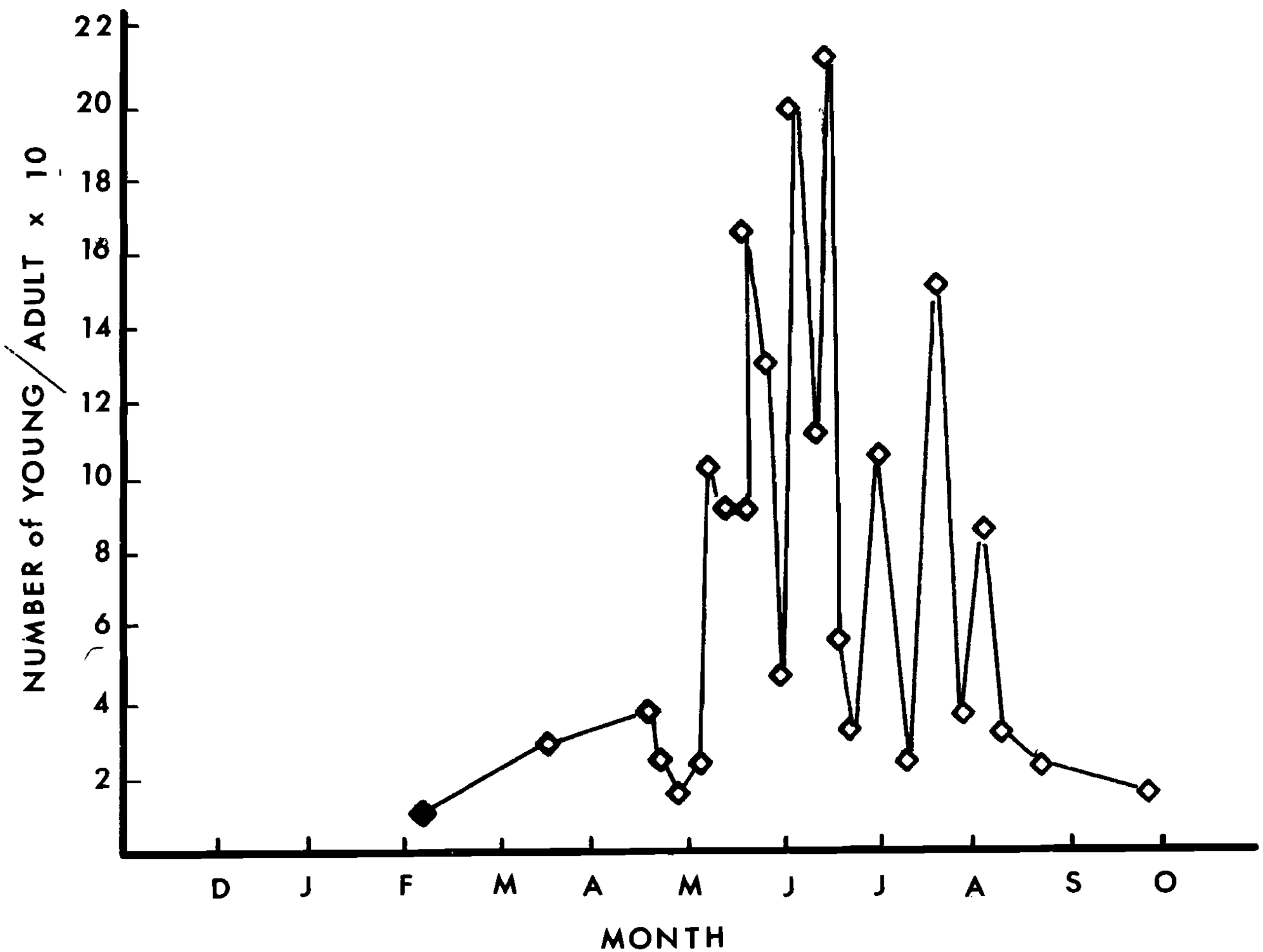
RESULTS AND DISCUSSION

Population Density and Seasonal Standing Crops of Snails

Variations in population density are summarized in Figure 1. Population density remained relatively stable during the first four months of this study and then declined through the early spring, reaching a minimum density of approximately 10 individuals per m^2 of watercress by mid-April. Although observed values fluctuated throughout the next three months, the general trend was for population density to increase. A maximum density of 145 snails per m^2 was recorded by late July. The density declined throughout the remainder of the study, so that by the first of October, 1974, the density was 26 snails per m^2, a value that was similar to the densities observed the previous fall and winter. The rather marked increases and decreases in densities during the period April through July were probably the result of reproduction and high mortality of young snails, and observed density peaks suggest two periods of maximum reproduction.

When total standing crops of snails inhabiting the spring are estimated, some rather interesting results are obtained. The average total surface area of watercress in the pool was determined for the winter, spring, summer, and fall periods. This was accomplished by calculating the average surface area of plant material appearing in the cylinder samples for each season and then estimating the total number of cylinder samples

Figure 1. Seasonal variation in population density of *P. anatina*.


NUMBER of YOUNG/ADULT x 10
22
20
18
16
14
12
10
8
6
4
2
D
J
F
M
A
M
J
J
A
S
O
MONTH

of watercress that could be taken from the pool during each period. The product represented the total surface area of watercress present. Values obtained were; winter 104.1 m^2, spring 187.8 m^2, summer 371.8 m^2, and fall 221.4 m^2. Assuming the density estimates representative of abundance, the average density times the total plant surface area yielded standing crop. On this basis the total *P. anatina* population inhabiting the spring in January was 3227 snails, and for mid-April the standing crop was approximately 2567 individuals. For the period of maximum density in July the standing crop was estimated at 53,911 individuals. By the end of September standing crop had declined to approximately 554 snails. Unfortunately, no similar data were found in the available literature to compare with these estimates.

