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THE REGULATION OF DENSITY IN A NATURAL POPULATION
OF THE POND SNAIL, LYMNAEA ELODES

by

Robert Michael Eisenberg

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in The
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1965

Doctoral Committee:

Professor Frederick E. Smith, Chairman
Professor Nelson G. Hairston
Assistant Professor George W. Saunders
Professor Frederick K. Sparrow

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INTRODUCTION

The study of animal populations has progressed from the strictly descriptive field approach and the strictly laboratory approach to an integration of the 2 approaches where careful laboratory experimentation is used as a tool in the analysis of field descriptions. This integrated approach can result in the ability better to predict population events under natural conditions. In this study the next logical step has been taken of experimentation carried out in the field under natural conditions.

One of the major questions in ecology is what determines the numbers of animals in natural populations. There is a number of widely divergent views on the overall classification of the mechanisms responsible for keeping the numbers of animals in populations at their observed levels in nature, and as these views diverge so do the actual mechanisms proposed. Two views are dominant. One is that the numbers of animals in natural populations are determined independently of population density with the weather being the major determining factor, while the other view is that natural populations are regulated in a density-dependent fashion and that this regulation is mediated through intra- and interspecific relationships which result directly from density feedback. Advocates of density-dependence do not or should not deny the importance of weather as a factor influencing the number of animals in nature, since it can obviously disturb populations strongly. They hold, however, that the average levels achieved are not determined by density-independent processes.

A number of quantitative studies have been done on natural populations

(for example: Davidson and Andrewartha, 1948; Reynoldson, 1961; Paris, 1963; Hall, 1964; Cooper, in press). Some of the above studies were completely descriptive and some combined laboratory with field work. In each case the author was fairly certain as to whether the population being studied was regulated or if the numbers were determined mainly by density-independent processes. But the problem in the past and presumably that of the future is that the interpretation of this type of work has not been completely acceptable to ecologists in general. The ecological literature contains many statements of theory and rebuttal on the topic of what determines the numbers of animals in natural populations (Thompson, 1956; Milne, 1957; Birch, 1957; Andrewartha, 1957; Nicholson, 1957; Hairston, Smith, and Slobodkin, 1960; Smith, 1961; Klomp, 1964). The problem yet unresolved is whether a population can have its numbers determined solely by density-independent processes and be maintained in this fashion from generation to generation, or whether regulation has to be invoked to explain the numbers of animals in natural populations.

A simple experiment which should yield results unequivocally supporting either density-dependence or density-independence is one in which the densities of isolated units of a natural population are artificially increased and decreased. The examination of these units in time would reveal whether or not convergence in density of unaltered and altered units has occurred. Since the only variable here is density, density-independent models must predict that convergence would not occur and that altered and unaltered units would remain disparate in time. As various density-independent processes acted on the subpopulations, they would fluctuate, but a plot of the logs of densities with time would give a series of quasi-parallel lines. On the other hand, density-dependent

models would predict that altered and unaltered situations would converge in time, although the level at which convergence occurred would almost certainly be influenced by density-independent processes.

The basic idea of altering densities of isolated units of a natural population as a test for density-dependent regulation has been suggested at least twice in the literature. Nicholson (1957b) first suggested it and Solomon (1961) restated Nicholson's basic ideas along with a plea that the work be done.

The major goal of this study was to perform the experiment as described above and test the hypothesis of density-dependent regulation, and hopefully to get at some of the mechanisms of regulation, if indeed it did occur.

A population of the pond snail, Lymnaea elodes living in a small pond, was chosen for the experimental device. The small pond afforded a discrete habitat which could easily be subdivided and the snail, an animal with limited powers of dispersal, which could be isolated effectively with simple enclosures.

THE STUDY AREA

Payne Pond is a small permanent pond located about 5 miles north of Ann Arbor, in Washtenaw County, Michigan. It is bordered along about half of its margin by an open horse pasture, and along its other half by an over-grown field. As a result of recent highway construction, a small portion of the southern end of the pond was filled and now borders the highway right-of-way. The pond has no permanent inlets or outlets. Rain run-off enters from a series of swales from the pasture and from a small temporary pond located in its northern end, and from adjoining fields. High water is drained off through a culvert at the southern end of the pond which runs under the highway. Due to the highway construction mentioned above, the maximum water level of the pond was reduced about 6 inches. In order to compensate for this a small sod dam was built near the culvert entrance, restoring the original water level. The surface area of the pond varies with rainfall but rarely is less than 2 or more than 3 acres. Minimum water levels are usually reached in the fall and are maintained until the ice cover melts and the spring rains begin. Maximum water levels are usually reached in the late spring or early summer after which time the pond water level again begins to drop due to low summer precipitation. This series of events can be considerably altered by high winter precipitation which can fill the pond to near maximum levels before the spring thaw. The pond is shallow with a maximum depth of about 4 feet. The margin is gently sloping, resulting in a wide border area only inches in depth. During the summer, this shallow margin, out to a depth of about 18 inches, becomes overgrown with emergent vegetation, i.e., Sagittaria latifolia, Alisma plantago-aquatica,

Eleocharis spp., etc. This lush growth of vegetation generally coincides with a lowering of the water level in the pond. It is this marginal area of the pond that forms the major portion of the Lymnaea elodes habitat.

LIFE HISTORY

Lymnaea elodes (palustris) Say [Stagnicola palustris elodes (Say), see Baker, 1928] is essentially restricted to 1 generation per year in Payne Pond. The snails overwinter along the exposed margin of the pond as small juveniles (1 to 5 mm). As the pond thaws and the water level rises in the spring, this area is submerged and the snails become active and begin to grow. They reach adult size (15 to 30 mm) in late spring and early summer at which time they begin to reproduce. The adults do not appear to grow much once reproduction has begun. The snails reproduce through June and most of July during which time the water level of the pond is generally falling. It is during this period of reproduction and falling water level that young snails estivate along the margin above the water line.

Throughout the reproductive period only 2 size classes of snails are usually found: the adults and the small young of the year. Thus snails produced in one year do not attain adult size that same year. In late summer and early fall both young and adults become increasingly difficult to find until they have essentially disappeared from the pond. Occasionally in the spring an adult that has overwintered is found, but the numbers of these snails in the spring of 1964 represented an insignificant fraction of the summer adult population.

OVERALL PLAN OF THE STUDY

The study can be divided into three parts. The first deals with a purely descriptive approach to a portion of the snail population in the pond that was not under enclosure. This part also involves a limited amount of laboratory work on the growth, reproduction, and predators of the snails. The major purpose of this part of the study was to obtain a description of the general dynamics of the snail population which could be used as a basis for comparison with the results obtained from the experimental work with isolated populations. The second part of the study concerns itself with the alteration of adult densities in a number of isolated populations and the effects of these artificial alterations on adult density per se. The third part of the study deals with the effects of the alterations in adult densities on the dynamics of the subsequent snail populations in the altered situations. In addition, a number of treatments other than adult density alterations were carried out and the effects of these treatments on their respective isolated populations were carefully examined.

THE SNAIL POPULATION OUTSIDE THE PENS

Sampling

The snail habitat in Payne Pond presents a heterogeneous area for sampling. Water depth and vegetational characteristics show strong zonation from the margin toward the center of the pond. A method well suited to sampling this type of habitat is that of taking samples at equal intervals from transects which traverse the habitat, perpendicular to the pond's margin. In sampling the snail population not under enclosure transects were used exclusively.

In order to follow the general dynamics of a portion of the snail population not under enclosure, a section of about 20 feet of margin was selected. This was adjacent to and north of the pens, and appeared to have the same general environmental characteristics as the area under enclosure. At each sampling time this area was divided into 3 or 4 equal parts, the middle 2 or 3 divisions determining the positions for 2 or 3 transects, respectively. The lengths of the transects were determined by the total length of submerged area in the pens at the time of sampling. Transects were begun just inside the waters edge, or if the pond level was higher than the backs of the pens, at the backs of the pens. In this manner the area sampled outside the pens was adjusted on each sampling date to coincide with the submerged area in the pens. Samples were taken weekly from April 16 to July 30, 1964, except on June 4 and June 25, 1964, when no samples were taken. Samples were also taken on November 1, 1964, after the water margin was beyond the transect area.

With the exception of the April 16 sampling, when 1 foot intervals were used, all samples were taken at 2 foot intervals along the transects.

Generally 3 transects and 12 to 24 samples were taken. When young and eggs were abundant and 3 transects were taken, in order to reduce the work load, one of the 3 was arbitrarily omitted from the examination for young and eggs.

With the exception of the February 22, 1964, samples, when a 5-inch diameter device was used to sample frozen soil (see Hairston and Byers, 1954, for description of the sampler), a 3-foot length of 4-inch diameter stovepipe was used to take all transect samples. The stovepipe proved to be very adequate for both submerged and exposed, unfrozen areas. Samples taken with this device included a 2- to 4-inch deep plug of the bottom substrate, plus whatever water and vegetation lay on top. Each wet sample was first drained of excess water through a 35 mesh screen sieve and then placed in a plastic bag. They were then brought into the laboratory and each was placed in a white enamel pan which was filled with enough water to submerge the entire sample.

Snails were removed from the samples by careful visual examination. This removal was greatly facilitated by a number of behavioral traits exhibited by the snails. They showed a tendency to crawl on the bits of vegetation in the samples or to move to the sides of the enamel pans. Snails were also located by means of the trails they left in the settled sediment in the bottoms of the pans. In addition a large number of snails were found moving around, foot up, on the surface of the water. With wet samples the procedure of removing snails was begun as soon as the samples were submerged in the enamel pans, but with dry or frozen samples there was usually a 12- to 24-hour period before the snails became active enough to be found easily and removed from the samples.

While the population was reproductive, eggs were found by carefully

examining each bit of vegetation and debris in the samples for the presence of egg masses. After the samples had been thoroughly examined they were sieved through an 18 mesh screen sieve and the sieve residue was examined for the presence of loose egg masses.

The process of examining the samples was followed continually on the day the samples were taken, or in the case of dry or frozen samples, on the day following sampling. On the first day of intensive examination the greatest majority of the snails were removed from the samples, but they were periodically examined for an additional 2 or 3 days. During the general hunting procedure and before discarding samples were carefully examined for the presence of dead adult shells. Also, snail predators were removed from the samples when they were found.

On several occasions, samples ready for discarding were pooled and kept in the laboratory for several days, over which time they were periodically examined for snails. This procedure always resulted in the finding of a few additional snails, but always of the small young and less than 1% of the total obtained from the regular time interval of examination.

On one occasion a known number of partially grown adults was added to a group of snail-free samples and these were agitated to simulate the conditions after sampling. All snails added were found with ease. -It is felt that adults, both living and dead, were removed from samples in a quantitative fashion due to their large size relative to the size of the samples. No test of efficiency of the extraction method was made for the small snails, but snails of the size of young at hatching were obtained from the samples in large numbers and with apparent facility. It is also thought that egg masses due to their large size and usual attachment to

solid substrate were removed from the samples with a high degree of efficiency.

All snails from the samples were counted and measured. Adults were measured with a pair of vernier calipers to the nearest 0.1 mm and young with an ocular micrometer to the nearest micrometer unit (17.3 units = 1.0 mm). Snails were measured for greatest length from the base of the apex to the end of the aperture. Young measured with the ocular micrometer were first oriented with their apertures facing up. The numbers of eggs and egg masses were counted. All snails and egg masses from the transect samples were discarded after counting and measuring, and not returned to the pond.

Each time the pond was visited the temperature of the water in the study area was taken with a mercury thermometer and the water level was recorded from a celluloid ruler fixed to a cedar post at the pondward end of pen 28.

Results

The results of the weekly transect samples of the snail habitat not under enclosure are given in Figure 1. There appears to have been little mortality in overwintering snails during the first few weeks of sampling, followed by a fairly constant rate of loss over the remainder of the sampling period. For the period from April 16 to July 23 the death rate was 0.041 per day. The presence of eggs was first noted on May 28 and egg production reached its peak (45.08/sample) on June 18. The numbers of young reached maximum levels (82.25/sample) on July 9. Both eggs and young showed fairly rapid increases followed by a very rapid decline. On July 30, neither eggs nor adults were found and only 4.0 young per sample

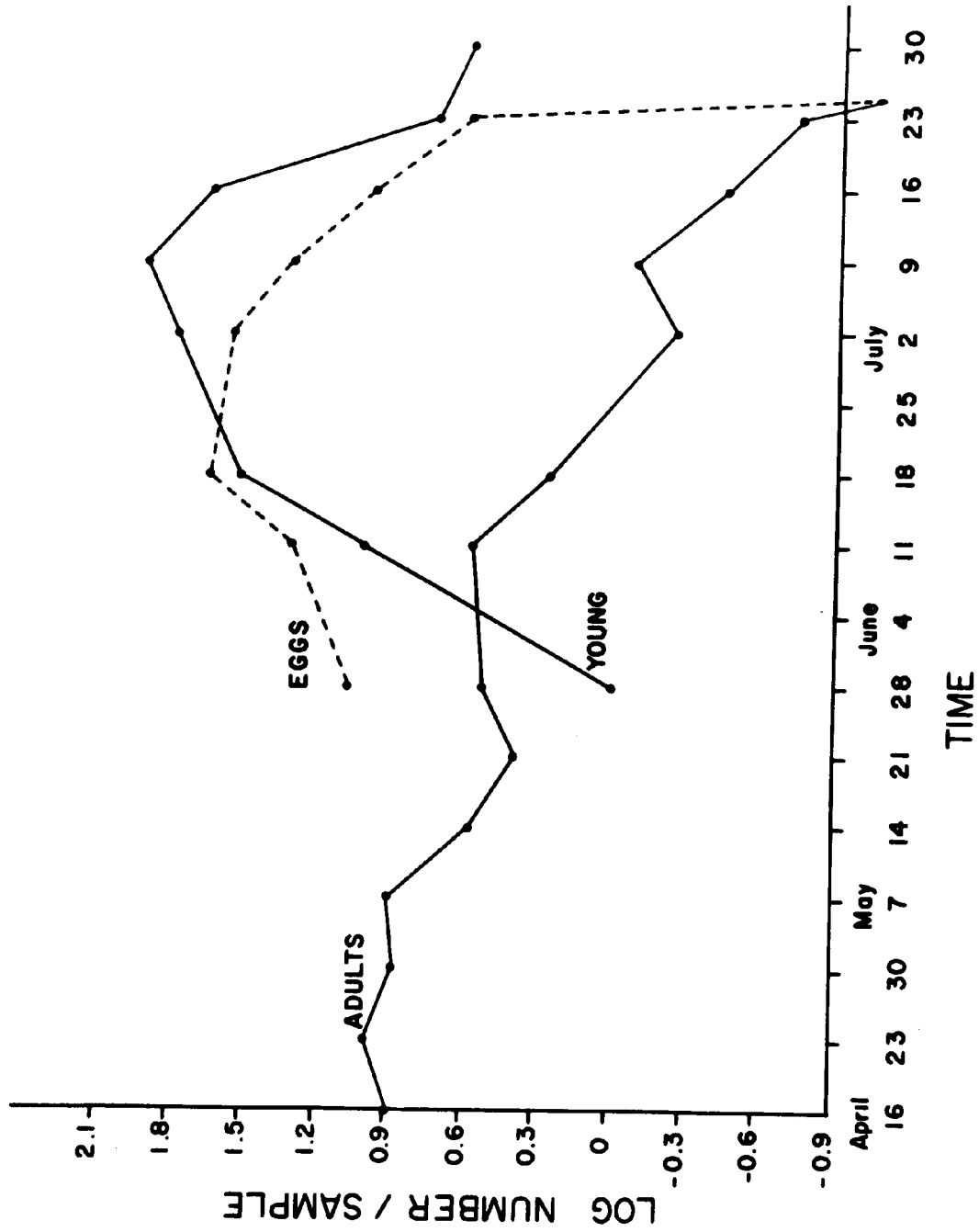


Figure 1. Description of the snail population not under enclosure from April 16, 1964, to July 30, 1964.

were found (note: these samples did not include the exposed zone of pond bottom).