Reproductive Season

Egg masses were observed in the pool throughout the year, but were most abundant during the warmer months. An average of six masses per sample of watercress was found in winter samples compared to an average of 70 egg masses per sample during the late spring. Based on the number of egg masses observed, *P. anatina* began its reproductive season during late April and exhibited two periods of maximum egg deposition. The first and greatest period occurred in mid-May and the second, less pronounced period during July and August. These observations support the hypothesis that reproduction accounted for the recorded seasonal increases in standing crop. Figure 1 shows a marked increase in population density within three weeks after the onset of increased egg deposition. This three week period may be the hatching period for this population.

Duncan (1959) described the reproductive behavior of P. fontinalis in a pond at Stanmore, England. In 1954, he found that the main reproductive period occurred during April and May, although egg masses were found until the last week of August. Some of the snails that hatched during the spring season reached maturity by July and August when a second breeding season occurred. Duncan found that the snails breeding then were all much smaller than those in the April and May season. It was evident that they reached sexual maturity before they reached the same size as the spring breeders. Duncan concluded that the warmer temperatures in the summer produced rapid metabolic activity allowing a more rapid development of the second generation and a subsequent, second breeding season. At Stanmore, reproductive activity ceased in September. During 1955, the Stanmore population did not produce a second generation in the fall (Duncan, 1959). Duncan attributed this to an exceptionally warm summer which caused slowed development. He stated that growth was not solely governed by temperature. A second breeding season was not found in populations at two other locations in the fall of the same year. In the Lake District, 188 km further north of Stanmore, only one generation was the general rule. The reproductive season in that region occurred a little later, continuing until the last week of July. Growth was less rapid and shell length at maturity much shorter.

DeWitt (1954a) studied an April population of _P. gyrina_ in Michigan consisting entirely of sexually mature individuals which had begun to oviposit. By May the adults were replaced by juveniles, and egg masses were scarce from June through October. In August a high percentage of this population consisted of individuals within the same size range as that which had oviposited in the spring. As at Stanmore in 1954 a second generation occurred. DeWitt observed, as Duncan had in _P. fontinalis_, snails which hatched in the spring developed at a rate that enabled them to reach sexual maturity in the fall and some of these snails oviposited. Snails from the second generation did not reach maturity until the following spring.

Hunter (1961) reported the reproduction of _P. fontinalis_ in Loch Lomond began from late May to late June. There was no replacement of one generation with another, as DeWitt found with _P. gyrina_.

Brown (1937) reported March as the main period of reproduction for an Illinois population of _P. anatina_. She found reproduction declined during the summer months and a second season occurred in September, which reached a maximum activity in November when 80 % of a laboratory population produced egg masses. In Kansas, the reproductive season of _P. anatina_ begins in February and continues into the fall (Leonard, 1959). The relatively stable water temperatures in Ross spring may have influenced the reproductive behavior of the resident population. Many researchers agree that temperature affects the reproductive behavior of _Physa_. Duncan (1959) and DeWitt (1954b) related observed reproductive behavior to temperature, but Hunter (1961) disputed any direct effect of temperature. He found no evidence that the incidence of extent of a subsidary breeding season was in any way related to summer temperatures occurring at the time. He contended that the variations found in sizes attained by snails could be correlated with conditions prevailing the preceding year. However, DeWitt (1955) stated reproduction in P. gyrina, under natural conditions, is directly related to temperature. He observed oviposition began when temperatures in the pond he studied reached 10 C-12 C. Duncan (1959) found temperature the basic, though indirect factor, governing oviposition through its control of the rate of development. In both years of his investigations at Stanmore, his observations showed temperatures between 7 C and 11 C critical in the initiation of oviposition. He found 7 C the temperature at which growth was initiated again after the winter lag. Since water temperature was never below 11 C in the Ross spring and snails of all sizes were found throughout the year, it is possible that there was less lag in reproduction of overwintering animals. The Ross spring temperatures of 11 C to 16 C fall within the range given by Duncan (1959) and DeWitt (1954b) as the range in which reproduction and development of Physa could occur. This would account for the presence of egg masses during the winter in Ross spring.

Natality

It was hypothesized that observed variations in the estimated density of the Ross spring Physa population were due primarily to reproductive and survival behavior. Observations reported in the previous section supported this hypothesis, since maximum reproduction, in terms of egg masses deposited, coincided with the period of maximum population density. Additional observations and data analysis were designed and executed to provide additional evidence in the form of seasonal natality and survival rates.

Average seasonal egg production of the study population was estimated from field data in the following manner. During certain months the total number of eggs in five separate egg masses, selected at random from samples, were used to calculate the average number of eggs per egg mass for that month. A seasonal average was then determined from the averages. Averages from March, April, and May's samples were used to determine the average for spring period. Summer averages were determined from the cases selected in June, July, and August. The fall average was determined in September, while the winter average was determined in January. Fall and winter are periods of decreased reproductive activity and results based on a single month were believed representative. Total eggs present in a given sample was equal to the number of egg masses per sample times the appropriate seasonal value for the average number of eggs per mass.

It was reasoned that if the approximate number of eggs present was known and if development time and percentage of eggs hatching were known, then the number of young snails entering the population per unit of time could be estimated.

Hence, it would be possible to predict the population density at a future time given an initial population density plus a natality value. Of course, to be realistic the predicted population density should be corrected for mortality.

The initial task was to derive a value to represent the expected proportion of an egg mass to hatch, or the percentage hatchability. This value was determined in the laboratory.

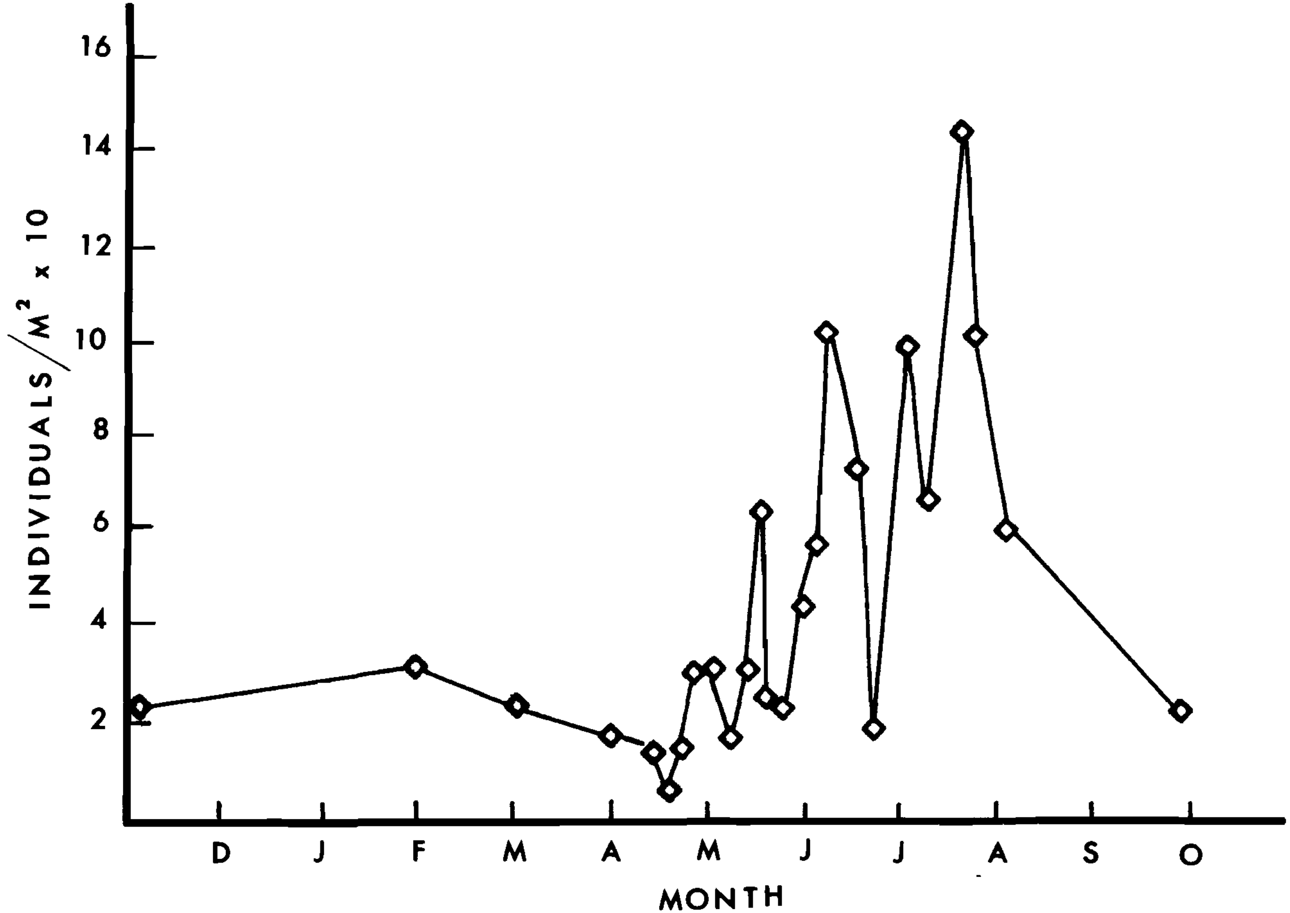
Fourteen egg masses, collected from isolated snails, were transferred to culture vessels of spring water and maintained at 16 C. Cultures were examined several times daily and a record was kept of how long it took for hatching to begin as well as the number of eggs that hatched. Brown's (1937) study of *P. anatina* showed hatching required four to 17 days, at 19 C to 22 C, and she estimated 33 % hatchability. Duncan (1959) found *P. fontinalis* usually hatched in about 17 days at 19 C. At 16 C the Ross spring eggs began hatching 10 to 29 days after deposition, with the average hatching time being 18 days. Hatchability of individual egg masses ranged from 6 % to 100 % and averaged 72.3 %.

The number of young produced per mature snail (specific natality) of the study population was calculated by multiplying the seasonal average number of eggs per mass by percentage hatchability times the average number of cases divided by the number of mature snails found in each sample. Snails were considered mature if they measured 4.5 mm in length, the length at which oviposition was observed to begin in laboratory populations.

Figure 2 summarizes the estimated specific natality for the Ross spring population throughout the study period. Actually, values were advanced 18 days to account for developmental time. For example, the specific natality value shown in the figure for the first of May was based on the number of eggs present in samples taken during the second week of April. Natality was lowest during winter, when an average of 12.6 young were produced per mature snail. During spring estimated specific natality increased to an average of 65.5 young per mature individual. The first natality peak 214.0 young per mature snail was reached in the spring. Summer specific natality averaged 85.1. The second peak in natality, reached during the summer, was 148.0 young per mature snail. By September values dropped to 61.2 young per mature snail.