Egg masses in the transect samples ranged in mean clutch size from 20.86 eggs on May 28 when 14 masses were found to 45.00 eggs on July 23 when only 1 egg mass was found. However, the mean number of eggs per mass did not increase in a regular fashion with time and, except for the July 23 samples, it was never over 30 eggs per mass. Of the 77 egg masses found, 67 had between 10 and 40 eggs. The largest clutch contained 48 eggs.

In Figure 2, the size frequency distributions of adults (overwintering snails) from the weekly transect samples are plotted. The open circles on the graph are the mean sizes of the snails within a transect series. A smooth curve drawn through these open circles approximates a growth curve for the snails under the environmental conditions over this time interval, uncorrected for differential mortality. The growth rate slowed in late May and early June when the population became reproductive. The increase in mean adult size after May 28 was achieved without an increase in size of the larger size categories. The February 22 distribution in this figure represents the snails (estivating) from the margin samples whose distributions of abundance were used in locating the snail pens (see section on The Snail Populations in the Pens; Location and Construction of the Pens). Little growth occurred in the snails before April 16. Of particular interest is the range of sizes in the February 22 samples. Only 1 snail out of 328 is larger than 4.0 mm, and size cuts off sharply at 1.2 mm.

The size frequency distributions of the new generation snails from the transect samples are given in Figure 3. On May 28, in addition to eggs from newly matured adults, a few partly grown young were found.

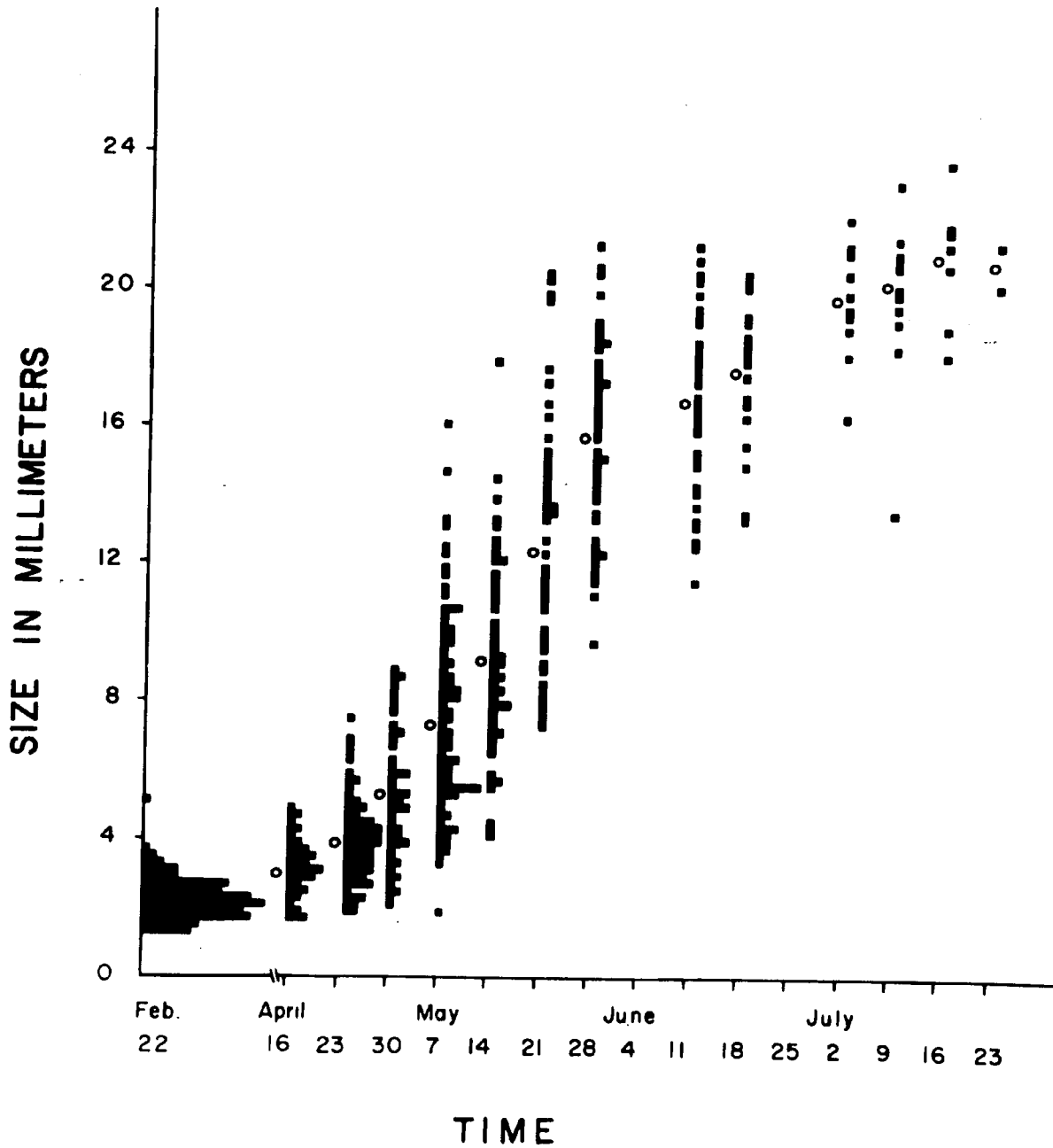


Figure 2. Size frequency distributions of adults (overwintering snails) from the snail population not under enclosure. Each square represents 1 to 3 snails.

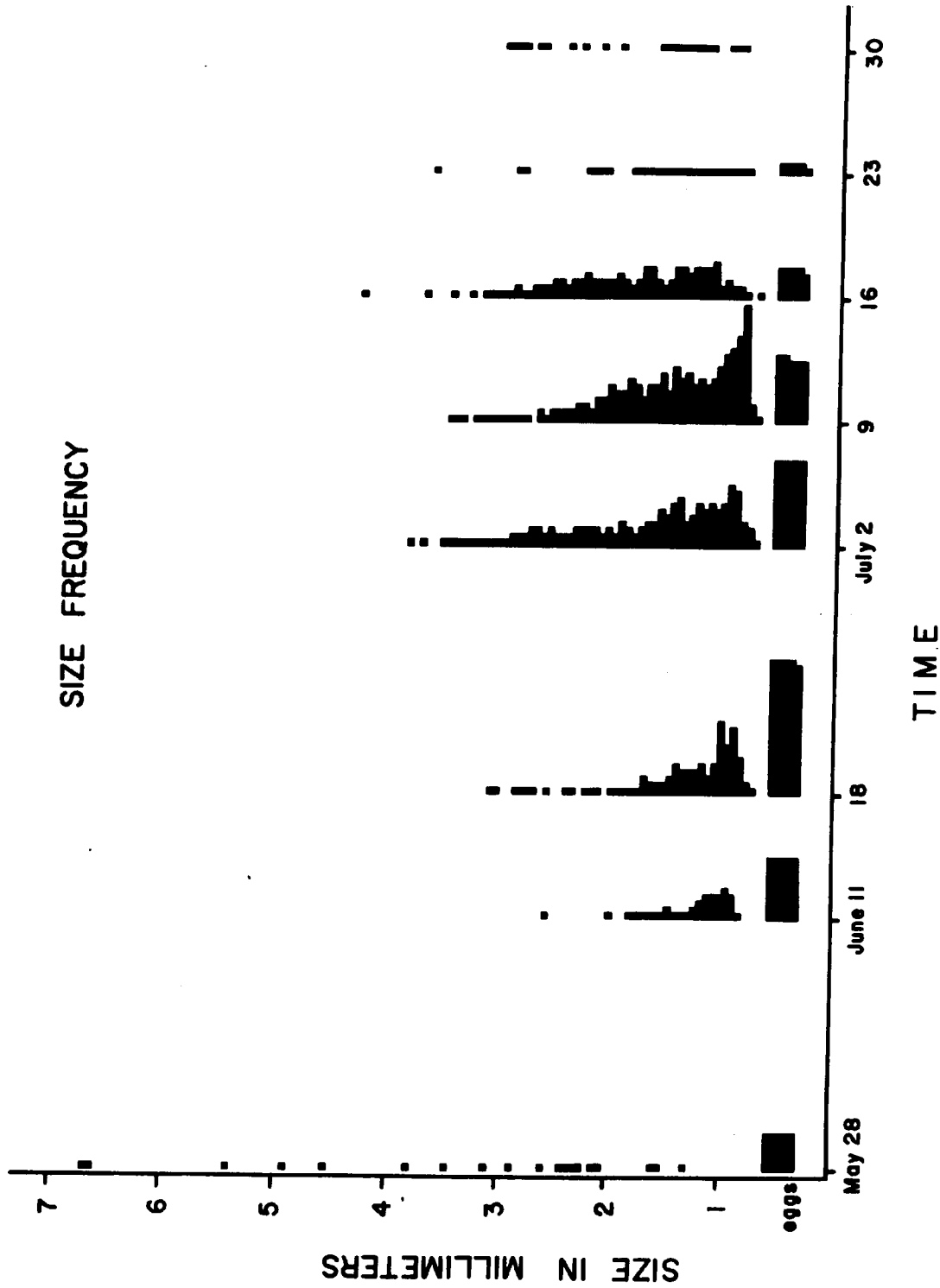


Figure 3. Size frequency distributions of young snails from the snail population not under enclosure. Each square represents 1 to 5 snails or eggs.

They probably were produced by the few overwintering adults that were known to be present in the pond, at densities too low to be expected in samples. These young never appeared in later samples, nor could any of their age be found anywhere in the pond.

With the exception of the May 28 samples, the maximum size attained by young snails was only 4.3 mm. The size ranges in these histograms are thus similar to those from the February samples of estivating snails. The major difference between the 2 is the presence of many snails between 0.8 and 1.2 mm in the summer samples.

A summary of the raw data from the transect sampling is presented in Table 1.

TABLE 1

THE RESULTS OF TRANSECT SAMPLING FROM OUTSIDE OF THE PENS
FROM APRIL 16, TO JULY 30, 1964, AND NOVEMBER 1, 1964

Date	No. of Adults	No. of Samples	No. of Young	No. of Samples	No. of Eggs	No. of Egg Masses	No. of Samples
4-16	115	15	0	15	0	0	15
4-23	174	18	0	18	0	0	18
4-30	120	16	0	16	0	0	16
5-7	189	24	0	24	0	0	24
5-14	91	24	0	24	0	0	24
5-21	59	24	0	24	0	0	24
5-28	82	24	23	24	292	14	24
6-4	---	--	---	--	---	--	--
6-11	46	12	153	12	250	10	12
6-18	22	12	408	12	541	20	12
6-25	---	--	---	--	---	--	--
7-2	10	18	733	12	446	19	12
7-9	15	18	987	12	256	9	12
7-16	7	18	530	12	117	4	12
7-23	2	11	61	11	45	1	11
7-30	0	7	28	7	0	0	7
11-1	0	24	77	24			

GROWTH AND REPRODUCTION

Laboratory

Egg hatching intervals

Adult Lymnaea elodes collected from Payne Pond were acclimated to 20° and 25° C in constant temperature boxes in the laboratory. After 2 to 3 weeks the egg masses deposited by these snails were isolated and maintained at the temperatures at which they were produced to determine the time interval to hatching. This interval varied from 8 to 9 days for eggs at 25° C and from 11 to 12 days for eggs at 20° C.

Sizes of young at hatching

The sizes of young snails at hatching were determined by isolating 12 egg masses from a laboratory culture of adult, Payne Pond Lymnaea which was kept at room temperature, and removing the young as they hatched. To facilitate handling and measuring, the snails were killed in 70% alcohol as they were removed. These young were measured in the identical fashion to the young from the transect samples. The size distribution of the 281 snails produced by the 12 egg masses was:

Size (mm)	%
0.8	17.1
0.9	65.8
1.0	16.4
1.1	0.7

Growth rates

Growth rates for snails at 20 and 25° C from the time of hatching were determined from groups (cohorts) of 5 snails selected from individual egg masses deposited at the appropriate temperatures. Freshly hatched young

were first maintained together in finger bowls that had previously been conditioned so that they contained a rich algal growth attached to the glass substrate. After 3 to 4 days the young were segregated into separate, similarly conditioned finger bowls. After the snails had attained a size of approximately 2.0 mm their food supply, which up to this time consisted entirely of the algae in the finger bowls, was supplemented with super-abundant amounts of dried, frozen spinach. The measurement of small snails (up to about 5.0 mm) was done in the same fashion as the young from the transects, but snails over 5.0 mm were measured against a piece of millimeter graph paper and their lengths were estimated to the nearest 0.1 mm. Because of the very rapid growth of these snails their shells were very delicate and they had to be handled with great care. Every 3 or 4 days, when the snails were measured, the water in the bowls was changed with preconditioned water and new food added, while old, uneaten food was removed.

In figure 4, the averaged growth curves for 4 of the above 12 cohorts of Lymnaea grown at 20 and 25° C are presented. These curves represent the maximum and minimum rates obtained for each temperature. Some 25° cohorts did not grow as well as the maximum 20° group. In the minimum 20° cohort shown in the figure, the increments of growth for 7 day intervals beginning at time zero (hatching date) increase steadily from 1.1 mm (0 to 7 days) to 3.0 mm (9 to 16 days).

Reproduction

Two cohorts of snails from the 25° growth study were maintained through a portion of their reproductive period. First eggs were deposited 31 and 34 days after hatching by snails 20.4, 21.6, and 19.2, 22.9 mm respectively for the 2 cohorts. The growth rates in these 2 cohorts

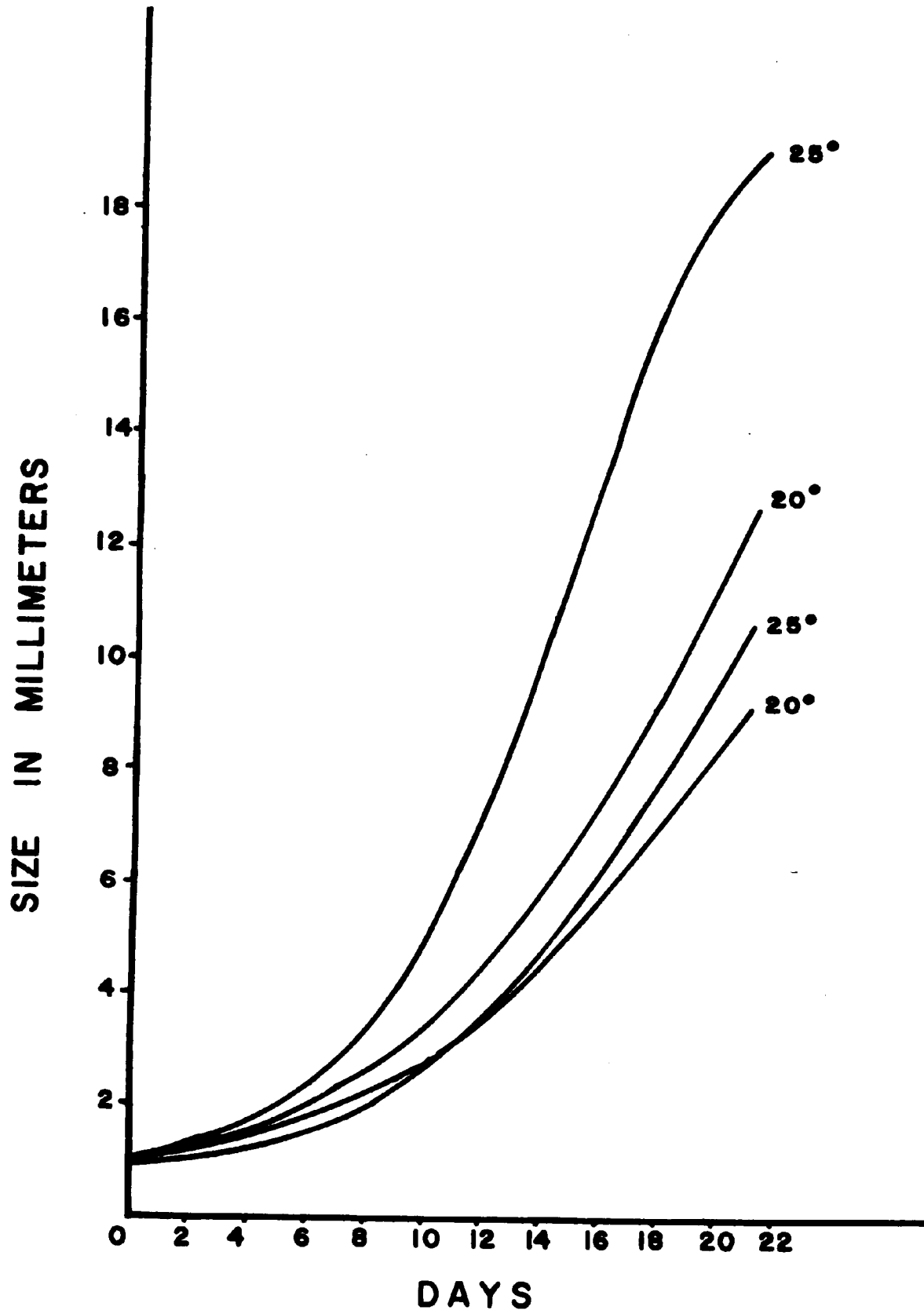


Figure 4. Growth curves for snails grown in the laboratory at 20 and 25° C.

were the minima obtained for the temperature. The lower 25° C growth curve in Figure 4 is from the cohort that first produced eggs at 34 days. The 9 snails (1 died prior to reproduction) in these 2 cohorts deposited 31 egg masses and a total of 2653 eggs in 11 days for a mean number of eggs per mass of 85.58 ($s = 27.3$).

PREDATION

Field

A number of direct observations of snail predation was made in the field. Those animals actually seen in the process of killing and eating snails were: large dragonfly nymphs eating large, adult snails; leeches eating small snails; a bug, Belostoma (both early instars and adults), eating both adult and small snails; several species of sciomyzid fly larvae eating small snails and one species that deposited its eggs on the shells of estivating adults and whose larvae killed the snails.

Several methods were tried in an attempt to quantify the sciomyzid larvae in the pond, but none was successful. The regular sampling for snails both inside and outside of the pens did produce some larvae, but not enough for reliable estimates of the fly larvae densities. Observations of adults around the pond and of larvae and the puparia and adults they produced indicated that 4 or 5 species of sciomyzids were present in the area.

An impression of the fly larvae population, based mainly on the facility with which they were collected for laboratory work, indicated that there were 2 peaks in larval abundance. These were in April and May when the overwintering snails were most abundant and again in late June and early July when the young of the year were most abundant. From mid May to mid June and again in late July the larvae appeared to be almost completely absent from the pond.

There was no indication from the field observations of any significant degree of predation on the snail's eggs. A few isolated observations were made of single egg capsules in egg masses filled with protozoa. Further-

more, while it was found in the laboratory that adults of Lymnaea elodes will, in the absence of alternative food, cannibalize their freshly hatched young, there is no evidence that this occurs in the field.

Laboratory

A number of possible predators were brought into the laboratory from Payne Pond. A wide variety of animals, from newts to crayfish, were found to prey on the snails under laboratory conditions and with no other food available. But the value of such determinations is highly questionable since predator food preference in nature is not known.

In the laboratory the only quantitative predator experiments were those using sciomyzid larvae collected from the pond. Neither the exact ages of the fly larvae used were known nor how many, if any, snails they had already consumed in the field. On April 22, 5 small larvae (about 8 mm long) were placed in separate finger bowls along with a large number of Lymnaea collected on the same day. A superabundance of snails was always kept in the finger bowls. The 5 larvae consumed 142 snails from 2.3 to 8.0 mm in length during a total combined larval feeding life (until feeding stopped prior to pupation) of 44 days. Thus approximately 3.2 snails were consumed per larval feeding day. It was found that the same types of sciomyzid fly larvae as used in this experiment would not, even when starved, attack adult snails (15 mm or larger).

FIELD AND LABORATORY

The temperature of the water in the study area varied a great deal, both diurnally and from day to day, during April and May when the overwintering snails were growing to adult size. The shallow nature of the margin habitat made it subject to extremes in temperature, especially on clear, sunny days. On April 5, an overcast day, the water temperature was 7 to 8° C at 4:00 p.m., while on April 6, which was clear and sunny, the temperature of the water was 21.5° C at 3:30 p.m. Throughout April it was common to find early morning temperature of around 10° C and afternoon temperatures of 21 and 22° C. In May few temperatures below 15° C were recorded and on sunny afternoons the temperature reached 30° C. In June and July few temperatures below 18° C were observed and most of the day the water temperature ranged from 25 to 30° C.

Since there was so much variation in temperature in the pond while the overwintering snails were growing there can be no direct comparison made between their growth and the growth of snails in the laboratory under constant temperature conditions.

However imperfect the laboratory data on growth and reproduction are in relation to actual field conditions, one thing is clearly demonstrated by them. A generation time of about 40 days is probably a reasonable estimate for temperatures between 20 and 30° C and it therefore seems not unreasonable to expect that under ideal conditions (i.e., abundant food, low mortality) the snails in the pond should have been able to complete 2 and perhaps 3 generations during the spring and summer (April through August) instead of the single generation which was observed.

Examination of the size frequency distributions of the new genera-

tion snails from the transect samples (Figure 3) gives little indication of growth in these snails. There appears to be 2 possible reasons for this. Either they were not growing more than the slight amount that is indicated in the figure, or they were growing more but the larger size categories were being removed from the population.

In Figure 5 are the results of an experiment run in the field in an attempt to discover what was happening to the young snails in the pond. An enamel pan (area = 201 square inches) was submerged in the transect sampling area from July 9 to July 14. On July 14 the sediment that had collected in the pan was removed, preserved in 70% alcohol and brought into the laboratory. The sediment was carefully examined under a dissecting microscope and all whole, dead snail shells were removed along with any fragments containing a complete apex. About 90% of the shells found were whole.

Of the 3 histograms in Figure 5, 2 have been reproduced from the July 9 and July 16 samples from Figure 3. The middle histogram represents the dead shells sedimented into the enamel pan from July 9 to July 14. The July 9 and July 16 histograms are each based on 12 samples and the sediment histogram has been adjusted so that the area of the pan and the time interval of sediment collection are equivalent to the area sampled by 12, 4-inch cores and an interval of 7 days. The straight line on this graph drawn through the 3 histograms connects the mean size of a cohort of laboratory snails grown at 25° C with superabundant food, from the time at hatching to 7 days of age. If the growth of the young in the pond were proceeding at this rate, the majority of the young sampled in any one week would have been unhatched eggs the week before.

The efficiency of the sediment method for collecting dead shells is

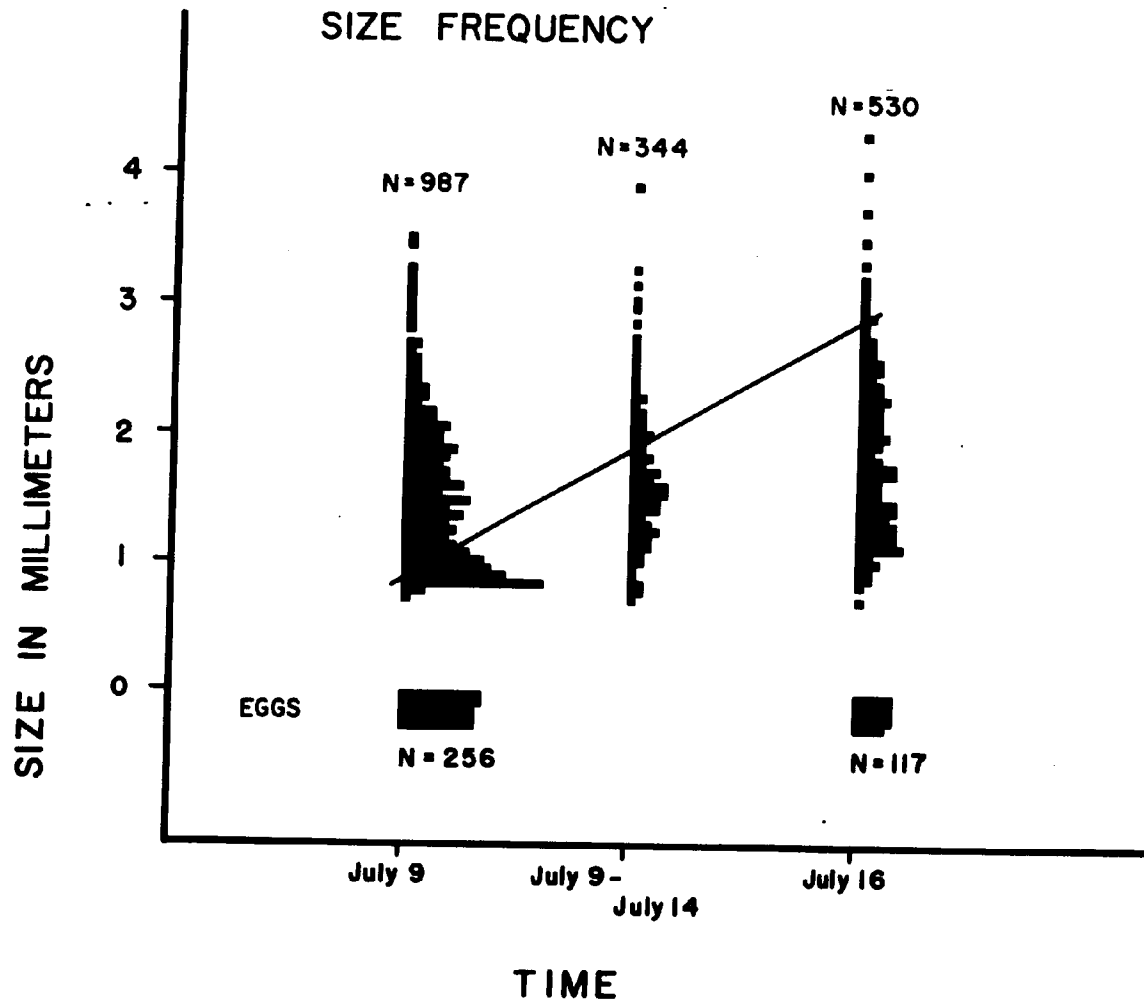


Figure 5. Size frequency distributions of young snails from 2 July samples and of dead shells sedimented in the sampling area. Each square represents 1 to 5 snails or eggs.

not known, but the indication is that it is quite high. If it is assumed that the hatching interval during this period was 10 days, then during the week from July 9 to July 16, $7/10$ of the July 9 eggs would have hatched ($.7 \times 256 = 179.2$). Thus, on July 16 one would expect to find, assuming no mortality of young or eggs, $987 + 179$ or 1166 young snails. But only 530 were found on July 16, leaving 636 to be accounted for. The sediment pan produced 344 or just over 54% of this loss.

The distribution of the sizes of the dead snails from the sediment is intermediate between those of July 9 and July 16. Thus, no evidence of strong size-selective mortality is present.

There is evidence that the young in the field were growing at only a fraction of the rates observed in laboratory snails. Of the 530 young found on July 16, approximately 350 ($530 - 179 = 349$) must have been young and not eggs on July 9. Since the indication from above is that there was no strong size-specific mortality, then the median snail from one week should also be the median snail, after correction for newly hatched young, the following week. Using this line of reasoning, an estimate of field growth over a 7 day interval can be obtained by considering the periods June 11 to June 18, July 2 to July 9, and July 9 to July 16. For these 3 periods it was determined that the median snail grew on the average 0.3 mm in 7 days. This is only about $1/7$ of the growth increment in 7 days achieved by snails, beginning at the same median sizes, in the lowest 20° C cohort shown in Figure 4.