Duncan (1959) observed that the number of eggs in a mass was not proportional to the size of _P. fontinalis_ in the laboratory, but depended on where the animal was in its oviposition cycle. DeWitt (1954b) found, under natural conditions, a significant positive correlation between the number of eggs per mass and the size of _P. gyrina_. Duncan's observations were made through recording the number of eggs per case in relation to the development of the genital systems which he determined through dissection. DeWitt's observations were made from collecting egg masses from isolated snails for an entire year. DeWitt found that the snails which began oviposition in the spring were smaller and laid fewer eggs per case. He found (DeWitt, 1954b) _P. gyrina_ initially laid masses that tended to contain the maximum number of eggs. The number of eggs per mass and the number of masses he found pro-

Figure 2. Seasonal variation in specific natality of *P. anatina* inhabiting Ross spring.


INDIVIDUALS/M² x 10
16
14
12
10
8
6
4
2
D
J
F
M
A
M
J
J
A
S
O
MONTH

gressively declined.

Cultures of *P. anatina* were set up in the laboratory to determine the relationship between size and egg production. Two groups of *P. anatina* of differing sizes were cultured. Each snail was isolated, and all were sexually mature. The younger group containing ten snails of average size index 7.6, produced only 0.4 young per snail per day. The older group also containing ten snails, with an average size index of 39, produced 1.7 young per snail per day. Thus the younger snails tended to produce fewer eggs than older, larger snails.

DeWitt (1954b) indicated that in *P. gyrina* there was a definite relationship between population density, the size attained by the snail before sexual maturity, and egg production. As the number of snails reared together was increased the size at commencement of oviposition decreased and the mean number of eggs per snail decreased. An experiment was conducted in the laboratory to investigate the relationship of population density to egg production in the study population of *P. anatina*. Four snails of an average size index of 6.0 were cultured at 16 C. Ten snails of an average size index 7.6 were isolated individually. The four smaller snails produced 2.4 young per snail per day. The ten isolated snails produced 0.4 young per snail per day. The denser population yielded a higher natality. This is the opposite relationship DeWitt found. Additional experiments of this type are needed.

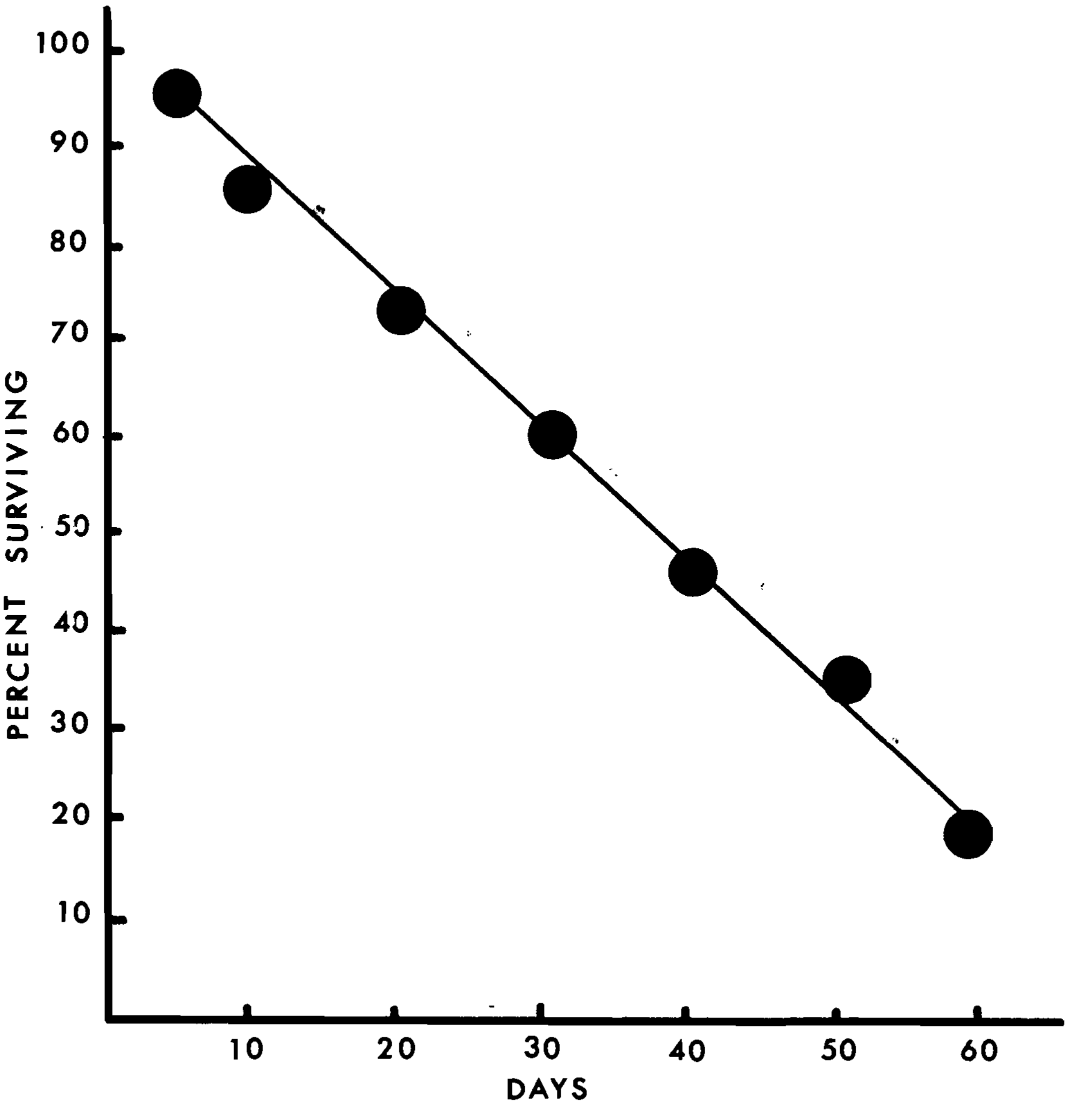
Survivability

Data on survivability of young snails for the Ross population were recorded in the laboratory. Snails hatched from 14 isolated egg cases were placed into separate cultures with spring water and watercress. Each group was observed over a 60 day period and the number of snails surviving from each egg case was recorded. Figure 3 shows the average number of snails surviving from the 14 groups for each ten day interval of the 60 days. Mortality appeared constant and averaged 12.6 % per ten days, ranging from 10 % to 16 %. After the 60 days, only 24 % of the original numbers of young survived, indicated a mortality of 76 %. The periodic decreases in population density recorded in Figure 2 is believed to be largely due to the high mortality occurring in the first 60 days after hatching.