In Figure 6, the relation between the numbers of young per sample from the weekly transect samples and the accumulated estimate of the numbers of eggs per sample hatched during the season is shown. An egg development period of 10 days was used. Estimates of the numbers of

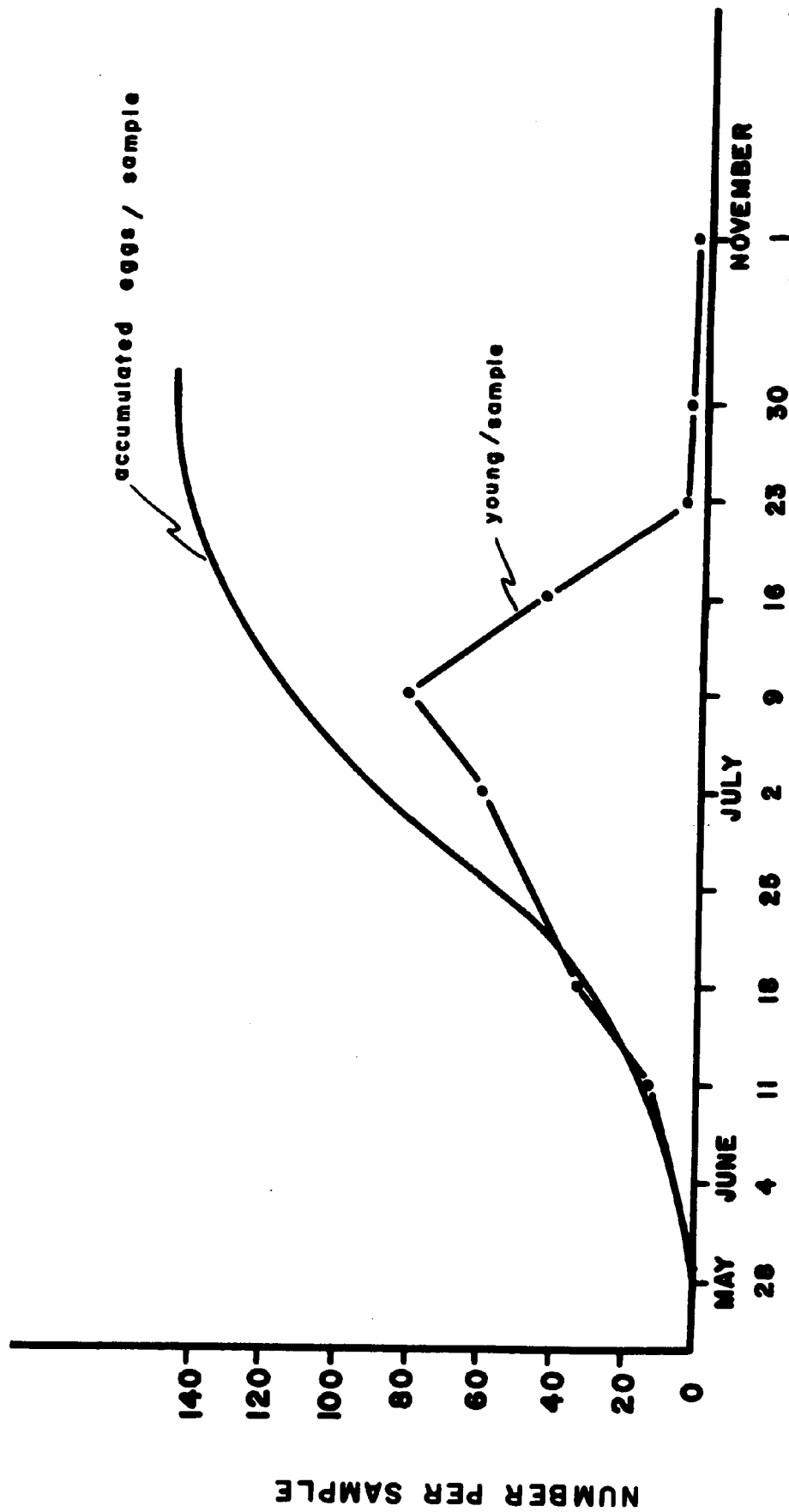


Figure 6. The relation between the numbers of young per sample and the accumulated estimate of the numbers of eggs hatched during the season.

eggs per sample on the 2 dates (June 4 and June 25) when samples were not taken were obtained by extrapolating from adjacent data.

The figure shows little loss of young up through June 25, at which point the actual number of young obtained per sample begins to fall rapidly below that expected on the basis of accumulated eggs. The last value of young per sample on the graph is from the November 1 samples taken from the then dry transect area and represents only 3.2 young per sample. This is opposed to a season's estimated accumulation of 145.7 eggs per sample. The difference between accumulated eggs and the number of snails left represents a 97.8% mortality of young assuming all eggs hatched.

THE SNAIL POPULATIONS IN THE PENS

Location and Construction of the Pens

On February 22, 1964, a series of samples was taken from 4 evenly spaced transects across a homogeneous portion of the exposed, frozen soil of the margin of the pond. Seven samples were taken from each transect at 2 foot intervals. On the basis of the distribution of the snails in these samples, and with the aid of vegetational bands along the margin of the pond, and with a knowledge of the preceding spring and summer water levels, grids were laid out for 28, 3 x 15 foot enclosures (pens) in 2 groups of 13 (pens 1 to 13) and 15 (pens 14 to 28) pens each. The pens were built perpendicular to the shoreline. Each pen was supported with 6 evenly spaced 3 inch by 7 foot cedar posts driven or dug about 3 feet into the ground. The sides and shoreward ends of the pens were covered with 14 x 16 mesh plastic impregnated steel screen which was attached to the posts with wire staples. Pens within a group shared common supports and sides. The pondward ends of the pens were first covered with 16 x 18 mesh aluminum insect screening and then with no. 202 Nytex nylon monofilament cloth (202 micron openings). The screen and nylon cloth were attached to the end supports with quarter inch molding backed with strips of insulating material to insure a tight fit. All ends and sides were buried into the ground to a depth of 4 to 6 inches. The snails showed little tendency to crawl onto the screen sides or ends of the pens and no tendency to burrow more than a fraction of an inch into the bottom substrate.

The heavy work of placing cedar posts and putting up the sides of the pens was begun on March 1, 1964, when the ground and the pond were frozen

and the water margin about 30 feet from the construction area. This work was completed on March 25, 1964, while the ground and the pond were still partially frozen and the water margin still several feet from the pens.

After the cedar posts were all in place and before the screen sides were put up, 2 by 4's were nailed to the posts, connecting in pairs the 3 sets of posts supporting each pen. These 2 by 4's later served as supports for 8 foot sections of 2 by 10's which were used as catwalks for examining and sampling from the insides of the pens. Once the pens were completely built they were not entered until the fall when they were completely dry. The end material of the pens was not put in place until May 26 and 27, 1964, so that up to this time the pond fauna could mix freely in the partially built pens.

Adults

Density estimates and manipulations

On June 1, 1964, after the pens had been closed, estimates of the adult densities in them were begun using a simple mark-release-recapture index (Lincoln Index, unmodified). Every effort was made to meet the basic assumptions of the method. Three successive estimates for each of 26 pens from June 1 to June 10 gave results that appeared to be consistent. The estimates obtained by pooling these data are shown on the first column of Table 2. Pens 27 and 28 were not sampled for lack of time.

On the basis of these estimates 6 pens were selected from each of the 2 groups of pens. These 12 pens were divided into 3 sets of 4 pens each in such a manner as to achieve similar means and variances among the sets. Further criteria for selecting the pens within a set were that half (2 pens) of each set be located in each of the 2 groups of pens and

TABLE 2

ADULT DENSITY ESTIMATES AND MANIPULATIONS IN PENS

(R = reduced; I = increased; C = control)

Pen No.	Lincoln Index Estimates 6/1-6/10	Manipulations 6/10-6/15	Lincoln Index Estimates 6/17-6/23	Manipulations 6/21-6/30	Census 6/25-7/7	Final Spring Estimate	Fall Estimate of Spring Adults
1	594	--	--	--	--	--	902
2(R)	504	- 403	1012	- 880	--	259	193
3	515	--	--	--	1272	--	129
4(I)	655	+2620	--	+4400	--	5539	5157
5(C)	653	--	--	--	--	1139	1160
6	406	--	--	--	--	--	902
7	684	--	--	--	1006	--	64
8	579	--	--	--	--	--	580
9(C)	708	--	1277	--	--	1139	1096
10(R)	716	- 573	--	- 880	--	259	516
11(I)	722	+2888	--	+4400	--	5539	5737
12	640	--	--	--	--	--	967
13	790	--	--	--	--	--	580
14	656	--	--	--	--	--	967
15	975	--	--	--	--	--	1740
16(C)	506	--	925	--	--	744	580
17(I)	540	+2424	--	+2800	--	3544	2643
18(R)	562	- 450	--	- 560	--	184	322
19	691	--	--	--	--	--	774
20(I)	506	+2260	--	+2800	--	3544	2901
21(C)	564	--	1052	--	--	744	1096
22	536	--	--	--	709	--	0
23	475	--	--	--	--	--	1031
24	720	--	--	--	779	--	129
25(R)	625	- 500	--	- 560	--	184	193
26	523	--	--	--	--	--	322
27	---	--	--	--	--	--	1031
28	---	--	--	--	--	--	1418

that no 2 adjacent pens be assigned to the same set. One of these 3 sets was arbitrarily selected to have its adult densities increased to 5 times the original density estimates, a second to have its densities reduced to $1/5$ of the original estimates, and the third set to remain unchanged as a control.

Reduction in the pens was accomplished by carefully examining the pens and removing the required number of snails. Snails removed were used to raise the densities in the increased pens, but the majority of the snails for this purpose was collected from an area of the pond about 50 yards to the south of the pens. These manipulations were begun on June 10 and completed on June 15, 1964, and are shown on column 2 of Table 2.

From June 17 to June 23, 1964, a number of additional adult density estimates was made as a check on the first estimates. Both old marks and a new series of marks were used to obtain these estimates (column 3, Table 2). In all cases the new estimates were higher than the first estimates. With the evidence presented by these new estimates it was decided that those used as a basis for manipulations were not reliable, and adjustments were begun in the already altered pens. At the time (June 21) it was not known what the levels of manipulations would be, but the new estimates indicated that the old ones were consistently and considerably low.

As an alternative method for estimating the adult densities, 2 pens, not previously assigned treatment, were selected from each of the 2 groups of pens. All of the vegetation in these 4 pens was either pulled out or cut off below the surface of the water, and all snails found were removed. The removal of snails was mainly accomplished by running a dip

net through the pens and effectively straining the contents of the water and the sediment in them. These 4 pens were continually examined until no more snails could be found. Both living and recently dead shells were removed in the above manner, giving 4 censuses of total pen populations.

The censusing of the adults was begun on June 25 and the majority of the snails had been removed from 2 of the pens by June 26, although the last snails were not removed from these 4 pens until July 7, 1964. However, since it was felt that time was the more important factor to consider, alterations in manipulations were carried out on the basis of partial censuses. An estimate of 1100 snails per pen was used for the pens in group 1 to 13 and 700 snails per pen for the group 14 to 28. Thus either 880 or 560 snails was removed from the reduced pens and either 4400 or 2800 snails were added to the increased pens. All manipulations were completed on June 30, 1964 (see column 4, Table 2).

The final numbers of adult snails removed from the 4 censused pens are presented in Table 2 (column 5) and also below:

Pen No.	Total Number of Shells
3	1272
7	1006
$\bar{X} = 1139$	
22	709
24	779
$\bar{X} = 744$	

The original experimental design called for alterations in adult density on the order of $1/5X$, X , and $5X$, for the 3 sets of 4 pens in the basic design. This would have given a total difference between the reduced and increased sets of 25 fold. Based on the mean number of all adults from each of the 2 groups of censused pens, the actual levels of altera-

tion achieved are presented in Table 3. Also in this table are the levels of alteration that were achieved on June 15 when the first manipulation based on the first Lincoln Index estimates were completed, and on June 26 after readjustment had begun and the pens in group 14 to 28 had been over-manipulated.

TABLE 3
LEVELS OF ALTERATION ACHIEVED IN THE INCREASED
AND REDUCED SETS OF PENS

Pen No.	Ratio of Treatment/Control		
	June 15	June 26	June 30
<u>Increased</u>			
4	3.3	4.5	4.9
11	3.5	4.5	4.9
17	4.3	6.4	4.8
20	4.0	6.4	4.8
<u>Reduced</u>			
2	0.65	0.42	0.23
10	0.50	0.31	0.23
18	0.40	0.15	0.25
25	0.33	0.14	0.25

As mentioned earlier, every effort was made to meet the assumptions of the mark-release-recapture method. The problem of dispersion over the pond was solved by the confinement of the pens, but it is obvious by the low nature of the early estimates that at least during the period from June 1 to June 10 marked individuals did not mix randomly or were not re-

moved randomly from the pen populations. In pens 1 to 13, for example, half of the snails appear to have been missed in the Lincoln Index estimates of June 1 to June 10.

After manipulations were completed, only one further estimate of adult density was made in the pens. On September 6, an extensive series of samples was begun from all 28 pens. Samples were taken, using the same stove pipe sampler as described in the preceding section, from a zig-zag transect which moved from side to middle to side at 2 foot intervals beginning at the center of the shoreward ends of the pens and ending at the right hand corner (facing the pond) of the pondward ends. On each sampling day 1 sample was taken from the same location in each of the 28 pens. In this fashion the entire lengths of the pens were covered and the design yielded 4 samples each from the sides and the centers of the pens. The series of samples took until October 17 to complete. During this time interval the level of the pond was falling and always below the level of the samples being taken so that all 8 of these samples were dry soil cores, and presumably contained only estivating snails.

Samples were treated and sorted in an identical manner to those from the snail population not under enclosure. The results are shown on the last column of Table 2.

Results

In Figure 7 the number of adult snails (living and dead) expected per pen on the basis of the spring estimates (column 6, Table 2) are plotted in relation to the total number of adults, adjusted to a per pen basis, obtained from the September-October series of samples (column 7, Table 2). The straight line drawn on this figure has a slope of 1 and passes through the origin of the graph and represents perfect agreement

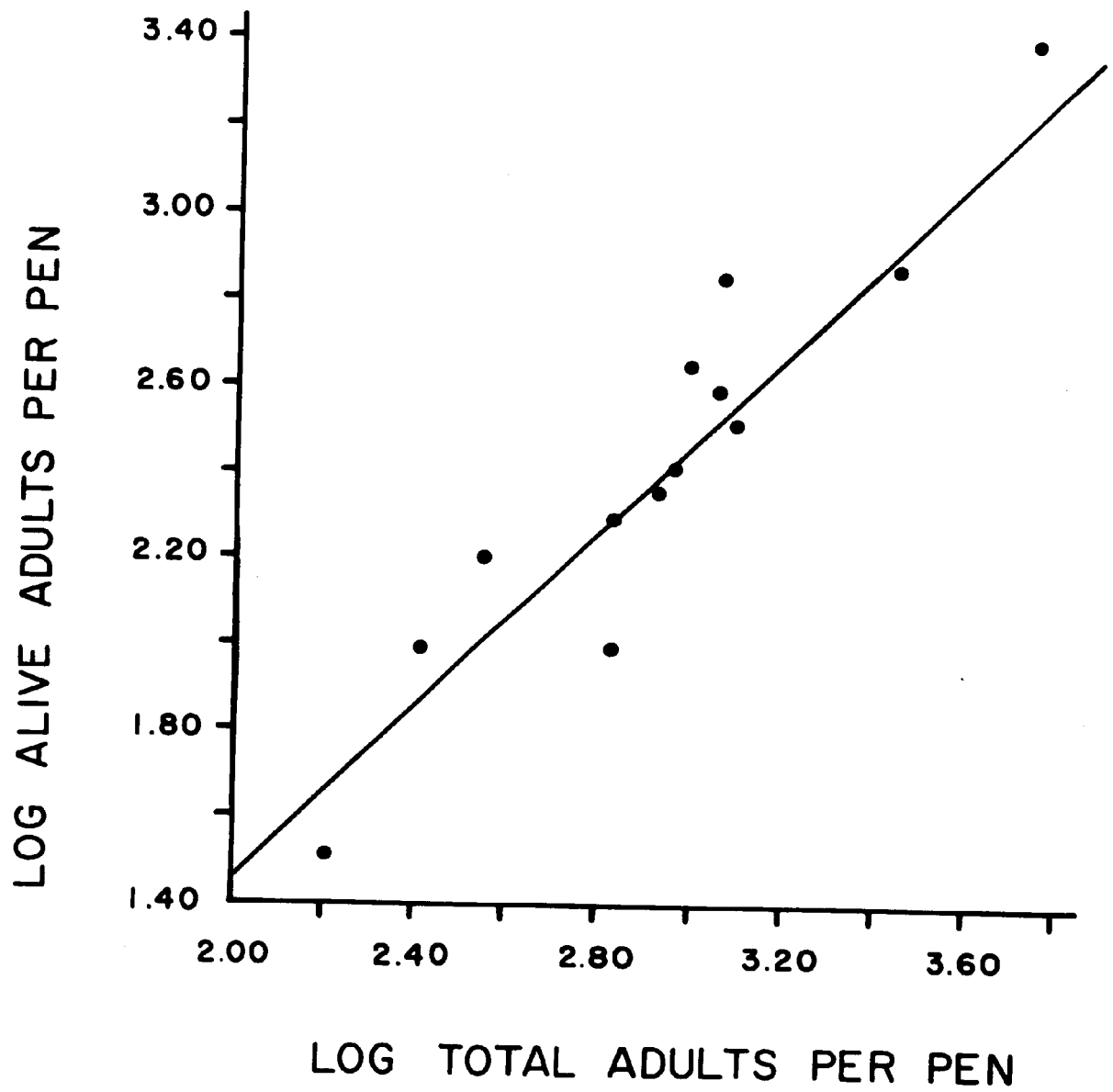


Figure 7. The relation between the total number of adults per pen and the number of living adults per pen. Each point represents a pair of pens.

between expected and observed results. The agreement of the data to this line, especially that from the altered pens, indicates that the desired levels of alteration of adult density were closely approximated and were maintained over the time of the study. Of major concern here earlier was the possibility of snails crawling out or being removed by some agent (i.e., birds).

For individual pen estimates of adult density, both initially and in the fall, the 8 sample series of September-October (fall series) is considered to be the most reliable and will be used in this paper whenever observed adult densities are mentioned.

The relationship between the number of living adults and the total number of adult shells from the fall series is shown in Figure 8. To reduce sampling error, each point on the graph represents the sum of a pair of similarly treated pens. Pens were paired with their closest similar neighbor beginning with pen 1. In this manner, pen 1 which received no specific treatment and therefore acted as an extra control, was paired with pen 5 which was designated a control in the original 12 pen design; and pen 2 which was reduced was paired with pen 10; etc. A straight line with a slope of 1 has been drawn through the median point on the graph. Since the axes are on a logarithmic scale, the close agreement of these data to this line indicates that the proportion of adults surviving until fall was similar for all treatments. In other words, there was no regulation of adult density among the various treatments through differential survival.

Other Pen Treatments

Treatments other than alterations of adult density were given to a number of pens. On June 19, 2 pens (27 and 28) which had received no

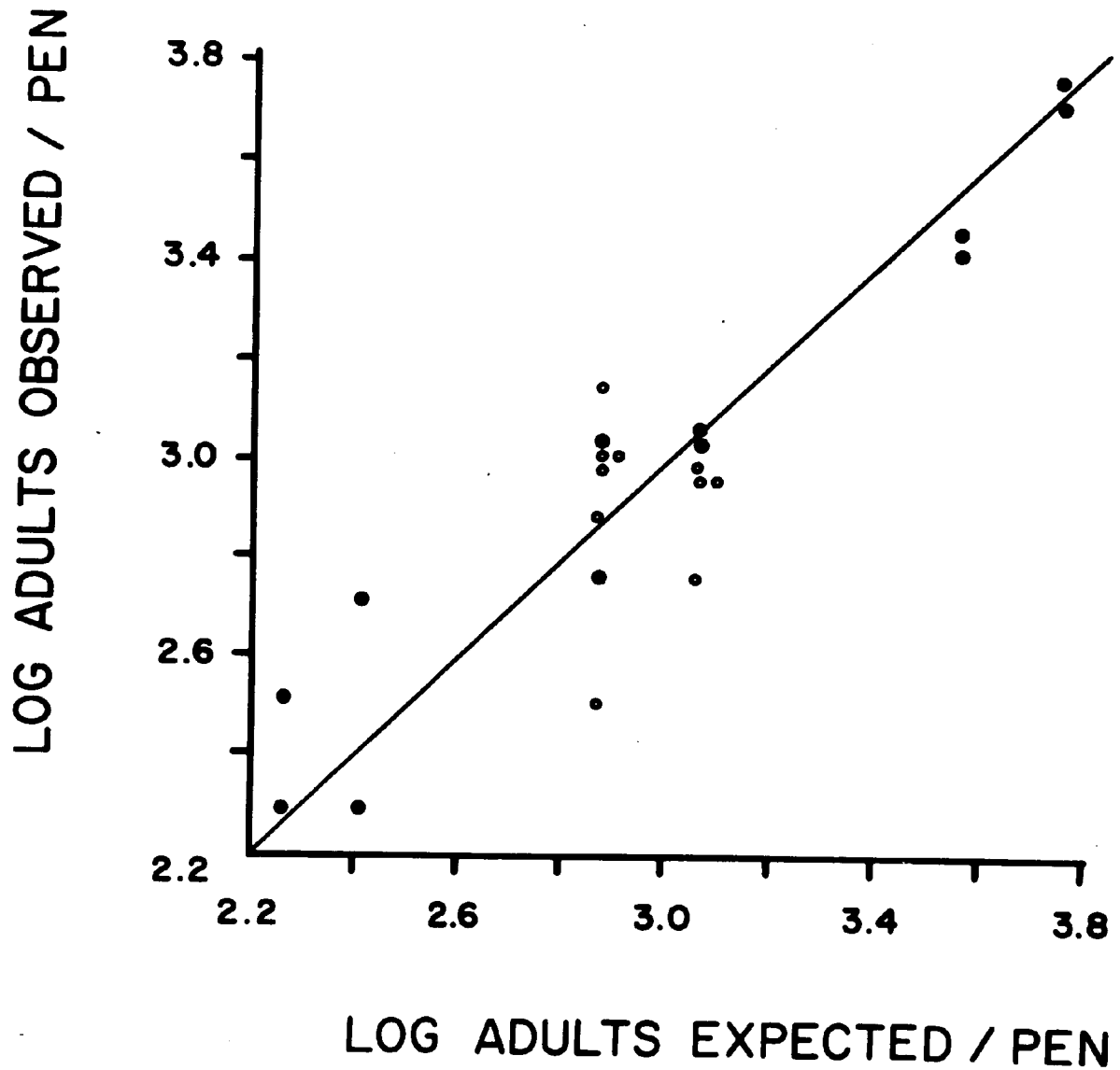


Figure 8. The relation between the numbers of adults expected and observed per pen. Solid circles are the 12 pens in the basic design. Open circles are other controls (6), fed pens (2), and predator added pens (2).

previous treatment were each supplied with a 10 oz. package of A&P frozen spinach. The spinach was distributed throughout the submerged portions of the pens. This treatment was continued at 3 or 4 day intervals until July 30, 1964.

At the time the pens were being built, 2 pens (13 and 15) were selected which were entirely closed in, in an attempt to exclude predators. These were framed in with 2 by 4's about 30 inches above the ground. The side and end material was extended up to this frame and screen covers made of 16 x 18 mesh aluminum insect screening supported on 2 by 2 frames were constructed for the tops. Unlike the other 26, the ends of these were closed off before the water level in the pond reached them, so that there was no opportunity for the free movement of animals into or out of these pens.

On July 11, 1964, 2 pens (12 and 14) were selected and 100 Belostoma (mainly early instars) collected from the pond at large were added to each.

Aside from the 12 pens in the basic design, the 4 which were censused, and the 6 just mentioned above, 6 pens (1, 6, 8, 19, 23, 26) received no treatment at all and therefore acted as 6 extra controls.

The disposition of all 28 pens is summarized in Table 4.

Young and eggs

All samples of young snails were taken with the 4 inch diameter stove pipe sampler. On 3 dates in July (July 7, 20, and 27), 2 samples were taken per pen from the 12 pens in the basic design. On the last 2 of these dates, 2 samples were taken from each of the pens receiving additional food. All of these samples were taken along the central axis of the pens (1-1/2 feet from either side) and the exact location of the samples was determined by the water level in the pens. On July 7 when the pens were

TABLE 4
THE DISPOSITION OF THE 28 PENS

Treatment	Pen No.
Reduced	2, 10, 18, 25
Control	5, 9, 16, 21
Increased	4, 11, 17, 20
Food Added	27, 28
Belostoma Added	12, 14
Completely Closed	13, 15
Censused	3, 7, 22, 24
No Treatment (controls)	1, 6, 8, 19, 23, 26

full, 1 sample was taken from the middle of each half of each pen, while on July 27 when they were almost dry, samples were taken at 1 foot intervals beginning 1 foot from their pondward ends.

The 8 sample series from September 6 to October 17 (fall series) mentioned in the section on adults was also carefully examined for the presence of young snails and represents the most extensive series of samples for this group of snails.

The handling and sorting procedures for these samples were identical to those for samples taken from the unenclosed snail population.

On July 10, a time limited search for eggs was carried out in the 12 pens in the basic design and the 2 fed pens. Each was thoroughly examined and all egg masses found within 10 minutes, except for the fed pens where eggs were so numerous that the searching time was reduced to 4 minutes, were placed in glass containers. The containers were brought into the laboratory where the numbers of eggs and egg masses were counted,

after which the egg masses were returned to their respective pens in the field.

Results

On 3 successive dates in July when samples were taken from the 12 pens in the basic design, an inverse relationship was found between the numbers of young and adults within the 3 sets (Figure 9). On all 3 dates the reduced pens had the highest number of young and the increased pens the lowest number of young. As early as July 7, only 1 week after the final manipulations had been completed, the regulation of density as expressed in the numbers of young obtained from the 3 treatments was complete to the point of overcompensation. The maintenance of this inverse relationship over 3 sampling periods is in itself significant.

On July 20 there was over a 4-fold difference in the numbers of young from the fed pens as compared with the controls. This difference was over 9 fold on July 27 (see Figure 9 and Table 5). The greatest difference found among the 3 sets in the basic design was a little under 2 fold between the controls and the reduced pens on July 27. The large differences between the fed pens and the controls, or even the reduced pens, indicates strongly that the snails in the unfed pens were severely food limited and the additions of what seemed to have been relatively small amounts of food in the form of frozen spinach were enough to at least partially release the snails in the fed pens from the limitation.

The broken line in Figure 9 connects the last July samples with the numbers of young from the fall series. In the fall, the inverse relation between young and adult densities did not hold. The numbers of young were greater in the fall than in the last July samples. It is suspected that this was due to the fact that the July 27 samples were

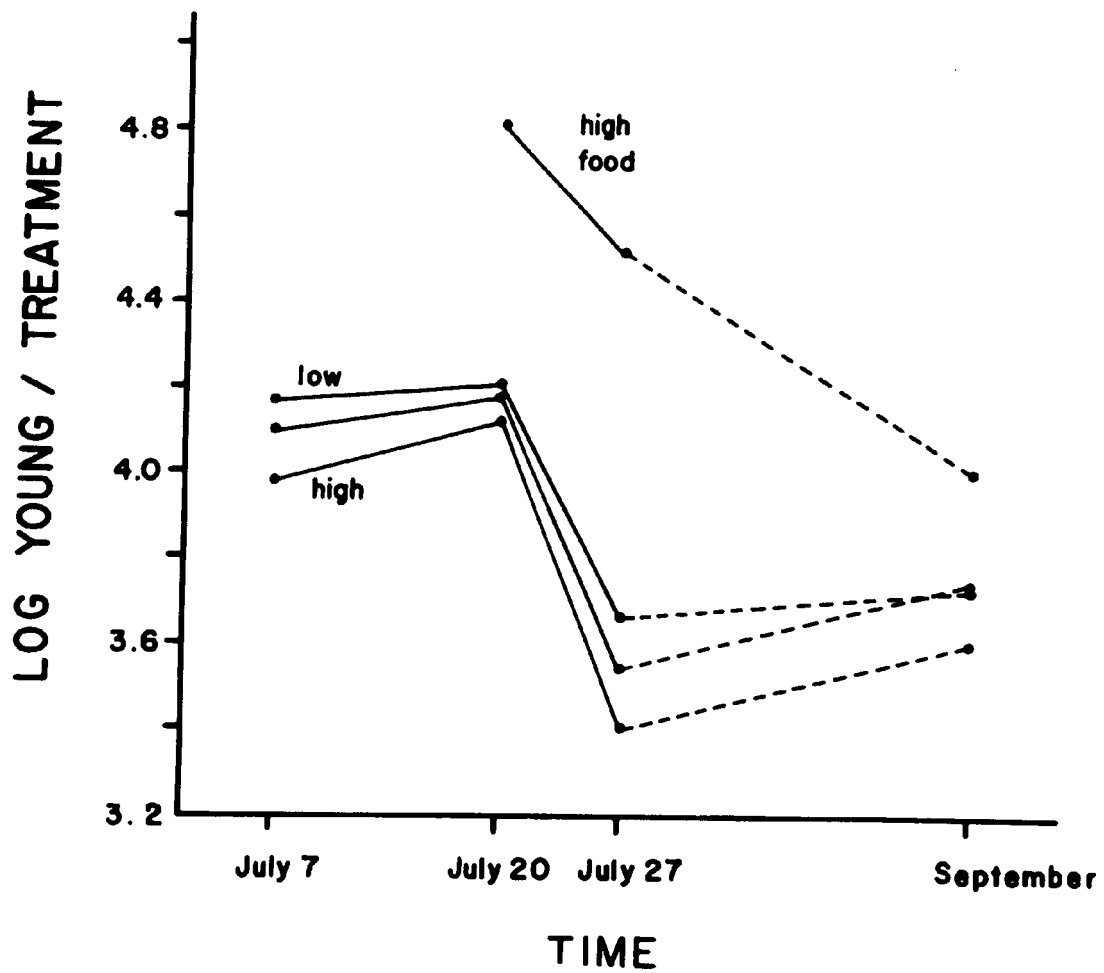


Figure 9. Relation of the numbers of young snails to treatments in the 3 sets in the basic design and the fed pens during July and in the fall. Numbers adjusted to a per pen basis. The control set is unlabeled. (High food = fed, low = reduced, high = increased).