Growth and Maturity

The variations found in the size of *Physa* at sexual maturity supports the plasticity of this genus. Duncan (1959) found the size attained at sexual maturity varied in the same population at Stanmore. He found that snails breeding in the spring season measured an average of 10 mm in length while the second generation reached 7.1 mm by fall and were spawning by this time. Brown (1937) found *P. anatina* began ovipositing between 5.3 mm to 9.3 mm in length. The Ross population of *P. anatina* began ovipositing in the laboratory at an average length of 4.5 mm when cultured at 16 C. Determination of growth rate for *P. anatina* was made in the laboratory. Ten newly hatched snails were isolated individually in cultures. Each snail was measured and its size index determined daily for the first ten days. After the first ten days they were measured at five day intervals. These ten snails exhibited an average growth rate of 0.01 index units per day for the first 30 days. During the

Figure 3. Percentage of newly hatched snails surviving.



100
90
80
70
60
50
40
30
20
10
PERCENT SURVIVING
10
20
30
40
50
60
DAYS

second 30 days their growth rate increased to 0.02 units per day. Hunter (1961) found that newly hatched P. fontinalis could gain 1.1 mm in length the first 20 days. The shell increase corresponding to the newly hatched Ross snails' index was 1.2 mm the first 20 days.

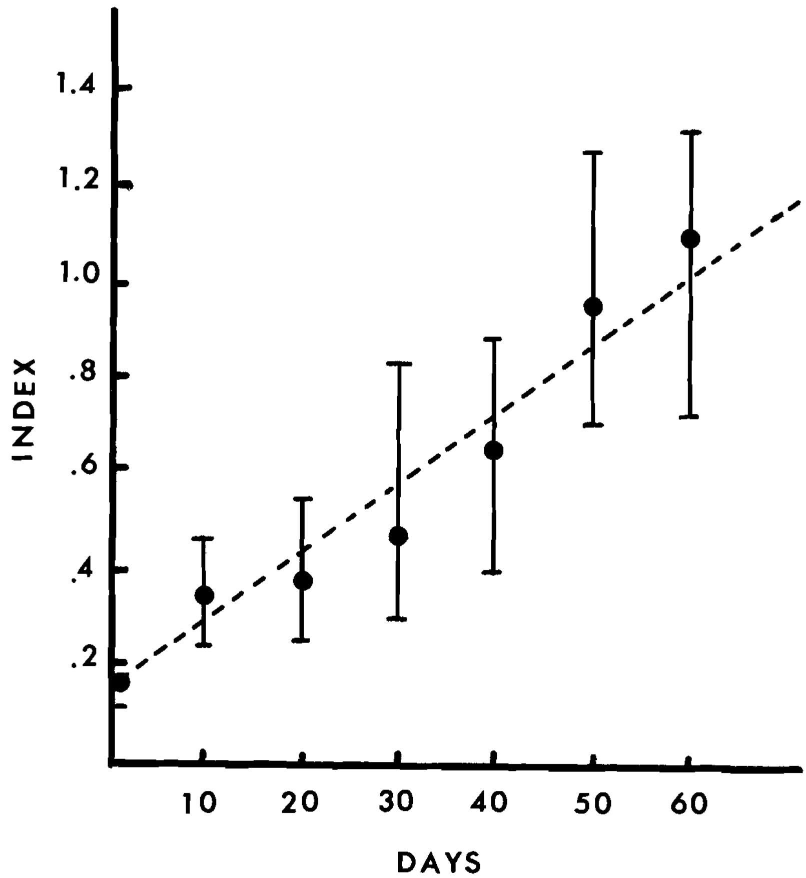
Growth rates of two older groups of snails were recorded. A mid-sized group with an average size index of 22.0 increased an average of 0.11 units per day. The size index of the older group averaged 45.0. These snails grew an average of 0.58 index units per day. This indicated the older snails were growing at a more rapid rate.

Population Structure

In order to study population age structure a method was needed for grouping snails into age classes. An egg mass was selected which had over 20 developing embryos to insure at least ten would be available for the determination. When hatching occurred, ten of the newly hatched snails were measured and each isolated in a shallow, covered dish of spring water with food. For the first ten days the snails were measured daily and the size index of each recorded. After the initial ten days they were measured at ten day intervals for 50 more days. A second group of snails was obtained and measured in the same manner, to determine if their growth rates would be the same. No significant difference ($p=0.05$) was found between the two groups when their average indexes were analyzed statistically.

Figure 4 shows the range of measurements of the ten snails on each of the days measured. There was overlap in the range

Figure 4. Range and average age index for ten snails from hatching to 60 days.


1.4
1.2
1.0
.8
.6
.4
.2
INDEX
10
20
30
40
50
60
DAYS

of size indices from one interval to the next so four age intervals were selected to represent population age structure. The first interval contained snails which were younger than 20 days and exhibited an index of 0.35 or less. The second interval represented snails considered to be 20 to 40 days old and consisted of snails with indexes of 0.36 to 0.70. The third interval represented snails between 40 and 60 days old. These snails had indexes of 0.71 to 1.0. The last interval contained the oldest snails, all over 60 days old and exhibiting indexes greater than 1.0.