TABLE 5

THE RESULTS OF SAMPLING INSIDE THE PENS FOR YOUNG, ADULTS, AND EGGS

(R = reduced; I = increased; C = control; F = fed)

Pen No.	Number of Young (No. of samples)				Total Number of Adults (No. alive) per 8 Samples From September-October	Number of Eggs per 10 Minute Search from July 10	Mean Number of Eggs per Egg Mass
	7/7	7/20	7/27	September- October			
	(2)	(2)	(2)	(8)			
1	-	-	-	152	14(4)	--	--
2(R)	60	26	6	66	3(3)	149	24.8
3	-	-	-	24	2(0)	--	--
4(I)	10	4	1	9	80(24)	309	15.4
5(C)	38	18	4	96	18(0)	328	21.4
6	-	-	-	64	14(4)	--	--
7	-	-	-	27	1(0)	--	--
8	-	-	-	67	9(2)	--	--
9(C)	38	125	1	96	17(12)	803	--
10(R)	34	38	8	80	8(2)	485	19.1
11(I)	22	13	3	68	89(52)	300	25.5
12	-	-	-	42	15(4)	--	13.0
13	-	-	-	14	9(6)	--	--
14	-	-	-	32	15(10)	--	--
15	-	-	-	106	27(16)	--	--
16(C)	96	60	6	107	9(4)	222	17.4
17(I)	78	122	2	105	41(15)	127	23.8
18(R)	61	52	16	96	5(2)	213	24.6
19	-	-	-	65	12(4)	--	--
20(I)	38	64	33	64	45(8)	411	19.6
21(C)	23	33	43	44	17(3)	388	18.5
22	-	-	-	7	0	--	--
23	-	-	-	66	16(1)	--	--
24	-	-	-	42	2(1)	--	--
25(R)	73	135	41	103	3(1)	540	28.4
26	-	-	-	78	5(2)	--	--
27(F)	-	381	160	145	16(0)	7,247	45.3
28(F)	-	129	99	175	22(10)	11,517	48.0

from a small submerged portion of the pens and were of "active" snails, while the fall samples were from the entire pens and were of estivating snails.

The size frequency distributions of the young snails from the 3 series of July samples from the 3 treatments in the basic design (Figure 10) give no indication of growth over the sampling intervals. In this respect and also in respect to the actual size distributions of the snails (maximum size was 4.3 mm) these young are very similar to the young snails from the transect samples from outside the pens (Figure 3). There are no convincing differences in the size distributions of young snails from among the 3 sets of treatments.

No relation was found between the number of eggs per pen from the July 10 time limited search and the total number of adults per pen (Figure 11). There was no significant difference in the total number of eggs per pen among the 3 treatments. But the numbers of eggs from the fed pens showed a striking (25 fold) increase over the numbers of eggs from the 12 pens in the basic design. As with the number of young from these pens, this difference can only be attributed to the food additions made to these pens.

There was a significant relation found between the mean number of eggs per egg mass and the number of adults per pen in the 12 pens of the basic design (Figure 12). There was also a significant difference (one-way analysis of variance on logs: $F_{2,235} = 32.40$, $.05 > P > .025$) in the number of eggs per egg mass among the 3 treatments. The mean clutch size in the fed pens (46.91) was over 2 fold larger than the mean clutch size in the control pens (20.16). In the reduced pens the mean clutch size was 26.06 and in the increased pens it was 16.14 eggs per egg mass. In the

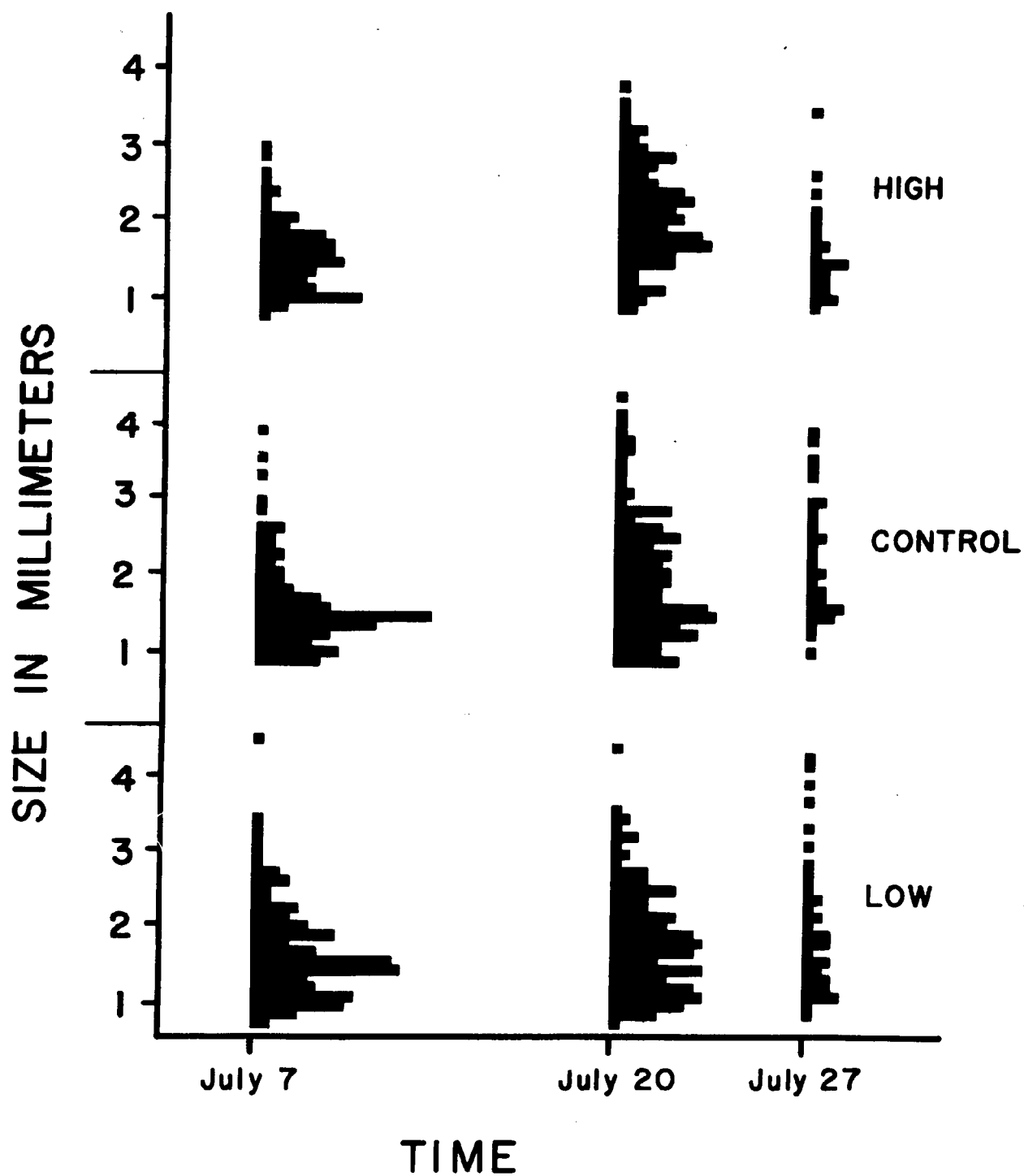


Figure 10. Size frequency distributions of young snails in the 3 treatments in the basic design during July. Each square represents 1 to 2 snails. (low = reduced, high = increased).

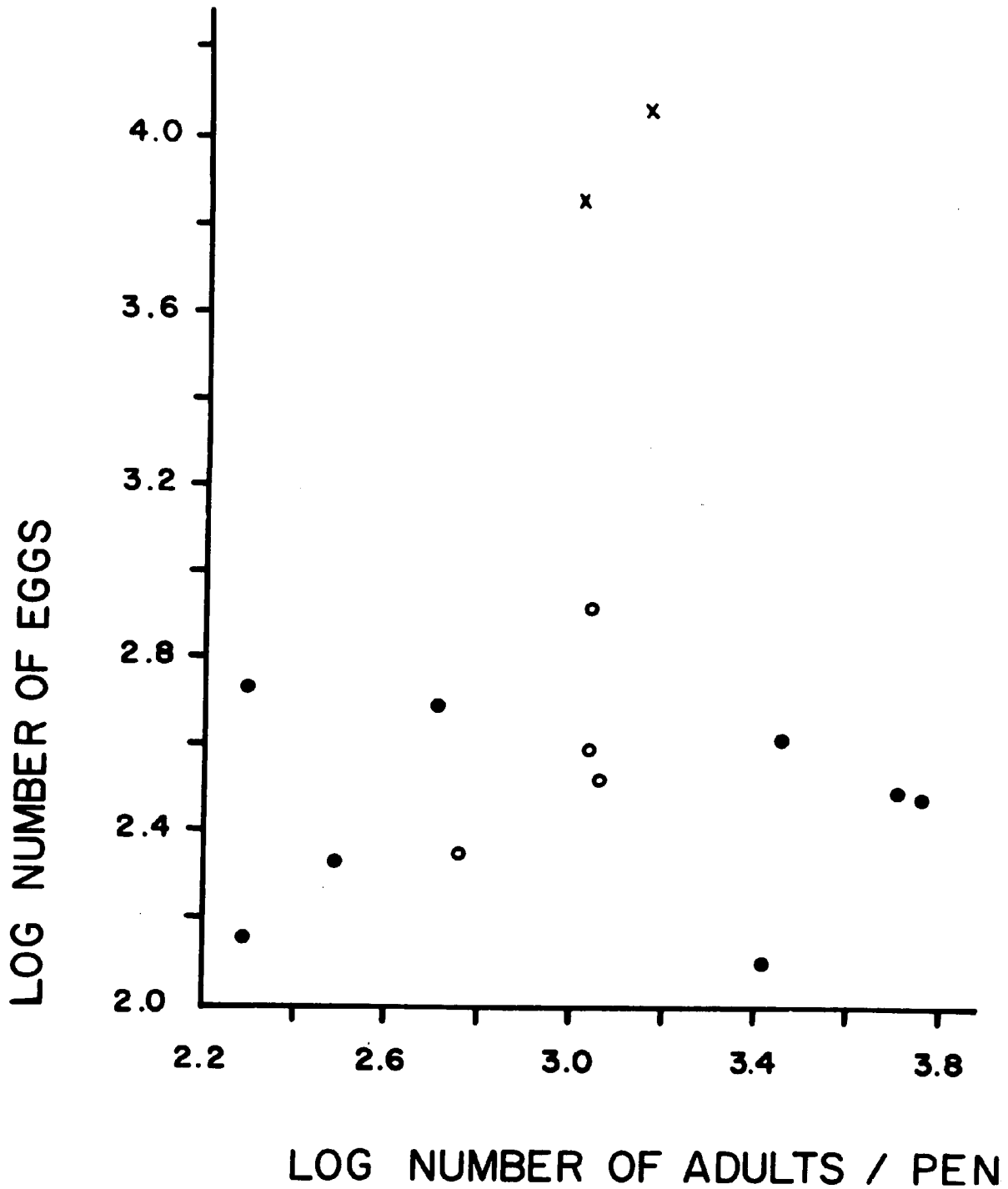


Figure 11. Relation between the number of eggs from the July 10 time-limited search and the number of adults per pen from the fall series. Solid circles on the left are reduced pens and on the right are increased pens. Open circles are controls and x's are fed pens.

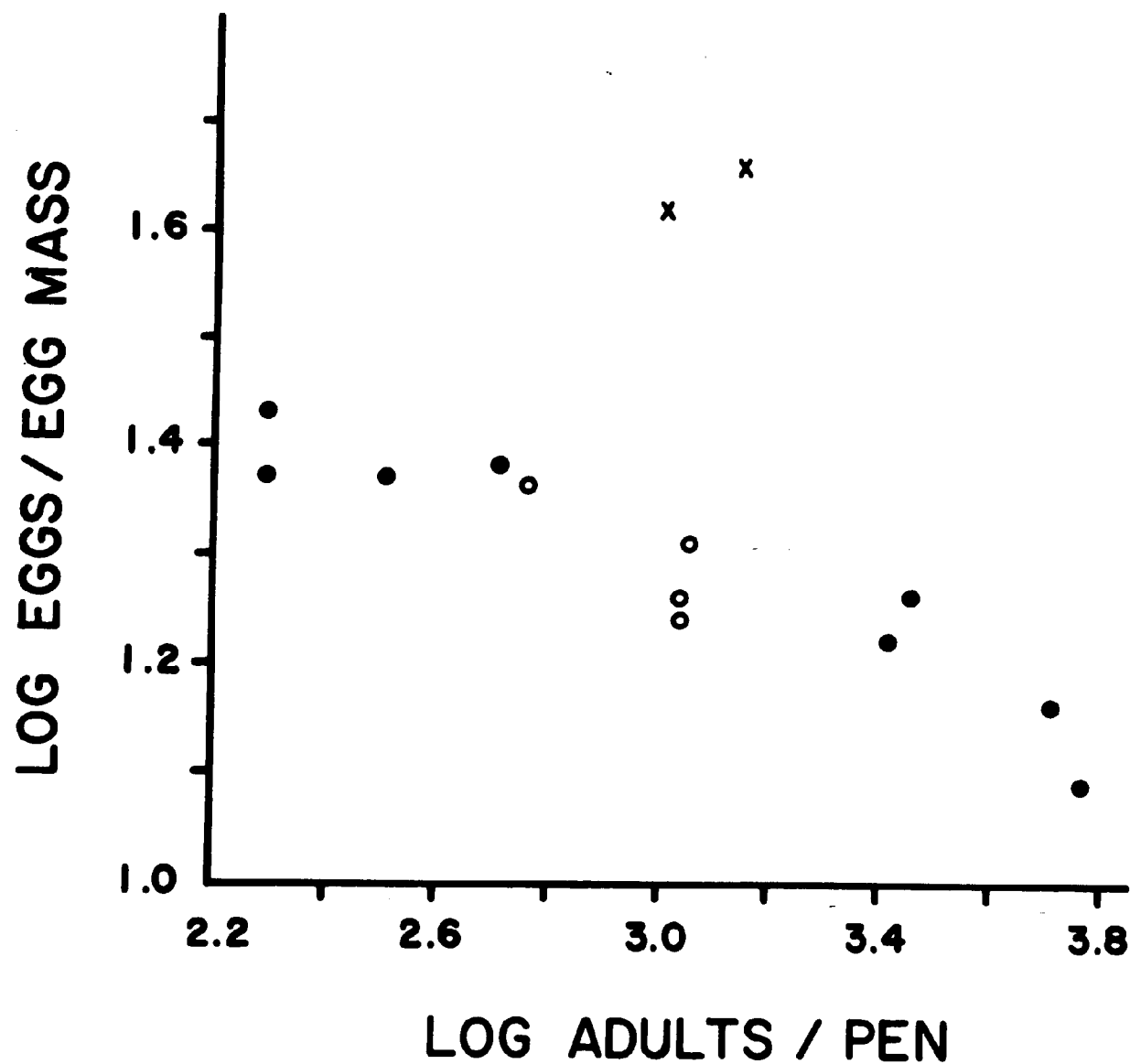


Figure 12. Relation between the number of adults per pen and the mean number of eggs per egg mass in the 12 basic and 2 fed pens. Symbols are identical to those in Figure 11.

fed pens the mean clutch size was only a little less than half of that for laboratory snails grown at 25° C with superabundant food (85.58).

In Figure 13, the relation between the numbers of young per pen and the total numbers of adults per pen, based on the fall series, is plotted. The total numbers of young per pen among the 3 treatments in the basic design are not significantly different. The difference remains not significant when the 6 extra control pens are included in the analysis. The fed pens, however, have significantly more young in them than the unfed pens. But, what was over a 25 fold difference in egg numbers between the fed pens and the 12 pens in the basic design, is now just a 2 fold difference. Obviously there has been a much higher mortality of young snails in the fed pens than in the pens in the basic design.

When the total number of young from all 3 sets of July samples is plotted in relation to the number of young obtained from these same pens in the fall series, a significant relation is found between the 2 sets of data (Figure 14). Ignoring the fed pens, a corner test of association gives a sum of plus 12 ($.05 > P > .02$). In other words, pens, regardless of treatment, which had high numbers of active young during July, also tended in a significant fashion to have high numbers of estivating young in the fall. This indicates the presence of individual differences among the pens which were expressed independently of the treatment they received. Without sufficient replication in the experimental design, this type of individual difference could have masked the final results.

The results from the closed pens (13 and 15) and those (12 and 14) to which predators (Belostoma) were added are inconclusive. There were no clear effects of either of these treatments on either the adults or the young.

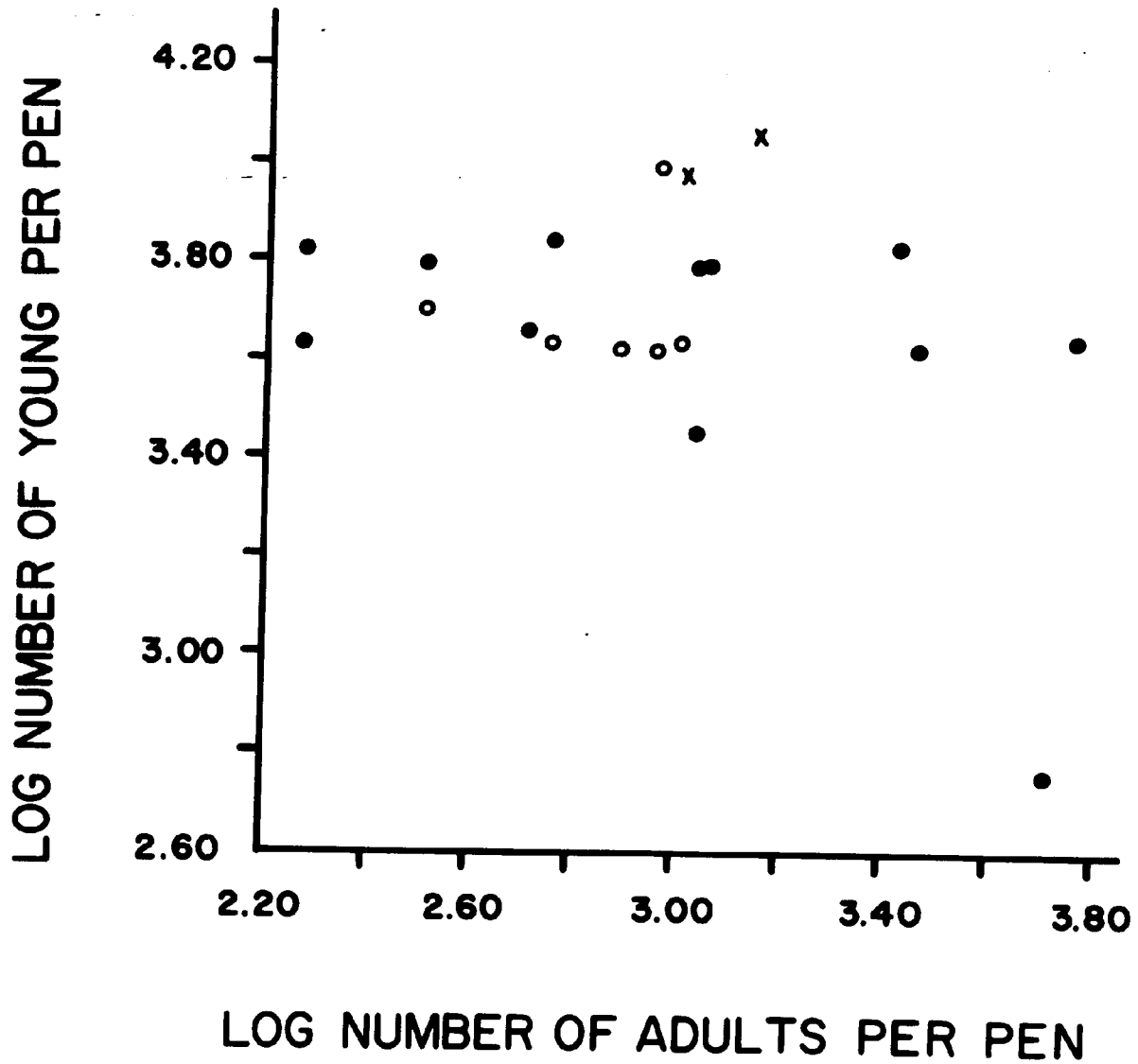


Figure 13. Relation between the number of adults and young snails per pen based on the fall series. Solid circles are the basic 12 pens, open circles are the 6 other controls, and x's are the 2 fed pens.

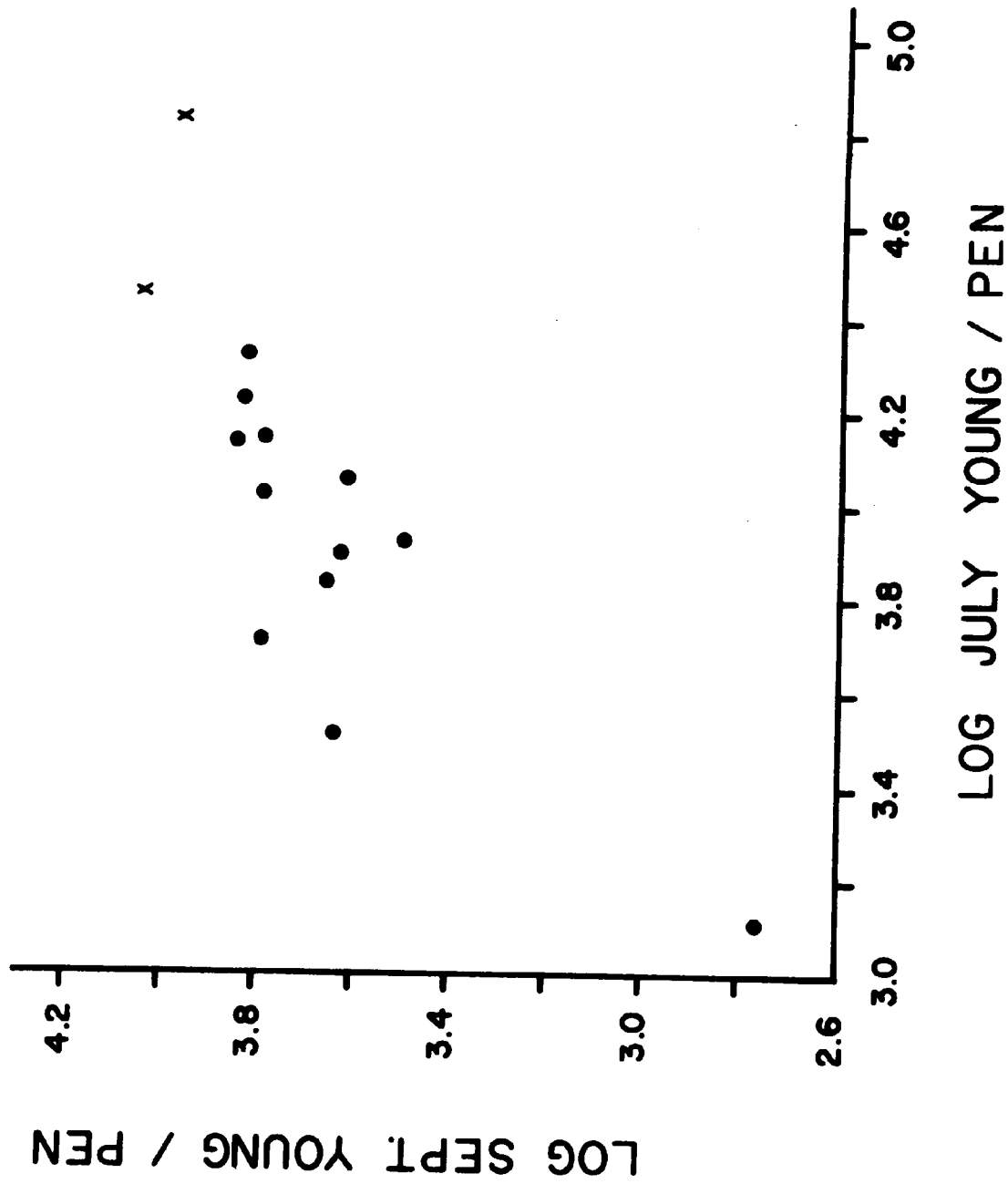


Figure 14. Relation between the number of young snails from July and the fall series from the 12 basic and 2 fed pens. Numbers adjusted to a per pen basis.

The closing of pens 13 and 15 did not in fact exclude predators from them. Early in June, pen 13 contained an estimated 1000 or more young crayfish, and while the numbers of crayfish in it were not followed, their presence was obvious throughout June and July. In addition to the crayfish in pen 13, sciomyzid fly larvae were observed in both pens as well as emerging adult dragonflies. Access to these pens by predators could have been had when their tops were off for inspection or at all other times through small openings around the imperfectly fitting tops. Early in June at the time of the first Lincoln Index estimates, these pens appeared to have larger populations of adults of a smaller size than the other pens. It is thought that this may have been due to the early closing off of their ends and the fact that the enclosed area contained most of the area in which snails estivated, while once the pond level rose the snail habitat covered an area greater than that covered by the pens. The fact that pen 13 contained the crayfish and only produced 14 estivating young in the fall may or may not be significant.

The additions of the Belostoma to pens 12 and 14 were made at a time when the water level in the pens was beginning to drop and should not be considered as an adequate test of this predators effect on the snail population.

Throughout the sampling for young snails pen 4 was consistently low in the numbers of young found. This difference is real, but the reason for its existence is unknown.

The results of sampling within the pens for eggs, young, and adults are summarized in Table 5.

DISCUSSION

The Demonstration of Regulation

When the basic experimental design of altering densities in pens was first conceived, it was thought that the most that could be expected, if regulation did occur during the time of the study, would have been a statistically significant convergence in the densities of the altered with the unaltered sets of pens. But convergence, and hence regulation, as expressed in the densities of young snails, was found to be far more complete and to occur more rapidly than was thought possible. The first set of samples of young snails from the 3 sets of pens in the basic design in July revealed an inverse relationship between adult and young densities. This same relationship was further borne out in the 2 subsequent samples of young (see Figure 9). The inverse relationship found may be compared with the over-adjustment of temperature to thermostatic control, a common phenomenon in feed back systems.

The results of the time limited search for eggs in July showed no significant difference in the number of eggs per pen among the 3 treatments in the basic design. However, it did show a significant difference among the 3 treatments in the mean clutch sizes and also a significant inverse relationship between observed adult densities and the mean clutch size in the 12 basic pens. As with the numbers of young above, these data show regulation in the system.

Since the only variable in this system was adult density, it must be assumed that the results obtained were due to the alterations in adult density. The inverse relations and the convergences must be attributed to feed back from adult density, and from both increased and de-

creased densities. This type of result is exactly what would be predicted by density-dependent models. These results should be considered as an unequivocal demonstration of the existence of the regulation of numbers in a natural animal population, a demonstration that the author has been unable to find duplicated for any other natural animal population in the ecological literature.

The absence of any regulation through adult survival in the altered pens was not expected but was not entirely surprising. Since the snails in the pond essentially reproduce in only 1 year, all that is required of the system for regulation to be achieved is that adult density be inversely expressed in fecundity, or short of this immediate relationship, that there be an inverse relation between adult density and young survivorship. That one or both of these things happened in the snail populations in the altered pens is abundantly clear from the data.

A number of investigators have used density manipulations under more or less natural conditions, but in each case reviewed, serious questions remain unanswered or the experimental design was not adequate for a test of regulation. Kajak (1963) manipulated the densities of a species of tendipedid in submerged cages in a lake, but his cages were not free of emigration and immigration and a replicated design was not used. He found that artificial increases were, in general, not maintained, but decreased to the general level of the population in the lake around the cages. But, when the population in the lake around the cages was itself increasing, the artificially high levels in the cages were maintained better. However, some species, noted as absent from the cages at the beginning of experiments, were found in some cases to have attained very high densities at their ends (0 to 1776 in one extreme case). While the

results of this work are of some interest and to some would certainly indicate a regulated system, they remain equivocal. Andrzejewsky (1961) artificially manipulated the densities of a homopteran in meadows. In a set of cages in a natural meadow, where either 250, 500, or 1000 homoptera were added per cage, he found a 90% mortality in all cages during the first 3 days of the study. This was followed on the 6th day by the intermediate (500) cage having the highest density of animals. This intermediate cage remained the highest with the high (1000) and low (250) cages with respectively lower densities over the remainder of the study (6 more days). However, a replicated design was not used and the author does not indicate whether or not the differences in density observed among the 3 treatments were significant, making the interpretation of the results difficult. Economic entomologists have used elegant designs in manipulative experiments in attempts to evaluate the effects of varying densities of pest species of insects on economically important crops (Bowling, 1963a; Lloyd, et al., 1962). But their major interest has been the effect of the pest on the crop and not the density effect per se within the pest species populations. In one of the more careful studies to date, and with a specific eye to regulation, Lomnicki (in press) artificially increased the density of adults in a natural population of the snail, Helix pomatia. He found no regulation in adult survival, but he did not follow reproduction.

As mentioned in the introduction, a variety of populations has been studied in an attempt to discover how their numbers are determined (regulated or in a density-independent fashion) and the mechanisms involved. Work on the Spruce Bud Worm (Morris, 1963) should perhaps be considered the most complete in this respect. But descriptive approaches,

even if they are coupled with extensive laboratory experimentation, cannot substitute for direct experimental evidence obtained under natural conditions. As long as results are descriptive they will remain equivocal in the minds of some, and general agreement on the subject of regulation will not be reached by ecologists.