Population structure was studied in the spring over an entire year. Size indexes for all snails collected during the study were recorded. Each snail's index number was then placed into the appropriate age class interval. The percentage of each age class present in the population was then estimated by determining the percentage of each age class present in the pooled samples. The population age structure over the entire year was then shown as the percentage present of each age class on each sampling date, (Figures 5-8).

Fortthe first three sampling periods the population age structure remained relatively stable (Figure 5,A,B,C). The proportion of older snails (age greater than 60 days) increased during the early spring. By April 28 the percentage of young snails in the population was increasing (Figure 6). This trend continued throughout the next three months. The periods of maximum population density and maximum egg production are reflected by the population age structure. By the end of May nearly 80 % of the population consisted of individuals less than 20 days

Figure 5, A-F. Percentage of snails occurring in each age class from September 11 through April 12.

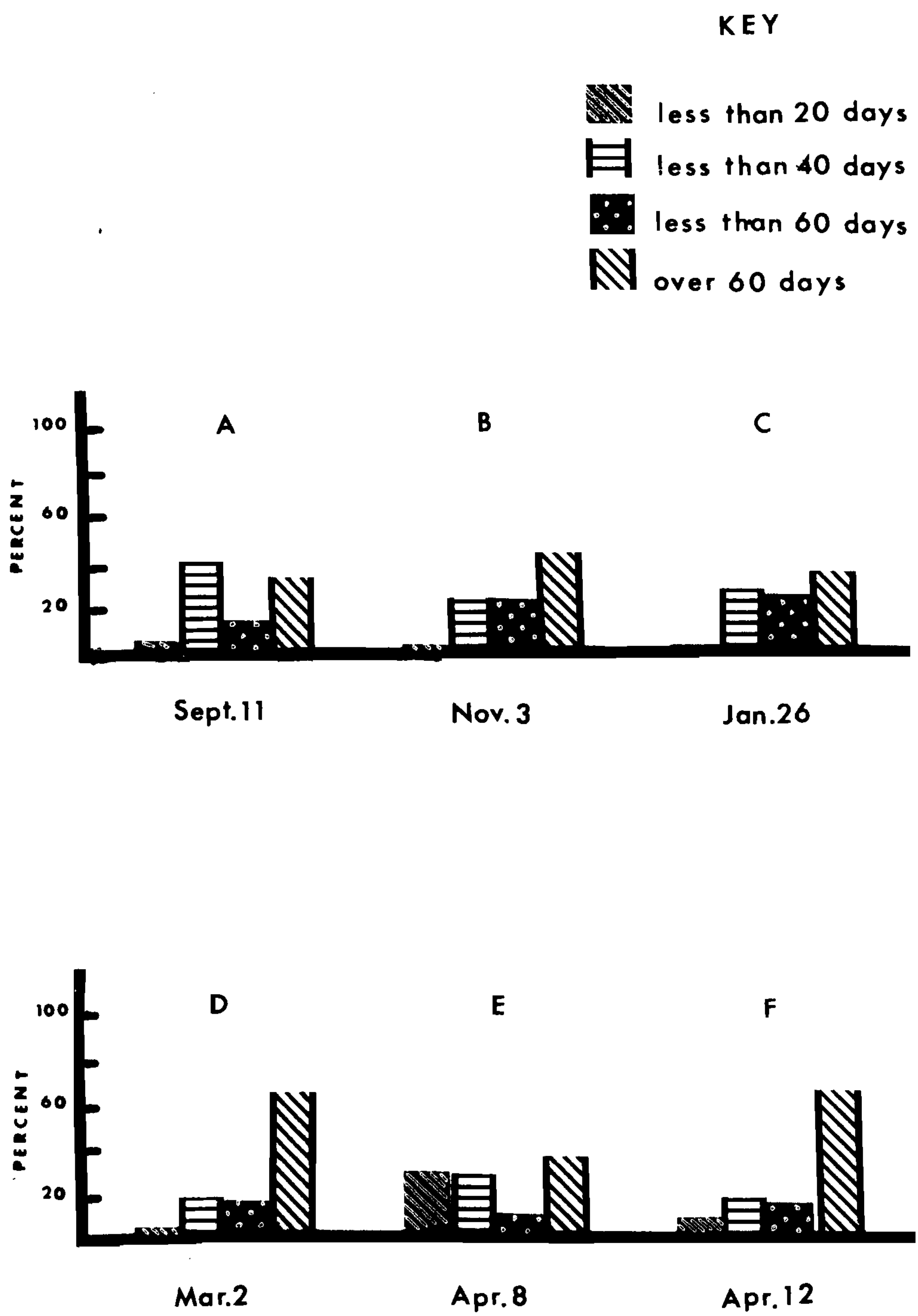

KEY
less than 20 days
less than 40 days
less than 60 days
over 60 days
100
60
20
PERCENT
A
B
C
Sept.11
Nov. 3
Jan.26
100
60
20
PERCENT
D
E
F
Mar.2
Apr.8
Apr.12

Figure 6, A-1. Percentage of snails occurring in each age class from April 16 through May 22.

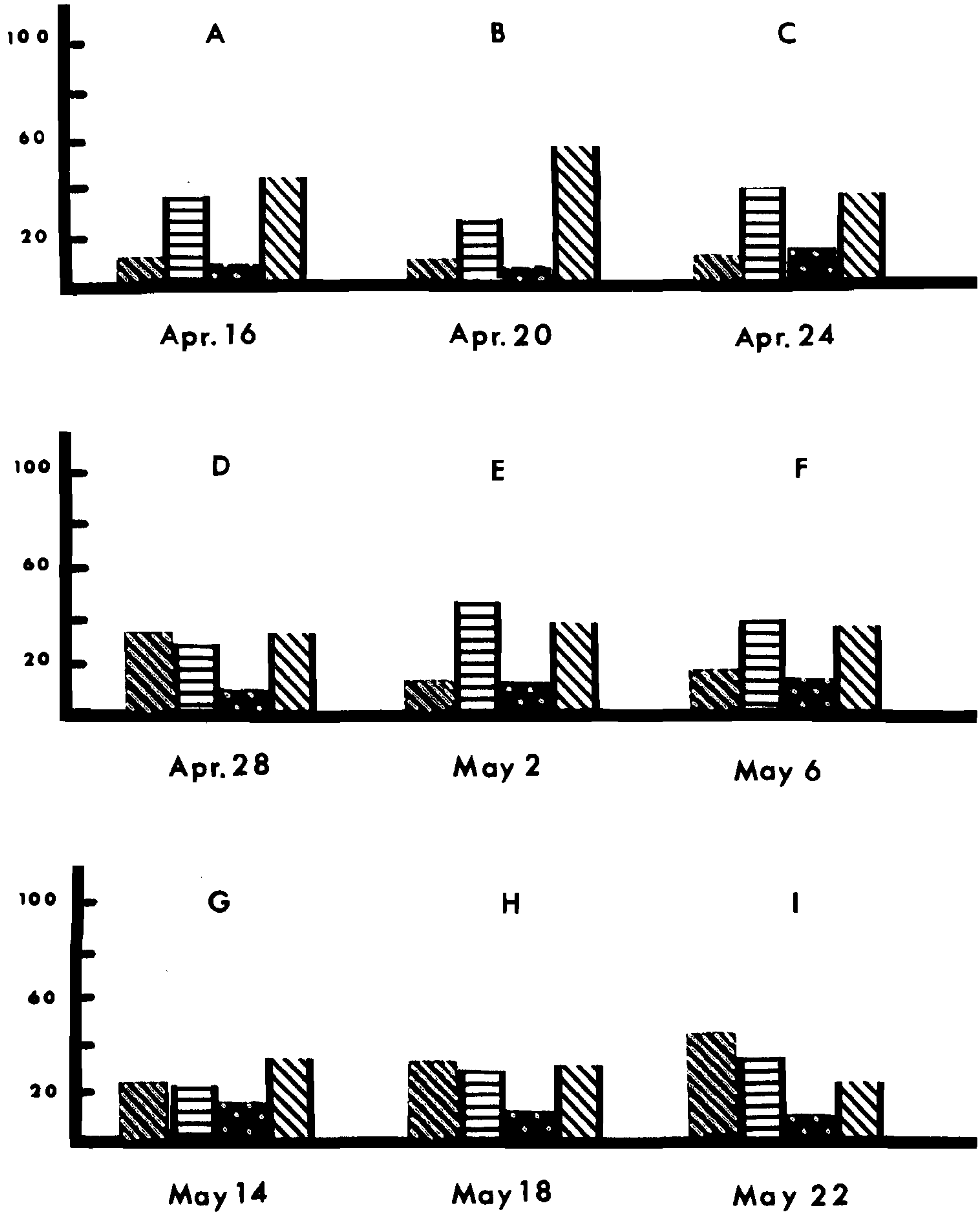

A
B
C
100
60
20
Apr. 16
Apr. 20
Apr. 24
D
E
F
100
60
20
Apr. 28
May 2
May 6
G
H
I
100
60
20
May 14
May 18
May 22

Figure 7, A-1. Percentage of snails occurring in each age class from May 26 through July 21.