Mechanisms of Regulation

The mechanisms of the regulation of density in the snail population are not as clear as the demonstration of their existence. The results from the fed pens indicate that the snails, both in the pens and in the pond at large, were under a severe food limitation. Further, a comparison of the clutch sizes and growth rates of field with laboratory animals indicates that even in the fed pens, the snails were realizing only a portion of their potential for growth and reproduction.

The results from the basic experimental and fed pens indicate that in the altered pens of the basic design, the regulation of density was achieved through an adjustment in adult fecundity as influenced by the food supply. Egg number similarity alone in these pens would have led to convergence in the numbers of young. However, the actual level at which convergence occurred must have been a function of other factors and these may not have been regulatory. For the snail population outside of the pens, young snail mortality was estimated to be 97.8%. Assuming egg production in the pens was similar to that in the pond, a slightly lower (about 93%) mortality is indicated here. However, there is no way of determining at present whether or not this mortality was regulatory in nature. There are 2 things that indicate that mortality may be a potential regulatory force in the snail population. First there was the loss of the inverse relation of young to adult densities in the 12 pens of the

basic design, and second, the extremely high mortality that was indicated in the fed pens. Comparing the fed pens and the 12 pens in the basic design, what was over a 25-fold difference in the number of eggs in July, and 4- and 9-fold differences in the number of active young on 2 other occasions in July, resulted in little over a 2-fold difference in the number of estivating young in the fall. So here at least, in the fed pens, it cannot be said that regulation was achieved through adult fecundity. However, within the framework of the experimental design, that is, 20-fold differences in adult density, it appears that survival is immaterial to regulation, because at least within this 20-fold range, food will be limiting and regulation will occur in egg production.

Food Limitation

The idea of food limitation is not a new one in ecology and some broad generalizations have been made concerning its role in determining the numbers in natural populations (Hairston, et al., 1960). Malacologists in the past have considered fresh water snails not to be food limited (Boycott, 1936), but Boray (1964) states that one of the factors influencing snail populations is the presence or absence of suitable food.

In the present study food limitation in the Lymnaea population has been clearly demonstrated, but it is felt that the limitation is one of a relative rather than an absolute nature. There is a superabundance of vegetation and coarse debris in the pond that the snails can and do eat, but apparently there is a shortage of "high quality" food that is required for maximum growth and reproduction. Even in the increased pens of the basic design there was little evidence, with the possible exception of a few grass cuttings, that the snails were actually damaging the habitat (i.e., the vegetation) in their quest for food.

It is quite uncommon to find accounts of animals starving to death in nature, but there are a number of examples of the effects of food

quality and food quantity on animals in natural and artificial situations. Lack (1954) cites a variety of evidence showing a clear relationship between food supply and clutch size in a number of bird species. Of particular interest is the work of Swanberg (1954) who supplied certain wild nutcrackers with hazelnuts during "bad" nut years and found that the clutch sizes in these birds were larger than those of birds not supplied nuts. Reynoldson (1961) obtained increased fecundity in a natural population of a flat worm by periodically supplying the habitat with food in the form of cut-up earth worms.

A great deal of work has been done by economic entomologists on arthropod pest nutrition (see review by Fraenkel and Lipke, 1956). Both Bowling (1963b) and Okigbo and Gyrisco (1962) found that pest insect densities increased with increased applications of nitrogen to cultivated fields. Henneberry (1962) and Henneberry and Smith (1960) found that mite densities increased on individual plants that had been supplied with elevated nitrogen levels. In the latter study they found 60- to 80-fold increases in mite density with nitrogen additions.

In the case of the snails the nature of the food limitation is not known, but events during the snail's life history indicate what it might be. In the spring when the snails begin to grow, there is almost no emergent vegetation in the habitat, but a great deal of debris from the previous year's growth. In the habitat area the water is shallow and clear and this debris becomes heavily encrusted with epiphytic growth. As the season wears on the new emergent vegetation becomes more and more prominent and also large portions of the surface of the water become covered or obscured with duckweeds (Lemna trisulca and Spirodella polyrhiza). The growth of these vascular plants may not only act to cut down on light

transmission to the **epiphytes**, but they may also compete with them for essential nutrients (i.e., nitrate). Perhaps it is only coincidence, but at the time of the year when the vascular plants begin to dominate the habitat, the snails slow, or stop growing and begin to reproduce.

In the 4 pens which were censused, some young snails and eggs were not removed and during the course of the summer a number of snails attained adult size. In the fall series of samples from these 4 pens, 9% of the young were over 8.1 mm long, while only 1 other young snail from the entire fall series of samples attained this size (8.4 mm), and this snail was from the fed pens. Obviously conditions in these 4 pens were different from the other pens and the pond at large, but the cause of this difference is not clear. Not only were most of the adult snails removed from these pens, but all of the vegetation in them was either pulled out or cut back below the water level. In addition it is not known how this treatment affected the other organisms (i.e., predators) in these pens.

It does not seem unreasonable to propose that the type of food limitation found in the pond snail may not be at all uncommon among animals of similar trophic classification in the aquatic and semi-aquatic environment, and the possibility of its existence in terrestrial situations cannot be overlooked.

Predation

The actual role of predators, if any, in the regulation of the Lymnaea population in Payne Pond is not known. There is however an indicated 93 to 98% mortality in the young snails in the pens and the pond, and predation is no doubt responsible for a large percentage of this loss.

Due to the important economic and medical position held by snails as vectors of trematode infections in large parts of the world, the possi-

bility of their biological control using predators has been examined (see review of snail predators by Michelson, 1957). But the actual role of any predator in the regulation of a natural population of fresh water snails is unknown. Introductions of the large predaceous pulmonate, Marisa conrui-
atietis into Puerto Rico resulted in greatly reduced numbers of the snail Austrolorbis glabratus in certain of its habitats (Ferguson, et al., 1958), but the authors were uncertain as to whether this was due to predation by Marisa or to competition between the 2 species of snails.

A group of snail predators that have recently received a great deal of attention is the schiomyzid flies whose larvae are specific predators of snails (Berg, 1953; Berg, 1961, Knutson and Berg, 1964; Berg and Neff, 1959). However, there is no evidence to date as to the specific effect of schiomyzid fly larvae predation on a natural population of snails.

It is difficult to imagine the mortality of the snails in a habitat like Payne Pond to be due to a single specific predator. Productive bodies of water like this pond contain a wide variety of invertebrate predators. Most of these are seasonal in their occurrence. Predaceous beetle larvae are most common in the spring, and the bug, Belostoma does not occur in any numbers until late in the summer, while schiomyzids appear to be very scarce except for 2 short peaks in abundance. It seems much more reasonable to assume that while a few more or less specific snail predators may account for an unequal share of the snail mortality, that the remaining large number of less specific predators may take an equally large fraction of the snails lost to predation. Under certain conditions the combined effects of all predation could exert a regulatory influence on the snail population. However, the only way to determine the role of specific predators or predators in general, is to experimentally

manipulate them under natural conditions.

While there was no indication of any strong size-specific mortality in the young snails in the pond, the fact remains that they did not, in general, grow larger than about 4 mm. Part of this was accounted for by the slow growth rate in the field, but this does not explain why a few larger snails were not found. The most reasonable explanation for this lack of larger snails appears to be mortality due to predation. But as indicated above, the only way to determine if this were truly the case would be to experimentally exclude snails of the new year class from all sources of predation.

Differences Between the Pens and the Pond

There were 2 obvious differences between the isolated pen populations and the snail population in the pond at large. The survivorship of adults in the pens was much higher than that in the pond. Approximately 37% of the adults recovered from the pens in the fall series of samples were alive, while no living adults were recovered from the 3 transects taken from the outside sampling area in November. The reason for this difference is not known, but it might have been due to the exclusion from the pens of a predator or predators whose late arrival to the pond kept it (them) from generally getting into the pens. Also, approximately 3 times as many estivating young were found in the pens as in the transect area outside the pens. Again the reason for this difference is not known.

It is not felt that these differences could have in any way influenced the outcome of the experiments in the pens.

The Timing of Adult Alterations

Assuming that egg production in the pens was similar to that in the transect area, about 65% of the season's egg production had occurred in the pens by June 25, 5 days before the manipulations of adults were completed. If it is further assumed that there was no density regulation, the expected levels of abundance of young snails in the altered pens can be calculated, corrected for the timing of manipulations.

If the number of eggs produced per adult at each sampling date in the transect area is plotted and a smooth curve drawn through these data, the number of eggs per adult per day can be taken directly from the graph. Also, the number of adults in each pen in the basic design can be determined on a day by day basis by using the census means (1139 and 744) for the dates before June 10 when manipulations were begun, and after June 10 these same numbers plus or minus the alterations made. Assuming no adult mortality over the period, the number of adults present can be multiplied by the number of eggs per adult for that same day to give the number of eggs produced in the pens for that day. Using a 10 day interval to hatching the accumulated number of young produced per pen to any day can be calculated.

The results of these calculations in the form of ratios of abundances in altered to control pens are given in Table 6 for the 3 dates in July when active young were sampled from the pens. In the absence of density regulation these ratios rather than those given in Table 3 should have been approximated. A comparison of the ratios from Tables 3 and 6 shows some convergence, but with any density regulation in the pens the degree of convergence would be reduced. At any rate the amount of convergence shown here is not significant when compared with the actual results which showed total convergence.

TABLE 6

EXPECTED LEVELS OF ABUNDANCE OF YOUNG SNAILS IN INCREASED
AND REDUCED PENS, CORRECTED FOR THE TIMING OF MANIPULATIONS,
ASSUMING NO DENSITY REGULATION

Pen No.	Ratio of Treatment/Control		
	July 7	July 20	July 27
<u>Increased</u>			
4	3.2	4.1	4.2
11	3.4	4.2	4.3
17	4.2	4.5	4.5
20	4.1	4.4	4.5
<u>Reduced</u>			
2	0.65	0.43	0.39
10	0.58	0.40	0.37
18	0.48	0.36	0.34
25	0.43	0.34	0.32

Density-Dependence vs. Density-Independence

Natural populations have the capacity to increase geometrically, but they do not in fact increase without limit, nor do they generally become extinct in the space of "ecological" time. There appear to be more or less the same numbers of animals of the same kinds in nature from year to year (Richards, 1961). The numbers of animals, however, within the range of this "more or less" fluctuate. For some populations the fluctuations may be of the order of 10 fold, while for others 100 fold or greater (for examples from literature see Solomon, 1964). However, there is no reason to assume that there exists a fixed level around which a natural population tends to fluctuate from year to year. What must be assumed is that natural populations tend to achieve some sort of equilibrium with their environments, and since the environment

is not a constant, as it changes the numbers of animals would also be expected to change.

In the simplest terms possible, what is being said above is that the numbers of animals in natural populations are determined in some meaningful manner as opposed to a haphazard one. This author chooses to call the state of such a population "regulated" and to define regulation as follows: the maintenance of the numbers of animals in a natural population, brought about as a result of negative feed back from population density, within a certain range, around some level that is determined by the whole of the environment. Defined in this manner, regulation can only be density-dependent, and the phrase "density-independent regulation" is a contradiction in terms.

The test for the presence of regulation and the demonstration of its existence in the pond snail population have been given earlier in this paper. However, we must remain cognizant of the "time" factor involved if we are to escape from trivial argument. It cannot be expected that the numbers in a natural population will increase during periods of reproductive inactivity. Therefore when speaking of time in regard to regulation, we should probably consider a single generation time as our smallest unit of measure. A single generation time was sufficient for the complete regulation of the pond snail population but this may not be so for all populations.

In their book, The Distribution and Abundance of Animals, Andrewartha and Birch (1954) state that expressions like "regulate" and "control" stem from the dogma of density-dependence, are allegorical, and should be viewed with caution unless carefully defined. They choose to avoid using these terms freely but rather talk about what "determines" and "limits" the numbers of animals in nature. It is not entirely clear whether they

are denying completely the regulation of numbers as defined above, but in some instances this appears to be the case. In regard to a study of Thrips imaginis, they state, "All variation in maximal numbers from year to year may therefore be attributed to causes that are not related to density: not only did we fail to find a "density dependent factor," but we also showed that there was no room for one." And again when talking about a study of the grasshopper, Austroicetes cruciata, whose numbers were not counted, they say that fecundity was determined by the food supply but that food ran out not because it was eaten by the grasshoppers, but because in the absence of rain it became unsuitable. From this they conclude, "The supply of food was therefore quite unrelated to the number of grasshoppers, and it cannot in any way be construed as a density dependent factor."

Part of the problem at least that leads to the major disagreement between the schools of density-dependence and density-independence, and which must be confusing to one reading the literature for the first time, is a semantic one. With the definition of regulation given above and the 2 examples from Andrewartha and Birch, the following hypothetical example is presented in the hope that part of the problem can be clarified.

Consider a natural population that is limited only by its food supply and let the numbers of this animal vary as some direct function of the food supply. For the sake of simplicity let the animal be a herbivore and the food supply a specific plant and furthermore let the abundance of the plant be some direct function of rainfall such that it is determined by the rainfall in the season preceding its growth. Within such a hypothetical system, knowing the amount of rainfall in the spring (say this is the preceding season) would enable one to accurately predict the abundance

of the plant in the summer (say this is the growing season) and also the abundance of the animal if it had earlier been determined what the relationships between rainfall, plant abundance, and animal abundance were.

The above relationships might be presented in the following manner.

let $D(\text{density of animal}) = f(F)(\text{abundance of plant})$

and let $F(\text{abundance of plant}) = f(R)(\text{rainfall})$

and let the density of the animal (D_1) at any time T_1 be related to the density (D_2) at time T_2 such that for every increase or decrease in rainfall from T_1 to T_2 there is a constant factor by which the density of the animal either increases or decreases, so that

$$D_2 = D_1 e^{k(R_2 - R_1)}$$

where k is the constant for the system that has previously been determined by observation and which relates animal density to plant abundance and hence to rainfall.

The question that should now be asked, given that the above system operates as proposed, is whether this hypothetical population is regulated or if its numbers are determined by density-independent processes. As in the Thrips, the causes of the changes in density may be attributed to factors other than density, in fact rainfall is adequate in this particular system. Also, like the grasshoppers, it is rainfall that determines the amount of food that will be available and the animals cannot influence the amount of rain that will fall. What kind of system does this model describe? Up to this point nothing has been said about mortality, fecundity, etc., and these subjects need never be considered if one is only interested in predicting density changes in this particular system. But if one is interested in how this system operates, the question

must be asked as to how the animals adjust their density to changing levels in the food supply. In order for this system to be maintained there must be a feed back from density interacting with food so that the animals can come into some sort of equilibrium with their food supply. If this were not the case, only random fluctuations would be expected in density and with random fluctuations the correlation of density with rainfall would disappear. This system then is a regulated one, and while density-independent processes may influence the numbers in the population they cannot be responsible for its maintenance.

Predictability is something that is sought after by all ecologists, but the attainment of the ability to predict (as in this hypothetical case) should not mask those things of greatest theoretical interest; namely the mechanisms, which generally must be understood and quantified in order to make prediction possible.

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