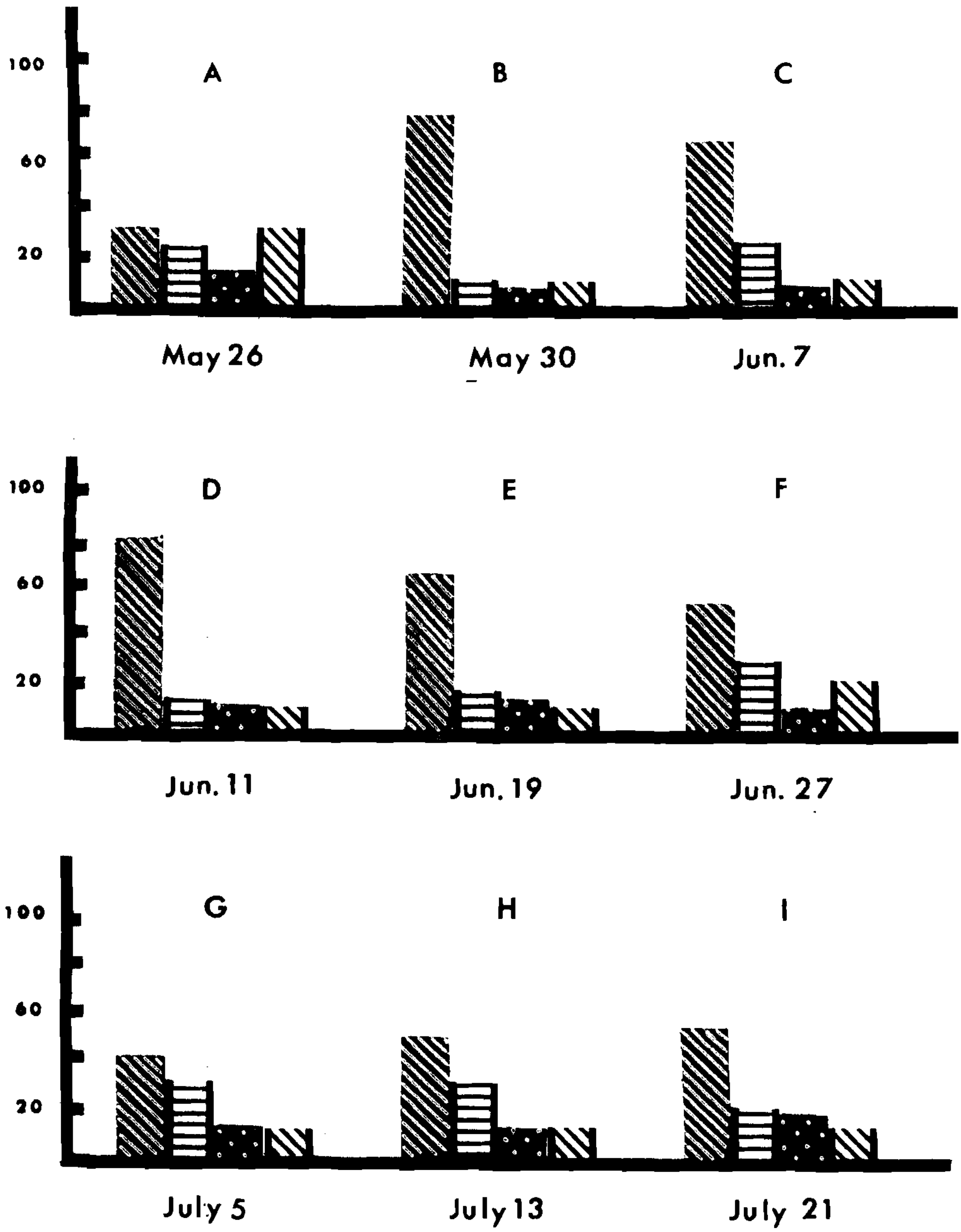
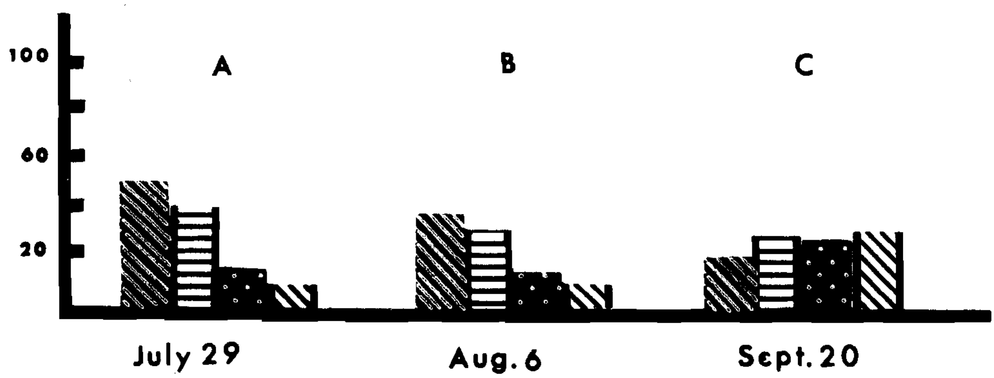

100
60
20
A
B
C
May 26
May 30
Jun. 7
100
60
20
D
E
F
Jun. 11
Jun. 19
Jun. 27
100
60
20
G
H
I
July 5
July 13
July 21

Figure 8, A-C. Percentage of snails occurring in each age class from July 29 through September 20.


100
60
20
A
B
C
July 29
Aug. 6
Sept. 20

old (Figure 7). The percentage of young snails then gradually decreased through the remainder of the summer and by September 20 the relative proportion of young had decreased to levels approximating that recorded the previous September (Figure 8).

Some relationships are apparent among data obtained on population structure, density of snails, and hatching. Figures 1 and 2 highlight these relationships. The peaks for estimated specific natality closely coincide with those of peak density. This not only supports the hypothesis that the peaks in standing crop and density were due to natality, but supports the proposed 18 day developmental period. While the first peak in density was probably due to the great upsurge in natality, the second and maximum peak was reached when the first increase was added to by a second period of natality. Note from the population structure figures that after the first period of natality in May and June the percentages of the age classes began to level off. The second age class began to increase as the snails grew out of the first age class. Young produced from the second period of natality added to those surviving from the first period. This accumulative effect caused the peak in density and total standing crop of the population. Mortality and growth of individuals then caused the age structure to level off.

SUMMARY

A study of the population dynamics of Physa anatina Lea inhabiting Ross spring revealed the population density to be related to the amount of watercress present in the spring's pool. Seasonal density of snails ranged from 10 snails per m^2 of plant surface area in the early spring to 145 snails per m^2 in late July. The fluctuations in density and total standing crop of snails were found to be related to the peaks in reproductive activity.

It was found that the Ross population began its reproductive season in late April and continued through July and August with some reproduction year round. Two peaks in natality occurred, the first and greatest in mid-May and the second during July and August. The accumulative effect of these peaks in natality resulted in the July peak in density and standing crop.

Laboratory investigations showed eggs from the Ross population hatched in an average of 18 days from deposition. Hatchability averaged 72.3 % while survivability of the young was 24 % after the first 60 days. Specific natality ranged from an average of 12.6 young per adult during the winter to 85.1 during the summer.

Investigation of the population age structure further supported two peaks in natality and the effect of natality on the density and total standing crop of snails. Age structure of the Ross population remained stable during the winter and

until late April. By May the percentage of young began increasing and reached a maximum in late May.

Reproductive activity was believed related to water temperatures occurring in the spring. Due to the relatively stable temperatures of this aquatic habitat the population showed some natality year round. The age structure investigations supported continuous reproduction since all four age classes were continuously present.

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